Plant and snail communities in three habitat types in a limestone landscape in the west of Ireland, and the effects of exclusion of large grazing animals

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by

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based on research carried out under the supervision of

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DECLARATION

I hereby declare that this thesis has not been submitted as an exercise for a degree at this or any other university. It is entirely my own work except where indicated and clearly acknowledged in the text. I agree that the library may lend or copy this thesis upon request.

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SUMMARY

This thesis documents the plant and snail communities found in woodland, scrub and grassland in the Burren region in the west of Ireland. The flora of the Burren is renowned and has been well-studied, but the vegetation communities are less well-understood. In relation to molluscs, their distribution in Ireland is quite well-documented, but studies on molluscan ecology and community structure are lacking, particularly for land snails. Additional work with the molluscan data includes an examination of the population structure and an assessment of methodological issues. This thesis also investigates experimentally the short-term changes in plant and snail communities following cessation of grazing by large herbivores. This study is exceptional in assessing the effects of grazing by looking at multiple habitats using a replicated, balanced multi-site design. The project design enables the study of ecological change on a number of scales – quadrat, site, habitat and landscape.

Scrub encroachment is a big issue for many land owners and managers in the Burren, with hazel, *Corylus avellana*, being the most significant species involved. The woodland and scrub habitats selected for study were hazel-dominated, and all of the grasslands had hazel scrub nearby. The findings of the vegetation study indicate that, unsurprisingly, the vegetation of woodlands and grasslands differ substantially, with soil fertility as well as light penetration being important in the separation. Interestingly, the scrub vegetation differed floristically from both woodland and grassland. Further, it could be split into two distinct subsets – 'woody' and 'grassy'. These elements formed reasonably distinct entities which were related to the woodland and grassland vegetation communities respectively, but were distinct from either.

A total of 30 species of snail was recorded, which is approximately 45% of the total number of land snails in Ireland. This included a number of species from the 'Red List' for Irish non-marine molluscs. The woodlands and scrub had higher abundances of snails and were more species rich than the grasslands. The amount of litter in a quadrat was found to be an important factor correlated with species richness of snails, while plant species richness was not found to be correlated with snail richness.

With regard to population structure of snails, the populations at the study sites were shown to be composed mainly of juveniles, with only 28% adults. The inclusion of dead and immature individuals in the results added six to the species list, but these species occurred in very low numbers. The relative abundances of species was shifted, however, if only adults were included. The advantages of using a 0.5mm sieve mesh size for processing samples were shown by the large numbers of snails found in this smaller size fraction and by the demonstration that a number of species are under-estimated when sampling using a 1mm sieve mesh. However, these advantages need to be weighed against the benefits gained in terms of decreased lab work time.

The changes in the vegetation brought about by the cessation of grazing were rapid and dramatic in the grasslands. Many plant species declined in abundance and several flowering plant species disappeared. There was a major build-up of litter, and cover of grasses increased significantly. Both diversity and species richness of plants decreased. The woodlands presented contrasting findings to the grasslands, with plant diversity increasing significantly. Species richness increased also, although the change was not statistically significant. The amount of bare earth decreased sharply, and the cover of field layer plants increased in parallel. There was little detectable pattern of change in the scrub vegetation; this can be ascribed to the heterogeneity and variability of the habitat and the restricted timeframe of the 24-month study period.

A large change was seen in the snail communities in the grasslands - in this case, abundance and species richness increased. The changes were linked with the litter build-up, and the denser, taller vegetation within the fenced plots. Few individual species showed strong trends, with the pattern instead being a small and variable, but relatively consistent, increase across all species. The snail communities showed little appreciable changes in the woodlands and scrub during the timespan of this survey. Again, a period of 24 months may not have been long enough for measurable changes to manifest themselves.

Land abandonment is a major threat in many ecosystems and the cessation of existing management regimes (e.g. grazing) is likely to have a large impact on plant and animal communities. Changes have been seen in the Burren in recent decades, with perhaps the most dramatic example being the expansion of hazel scrub. This has been attributed mainly (though not exclusively) to changes in grazing practices. The network of fenced exclosures, and their associated control plots, set up during this project are an important resource for the study and documentation, now and in the future, of how changing management practices are affecting plant and animal communities. Already, the loss of some plant species has been documented from grasslands in the absence of grazing, indicating how essential grazing is for the maintenance of semi-natural grasslands in the region. However, this loss of diversity is off-set by the success of the snails in the ungrazed plots, reminding us that solutions are rarely straightforward in conservation management, and that a variety of structural elements (e.g. grazed and ungrazed patches) is probably optimal for biodiversity.

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All photographs were taken by the author unless otherwise stated.

Common names are sometimes used for tree and shrub species. A list of these, and their scientific names, is provided in Appendix 1. Nomenclature follows Stace (2010) for scientific names for these and all other species referred to in the thesis, and Scannell and Synnott (1987) for common names.

LIST OF ABBREVIATIONS AND ACRONYMS

Abbreviations specific to this project:

F	Fenced plot	
C	Control plot	
T	Treatment (= fencing)	
H	Habitat	
W	Woodland	
S	Scrub	
G	Grassland	
Y1	2006 (i.e. year one of the study)	
Y3	2008 (i.e. year three of the study)	
1	Site 1 – Ballyclery	(Woodland)
2	Site 2 – Glencolumbkille	(Woodland)
3	Site 3 – Glenquin	(Woodland)
4	Site 4 – Gortlecka	(Woodland)
5	Site 5 – Carran	(Scrub)
6	Site 6 – Knockans	(Scrub)
7	Site 7 – Rannagh	(Scrub)
8	Site 8 – Roo	(Scrub)
9	Site 9 – Caher	(Grassland)
10	Site 10 – Gregan	(Grassland)
11	Site 11 – Kilcorkan	(Grassland)
12	Site 12 – Slieve Carran	(Grassland)

Other abbreviations/ acronyms used:

AD	Anno Domini
ANOVA	Analysis of variance (statistical method)
BC	Before Christ
BP	Radiocarbon years before present
c.	Circa
C	'Competitor' (sensu Grime et al., 1988)
cSAC	candidate Special Area of Conservation
CSO	Central Statistics Office
DBH	Diameter at breast height
EPA	Environmental Protection Agency
EU	European Union

GIS	Geographic Information System
GPS	Global Positioning System (device used in the field to record locational information)
IUCN	International Union for the Conservation of Nature
JNCC	Joint Nature Conservation Committee
LOI	Loss-on-ignition, given as a percentage
LSD	Least significant difference
LU	Livestock units
MAVIS	Modular Analysis of Vegetation Information System (computer programme; Smart, 2000)
N	Nitrogen
NBDC	National Biodiversity Data Centre
NMS	Non-metric Multidimensional Scaling (statistical ordination method)
NPWS	National Parks and Wildlife Service
NSS	National Soil Survey
NVC	National Vegetation Classification (Rodwell, 1991, 1992)
OSi	Ordnance Survey Ireland
P	Phosphorous
p.a.	per annum
PC-ORD	Statistical analysis computer programme (McCune and Mefford, 2006)
pNHA	proposed Natural Heritage Area
R	'Ruderal' (sensu Grime et al., 1988)
RBINS	Royal Belgian Institute of Natural Sciences
REPS	Rural Environment Protection Scheme
RIMD	Republic of Ireland Molluscan Database
S	'Stress-tolerator' (sensu Grime et al., 1988)
SPSS	Statistical analysis computer programme (PASW Statistics (SPSS) Version 18.0.0, 2009)
Total P	Weight of total phosphorus per unit volume of soil (µg/ml)
UK	United Kingdom
USA	United States of America
USDA	United States Department of Agriculture

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Chapter One:

General introduction

"*The Burren has been aptly described as '150 square miles of paradoxes'.* "
(Dunford, 2002, citing Robinson, 1999)

"*Of this barony it is said that it is a country where there is not water enough to drown a man, wood enough to hang one, nor earth enough to bury them. This last is so scarce that the inhabitants steal it from one another and yet their cattle are very fat. The grass grows in tufts of earth of two or three foot square which lies between the limestone rocks and is very sweet and nourishing."*
Ludlow, Cromwellian Army Officer, 1651

General introduction

The Burren is famous for its flora, fauna and geology, as well as its cultural heritage, both past and present. Its impressive biodiversity is indebted in no small way to the agricultural traditions of the area. From a natural history point of view, the limestone pavements and the species rich grasslands are among the most famous aspects, but also significant are the hazel woods and well-developed areas of scrub. Areas of long-established hazel scrub are very important habitats in their own right, often supporting luxuriant and scientifically significant mosses and lichens, as well as a number of rare or scarce plants (e.g. Kirby, 1981, Coppins and Coppins, 2005).

Large areas of the Burren limestone may appear bare, but there is in fact a rich vegetation to be found throughout the area. As well as the bare rock which is so striking, large parts of the region are covered, though sometimes sparsely and unevenly, with soil. These areas support vegetation mosaics formed of patches of calcareous and mesotrophic grassland, dry heath and/or hazel scrub and woodland. Indeed, much of the Burren is characterised by a patch-like arrangement of vegetation communities. Scrub and woodland are more common in the east of the Burren, and grasslands and heaths are most expansive in the central and upland parts (Webb and Scannell, 1983). There are also rich and interesting communities of plants in the grikes in the limestone pavement. Dickinson et al. (1964), and more recently Murphy and Fernandez (2009), explain how the morphology of the limestone can support a range of 'microclimates', which helps a variety of plant communities to survive.

Calcareous grasslands in the Burren are often very species rich, but there is a second common type which is more mesotrophic (with species such as cock's-foot, *Dactylis glomerata*, and Yorkshire fog, *Holcus lanatus*) (Parr et al., 2009b). Parr et al. also record two main types of heath in the Burren – one characterised by mountain avens (*Dryas octopetala*) and the other by ling heather (*Calluna vulgaris*). Limestone pavements and species rich grasslands are among the best-known habitats of the Burren, but the hazel woods and well-developed areas of scrub are not to be ignored. Their biodiversity has been largely overlooked, even by biologists - e.g. *"...scrub on its own is considered to be of little conservation value...*" (Laborde and Thompson, 2009). These wooded areas are now set in a changing landscape, however, with much of the grassland and pavement that

surrounded them in the past now being taken over by young, secondary hazel scrub. This newer scrub may also interfere with farming by blocking access trackways and taking over valuable farmland. One of the main theories about why this is happening (along with the possible influence of climate, and a definite drop-off in human use, e.g. for fuel) is changes in farming, and more specifically, grazing practices. It is ironic that it is farming, over millennia, which has made the Burren what it is today (floristically speaking at least), and that the greatest current threat to the biodiversity of the Burren is undergrazing and neglect (Dunford, 2002).

This thesis aims to document the plants and snails found in woodlands, scrub and grasslands in the Burren, and to assess if distinct communities exist in each of these habitats. The principal environmental drivers are identified. Fenced exclosures are used to experimentally investigate how diversity, abundance and community structure of plants and snails is affected by cessation of grazing. Additionally, some methodological issues in malacology are investigated.

Study area - the Burren

The Burren is a karstic landscape located on Ireland's Atlantic seaboard (Figure 1). It is renowned as one of the most outstanding archaeological landscapes in Europe (Grant, 2010). It is also famous as one of the most botanically interesting and biodiverse areas in Ireland, and it is in the Burren that many of Ireland's rarest and most fascinating mixtures of plants can be found. As Tansley (1965a) aptly said, it possesses a "*curiously mixed vegetation*". For example, the Mediterranean dense-flowered orchid (*Neotinea maculata*) can be found growing next to the alpine spring gentian (*Gentiana verna*), often at sea level. Calcicole and calcifuge species can also be found growing side by side. Dunford (2002) states that almost three-quarters of Irish (native) plant species (635 spp = 70.5%) are to be found there. Further details on the unusual Burren flora can be found in publications such as Webb and Scannell (1983), Nelson and Walsh (1991), D'Arcy and Hayward (1992), Nelson (2000) and O'Connell and Korff (2001). The plant communities of the Burren are less well studied, but see Ivimey-Cook and Proctor (1966) for a very extensive and detailed, if somewhat outdated, conspectus on plant communities. McGough (1984) provides a classification of Burren grasslands, and Jeffrey (2003) a review, while Parr et al. (2009b) and Murphy and Fernandez (2009) provide recent and objective vegetation classifications for plant communities of, respectively, upland grasslands and limestone pavements. These are discussed in more detail later in this chapter.

The Burren is remarkable also for its size – it ranks as one of the largest limestone pavement dominated landscapes in Europe (National Parks and Wildlife Service, 2009, Grant, 2010). Murphy and Fernandez (2009) report that Ireland has the largest area of limestone pavement in the EU, at 31,000ha, the majority of which is in the Burren region. This compares with less than 3,000ha in all of the UK (Joint Nature Conservation Committee, 2007, Ward, 2007). Ward (2007) reports that the three main Burren candidate Special Areas of Conservation (cSACs) - East Burren, Moneen

Mountain and Black Head – Poulsallagh, contain 18,000ha of limestone pavement between them. Five adjacent cSACs contain another 450ha, bringing the total in the immediate region to approximately 18,450ha.

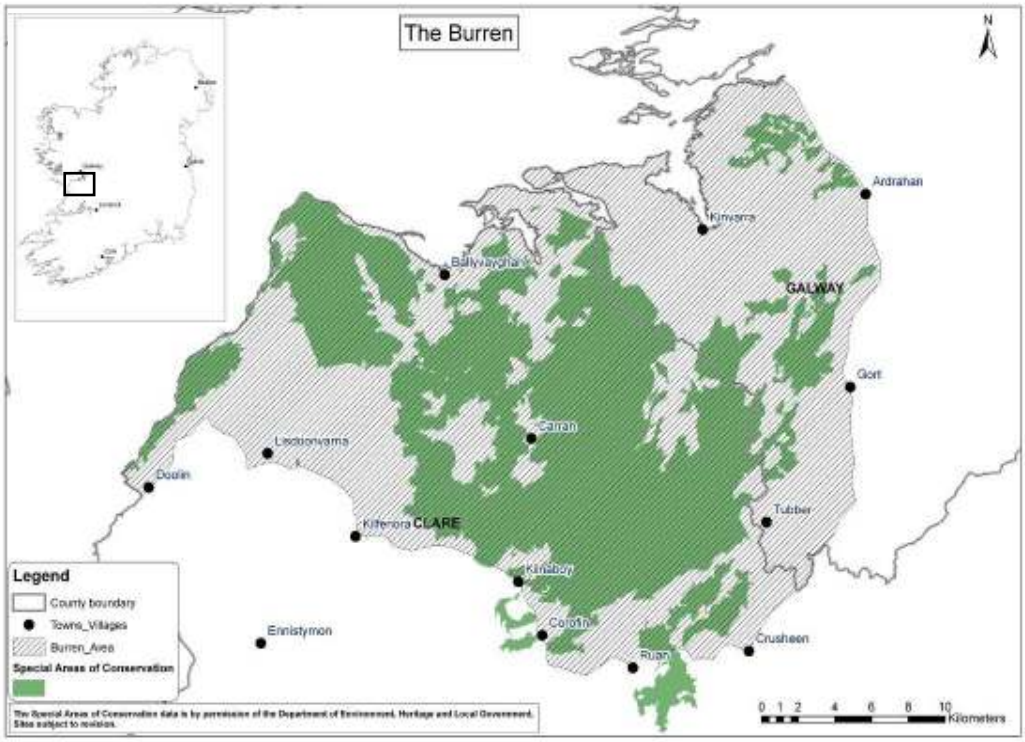


Figure 1 Location and approximate extent of the Burren. (Map produced by Burren Farming for Conservation Programme, 2010, and reproduced with permission from the National Parks and Wildlife Service, NPWS.)

Geology

The Burren is made up principally of Carboniferous limestone which rests upon a deeply buried foundation of Galway granite (Figure 2) (Simms, 2001). It is more than 1,000m thick and was laid down at the end of the Lower Carboniferous period, approximately 325 million years ago (Drew and Daly, 1993). Thus the Burren was once a limey mud at the bottom of a shallow tropical sea, the evidence for which lies in the abundance of coral fossils to be found in the area (Feehan, 2001). Fossils of older ages are obliterated by the presence of the granite, and younger fossils are absent because of the erosion of the material overlying the limestone (D'Arcy and Hayward, 1992). The limestone disappears in the south under beds of Namurian black shales and flagstones. The Namurian deposits once overlay most of what is now the Burren, but have been stripped away in the north to expose the limestone. These Namurian layers were laid down in the Upper Carboniferous period, about 280 million years ago and were eroded away by the bulldozing action of the glaciers (D'Arcy and Hayward, 1992, Feehan, 2001). It has been suggested that the Burren has retained its present height only because it is relatively recently that the protective Namurian

covering has been stripped from it. During the Pleistocene Period at least one ice sheet covered the whole of this area. It finally melted and retreated, after many successive advances and retreats, about 10,000 years ago (D'Arcy and Hayward, 1992, Drew and Daly, 1993).

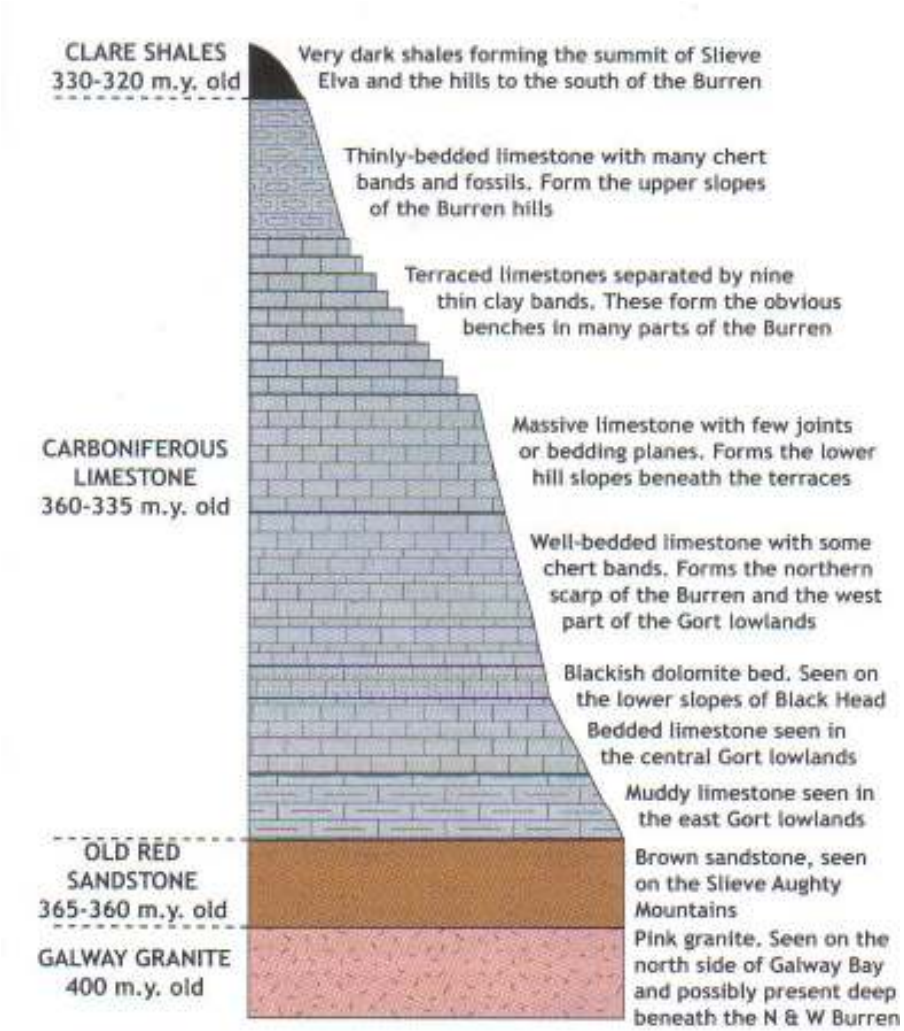


Figure 2 Vertical section through the rocks beneath the Burren and Gort lowlands (not to scale). [Taken from Simms (2001).]

Limestone is an unusual rock type, both because of its relatively high solubility and because it leaves relatively little weathering residue (Webb and Scannell, 1983). The Burren is, for the most part, made up of pure limestone (except for occasional chert beds: Webb and Scannell, 1983). This pure limestone dissolves relatively quicker than other types of limestone. Karstification is the process whereby limestone (or similar carbonate rocks) is slowly dissolved by water. Pre-existing fissures and fractures in the rock are slowly enlarged as water passes through them (Drew and Daly, 1993). Interestingly, karstification begins more easily if the carbonate rock has a covering of soil. Over time, many of the features that are familiar within a karstic landscape, such as grikes (vertical joints or cracks between the slabs of rock), swallow holes, dry valleys, turloughs (seasonal

lakes), dolines (depressions formed by cavern collapse) and poljes (similar to dolines but larger) are formed.

Due to the nature of carbonate rocks there is usually very little surface water flow in karst areas - most of the water flows underground in often complex systems of conduits, caves and channels. For example, the only river which maintains a surface flow to the coast at all times is the 4km-long Caher River, in the north-west of the Burren. Nelson and Walsh (1991) note that "*any rain that falls will quickly drain away underground – within a few seconds most water has run off the Burrens surface*.".

While the limestone pavement itself can be mapped and its extent quantified (Figure 3 shows the area and extent in Ireland), the exact area which is covered by 'the Burren' depends on how its boundaries are drawn up. It is bounded to the north and west by Galway Bay and the Atlantic, and by the Namurian shales which overlie it in the south. The eastern boundary is somewhat arbitrary, however. It is sometimes taken to be where the uplands give way to the lower ground to the east of the Turloughmore hills, but others (e.g. Webb and Scannell, 1983) take the main Ennis to Galway road (the N18) as the boundary. O'Ceirnín (1998) puts the area of the Burren at 270km^2, and Drew and Magee (1994) estimate it to be 367km^2. Williams et al. (2009) say that the Burren is 720km^2, due mainly to the fact that they include large tracts of lowland limestone country. A particularly broad definition of the Burren, following that of the Burren Farming for Conservation Programme is provided in Figure 1.

Climate

The climate of the Burren is cool, temperate and oceanic, being very influenced by the North Atlantic drift. This means that while the weather may be changeable and unpredictable, it is equable and there are few extremes. Winters are generally mild (few frosts), and summers cool, and rainfall occurs year-round. Average temperature, sunshine, rainfall and wind conditions are listed below (Table 1) from the nearest Meteorological Station in Shannon. However, as Figure 4 shows, rainfall in the Burren is somewhat higher than that at Shannon. Drew (1990) quotes figures (from a series of long-term rain gauges located in the Burren) in the range of 1,239mm/yr for Corofin (just south of the Burren) and 1,729mm/yr for Corkscrew Hill (+/- mid-Burren), with an average across the whole Burren of 1,527mm/yr.

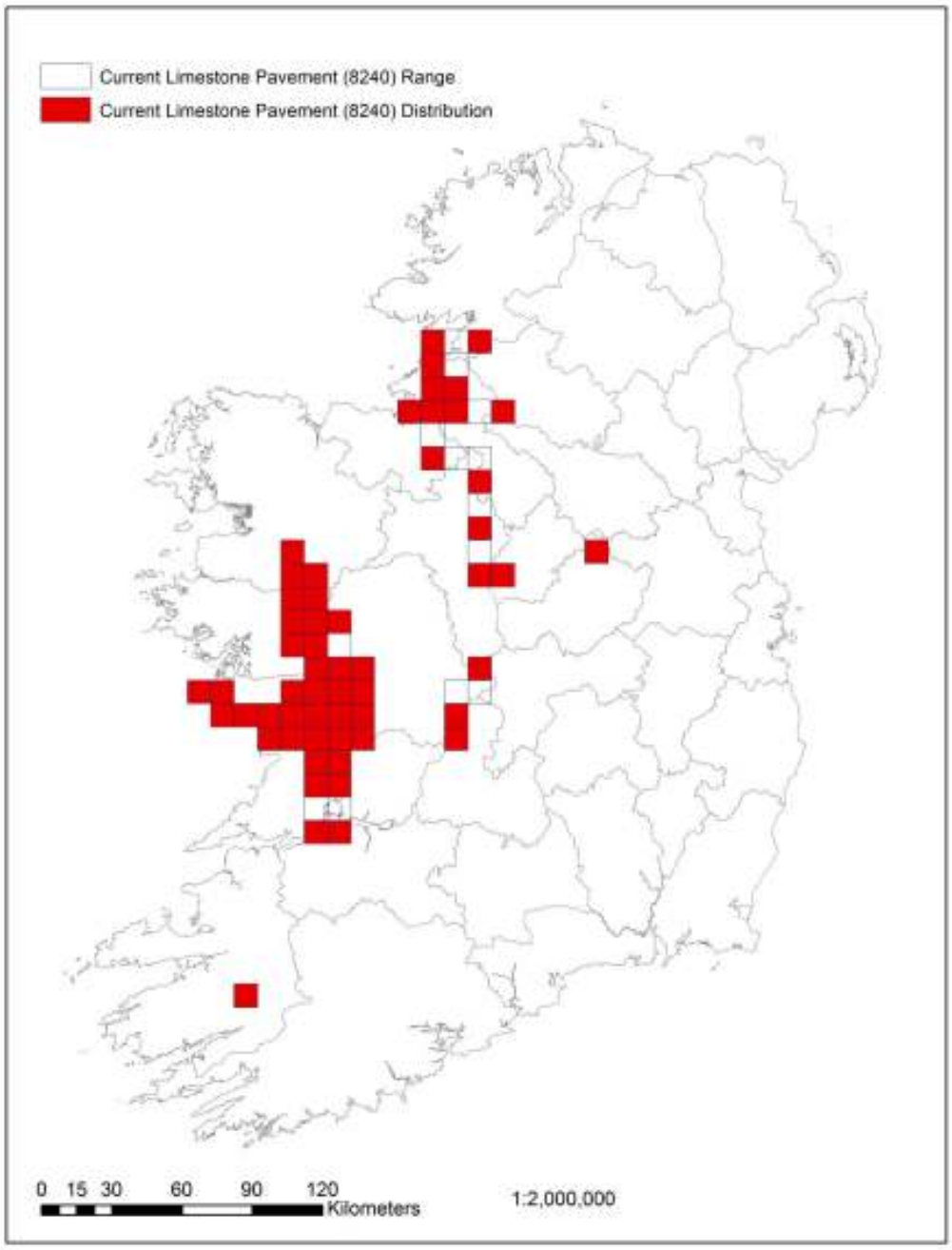


Figure 3 Occurrence of limestone pavement in Ireland. (Reproduced from Murphy and Fernandez, 2009.) [The *distribution* represents areas where limestone pavement is present, and is a sub-set of the range. The *range* is the outer limits of the overall area in which a habitat is found. It is an envelope within which areas actually occupied occur, with additional areas included if there are fewer than two 10km-squares between actual occurrences (Ward, 2007).]

Table 1 Main aspects of the Burren climate. Based on the 30-year averages (1961-1990) from Shannon Airport, the nearest Meteorological Station to the Burren. (Cited from BurrenBeo, 2011).

Temperature	**Rainfall**
Mean Daily Temperature (Celsius): 10.1 (Hottest - June 15.7, Coldest - January 5.4) Mean Daily Maximum (Celsius): 13.5 (Hottest - July 19.4, Coldest - January 8.2) Mean Daily Minimum (Celsius): 6.8 (Hottest - July 12, Coldest - January 2.6) Absolute Maximum (Celsius): 31.6 (June) Absolute Minimum (Celsius): -11.2 (January)	Mean Annual Rainfall (mm): 926.8 (Wettest - December 99.6, Driest - April 55.5) Mean number of days with >0.2mm rain: 214 Mean number of days with >1mm rain: 160 Mean number of days with >5mm rain: 66
	Other
Sunshine	Mean Annual Wind Speed (knots): 9.8 (Windiest - Feb. 11.1, Calmest August 8.6)
Mean Daily Sunshine (hours): 3.48 (Max - May 5.77, Min - December 1.42) Maximum Daily Sunshine (hours): 15.8 (June) Mean Number of Days with no Sun: 62	Mean Number of days with snow/sleet: 10.9 (Most snow - January 3.4 days) Mean Number of days with hail: 21.7 (Most hail - March 4.3 days) Mean Number of days with thunder: 6.3 (Worst thunder - January 0.9 days avg) Mean Number of days with fog: 31.8 (Foggiest month - January 4.1)

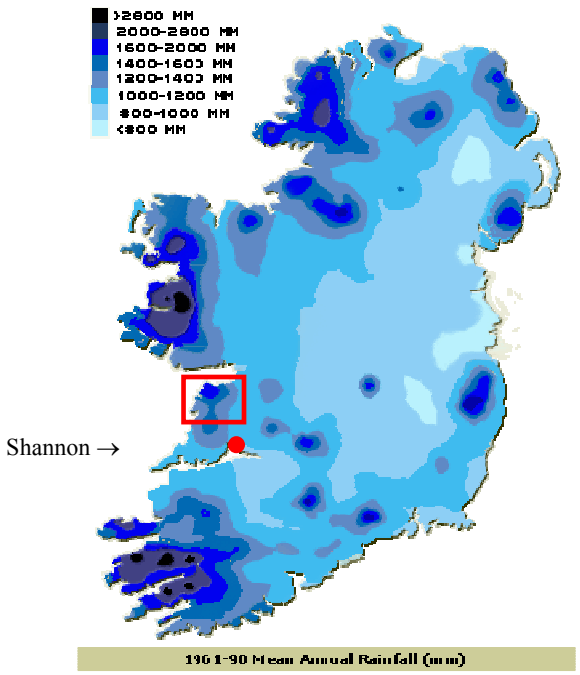


Figure 4 Mean annual rainfall (mm) for the island of Ireland (source: MetÉireann).

Soils

Soil types

The soils of Clare were surveyed between 1965 and 1968 as part of the National Soil Survey (NSS) organised by An Foras Talúntais (The Agricultural Institute), and this work culminated in the publication of 'The Soils of Co. Clare' (Finch, 1971). The main purpose of these surveys was to inform land use planning. Soils were mapped at the 6 inches to 1 mile scale (1:10,560), with 'soil series' (a basic category in soil classification, having similar type and arrangement of horizons, and having developed from a similar parent material) being the primary mapping category. The soil series are grouped into 'great soil groups' which are closely related soil series. (Note that Co. Galway was not surveyed at this time.)

The main great soil group to occur in the Burren is the 'rendzina', but 'brown earths', 'grey-brown podzolics' and 'gleys' occur also (Finch, 1971). Thus there is much variability in the soil type, and therefore also in quality, fertility, depth and usage potential. Their origins are also quite different, with the mineral soils being derived from glacial drift and the rendzinas deriving directly from the Carboniferous limestone bedrock. Brown earths are mature, well-drained, mineral soils, and may be acid or alkaline, depending on their parent material. They are generally good soils for agriculture. The grey-brown podzolics are associated with leaching, and in particular, the leaching of clay, but they are generally "good all-purpose soils" (Finch, 1971). They are found throughout the Burren, albeit in scattered patches, and are often deeper than the other mineral soil types (e.g. the brown earths). Both of these soils types are more fertile than the 'typical' Burren rendzina soils, and often result in pockets of green which contrast with the rest of the landscape. Gleys are soils with poor drainage and water-logging. They are found in low-lying areas of the Burren, also in small hollows on some hilltops – but their extent is very limited.

Rendzinas are free-draining, shallow soils, often high in organic matter, derived from a parent material which is high in carbonates (>40-50%) (Finch, 1971). They are the most common soils in the Burren, and fall into two main soil series: the 'Burren series' and the 'Kilcolgan series'. Many of the rendzinas are well suited to extensive winter grazing because of their strong structure and good drainage, making them quite resistant to poaching and waterlogging. Furthermore, because they are free-draining and of relatively nutrient-poor status, they facilitate stress-tolerant species, while discouraging more vigorous species (for example, many grasses). This is one of the features which contributes to making the Burren so special botanically.

Another (and rather controversial - e.g. Dunford, 2002) soil type has been reported from the Burren – loess. This type of soil has its origins in what was essentially rock dust (glacially-produced ground-down rock powder), which has been wind-blown and deposited elsewhere (Jeffrey, 2003).

It is fine in texture, non-calcareous (pH +/- 6.5, Dr David Jeffrey pers. comm.) and free-draining. Jeffrey (2003) reports that loess is found extensively in the UK, and that he (Jeffrey, 1995), O'Donovan (1987) and Moles et al. (1995) have found it in the Burren also. However, in a later publication, Moles and Moles (2002) withdraw their suggestion that there is a loessic origin for the soils they investigated.

A GIS (Geographic Information System) map of soils for the entire country has been produced by Teagasc (The Irish Agriculture and Food Development Authority) (Fealy et al., 2006). Soils and subsoils have been mapped, using a "*first-approximation soil classification for those areas not previously surveyed by the NSS, using a methodology based on remote sensing and GIS*" (Fealy et al., 2006). According to this system most of the sites in this study are found on shallow well-drained mineral soils which are mainly basic in nature (more details provided in soils section in Chapter Two).

Soil history

There has been much debate about the past vegetation and soil cover of the Burren, both of which are closely linked. Moles and Moles (2002) note that soil cover in the Burren is incomplete and patchy, with large amounts of exposed rock. Farrington (1965) postulated that the drift deposition itself (by retreating glaciers) was irregular, particularly on the Burren uplands, with some areas never having had much cover.

However, in order for woodland to have occurred (discussed in the next section) more substantial deposits of soil that those present now are likely to have existed. (However, yew woods do occur on limestone pavement in Killarney: Kelly, 1981, Perrin, 2002). In addition, the very numerous prehistoric structures, field systems, settlements and tombs that are found in now-barren parts of the region are suggestive of a landscape more capable of supporting humans and their needs (Drew, 1983). Indeed Watts (1983) points out that judging by the wealth of monuments, the Burren has been one of the most densely populated regions in Ireland since Neolithic times.

Drew (1982) found evidence of a brown earth soil in the region from underneath old protected land surfaces (e.g. underneath ancient stone walls). In further work he used paleosols – older soils preserved by burial underneath other sediments or rocks – and solution features on exposed rocks to add support to the theory of a formerly more extensive covering of soil in the Burren (Drew, 1983). He states that soil cover was damaged by erosion which occurred after deforestation. He suggests that this erosion of what he describes as "*an extensive cover of mineral soil*" happened over a short period of time. Furthermore, he asserts that deforestation by man since approximately 2000 BC has possibly been the most significant factor in causing mass soil erosion in karst systems in general.

Feeser and O'Connell (2009) noted that analysis of material washed into grikes supports the theory that considerable soil loss has taken place – but their findings indicate that this occurred during the first millennium AD, or even in the early part of the second.

Vegetation history

Even though some of the findings have been refined or superseded, the detailed account of vegetation history in the Burren during the Holocene (the period since the last glaciation) provided in Watts (1984) is still valuable. It is based largely on cores taken from two small water bodies in the south-east of the region. The sequence of invasion of tree species after the final retreat of the ice is broadly similar to that put forward by Mitchell (2006) for the whole of Ireland. The account here largely follows the sequence of Watts, with additions from other authors.

Juniper (*Juniperus communis*) formed a significant part of the pioneer vegetation and birch (*Betula*) was next to follow (Kirby, 1981). At a certain point there were probably substantial stands of birch in the region, but because herbs make up a significant proportion of the pollen record also, it has been deduced that there was open landscape present too. Mitchell (2006) reports that hazel was the next major tree species to colonise the country, followed by Scots pine. Watts, however, suggests that hazel and pine arrived, in the Burren region at least, simultaneously. He states that this record of pine may indeed be the earliest for Ireland. Hazel cover across Ireland peaked at about 9,000 BP, but it continued to be a major component of woodlands at least until 3,000 BP (Feehan, 2003). The arrival of elm (*Ulmus*) and oak (*Quercus*) in the Burren, in lower quantities than elsewhere in Ireland, happened after the hazel and pine. Overall, the picture at this stage (early Holocene) is one of woodland – pine, elm, hazel and birch – with open ground, as opposed to the dense forest of oak and elm that is thought to have covered much of the rest of Ireland, at least on better soils (Crabtree, 1982, Watts, 1984).

Once yew (*Taxus baccata*) arrived in the Burren it quickly came to constitute about 20% of the pollen (Watts, 1984). It peaked in occurrence at 4,550 BP, followed by a substantial decline. After the yew decline, Watts suggests that woodland cover decreased and the landscape became more open. Increases in the pollen of grass, heather, bracken and plantain occurred, along with a rise in birch and holly (*Ilex aquifolium*). Feehan (2003) states that by 3,500 BP most of Europe had had its tree cover removed by early farming communities, and it is probable that this was the case across Ireland and the Burren also (Kirby, 1981).

At approximately 2,500 BP there was an increase again in the cover of yew and ash, along with a temporary halt in the decline of pine and elm (Watts, 1984) – a return to a more wooded landscape (Feehan, 2003). This corresponds with a climate deterioration which seems to have contributed, along with other factors such as soil impoverishment and erosion, to a lull in farming activity in general across Europe (Feehan, 2003). In the Burren, the late Iron Age lull was picked up at Lios

Lairthín Mór (Jelicic and O'Connell, 1992), at Molly's Lough (Lamb and Thompson, 2005), and at Rockforest (Roche, 2010), leading to the conclusion that there was a pronounced decline in human activity, paralleled by an increase in woodland cover, at that time.

At 1,500 BP pine had virtually disappeared from the pollen record. Watts (1984) states that the causes are unknown, and Roche (2010) cites Bennett (1984) in listing climatic change, the expansion of blanket bog, competition with alder (*Alnus glutinosa*), soil deterioration and human activity as possible causes (although the expansion of blanket bog and competition from alder are unlikely to have been major factors, Dr Jenni Roche, pers. comm.). At around the same time there was a concurrent decrease in woodland cover (all tree species declined), accompanied by an increase in species typical of open habitats.

The latest research on vegetation history in the area (Feeser and O'Connell, 2009) suggests, however, that hazel-dominated woody habitats remained until much later than previously thought: using palynological studies, significant wooded areas have been shown to have existed between 1500 BC and 500 BC. According to Feeser and O'Connell, hazel cover was extensive in the region until possibly as late as 1600 AD. This date ties in with the date put forward by Mitchell (1982) for the beginning of a major 'onslaught' on the woodlands of Ireland. Kirby (1981) also notes that pollen output levels suggest that there were significant areas of secondary hazel scrub in Ireland from approximately 5,000 BP to around the late 16th century AD.

A study based in the nearby (and botanically and geologically similar) island of Inis Oírr has shown that woodlands existed there too at various times since the last glaciation (O'Connell and Molloy, 2005). They were dominated by hazel and pine for the most part, and had a rather open character. The woodlands are thought to have been cleared in the 1400s/1500s. O'Connell and Molloy note that the "*present-day almost treeless landscape is thus of relatively recent origin*."

Agriculture – the 'winterage' system

"*The Burren is a pastoral landscape… Grazing has been the primary land use here for almost 6,000 years.*"
"*Winter grazing is the key to maintaining the Burren's rich biodiversity.*"
(BurrenLIFE, 2010b)

The biodiversity of the Burren owes much to the agricultural traditions of the area. These traditions are many and varied, but one system, known locally as 'winterage', but more widely as 'reverse-transhumance', involves beef cattle being grazed on the rougher uplands between October and April (Dunford, 2001). Transhumance, or 'booleying' (Keville O'Sullivan Associates Ltd., 2008), is the traditional seasonal movement of livestock by farmers, typically from upland areas in the summer to lowland areas in the winter, allowing the complementary exploitation of resources in

both areas (Ruiz and Ruiz, 1986). In the Burren, cattle are grazed in the lowlands in summer time, but out-wintered on higher ground, a reversal of most other transhumance systems. This system was developed in order to take maximum advantage of the unique combination of limestone terrain and oceanic climate which exists in the Burren. One element of this is the fact that the limestone rock absorbs heat during summer, and releases it slowly during the winter, thus greatly reducing frost and lengthening the growing season, and making it a hospitable environment for farm animals (Watts, 1984, Drew, 1997, Dunford, 2002). Additionally, the uplands can lack drinking water for grazing animals in the summer time, but are generally relatively warm, dry areas in winter, with sources of calcium-rich fodder, water and shelter. For local farmers, this was, and still is, a viable, low-cost alternative to housing cattle in slatted sheds and feeding them large quantities of silage.

This farming system has a number of distinct advantages for the botanical diversity of the region. Foremost is the fact that much of the dead and dying biomass is removed during the winter, allowing the emergence and growth of herbs in spring which might otherwise have been choked and out-competed (Dunford, 2001, 2002). They can then thrive in an environment from which much of the competition has been removed, and in which there is relatively little (summer time) disturbance. The winterage system has been credited as one of the main contributing factors to the great diversity of flowering herbs in the region (O'Donovan, 2001, Dunford, 2002).

Recent changes – farming and landscape

Changes in farming

In recent times a number of factors have been driving changes in farming in the region. Some are common to farming throughout the country, including changing demographics (Figure 5) and falling incomes (Williams et al., 2009). Additionally, the age profile of Irish farmers is increasing (e.g. The Heritage Council, 2010). This has also been outlined by Frawley and O'Meara (2004), who show that in parts of Co. Galway 84% of farmers are over 40 years of age. Central Statistics Office (CSO) figures suggest that only 8% of farmers in the Republic of Ireland were under 35 in 2005, compared to 14% in 1995 (Anon., 2008). Dunford (2002) found that an off-farm income is now part of the domestic economy of over half of Burren farms. This of course leaves less time for labour-intensive farm tasks such as out-wintering stock.

Other factors involved include a move away from mixed farming (which would have included sheep and/or goats), and an increase in the use of less hardy breeds of cattle because they gain a more competitive price at the marketplace. The traditional breeds of beef cattle (e.g. Shorthorns) required little or no supplementary feeding while on the winterages, whereas the Continental breeds which have gained in popularity in recent decades (such as Charolais and Limousin: Dunford and Feehan, 2001) typically need much more nutritional supplementation and husbandry (Dunford, 2002). There has also been a substantial changeover from a system of grazing older beef animals

(and, on many farms, sheep and goats) to a suckler cow system. This involves the production of weanlings or young calves for the export market from non-dairy, or suckler, cattle. This change has been largely driven by the EU 'Suckler Cow Premium' (Anon., 2009). Moran (2009) notes that in-calf cows have high nutritional requirements, which has resulted in an increased rate of silage feeding. Silage-fed animals forage less, contributing substantially to the problem of undergrazing. Silage feeding can also lead to poaching and point source pollution (BurrenLIFE, 2010b). Other policies, such as the recent 'Farm Building Scheme' which provided grant-aid for the building of slatted sheds for housing animals, have also brought big changes in Burren farming practices (Dunford, 2002, Williams et al., 2009). A survey which involved approximately one in six farm families in the Burren has shown that the farmers themselves view the building of slatted sheds as one of the main changes that have occurred in farming in recent years (Walsh, 2009b).

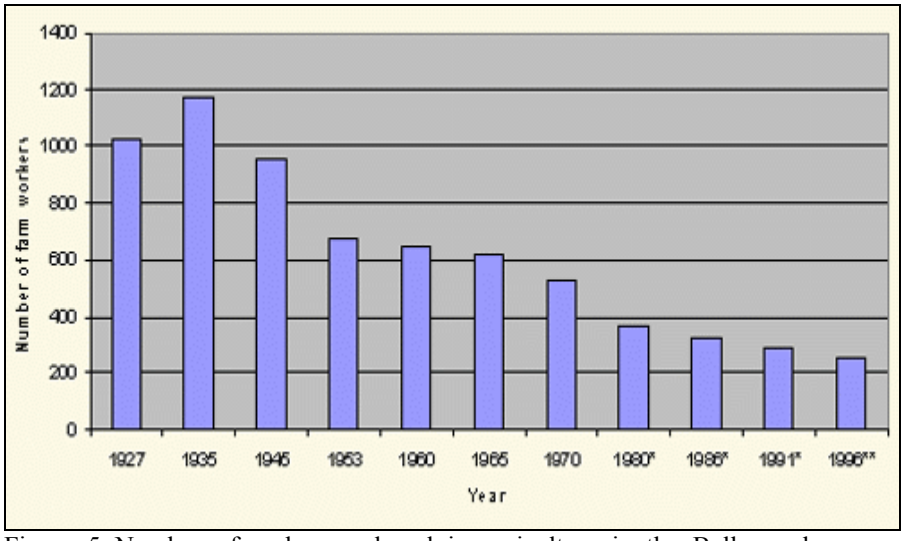


Figure 5 Number of males employed in agriculture in the Ballyvaughan area, which covers approximately 75% of the Burren. Both * and ** refer to number of males *and* females employed. Source: Central Statistics Office (cited in Dunford, 2002).

All of these factors combined have resulted in a decrease in grazing pressure, a decrease in the practice of out-wintering cattle, and a changeover to a more specialised and intensive style of farming. The farmers surveyed by Walsh (2009b) said that the changes are happening because of a need to maximise income, and also to 'make life easier' for part-time or elderly farmers.

Changes in the landscape

One of the most dramatic and noticeable results of the changes in agriculture outlined above is the dramatic spread of hazel scrub. A recent report from The Heritage Council (2006) states that the area of land under hazel scrub in one part of the Burren has doubled in a 31-year period (1974-2005), and that the rate of spread of hazel in this area was 4.4% p.a. between 2000 and 2005.

Dunford (2002), reporting on the results of a survey of 65 Burren farmers, states that hazel scrub is considered a problem on the farms of two-thirds of the respondents.

Thus the Burren winterages and uplands may go the way of other areas of 'marginal' land, which are often the first areas to be abandoned as farming changes (MacDonald et al., 2000, Pineda, 2001). As noted by Dunford (2002), and also in Tomazic (2003), Eler (2004) and Vidrih et al. (2008), abandonment has resulted in dramatic changes in some of Europe's other karstic landscapes, such as the Kras region of Slovenia, mainly through scrub and woodland development. Both Dunford (2002) and Parr et al. (2009a) say that land abandonment has been identified as one of the main threats to nature in the Burren.

Grazing & grazers

"*Grazing is a natural process affecting the composition and structure of plant communities. It is generally accepted that grazing is an essential tool with which to achieve nature conservation objectives in grassland. The key objectives are the control of successional change toward scrub and woodland and the creation of structural heterogeneity in the vegetation…"*
(Tallowin et al., 2005)

A (short) history of grazing animals in Ireland and the Burren

It is well acknowledged that large grazing animals have historically been a part of many ecosystems across Europe (Hester et al., 1996, Anon., 2005, Mitchell, 2005). In fact, some authors go so far as to say that they drove and shaped the vegetation (Vera, 2000). This theory is not universally accepted (Mitchell, 2001, Svenning, 2002, Kirby, 2003b, Kirby, 2004a, Mitchell, 2005), but it does highlight the fact that the assumption of a dense forest cover across north-western Europe has not been satisfactorily tested (Mitchell, 2001).

The extent to which grazers have influenced the vegetation (both in terms of composition and dynamics) in Ireland during the early Holocene (i.e. before the arrival of man and agriculture) is not completely clear, but Mitchell (2005) claims that large herbivores were so uncommon in Ireland that the island can in fact be considered as a control, enabling comparisons with nearby areas that were certainly grazed (i.e. Britain and the rest of north-west Europe). Mitchell, quoting Woodman et al. (1997) and Roberts (1998), states that wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*) were the only large herbivores present, and that the numbers and/or extent of red deer in Ireland is debatable, with little evidence having been found of their presence in Ireland during the early Holocene. Watkinson et al. (2001), however, state that there would have been few woodlands in the British Isles which have not had large grazing mammals.

Woodman et al. (1997), in the 'Irish Quaternary Fauna Project', drew together much of the existing information on the Quaternary fauna of Ireland, and added to it by providing radiocarbon dates for

a number of finds. They report that the first reliable records of domesticated cattle in Ireland come from approximately 5,000 years BP, and horse bones have not been found before 4,000 years BP (also reported for Co. Clare in Keville O'Sullivan Associates Ltd., 2008). Feehan (2003) states "*The Burren has been farmed almost since the arrival of the agricultural way of life in Ireland: a court tomb on Roughan Hill has been dated to 3500 BC*." A similar date, 3800 BC, has also been put forward by Grant (2010). O'Connell (1994) suggests that farming began in the Burren around 5,800 BP, and Lynch (1988) reports on evidence of a Neolithic farm economy from excavations at the Poulnabrone dolmen dated to 5,500 BP.

It is likely that early Neolithic farmers in the Burren brought with them cattle, pigs, sheep and goats (D'Arcy, 1995, Dunford, 2002), though evidence of domestic animals in prehistoric times is very limited (Feehan, 2003). Dunford (2002) quotes de Valera and Ó Nualláin (1961) and Lynch (1988) when stating that cattle were important in the Neolithic, but that mixed farming was prominent, with sheep and goats also being kept. While the impact of man (and agriculture) around that time was seen in pollen diagrams through a lessened tree cover (there was a "major expansion in settlement and farming activity in the uplands": Grant, 2010), this impact seems to decrease again in the late Iron Age, when the amount of tree pollen recorded rises (Mitchell, 1982). This finding is common to the rest of Ireland (Feehan, 2003).

By the start of the Early Christian Period (c. 500 AD) agriculture in the Burren, as elsewhere in Ireland, had begun to recover from the quiet period during the Iron Age. Archaeological investigations at Cahercommaun stone fort in the Burren have yielded an insight into farming about 800 AD, suggesting that cattle were the most common farmed animal, at least in that locality, but that mixed farming was practised. Keville O'Sullivan Associates Ltd. (2008) state that dairy and dry cattle were the most important farm enterprises in Co. Clare in this period. The finding of a large number (55) of spindle-whorls at Cahercommaun led to the conclusion that wool was processed there, and that sheep were probably also common in the region at the time (Cotter, 1999).

Cattle were of huge importance in Ireland in the Middle Ages (i.e. the Early Christian and the Medieval Periods) (Feehan, 2003). Dunford (2002) notes that the high number of tower houses, with associated walled livestock enclosures, serve as proof of the agricultural significance of the Burren in Medieval times.

Dineley's journal of 1681 provides the following mention of the farming systems of the Burren: *"...which raiseth earlier Beef and Mutton, though they allow no hay, than any land in this Kingdome, & much sweeter by reason of the sweet herbs intermixed and distributed every where."* (Dineley, 1681). Dunford (2002) writes that, following the major redistributions of land in the 17th century, sheep farming seems to have become more popular. Feehan (2003) notes the Burren as

one of the main areas in the country for sheep farming in the late 18th century – this was in contrast to many other parts of the country, where cattle held sway. Kirby (1981), referring to Ainsworth (1961), says that extensive sheep farming was practised in the Burren between 1650 and 1880, and that many authors claim that cattle rearing, although taking place in the Burren at the time, was not as common as sheep rearing. In 1808 Hely Dutton produced a 'Statistical Survey of the County of Clare' (Dutton, 1808) for the Dublin Society, in which he documents many aspects of agricultural and rural life. The overall picture which emerges regarding farming in the Burren is one dominated by sheep, though cattle were also reared. He mentions that *"immense numbers are annually reared"*, and that because of the wild plant mixtures that they were grazing on, *"the mutton ... is amongst the best in Ireland..."*. Furthermore, he specifies that the rocky areas of the Burren (*"...those vast tracts of rocky ground..."*) were *"devoted almost exclusively to the rearing of sheep"*.

By the middle of the 19th century life (and agriculture) had changed dramatically throughout Ireland. The human population was the highest it had ever been and much of the population was desperately poor. In many areas, the Burren included, the general population subsisted on a diet made up mostly of potatoes. A succession of bad potato harvests led to widespread starvation, disease, death and emigration in the period 1845-47. The population of Co. Clare was reduced by 24% during the period 1841-1851 (O'Neill, 1974). Leading up to this, the Burren had a population at least ten times its current size (D'Arcy, 1995). The landscape was almost certainly devoid of trees and scrub at this time, except in all but the most inaccessible of places, because timber was in high demand as fuel and building material (Dunford, 2002).

Since the famine, the pressure on the Burren as an agricultural landscape has been less, and it has been reverting, slowly for the most part, to a more wooded appearance (Kirby, 1981). Two of the major factors which had been keeping hazel scrub in check, sheep grazing and clearance for fuel, all but disappeared. The most popular farmed animals after the famine were, once again, cattle; sheep farming decreased substantially (Dunford, 2002).

In addition to these two factors, some authors add a third – the influence of goats, whether farmed or feral. For example, Whitehead (1972) suggests that the killing and/or exporting of large numbers of goats during the second World War drastically reduced the population. He states, however, that it "*was not long before the local people began to regret the shortage of goats, for the scrub soon started to spread and became well-nigh impenetrable in parts where their cattle used to graze.*" Feehan (2003) asserts that it was goats and sheep in fact, rather than cattle, which were the most important animals in early Irish farming. He also states that while goats were not that common during the Early Christian Period, they came to be so by the Early Modern Period, and were 'typical' on small farms in the late 1800s.

Current grazing situation in the Burren

Suckler cows are stocked on 90% of Burren farms, and the average herd size is 31 cows - based on the results of a survey presented in Dunford (2002). Almost half of the 65 Burren farmers surveyed also had sheep (on average, 60 ewes), but there is a decreasing trend in sheep farming. Just under 20% of farmers had a dairy herd (average size 32 cows), though not all herds were based in the Burren. Surprisingly, the formerly widespread system of beef/drystock animals made up only 4.6% of the sample.

Stocking rates for winterage areas were estimated by respondents to Dunford's survey to be 0.56 LU/ha (livestock units per hectare) over the six-month winterage period. Grasslands in the uplands were used for summer grazing by over half of the respondents, although the degree of usage varied. Silage bales were used by 40% of the farmers surveyed to feed animals on the winterages, while 18% of farmers said that they fertilised winterage grasslands, application of fertiliser being by hand in many cases.

Accurate estimates of the size of the feral goat population in the Burren are hard to come by. Kirby (1981) stated that the only documentary evidence of goats in the Burren (to that date) was to be found in Whitehead (1972). Whitehead wrote that in the 1930s there were hundreds of goats in the Burren, but that many were killed and exported during the second World War, and "*only a few remain*". Bullock and O'Donovan (1995) quote wardens as estimating that the population of feral goats in the Burren was, at that stage, in the low thousands. Indeed, Bonham and Fairley (1984) found that there was an extremely high survival rate for goat kids in the Mullaghmore area – 100% in 1980. They reported finding 138 goats, in two herds, in the National Park at that time, and Byrne (2001) reports between 63 and 85. She also reports a large cull (>200 individuals) in 1994. Moles et al. (2005) state that there were 212 individuals in the vicinity of the National Park at that time. Viney (2011) suggests that there are currently about 1,000 feral goats in total in the Burren, and this estimate is supported by Werner (2010), though with the caveat that it is a very approximate value. The local National Parks and Wildlife Service (NPWS) conservation ranger thinks that there may be more (Emma Glanville, pers. comm.), and accounts from local farmers tend to support this latter view. Most of the goats are relatively recently escaped domestic dairy goats, but there are suggestions that some are of more ancient stock (Werner, 2010).

There are no deer herds in the Burren, although a few deer have been seen running with goat herds in the area of the National Park (local farmers, pers. comm.), and deer sometimes wander into the Burren from the outer edges (e.g. red deer, *Cervus elaphus*, have been seen near Kinvara: local landowner, pers. comm.). Thus the influence of deer as grazers in the Burren is considered here as negligible. With respect to other grazers, rabbits are not common in the region, but hares are plentiful.

The impacts of different grazers

"*Grazing is always to some extent selective…"* (Morris, 1990)

Species of herbivorous animals graze (i.e. feed mainly on grasses) and browse (i.e. feed on woody plants) differently, and utilise different plants or groups of plants. Some plants are avoided by most animals, e.g. those with spines, like thistles, and those with glandular hairs (Morris, 1990), and most animals find grasses and herbs more palatable than woody plants. Goats are an exception however (Figure 6), being fond of most scrubby plants, along with thistles, docks and nettles, among others (Whitehead, 1972, Mayle, 1999). Cattle tend to graze by wrapping their tongue around their food plant(s) and pulling (the "wrap-around-and-pull" method mentioned in Bacon, 1990), while sheep have a nibbling mouth-action which crops the sward very short. Cattle are not particularly selective grazers (Mayle, 1999), and are better suited to dealing with tall or rank vegetation than are sheep, for example. Sheep have a tendency to select flowers and herbs (Bacon, 1990). Cattle are content to eat coarse grasses, which sheep will avoid, and they will do so early in the season, encouraging the growth of other less competitive species (Feehan, 2003). Cattle hooves create breaks in the turf, and also break up litter, both of which impacts may be beneficial in the management of calcareous grasslands (Bacon, 1990, Moles et al., 2005) and also in woodlands (e.g. Mayle, 1999).

Goats are mainly browsing animals, and hence are very useful for conservation grazing in scrubby areas (Bacon, 1990). However, dietary analysis of faeces from Burren goats showed that they had high percentages of grasses in their diets (Byrne, 2001). Rook et al. (2004) state that goats and sheep can browse on tougher species more so than cattle because they are better able to select the high quality parts of the plants.

When an area is grazed only by cattle, characteristic rings of higher vegetation are evident, encircling dung pats (at least at low to moderate stocking densities). These are known as 'zones of repugnance' and, combined with the dung pats, may cover over 20% of the area available for grazing (Nolan, 1995). Sheep will graze such areas, however. Perhaps one of the best options for optimally grazing any grassland is to use mixed grazing, e.g. sheep and cattle, thus ensuring a more efficient and varied grazing regime.

Hazel scrub and woodlands are also used by grazing animals. Cattle tend to spend more of their time in the scrub/woodland in bad weather (Kirby, 1981, local farmers, pers. comm.). Kirby considers scrub an unproductive habitat for cattle, with a low amount and quality of forage material available to them. He does, however, acknowledge that they eat hazel leaves and even the stem tips (Table 2). Other grazers of hazel in the Burren are goats, sheep and insect larvae. Kirby notes, however, that goats and cattle are the principal grazers of hazel leaves.

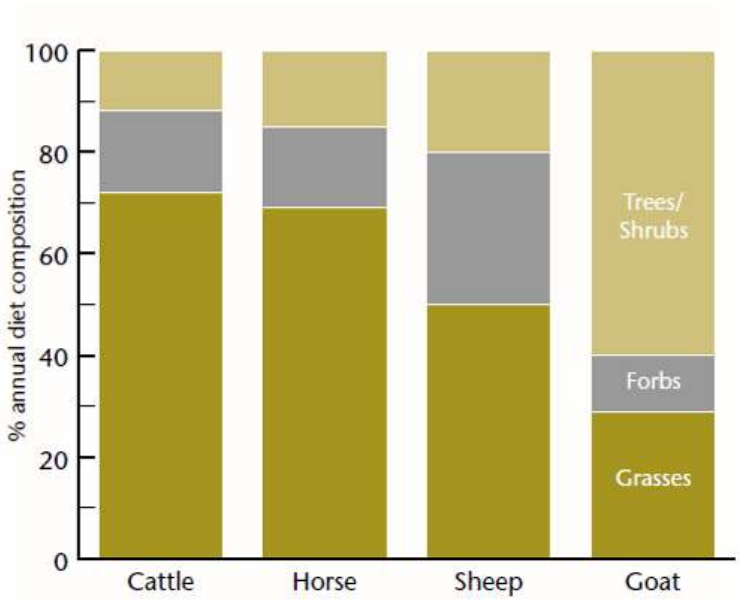


Figure 6 Variation in the diet of domestic stock (Mayle, 1999).

Table 2 Grazers of hazel, and parts of hazel grazed/eaten (from Kirby, 1981).

	Flowers	**Fruits**	**Seedlings**	**Bark**	**Leaves**	**Stem tips**
Goats			X	X	X	X
Cattle			X		X	X
Sheep			X		X	X
Mice	X	X				
Squirrels		X				
Pine martens		X				
Foxes		X				
Birds		X				
Badgers		X				
Insect larvae	X	X			X	

Hazel seedlings are heavily grazed in grasslands (Kirby, 1981, Laborde and Thompson, 2009), but the plant becomes more resistant once it has reached approximately 1.5m in height (Kirby, 1981).

The most important elements of the physical damage done to hazel scrub/woodlands by grazing animals can be summarised thus (adapted from Kirby, 1981):

1 – Trampling, flattening or other damage to the hazel plants, and also the herb and moss layers (on occasion the damage can be major to these lower layers).

2 – Grazing of species in the herb layer.

3 – Bramble, *Rubus fruticosus* agg., broken up (especially by cattle in colder periods), thus decreasing the general density of the scrub.

Kirby points out, however, that damage to the herb layer is usually minimal as cattle use the scrub mostly at a time of year when many of the herb species are dormant or not visible above ground.

The addition of nutrients through dunging is another important impact (Hester et al., 2000, Byrne, 2001, Watkinson et al., 2001), as is the reduction or elimination of tree/shrub regeneration (Watkinson et al., 2001). Morris (1990) believes that the effects of trampling are often under-estimated, and may be quite considerable. The lack of knowledge on the specific effects of trampling is acknowledged in Chappell et al. (1971), who describe trampling as a 'multifactorial effect'.

Habitat types under study – definitions

This study concentrates on three distinct habitat types which we call 'woodland', 'scrub' and 'grassland'. These habitat types were chosen because they form part of a dynamic continuum which is of great current relevance due to recent increases in rates of scrub encroachment in the Burren region (Dunford and Feehan, 2001, O'Donovan, 2001, The Heritage Council, 2006). Figure 7, Figure 8 and Figure 9 show examples of each of the habitat types.

Woodland

Woodland in the Burren is somewhat unusual in that it is dominated by hazel, *Corylus avellana*, a multi-stemmed shrub or small tree. All sites which we call woodland have a closed canopy of hazel which is >5m tall, and possess a typical woodland ground flora. Many ecologists struggle to consider this vegetation type 'woodland' in the typical sense, but with its closed canopy and woodland ground flora, it matches typical woodlands in all ways but height and structural complexity. Rackham (2006) points out that hazel only produces pollen when it is unshaded (i.e. when it is a canopy species), and he infers that the copious amounts of hazel pollen found in cores indicate that hazel was frequently a canopy tree in woods of times past.

It should be noted that woodlands of the more accepted sense (i.e. dominated by taller trees such as ash, *Fraxinus excelsior*) exist in the Burren also, but these are few and far between and were intentionally not chosen for this study. Examples of areas with ash-dominated woodland in the Burren include: Ballyallaban, Clooncoose (though this site was largely destroyed in the 1980s), the Glen of Clab/Poulavallan, Glencolumbkille, Mullaghmore, Slieve Carran and Turloughmore.

Scrub

The straightforward definition of scrub used by Tansley (1965a) is the one followed here: "*Communities dominated by shrubs or bushes"*. Additionally, all scrub sites in this study are dominated by hazel, with bushes <5m tall (a cut-off used also by other authors: Kelly and Kirby, 1982, Fossitt, 2000, Mortimer et al., 2000, Day et al., 2003). A closed canopy does not exist, though bushes may merge to form patches of closed canopy in places. The vegetation is thus very patchy and heterogeneous in nature. Some areas are dominated by woody plants and others by herbaceous plants. At times in this thesis the scrub has been split into 'woody' and 'grassy' sub-categories to allow further elucidation of patterns. A cut-off point of 50% cover of shrubs in the

Figure 7 Hazel woodlands in the Burren. Above – Ballyclery, showing moss-covered rocks; below – Glencolumbkille, with developing bramble.

Figure 8 Hazel scrub. Above – Carran, with hazel scrub seen stretching to the horizon; below – Roo, a species rich grassland patch.

Figure 9 Grasslands in the Burren. Above – Gregan, with some outcropping rock; below – Caher. Scale is provided by the author, and fieldwork helper Shane Casey

vegetation quadrats was used to make the split. This was chosen because a number of authors have found that once scrub/woody cover exceeds 50% large changes occur in the flora and fauna (Ward, 1990, Magnin and Tatoni, 1995).

Grassland

The grasslands in the study are unimproved or semi-improved (sensu Fossitt, 2000) and generally quite species rich. None were thought to have been ploughed or re-seeded, and all have adjacent scrub and outcropping rock.

Vegetation of the three habitat types

The first detailed investigation into the plant communities of the Burren was that of Ivimey-Cook and Proctor (1966). In a review of issues relating to Burren plant communities, Jeffrey (2003) notes that "*the definitive account of the plant communities by Ivimey-Cook and Proctor (1966) remains valid and useful*." The communities they list which are relevant to this study are given in Table 3. It should be noted that their work is heavily based on the earlier work of Braun-Blanquet and Tüxen (1952) who carried out a brief but penetrating study of Irish vegetation. Theirs was pioneering work in the Burren, as in many other parts of the country.

Table 3 From their 'conspectus of communities', the plant communities of Ivimey-Cook and Proctor (1966) which are relevant to this study.

Class: Molinio-Arrhenatheretea R. Tx. 1937.
Order: Arrhenatheretalia Pawl. 1938
Alliance: Cynosurion R. Tx. 1947.
Centaureo – Cynosuretum Association Br.-Bl. and R. Tx. 1952.
Class: Festuco-Brometea Br.-Bl. and R. Tx. 1943.
Order: Brometalia erecti Br.-Bl. 1936.
Alliance: Bromion Br.-Bl. 1936.
Dryas octopetala – Hypericum pulchrum Association.
Antennaria dioica – Hieracium pilosella Nodum.
Class: Querco-Fagetea Br.-Bl. and Vlieger 1937.
Order: Fagetalia sylvaticae Pawl. 1928.
Alliance: Fagion sylvaticae R. Tx. and Diem. 1936.
Corylus avellana – Oxalis acetosella Association.

Grasslands

"*Burren grasslands are notoriously complex and difficult to describe scientifically, due to the high degree of variation in soil and vegetation characteristics over very short distances."*
(Dunford, 2002)

"*Although internationally renowned and much visited, few have tried to classify the grasslands of the Burren."* (Parr et al., 2009a)

The Arrhenatheretalia are, in general, anthropogenic grasslands of basic to slightly acid soils, and the *Centaureo - Cynosuretum,* in particular, are grasslands dominated by species such as *Cynosurus cristatus, Dactylis glomerata* and *Festuca rubra*, along with a suite of common agricultural grassland species such as *Achillea millefolium, Centaurea nigra, Trifolium pratense* and *T. repens.* In the Burren, there are typically additional limestone grassland species present (Ivimey-Cook and Procter, 1966). O'Sullivan (1982) describes a further three sub-associations for the whole of Ireland, the 'galietosum' sub-association being applicable to those grasslands found in the Burren region.

The grasslands in the Brometalia erecti are anthropogenic and found over limestone in dry, base-rich areas (Ivimey-Cook and Procter, 1966). They are seldom mown or manured. Ivimey-Cook and Proctor note that there are a number of types of these grasslands in the Burren, and that the distinction between them can often be difficult to make. In general they are species rich communities, containing many of the characteristic Burren plants. O'Sullivan (1982) and White and Doyle (1982) also divide the Brometalia erecti grasslands into a number of sub-categories (White and Doyle draw heavily on the work of O'Sullivan, but add a few rarer associations (O'Neill et al., 2009)). Shimwell (1971) also worked on the categorisation of the plant communities of limestone grasslands in the British Isles. His findings differ somewhat from Ivimey-Cook and Proctor (1966) in the details. Many of his findings were integrated into the National Vegetation Classification (NVC) system (see below).

The *Centaureo – Cynosuretum* are generally found on deeper soils with a higher clay content, and grasslands in the Brometalia erecti are typically confined to shallower, more organic soils (Ivimey-Cook and Procter, 1966, O'Sullivan, 1982).

The NVC (National Vegetation Classification) of Great Britain (Rodwell, 1991, 1992) is a very useful reference as it constitutes a comprehensive categorisation of vegetation types, and it is the most logical system with which to compare findings, in the absence of such a system in Ireland (although the 'Irish Semi-natural Grasslands Survey' is underway and has produced interim results – see O'Neill et al., 2009, and below, for more details). A review and synopsis of Burren grassland

and heath communities, which utilises some of the NVC communities is provided in Jeffrey (2003) (Table 4).

Table 4 Review of Burren vegetation types by Jeffrey (2003). Only those relevant to the current study are included. (Adapted from Jeffrey (2003)).

Community	Substrate	Notes
Old meadow (MG5)*	Drift or loess on limestone	Probably the most widespread grassland type
Sesleria albicans grassland (CG9)*	Thin drift or loess on limestone	
'Mesobromion' (cf. CG1-2)*	Calcareous drift and thinly covered outcrops	Limited in extent and in mosaics with several other communities
Corylus/Prunus spinosa scrub [Corylo-Fraxinetum (Kelly and Kirby, 1982)]	Drift or loess on limestone	

* MG5 (*Cynosurus cristatus – Centaurea nigra* grassland), CG9 (*Sesleria albicans – Galium sterneri* grassland), CG1 (*Festuca ovina – Carlina vulgaris* grassland), CG2 (*Festuca ovina – Avenula pratensis* grassland),

Parr et al. (2009b), in a detailed study of grassland and heath vegetation of conservation interest in the Burren uplands, used statistical analyses to classify the vegetation objectively. They found that the grasslands in the 'high Burren' – i.e. in upland areas away from more productive farmland – fell into two main categories which they named the *Sesleria albicans – Breutelia chrysocoma* group and the *Dactylis glomerata – Holcus lanatus* group. The first group comprises essentially very low productivity grasslands (similar to CG9 in the NVC classification) and grasslands in the second group (most similar to MG5) are more productive, although they are still used for grazing only in winter time. Each of these groups was further broken into three sub-groups (refer to original publication for further details).

A survey of limestone pavement and associated habitats in Ireland (Murphy and Fernandez, 2009) similarly produced a classification resulting in two grassland types which are commonly found associated with limestone pavements (denoted 'Type 1' and 'Type 2'). These had affinities to CG9, CG10 and CG13 of the NVC (CG10: *Festuca ovina – Agrostis capillaris – Thymus praecox* grassland. CG13: *Dryas octopetala – Carex flacca* heath), as well as to the *Sesleria caerulea – Breutelia chrysocoma* group and a heath category from Parr et al. (2009b). However the overall number of relevés used in the study was small (n=15), and of these, only ten were from the Burren.

Finally, the interim report of the 'Irish Semi-natural Grasslands Survey' (O'Neill et al., 2009) lists four main grassland types for Ireland (but note that Co. Clare is not among the counties which have been surveyed to date). The group into which the Burren grasslands would most likely fit is the *Plantago lanceolata – Festuca rubra* group (summarised as "*dry neutral or calcareous grassland including semi-improved swards*"), which contains within it seven different vegetation types. Types 'a' and 'b' are those which correspond most closely with the grasslands under survey in this study (Table 5).

Table 5 Vegetation types from the Irish Semi-natural Grasslands Survey which most closely relate to the grasslands in the Burren (after O'Neill et al., 2009). Both are within the *Plantago lanceolata – Festuca rubra* grassland group.

	Vegetation type	Comment	NVC equivalent
a	*Succisa pratensis – Carex flacca*	Very species rich swards, typically from well-drained pastures with some calcareous influence, and on steeply sloping ground.	**CG10** *Festuca ovina – Agrostis capillaris – Thymus praecox* grassland
b	*Trifolium pratense – Plantago lanceolata*	A common sward type, consisting of relatively mesotrophic, dry, lowland pastures and meadows on well-drained mineral soils.	**MG5** *Cynosurus cristatus – Centaurea nigra* grassland

In addition to the vegetation classifications outlined above, there exists in Ireland a widely used habitat classification system: 'A Guide to Habitats in Ireland' (Fossitt, 2000). Unlike a vegetation classification, this uses soils, geology and landscape features, in addition to plant communities, to define each habitat. The habitat category into which the Burren grasslands would fall is GS1 - Dry calcareous and neutral grassland, which encompasses all unimproved and semi-improved grasslands on calcareous and neutral soil. This habitat type is associated with free-draining mineral soils and low-intensity agriculture.

Some management considerations

"*Most calcareous grasslands of nature conservation interest are now, or have been in the past, grazed.*" (Bacon, 1990)

Grasslands occupy just under three-quarters of the land area of Ireland, the majority of this being improved agricultural grassland (O'Sullivan, 1982). O'Neill et al. (2009) report that semi-natural grasslands contribute only a small percentage of the total. These semi-natural grasslands are under threat of abandonment on the one hand, and intensification on the other, with fertiliser application, drainage and reseeding being among the accompanying damaging operations (O'Neill et al., 2009).

Management (e.g. grazing, mowing) is of immense importance in the maintenance of most grassland types. In calcareous grasslands, where the threat of scrub encroachment is often present, management is imperative, and very often takes the form of grazing (Ward, 1990, Mortimer et al., 2000, WallisDeVries, 2002, O'Neill et al., 2009). Calcareous grasslands are especially important habitats from a conservation point of view because their biodiversity is high, and they harbour many rare and uncommon species from many taxonomic groups (McLean, 1990, WallisDeVries, 2002).

Bacon (1990) cites three of the most important variables to be considered in the use of grazing as a management technique for calcareous grasslands: time of year; intensity of grazing and type of grazing stock. The time of year in which grazing occurs is typically linked to the productivity of the

grassland. Thus in the case of the low productivity grasslands of the Burren, winter time grazing is usually optimal. For more productive grasslands, summer grazing is often needed also, to ensure adequate control of the growth of vigorous species. Winter grazing has the advantage of stock not eating flowering herbs, and minimal disturbance to many invertebrates which are likely to be fairly inactive and "*tucked well down into the available cover*" (Bacon, 1990). The intensity of grazing is also crucial – it is generally better to have low numbers of stock on the land for longer, rather than high numbers for a short time. This ensures more even grazing throughout a site, and less damage from poaching (Bacon, 1990). Aspects relating to the species of stock used have been discussed above in the section titled 'Grazing and grazers'.

Woodlands

According to Ivimey-Cook and Proctor (1966) the woodlands of the Burren fall under the Querco-Fagetea of Braun-Blanquet and Tüxen (1952) – deciduous woodlands on base-rich soils – and they classified them in the *Corylus avellana – Oxalis acetosella* association. They are described as being very species rich and having a well-developed bryophyte flora. Kelly and Kirby (1982) considered the Burren hazel stands to fall under the association Corylo-Fraxinetum Br.-Bl. et Tx. 1952 (as did White and Doyle (1982)), and largely into the sub-association neckeretosum (which includes the *Corylus avellana – Oxalis acetosella* of Ivimey-Cook and Proctor (1966)). In his synopsis of Burren vegetation types, Jeffrey (2003) also uses the classification of Kelly and Kirby (1982). The Corylo-Fraxinetum is characterised by "*a wealth of broadleaved herbs*" and luxuriant ferns (Kelly and Kirby, 1982). In the sub-association neckeretosum there is an abundance of bryophytes (though usually less species rich than in acid woodlands), but the field layer may be more depauperate. There is typically a high soil pH and a large amount of exposed rock (Kelly and Kirby, 1982, Kelly, 2005).

Using the results of the 'National Survey of Native Woodlands' the woodlands of Ireland were classified into four main groups (Perrin et al., 2008a, 2008b). The hazel woods of the Burren are found within the *Fraxinus excelsior – Hedera helix* group, and fall under the subtype *Corylus avellana – Oxalis acetosella.* These are described as stands of hazel which are quite species rich, with a low canopy height (5-8m). There are generally a wide variety of broadleaved herbs present, and the bryophyte layer is well developed. This vegetation type was found by Perrin et al. (2008b) to have affinities to the NVC category W9a (*Fraxinus excelsior – Sorbus aucuparia – Mercurialis perennis* woodland, typical sub-community) (Rodwell, 1991). The corresponding Fossitt (2000) category is WN2 – Oak-ash-hazel woodland.

Some management considerations

"*Low intensity grazing by domestic stock should benefit a range of ancient and semi-natural woodland types by increasing structural and species diversity.*" (Mayle, 1999)

"*A priority for the management of Irish woodlands is to devise grazing regimes that permit adequate tree regeneration whilst maintaining biodiversity.*" (Kelly, 2005)

At 9%, Ireland has one of the lowest total covers of woodland in Europe, with most of this being conifer plantation (Perrin et al., 2008a). Semi-natural woodland is therefore a sparsely distributed habitat in Ireland, estimated at <2% cover (Gallagher et al., 2001, quoted in Perrin et al., 2008a). These woods are subject to a number of threats. Many are overgrazed, with deer being the main culprits in many areas (e.g. oakwoods in Killarney and Wicklow; Kelly, 2005). Cattle are the most frequent large herbivore (evidence of cattle grazing was found at over 30% of woodlands visited during the National Survey of Native Woodlands, with deer grazing being evident at just over 20% of sites; Perrin et al., 2008a). Whitehead (1972) notes that goats can do a lot of damage in woodlands due to bark stripping. This is particularly the case in winter, when other food sources may be lacking. Hester et al. (1998) state that goats can have "*dramatic detrimental effects on woodland structure and regeneration*". Rackham (1993) considers that grazing is the main threat to ancient woodlands in Britain, and Hester et al. (1998) cite the lack of control of the numbers of wild grazers as one of the most serious management issues facing woodlands in Britain and Ireland. McEvoy et al. (2006) state that many woods in Northern Ireland are grazed as a result of trespassing stock. Neglect is also a threat (e.g. Watkinson et al., 2001), however, with many younger woodlands not being managed at all, and many older woods having been abandoned (Perrin et al., 2008a). Mayle (1999) notes that both neglect and overgrazing are causes of loss in woodland habitats. Invasive species are another major issue, with species such as *Rhododendron ponticum* spreading rapidly in many acid woodlands (Perrin et al., 2008a).

Scrub

Scrub is a vegetation type which is difficult to define, and has been little studied (Mortimer et al., 2000). For example, Kirby (1981) reports that, while there were a small number of British vegetation studies which, to that date, had included hazel scrub, only one of them had attempted to classify it. It is, nonetheless, an important vegetation type, and particularly so in the Burren, where *"encroachment of scrub is a major threat to the species richness and floral diversity of the calcareous grasslands"* (The Heritage Council, 2006).

Scrub can defy classification because it is often seral (Mortimer et al., 2000), and thus effort may be concentrated in the start- or end-communities of the succession (e.g. grassland or woodland). It may also be the case that scrub forms an edge community, or an ecotonal one, its importance again

often being overlooked. There are also logistical and physical difficulties associated with working in scrub habitats - they are often thorny, spiny and unpleasant places to survey.

One of the earliest (and still one of the most useful) investigations of scrub was by Tansley (1939, 1965a, 1965b). He paid particular attention to the hazel scrub of the Burren, quoting it as one of the best examples of 'climax scrub' (this type of scrub occurs in places where *"local edaphic conditions may help prevent the growth of trees though they are just good enough for shrubs to maintain themselves"*). [Mortimer et al. (2000) add altitude and exposure as factors which may also limit tree growth.] Tansley makes the distinction between this type of scrub and 'seral' scrub, which is essentially a vegetation type which is intermediate in a succession series (e.g. grassland reverting to woodland after abandonment may go through a scrub stage). His definition of scrub in the more general sense, though very simple, is also useful to bear in mind: *"Communities dominated by shrubs or bushes"*. Interestingly, Ivimey-Cook and Proctor (1966) also note that *"There seems to be no indication that the hazel scrub represents a seral stage leading to ashwood in this region."*

Kirby (1981) looked in detail at hazel scrub in the Burren, and placed it in the association Corylo-Fraxinetum Br.-Bl. et Tx. 1952. He defined a number of types of scrub, based mainly on growth form and substrate (Table 6).

Following Ivimey-Cook and Proctor (1966) (see Table 3), the scrub in the Burren would be most likely to be classified under the Querco-Fagetea (deciduous woodlands on base-rich soils), *Corylus avellana – Oxalis acetosella* association, as are the hazel woodlands in the region. This classification has been superseded for the hazel woodlands in the Burren, however, by that used by Kelly and Kirby (1982) – association Corylo-Fraxinetum Br.-Bl. et Tx. 1952 (sub-association neckeretosum). The scrub communities encountered do not fit neatly into either of these classifications. Braun-Blanquet and Tüxen (1952) described a heterogeneous hedge and bush community, the *Crataegus – Primula vulgaris* association, with several of the relevés coming from the Burren. Although both Ivimey-Cook and Proctor (1966) and Kelly and Kirby (1982) failed to find this floristically distinct, it is possible that the scrub communities of the Burren fit best within this association.

It should be noted that in 'Studies on Irish Vegetation' there are two chapters relating to the vegetation of mantel and saum in Ireland (Dierschke, 1982, Wilmanns and Brun-Hool, 1982). These are ecotonal habitats, found at woodland margins, and so do not equate with the hazel scrub of the Burren.

The Burren scrub does not fit clearly into any of the five NVC scrub categorisations, but scrub may form an important component in a number of the other communities (Rodwell, 1991). For example,

W9 (*Fraxinus excelsior – Sorbus aucuparia – Mercurialis perennis* woodland), in the more oceanic parts of the British Isles, can be present as 'permanent scrub'. Additionally, W8 (*Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland) may have hazel as the dominant tree species. The JNCC (Joint Nature Conservation Committee) report "*The nature conservation value of scrub in Britain*" (Mortimer et al., 2000) refers to several different types of scrub, but none of these is directly referable to the hazel scrub of the Burren. Fossitt (2000) has a scrub category, WS1, which is a broad group encompassing areas that have ≥50% cover of shrub, stunted trees or brambles. Canopy height is ≤5m, though there may be occasional tall trees.

It seems clear that both seral and 'climax' scrub exists in the Burren. Stands of long-established hazel scrub are quite likely in many instances to represent a 'climax' woodland community in the Burren, but areas which are being colonised/recolonised by young hazel are generally seral – and these are the areas which constitute a major conservation issue (WallisDeVries, 2002, The Heritage Council, 2006).

Table 6 Types of hazel-dominated scrub and woodland found in the Burren (from Kirby, 1981).

A.	Hazel of average height 1.07m +/- 0.15, cover ≤40%. Canopy discontinuous. Mix of light- and shade-tolerant species.
	(Groups B - F have continuous canopy of hazel, ≥3m.)
B.	This group is considered immature in relation to the others (C, D, E and F), but more developed than group A.
	(Groups C + D represent typical/mature hazel scrub in the Burren. They lack light-tolerant species, and do not represent "*an incipient or transient community*".)
C.	On rocks, with extensive cover of bryophytes.
D.	On soil, with extensive cover of herbs.
E.	Mature hazel scrub, with fewer taxa than C or D. Often high cover of rock.
F.	Ash-hazel woodlands.

Some management considerations

"Hazel-dominated scrub is part of the Burren landscape." (BurrenLIFE, 2010a)

The importance of scrub as a habitat in its own right is often overlooked – e.g. *"In most situations, scrub is primarily considered as a threat to other habitats"* (Mortimer et al., 2000), and *"scrub on its own is considered to be of little conservation value"* (Laborde and Thompson, 2009). However, it is a structurally and floristically heterogeneous habitat (Brown et al., 1990), often with great

associated diversity due to the fact that is encompasses elements of woody vegetation and of more open, grassy/herb-rich vegetation (Mortimer et al., 2000, WallisDeVries, 2002, Coppins and Coppins, 2003, 2005, Tallowin et al., 2005, Laborde and Thompson, 2009). In addition, in a country with as little woodland cover as Ireland, the importance of areas of scrub as alternative woody habitats should not be underestimated.

Many of the management issues mentioned already as being important in grasslands and woodlands are also relevant in scrub habitats, e.g. abandonment, intensification of land use, changes in grazing regimes, etc. These have led to an unprecedented spread of hazel scrub in many parts of the Burren. Recent studies have shown that dense hazel scrub covered 14% of the 'high' Burren in the early 2000s, and that at least 5-10% more of the region has scattered and increasing scrub (The Heritage Council, 2006, BurrenLIFE, 2010a). Management of scrub is complex, however – *"Scrub control is difficult, time-consuming, labour intensive and expensive"* (BurrenLIFE, 2010a), not least because of the heterogeneity of the habitat. A fine balance is needed, whereby grazing levels are enough to keep scrub encroachment in check, but not heavy enough to cause damage to the grass and flower-rich areas through, for example, overgrazing and excessive trampling (Ward, 1990, Mortimer et al., 2000).

Studies in the Burren have suggested that winter grazing by cattle may not in itself be enough to stop hazel scrub encroachment (Dr Sharon Parr, pers. comm.) – hazel seedling survival rates of >80% have been recorded, with recruitment more than compensating for losses. In the areas monitored, there were more hazel seedlings at the end of the monitoring period than at the beginning, although they were shorter in stature. Sheep grazing may help to control the spread of hazel, but additional scrub control measures by farmers are likely to be needed, e.g. removal, treatment of stumps, etc. (BurrenLIFE, 2010a).

The JNCC report 'The nature conservation value of scrub in Britain' describes the situation well:

> "*Scrub often exists as a mosaic with grassland and other open vegetation. Spatial patchiness is an extremely important habitat feature for many plants and animals. In the case of invertebrates, fine-scale mosaics of structure and plant compositions provide a diversity of niches and a variety of food and shelter. Edges are particularly important and intimate mixtures of grass, scrub and woodland may be advantageous to many insects. Similar structural patchiness can result in very rich bird communities. The maintenance of such mosaics is a difficult management challenge*." (Mortimer et al., 2000).

The ever-present threat of scrub expansion into semi-natural calcareous grasslands is made all the more ominous by the fact that individuals of woody scrub species can exist in a relatively tightly grazed sward as what Ward (1990) termed 'incipient scrub' – very low-growing woody plants, with well-established rootstocks which can thus grow tall and strong in a very short space of time if

grazing pressure is relieved. This is particularly likely where grikes and fissures in the limestone facilitate deep-rooting plants and may also provide some degree of protection from grazing. This has been reported as commonly occurring in the Burren by staff of the BurrenLIFE Farming for Conservation Programme (Dr Sharon Parr, pers. comm.).

Hazel (*Corylus avellana*)

"*Very few trees have had, or continue to have, so pervasive a role in the Irish landscape as hazel*." (Feehan, 2003)

"*...from the first woodland disturbance more than five thousand years ago, until the Tudor clearance in the late sixteenth century, there must have been very extensive areas of secondary hazel scrub in Ireland*." (Mitchell, 1976)

Webb and Scannell, in 'The Flora of Connemara and the Burren' (1983), describe hazel as being dominant in scrub over large areas of the Burren, and very abundant in sheltered places. They reiterate the importance of shelter from wind; they note that the buds on the leading shoots are often killed if exposed to strong winds, and that a marked increase in the height of the bushes can be seen in sheltered areas (noted also in Kirby, 1981, and Kelly and Kirby, 1982). Webb and Scannell also note the impact of grazing on the plant, but observe this to be less severe than with many other woody species. Kirby (1981) says that hazel is vulnerable to grazing (and particularly sheep grazing) when at the seedling stage, but that once it is >1.5m in height the effects of grazing are minimal. As well as forming stands of scrub in which it is the dominant plant species, hazel is also common as an understorey tree in, for example, oak or ash woodlands (Fossitt, 2000, Perrin et al., 2008a, 2008b).

The growth form of hazel is unusual in that it typically has many trunks. It is described in Rose (1981) as "*many-stemmed deciduous shrub to 8m*", in Fitter and Peat (1994) as "*a shrub, 1-6(-12)m, with several stems, usually seen coppiced, rarely a small tree*" and in Stace (1997) as "*several-stemmed shrub to 6(12)m*". Some individuals many have many medium girth trunks, and hundreds of smaller shoots (e.g. Figure 10). Coppins and Coppins (2003) describe it thus:

> "*A typical hazel stool has a cluster of thin, medium and thick stems. ... The ageing stems tend to gradually lean outwards, probably from the weight of the canopy they support. This creates a gap in the overall canopy, which enables new, young stems to arise and fill the space. Damage to the canopy from winter storms will break off canopy twigs, and abrasion from stems rubbing together in windy weather allows fungal pathogens ... to invade, and gradually kill off individual stems. This all leads to a considerable turnover of stems within a stool.*"

The number and girth of shoots/trunks depends on factors such as soil depth and grazing pressure. Ageing a hazel tree, or making use of standard survey measurements such as DBH (diameter at breast height), are thus very challenging.

Figure 10 Hazel tree, showing multiple stems.

Hazel was much prized in times past. Hazel nuts are nutritious and its wood has many uses (bowls, spindles, small tools and furnishings, wattles for walls and hoops for casks: Feehan, 2003, fuel, fencing, thatching and as a fodder source: BurrenLIFE, 2010b). Hazel responds well to cutting, making it an ideal species for coppicing. It is unclear to what extent hazel was actively coppiced in Ireland (however, Feehan, 2003, states that there were extensive coppices in existence in the 19th century, as does McEvoy et al., 2006, referring to Northern Ireland, but Perrin et al., 2008a, record 'mature coppice' at only 18% of native woodlands surveyed), as compared to Great Britain, where there is ample evidence of coppicing. However there is no doubt as to the value which was placed on it and its products. For example, hazel is listed as one of the seven ‘Nobles of the Wood’ in the Old Irish tree list from the 8th century (Kelly, 1998). In current times, however, hazel scrub or woodlands are not generally actively used or managed by landowners, and indeed, it has come to be perceived as a threat and a nuisance in some areas, e.g. parts of the Burren.

Hazel seedlings are a relatively rare sight in the Burren (Kirby, 1981, and pers. obs.). However, the species regenerates readily by suckers, thus ensuring regeneration success (Kirby, 1981). Studies in

Britain on the post-dispersal fate of hazel nuts (Laborde and Thompson, 2009) have found that hazel will regenerate from seeds, but that there is a very high predation rate, especially from rodents (e.g. wood mouse, *Apodemus sylvaticus*, and grey squirrel, *Sciurus carolinensis*). However, 'scatter-hoarders', such as mice and squirrels, will inevitably forget or fail to re-find some buried caches, thus promoting hazel encroachment if the cache is at the edge of the scrub, or in open grassland. Granivorous rodents therefore may play an important role in succession in grassland/scrub mosaics. In particular, the grey squirrel was found to be a voracious consumer and hoarder of hazel nuts (10,000 - 12,000 nuts scatter-hoarded in a 30m strip of grassland next to the scrub during the three-year study of Laborde and Thompson, 2009). Grey squirrels have not yet invaded the Burren but red squirrels are found there (local NPWS conservation ranger, Emma Glanville, pers. comm.).

If seedlings grow, they may have a better chance of survival in grasslands, as they cope better in direct sunlight (Kollmann and Schill, 1996), but they are of course at increased risk from grazers. Laborde and Thompson (2009) mention the concept of 'incipient scrub' (taken from Ward, 1990, who recorded suppressed plants up to 14 years old) – short or stunted hazel plants in grasslands, which can grow tall quickly if grazing is relaxed. The importance of continued grazing in suppressing scrub is thus obvious.

Hazel has a remarkable capacity to grow where it appears that there is little or no soil. Many hazel trees in the Burren appear to grow straight out of the limestone pavement, but on closer inspection a layer of moss and humus, or a grike filled with soil, is usually revealed. The hazel scrub in the Burren is used by animals for grazing, but mostly for shelter (Kirby, 1981, Burren farmers pers. comm.). As well as the ten or so species of animal listed in Table 2 (above) which feed on hazel, Mortimer et al. (2000) report that 253 species of insect feed on hazel in Britain, a relatively high number (it ranked sixth in number of insects in a list of 31 woody scrub plant genera). Coppins and Coppins (2003, 2005) point out the often unrecognised value of hazel as a host for lichens. They put forward the theory that Atlantic hazelwood is a distinct habitat type, and one which is exceptionally rich in lichens. In addition, they point out that hazel does not need to be coppiced to self-perpetuate, and that not all hazel stands in Britain have been coppiced – a view espoused by many naturalists.

Molluscs

Terrestrial molluscs – an introduction

Phylum Mollusca is one of the most diverse and speciose animal phyla, being outnumbered only by the Arthropoda. There is a great degree of uncertainty regarding the total species count, but it is likely to be as large as 200,000 (Ponder and Lindberg, 2008). The phylum comprises animals as diverse as snails and slugs, bivalves, marine chitons, cuttlefish and octopus. It is in the marine

environment that molluscs reach their maximum diversity. In Ireland, a total of 177 non-marine molluscs have been recorded (Byrne et al., 2009). (In this context, non-marine means all molluscs not found in the sea or the intertidal area.) This number includes land and freshwater snails, slugs and bivalves, along with some brackish-water species. Of the total of 177, approximately 50 are aquatic, 32 are slugs, and the remainder are terrestrial snails (Dr Roy Anderson, pers. comm.). Alien species make up 27 of this total, the most notorious perhaps being the zebra mussel (*Dreissena polymorpha*), a freshwater bivalve. These alien species are most often confined to glasshouses, however, and most have not established populations in the wild.

The terrestrial molluscs found in Ireland belong to the Class Gastropoda, the only molluscan group to have colonised land. The Gastropoda is the second most speciose animal class, and contains a huge diversity of marine species (Aktipis et al., 2008). Gastropods are distinguished from all other molluscs by undergoing torsion during development. Most, though not all, are characterised by having a single shell (many species have lost the shell and are known as slugs). The size range of gastropods is from <1mm to almost 1m (Aktipis et al., 2008).

The two subclasses of Gastropoda which are found in Ireland are: Prosobranchia (mainly aquatic, sexes are separate, and they have an operculum or horny lid on the foot with which they can close off their shell) and Pulmonata (these species have a lung and are hermaphrodite) (Cameron, 2003). There are only two species of Prosobranchia found in Ireland: *Pomatias elegans* (restricted to one small site in Ireland; not found as part of this study) and *Acicula fusca* (a tiny under-recorded species; found in moderate numbers during this study).

Development in snails is direct, i.e. there is no metamorphosis. Land snails generally lay eggs and, while most species have preferred breeding seasons, many will breed opportunistically whenever conditions are suitable (although few species are active during winter) (Kerney and Cameron, 1979). Williams (2009) describes nicely the development of the shell during the lifetime of a snail: "*Formed inside the egg, where it is known as the 'protoconch', the rudimentary shell becomes the apex of the adult shell, with growth occurring as a result of material being added to its lip*." Cameron (2003) writes that there is generally a maximum adult size, and once this is reached some species will add to the mouth of their shell a lip, teeth or lamellae. Most species live for less than one year, but some that are larger may live for a number of years (Kerney and Cameron, 1979)

Snails are of direct importance to humans in a number of ways. They are widely used as a food source (e.g. Williams, 2009), for jewellery and they can be vectors for disease and significant crop or garden pests. There are also important medicinal and pharmaceutical uses for molluscs and mollusc-derived products (e.g. Aktipis et al., 2008, Williams, 2009).

Terrestrial molluscs are, for the most part, herbivorous, although some larger species are omnivorous, being opportunistic feeders (see below for more details). They play a very important role in ecosystems by consuming large quantities of dead and decaying plant matter – their main food source. They also provide a vital source of food as prey for animals such as birds, hedgehogs, beetles and amphibians (Williams, 2009).

Terrestrial molluscs have a number of relatively universal habitat requirements. Most of them need moisture, shelter and calcium (for building and maintaining their shell, though this requirement varies among species) (Kerney and Cameron, 1979). There are, of course, exceptions – e.g. some molluscs do best in open, short, dry grassland (e.g. xerophiles such as *Helicella itala* and *Vallonia costata*), and a few are found on heathlands (e.g. *Columella aspera*).

Molluscs as grazers

"*Most species of slug and snail feed on rotting vegetation, fungi, algae and lichens; healthy green plants are not much attacked – although flowers, fruit and seed, and underground storage organs like potatoes or carrots are taken."* (Kerney and Cameron, 1979)

Most terrestrial molluscs are saprophagous herbivores, though a few species are carnivorous/ omnivorous (most communities of snails will, however, contain species with each of these feeding preferences, Schamp et al., 2010). Among the species found in the Burren, *Oxychilus* spp and *Aegopinella* spp are some of the most common carnivorous/omnivorous species, often preying on other molluscs. Most species feed on dead plant material however (Mason, 1970, Kerney and Cameron, 1979, Falkner et al., 2001), and are important in the decay of plant material in many ecosystems (Chatfield, 1976).

O'Donovan (1987) studied in detail the grazing effects of the snail *Helicella itala* on biomass and productivity in Burren grasslands, as well as on nutrient turnover. She found that, in laboratory conditions, they preferred the flowers of *Dryas octopetala*, *Sesleria albicans* [*caerulea*], the leaves of *Thymus polytrichus* and litter, over bryophytes, *Teucrium scorodonia* and *Succisa pratensis*. Molluscs are indeed known to be selective feeders (Grime et al., 1968, Chatfield, 1976). O'Donovan's work revealed that approximately 1 - 2.8% of the productivity of the sward was consumed by *H. itala* each year (an individual was estimated to eat approximately 4mg dry weight day^{-1}). She concluded that "…H. itala *does not have a great effect on the productivity of the sward…".* With respect to nutrient turnover, while the amounts measured were small, the returns of nitrogen and phosphorus to the soil in snail faeces may be important, especially given that some nutrients are limiting in the Burren grasslands.

Other work on the effects of molluscs as grazers has shown that they can be important predators of seedlings in grasslands (Hulme, 1994). However, Grime and Blythe (1969) did not find traces of

seedlings in any of the faeces they examined from four of the large snail species they studied from a limestone gorge in England. In this study, species fed mainly on senescent or older green leaves on flowering plants. The preference for senescent leaves is reiterated by Speiser (2001), who speculates that it is their low toxin content that makes them more attractive. Speiser also notes that molluscs generally eat "*only small amounts of grasses*", and that green plant material is generally a small component of their diet (though some species were found to consume live nettles and mosses).

Molluscs appear to be more efficient than other invertebrates at assimilating litter; this is attributed to the presence of cellulases and other polysaccharidases in their guts which enable them to decompose plant structural polysaccharides (Mason, 1970, Kerney and Cameron, 1979). The molluscs investigated in Mason's study fed most commonly on higher plant material (rather than fungus or animal material) and, in particular, on dead material (Mason, 1970). Mason concludes that "*snails are thus largely saprophagous, but there are marked differences in preferred secondary foods*".

Project rationale and objectives

This project was conceived in response to a lack of information on the impacts of some land uses, and land use changes, on biodiversity in Ireland. One of the major changes anticipated in coming years, and particularly in the west of Ireland, is the increased abandonment of marginal (i.e. less agriculturally productive) land (e.g. Dunford, 2002, The Heritage Council, 2010). Lands which were grazed for many generations may face significant changes.

One of the possible outcomes land use change in the Burren area is an increased rate of scrub encroachment (Mortimer et al., 2000, Dunford, 2002, Feehan, 2003). In fact, this has already begun (The Heritage Council, 2006). This is undoubtedly due to a complex mix of factors, but changes in farming practices are foremost among them. The hazel scrub has spread beyond the control of many individual landowners, resulting in government-funded schemes being initiated which have major parts dedicated to helping to manage and curb it (e.g. BurrenLIFE, and the Burren Farming for Conservation Programme). Among the problems caused by scrub encroachment are damage to archaeological monuments, blocking of grazing access tracks, direct loss of grazing lands and conversion of habitats like limestone pavement and species rich calcareous grassland to what is perceived to be a less diverse and valuable habitat.

This project sets out firstly to document the plant and snail diversity of three different habitat types in the Burren region – grassland, scrub and woodland. These habitats exist along a continuum, and this study is, to our knowledge, unique in Ireland in its focus on habitats in a successional sequence. Additionally, there have been very few ecological studies on terrestrial molluscs in Ireland. The second overarching aim of this work is to monitor the changes that are occurring in the

plant and snail communities once grazing ceases. This was done in the three study habitats using twelve long-term experimental exclosures. This methodology is unusual in that very few studies have set up multiple long-term exclosures – for reasons such as logistics, costs, timescale issues, etc.

Additional aims of this work include providing a detailed account of some aspects of the biodiversity associated with scrub as a habitat itself. As Mortimer et al. (2000) state "*A major constraint on the conservation of scrub and its associated species is the widely-held opinion that scrub is of low conservation value and primarily a threat to other more valuable habitats*." It is hoped that this study can shed some light on the debate as to whether we should "*just let nature take its course*" (Feehan, 2003) or whether we should actively manage hazel scrub, preventing it from replacing limestone pavement and grasslands. An assessment of some malacological methodologies is also undertaken.

There have been a number of calls for long-term experimental studies in the Burren – e.g. the British Ecological Society (Webb, 1962a), O'Donovan (1987), Byrne (2001), Osborne and Jeffrey (2003) and Moles et al. (2005). The current study goes some way towards answering these calls.

Aims of this thesis - summary

1. To gain ecological information on, and assess biodiversity in, two taxonomic groups (vascular plants and snails) in three habitats (woodland, scrub and grassland) in the Burren region.
2. To investigate how far distinct snail communities exist in each of grassland, scrub and woodland.
3. To determine the main environmental drivers of plant and snail communities.
4. To assess some commonly used malacological methods and make recommendations for future studies.
5. To investigate experimentally the responses of the communities of vascular plants and snails to the removal of grazing by the use of fenced exclosures.
6. To draw together the information gathered on both groups (i.e. plants and snails) to gain a deeper insight into the effects of the cessation of grazing on biodiversity.

Chapter Two:

Study sites, experimental design and ancillary projects

Introduction

The data presented in Chapters Three - Six were collected at the same twelve study sites. To avoid repetition, some aspects relevant to the study sites are presented here (e.g. physical parameters such as location, altitude, etc.; details on the soils and the age of the habitats), along with the overall experimental design, and a description of one of the principal methods of analysis which is used in a number of the chapters. Additionally, a number of ancillary projects ran alongside this one, and they are mentioned briefly here.

Site selection and experimental design

Site selection

This project investigated experimentally the impact of the removal of grazing by large mammalian herbivores on plant and snail communities in a range of habitats in the Burren area of Counties Clare and Galway in the west of Ireland. This was done by recording and monitoring changes in the vegetation and in the snail fauna in a network of permanent plots within fenced exclosures over a period of three years. Figure 11 shows the location of the twelve study sites within the study area. The study sites were chosen by searching the study area, by liaising with local National Parks and Wildlife Service (NPWS) staff, and also by talking with local landowners.

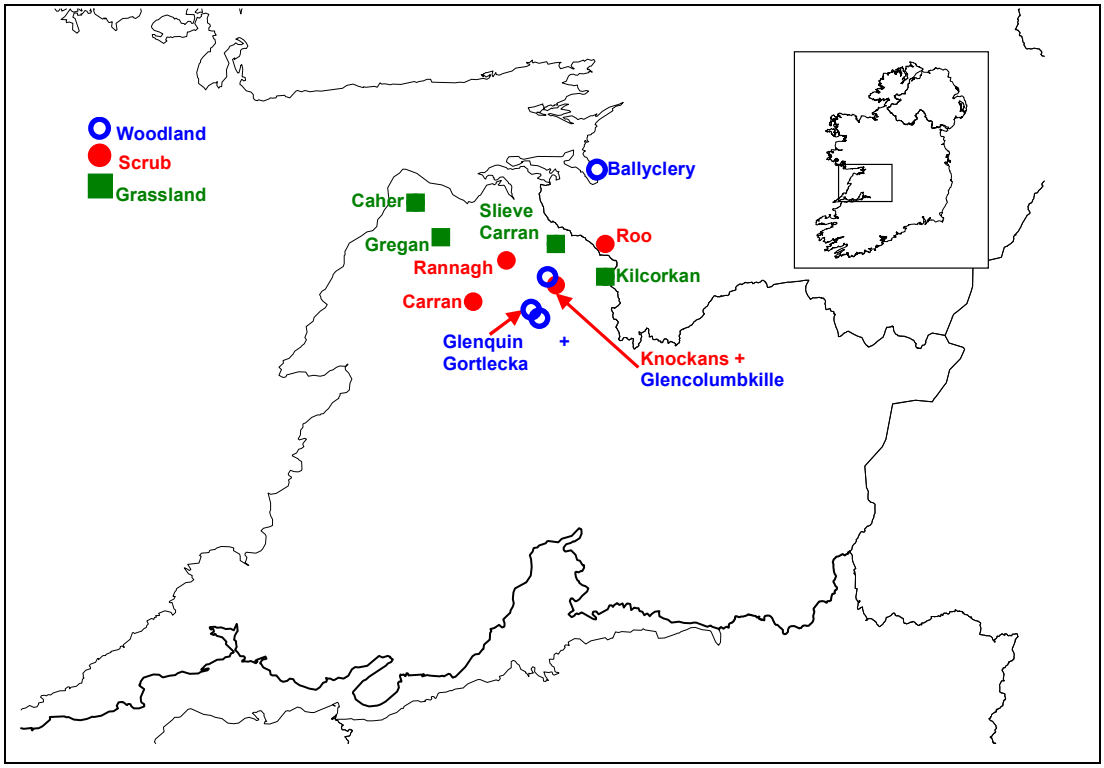


Figure 11 Study area and location of the twelve study sites.

Three habitat types were chosen for study: woodland, scrub and grassland (refer to Chapter One for more details). Areas which were very steep were avoided, as were wet areas (i.e. all sites are located on free-draining land). To avoid the influence of the sea (i.e. salt spray) sites near the coast were not chosen (one exception: the woodland site, Ballyclery, is approximately 700m from the sea in a sheltered inlet - thus it is not influenced by sea spray). Soil cover, at least over most of the plot, was a prerequisite, so while there are areas of exposed rock in some plots, it does not dominate in any. Plots varied in elevation between 13m and 187m above sea level, and had a range of aspects (Table 7). Exposure was measured on a subjective scale, with sites varying between sheltered and very exposed (1 = sheltered, 2 = moderate exposure, 3 = exposed, 4 = very exposed).

Species of grazer (cattle, and to a lesser extent, feral goats) and grazing level (moderate) were taken into account at the site selection stage, with the initial aim having been to have these constant across all sites. This proved impossible, however, due to difficulties in locating sites which were similar enough across a range of other factors (such as habitat type, slope, soil cover, etc.). As a result, some sites have grazers other than the focal species (donkeys at Ballyclery; sheep and horses at Glenquin). In every case, however, the grazing regime, including the approximate stocking rate and grazing duration, has been defined through survey questionnaires with landowners/land managers (see below). Grazing level was also recorded in the field on a subjective four-point scale as follows:

0	no grazing
1	light grazing
2	moderate grazing
3	heavy grazing

All sites had a grazing level of ≥1 at the beginning of the experiment (i.e. no ungrazed or abandoned sites were chosen for study). A grazing level of 3 was recorded only once (Glenquin, control plot, 2006). This information may seem to be relatively crude, but it serves as an adequate measure to facilitate broad comparisons. Watkinson et al. (2001) point out the importance of attempting to quantify grazing levels to help inform investigations, pointing out that regardless of how inexact the methods may appear to be, it is better to have a crude measure than none at all.

Experimental design

Four replicate sites were chosen for each of the habitat types in the study (woodland, scrub and grassland). At each of these twelve sites, fenced and control plots were set up, each containing five fixed 2 x 2m quadrats (Figure 12), giving a total of 120 quadrats across the entire study. A stock-proof fence was erected at each site in 2006 to keep out large grazing animals. Each plot was approximately 20 x 20m, and fenced and unfenced plots were in close proximity (between 3m and 20m apart). Within each plot (i.e. both fenced and control) the five 2 x 2m quadrats were arranged in a grid formation (Figure 12). These were fixed quadrats, marked using underground metal markers at all corners, enabling them to be re-found using a metal detector. The corners of the

unfenced/control plot were also marked with underground metal markers. GPS (Global Positioning System) readings were taken at the corners of the control plots, and in the centre of all plots.

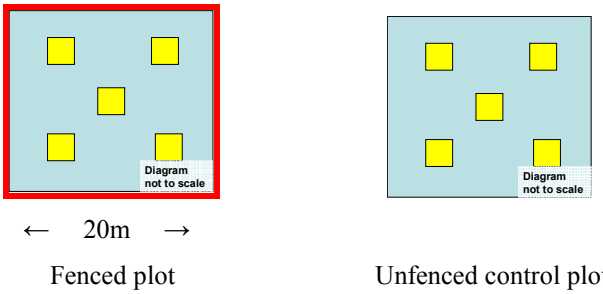


Figure 12 Schematic diagram (not to scale) showing layout of fenced and control plots at each site, with five 2 x 2m quadrats inside each one.

Fencing

The fences were erected in late summer and autumn 2006, with one exception (Gortlecka, erected December 2006). Where landowners agreed that the fences could remain indefinitely, galvanised metal posts were used (these are more durable, but also more expensive). The remaining five fences were constructed using treated wooden posts. Each fence was composed of sheep wire overlaid with chicken wire, and two strands of barbed wire running on top (Figure 13), and was approximately 1.5m high. This is sufficient to keep out domestic stock such as cattle, sheep, horses and donkeys, as well as feral goats. The exclosures are hare-proof, but not rabbit- or badger-proof due to their ability to dig underneath. However, rabbits are relatively uncommon in the area, and during the five years that the fences have been standing, only one attempt was made by a badger to dig its way into an exclosure. (Using a large stone to block its efforts was sufficient to deter it.) The fences were erected by a professional fencing contractor, and care was taken in order to minimise disturbance to the habitats.

Figure 13 Fenced exclosure at Caher (grassland site).

Long-term monitoring

As noted in Chapter One, there have been many calls for long-term experimental studies in the Burren, including those from the British Ecological Society (Webb, 1962a), O'Donovan (1987), Byrne (2001), Osborne and Jeffrey (2003) and Moles et al. (2005). But what are the advantages of long-term studies? Are the extra costs and complicated logistics justified?

Magurran et al. (2010), in a review of long-term ecological research, noted the importance of long-term datasets, not least due to the growing need for baseline data so that efforts to reduce biodiversity loss can be assessed: "*Data that can be used to monitor biodiversity, and to gauge changes in biodiversity through time, are essential*." This paper mentions some of the longest running, and best known, ecological experiments, such as the 'Park Grass Experiment', which was set up initially in 1856 (Silvertown et al., 2006). Magurran et al. also mention some of the drawbacks – it is not always easy, for example, to determine whether a community is changing due to anthropogenic influences, or to some natural background dynamic. Bakker et al. (1996) discuss the importance of long-term studies in terms of assessing the success of management practices, and also in terms of monitoring change in relation to environmental policy (e.g. the effects of drainage on habitats and species). They also point out the great importance of being able to extrapolate beyond the time frame of the study. In a critique of permanent plot methods in tropical rain forests, Sheil (1995) states that studies based on permanent plots "*play a major role in ecological and management research*".

Sheil (1995) also points out some potential pitfalls, such as the damage caused within plots during surveying, the fact that (unwanted) attention can be drawn to permanent sampling areas by the erection of fencing and markers. Perrin (2002) lists ongoing maintenance as a further difficulty with permanent plots, and Mountford and Peterken (1998) state that many planned long-term studies fail due to loss of interest or financial support, or due to changes in personnel and/or responsible organisations.

Overall, however, once sufficient effort is made to foresee and tackle potential issues, long-term monitoring is not just extremely valuable, but essential to furthering our understanding of ecological processes. Studies which instead use laboratory work, down-scaled timeframes, or which survey a range of sites of different conditions rather than tracking individual sites over time, while valuable, are "*adjuncts to, rather than substitutes for, controlled, long-term field experiments*" (Morgan and Jefferson, 2007). The same authors point out that money has been underused or even wasted by having useful experiments running only in the short-term, ending before they could generate their most powerful data.

Data analysis using Non-metric Multidimensional Scaling (NMS)

Ordinations

An ordination is a scatter of points, each of which is positioned in relation to all the others in such a way as to represent its relationship to them (Kent and Coker, 1992): points that are closest together are most similar. The points are arranged along a varying number of axes (the way in which this is decided upon varies among ordination methods). Ordinations are used to present graphically the most important patterns in a dataset. Thus they provide a summary of complex relationships, plotted on a low number of axes (McCune and Grace, 2002). The number of axes used depends on the level of complexity in the patterns that the ordination can pick up, and this is balanced against interpretability (McCune and Grace, 2002). The aim is to achieve a balance between ease of understanding and interpretation, and the retention of a sufficient amount of the original information and data structure. Ordination methods depend on the covariance of variables in a dataset – something which is often very problematic in other methods, such as regression.

Non-metric Multidimensional Scaling (NMS)

The ordination method used in this thesis is 'non-metric multidimensional scaling' (NMS), a type of indirect gradient analysis. All analyses were carried out using the PC-ORD 5 computer package (McCune and Mefford, 2006). NMS is a very robust ordination technique, well suited to extracting patterns from ecology and community data which are often non-normal and 'zero-heavy' (McCune and Grace, 2002, Perrin et al., 2006b, Nekola, 2010). Measures of stress and instability, along with consistency of output/results over multiple runs, are used to measure the degree of reliability which

can be attached to NMS ordination results (McCune and Grace, 2002). Stress values of between 10 and 20 are considered acceptable in ecology, and allow reasonable confidence in the results. McCune and Grace (2002) warn, however, that values in the range of 35-40 mean that points are essentially arranged at random. McCune and Grace (2002) recommend striving for an instability value of <0.0001, but state that 0.001 is acceptable if the stress is low. Typically ordinations will be run four to five times using the 'slow and thorough' option in PC-ORD. The repetition allows the investigator to judge if the result is consistent.

Representing species on ordinations

The most common type of data presented in an ordination are sample units, or quadrats, which appear as points, arranged according to how similar they are. There are, in addition, a number of ways of presenting species on an ordination. It is possible to represent the species in 'sample space' (i.e. they can also be graphed as points on an ordination), but this is advised against (McCune and Grace, 2002) because species correspond to a volume of space, rather than to a point (as is the case with quadrats). To better represent species overlays are possible on ordinations of quadrats. These are used in this thesis. One option is to overlay species, one by one, on ordination diagram(s). This method has obvious limitations, especially when aiming to present information relating to multiple species. Thus the most useful method is to add the species data into the second matrix. Those which are influential on the data will appear in the biplot (i.e. will be shown simultaneously with the sample units on the ordination, the length of their associated line being proportional to the strength of their influence on the data). By this means, the species data can additionally be tested for correlations with the axis scores.

Data preparation/screening

Outliers can have a large influence on data analysis and interpretation of results. Outlier analysis was performed in advance of each analysis using PC-ORD 5 (MjM Software, Oregon). A cut-off of two standard deviations from the grand mean was used to identify outliers (McCune and Grace, 2002). These were all noted, assessed and considered for exclusion.

Species which are rare in a dataset can contribute significantly to 'noise' (variation in data which is random, i.e. not related to an underlying pattern), making it harder to detect actual patterns. McCune and Grace (2002) state that "*species occurring in fewer than two samples provide virtually no information as to pattern with respect to underlying gradients, so for those type of analyses they should probably be removed*." Accordingly, for NMS analyses, species which occurred in ≤2 quadrats were deleted.

Variables overlaid on ordination diagrams – are the relationships significant?

Following ordination, it is usual to attempt to relate the patterns seen to other variables (these may be measured variables [e.g. pH, altitude], or derived variables [e.g. species richness or total cover of sedges]). This can be done in two principal ways: using overlays on the ordinations, or by calculating correlations between the variables and the ordination axis scores (McCune and Grace, 2002). Overlays are especially useful in showing up patterns that are non-linear (these may be missed by correlations). Additionally, they are flexible and greatly help elucidate whether and how variables are patterned on an ordination (McCune and Grace, 2002). Variables can be overlaid one at a time, or methods such as 'biplots' can be used to overlay numerous variables at one time. Species data can also be overlaid using this method, as discussed above.

Correlation coefficients (r) give us a measure of the (linear) relationship between the axis scores (of sample units) and selected variables. Spearman's rank correlation coefficients were calculated between variables (and species) and ordination axis scores using SPSS (PASW Statistics (SPSS) Version 18.0.0, 2009). This non-parametric statistic was chosen in order to avoid any assumption of normality in the datasets. McCune and Grace (2002) state, however, that correlation values should be treated with caution. Ordination scores are not strictly independent of each other (however, this becomes less of an issue with medium to large datasets). Additionally, outliers can have a large influence on coefficients, resulting in a strong correlation which does not reflect patterns in the bulk of the data. The fact that correlation coefficients will misinterpret non-linear relationships must be borne in mind also.

Successional vectors

Another method of overlaying information on an ordination is to use successional vectors. With this method, data points are connected in sequence. This method is appropriate when sample units have been followed over time. Successional vectors are used in this study to show how quadrats have changed in snail species composition (and therefore in their position in the ordination) between 2006 and 2008.

The study sites - history and other relevant information

Questionnaire results

A questionnaire was compiled and administered to landowners/managers of all study sites in order to gather information on past and present management, with particular emphasis on stocking levels and type of grazing stock. A copy of the questionnaire is provided in Appendix 2. Among the results are a list of the main grazers (both domestic and feral/wild) for each site (Table 7), along with details on the times of year and duration of grazing of domestic stock. Most of the sites are grazed in winter time only, and all have cattle as the main grazers. Two sites have additional types

of domestic stock, and a number of sites are occasionally grazed by feral goats. The number of cattle per hectare is also given in Table 7.

One of the most important issues highlighted by the results of the questionnaire was a management event at Kilcorkan. The area where the grassland exists now was 'reclaimed' approximately 30 years ago. Prior to that, the area had consisted largely of rock and scrub, but also contained areas with significant soil cover because cultivation ridges or 'lazy beds' are mentioned. The site was cleared (by bulldozer), the soil re-distributed and it was re-seeded. It was fertilised with low amounts of nitrogen until about twelve years ago. This significant disturbance needs to be kept in mind when interpreting findings from this site.

Continuity of habitat/vegetation type

Each landowner was asked how far back they could confirm the existence of the habitat/vegetation type at the study site (Table 8). It is of particular interest to note for how long scrub or woodland may have existed at the study sites, and time periods longer than human memory are important. To this end, the Historic Maps Archive on the Ordnance Survey of Ireland (OSi) website (Ordnance Survey Ireland, 2011) was used. This service allows the user to view maps from the original and first large scale ordnance survey (carried out between 1829 and 1842, at a scale of six inches to one mile), and those maps produced at the later survey dates of 1888-1913 (scale: 25 inches to one mile). These maps are acclaimed for their accuracy (Ordnance Survey Ireland, 2011). The results from these investigations are presented in Table 8. Additional maps were accessed in the Map Library of Trinity College Dublin – William Petty's 'Down Survey' map (1655-1656), Henry Pelham's 'Grand Jury Map of County Clare' (1787) and William Larkin's map of Galway from 1819. The 'Down Survey' maps were found not to cover the current study area in north Clare. Pelham's map showed all of the twelve study areas as being open, though small woodlands are shown nearby in the cases of Caher (grassland), Knockans (scrub) and Gortlecka (woodland). Larkin's map of Co. Galway consists of one small scale map of the county, and 16 larger scale maps. On the small scale map, only very large woods are shown, and the areas around the two Galway study sites (Roo and Ballyclery, scrub and woodland respectively) are shown as open. In the larger scale maps, both sites again appear to be shown as open, but the quality is poor, making interpretation challenging. Trees are shown clearly in other areas, however, lending strength to the interpretation of open habitat.

Kirby (1981) researched the cartographic history of woodland cover in the Burren in detail and reports that OSi maps show the following general progression for the Burren. Around the 1840s there were scrubby areas in the Burren, but scrub was probably not extensive. By 1893 both dense and scattered scrub existed, and by 1915 scrub had increased in both density and distribution across the Burren. Woodland had also developed in a number of places by this time. Kirby contends that

almost all wooded areas in the Burren have developed within the past 100 years – i.e. from the date of his thesis in 1981.

However, there are a number of reasons to query this. For example, speaking specifically about the woodland at Slieve Carran (an area just to the north of the grassland site of that name included in this study), Rackham (2006) states that, while this woodland does not appear on either the 1840 or 1913 OSi maps, he believes that at least the upper part of the present-day wood is ancient woodland. Another woodland specialist believes that the big old coppiced ash trees on the scree slope at Slieve Carran are the best candidates that he has seen for ancient/pre-famine trees in the Burren (Dr Daniel L Kelly, pers. comm.).

Kirby himself acknowledges a number of other reasons for woodland or scrub failing to be recorded on the OSi (and other) maps (Kirby, 1981). Firstly, information pertaining to what was perceived as 'wasteland' may not have been recorded, and it is possible that areas of scrub may have been seen in this way. Woodland is likely to have been conscientiously marked as such on all maps, but the treatment of scrub (and possibly coppice or felled areas) may have been more variable. Secondly, he points out that Westropp (1909) wrote that "*ivy, like hazel, was too common for distinctive naming*" in his 'The forests of the counties of the lower Shannon Valley' – thus raising the possibility that plants that were extremely common were sometimes omitted. Might this have happened with hazel scrub? Kirby also points out that Foot (1871) failed to mention hazel in his otherwise seemingly comprehensive paper on plants in the Burren. Interestingly, as Kirby also points out, *Bellis perennis, Primula* spp or *Hedera helix* do not get a mention either.

Table 7 Location, species of grazer, and other details relating to each of the twelve study sites.

	Site Name	Grid Reference	County	Main Conservation Designation(s)*	Ownership	Altitude (m)	Slope (degrees) (F,C) ***	Aspect	Exposure	Main grazing animals	Grazing time	Grazing level estimate (F,C)***	Cattle ha^{-1} +
WOODLAND	Ballyclery	M378121	Galway	pNHA	Private	13	8, 8	NW	Moderate	Cattle, donkeys (red deer - rare)	Winter	2, 2	3.09
	Glencolumbkille	R326993	Clare	cSAC	Private	54	3, 6	S	Sheltered	Cattle, feral goats	All year	1, 1	0.88
	Glenquin	R306960	Clare	cSAC	Private	79	6, 12	E	Sheltered	Cattle, sheep, horses (feral goats & deer - rare)	All year	2, 3	1.65
	Gortlecka	R308950	Clare	cSAC	An Taisce **	46	8, 16	E	Sheltered	Cattle (feral goats - occasional)	Winter	1, 1	0.53
SCRUB	Carran	R240967	Clare	cSAC	Private	117	2, 2	W	Exposed	Cattle	Winter	2, 2	3.30
	Knockans	R328985	Clare	cSAC	Private	63	3, 2	NNW	Moderate	Cattle	Winter	1, 1	2.97
	Rannagh	M272012	Clare	cSAC	Private	144	2, 1	E	Moderate	Cattle	Summer	2, 1-2	1.48
	Roo	M391035	Galway	cSAC	Private	17	0, 0	n/a	Sheltered	Cattle	Winter	1, 1	0.40
GRASSLAND	Caher	M164081	Clare	cSAC	Private	94	4, 4	W	Moderate	Cattle (feral goats - rare)	Winter	2, 2	1.06
	Gregan	M207025	Clare	cSAC	Private	187	1, 1	SW	Very exposed	Cattle	Winter	2, 1	0.67
	Kilcorkan	R390995	Clare	cSAC	Private	25	3, 2	NW	Moderate	Cattle (feral goats - rare)	Winter	2, 2	0.95
	Slieve Carran	M329038	Clare	cSAC, National Park	National Parks and Wildlife Service	164	6, 6	NE	Very exposed	Cattle, feral goats	Winter	1, 1	0.33

* pNHA = proposed Natural Heritage Area, cSAC = candidate Special Area of Conservation

** An Taisce = the National Trust for Ireland

*** Measurements/estimates for fenced (F) and control (C) plots are presented separately.

+ Figures calculated from information received from farmers in management questionnaire.

Table 8 Past records of habitat type at each of the twelve study sites.

	Site name	Question to landowner: "How many years can you confirm that the habitat has been present?"	Pelham/ Larkin (1787/ 1819)	1837 - 1842 OSi 6":1 mile map	1888 - 1913 OSi 25":1 mile map	Tentative conclusion
WOODLAND	Ballyclery	>30 years	Open	Rough pasture with outcropping rock.	Open ground with outcropping rock.	Woodland developed >30 but <100 years ago.
	Glencolumbkille	*Don't know/ no answer given*	Open	Rough pasture with outcropping rock. Large boulders and cliff/ break in slope.	Scrub with outcropping rock.	Woodland may be ~100 years old.
	Glenquin	Area was more open in the past (15/20years ago), but was still scrubby. Would have been +/- the same 40 years ago.	Open	Rough pasture with outcropping rock. Open ground/cleared fields nearby.	Outcropping rock.	Woodland developed >40 but <100 years ago.
	Gortlecka	>10 years	Open	Rough pasture with outcropping rock and scrub.	Scrub and outcropping rock	Woodland may have existed up to 200 years ago.
SCRUB	Carran	Area was more open in the past (>10 years ago), but always had some scrub.	Open	Rough pasture with outcropping rock. Scrub nearby.	Rough pasture with outcropping rock.	Scrub may have existed up to 200 years ago.
	Knockans	Probably more open 10 years ago, but always scrub present.	Open	Rough pasture with outcropping rock.	Rough pasture, outcropping rock, and exposed flat rock nearby.	Scrub developed >30 but <100 years ago.
	Rannagh	*Don't know/ no answer given*	Open	Rough pasture.	Rough pasture with outcropping rock.	Scrub has developed some time in the past 100 years.
	Roo	Hasn't changed in many years	Open	Rough pasture with outcropping rock.	Scrub and outcropping rock.	Scrub may have developed over 100 years ago.
GRASSLAND	Caher	>10 years	Open	Rough pasture with outcropping rock.	Rough pasture with outcropping rock. Symbol which may denote scrub.	Has probably been open ground for up to 200 years.
	Gregan	15 years	Open	Rough pasture.	Rough pasture with outcropping rock.	Has probably been open ground for up to 200 years.
	Kilcorkan	30 years	Open	Rough pasture with outcropping rock and boulders.	Rough pasture with outcropping rock.	Has probably been open ground for up to 200 years.
	Slieve Carran	*Don't know/ no answer given*	Open	Open ground. Field demarcated. Surrounded by rough pasture with outcropping rock.	Open ground. Field demarcated.	Has been open ground for approximately 200 years.

Soils

In the field

At each site a small soil pit was dug, down to the bedrock. The location for the pit was generally between the control and the fenced plots, in order to be representative of both. The soil depth at the location for the pit was checked before digging to ensure that the soil was sufficiently deep to be representative of the area, and to ensure a good chance of identifying soil horizons should they exist. The depth of the pit was recorded, along with details such as colour, stoniness and identifiable horizons (Table 9).

Table 9 Soil descriptions from soil pits at each site.

	Site Name	Soil pit depth (to bedrock) (cm)	Comments
Woodland	Ballyclery	9	Uniform, no identifiable horizons. Mid-dark brown, stony below.
	Glencolumbkille	11	Uniform, no identifiable horizons. Mid-brown.
	Glenquin	16	- 2cm layer of dark brown soil on top. - Underneath more uniform, dark brown and crumbly.
	Gortlecka	8	Uniform, no identifiable horizons. Dark brown.
Scrub	Carran	10	Uniform, no identifiable horizons. Very dark brown with a large amount of organic material (e.g. roots).
	Knockans	10	- 1.5cm of mid-brown soil with lots of roots and other organic material. - 8.5cm of more uniform soil below.
	Rannagh	14	Uniform, no identifiable horizons. Dark brown.
	Roo	8	Uniform, no identifiable horizons. Mid-brown with roots and organic material mixed in. Stony below.
Grassland	Caher	21	- 11cm of mid-brown soils with roots and organic material. - 10cm of a lighter brown, more orange soil.
	Gregan	19	Uniform, no identifiable horizons. Very dark and peat-like, with a high organic matter content.
	Kilcorkan	14	+/- Uniform, no identifiable horizons. Dark brown, with increased organic matter near top, but not differentiated into horizons.
	Slieve Carran	16	Uniform, no identifiable horizons. Mid-brown in colour.

The average soil depth at each site was calculated by taking 15 readings (to the nearest cm) in each plot, using a thin metal pin stuck into the ground (Table 10).

To allow for later analyses, soil samples were collected in the field. This was done separately at the fenced and control plots at each site, using a standard 10cm soil corer. Five cores were taken from each plot, taking care that samples were widely spaced across the plot to ensure representativeness, and these were then mixed to make a bulk sample. It should be noted that at some sites it was difficult to collect a soil sample due to the shallowness of the soil and the high amounts of organic matter and roots present.

In the laboratory

pH

The pH readings were taken from soils on the day of sampling; two replicates of each, which were then averaged. Centrifuge tubes were filled up to the 10ml mark with soil. These were topped up to the 20ml mark with distilled water (and in one case, because the soil had a high organic matter content, to 30ml). This was then shaken vigorously, and left to stand for approximately one hour. pH readings were taken after two minutes, using a pH meter which was calibrated daily.

Further analyses

The remaining soil from each plot was crumbled, air-dried and passed through a 2mm sieve in preparation for further laboratory-based analyses. These were:

1. % loss-on-ignition (% LOI),
2. textural analysis (% sand/silt/clay),
3. % calcium carbonate ($CaCO_3$) and
4. total phosphorus (Total P).

These laboratory-based analyses were carried out by an undergraduate student (Kirrane, 2008). The methods used and results are presented in Appendix 3.

Desk study

The soil types at each of the study sites were identified from the Environmental Protection Agency (EPA) soil map (Fealy et al., 2006). Eleven out of twelve sites were categorised as having shallow, well-drained mineral soils, which are mainly basic (BminSW). Most sites had soils with a parent material described as 'calcareous bedrock at surface' (RckCa). The one exception was Roo (a scrub site) which had a soil type described by Fealy et al. as shallow lithosolic – podzolic, potentially with peaty topsoil – derived from calcareous rock or gravel, with/without peaty surface horizon (BminSRPT). Taking into account that the spatial resolution of the EPA map may lead to some local-scale inaccuracies, and the fact that data on soil pH and % LOI collected here do not support the suggestion of a different soil type, it is most likely that the soil at Roo is in fact similar to that found at the other study sites, i.e. that it is a basic, shallow, well-drained mineral soil.

Summary of soil data

A summary of the measured soil parameters, along with some derived data, is provided in Table 10.

Table 10 Summary of soil details from each of the twelve study sites. (See also Appendix 3.)

	Site Name	Plot	Ave. soil depth (cm)	pH	% LOI	% sand	% silt	% clay	Soil texture (derived from % s/s/c)*	$gCaCO_3/ml$**	Total P (µg/ml)	Soil type (EPA)
Woodland	Ballyclery	F	8	7.35	26.15	72	21	11	Sandy Loam	0.0156	159.70	BminSW
	Ballyclery	C	8	7.295	19.79	62	18	10	Sandy Loam	0.0301	204.33	
	Glencolumbkille	F	12	6.56	28.31	84	6	10	Loamy sand	0.0199	180.30	BminSW
	Glencolumbkille	C	7	6.73	26.69	84	8	8	Loamy sand	0.0463	164.57	
	Glenquin	F	9	6.965	38.18	47	36	17	Loam	0.0449	372.70	BminSW
	Glenquin	C	10	7.005	35.17	74	12	14	Sandy Loam	0.0454	412.41	
	Gortlecka	F	6	6.89	29.08	52	34	14	Sandy Loam	0.0587	159.27	BminSW
	Gortlecka	C	4	6.885	40.91	55	21	24	Sandy Clay Loam	0.0485	98.92	
Scrub	Carran	F	4	6.865	63.19	74	6	20	Sandy Clay Loam	0.0351	145.19	BminSW
	Carran	C	3	6.725	67.21	75	4	20	Sandy Clay Loam	0.0327	187.92	
	Knockans	F	4	6.765	41.58	72	12	16	Sandy Loam	0.023	120.41	BminSW
	Knockans	C	4	6.58	49.65	76	10	14	Sandy Loam	0.0166	128.01	
	Rannagh	F	5	6.575	60.63	78	6	16	Sandy Loam	0.0095	137.75	BminSW
	Rannagh	C	4	6.8	59.55	69	13	18	Sandy Loam	0.0278	207.05	
	Roo	F	14	6.15	26.08	64	24	12	Sandy Loam	n/a	139.31	BminSRPT
	Roo	C	9	6.305	21.19	78	14	8	Loamy sand	n/a	157.28	
Grassland	Caher	F	13	6.9	28.48	40	48	12	Loam	0.0148	164.04	BminSW
	Caher	C	13	7.07	33.09	50	36	14	Loam	0.0315	204.47	
	Gregan	F	6	6.745	85.67	82	1	17	Sandy Loam	0.017	161.22	BminSW
	Gregan	C	9	6.645	69.87	86	4	10	Loamy sand	0.0092	246.25	
	Kilcorkan	F	8	7.245	22.78	68	20	12	Sandy Loam	0.0308	170.14	BminSW
	Kilcorkan	C	8	6.68	19.04	64	30	6	Sandy Loam	0.043	188.68	
	Slieve Carran	F	19	6.04	21.06	57	30	13	Sandy Loam	n/a	202.89	BminSW
	Slieve Carran	C	13	6.39	22.43	65	21	14	Sandy Loam	n/a	241.24	

* Refer to Appendix 3 for details on how % sand/silt/clay data were used to determine soil texture

** $CaCO_3$ amounts were not calculated for sites with pH <6.5.

Ancillary projects

In order to maximise the scientific and ecological benefits gained from the exclosures erected as part of this PhD project, a number of ancillary projects were designed and initiated.

Ants and anthill vegetation

In 2007 two ant-related projects took place. One investigated ant species and another the vegetation associated with anthills. Ant species were searched for in the field at all study sites by Robin Niechoj, a researcher from University of Limerick. No ants were found in woodland sites (in spite of extra and dedicated surveys in this habitat). The species found at the scrub and grassland sites are listed in Table 11.

Table 11 Ant species found at scrub and grassland sites.

	Site Name	*Myrmica ruginodis*	*Myrmica scabrinodes*	*Lasius flavus*	*Myrmica sabuleti*	*Formica lemani*	*Lasius platythorax*	*Leptothorax acervorum**	Species total for site
Scrub	Carran	x	x	x		x		x	**5**
	Knockans	x	x	x	x	x			**5**
	Rannagh	x	x	x	x		x		**5**
	Roo	x	x	x	x	x	x		**6**
Grassland	Caher	x	x	x	x	x	x		**6**
	Gregan	x	x		x				**3**
	Kilcorkan	x		x					**2**
	Slieve Carran	x	x						**2**
	No. of sites	**8**	**7**	**6**	**5**	**4**	**3**	**1**	

* This species possibly overlooked in some sites

Anthill vegetation was studied at five of the sites (Carran, Knockans, Rannagh, Roo and Caher); these were suitable for this study as they contained multiple large anthills in the vicinity of the exclosures. The vegetation of the anthills was compared with surrounding vegetation and found to differ in a number of aspects – e.g. there was significantly more bare earth on the anthills, and plant species diversity was higher in the surrounding vegetation. Certain plant species were found to have an affinity for the anthills, e.g. *Thymus polytrichus*. A manuscript is to be submitted for publication shortly (Howard-Williams et al., in prep.).

Lichens

The epiphytic lichens of hazel trees/shrubs at each of the scrub and woodland sites were examined in detail by Campbell (2008) as part of an MSc research project. The results listed 47 species (37 from woodlands, 40 from scrub). Scrub was found to be more diverse in lichens than woodland and, using both cluster analysis and ordinations, the species composition of both habitats was shown to be different. The scrub contained more light-demanding, pioneer species, while the woodlands contained, for example, species in the *Lobarion* alliance, a group of relatively rare lichens of international importance which typically need more sheltered, humid and dark conditions. The composition of the lichen flora appeared to be influenced by factors such as girth of stem (a possible surrogate for age, but this is complicated by the multi-stemmed growth form of hazel), cover of bryophytes and canopy height. Previous published studies on lichens in the area are few: Dickinson and Thorp (1968), Kirby (1981) and McCarthy and Mitchell (1988). Appendix 4 provides the lists of lichens found at each site.

Bryophytes

In 2009 two research students (one MSc and one undergraduate), under the supervision of Dr Daniel L Kelly, sorted and identified bryophyte samples collected from the study sites in 2006. Mosses and liverworts had been collected systematically from all 120 vegetation quadrats. Sampling was generally limited to patches ≥5 x 5cm, and only bryophytes living on or near the ground were collected – i.e. epiphytes were collected separately and were not included in these studies. Three out of each group of five samples (i.e. from within a plot) were worked through by the bryology students, and all specimens were identified to species level (with a few exceptions for difficult taxa or damaged specimens). The full results are to be found in Walsh (2009a) and Lu (2009), and are summarised here and in Appendix 5.

A total of 55 species of bryophyte were identified, with 33 species from the grassland sites, 41 from the scrub and 44 from the woodlands. The suites of species found in grasslands and woodlands separated out well on NMS ordinations, and so too did the scrub quadrats once they were divided into ‘woody’ scrub and ‘grassy’ scrub. Factors such as calcium carbonate levels and canopy cover were found to be among the important explanatory variables. It was also found that there was a relationship between bryophyte and vascular plant species richness in grasslands, but this relationship did not hold for the other two habitat types.

Chapter Three:

The vegetation of woodlands, scrub and grasslands in a limestone landscape of high biodiversity value, and the short-term effects of excluding large grazing animals

"*The finer consequences of grazing changes as they affect all departments of the ecosystem are very incompletely known, however…*" (Boyd, 1960)

"*The main threat recorded for Annex I grassland habitats surveyed in 2009 was encroachment/undergrazing, highlighting the urgency with which the problem of land abandonment needs to be tackled*."
(O'Neill et al., 2009, from the Irish Semi-natural Grasslands Survey Annual Report)

Introduction

Grazing animals are known to have significant impacts on biodiversity (for example, Gibson, 1997, Hester et al., 2000, McIntyre et al., 2003, Perrin et al., 2006a, Van Uytvanck and Hoffmann, 2009). It is often unclear however, whether these impacts are positive or negative over different time frames, how they relate to grazing intensity, and whether and how they apply to diversity across the scales of species to communities to ecosystems. For example, fenced exclosures have demonstrated that diversity in oakwoods may be threatened by either high grazing levels or the absence of grazing (Mitchell and Kirby, 1990, Kelly, 2000). It is also difficult to make general statements on the effects of grazing animals based on individual studies due to the amount of variability possible in and among such studies. In any case, there is clearly a lack of experimental data on the effects of grazing on the vegetation of both Irish woodlands/scrub on base-rich soils, and on semi-natural grasslands. For example, Osborne and Jeffrey (2003) point to the "*absence of experimentally based studies*" on grazing impacts in the Burren, and they recommend the establishment of permanent monitoring plots.

In this chapter the vegetation of woodlands, scrub and grasslands at the twelve study sites in the Burren is described. The relations within and between the vegetation communities are investigated, along with environmental drivers. The effects of the cessation of grazing on plants (richness, diversity, individual species abundances) are assessed using the fenced exclosures.

Selective review of grazing exclusion studies

Grazing exclusion studies outside of Ireland

Grasslands

There have been many studies focussing on the effects of grazing on grassland species composition (recent examples and reviews from the UK include: Smith and Rushton, 1994, Smith et al., 1996, Gibson, 1997, Smith et al., 2000, Tallowin et al., 2005, Stewart and Pullin, 2006, Scimone et al., 2007, Critchley et al., 2007, Marriott et al., 2009), but relatively few have used the experimental method of grazing exclosures, favouring instead the comparison of sites with different

managements (or management histories). Morgan and Jefferson (2007), in a review of long-term experimental studies of lowland grasslands and heaths in the UK, found twelve studies which had grazing as an experimental treatment (though not all of these would necessarily have used exclosures). Many of the exclosure studies in existence focus on excluding sheep, and/or are based in upland habitats (e.g. the long-running experiment described in Hill et al., 1992, and the more recent work of Evans et al., 2006).

Recent studies from further afield which used grazing exclosures in grasslands include Hansson and Fogelfors (2000), Sternberg et al. (2000), Jacquemyn et al. (2003), Alrababah et al. (2007), Gill (2007), Pavlu et al. (2007), van Staalduinen et al. (2007), Mayer et al. (2009) and Skornik et al. (2010). These experiments range in timescale from 3 to 90 years, and are located in parts of the globe as diverse as Sweden, the Mediterranean, Mongolia and the USA. The species of grazing animal varied, but cattle were the most common grazers to be excluded. In general, a majority of studies found either a reduction in species richness or a change in species composition with cessation of grazing.

Of particular relevance to the situation in the Burren are the studies based in alvar grasslands, and particularly those on the island of Öland in Sweden (well summarised in Rosen, 2006, but see also Zobel and Kont, 1992, Partel and Zobel, 1995, and Partel et al., 1998 for details on vegetation and succession in alvar areas in Estonia). Alvars are areas of land used for pasture which have thin deposits of soil overlying limestone bedrock. Öland has the largest area of alvar in the world at 25,500ha (Rosen, 2006). This area is high in biodiversity, and is particularly rich in phytogeographical elements, and endemic and rare species. A drop in the human population on the island at the end of the nineteenth century (following a famine) meant that the land was less intensively used and scrub encroachment began to become an issue. It continued to such an extent that it became uneconomical to farm the land, thus causing an acceleration in the spread of scrub. It is only since the 1990s that grazing has again been used as a widespread and effective land management tool in the region, thanks largely to funding through the EU LIFE programme (final project report: Rundlof Forslund and Lager, 2000).

A series of permanent plots have been monitored in the region since the early 1970s, and an increase in scrub cover, mostly *Juniperus communis*, in the absence of grazing has been shown to lead both to a decline in vascular plant species richness, and also to a decrease in the structural heterogeneity of the landscape (Rosen, 2006). A lack of grazing in grass-dominated areas has meant that taller more robust species did well at the expense of smaller plants, and there was also a decrease in plant species number. Interestingly, this was offset at some sites by an increase in anthills (due to the absence of trampling), which facilitated increases in plant species richness (Rosen and Bakker, 2005).

Woodlands

"*Controlled grazing studies have revealed that large herbivores (wild and domestic) have a substantial influence on forest composition and dynamics.*" (Hester et al., 2000)

"*The general effect of sustained heavy grazing and browsing* [by deer] *is a reduction in the richness of biological communities*." (Fuller and Gill, 2001)

Cattle as grazers

A survey of cattle-grazed woodlands in Britain was carried out by Armstrong et al. (2003) with the aim of gathering information on the sites themselves, the reasons for grazing, the stocking rates, the impacts, and a number of other variables of interest. They note that there are virtually no published studies of the impact of cattle grazing on woodlands in Britain, even though cattle are increasingly being used as a tool for conservation management in woodlands because of perceived benefits (such as reduction of cover of certain species and the breaking up of litter and other matted vegetation). They found that the main reasons for having cattle in woodlands varied by region, with nature conservation aims being most important in England, and production being most important in Scotland. Within areas where cattle production was important, the woodlands were used mainly for shelter in winter, rather than as a source of forage. From the nature conservation point of view, the most common aims were encouragement or prevention of tree regeneration, depending on the situation, and also the reduction in cover of certain highly competitive species (e.g. bramble, bracken, *Pteridium aquilinum*, and some grass species). They found that objectives were being achieved at most sites. These patterns of woodland usage by landowners are in contrast to the situation in Ireland, where almost 40% of native woodlands are grazed by livestock. Perrin et al. (2008a) note livestock grazing as the most common management type in native woodlands, and found that cattle graze in over 30% of them (deer are the second most common grazer overall at 20%). Cattle grazing is most common in lowland woods in Ireland, and the highest percentage of cattle-grazed woods in the country is in Co. Clare, at 55% (Perrin et al., 2008a).

Exclosures of some sort were in place at approximately one-third of the cattle-grazed sites surveyed by Armstrong (2003), but findings from these have rarely been analysed or written up, and control plots were lacking in all cases. Interestingly, the survey found only three sites in which cattle were the only large mammalian grazer (sheep and/or deer were normally present also), in contrast to the picture for the Burren, or for Ireland as a whole. Overall, excessive cattle grazing pressures were found to lead to decreased regeneration levels. Other aspects of woodland ecology such as effects of cattle grazing and trampling on field layer vegetation were not covered in this survey, but were listed under 'future research needs'.

In Belgium, Van Uytvanck and Hoffmann (2009) found that cattle grazing in woodlands reduces bramble cover, and thus impacts positively on aspects of the ground flora, but only up to a

moderate density of grazers. Beyond this, trampling damage and the direct effects of grazing begin to impact negatively on other species.

Other grazers

There have been numerous long-term studies of woodlands in Britain (see, for example, Kirby et al., 2005, Keith et al., 2009). Of those which looked at grazing, the majority related to deer, with a smaller number relating to sheep. Some of these have used grazing exclosures, but most used other methods to study the effects of grazing on the vegetation. One of the best known long-running woodland study sites is Wytham Woods, Oxford, a *Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland (category W8 from Rodwell, 1991) (for accounts of species changes see: Kirby et al., 1996, Kirby and Thomas, 2000, Corney et al., 2008, Mihók et al., 2009). Morecroft et al. (2001), in a paper detailing the findings from three deer exclosures set up there in 1997 (and which were surveyed in 1998 and 1999), report that the changes seen within this timeframe were limited, but included a significant increase in dicotyledon forbs within the exclosures. They list the following changes seen in Wytham Woods in recent decades as being presumed to have been caused by deer-grazing: a decrease in the shrub layer, a decrease in bramble, a decrease in some woodland herbaceous species (particularly *Mercurialis perennis* and *Circaea lutetiana*) and an increase in unpalatable and/or grazing-tolerant species such as the grass *Brachypodium sylvaticum*.

A long-running exclosure experiment exists in the New Forest, Hampshire, and is reported upon in Putman et al. (1989). The paper relates the findings of 22 years of deer exclosure in this oak-beech woodland. Clear differences were evident between the grazed and ungrazed plots, with a dense layer of bramble, along with substantial growth of tree saplings, characterising the ungrazed area. Species diversity was highest in the ungrazed plot, but the biomass of the herb layer was lower. There were more grasses in the grazed plot (an exception was the grass *B. sylvaticum*, which was found in the ungrazed plot only). Putman et al. state that the species composition of the grazed plot reflected the selectivity of the grazing animals and the more open conditions which prevailed (as a result of the grazing). They note that the species composition of the two plots were remarkably similar, even after 22 years, and suggest that isolation from sources of possible colonisers may account for the lack of 'new' species in the ungrazed plot.

Latham and Blackstock (1998) report on a 20-year old exclosure in alder woodland in Wales (sheep and ponies were the main grazers excluded). They found that the field layer inside the fenced area was better developed, had more litter, dead wood, bryophytes and woodland species. Pigott (1983) found that after 26 years of exclusion of sheep from an oak-birch woodland near Sheffield, regeneration of the two main tree species was much increased. A closely-cropped grassy field layer had been replaced by a more heterogeneous vegetation, with *Vaccinium mytillus,* in particular, doing well. Hester et al. (1996) and Mitchell et al. (1996) both report on the effects of

sheep grazing on regeneration in an upland broadleaved woodland, based on seven years of exclosure. They found that regeneration greatly increased, across a range of tree species, once grazers were excluded. Finally, in a review of the impact of large grazing animals on semi-natural upland woodlands Mitchell and Kirby (1990) recommend a low level of grazing (rather than heavy grazing or no grazing), as this is likely to provide the greatest diversity in both vegetation structure and species composition.

Scrub

Grazing studies based on scrub of any sort from Britain or Ireland are few. To this authors knowledge, the only published studies which focus on the exclusion of grazing animals from hazel scrub are those of Moles et al. (2005) and Deenihan et al. (2009), both based in Ireland and discussed below.

The use of goats to help control scrub in chalk grasslands in Britain was investigated by Oliver et al. (2001), who found that both the browsing and grazing activities are beneficial to plant diversity (browsing functioned to reduce the scrub itself, increase species diversity and increase chalk-specialists, whilst grazing reduced vegetation height and competition, also increasing biodiversity). In the USA, Rosenstock (1996) studied the effects of livestock grazing on the vegetation (and small mammal populations) of a semi-arid shrub-grassland. Results included substantially more litter in the ungrazed sites, and taller grass with a higher cover. Hongo et al. (1995) investigated the recovery of overgrazed shrub-steppe in north-west China, finding diversity was decreased when grazers were excluded, but soil organic matter increased and water balance improved – both desirable changes in overgrazed steppe habitats.

Grazing exclusion studies in limestone habitats in Ireland

O'Donovan temporary exclosures

Experimental grazing studies in calcareous habitats in Ireland are quite few. Work by O'Donovan (1987, 1995, 2001) looked at the influence of large vertebrate grazers on vegetation productivity in an area of *Sesleria*-dominated grassland in the Burren National Park. She measured the grazing pressure using three small portable exclosures measuring 1.5 x 1.5 x 1m. Using data from six-weekly harvests between March and December 1982, O'Donovan found no significant difference in the biomass between inside and outside the exclosures. She notes that the harvests were very heterogeneous due to the mosaic-like nature of the vegetation and that the grazing pressure may have been too low during the sampling period to have been picked up with the methods used. Additionally, she points out that the exclosures may have been too small, too few, and/or moved too frequently to allow changes in productivity/biomass to be measured. A second period of observations (January - April 1985) showed the beginnings of a trend, with an average difference of 30% between inside and outside.

The exclosures were also left in place for an entire year (June 1983 to July 1984) in order to ascertain if there were longer-term changes in productivity. In this case, an appreciable difference in the biomass between inside and outside was detected. This difference amounted to approximately 25% of the sward's annual productivity – i.e. grazing animals had removed a quarter of the biomass produced by the habitat in that year.

Gortlecka exclosure

A study by Moles et al. (2005) involved fencing off a small area of land (6.3 x 6.3m) consisting of a grassland/pavement/scrub mosaic in the townland of Gortlecka, between Lough Gealain and Mullaghmore in the Burren National Park in 1991. The fence excluded cattle, but was not entirely goat-proof. There was a corresponding unfenced area directly adjacent, acting as a control. The most important finding to emerge from the study was that when large herbivores were excluded, competition intensified and there was a steep decline in plant diversity. There were notable reductions in frequency for most plant species. Only the grasses apparently increased in abundance. Moles et al. conclude by stating that the disturbance provided by grazing animals is of the utmost importance in the conservation of biodiversity in grasslands in the Burren.

Deenihan et al. (2009) continued the study at Gortlecka by mapping the distribution of five 'habitat' types in 1991, 1997, 2003 and 2006. The habitat types, as assigned by the authors, were: 'pavement', 'sward', 'mix of pavement and sward' [similar cover of each], 'scrub' and 'heather'. Deenihan et al. traced how the extent of each of these habitat types changed over time. Their findings showed a shift towards increased heather and scrub cover over a 15-year period, paralleled by a shift away from grassland and pavement. They suggest that there has been a loss of diversity as a result. Of note also is the fact that a similar (but smaller in scale) shift towards heather and scrub was noted in the vegetation in the control area, inferring that the management regime in place within the National Park as a whole may not be functioning adequately to halt scrub encroachment. The findings from such a small and unreplicated study are, however, of limited applicability on a broader scale.

'Bonham' exclosures

The 'Bonham' exclosures on Mullaghmore in the Burren National Park were set up in April 1980 by Francis Bonham, a postgraduate student of University College Galway, with the involvement of the 'National Parks Department' (Bullock and O'Donovan, 1995). The lower exclosure is 33 x 20m in size and the upper is 30 x 12m. The lower exclosure is situated at the edge of a limestone terrace, and consisted of a high proportion of bare rock, with some hazel (*Corylus avellana*) cover and occasion patches of low-growing herbaceous vegetation. The upper exclosure consisted of some hazel scrub/woodland at the base of a scarp, and some herbaceous vegetation, and is more sheltered. Bonham carried out a baseline botanical survey of the two exclosures, and their adjacent controls, in August 1980 using a detailed point quadrat method. His aim was to assess the effects of

the grazing of cattle (at the upper exclosure) and feral goats (at the lower exclosure) on the vegetation. In fact, both species of grazer can be found in the vicinity of both exclosures (Bates, 1988, Byrne, 2001.) He had planned to re-survey the exclosures over a number of years, but the work was never finished nor published.

In 1988 Bates carried out a re-survey of these exclosures, but did not use the point-quadrat method of Bonham (Bates, 1988). He found that the vegetation composition of the lower fenced and control plots was similar (using the Sørensen coefficient of similarity). However, he found that hazel was taller and had higher cover inside the lower exclosure, compared to the control, but he did not test this statistically, nor did he provide data from the beginning of the study for comparison. At the upper exclosure, hazel was again found to be taller within the fenced plot, and to have a higher cover. Sørensen's measure of similarity showed that the vegetation was similar outside and within in the parts dominated by hazel, but for the parts dominated by herbaceous vegetation, the coefficient was lower (67%). There was substantially more total biomass inside the fence than outside.

The effects of cattle and feral goats on the ecology of some of the habitats of the Burren National Park were the focus of a PhD thesis by Byrne (2001). As part of this work, she carried out a detailed re-survey of the two 'Bonham' exclosures in 1996, using Bonham's original survey methodology. In summary, she found a substantial increase in hazel at the upper exclosure, and only a slight increase at the lower, presumed to be because of its more exposed location. Cover of hazel had not changed noticeably in either control since the establishment of the plots in 1980. Cover of forbs and grasses had decreased by a third inside the upper exclosure, with no such changes seen in the control. The number of grass species recorded declined sharply (from 13 to six) between 1980 and 1996. Differences were more difficult to detect in the lower exclosure, but the combined percentage cover of trees, shrubs and grasses had increased at the expense of all other plant categories within the exclosure. This was due in particular to the expansion of hazel and *Sesleria caerulea*.

Woodland exclosures

The only published study into the effects of the exclusion of grazers from base-rich woods in the Republic of Ireland is that of Perrin et al. (2006a), which focused on regeneration and stand dynamics. This work (and a complementary study which focusses on ground flora which is in completed manuscript form: Perrin et al., in prep.) details the effects of long-term (>30 years) exclusion of grazers in two woodlands (one yew- and one oak-dominated) in Killarney National Park, Co. Kerry. It was found that heavy deer grazing has a strong negative effect on regeneration and survival of a number of tree species, but that other factors such as light availability are important also. They found that while ground cover increased inside the fenced plots, this was driven by major expansions in just a few species – mainly bramble (*Rubus fruticosus* agg.) and ivy

(*Hedera helix*). Herbaceous species increased in abundance when grazing first ceased, but then showed a decline, resulting in a long-term decrease in species richness in ungrazed plots. This study was, however, quite limited both in terms of its replication and its representativeness, yew woods in particular being a rare habitat type.

Cooper and McCann (2011) investigated the effects of exclusion of cattle from two adjacent wet oakwoods in Northern Ireland. They found significant decreases in ruderal species and grasses after ten years, while woodland species (both graze-resistant and graze-sensitive) increased. They believe that relief of grazing pressure and a changed light environment are the main causes of the changes. They suggest that, following exclosure, it is mainly light-dependent ruderal species which are lost from woodlands. This study is again limited in terms of replication and geographical spread.

Grazing exclusion studies in other habitats in Ireland

Other woodland types

McEvoy et al. (2006) looked at the effects of livestock grazing on a large number of woodlands of different types across Northern Ireland. The study came about in response to the fact that many modern agri-environmental schemes recommend removal of grazers from woodlands (due to concerns about overgrazing and reduced regeneration), without regard for the fact that grazing of some form has long been an integral part of the functioning of woodland ecosystems. They note that exclusion of large grazing animals can cause substantial changes in the structure and composition of woodland floras, and that continuation of grazing can help maintain biodiversity (of both flora and fauna). Overall, they found that woodlands which are grazed are slightly more species rich, have lower cover of dominant species in the field layer and shrub layer (e.g. lower cover of bramble) and have more bare ground in comparison to ungrazed woods. Interestingly, from a total of 100 woodlands chosen randomly for survey, none showed obvious signs of deer grazing. Sheep were the most common grazer in upland areas, and both cattle and sheep were common in lowland woods.

Kelly (2000) documents the changes seen in a heavily (deer-)grazed acidic oakwood in the south-west of Ireland, after 26 years of exclosure. One of the main findings was an initial increase in species richness and diversity (lasting only a few years), following by a decline. By year 26, the Simpson's diversity measure, mean number of vascular plants and total number of angiosperm herbs (this group had seen the most substantial initial increase) had all fallen to below the values they had had at the start of the experiment. A small number of species, mainly *Luzula sylvatica* and holly, had increased, leading to the competitive exclusion of other species. Kelly concluded that an intermediate grazing level (as opposed to heavy or no grazing) is necessary for maintaining woodland diversity.

A number of studies involved plantations. For example, Smith (2003), in a large scale exclosure experiment, investigated a number of factors which may affect the restoration of native woodland on conifer clearfells, including grazing effects. He employed a series of 21 grazing exclosures, located in counties Wicklow and Kerry, each with a corresponding unfenced control plot. Browsing by large herbivores was found to be the most important factor inhibiting tree growth and survival in the trees which were planted into the control plots. There was no significant effect of grazing pressure on the field layer vegetation developing in the control plots. He comments that this is surprising given the large density of herbivores at the study sites (mainly deer, sheep and feral goats). He suggests that insufficient time may have elapsed in order for the effects to become measurable (the sites were monitored for three years).

Sheep as grazers have been looked at in a number of studies, e.g. McEvoy and McAdam (2008), who looked at their effects on young oak and ash trees in plantations. They found that the most significant effects were on height and biomass of the surrounding sward, and that young trees were only slightly damaged. Another plantation study is that of Strevens and Rochford (2004), focusing on hare-grazing in plantations. They found that, while there was significant damage, it was local and did not usually cause the death of the tree. They noted that deciduous trees were more susceptible than conifers.

Heathlands and peatlands

A number of studies investigating the effects of grazing have taken place in peatland/heathland ecosystems in Ireland. These were driven, at least in part, by the problem of overgrazing which existed on Irish peatlands but which has been ameliorated following reforms in agricultural grant aid systems. In the mid-1990s, McFerran et al. conducted a series of investigations into the effects of grazing (and other management practices) on invertebrates of heathlands and other upland vegetation types (McFerran et al., 1994a, 1994b, 1994c, 1995). Their findings included a grazing influence on spider and beetle community composition, though this influence varied among species and among groups. Bleasdale (1995) used grazing exclosures in upland habitats to investigate the influence of sheep grazing on the vegetation. The expansion of the grass *Nardus stricta* was found to be a problem in heavily grazed areas. Finally, Dunne (2000) carried out an inventory and survey of grazing exclosures on blanket bog, heath and upland grassland (the main grazer in all cases was sheep) on National Parks and Wildlife Service (NPWS)-owned lands. She found that the results of excluding grazers were varied, and depended on the condition of the vegetation prior to the erection of the exclosures. The vegetation type, the local site conditions and subsequent management were all important factors also. In some dry heathland sites, a relatively quick vegetation recovery was recorded once grazing ceased, and some blanket bogs also showed good signs of recovery, but in sites with severe damage, recovery was slow.

Turloughs

Moran et al. (2008) found that, along with hydrological regime, grazing is one of the main factors controlling the composition of plant communities in turloughs ('vanishing lakes'). Vegetation structure and amount of litter were found to be important variables, and grazing intensity was important in explaining floristic differences (e.g. at higher grazing intensities there were more rosette-forming species present). Overall, grazing had a positive effect on species richness. Conversely, Ryder et al. (2005) found that grazing impacted negatively on dipteran (flies) diversity in turloughs.

Objectives of this chapter

This chapter aims to present details of the vegetation found at each of the habitat types, woodland, scrub and grassland in the study region of the Burren, west of Ireland, along with an account of the factors influencing the variation seen both within and among habitat types.

Further, through the use of a network of fenced experimental exclosures and their associated unfenced control plots, the short-term effects of the cessation of grazing on the plant communities will be assessed. Differences in species richness and diversity and the effects on some individual species are investigated.

Methods

Study area and study design

The impact of the cessation of grazing on plant diversity was investigated experimentally in three habitat types in the Burren in the west of Ireland. Changes in the vegetation in woodlands, scrub and grasslands were recorded in a network of permanent plots between 2006 and 2008 using fenced exclosures. Details on the habitat types and the study area can be found in Chapter One, and see Chapter Two for locations of study sites and experimental set-up. In summary, the network of study sites consisted of twelve locations - four each for woodland, scrub and grassland. At each of the twelve sites there were two 20 x 20m plots – one fenced and one unfenced (the control). Each plot contained a grid of five fixed 2 x 2m quadrats, and these were used for the vegetation sampling (see Figure 12, Chapter Two).

Data collection

Fieldwork was carried out in late summer. In 2006, eleven of the sites were surveyed between 26th July and 4th September. The twelfth, Gortlecka, was not surveyed until December 2006. This late survey date is unlikely to have had a significant effect on the data gathered, although some species may have had their covers under-estimated. To mitigate against this, the cover values for canopy species at this site were checked the following year. Sites were resurveyed in 2008 within ten days

of their first survey date (except for Gortlecka, which was resurveyed in late August with the other sites).

All vascular plants present in the 2 x 2m quadrats were recorded in 2006 and 2008, along with their percentage cover values estimated to the nearest 5%. At covers of <5%, a modified version of the Domin scale was used (+ = tiny, or one plant; 1 = 1-2 plants, but <1% cover; 2 = several plants, but still <1% cover; 3 = 1-4% cover). These cover scores (i.e. '+', '1', '2' and '3') were converted to an approximately equivalent percentage for database entry (0.2%, 0.5%, 1% and 3% respectively). A list of vascular plants was also recorded from the entire plot (i.e. *outside* the quadrats but *inside* the 20 x 20m plot), with each species being given a rating on the DAFOR scale (D=dominant, A=abundant, F=frequent, O=occasional, R=rare; Kent and Coker, 1992). In the main vegetation database all plants were assigned to one of the plant groups listed in Table 12.

The cover values for a number of categories which summarise either a functional or a structural aspect of the vegetation were also recorded (Table 13). There are a number of species which do not sit neatly in just one category. For example, ivy can be found growing anywhere from the ground to the canopy in a woodland. It was treated as a 'low woody' species for overall cover values, but note was taken of the proportion of the cover which was at 'ground' and 'canopy' level. Other species to which this may apply include bramble and *Lonicera periclymenum* (Kelly and Kirby, 1982).

Table 12 Plant group, abbreviations used and description.

Plant group	**Full name**	**Description (where necessary)**
W	Woody	Woody species (in the shrub and canopy vegetation layers)
LW	Low woody	Woody species which are low-growing and are not trees or shrubs (e.g. bramble, ivy, *Calluna vulgaris*)
FO	Forb	Broadleaved herbaceous species, excluding grasses, sedges, rushes and ferns
O	Orchid	
G	Grass	
C	*Carex* spp (sedge)	
J	*Juncus* spp (rush)	
F	Fern	

Table 13 Categories to which cover values were assigned, both at quadrat and plot level.

Vegetation class	Description
Grass	Cover of all grasses
Sedge	Cover of all sedges
Fern	Cover of all ferns (includes bracken)
Pteridium	Cover of bracken only
Bare earth	Cover of exposed soil
Bare rock	Cover of exposed rock *
Litter	Cover of dead/decaying plant material
Ground layer	Cover of bryophytes
Herb layer	Cover of grasses + sedges + ferns + rushes + forbs
Low woody	Cover of all species which are woody, but which are not trees or shrubs (e.g. bramble, ivy, *Calluna vulgaris*)
Shrub	Cover of woody plants in the shrub layer (i.e. below the canopy)
Canopy	Cover of all woody species in the canopy

* may have scattered lichens

Vegetation height was recorded in each quadrat. In the woodland, canopy height was estimated by eye to the nearest metre (maximum was 11m). In the grassland, nine readings (to the nearest centimetre) were taken using a metre stick and then averaged. In the scrub, a mixture of these two methods was used, depending on the vegetation in the quadrat in question.

A number of environmental variables were recorded at each plot (see Chapter Two for more details) including altitude; aspect; slope; exposure; species of grazer; grazing level; number of cattle per hectare (derived from questionnaire results), grid reference and a number of soil-related variables – depth, pH, % loss-on-ignition (% LOI), %sand/silt/clay, texture, $CaCO_3$, and total P.

Quadrats were labelled using an intuitive system of abbreviations (Table 14). A quadrat labelled 'Y1W3F2' (reading from the right-hand side of the label) is the second quadrat inside the fenced plot (F2), at the third woodland site (W3, =Glenquin), in year one (Y1, =2006).

Table 14 Quadrat labelling abbreviation system

Year	Habitat	Site (refer to Figure 11, Chapter Two)	Plot/Treatment
Y1 = 2006	W = woodland	1 = Ballyclery	F = fenced
Y3 = 2008	S = scrub	2 = Glencolumbkille	C = control/unfenced
	G = grassland	3 = Glenquin	
		4 = Gortlecka	
		5 = Carran	
		6 = Knockans	
		7 = Rannagh	
		8 = Roo	
		9 = Caher	
		10 = Gregan	
		11 = Kilcorkan	
		12 = Slieve Carran	

Species nomenclature/identification issues

Common names are sometimes used for tree and shrub species in this thesis. A list of these, giving common and scientific names, is provided in Appendix 1. Scientific names are used for all other species. Some taxa which occur frequently in the text are referred to by genus name only, such as *Rubus* and *Pteridium*, but only where the identity of the species is unambiguous. Nomenclature follows Stace (2010) for scientific names and Scannell and Synnott (1987) for common names.

Some species groups are generally acknowledged to be difficult to identify to species level - e.g. "*...certain groups, like the brambles, hawkweeds, eyebrights and dandelions, often defeated us...*" (Rodwell, 1991). In addition to those mentioned by Rodwell, difficulties were encountered with sedges (*Carex* spp) and the grass genus *Agrostis*. In many, but not all, cases identifications of specimens from these two genera were made to species, but because this generated a mixture of species-level and genus-level records, these were all entered in the database (and analysed) at the genus level.

In the case of the sedges were, many were recorded to species level, but there were some gaps and uncertainties (often due to the absence of inflorescences, damage caused by grazing, etc.), and thus records were sometimes amalgamated. An exception was made with the woodland data when this was being dealt with in isolation from the other habitat types as only *C. sylvatica* and *C. flacca* were present, and they were readily distinguishable. The species of *Agrostis* which occur in the Burren are *A. canina* (local distribution), *A. capillaris* (frequent), *A. gigantea* (one station south-east of Gort) and *A. stolonifera* (abundant) (Webb and Scannell, 1983). Some of the specimens encountered were indeterminable, and so all records were entered as *Agrostis* sp. The hawkweeds (*Hieracium* spp) are represented in the Burren by six species (Webb and Scannell, 1983), of which *H. anglicum* and *H. sanguineum* are the most common. Specimens encountered during this project were few in number, and did not readily fit the description of either of these species, and/or were too small or under-developed to identify with confidence. Numerous microspecies of bramble have been recorded in Ireland, but no attempt was made to distinguish these here - records were entered as *Rubus fruticosus* agg. The genus *Taraxacum* is similarly complex, and was recorded in all cases as *Taraxacum* agg.

A number of pairs of similar species which could not be readily distinguished were encountered. *Viola reichenbachiana* and *V. riviniana* cannot be reliably distinguished on vegetation characters alone (Kelly and Kirby, 1982, Rodwell, 1991). The *Primula* species, *P. veris* and *P. vulgaris*, need to be seen in spring for reliable identification. The two similar species of *Festuca* grasses (*F. ovina* and *F. rubra*) need to be looked at, for the most part, under a stereo-microscope to tell them apart. In many instances they were not recorded to species level in the field, and thus it was decided to amalgamate them. Young, under-developed shoots of *Asperula cynanchica* closely resemble the small straggling shoots of *Galium sterneri*. Therefore close inspection of all material under a

stereo-microscope is desirable. While many specimens were collected (all of these were examined and identified), there were some remaining quadrats from which specimens had not been collected, and so it was necessary to pool records for these two species.

There has, historically, been considerable debate about the identity and status of the all-white orchid with unspotted leaves that can be seen frequently in the Burren. It has been named variously as *Orchis o'kellyi, O. maculata* var. *okellyi, Dactylorhiza fuchsii* var. *o'kellyi,* and *D. fuchsii* subsp. *fuchsii* var. *okellyi* (see, for example, Stelfox, 1924, Webb and Scannell, 1983, Nelson and Walsh, 1991, Webb et al., 1996, Viney, 2003). Stace (1997) does not mention it, but Webb et al. (1996) note it as a variety of *D. maculata* subsp. *fuchsii*. As it is readily distinguished in the field, is has been retained here as a separate entity, using the name *D. fuchsii* var. *okellyi*, following Sayers and Sex (2009).

Other specimens which were not identified to species level due to factors such as damage, small size, developmental stage, etc. are (in decreasing order of frequency in the dataset): *Poaceae* indet., *Orchidaceae* indet., forb indet., *Compositae* indet., *Rosa* sp., *Apiaceae* indet., *Dryopteris* sp., *Polypodium* sp., *Cirsium* sp., *Sonchus* sp., *Cardamine* sp., *Hypericum* sp., *Epilobium* sp., *Rumex* sp., *Veronica* sp., *Dactylorhiza* sp. and *Poa* sp.

Finally, there are a number of vernal species which, if present, are likely to have been significantly under-recorded (or missed) within this dataset due to the timing of sampling, including *Anemone nemorosa, Conopodium majus, Hyacinthoides non-scripta* and *Ranunculus ficaria* (Kirby, 1981, Kelly and Kirby, 1982).

Analytical approach

Sørensen coefficient of similarity

To measure the extent to which the suites of species from the three different habitats were similar, the Sørensen coefficient (S_s) was used (Kent and Coker, 1992). The data were converted to presence/absence, and only data from 2006 were used. Values range from 0 (no species in common) to 100 (species lists exactly similar).

$$S_s = \frac{2a}{2a + b + c}$$

a = number of species common to both lists
b = number of species in first list
c = number of species in second list

MAVIS – NVC classifications and Ellenberg indicator values

Modular Analysis of Vegetation Information System (MAVIS) Plot Analyzer v. 1 (Smart, 2000) is a computer programme which can be used to make links between vegetation data collected in the field and a number of different classification systems. Using MAVIS allows objective comparisons to be made. In this case, the data were compared to the National Vegetation Classification (NVC), a system devised for Britain (Rodwell, 1991, 1992).

The Czekanowski (or Sørensen) method is used to calculate matching coefficients between the inputted data and already existing data, and the top ten coefficients are given in the MAVIS output. MAVIS has been relatively widely used both in Britain (e.g. Corney et al., 2004, Kirby et al., 2005, De Vere, 2007, Corney et al., 2008) and in Ireland (e.g. O'Neill et al., 2009, Parr et al., 2009b, Sullivan et al., 2010).

MAVIS classifies data across the full range of NVC vegetation types – something that is very valuable when data collected do not obviously fall into a particular NVC category. A number of cautionary notes apply, however. Kirby (2003a) points out that the scarcity and/or absence of some key species from Ireland may be troublesome. An obvious example is that of *Mercurialis perennis*, a very common species in Britain, and one which is used in the definition and separation of a number of woodland vegetation types. In Ireland, however, this species is very rare (Webb et al., 1996), and in most of the areas where it does exist, there are doubts about its native status (Webb and Scannell, 1983, Reynolds, 2002). Additionally, the presence of some anomalous species, especially in combination with the absence of some key species, may mean that the 'correct' community does not get the highest score. To avoid this being a significant issue, all outputs from MAVIS (and similar programmes) should be assessed and interpreted carefully by an ecologist. Finally, differences between Ireland and Britain, such as in climate, are likely to mean that correspondence with communities will not be exact, and this too must be borne in mind when interpreting outputs.

MAVIS was also used to generate average 'Ellenberg values' for fertility, wetness and light for each quadrat. Ellenberg values are scores assigned to individual plant species as indicators of certain environmental factors. Ellenberg values were originally published as lists which related mainly to central European species (Ellenberg et al., 1991), but these have been updated by a re-calibration of the original scores using British data by Hill et al. (1999). Using many species together (e.g. a quadrat list), rather than taking values for individual species, gives a better approximation of the actual environmental conditions (Diekmann, 2003). The Ellenberg light (L) scale ranges from 1 (deep shade) to 9 (plants grow in full light), the moisture or wetness (F) scale ranges from 1 (extreme dryness) to 12 (submerged plant) and the fertility or nitrogen (N) scale is from 1 (extremely infertile) to 9 (extremely rich/fertile) (Hill et al., 2004).

The data were also related to Grime's triangular C-S-R model, which classifies plants in relation to one of three kinds of ecological strategy (e.g. Grime et al., 1988):

C = competitors (plants which thrive in conditions of low stress and low disturbance),

S = stress-tolerators (species which do well in areas with high stress but low disturbance), and

R = ruderals (species which cope well with disturbance, but not stress).

Non-metric Multidimensional Scaling (NMS)

Vegetation community data were analysed using NMS (PC-ORD 5; McCune and Mefford, 2006). As detailed in Chapter Two, NMS is an ordination technique often used with ecology and community data. It is well suited to extracting patterns from data which are often non-normal and 'zero-heavy' (McCune and Grace, 2002, Perrin et al., 2006b, Nekola, 2010). All data were screened using outlier analysis. In general, species data were also added to the second matrix and overlaid on the ordinations. Spearman's rank correlation coefficients were calculated between the variables and the scores from the ordination axes using SPSS (PASW Statistics (SPSS) Version 18.0.0, 2009).

ANOVA

General linear ANOVA models were constructed to test for differences in changes in numbers of plant species between 2006 and 2008. Using this method, effects can be assigned as fixed or random – random are those which introduce variance/noise into the dataset, but in whose actual values we are not specifically interested (except to account for the variance that they contribute). The factors used were 'habitat' (fixed), 'site' (nested within habitat, random) and 'treatment' (fixed). Tukey Simultaneous Tests were used for post-hoc analysis. Before computations, data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test), and transformed where necessary. All analyses were carried out in Minitab 13.3 (Minitab Inc, 2000).

'Wilcoxon signed ranks' test

In order to assess if there were significant differences in abundances of species between the two study years, (and also in some of the variables measured) the 'Wilcoxon signed ranks' test was employed (Dytham, 2003). This is the non-parametric equivalent of a paired t-test. Again, analyses were conducted in Minitab 13.3.

Results

The vegetation data - overview

A total of 240 vegetation quadrats, each 2 x 2m, were surveyed for vascular plants (120 in 2006, and all re-surveyed in 2008). These were located in twelve sites in the Burren, five within each 20 x 20m fenced or unfenced/control plot. There were 171 species recorded from the quadrats (data from both years combined). Plants were also recorded from the entire plot (i.e. *outside* the quadrats but *inside* the 20 x 20m plot), and this added an additional 40 species to the overall list. All species which occurred in at least two sites are listed in Table 16 (total = 127 species). At the top of the table are the most widespread species in the dataset, occurring in all three habitat types - *Corylus avellana, Crataegus monogyna* and *Pteridium aquilinum*. Hazel was also the most common species in the dataset overall.

The numbers of vascular plant species recorded in each habitat in 2006 are shown in Table 15. The woodlands had the lowest numbers of species, and also the lowest diversity index. The number of species recorded per site varied from a minimum of 33 at one of the woodland sites (Ballyclery), to a maximum of 102 in one of the grassland sites (Caher).

Table 15 Numbers of vascular plant species recorded from each of the three habitat types in 2006.

	Total no. spp recorded per habitat	**Simpson's Diversity Index**	**Mean no. spp (± S.E.) per site**	**Range in no. spp per 20 x 20m plot**	**Range in no. spp per 2 x 2m quadrat**
Woodland	73	0.56	39.5 ± 3.2	23 - 40	3 - 20
Scrub	142	0.79	84.7 ± 3.7	65 - 75	8 - 40
Grassland	130	0.91	73.5 ± 10.6	43 - 91	21 - 49

To investigate the degree of similarity in the suites of species found at each of the three habitat types Sørensen coefficients were calculated. The woodland and grassland habitats were the least similar (S_s = 0.22), while scrub and grasslands were the most similar (S_s = 0.42). Woodland and scrub had an intermediate Sørensen value of 0.30.

Table 16 Plant species, arranged by habitat affinity (only species found in ≥2 sites shown). Data further ordered by overall frequency of occurrence, and then within each 'plant group'. [W=woodland, S=scrub, G=grassland; plant groups defined in Table 12.]

		Plant group	Frequency in woodland sites (n=4)	Frequency in scrub sites (n=4)	Frequency in grassland sites (n=4)	Frequency in total dataset (n=12)	% Frequency in total dataset
All three habitats	*Corylus avellana*	W	4	4	4	**12**	**100**
	Crataegus monogyna	W	4	4	4	**12**	**100**
	Pteridium aquilinum	F	4	4	4	**12**	**100**
	Rubus fruticosus agg.	LW	4	4	3	**11**	**92**
	Taraxacum agg.	FO	4	4	3	**11**	**92**
	Viola riv/reich	FO	4	4	3	**11**	**92**
	Poaceae indet.	G	3	4	4	**11**	**92**
	Hedera helix	LW	4	4	2	**10**	**83**
	Hypericum pulchrum	FO	3	4	3	**10**	**83**
	Agrostis sp.	G	2	4	4	**10**	**83**
	Anthoxanthum odoratum	G	2	4	4	**10**	**83**
	Rosa spinosissima	LW	2	4	3	**9**	**75**
	Potentilla sterilis	FO	4	3	2	**9**	**75**
	Veronica chamaedrys	FO	3	4	2	**9**	**75**
	Sesleria caerulea	G	3	4	2	**9**	**75**
	Carex flacca	C	3	4	2	**9**	**75**
	Geranium robertianum	FO	3	3	2	**8**	**67**
	Solidago virgaurea	FO	2	4	2	**8**	**67**
	Forb indet.	U	2	2	2	**6**	**50**
	Asplenium ruta-muraria	F	2	2	2	**6**	**50**
W ONLY	*Ilex aquifolium*	W	4			**4**	**33**
	Asplenium trichomanes	F	4			**4**	**33**
	Euonymus europaeus	W	3			**3**	**25**
	Fraxinus excelsior	W	3			**3**	**25**
	Rosa indet.	LW	3			**3**	**25**
	Geum urbanum	FO	3			**3**	**25**
	Oxalis acetosella	FO	3			**3**	**25**
	Sorbus aucuparia	W	2			**2**	**17**
	Viburnum opulus	W	2			**2**	**17**
	Circaea lutetiana	FO	2			**2**	**17**
	Hypericum androsaemum	FO	2			**2**	**17**
	Mycelis muralis	FO	2			**2**	**17**
	Sanicula europaea	FO	2			**2**	**17**
	Carex sylvatica	C	2			**2**	**17**
	Asplenium scolopendrium	F	2			**2**	**17**
	Dryopteris affinis	F	2			**2**	**17**
	Dryopteris filix-mas	F	2			**2**	**17**
	Dryopteris indet.	F	2			**2**	**17**
W+S	*Prunus spinosa*	W	4	4		**8**	**67**
	Epipactis helleborine	FO	4	4		**8**	**67**
	Primula vulgaris	FO	4	3		**7**	**58**
	Brachypodium sylvaticum	G	3	4		**7**	**58**
	Arum maculatum	FO	3	2		**5**	**42**
	Conopodium majus	FO	3	2		**5**	**42**
	Fragaria vesca	FO	2	3		**5**	**42**
	Vicia sepium	FO	3	2		**5**	**42**
	Lonicera periclymenum	LW	2	2		**4**	**33**
S ONLY	*Teucrium scorodonia*	FO		4		**4**	**33**
	Trifolium pratense	FO		4		**4**	**33**
	Rubus saxatilis	LW		3		**3**	**25**
	Agrimonia eupatoria	FO		2		**2**	**17**
	Antennaria dioica	FO		2		**2**	**17**
	Cardamine flexuosa	FO		2		**2**	**17**
	Carlina vulgaris	FO		2		**2**	**17**
	Dactylorhiza fuchsii	FO		2		**2**	**17**
	Filipendula vulgaris	FO		2		**2**	**17**
	Hypericum indet.	FO		2		**2**	**17**
	Lapsana communis	FO		2		**2**	**17**
	Ranunculus bulbosus	FO		2		**2**	**17**
	Rubia peregrina	FO		2		**2**	**17**

Table 16 continued

		Plant group	Frequency in woodland sites (n=4)	Frequency in scrub sites (n=4)	Frequency in grassland sites (n=4)	Frequency in total dataset (n=12)	% Frequency in total dataset
S+G	*Achillea millefolium*	FO		4	4	**8**	**67**
	Centaurea nigra	FO		4	4	**8**	**67**
	Cerastium fontanum	FO		4	4	**8**	**67**
	Galium verum	FO		4	4	**8**	**67**
	Hypochaeris radicata	FO		4	4	**8**	**67**
	Lotus corniculatus	FO		4	4	**8**	**67**
	Orchidaceae indet.	FO		4	4	**8**	**67**
	Pilosella officinarum	FO		4	4	**8**	**67**
	Plantago lanceolata	FO		4	4	**8**	**67**
	Prunella vulgaris	FO		4	4	**8**	**67**
	Succisa pratensis	FO		4	4	**8**	**67**
	Trifolium repens	FO		4	4	**8**	**67**
	Avenula pubescens	G		4	4	**8**	**67**
	Briza media	G		4	4	**8**	**67**
	Cynosurus cristatus	G		4	4	**8**	**67**
	Dactylis glomerata	G		4	4	**8**	**67**
	Festuca ovina/rubra	G		4	4	**8**	**67**
	Holcus lanatus	G		4	4	**8**	**67**
	Asperula cynanchica/ Galium sterneri	FO		4	3	**7**	**58**
	Campanula rotundifolia	FO		4	3	**7**	**58**
	Euphrasia agg.	FO		3	4	**7**	**58**
	cf. *Leontodon* indet.	FO		3	4	**7**	**58**
	Linum catharticum	FO		4	3	**7**	**58**
	Potentilla erecta	FO		4	3	**7**	**58**
	Ranunculus acris	FO		3	4	**7**	**58**
	Ranunculus repens	FO		3	4	**7**	**58**
	Thymus polytrichus	FO		4	3	**7**	**58**
	Torilis japonica	FO		3	4	**7**	**58**
	Koeleria macrantha	G		4	3	**7**	**58**
	Geranium sanguineum	FO		4	2	**6**	**50**
	Gymnadenia conopsea	FO		3	3	**6**	**50**
	Lathyrus pratensis	FO		2	4	**6**	**50**
	Leucanthemum vulgare	FO		3	3	**6**	**50**
	Luzula campestris	J		3	3	**6**	**50**
	Carex caryophyllea	C		4	2	**6**	**50**
	Carex panicea	C		4	2	**6**	**50**
	Carex indet.	C		2	4	**6**	**50**
	Calluna vulgaris	LW		3	2	**5**	**42**
	Hypericum maculatum	FO		2	3	**5**	**42**
	Orchis mascula	FO		3	2	**5**	**42**
	Plantago maritima	FO		3	2	**5**	**42**
	Lolium perenne	G		3	2	**5**	**42**
	Bellis perennis	FO		2	2	**4**	**33**
	Filipendula ulmaria	FO		2	2	**4**	**33**
	Polygala vulgaris	FO		2	2	**4**	**33**
	Senecio jacobaea	FO		2	2	**4**	**33**
	Arrhenatherum elatius	G		2	2	**4**	**33**
	Molinia caerulea	G		2	2	**4**	**33**
	Phleum pratense	G		2	2	**4**	**33**
G ONLY	*Alchemilla filicaulis*	FO			3	**3**	**25**
	Coeloglossum viride	FO			3	**3**	**25**
	Odontites vernus	FO			3	**3**	**25**
	Rhinanthus minor	FO			3	**3**	**25**
	Rumex acetosa	FO			3	**3**	**25**
	Vicia cracca	FO			3	**3**	**25**
	Centaurium erythraea	FO			2	**2**	**17**
	Daucus carota	FO			2	**2**	**17**
	Hypericum perforatum	FO			2	**2**	**17**
	Lathyrus linifolius	FO			2	**2**	**17**
	Parnassia palustris	FO			2	**2**	**17**
	Pedicularis sylvatica	FO			2	**2**	**17**
	Pimpinella saxifraga	FO			2	**2**	**17**
	Potentilla anserina	FO			2	**2**	**17**
	Primula veris	FO			2	**2**	**17**
	Scorzoneroides autumnalis	FO			2	**2**	**17**
	Umbelliferae indet.	FO			2	**2**	**17**
	Carex pulicaris	C			2	**2**	**17**

Correspondence with NVC classifications

The MAVIS Plot Analyser (Smart, 2000) was used as a tool to objectively identify the closest NVC category for the vegetation found at each site (Table 17 and Table 18). The grasslands were the most clear-cut, with all sites emerging as MG5 (*Cynosurus cristatus – Centaurea nigra*) grassland, or a sub-community of this. Correspondences were quite high (50 - 60%). The woodlands too produced relatively consistent results, with repeated matching to W8d (*Fraxinus excelsior – Acer campestre – Mercurialis perennis*) woodland. One site classified as W10c (*Quercus robur – Pteridium aquilinum – Rubus fruticosus*) woodland. Correspondences were lower, at approximately 30-40%.

The scrub, not surprisingly, produced more complex results (Table 18). Because of this, the data were entered into MAVIS a second time, with the 'woody' and 'grassy' quadrats separated at each site (refer to the opening section of Chapter One for the rationale behind this split). For three of the four scrub sites the grassy quadrats contained elements of MG5, which relates well with the findings from the grassland sites. CG2 (*Festuca ovina – Avenula pratensis* grassland) was also common in the grassy elements. This vegetation type has been referred to by Jeffrey (2003) as possibly occurring in the Burren. The woody portions posed a larger challenge – surprisingly, not a single NVC woodland or scrub category emerged. Instead, a mix of grassland types were produced: mesotrophic (MG1, *Arrhenatherum elatius* coarse grassland and MG5, *Cynosurus cristatus – Centaurea nigra* grassland) and calcareous (CG2, *Festuca ovina – Avenula pratensis* grassland, CG4, *Brachypodium pinnatum* grassland and CG8, *Sesleria albicans – Scabiosa columbaria* grassland).

The results for the Knockans site were inconsistent, and should therefore be treated with caution.

Possible issues with using MAVIS on Irish plant datasets are dealt with in the discussion.

Table 17 The two closest NVC categories for each of the woodland and grassland sites, as generated by the MAVIS programme.

Habitat	Site	Closest NVC categories	% correspondence
Woodland	Ballyclery	**W8d** - *Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland, *Hedera helix* sub-community	34.82
		W21c - *Crataegus monogyna – Hedera helix* scrub, *Brachypodium sylvaticum* sub-community	29.85
	Glencolumbkille	**W8d** - *Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland, *Hedera helix* sub-community	40
		W21c - *Crataegus monogyna – Hedera helix* scrub, *Brachypodium sylvaticum* sub-community	36.71
	Glenquin	**W8d** - *Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland, *Hedera helix* sub-community	38.49
		W8e - *Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland, *Geranium robertianum* sub-community	35.29
	Gortlecka	**W10c** - *Quercus robur – Pteridium aquilinum – Rubus fruticosus* woodland, *Hedera helix* sub-community	36.68
		W8d - *Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland, *Hedera helix* sub-community	33.31
Grassland	Caher	**MG5c** - *Cynosurus cristatus – Centaurea nigra* grassland, *Danthonia decumbens* sub-community	50.77
		MG5a - *Cynosurus cristatus – Centaurea nigra* grassland, *Lathyrus pratensis* sub-community	49.62
	Gregan	**MG5** - *Cynosurus cristatus – Centaurea nigra* grassland	50.87
		MG5a - *Cynosurus cristatus – Centaurea nigra* grassland, *Lathyrus pratensis* sub-community	50.16
	Kilcorkan	**MG5a** - *Cynosurus cristatus – Centaurea nigra* grassland, *Lathyrus pratensis* sub-community	60.56
		MG5 - *Cynosurus cristatus – Centaurea nigra* grassland	59.08
	Slieve Carran	**MG5c** - *Cynosurus cristatus – Centaurea nigra* grassland, *Danthonia decumbens* sub-community	51.56
		MG5b - *Cynosurus cristatus – Centaurea nigra* grassland, *Galium verum* sub-community	51.2

Table 18 The two closest NVC categories for the scrub sites (as generated by MAVIS), with each site additionally split into its 'woody' and 'grassy' components.

Site	Closest NVC categories (with all quadrats from each site included)	% correspondence	Site (split into 'woody' & 'grassy')	Closest NVC categories (with sites split into 'woody' and 'grassy' elements) [n = number of 2x2m quadrats]	% correspondence
Carran	**MG1 -** *Arrhenatherum elatius* coarse grassland	41.07	Carran Woody (n=8)	**MG1 -** *Arrhenatherum elatius* coarse grassland	38.54
	MG1d - *Arrhenatherum elatius* coarse grassland, *Pastinaca sativa* sub-community	40.51		**MG1d -** *Arrhenatherum elatius* coarse grassland, *Pastinaca sativa* sub-community	37.97
			Carran Grassy (n=2)	**MG5c -** *Cynosurus cristatus – Centaurea nigra* grassland, *Danthonia decumbens* sub-community	48.87
				MG5a - *Cynosurus cristatus – Centaurea nigra* grassland, *Lathyrus pratensis* sub-community	46.99
Knockans*	**CG3B -** *Bromus erectus* grassland, *Centaurea nigra* sub-community	43.91	Knockans Woody (n=6)	**H6a -** *Erica vagans – Ulex europaeus* heath, typical sub-community	35.63
	CG2 - *Festuca ovina – Avenula pratensis* grassland	43.13		**CG4 -** *Brachypodium pinnatum* grassland	33.33
				CG4a - *Avenula pratensis – Thymus praecox* sub-community	31.08
			Knockans Grassy (n=4)	**CG2c -** *Festuca ovina – Avenula pratensis* grassland, *Holcus lanatus – Trifolium repens* sub-community	45.92
				MG5b - *Cynosurus cristatus – Centaurea nigra* grassland, *Galium verum* sub-community	44.85
Rannagh	**MG5a -** *Cynosurus cristatus – Centaurea nigra* grassland, *Lathyrus pratensis* sub-community	47.12	Rannagh Woody (n=4)	**MG1e -** *Arrhenatherum elatius* coarse grassland, *Centaurea nigra* sub-community	36.14
	MG5c - *Cynosurus cristatus – Centaurea nigra* grassland, *Danthonia decumbens* sub-community	46.45		**MG5a -** *Cynosurus cristatus – Centaurea nigra* grassland, *Lathyrus pratensis* sub-community	35.07
			Rannagh Grassy (n=6)	**MG5c -** *Cynosurus cristatus – Centaurea nigra* grassland, *Danthonia decumbens* sub-community	46.93
				MG5a - *Cynosurus cristatus – Centaurea nigra* grassland, *Lathyrus pratensis* sub-community	45.04
Roo	**CG2c -** *Festuca ovina – Avenula pratensis* grassland, *Holcus lanatus – Trifolium repens* sub-community	45.54	Roo Woody (n=4)	**CG2 –** *Festuca ovina – Avenula pratensis* grassland	37.94
	CG2 - *Festuca ovina – Avenula pratensis* grassland	45.11		**CG8b -** *Sesleria albicans – Scabiosa columbaria* grassland, *Avenula pratensis* sub-community	35.81
			Roo Grassy (n=6)	**CG2c –** *Festuca ovina – Avenula pratensis* grassland, *Holcus lanatus – Trifolium repens* sub-community	46.24
				CG2 - *Festuca ovina – Avenula pratensis* grassland	44.56

* The results generated for this site by MAVIS were mixed and inconsistent, and so should be treated with caution. See discussion for more.

Rare/notable species

A number of species with restricted distributions within Ireland were recorded during this survey. Some, such as *Rosa spinosissima*, were extremely common in the dataset – this species was found at eleven of the twelve study sites. This species is described as being frequent near the sea, but rather rare elsewhere (Webb et al., 1996). *Sesleria caerulea* was present at nine of the twelve sites. This species is locally abundant in the west of Ireland from Clare to south Donegal, rare in the centre of the country and unknown elsewhere. Species such as *Asperula cynanchica, Epipactis helleborine, Galium sterneri* and *Geranium sanguineum* are also locally frequent in the mid-west of the country but rare or unknown elsewhere (Webb et al., 1996, Preston et al., 2002a), and occurred frequently at the study sites. Other notable species which are largely confined to the limestone region in the west of Ireland (often centred on the Burren) are: *Antennaria dioica, Dactylorhiza fuchsii* var. *okellyi* and *Dryas octopetala*.

Epipactis atrorubens and *Filipendula vulgaris* are two species with extremely restricted distributions in Ireland. The former was recorded as a single record from just one site; the latter had multiple records from two sites. *Filipendula vulgaris* is remarkable in that the only area from which it is known on the island of Ireland is a small area of the Burren, just west of Gort. In this area it is quite frequent. *E. atrorubens* also has a very limited distribution – being found only in Clare and Galway (Preston et al., 2002a).

A number of species were recorded which are generally rare or of local distribution in Ireland: *Orobanche alba* (a species of very local distribution), *Thalictrum minus* (becoming increasingly rare in Ireland) and *Coeloglossum viride* (this was recorded at five of the study sites) (it is described as 'fairly rare, but easily overlooked', Webb et al., 1996, and as 'local' in Sayers and Sex, 2009).

Perrin and Daly (2010) list 29 species of vascular plants which they propose as ancient woodland indicators in Ireland. Sixteen of these species were found during this survey (Table 19). A number of additional species have been highlighted by other authors as being good candidates for ancient woodland indicator status. The species listed by Rackham (2003) and Kirby (2004b) which were found during this survey are presented in Table 20. Among the more notable of these is *Melica uniflora*, which was recorded from the Glencolumbkille site.

None of the species in the dataset is listed as protected on the Flora Protection Order (1999). One species is listed as 'Vulnerable' in the Red Data Book for vascular plants (Curtis and McGough, 1988) – *Filipendula vulgaris*. A status of 'Vulnerable' means that it was not considered endangered (at the time of compilation of the list), but could become so if its habitat is damaged in the future. Two of the plants found during the survey are protected species in Northern Ireland (*Dryas*

octopetala and *Primula veris*). Only two alien species were recorded during the survey: *Lonicera nitida* and *Mycelis muralis*.

Table 19 Putative ancient woodland indicator species in Ireland, and number of occurrences at study sites (data includes records from 2006 and 2008).

Ancient woodland indicator species in Ireland (Perrin and Daly, 2010)	No. woodland sites	No. scrub sites	No. grassland sites
Ajuga reptans	1	-	-
Allium ursinum	1	-	-
Anemone nemorosa	-	1	-
Arbutus unedo	-	-	-
Cardamine flexuosa	1	2	-
Carex sylvatica	2	-	-
Conopodium majus	4	2	2
Corylus avellana	4	4	4
Dryopteris aemula	-	-	-
Euonymus europaeus	4	2	-
Euphorbia hyberna	-	-	-
Galium odoratum	1	-	-
Geum rivale	-	-	1
Glechoma hederacea	-	-	-
Hyacinthoides non-scripta	-	-	-
Hypericum androsaemum	2	-	-
Luzula sylvatica	-	-	-
Lysimachia nemorum	1	-	-
Malus sylvestris	-	-	-
Oxalis acetosella	3	1	-
Populus tremula	-	-	-
Potentilla sterilis	4	3	2
Quercus petraea	-	-	-
Ranunculus ficaria	-	-	-
Rumex sanguineus	1	-	-
Silene dioica	-	-	-
Stellaria holostea	-	-	-
Ulmus glabra	-	-	-
Veronica montana	2	-	-

Table 20 Additional species found during this survey which are listed by other authors (Rackham, 2003, Kirby, 2004b) as putative ancient woodland indicators but which are not found on the Irish list (given in Table 19).

	Affinity with ancient woodland (Rackham, 2003)	Number of occurrences on lists for 13 regions of Britain (Kirby, 2004b)	Number of occurrences in this survey*
Melica uniflora	Strong	12	1 (1W)
Melampyrum pratense	Strong	10	1 (1S)
Viola reichenbachiana	Weak	10	5** (4W, 1S)
Epipactis helleborine	Strong	8	9 (4W, 4S, 1G)
Lathyrus linifolius	Strong	8	5 (1W, 1S, 3G)
Orchis mascula	Moderate	8	6 (4S, 2G)
Primula vulgaris	Weak	8	9 (4W, 3S, 2G)

* W = woodland site, S = scrub sites, G = grassland sites.

** *V. reichenbachiana* was not differentiated from *V. riviniana* in most instances in this study, but it is known to occur at at least five of the study sites.

Vegetation relationships among woodlands, scrub and grasslands

The vegetation data (in this section, only 2006 data included) were explored using NMS in order to investigate patterns in species composition. A large number of variables and species are overlaid on the ordinations, and/or appear in tables of Spearman's rank correlation tables. For convenience and for reference, the abbreviations used for all of these are presented here in Table 21 and Table 22.

Table 21 Abbreviations used, with explanations, for variables overlaid on the ordinations.

Abbreviation	Explanation
%clay	% of clay in the soil
%sand	% of sand in the soil
%silt	% of silt in the soil
Alt	Altitude of the site
Bare ear	Cover of exposed soil
Bare roc	Cover of exposed rock
C	Grime's 'C' category: competitors (derived from 'MAVIS')
CaCO3	% calcium carbonate (gCaCO3/ml) of the soil
Canopy	Cover of all woody species in the canopy
Cattle	Number of cattle per hectare
Cov Fern	Cover of all ferns
Cov Fiel	Cover of grasses + sedges + ferns + rushes + forbs
Cov Gras	Cover of all grasses
Cov Sedg	Cover of all sedges
CovPter	Cover of bracken
DryWgt	Weight of litter removed and dried
Fertility	Average 'Ellenberg score' for fertility (derived from 'MAVIS')
Graz lev	Subjective 4-point scale assessment of grazing level
Light	Average 'Ellenberg score' for light (derived from 'MAVIS')
Litter	Cover of dead/decaying plant material
LOI	% loss-on-ignition of the soil
Low wdy	Cover of all species which are woody, but which are not trees or shrubs
No. spp	Number of plant species per quadrat
pH	pH of the soil
R	Grime's 'R' category: ruderals (derived from 'MAVIS')
S	Grime's 'S' category: stress tolerators (derived from 'MAVIS')
SimpDiv	Simpson's Diversity Index
Slope	Slope of the site
Soil dep	Soil depth (cm)
Total P	Total phosphorus (µg/ml) of the soil
Veg hgt	Average vegetation height (m)
Wetness	Average 'Ellenberg score' for wetness

Table 22 Abbreviations and corresponding full scientific names for those species which are overlaid on some of the following ordinations.

Abbreviation		**Abbreviation**	
Achil mil	*Achillea millefolium*	Koele mac	*Koeleria macrantha*
Agros spp	*Agrostis* spp	Lathy lin	*Lathyrus linifolius*
Alche fil	*Alchemilla filicaulis*	Lathy pra	*Lathyrus pratensis*
Antho odo	*Anthoxanthum odoratum*	Leuca vul	*Leucanthemum vulgare*
Apiac sp	Apiaceae indet.	Linum cat	*Linum catharticum*
Arum mac	*Arum maculatum*	Loliu per	*Lolium perenne*
Asp/Gal	*Asperula cynanchica/Galium sterneri*	Lotus cor	*Lotus corniculatus*
Asple sco	*Asplenium scolopendrium*	Luzul cam	*Luzula campestris*
Avenu pub	*Avenula pubescens*	Molin cae	*Molinia caerulea*
Belli per	*Bellis perennis*	Odont ver	*Odontites vernus*
Brach syl	*Brachypodium sylvaticum*	Orchid	Orchidaceae indet.
Briza med	*Briza media*	Oxali ace	*Oxalis acetosella*
Callu vul	*Calluna vulgaris*	Pilo off	*Pilosella officinarum*
Campa rot	*Campanula rotundifolia*	Pimpi sax	*Pimpinella saxifraga*
Carex car	*Carex caryophyllea*	Plant lan	*Plantago lanceolata*
Carex flac	*Carex flacca*	Plant mar	*Plantago maritima*
Carex pan	*Carex panicea*	Poac sp	Poaceae indet.
Carex sp	*Carex* sp.	Poten ans	*Potentilla anserina*
Carex spp	*Carex* indet.	Poten ere	*Potentilla erecta*
Centa nig	*Centaurea nigra*	Poten ste	*Potentilla sterilis*
Circa lut	*Circaea lutetiana*	Primu vul	*Primula vulgaris*
Compo sp	Compositae indet.	Prune vul	*Prunella vulgaris*
Coryl ave	*Corylus avellana*	Prunu spi	*Prunus spinosa*
Crata mon	*Crataegus monogyna*	Pteri aqu	*Pteridium aquilinum*
Cynos cri	*Cynosurus cristatus*	R acetosa	*Rumex acetosa*
Dacty glo	*Dactylis glomerata*	Ranun acr	*Ranunculus acris*
Daucu car	*Daucus carota*	Ranun rep	*Ranunculus repens*
Epilo mon	*Epilobium montanum*	Rhina min	*Rhinanthus minor*
Epipa hel	*Epipactis helleborine*	Rosa spin	*Rosa spinosissima*
Euphr spp	*Euphrasia* indet.	Rubus fru	*Rubus fruticosus* agg.
Fe ov/ru	*Festuca ovina/ rubra*	Sanic eur	*Sanicula europaea*
Filip ulm	*Filipendula ulmaria*	Scorz aut	*Scorzoneroides autumnalis*
Filip vul	*Filipendula vulgaris*	Senec jac	*Senecio jacobaea*
Fraga ves	*Fragaria vesca*	Sesle cae	*Sesleria caerulea*
Fraxi exc	*Fraxinus excelsior*	Solid vir	*Solidago virgaurea*
Galiu apa	*Galium aparine*	Sorbu auc	*Sorbus aucuparia*
Galiu ver	*Galium verum*	Stell gra	*Stellaria graminea*
Geran rob	*Geranium robertianum*	Succi pra	*Succisa pratensis*
Geran san	*Geranium sanguineum*	Tarax sp	*Taraxacum* agg.
Geum riv	*Geum rivale*	Teucr sco	*Teucrium scorodonia*
Geum urb	*Geum urbanum*	Thymu pol	*Thymus polytrichus*
Gymna con	*Gymnadenia conopsea*	Trifo pra	*Trifolium pratense*
Heder hel	*Hedera helix*	Trifo rep	*Trifolium repens*
Holcu lan	*Holcus lanatus*	Veron cha	*Veronica chamaedrys*
Hyper pul	*Hypericum pulchrum*	Vi riv/rei	*Viola riviniana/reichenbachiana*
Hypoc rad	*Hypochaeris radicata*	Vicia cra	*Vicia cracca*
Ilex aqu	*Ilex aquifolium*	Vicia sep	*Vicia sepium*
Juncu art	*Juncus articulatus*		

Vegetation community relations among the three habitats

Data from all habitats from 2006 were analysed together using a matrix consisting of 120 quadrats and 110 species (species found in ≤2 quadrats were deleted). The resultant ordination solution was two-dimensional, and the total r^2 (i.e. the proportion of the variation explained) was 89%, with 12% relating to axis 1, and 77% relating to axis 2 (Figure 14). The stress was 12.78 and there was an instability of <0.00001 (see section on NMS in Chapter Two for more information on these measures).

The scrub quadrats were split between 'woody' and 'grassy' types, and all four resultant groups separate well on the ordination, indicating that distinct vegetation communities exist in each. The woodland quadrats are the most closely grouped, while the scrub quadrats (both woody and grassy) span the space between the grassland and woodland quadrats.

The most important variables were overlaid using a biplot. Using the default cut-off point of 0.2 for the r^2 value - the value used in deciding which of the variables to display in the biplot - resulted in a large number of variables being plotted. Interpretability was therefore reduced. To make the results clearer, the r^2 cut-off value was raised to 0.35. This produced a more manageable and interpretable suite of the most important variables (Figure 14).

Ellenberg's 'fertility' score, vegetation height and canopy cover were among the most important variables associated with the location of the woodland and woody scrub quadrats along axis 2 of the ordination, while Ellenberg's 'light', cover of field layer and Grime's 'R' category are associated with the grassland and grassy scrub quadrats. Fewer of the inputted variables appear related to axis 1, with the exception perhaps of 'number of species'. It should be remembered, however, that only 12% of the variation in the data is explained by this axis.

The species which were most influential on the spread of the quadrats within the ordination are presented in Figure 15. Again, for clarity and ease of interpretation, the r^2 cut-off value was raised to 0.35. Hazel and ivy are the species most strongly associated with the woodland quadrat positions at the upper end of axis 2, while the grass *Festuca ovina/rubra* is strongly associated with the grassland quadrats at the lower end. The following species appear negatively correlated with axis 1, and so may be important in discerning grassy scrub from grasslands: *Campanula rotundifolia, Carex flacca, C. panicea* and *Sesleria caerulea* (these are not shown in Figure 15 which uses an r^2 cut-off of 0.35, but do appear when $r^2 = 0.2$).

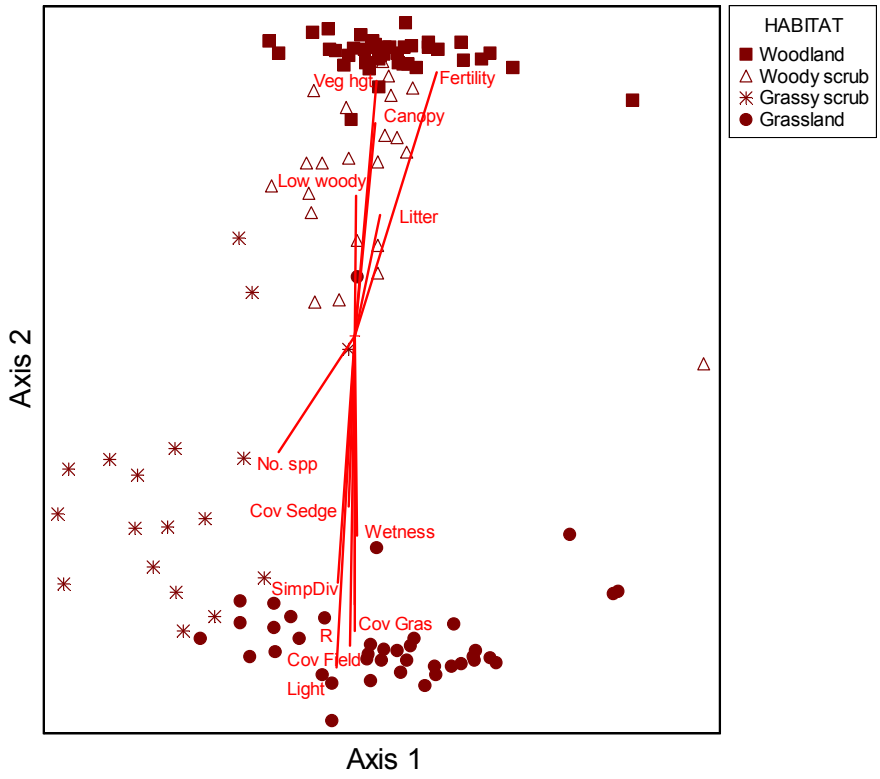


Figure 14 NMS ordination using all quadrats from 2006 (i.e. woodland, scrub and grassland). Each point corresponds to a quadrat and the most influential variables from the second matrix are overlaid. Axis 1 accounts for 12% of the variation in the data, and axis 2, 77%. Refer to Table 21 and Table 22 for explanations of overlay abbreviations.

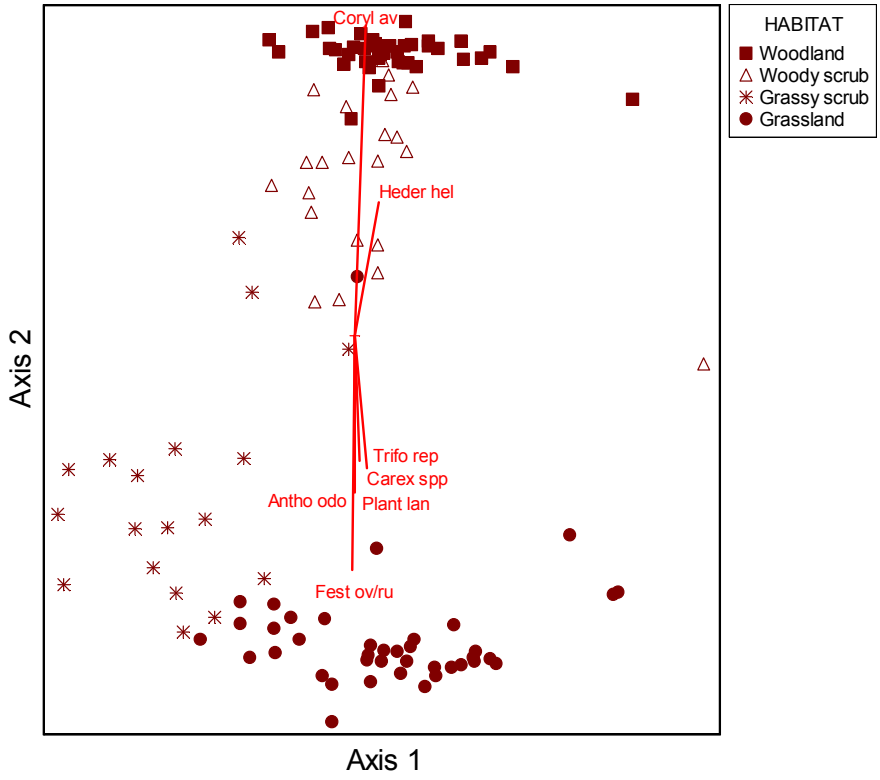


Figure 15 NMS ordination as per Figure 14, but with the most influential species from the second matrix overlaid.

Variation in vegetation composition within each of the three habitat types

In order to look in more detail at the extent of variation within habitats, and at some of the drivers of this variation, vegetation data from each habitat type were analysed separately.

Woodland

This analysis was based on a matrix of 40 quadrats and 33 species. An outlier existed in the data (quadrat Y1S3F1, 3.79 standard deviations from the grand mean). Investigation of the raw data revealed that this quadrat had the lowest cover of hazel of all the woodland quadrats (20%), and the highest cover of blackthorn. It also had among the highest covers of hawthorn. However, as it is a valid representation of the variation present in Burren woodlands, and following trials with this quadrat included and excluded to assess its influence on the dataset as a whole, it was decided to retain it. The total r^2 for the ordination solution was 93%, with 65% on axis 1, and 28% on axis 2. Stress was 12.39 and instability, <0.00001.

The ordination result (Figure 16) illustrates that canopy species had a large influence on the overall vegetation composition of individual quadrats. All species and variables used in the NMS analysis were assessed against their scores on the ordination axes for statistically significant correlations (Spearman's rank correlation coefficients, PASW Statistics (SPSS) Version 18.0.0, 2009) (Table 23, with only those significant at the <0.001 level shown). Axis 1 is primarily a gradient of decreasing light levels, with the photophilous hawthorn at one extreme and the shade-tolerant hazel at the other. Diversity appears to decrease with decreasing light levels. Axis 2 is more difficult to interpret, with both a wetness and grazing level gradient apparent.

Table 23 Variables and species which are strongly significantly correlated with axis 1 and/or axis 2 in Figure 16. Variables and abbreviated species names are explained in Table 21 and Table 22.

Axis 1	Spearman's rank correlation coefficient	p-value	Axis 2	Spearman's rank correlation coefficient	p-value
Crata mon	-.882	<0.001	Heder hel	-.892	<0.001
SimpDiv	-.802	<0.001	Low wdy	-.859	<0.001
Coryl ave	.753	<0.001	Cattle	-.686	<0.001
Light	-.677	<0.001	Graz lev	-.612	<0.001
			Fraxi exc	.602	<0.001
			Wetness	.570	<0.001
			pH	-.558	<0.001

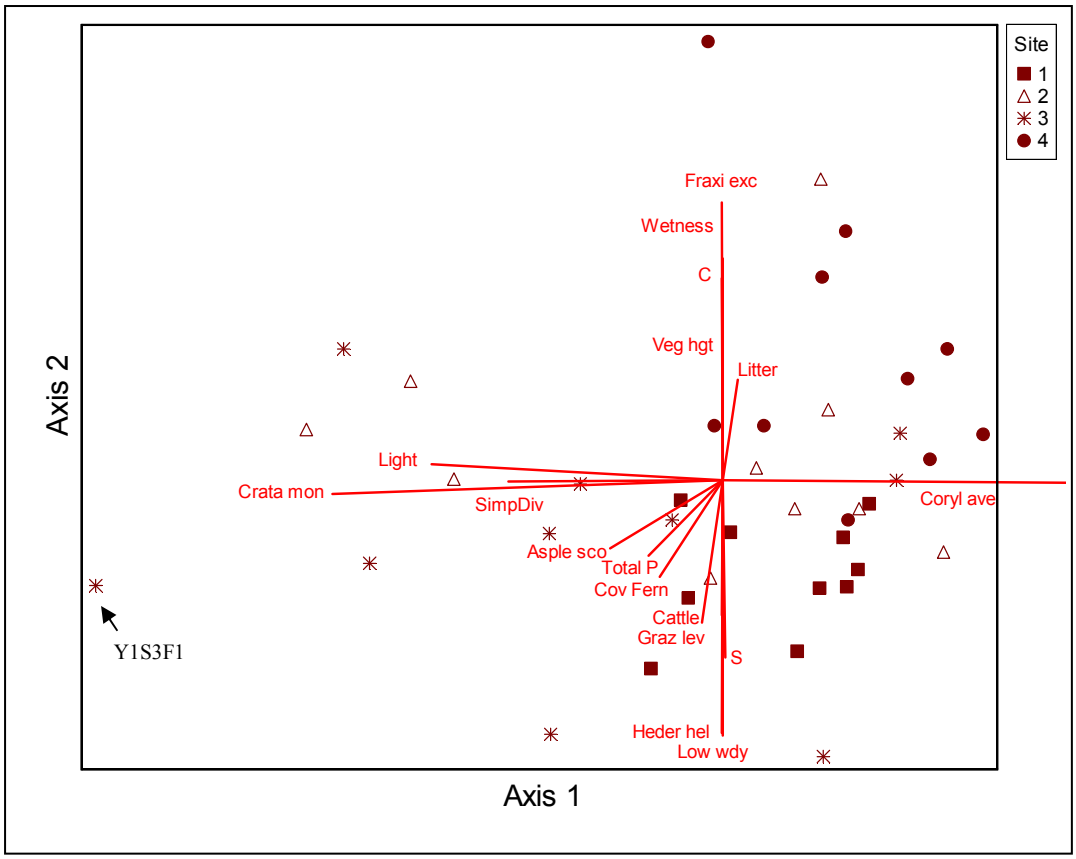


Figure 16 NMS ordination of woodland quadrats from 2006 (n = 40). Each point corresponds to a quadrat and the most influential variables and species from the second matrix are overlaid. Axis 1 accounts for 65% of the variation in the data, and axis 2, 28%. Refer to Table 21 and Table 22 for explanations of the overlay abbreviations. The outlier Y1S3F1 is labelled.

Scrub

When the scrub quadrats were analysed, and coded on the NMS ordination according to whether they were 'woody' or 'grassy' (Figure 17), the distinction between the two groups is clear. Three grassy quadrats plotted with the woody ones, and, on inspection, these were found to have moderately high covers of hazel (35-45% cover). One quadrat (Y1S5C1, from the control plot at the Carran site) appears to be quite different from all the others, although outlier analysis showed that it was not an extreme outlier, and so it was retained. This quadrat was dominated by blackthorn, and had high covers of species which are otherwise uncommon in the dataset, such as *Angelica sylvestris* and *Heracleum sphondylium*. There was also an unusually high cover for bracken in this quadrat. In this ordination solution the total r^2 was 90% (70% associated with axis 1, and 20% with axis 2), stress was 13.46 and instability was <0.00001. The data matrix consisted of 40 quadrats and 74 species.

The quadrats are coded by site in Figure 18, and the most influential variables are overlaid. As detailed above for the woodland result, a raised cut-off value for r^2 (0.35) was used in order to

provide a manageable number of variables for the biplot. For the sake of clarity, the species are overlaid on the ordination separately (Figure 19). Again, a cut-off value of 0.35 was used.

Axis 1, which accounts for the majority of the variation, appears to be a combination of light and fertility gradients, with higher fertility and lower light at the upper end of the axis (Table 24 and Table 25 – note that due to a large number of significant correlations, only those with a significance of $p<0.001$ are shown). The grassy and woody scrub quadrats are separated along this axis, with the woody quadrats being found at the upper end. Hazel and ivy are the species most positively associated with this axis, while a suite of species, including *Plantago lanceolata, Festuca ovina/rubra* and *Carex panicea*, are strongly negatively associated with it.

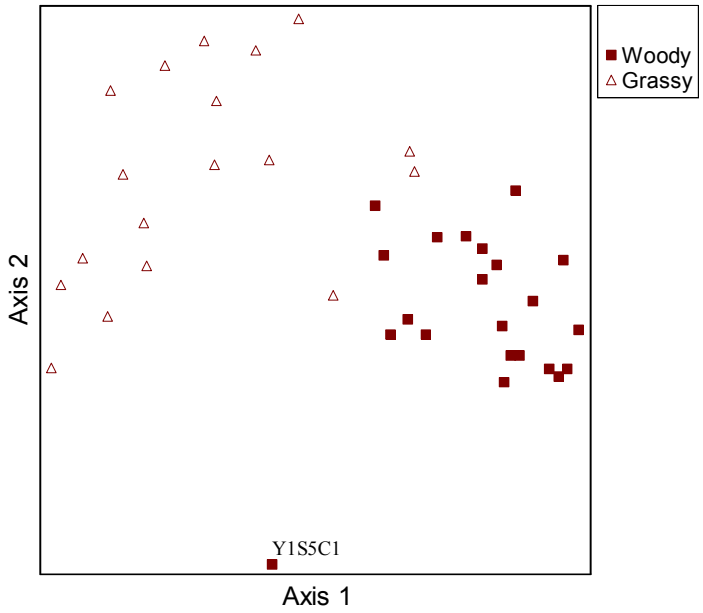


Figure 17 NMS ordination of scrub quadrats from 2006 (n = 40). Axis 1 accounts for 70% of the variation in the data, and axis 2 accounts for 20%. Quadrat Y1S5C1 is labelled as it is a marginal outlier.

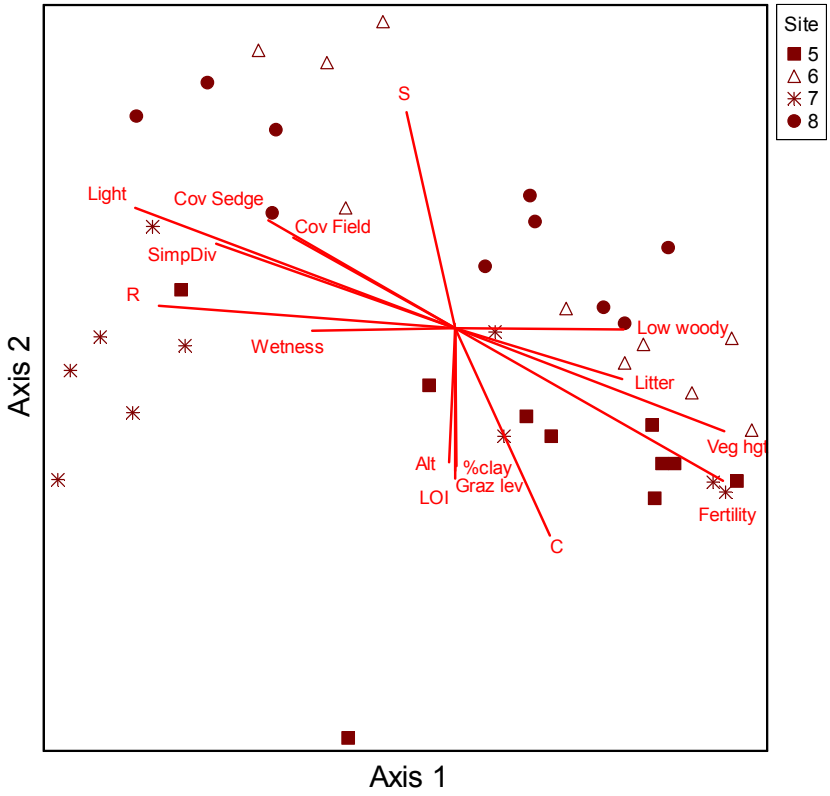


Figure 18 NMS ordination of scrub quadrats from 2006 with the most influential variables overlaid. Axis 1 accounts for 70% of the variation in the data, and axis 2 accounts for 20%. Refer to Table 21 and Table 22 for explanations of the overlay abbreviations.

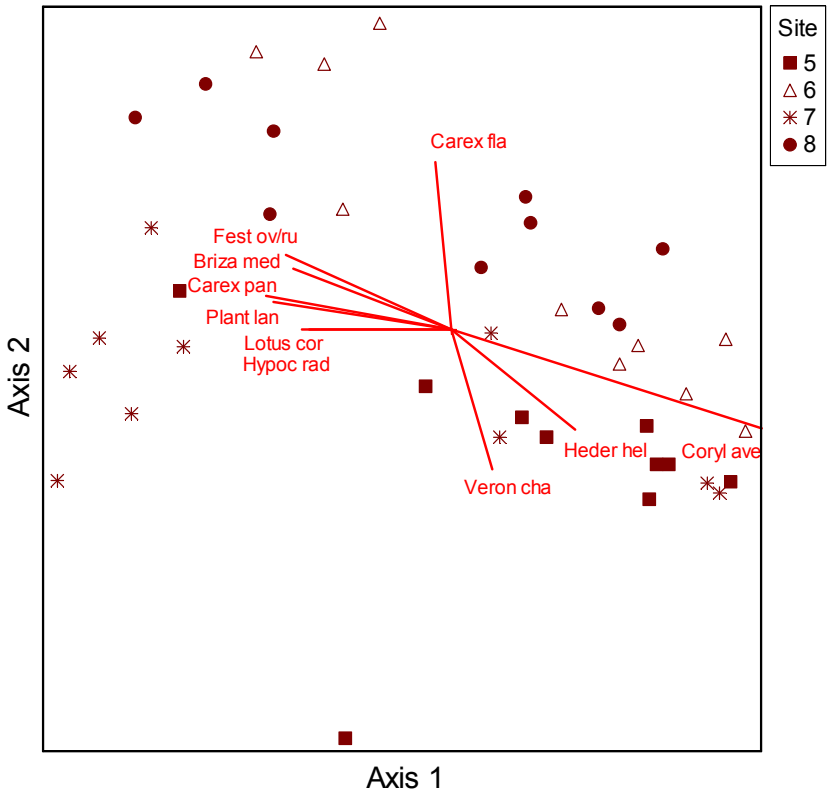


Figure 19 NMS ordination as per Figure 18, but with the most influential species from the second matrix overlaid.

Table 24 Variables which are strongly significantly correlated with axis 1 and/or axis 2 in Figure 18 and Figure 19 (NMS ordinations of scrub quadrat data from 2006). Abbreviated variable names are explained in Table 21.

Axis 1	Correlation Coefficient	p-value	Axis 2	Correlation Coefficient	p-value
Light	-.955	<0.001	Fertility	-.718	<0.001
SimpDiv	-.916	<0.001	LOI	-.705	<0.001
Veg hgt	.903	<0.001	%clay	-.703	<0.001
R	-.892	<0.001	S	.692	<0.001
Fertility	.879	<0.001	Cov Sedg	.685	<0.001
Cov Sedg	-.767	<0.001	Graz lev	-.673	<0.001
Cov Fiel	-.714	<0.001	C	-.664	<0.001
Litter	.693	<0.001	Alt	-.633	<0.001
Low wdy	.685	<0.001	CaCO3	-.622	<0.001
Cov Gras	-.637	<0.001	Light	.593	<0.001
C	.605	<0.001	%silt	.571	<0.001
DryWgt	.549	<0.001	Soil dep	.544	<0.001
Wetness	-.545	<0.001			

Table 25 Species which are strongly significantly correlated with axis 1 and/or axis 2 in Figure 18 and Figure 19 (NMS ordinations of scrub quadrat data from 2006). Abbreviated species names are explained in Table 22.

Axis 1	Correlation Coefficient	p-value	Axis 2	Correlation Coefficient	p-value
Coryl ave	.923	<0.001	Filip vul	.762	<0.001
Plant lan	-.798	<0.001	Carex flac	.718	<0.001
Fe ov/ru	-.770	<0.001	Heder hel	-.701	<0.001
Carex pan	-.762	<0.001	Geran rob	-.646	<0.001
Lotus cor	-.759	<0.001	Rosa spin	.645	<0.001
Galiu ver	-.750	<0.001	Veron cha	-.619	<0.001
Briza med	-.733	<0.001	Poten ere	.608	<0.001
Cynos cri	-.711	<0.001	Coryl ave	-.593	<0.001
Hypoc rad	-.708	<0.001	Geran san	.587	<0.001
Heder hel	.706	<0.001	Galiu ver	.573	<0.001
Trifo rep	-.680	<0.001	Trifo pra	.570	<0.001
Pilo off	-.612	<0.001	Epilo mon	-.564	<0.001
Poten ere	-.604	<0.001	Fe ov/ru	.560	<0.001
Succi pra	-.594	<0.001	Antho odo	.557	<0.001
Antho odo	-.588	<0.001	Briza med	.531	<0.001
Prune vul	-.579	<0.001			
Achil mil	-.574	<0.001			
Trifo pra	-.558	<0.001			
Thymu pol	-.544	<0.001			
Loliu per	-.529	<0.001			

Grassland

The grassland ordination returned a stress level of 14.87 and an instability of <0.00001. The solution explained 84% of the variation in the data (r^2 on axis 1 was 31% and on axis 2 it was 53%). The matrix consisted of 40 quadrats and 58 species. The four study sites separated quite clearly on the ordination diagram, indicating relatively distinct species compositions. The variables and species most associated with axis 1 are given in Table 26. Due to the high numbers of correlated variables and species, only those significant at the <0.001 level are presented. None of the variables were correlated with axis 2 at a significance level of <0.001.

Slieve Carran (site 12) appears to be characterised by high sedge cover. Kilcorkan (site 11) quadrats are associated with high covers of the species *Centaurea nigra* and *Trifolium repens*, as well as high 'R' values. Site 10, Gregan, was the most heterogeneous site, showing quite a degree of spread along axis 2. Taller vegetation, higher % LOI, % sand, higher fertility (Ellenberg scores) and the occurrence of species such as *Dactylis glomerata, Filipendula ulmaria, Koeleria macrantha* and *Sesleria caerulea* combine to mark out this site as distinct from the others. Quadrats from site 9 (Caher) are generally species rich, with higher covers of low woody species and bare rock than those from other sites (these variables were evident at $r^2 = 0.2$).

Table 26 Variables and species which are strongly significantly correlated with axis 1 in Figure 20 and Figure 21 (NMS ordinations of grassland data from 2006). Variables and abbreviated species names are explained in Table 21 and Table 22. None of the variables were correlated with axis 2 at a significance level of <0.001.

Axis 1	Correlation Coefficient	p-value
Centa nig	.912	<0.001
R	.811	<0.001
LOI	-.762	<0.001
Filip ulm	-.759	<0.001
Veg hgt	-.714	<0.001
Trifo rep	.672	<0.001
Pimpi sax	.658	<0.001
Sesle cae	-.642	<0.001
Alt	-.630	<0.001
Bare roc	-.580	<0.001
No. spp	-.568	<0.001
Antho odo	.565	<0.001
Thymu pol	-.563	<0.001
Koele mac	-.554	<0.001
Carex spp	.527	<0.001
Cov Sedg	.527	<0.001

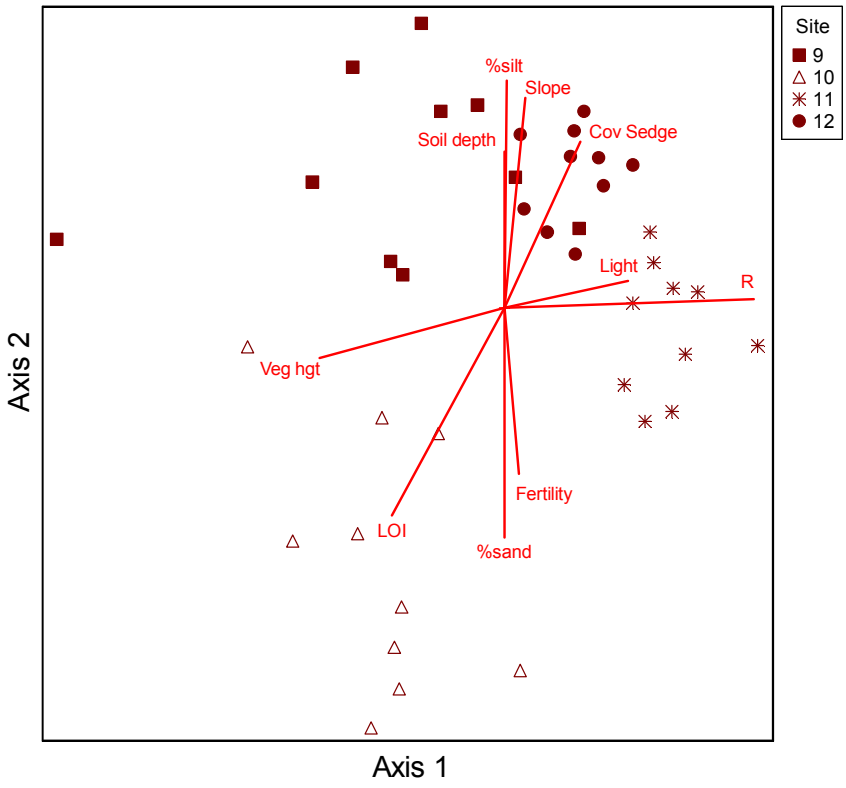


Figure 20 NMS ordination of grassland quadrats from 2006 (n = 40), with the most influential variables from the second matrix overlaid. Axis 1 accounts for 31% of the variation in the data, and axis 2, 53%. Refer to Table 21 and Table 22 for explanations of the overlay abbreviations.

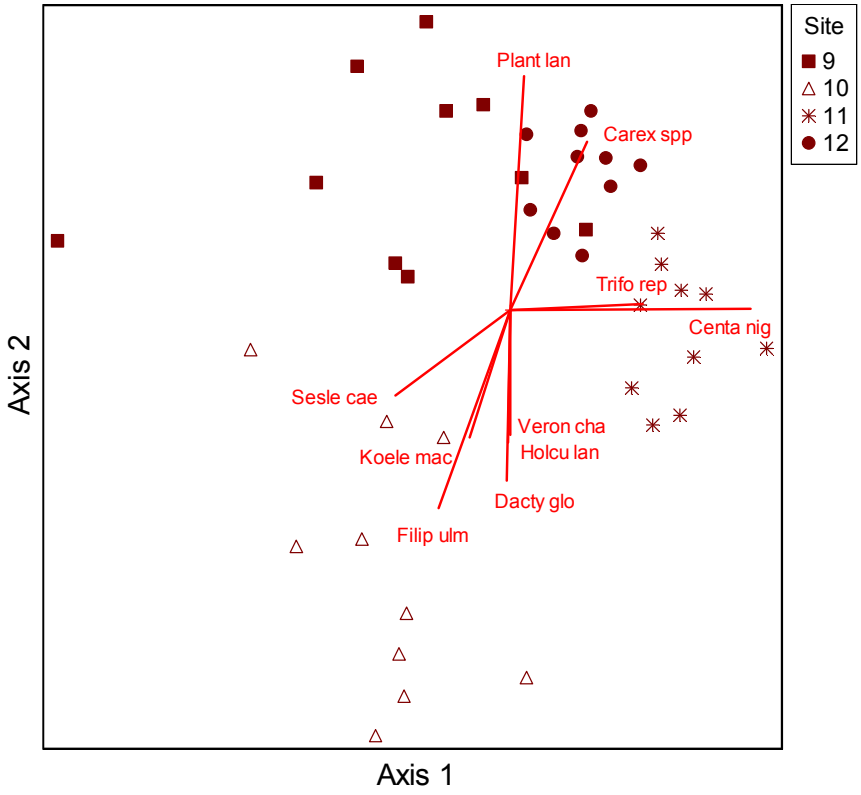


Figure 21 NMS ordination as per Figure 20, but with the most influential species from the second matrix overlaid.

The effects of cessation of grazing on the vegetation

Changes in numbers of species

To investigate if there were differences in the numbers of plant species per quadrat between 2006 and 2008, and, if so, to ascertain whether these were due to the experimental exclusion of grazers, an ANOVA 'general linear model' was constructed. 'Site' was included as a random effect, and was nested within habitat. Note that the effect of 'year' was accounted for by using 'change in species number' as the response variable, as opposed to simply using 'species number' for each of the two years. Thus the influences of 'habitat' and 'treatment' (i.e. grazed/ungrazed) on the changes in species numbers at each of the twelve study sites were investigated.

The results of the analysis (carried out on data transformed by addition of a constant and squaring) are given in Table 27 and Figure 22. There is a significant interaction ($p<0.001$) between 'habitat' and 'treatment', meaning that the effect of the treatment changes depending on the habitat in question. When there is a significant interaction the results above this level in the output table should generally not be interpreted. Post-hoc analysis (Tukey Simultaneous Tests) revealed that the changes in species numbers inside the fenced plot in grasslands were significantly different to the changes in the grassland controls ($p=0.0001$). This was not the case for either woodlands or scrub. Even with the three habitat types combined, the effect of fencing is still evident – illustrated in Figure 23.

In order to check if the initial richness of the habitat type was related to the magnitude of the change in richness (i.e. would habitats with high numbers of species change more than habitats with few species), the mean species richness per quadrat in 2006 for each of the habitats was plotted against the mean change in richness between 2006 and 2008 (Figure 24).

Table 27 Results from general linear model: mean changes in species number between 2006 and 2008 in quadrats in three habitat types, with fenced and control plots. (Data transformed by addition of a constant, and squaring.) [H = habitat, S = site, T = treatment]

Source	DF	Seq SS	Adj MS	F	P
H	2	212930	106465	5.23	0.031
S(H)	9	183123	20347	2.94	0.004
T	1	81432	81432	11.77	0.001
H*T	2	144567	72283	10.45	0.000
Error	105	726312	6917		
Total	119	1348364			

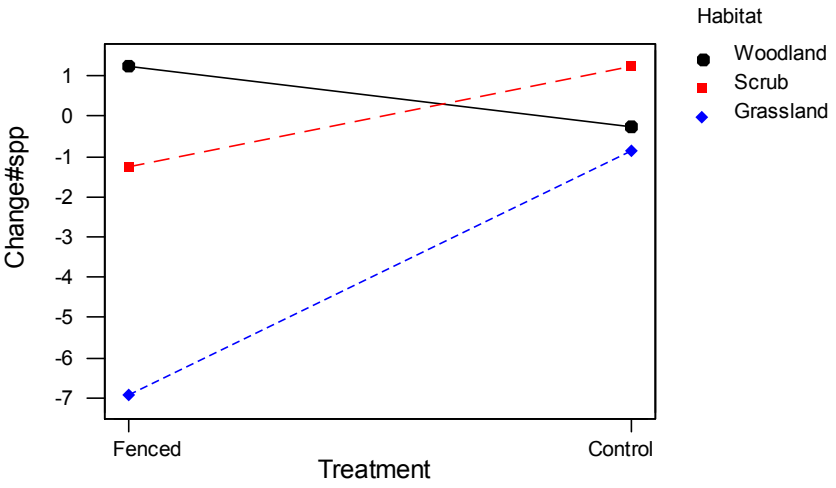


Figure 22 Interaction plot showing effects of treatment on the mean change in number of species between 2006 and 2008 in each of the three habitat types (plotted using untransformed data).

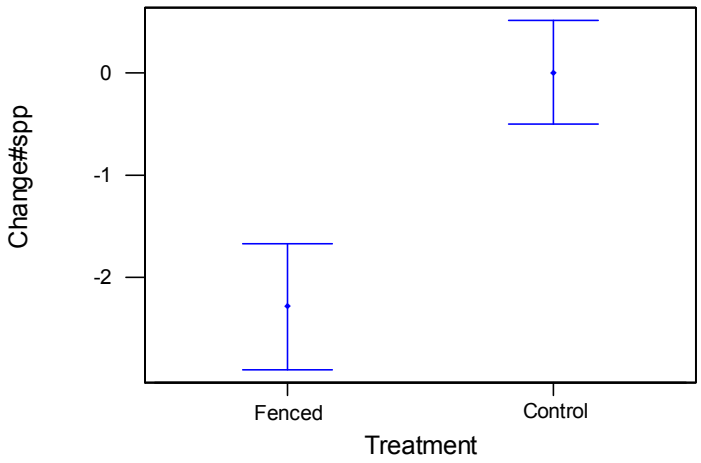


Figure 23 Effects of treatment on the mean change in number of species (between 2006 and 2008) for all habitats combined (+/- standard error, plotted using untransformed data).

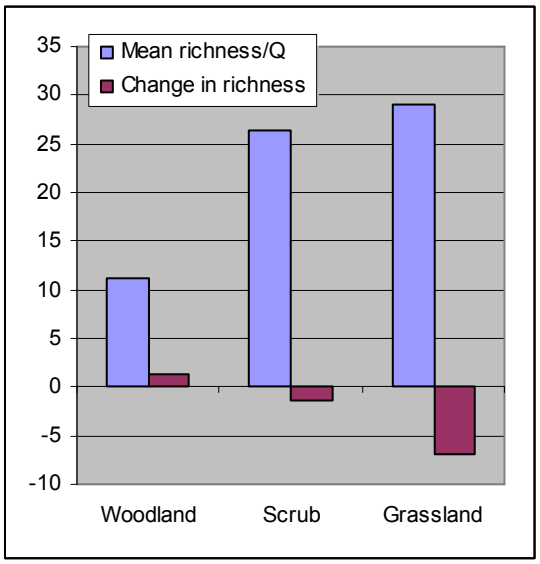


Figure 24 Mean species richness per quadrat for each of the habitats (2006 data) and mean change in richness between 2006 and 2008 (fenced plots only included in both cases).

Changes in diversity

Changes in diversity between 2006 and 2008 were also assessed using a general linear ANOVA model. The same variables as above were inputted: H = habitat, T = treatment, S = site (nested within habitat, and 'random'), and an interaction term H*T. Results again indicate a significant interaction between habitat and treatment (Table 28, Figure 25), with post-hoc analysis showing that there was a highly significant difference ($p<0.0001$) between the change in diversity seen in the woodland fenced and control plots (diversity increased more within the fenced plots). There was a more moderate, but still statistically significant ($p=0.0291$), difference between the changes seen in the fenced and control plots in the grassland sites (diversity decreased inside the fences but remained almost unchanged in the controls). No significant differences were found for the scrub plots.

Table 28 Results from general linear model: mean changes in Simpson's Diversity Index between 2006 and 2008 in quadrats in three habitat types, with fenced and control plots.
[H = habitat, S = site, T = treatment]

Source	DF	Seq SS	Adj MS	F	P
H	2	0.412985	0.206492	13.32	0.002
S(H)	9	0.139479	0.015498	5.04	0.000
T	1	0.000513	0.000513	0.17	0.684
H*T	2	0.109289	0.054644	17.78	0.000
Error	105	0.322694	0.003073		
Total	119	0.984959			

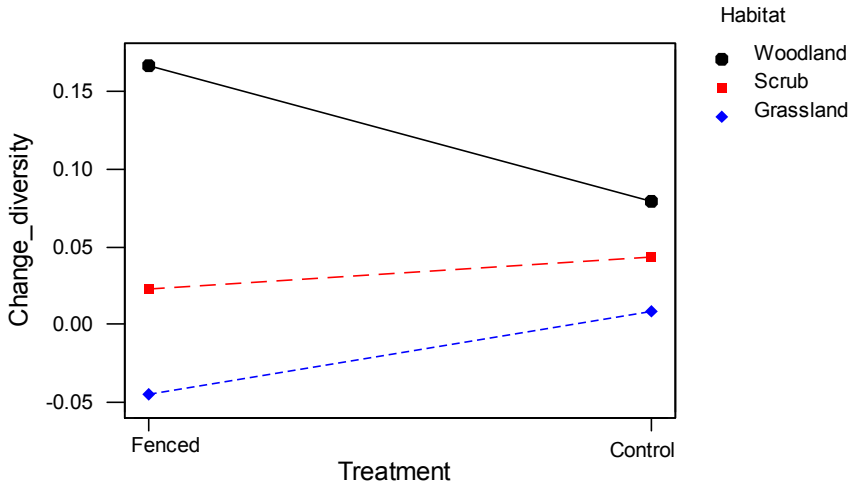


Figure 25 Interaction plot showing effects of treatment on the mean change in Simpson's Diversity Index between 2006 and 2008 in each of the three habitat types.

In order to check if there was any relationship between the initial diversity of habitats and the magnitude of the change in diversity following the experimental treatment their values were plotted (Figure 26).

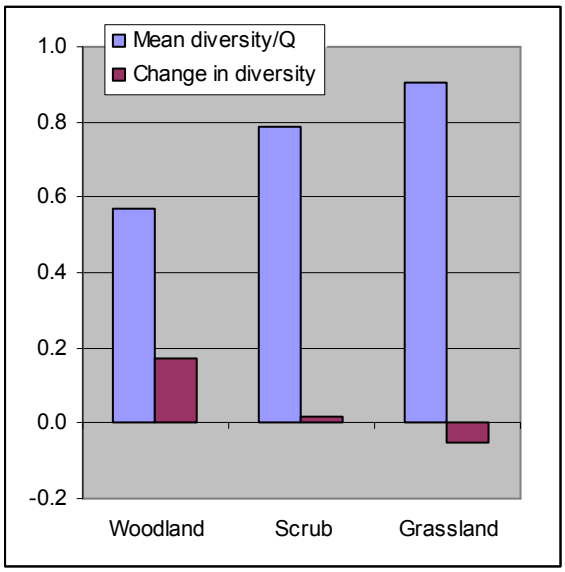


Figure 26 Mean diversity (Simpson's Diversity Index) per quadrat for each of the habitats (2006 data) and mean change in diversity between 2006 and 2008 (fenced plots only included in both cases).

Most notable changes - Woodlands

As outlined above, plant species richness increased inside the fenced plots, and diversity significantly so, at the woodland study sites. Mean species richness and diversity for fenced and control plots in both study years are presented in Figure 27. Nine species (or 16% of the total number of species recorded from woodlands in 2006) were lost, mostly from control plots, and all with low covers, indicating some stochastic species turnover. Eleven species were gained (19%), mostly in the fenced plots, and mostly with low cover values. The most significant gain was *Lysimachia nemorum* which appeared in one of the quadrats inside the fence at Gortlecka in 2008 at a cover of 5%.

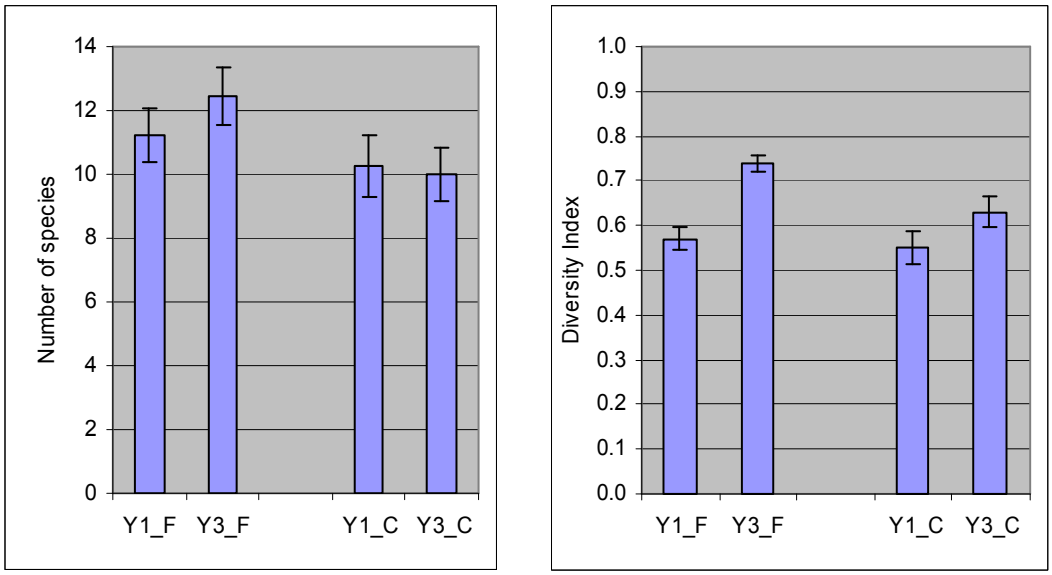
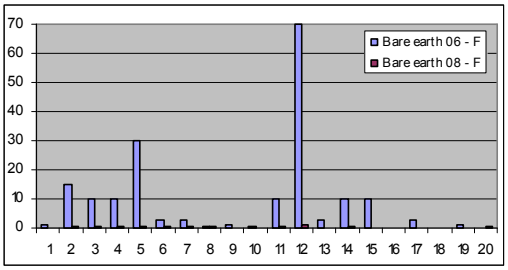


Figure 27 Average species richness [left] and Simpson's Diversity Index [right] in woodland quadrats in year one and year three in fenced and control plots (+/- S.E.).
[Y1 = year one, Y3 = year three; F = fenced plot, C = control plot]

Variables such as cover of field, grass, sedge and fern layers, cover of bare earth and bare rock, cover of litter and low woody species and dry weight of litter samples were analysed for differences in abundance between 2006 and 2008 using the non-parametric equivalent of a paired t-test, the 'Wilcoxon signed ranks' test (Dytham, 2003). This test necessitates at least six pairs of values and so all woodland quadrats were analysed together (i.e. sites were pooled, and n=20 in each case). The variable showing the strongest pattern was bare earth, with a significant decrease inside the fenced plot ($p<0.001$), and no corresponding decrease in the controls (Figure 28). Cover of field layer and cover of grasses showed significant increases in both the fenced and control plots, but as Figure 29 and Figure 30 show, the increases were larger inside the fenced plots.



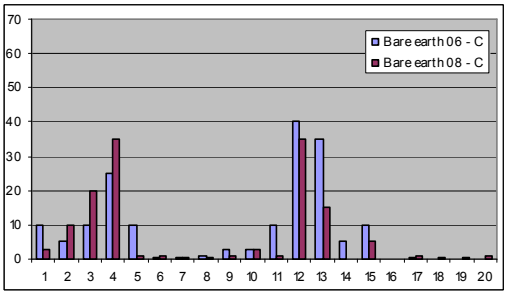
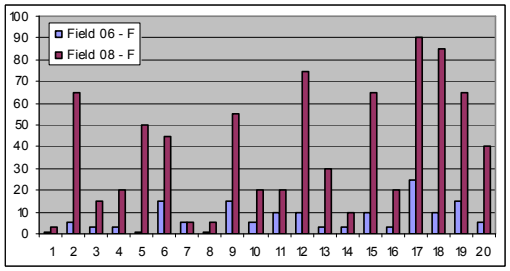


Figure 28 Changes in the % cover of bare earth in fenced (above) and control (below) woodland quadrats between 2006 and 2008.



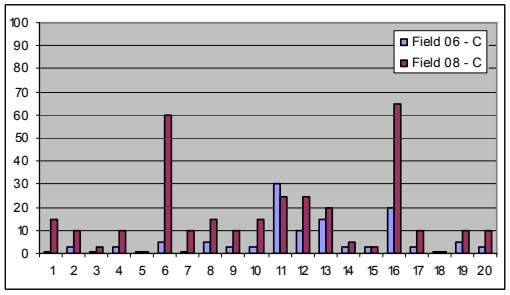
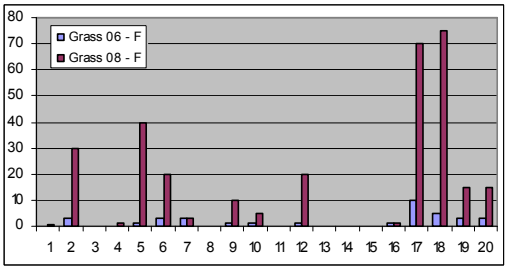


Figure 29 Changes in the % cover of the field layer in fenced (above) and control (below) woodland quadrats between 2006 and 2008.



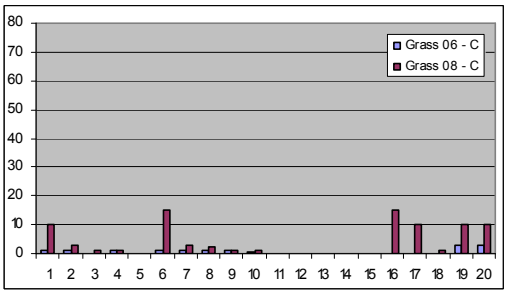


Figure 30 Changes in the % cover of grasses in fenced (above) and control (below) woodland quadrats between 2006 and 2008.

All species occurring in multiple quadrats (as a rule-of-thumb, species that occurred at ≥6 quadrats in at least one site, or ≥20 quadrats overall) were analysed in the same way as above. Two species exhibited significant increases in the fenced plots, which were not matched by significant changes in the control: *Geum urbanum* (p=0.036, Figure 31) and *Oxalis acetosella* (p=0.035, Figure 32). Several species exhibited significant increases in both the fenced and the control plots, but with the increases being larger in the fenced plots. These were *Brachypodium sylvaticum* (F: p=0.004, C: p=0.006, Figure 33), *Fragaria vesca* (F: p=0.015, C: p=0.036, Figure 34), *Rubus fruticosus* agg. (F: p<0.001, C: p=0.010, Figure 35) and *Viola riviniana/reichenbachiana* (F: p=0.004, C: 0.022, Figure 36).

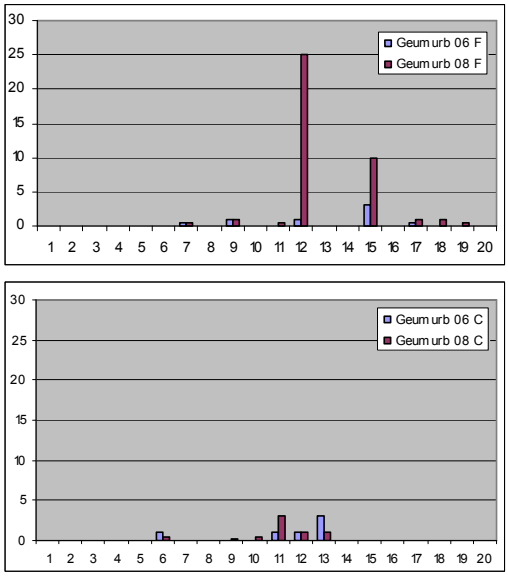


Figure 31 Changes in the % cover of *Geum urbanum* in fenced (above) and control (below) woodland quadrats between 2006 and 2008.

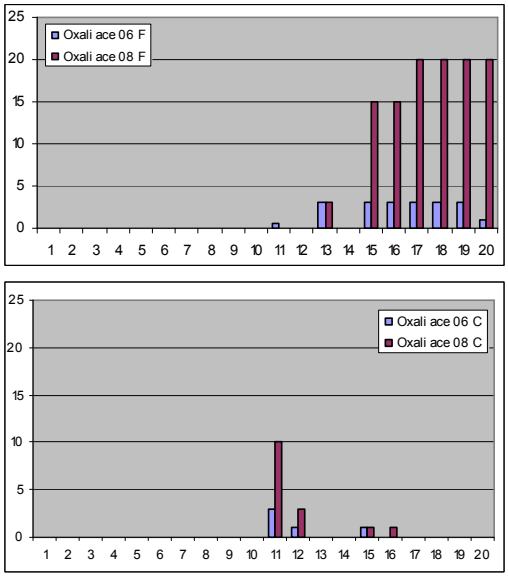


Figure 32 Changes in the % cover of *Oxalis acetosella* in fenced (above) and control (below) woodland quadrats between 2006 and 2008.

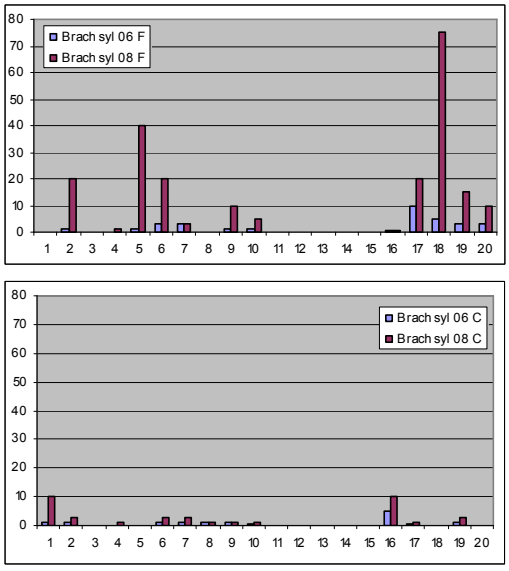


Figure 33 Changes in the % cover of *Brachypodium sylvaticum* in fenced (above) and control (below) woodland quadrats between 2006 and 2008.

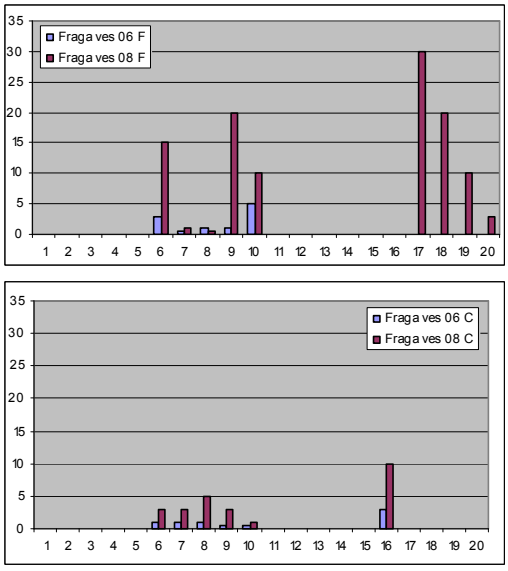


Figure 34 Changes in the % cover of *Fragaria vesca* in fenced (above) and control (below) woodland quadrats between 2006 and 2008.

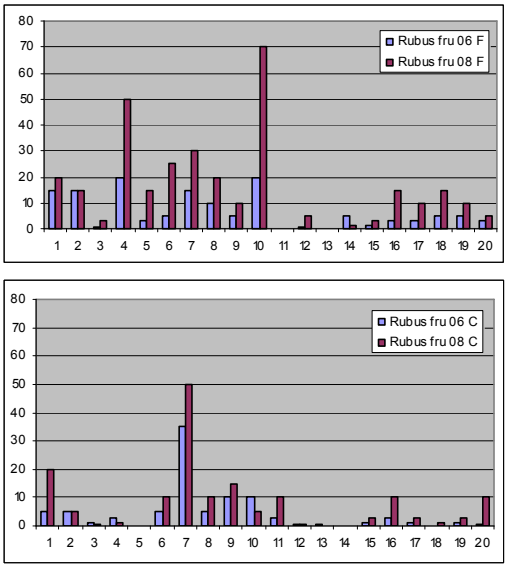


Figure 35 Changes in the % cover of *Rubus fruticosus* agg. in fenced (above) and control (below) woodland quadrats between 2006 and 2008.

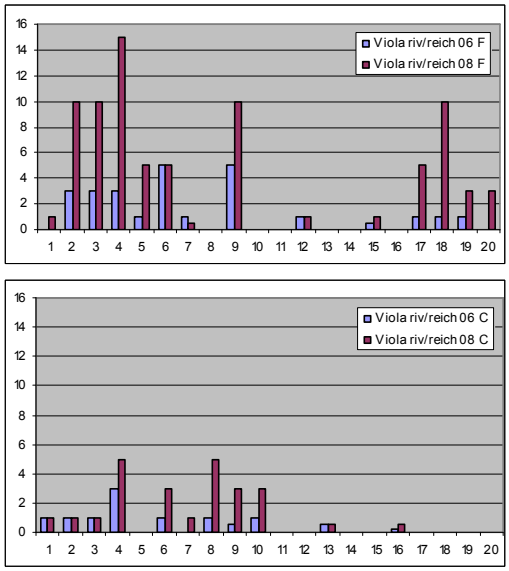


Figure 36 Changes in the % cover of *Viola riviniana/ reichenbachiana* in fenced (above) and control (below) woodland quadrats between 2006 and 2008.

Most notable changes - Grasslands

In contrast to the findings at the woodlands sites, both the plant species richness and the Simpson's Diversity Index decreased significantly inside the fenced plots at the grassland sites (refer to Figure 22 and Figure 25). Fourteen species (or 14% of the total number of species recorded from grasslands in 2006) were lost, and nine were gained (9%). Most had very few occurrences in the dataset. The mean species richness and diversity for fenced and control plots in 2006 and 2008 are presented in Figure 37. The differences in abundance between the study years were analysed further (Wilcoxon's test, n=20) for those species which occurred in multiple quadrats.

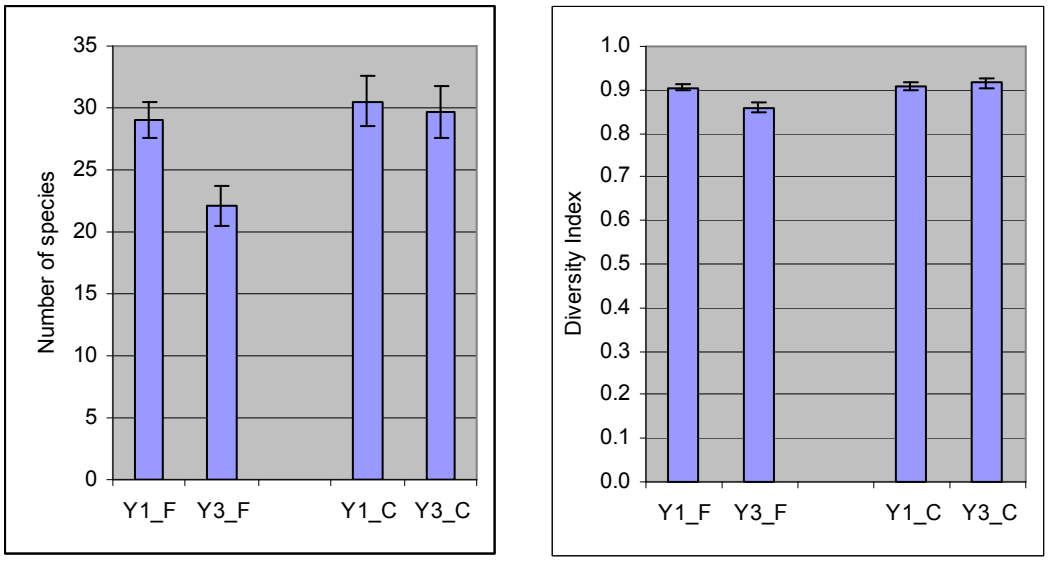


Figure 37 Average species richness [left] and Simpson's Diversity Index [right] in grassland quadrats in year one and year three in fenced and control plots (+/- S.E.).
[Y1 = year one, Y3 = year three; F = fenced plot, C = control plot]

Among the most dramatic changes seen in the grasslands was the complete loss of certain species from within some or all of the fenced plots. Foremost amongst these was *Euphrasia* agg., which was lost from all four grassland sites. Interestingly, and serving further to highlight the loss, this taxon showed a significant increase inside the control plots (F: $p<0.001$, C: $p<0.001$, Figure 38). Other species which were lost from one or more of the grassland fenced plots include *Linum catharticum* (F: p=0.022, C: p=0.889, Figure 39), *Odontites vernus* (F: p=0.036, C: p=0.753, Figure 40) and *Rhinanthus minor* (F: p=0.013, C: p=0.058, Figure 41). Each of these species exhibited significant changes inside the fenced plots, which were not matched by significant changes in the control, indicating an effect of the experimental treatment.

Among the other species showing a significant decrease were *Prunella vulgaris* (F: p=0.006, C: p=0.067, Figure 42) and the *Trifolium* species (*T. pratense* and *T. repens*) (F: p=0.003, C: p=0.003, Figure 43 and F: p=0.005, C: p=0.001, Figure 44, respectively). In the case of the latter pair, there was a significant change in both the fenced and the control plots, but the changes in the fenced quadrats were more marked.

Another species, *Cerastium fontanum*, showed a visible trend, though not statistically significant (F: p=0.097, C: p=0.813, Figure 45). This species appears to have been lost from five of the quadrats within the fenced plots, a loss not mirrored in the control plot quadrats.

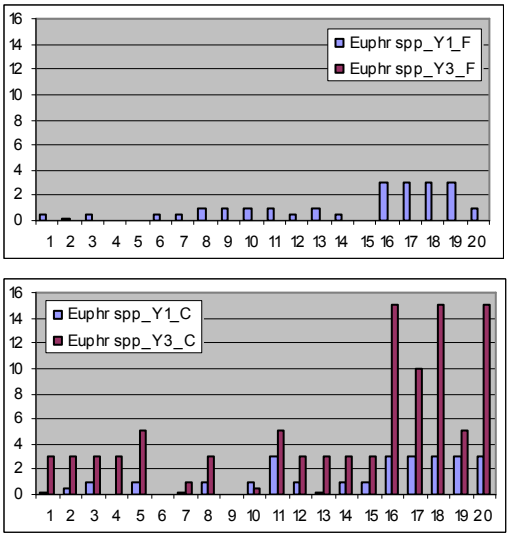


Figure 38 Changes in the % cover of *Euphrasia* spp in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

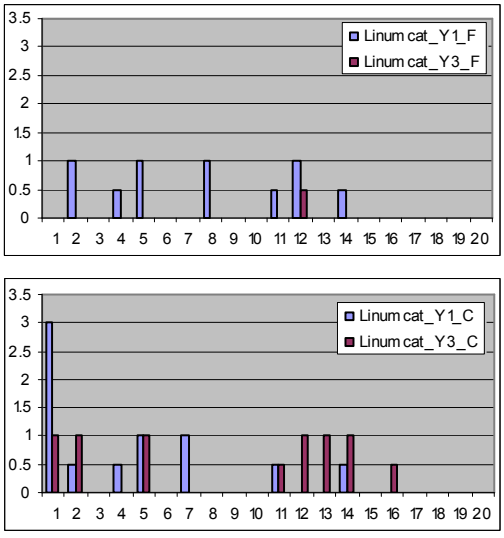


Figure 39 Changes in the % cover of *Linum catharticum* in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

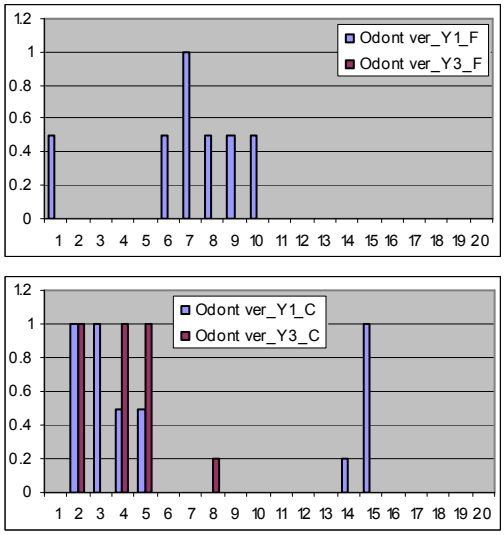


Figure 40 Changes in the % cover of *Odontites vernus* in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

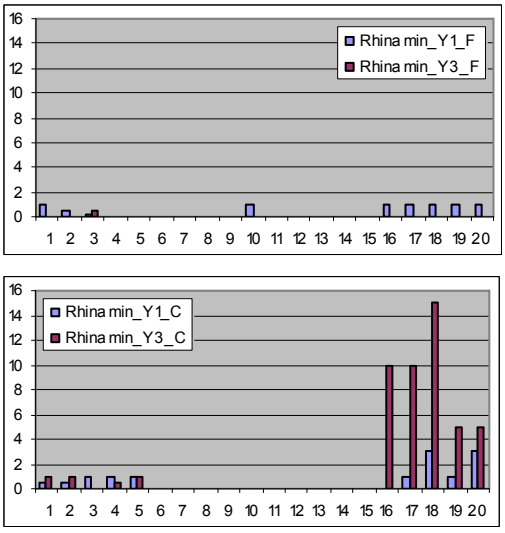


Figure 41 Changes in the % cover of *Rhinanthus minor* in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

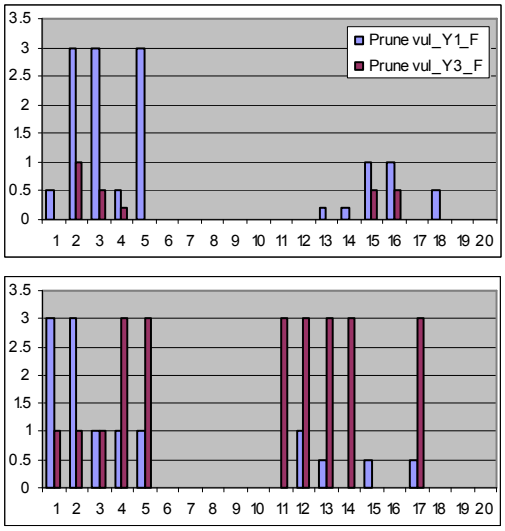


Figure 42 Changes in the % cover of *Prunella vulgaris* in fenced (above) and control (below) grassland quadrats between 2006 and 2008. (Legend removed for clarity.)

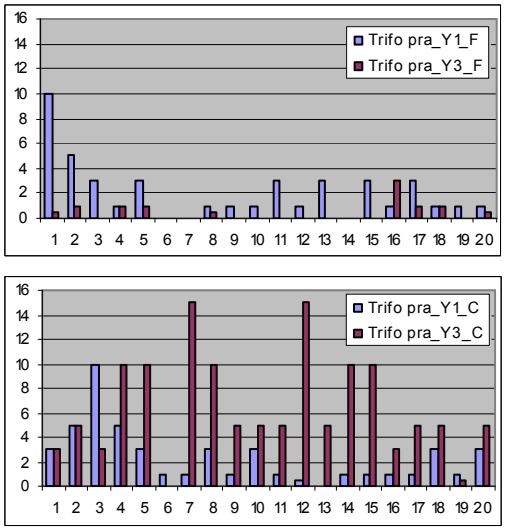


Figure 43 Changes in the % cover of *Trifolium pratense* in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

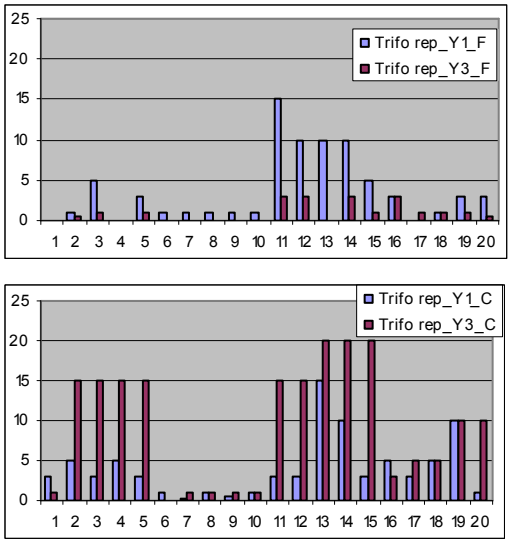


Figure 44 Changes in the % cover of *Trifolium repens* in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

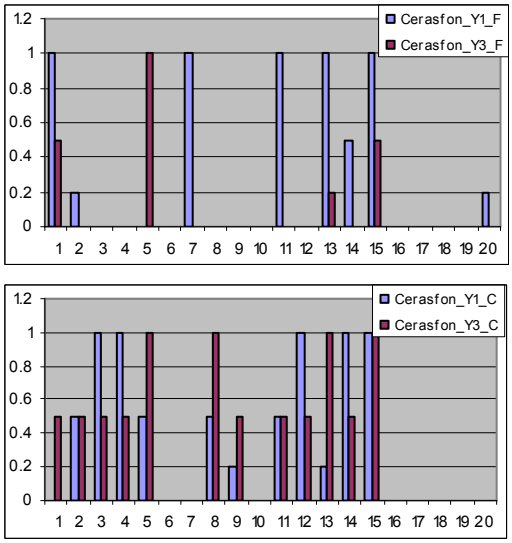


Figure 45 Changes in the % cover of *Cerastium fontanum* in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

A minority of species have thrived in the absence of grazing, showing significant increases inside the fenced plots. Examples are *Potentilla erecta* (F: p=0.003, C: 0.078, Figure 46) and *Pteridium aquilinum* (F: p=0.037, C: p=0.722, Figure 47).

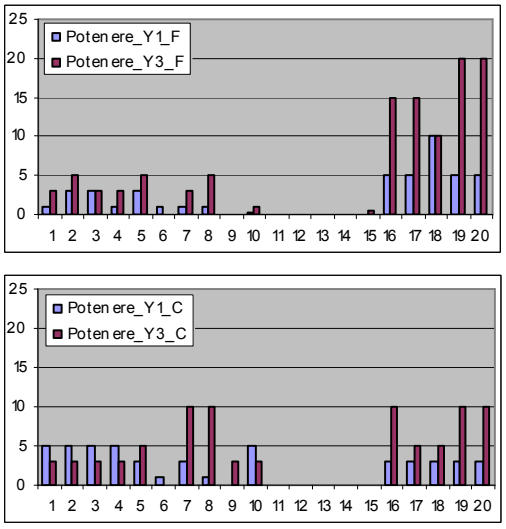


Figure 46 Changes in the % cover of *Potentilla erecta* in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

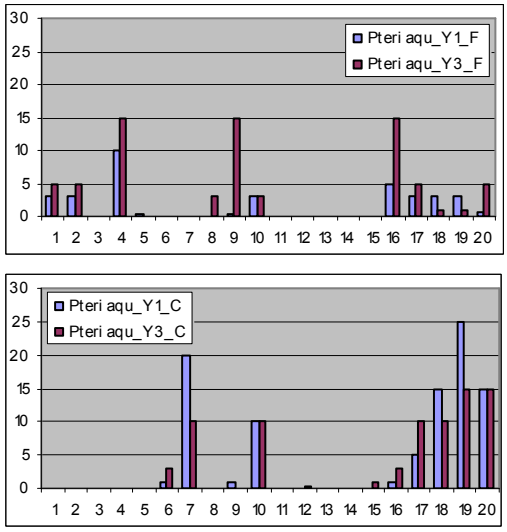


Figure 47 Changes in the % cover of *Pteridium aquilinum* in fenced (above) and control (below) grassland quadrats between 2006 and 2008

One of the most noticeable changes from amongst the other variables measured was the increase in the amount of litter present within the fenced exclosures. This was a very visible change, evident in the field (see photograph, Figure 71, Chapter Six). The amount of litter was measured in two ways – cover of litter for each quadrat was estimated in the field, and litter samples were collected, dried and later weighed. Cover of litter increased significantly in both the fenced and control plots (F: $p<0.001$, C: $p<0.001$), but as Figure 48 shows, the increase in the fenced plots is substantially larger and more consistent. The dry weight of litter did not increase significantly in the control plot quadrats but did so in the fenced (F: $p<0.001$, C: $p=0.401$, Figure 49).

The amount of grass cover in the grassland quadrats increased significantly during the course of the experiment (F: $p<0.001$, C: $p=0.045$, Figure 50), while the cover of bare earth dropped to almost zero across all fenced quadrats (F: $p<0.001$, C: $p=0.003$, Figure 51). Finally, vegetation height increased significantly in both the fenced and control plots but with a noticeably larger increase within fenced quadrats (F: $p<0.001$, C: $p<0.001$, Figure 52).

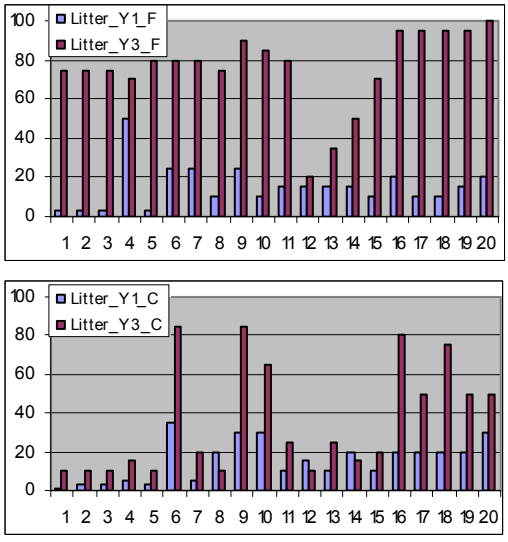


Figure 48 Changes in the % cover of litter in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

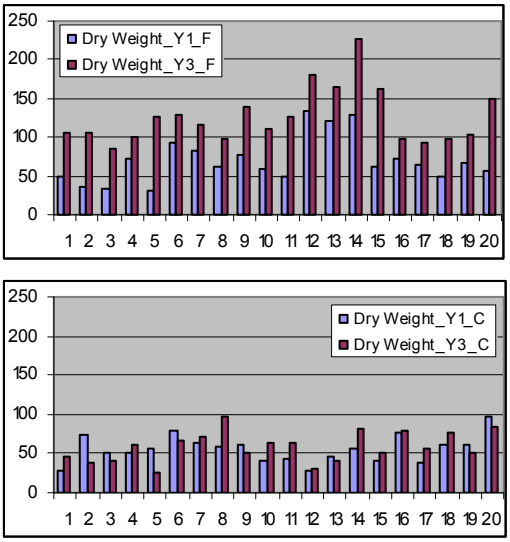


Figure 49 Changes in the dry weight (g) of litter in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

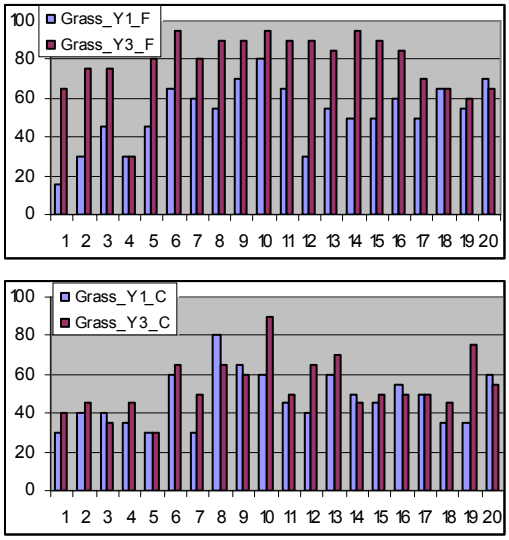


Figure 50 Changes in the % cover of grasses in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

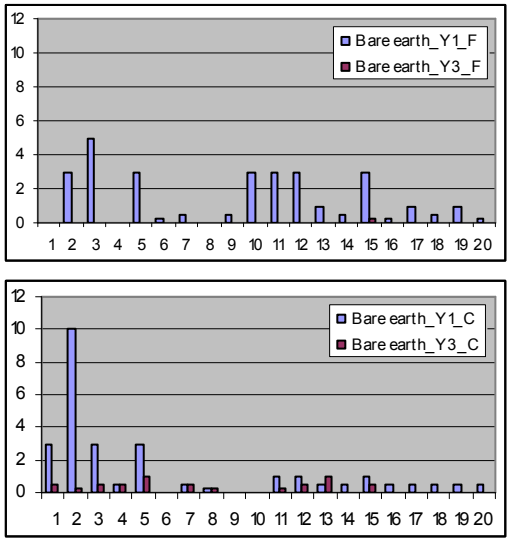


Figure 51 Changes in the % cover of bare earth in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

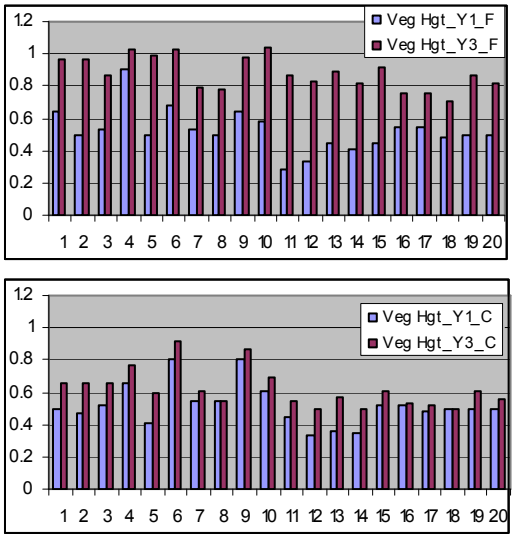


Figure 52 Changes in the vegetation height (m) in fenced (above) and control (below) grassland quadrats between 2006 and 2008.

Most notable changes - Scrub

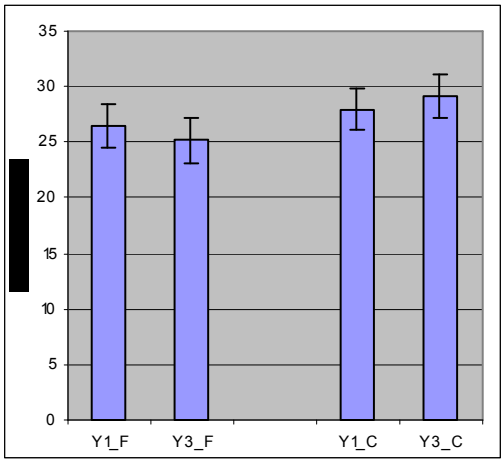
In the scrub sites, overall plant species richness did not change measurably inside the fenced plots, and nor did diversity (Figure 22 and Figure 25). The mean species richness and diversity for the fenced and control plots in 2006 and 2008 are presented in Figure 53. A total of 124 species were recorded during the two study years, with 115 recorded in year one. A total of 20 species (or 17%) were lost between year one and year three, and nine (or 8%) were gained. All scrub quadrats were examined together (Table 29, Figure 53), without a distinction being made between 'woody' and 'grassy' quadrats. As these may have, in effect, cancelled each other out, the mean species number per quadrat, and mean diversity score per quadrat, were re-calculated for woody and grassy scrub separately (Table 30, Figure 54).

Table 29 Mean species richness and diversity (+/- S.E.) at scrub fenced and control plots in 2006 and 2008.

Plot	Mean per 2 x 2m quadrat 2006	Mean per 2 x 2m quadrat 2008	% change
	Species number	**Species number**	
Fenced	26.5 +/- 2.0	25.2 +/- 2.1	- 4.7%
Control	28.0 +/- 1.8	29.2 +/- 2.0	+ 4.5%
	Simpson's Diversity Index	**Simpson's Diversity Index**	
Fenced	0.790 +/- 0.03	0.813 +/- 0.03	+ 2.9%
Control	0.798 +/- 0.03	0.841 +/- 0.03	+ 5.4%

Table 30 Mean species richness and diversity (+/- S.E.) in 'woody' and 'grassy' scrub quadrats in 2006 and 2008.

Plot	Mean per 2 x 2m quadrat 2006		Mean per 2 x 2m quadrat 2008		% change	
	Species number		**Species number**			
	Woody	Grassy	Woody	Grassy	Woody	Grassy
Fenced	21.6 +/- 2.7	32.3 +/- 1.1	19.8 +/- 2.6	31.8 +/- 1.4	- 8.3%	- 1.5%
Control	23.3 +/- 2.3	26.3 +/- 1.4	24.9 +/- 2.7	27.7 +/- 1.6	+ 6.7%	+ 5.3%
	Simpson's Diversity Index		**Simpson's Diversity Index**			
	Woody	Grassy	Woody	Grassy	Woody	Grassy
Fenced	0.693 +/- 0.04	0.697 +/- 0.04	0.724 +/- 0.04	0.766 +/- 0.03	+ 4.5%	+ 10.0%
Control	0.908 +/- 0.01	0.921 +/- 0.01	0.922 +/- 0.00	0.933 +/- 0.00	+ 1.5%	+ 1.3%



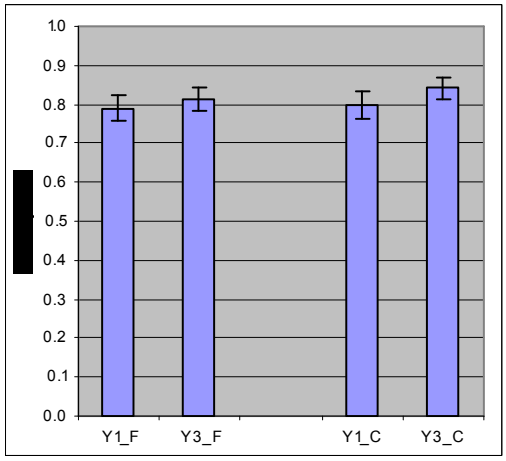
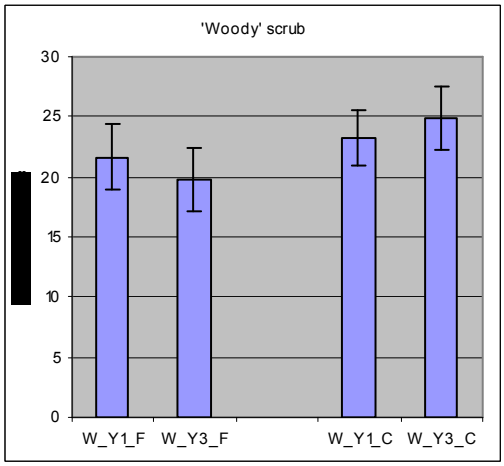
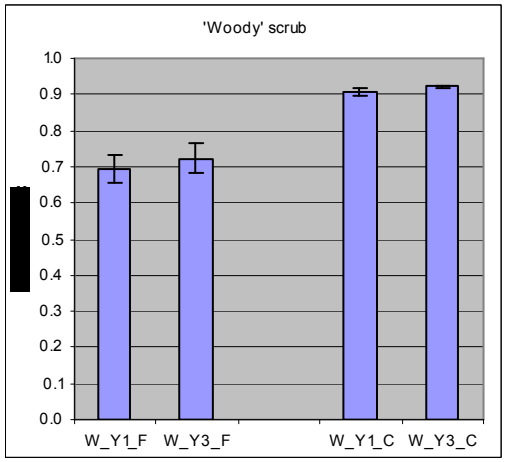
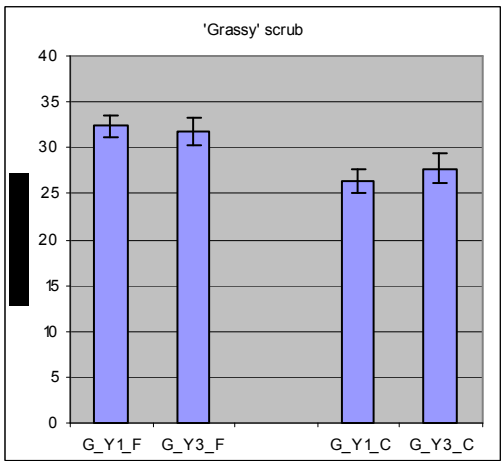


Figure 53 Average overall species richness [left] and Simpson's Diversity Index [right] in scrub quadrats in year one and year three in fenced and control plots (+/- S.E.).
[Y1 = year one, Y3 = year three; F = fenced plot, C = control plot]







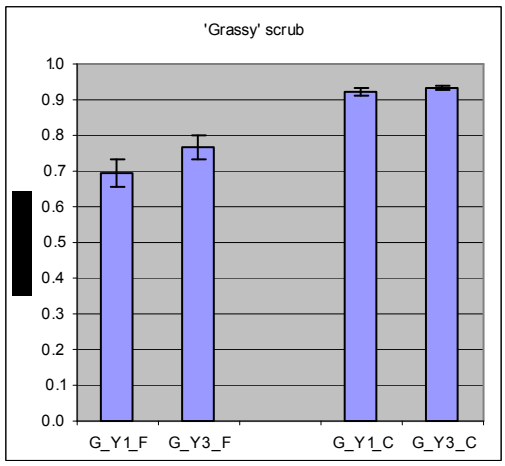


Figure 54 Average species richness [left] and Simpson's Diversity Index [right] in 'woody' scrub quadrats [top], and 'grassy' scrub quadrats [bottom] in year one and year three in fenced and control plots (+/- S.E.).
[Y1 = year one, Y3 = year three; F = fenced plot, C = control plot, W = woody, G = grassy]

There were a reduced number of replicates due to the scrub being split into its woody and grassy components, meaning that statistically testing for differences for individual species between years was generally not possible. Variables which appeared to exhibit trends (on examination of the raw data) were tested, however; these were: cover of litter, dry weight of litter samples and cover of field layer. There were significant increases in litter cover in both woody and grassy quadrats (Figure 55 and Figure 56). In the case of woody scrub, there was a significant increase in both the fenced and control plots (F: p=0.018, C: p=0.033), but the increase is larger in the fenced quadrats. The grassy quadrats show a clearer response to the experimental treatment, with a significant increase in litter cover being seen only in the fenced quadrats (F: p=0.009, C: p=0.093). Cover of field layer also showed a significant increase in both the fenced and control plots in the grassy scrub (F: p=0.024, C: p=0.022).

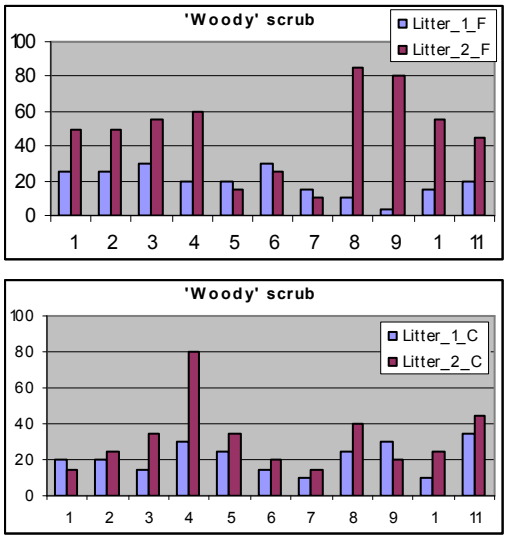
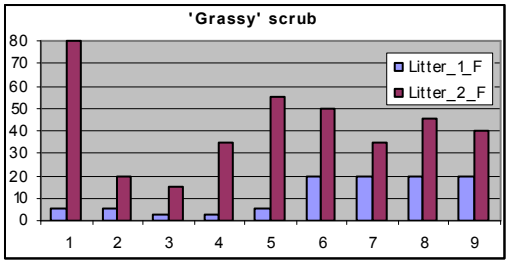


Figure 55 Changes in the % cover of litter in fenced (above) and control (below) 'woody' scrub quadrats between 2006 and 2008.



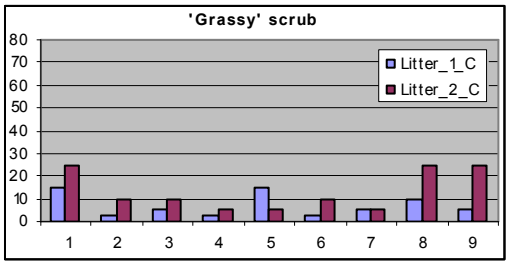
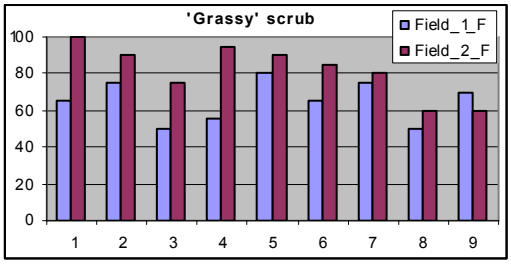


Figure 56 Changes in the % cover of litter in fenced (above) and control (below) 'grassy' scrub quadrats between 2006 and 2008.



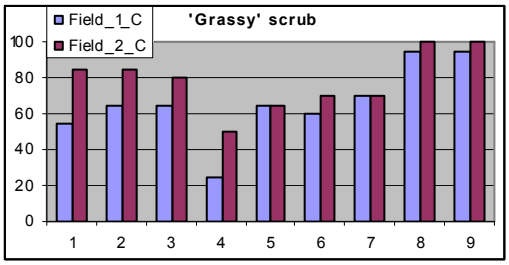


Figure 57 Changes in the % cover of the field layer in fenced (above) and control (below) 'grassy' scrub quadrats between 2006 and 2008.

Discussion

The vegetation of the Burren woodlands, scrub and grasslands

Species richness

A total of 211 vascular plant species were recorded at the twelve study sites during this survey. The total Irish (native) flora consists of just over 800 species (Webb, 1983), therefore 211 is quite a high proportion to record in a relatively small study area. Of particular note is the fact that 102 species were recorded from one of the grassland sites (Caher, 2006 data) – this alone represents approximately 12.5% of the Irish flora.

It is interesting to note the lack of overlap in the species richness of the woodland and grassland sites (Table 15). One possible criticism relating to this is that the smallest sampling unit, the 2 x 2m quadrat, was too small to adequately sample the woodlands. However, at the plot (20 x 20m), site (data from both fenced and control plots merged) and habitat (data from four sites merged) levels, the same pattern is evident – grasslands appear to harbour more species of vascular plants than woodlands. It is worth noting, however, that the woodlands were more species rich for lichens and bryophytes than grasslands (see 'Ancillary projects', Chapter Two).

The scrub habitat comes out with the highest total number of species, perhaps reflecting its ecotonal and heterogeneous nature, and the fact that it may harbour a suite of species with a wide range of ecological tolerances. The Sørensen coefficients calculated showed that, unsurprisingly, the woodlands and grasslands were the least similar in species composition. The grassland and

scrub sites had the most species in common. The relatively low coefficients of similarity overall indicate a fair degree of distinctness between the three habitats.

In order to investigate if the findings of greater (vascular plant) species richness in grasslands compared to woodlands is consistent with those of other studies, the Irish national survey reports on both woodlands and grasslands were accessed (Perrin et al., 2008a, Perrin et al., 2008b, O'Neill et al., 2009). The grasslands report gives a mean number of species (including bryophytes) per study site across four counties of 90.03. It is difficult to compare this directly with the findings of the current study because the figure includes bryophytes and is based on areas of the country containing mainly wet grasslands, rather than drier calcareous/neutral grasslands. The woodlands report (which covers all counties in the Republic of Ireland) states that there were, on average, 70 species (not including bryophytes) in sites which had woodland cover in the early 1800s, and a mean species number of approximately 60 for sites which did not – i.e. sites which hold younger woodlands. Again these figures are not directly comparable with the current study because all woodland types which occur in Ireland were included, and the species lists relate to entire sites (species lists compiled during this survey relate to 20 x 20m plots). Overall, however, when one allows for the limitations mentioned, the findings suggest that there may be a pattern of higher vascular plant species richness in grasslands compared to woodlands in Ireland in general.

Most common species

Hazel was the most common species in the dataset, and was also widespread, occurring at all sites. The high frequency of hazel is not surprising, as all the scrub and woodland sites were specifically chosen to be hazel-dominated, and all grassland sites were not far from a stand of hazel owing to the heterogeneous nature of the Burren landscape. The prominence of bracken, being also widespread and occurring at all sites, in the dataset is a little more remarkable. As this is a potentially invasive (although native) plant, its behaviour in the face of the exclusion of grazers will be important to document.

Also common and widespread (occurring at ≥9 sites) in the dataset were the low woody taxa *Rubus fruticosus* agg., *Hedera helix* and *Rosa spinosissima*, the forbs *Taraxacum* agg., *Viola riviniana/ reichenbachiana* and *Hypericum pulchrum,* the grasses *Agrostis* sp., *Anthoxanthum odoratum* and *Sesleria caerulea* and the sedge *Carex flacca*. Among these species, both *R. spinosissima* and *S. caerulea* have restricted distributions in Ireland, and can be regarded as 'Burren specialities'. *V. reichenbachiana* is noted in Webb and Scannell (1983) as being "*very precise in its requirements*" in the region, but "*usually present when these are forthcoming*". These requirements are shelter and a basic soil. While it was not always possible to tell the two *Viola* species apart during this survey, *V. reichenbachiana* was confirmed from all four woodland study sites, and from one of the scrub sites. *H. pulchrum*, although typically a calcifuge, is reported in Webb and Scannell as being frequent to abundant in the region. They suggest that the race which occurs on the Burren

limestones may be adapted to be more tolerant of alkaline soils. Grasses in the genus *Agrostis* were amalgamated in this study and recorded as *Agrostis* sp. due to issues with identification of some specimens, but the majority of records are likely to be either *A. capillaris* and *A. stolonifera*, these being the two most common species in the Burren (Webb and Scannell, 1983).

Species limited to woodland sites, but widespread within them, include holly and the fern *Asplenium trichomanes*. The latter species is typical of more open, rocky habitats (Webb and Scannell, 1983, Webb et al., 1996), giving an indication of the rockiness of the woods in the Burren. In the scrub, the forbs *Teucrium scorodonia* and *Trifolium pratense* are also widespread within that habitat, but limited to it. There were no species found exclusively in grasslands which occurred in all grassland sites, but a number were found in most (i.e. three out of four sites). Among these is the 'fairly rare' (Webb et al., 1996) orchid, *Coeloglossum viride*. A large proportion of the species recorded were found in both scrub and grassland habitats.

Correspondence with the National Vegetation Classification of Britain

To allow an objective comparison of the vegetation data collected with a well-recognised and established classification system, all quadrats from the first year of the study were entered into the MAVIS Plot Analyser (Smart, 2000). This tool enabled the relationships between the current dataset and the NVC classifications to be explored in detail.

Grasslands

Rather than being closely linked to a calcareous grassland category ('CG' in the NVC system) as might have been expected, the grasslands in the study emerged as being more closely aligned to the mesotrophic grassland type, MG5 (*Cynosurus cristatus – Centaurea nigra* grassland). These grasslands are characterised (Rodwell, 1992) by generally being species rich with a large proportion of forbs such as *Leontodon hispidus, Leucanthemum vulgare, Lotus corniculatus, Primula veris, Ranunculus bulbosus, Rumex acetosa* and *Trifolium pratense*. The grasses *Agrostis capillaris* and *Anthoxanthum odoratum* may be frequent or abundant. Rodwell notes that MG5 is one of nine recognised 'chalk grassland' types in Britain, making clear the link between this grassland type and the more calcicolous ones. The constant species (all of which are found at the study sites) are: *Agrostis capillaris* (*Agrostis* sp. recorded during this study, but likely to be composed largely of *A. capillaris* and/or *A. stolonifera*)*, Anthoxanthum odoratum, Centaurea nigra, Cynosurus cristatus, Dactylis glomerata, Festuca rubra, Holcus lanatus, Lotus corniculatus, Plantago lanceolata, Trifolium pratense* and *T. repens.*

Of the calcicolous grasslands, CG2 (*Festuca ovina – Avenula pratensis* grassland) is described by Rodwell (1992) as the "*core of this kind of vegetation*", referring in particular to the calcicolous grasslands typical of the south-east of England. This was considered to be one of the most likely categories of calcareous grassland to be found in the Burren by Jeffrey (2003). The constant species

are *Avenula pratensis*, Briza media, Carex flacca, Festuca ovina, Koeleria macrantha, Leontodon hispidus**, Linum catharticum, Lotus corniculatus, Pilosella officinarum, Plantago lanceolata, Poterium sanguisorba, Scabiosa columbaria** and *Thymus polytrichus* (* = not found in Ireland, ** = found in Ireland, but not recorded from the study sites).

It can be seen that there is considerable overlap between the communities recorded during this study, and both MG5 and CG2. Some of the species typical of these grasslands (e.g. *Avenula pratensis* and *Scabiosa columbaria*) do not occur in Ireland, and it is likely that this influences the outcome of the MAVIS programme. However, the MG5 community is sufficiently close in species composition to the Burren grasslands sampled to allow them to be placed in this category with reasonable confidence.

Of the three habitat types, the strength of the correspondence was largest for the grasslands (ranging from 50.8 to 60.6%), perhaps helped by the higher numbers of species recorded there. O'Neill et al. (2009), in the Irish Semi-natural Grasslands Survey report, found correspondences of between 52 and 76% for their grassland categories. Their datasets (and therefore, presumably, their species lists) were much larger than those in the current study, and thus the degree of correspondence achieved here is likely to be satisfactory, given the smaller sample sizes.

Woodlands

Three of the woodland sites were linked most strongly by MAVIS to W8d (*Fraxinus excelsior – Acer campestre – Mercurialis perennis* woodland, *Hedera helix* sub-community). W8 woodland has *A. campestre, Corylus avellana, F. excelsior, M. perennis, Rubus fruticosus* agg. and the moss *Eurhynchium praelongum* as its constant species. *A. campestre* and *M. perennis* do not occur at the study sites. One of the issues with using MAVIS, or any other system, for relating Irish quadrat data to the British NVC system is highlighted here by the absence (or nearly so) in Ireland of both *A. campestre* and *M. perennis*. This is a common issue because of Ireland having such a relatively depauperate flora in comparison to Britain. The absence of important diagnostic and characteristic species in Irish datasets could possibly lead to erroneous results, and this must be borne in mind.

The woodland at Gortlecka was linked most strongly by MAVIS to W10c (*Quercus robur – Pteridium aquilinum – Rubus fruticosus* woodland, *Hedera helix* sub-community). Rodwell (1991) states that this woodland type can grade into the W8d type, and so while at first it may seem an unlikely correspondence, it may not be incorrect. (Worth noting is that W8d is presented by MAVIS as the second most likely woodland type for Gortlecka.) The constant species of W10 are *Quercus robur* (not recorded in this survey)*, Lonicera periclymenum, Pteridium aquilinum* and *Rubus fruticosus* agg. Rodwell (1991) states that cover of ivy increases with oceanicity, and this may account in part for the placing of the woodland sites in the *H. helix* sub-communities of both woodland types.

The correspondences with NVC categories were much lower for the woodlands than the grasslands - in the range of 34.8 to 40.0%. It is not uncommon for woodland communities to have low values, however, with Kirby (2003a), in a review of the NVC after ten years of use, reporting that matching coefficients are "*often less than 50% for woodland samples*". He states that rather than meaning that a sample is atypical or 'wrongly' classified, it is possible that a reduced suite of species is the cause of the low coefficient. This may be due to a depauperate flora overall, as already mentioned, or it may be "*a consequence of comparing a limited species list (from for example five plots from one site) with the much longer list in the NVC table derived from tens of samples spread across many sites*" (Kirby, 2003a). It is possible that this effect is amplified in this study as the size of the basic sampling unit used is particularly small for woodlands – 2 x 2m. This size was used in this study as three different habitat types were being surveyed, and a compromise had to be reached with regard to the size of the basic sampling unit. The 2 x 2m quadrat was deemed to be the most appropriate overall, and additionally, the project was designed such that the quadrat data could be pooled, or the plot data (20 x 20m) used instead, should larger spatial scales be required.

Scrub

The scrub sites proved more challenging to categorise using MAVIS. Firstly, all quadrats at a site were entered and analysed together, and then the woody and grassy quadrats were separated and looked at separately. For three of the four sites, consistent results were achieved (i.e. the category suggested by MAVIS overall was also suggested for the woody and/or grassy subsets, depending on which one had the majority of quadrats in each case, see Table 18), allowing a fair degree of confidence in the findings.

The grassy scrub quadrats were assigned to either MG5 (Carran and Rannagh) or CG2 (Roo). The links and overlaps between these two categories, particularly in how they relate to the Burren grasslands, have already been covered in the grasslands section above. It is interesting to note that it is only in the scrub sites that MAVIS assigns grassland quadrats to CG2 (as opposed to MG5), suggesting that the scrub sites have a more calcicolous suite of species.

The woody scrub quadrats did not emerge aligned to any of the NVC woodland or scrub categories. Instead, a suite of grassland categories were suggested. Two sites (Carran and Rannagh) were matched with MG1 (*Arrhenatherum elatius* grassland). This is a category of coarse grasslands, with frequent or abundant *Arrhenatherum elatius, Dactylis glomerata* and *Holcus lanatus* (Rodwell, 1992). The calcareous grassland type CG2 was reported for both woody and grassy scrub samples for the site Roo. It is clear that the grassy nature of even the woody scrub quadrats is a very important facet of the vegetation. A potential issue is that the presence of open ground species, or disturbance indicator species, can heavily influence the NVC category which MAVIS will

suggest. Kirby (2003a) gives the example of two woodlands of the same type which may classify differently if one is younger and still has some open ground species present. It is quite likely that this is one of the main reasons for the classification of the woody scrub quadrats as grassland types.

The remaining site, Knockans, produced mixed and uncertain results, with one of the categories suggested by MAVIS for the woody quadrats being a heath type which is highly unlikely to occur in Ireland. It is perhaps not surprising that this site is mis-classified by MAVIS - there is a relatively large amount of limestone pavement at this site, and it is well acknowledged (Rodwell et al., 2000) that the NVC does not cover limestone pavement in a simple manner. Rather than having one, or a few, catch-all categories, limestone pavement is dealt with by being broken into its constituent parts, such as exposed rock, woodland communities (in the grikes, for example), grassland communities for grassy patches on the rock, etc. It may be for this reason that MAVIS struggled to place the quadrats from Knockans satisfactorily in an NVC category. The categories assigned to the grassy quadrats, CG2c and MG5b, relate well, however, to the suggestions for other sites, and so may be accepted with some caution.

Rare/ notable species

The Burren is well known for its unusual flora (e.g. Webb, 1962b, Webb and Scannell, 1983, Nelson and Walsh, 1991, O'Connell and Korff, 2001). Forty of the species recorded during this survey were rare, or had restricted distributions, or were putative old woodland indicators. Only two non-native species were recorded, *Mycelis muralis* (recorded from four sites) and *Lonicera nitida* (one record only). The lack of alien species in general is encouraging, indicating a relatively intact native semi-natural flora.

Lonicera nitida was found at one of the scrub study sites (Rannagh). It is not listed in the 'Flora of Connemara and the Burren' (Webb and Scannell, 1983). This species is commonly planted in gardens (Webb et al., 1996), and Reynolds (2002) notes that it is a "*common relic of cultivation*" in Ireland, i.e. it is a species which typically remains close to where it was originally planted, which is normally near houses or gardens. Its presence at Rannagh may be explained by the fact that there was a dwelling, now long-abandoned, nearby (within 50m).

Mycelis muralis:

> "*Although it is likely that* Mycelis muralis *is not native in the Burren its status remains enigmatic…*" (Clabby and Osborne, 1999)
>
> "*This plant is so abundant and apparently so much at home on the barer parts of the Burren that most people find it very difficult to believe that it is not native.*"
> (Webb and Scannell, 1983)

"*Its occurrence in the Burren, Co Clare, is exceptional as it grows in profusion over large areas of the limestone pavement. This is unusual given its occurrence in the rest of Europe in the herb layer of base rich woodlands … or at the very least in shaded locations*"
(Clabby and Osborne, 1991)

Webb and Scannell (1983) stated that, to their knowledge, *M. muralis* had never been seen in Ireland in the ground flora of base-rich woods (its characteristic habitat in its native range in Europe). In this study it was found at three of the woodland sites and one scrub site. Clabby and Osborne (1991) found this species to be quite frequent in shaded situations in Ireland, recording it from beech, ash and hazel woodlands. Much additional work has been undertaken on this species in Ireland in recent years (Clabby and Osborne, 1994, 1999, 2000). Reynolds (2002) notes that this species was first recorded from the Burren in the mid to late 1930s, and she too notes its occurrence in woodland. Clabby and Osborne (2000) suggest that the range of suitable microhabitats found in limestone pavement areas help to explain the rapid expansion of the species in the Burren region. It is worth noting too, that while this species was apparently not recorded in the Burren until the 1930s, there are earlier records of it from other parts of the country – e.g. Co. Kildare in the mid-1800s (Moore and More, 1866, cited in Reynolds, 2002), and Clabby and Osborne (1994) found a record from the Dublin area in a publication from 1726.

The use of species as indicators of ancient status for woodlands has always been contentious. Those species which appear to be useful indicators in one region, often emerge as poor indicators in another (see for example the lists for multiple regions in Britain, Kirby, 2004b). The recently compiled Irish list (Perrin and Daly, 2010) was used to identify indicator species from the current dataset. Those occurring most commonly (and in ≥3 woodland sites) were: *Conopodium majus, Corylus avellana, Euonymus europaeus, Oxalis acetosella* and *Potentilla sterilis*. Another species which is a strong indicator (according to Rackham, 2003, Kirby, 2004b) and which was common in woodlands and scrub at the study sites was *Epipactis helleborine*.

To facilitate comparisons of numbers of indicators among sites, the indicator species lists (from Table 19 and Table 20) were cross-checked against the species recorded at each of the study sites (Table 31). Gortlecka and Glencolumbkille rated highest. Based on the cartographic evidence (see Chapter Two) Gortlecka is likely to be the oldest site (scrub symbols present on maps from early 1800s), with Glencolumbkille likely to be the next oldest (scrub symbols present on maps from late 1800s/ early 1900s). Carran is likely to be the oldest scrub site. These findings tie-in relatively well with the results using the indicator species.

Four additional indicator taxa were recorded from the study sites which do not form part of the main vegetation dataset (either they were recorded outside of the study plots or outside of the study season, or are not vascular plants). In light of their value as old woodland indicators, they are included here; the saprophytic vascular plant *Neottia nidus-avis* (present in ten of the 13 of Kirby's

lists, Kirby, 2004b), the parasitic *Lathraea squamaria* (present in twelve out of 13 lists) and the lichens *Lobaria pulmonaria* and *L. virens* (listed by 'LichenIreland' (2011) and Dobson (2005) as old woodland indicators). Glenquin becomes the highest rated site when these additional species are included (all four were found at this site). Cartographic evidence for woodland at this site in the past is lacking, but it is known to have been wooded for >40 years at least. Given the high number of putative old woodland indicators present, it is highly likely that even if this exact area was not wooded, there has been continuous, if patchy, woody cover in the vicinity.

Table 31 Numbers of putative old woodland indicator species recorded at each of the woodland and scrub study sites.

		Number of putative indicator species using lists from Table 19 and Table 20
Woodlands	Gortlecka	13
	Glencolumbkille	12
	Ballyclery	10
	Glenquin	10
Scrub	Carran	8
	Rannagh	8
	Roo	8
	Knockans	4

It was not expected to find so many putative old woodland indicators, given the history of low woodland cover in the Burren (especially around the mid-1800s, when it is likely that most tree cover was removed - see section on the history of grazing and land use in the Burren, Chapter One). It should be borne in mind, however, that some of the species put forward on the lists for Britain may not necessarily act as reliable old woodland indicators for Ireland.

Vegetation communities – relationships, diversity and influential variables

Relationships among the three habitat types

Investigation of the entire dataset (i.e. quadrats from woodland, scrub and grassland analysed together) using non-metric multidimensional scaling (NMS) revealed one dominant axis of variation (77% of the variation, compared to 12% on the next axis). The relatively extreme separation of the quadrats along one main axis of variation is not surprising, given that three different habitat types were chosen a priori for study, and further, that these three habitat types are thought to exist along a successional continuum. The variation between quadrats at opposite ends of the ordination was driven by differences in factors such as vegetation height and canopy cover at one end of the spectrum, and differences in light penetration and consequent cover of grasses and field layer plants at the other. Species such as hazel and ivy were most associated with the position of the woodland quadrats at the upper end of the axis, while *Festuca ovina/rubra*, *Plantago*

lanceolata, Anthoxanthum, Centaurea nigra, Trifolium pratense and *T. repens* were most associated with the grassland quadrats at the opposite end.

The four habitat types (scrub was split into 'woody' and 'grassy' quadrats) plotted quite separately on the ordination. The woodland quadrats were the most tightly clustered, indicating a relative degree of homogeneity. The scrub quadrats span between the woodland and grassland points, with the woody scrub quadrats showing more variation along axis 2 (the main axis of variation), and the grassy scrub quadrats varying more across axis 1. Interestingly, the grassy scrub quadrats appear to be more species rich - the variable 'number of species' appears to be associated with their position on the ordination. High values for Simpson's Diversity Index are, however, associated more with the 'true' grassland points. This reflects the findings presented in Table 15.

Other outcomes of note are the fact that the woodlands appear to have higher soil fertility (Ellenberg scores), greater cover of low woody species and of litter than the grasslands. On the other hand, the grasslands have more ruderal species and are wetter (Ellenberg moisture scores) than the woodlands. The higher fertility which is suggested for woodland quadrats may stem from the fact that cattle are known to congregate in woodlands, especially in times of inclement weather. Their concentrated dunging may lead to raised fertility levels.

Variation in vegetation composition within the three habitat types

The vegetation of each of the three habitat types was analysed separately. The woodland NMS ordination showed that there was a fair degree of homogeneity of plant community composition within two of the woodland sites (Site 1, Ballyclery and Site 4, Gortlecka), with the other two sites being more heterogeneous. Overall, however, there was quite a lot of overlap, suggesting that the woodland sites are relatively similar in vegetation composition. The ordination result highlighted the importance of canopy species in determining similarity between quadrats. Samples dominated by hazel and hawthorn plotted at opposite ends of axis 1 (which explained 65% of the variation in the data), while ash and ivy plotted at opposite ends of axis 2 (28% of variation). Amount of light penetration and diversity were positively associated with hawthorn. Wetness, vegetation height, amount of litter and species which are good competitors, were all associated with the ash-dominated quadrats; and cover of low woody species, stress tolerant species and higher grazing levels were related to the quadrats with large amounts of ivy. This latter finding is unexpected – the presence of substantial amounts of ivy in a woodland usually indicates a low or absent grazing regime (e.g Kirby, 2001), but this generally refers to ivy cover on the woodland floor. When measuring the cover of ivy in this survey, its occurrence in all vegetation layers was noted, and so it may be that there were large amounts of ivy in the shrub or canopy layers (rather than in the ground/field layer).

The scrub vegetation was shown to be distinct from both the woodlands and the grasslands, and within it, there was obvious separation between woody and grassy elements. The ordination solution had one very dominant axis (70% on axis 1, 20% - axis 2) - a gradient of decreasing light and increasing vegetation height and canopy cover. This separated the majority of the woody quadrats from the grassy ones. As with the overall ordination (i.e. with all three habitats included), the grass-dominated quadrats were more diverse, and the woody quadrats had higher litter cover and higher Ellenberg 'fertility' values. Also, similar species were associated with the woody and grassy ends of the gradient (e.g. hazel with the woody, and *Plantago lanceolata* and *Festuca ovina/rubra* with the grassy).

In the case of the grasslands, the variation was somewhat more evenly distributed between axes (31% - axis 1 and 53% - axis 2), and all four sites separated quite distinctly on the ordination. Soil-related variables appeared to be particularly important in helping to explain the variation between quadrats (and between sites), with % LOI being the most influential (strongly negatively correlated with axis 1, and moderately negatively correlated with axis 2). Soil texture, soil depth and soil fertility were important also. High cover of sedges characterised the site Slieve Carran (site 12), and a high percentage of ruderals was associated with Kilcorkan (site 11). Caher (site 9) was comparatively more species rich, with more low woody species and bare rock than the other sites, and Gregan (site 10) appeared to be the most heterogeneous site, from a vegetation composition point of view.

Grazing experiment – vegetation changes

The results presented for the grazing exclusion work need to be interpreted in the context of the short-term nature of the current study. The fenced exclosures have been erected with long-term survey in mind, and they will provide a means for monitoring vegetation change into the future. The findings presented here are but the beginnings of this longer-term work.

The initial richness and diversity of the three habitat types was plotted against the changes in richness and diversity, in order to assess if initial levels had any influence on the magnitude of any subsequent changes. It might be expected that sites with higher initial values might change more, but this was not found to be the case. For species richness, both scrub and grasslands had much higher initial values than the third habitat, woodland, but only grassland showed a change of large magnitude. With diversity, it was in fact the habitat with the lowest initial diversity (woodland), which showed the largest change.

(a) Woodland

During the course of the study the woodland flora within the fenced plots increased significantly in diversity but there was no such increase in the control plots. This indicates that, at least in the short-term, woodland plant diversity is increased by exclusion of grazers. To help with the interpretation

of this, a number of facets of the changes seen were analysed – e.g. changes in percent cover of elements such as bare ground, and also of individual species. One of the major changes seen in the ungrazed woodland plots was a decrease in the amount of bare ground, and a concurrent increase in field layer woodland plants (also found by Morecroft et al., 2001, McEvoy et al., 2006, Perrin et al., in prep.).

The increase in diversity may be relatively short-lived, however, as it is likely to be associated with the initial recolonisation of the bare ground created by the trampling of grazing animals. Several other studies have demonstrated that longer-term surveys are necessary in order to adequately document changes in plant diversity which may occur in woodlands when grazers are excluded, as these changes may involve initial increases in diversity, followed by a decrease (e.g. Kelly, 2000, Perrin, 2002, Casey et al., 2006, Perrin et al., in prep.). Morgan and Jefferson (2007), in a review of long-term surveys, noted that studies which were of a high quality, but short-term, often failed to provide results, or gave findings which were different or reversed after a longer study period. McEvoy et al. (2006) found, in their survey of >100 woods in Northern Ireland, that grazed woods are significantly more species rich than ungrazed woods, lending more weight to the possibility that the diversity increase recorded in this study will indeed be temporary.

Perrin et al. (in prep.) suggest that the different rates of change in diversity which they documented at two woodland sites may be related to the existence of a skeletal soil over limestone pavement at one site – this may limit the ability of certain species to achieve dominance and out-compete other species. It will be interesting to see how the woodlands in the Burren fare in this respect, being also on thin soils over karst limestone terrain.

A number of individual species exhibited measurable (and significant) increases within the fenced plot during the timeframe of the study. Two species exhibited notable increases – *Geum urbanum* and *Oxalis acetosella*. Cooper and McCann (2011) also found increases in *G. urbanum* (they recorded *G. urbanum/rivale*, noting that while all specimens could not be separated, most were clearly *G. urbanum*), but these were not statistically significant. They class this species as 'graze-intolerant'. The pattern recorded in the current study for *O. acetosella* was particularly marked, with increases of several orders of magnitude observed in the absence of grazing/trampling (see Figure 32). As *O. acetosella* is an unpalatable species (Putman et al., 1989), it is likely that it is the release from trampling pressure which is driving the increase seen, rather than the lack of grazing. Latham and Blackstock (1998) acknowledge the dual action of large grazing animals in woodland habitats: "*These changes appear to be a consequence of the removal of both herbivory and physical disturbance caused by large herbivores.*" Perrin (2002) found that, after 30 years of experimental exclosures in the Killarney woods, *O. acetosella* was almost entirely restricted to grazed plots, having been outcompeted within fenced plots. Cooper and McCann (2011) also report a decline in

this species over a ten-year period. This highlights again the importance of longer-term studies into woodland ground flora changes.

Other species showing strong increases in the short term included the grass *Brachypodium sylvaticum* (which increased dramatically in cover in some quadrats), *Fragaria vesca*, *Rubus fruticosus* agg. and *Viola riviniana/reichenbachiana*. Putman et al. (1989) noted *B. sylvaticum* as being suppressed by grazing, and hence tending to flourish following exclosure. However, in contrast, McEvoy et al. (2006) noted that grasses tend to become more abundant in grazed woodlands compared to ungrazed ones, presumably due to their high tolerance of grazing. This is supported by Kelly (2000, 2005) and Corney et al. (2008). Several authors have found bramble to be one of the species which increases most significantly in the absence of grazing (Putman et al., 1989, Latham and Blackstock, 1998, McEvoy et al., 2006, Corney et al., 2008, Van Uytvanck and Hoffmann, 2009, Cooper and McCann, 2011, and Perrin et al., in prep.). Morecroft et al. (2001) found no significant change in bramble cover in a two-year study in Wytham Woods in England, but this is obviously a very short timeframe over which to assess change.

(b) Grassland

Within the grassland fenced plots there was a significant decrease in both species richness and diversity, pointing to the crucial role that grazers play in maintaining grassland plant communities. This finding, though perhaps surprisingly clear-cut for a short-term study, is not without precedent. Studies such as those of Gibson (1997), Hansson and Fogelfors (2000), Jacquemyn et al. (2003), Moles et al. (2005), Pavlu et al. (2007), Enyedi et al. (2008), Deenihan et al. (2009) and Skornik et al. (2010) have all found lower species richness and/or diversity in ungrazed grasslands, when compared to grazed sites. The rapidity of the changes seen here contrasts with the findings of Brown et al. (1990), who, in a study of the mechanisms controlling insect diversity in calcareous grasslands, state that there may be a delay in seeing the effects of cessation of grazing, with permanent grasslands left ungrazed sometimes taking years to lose floral diversity. They also note that these sites may for some time contain more insect species than grazed areas.

Perhaps the most dramatic finding of this part of the study was the rapid, and in some cases, complete loss of certain species. *Euphrasia* spp were completely lost from inside the fenced plots, across all four grassland study sites. *Linum catharticum*, *Odontites vernus* and *Rhinanthus minor* were also lost from those sites in which they had initially been recorded. Other species showed substantial declines – e.g. *Cerastium fontanum, Prunella vulgaris, Trifolium pratense* and *T. repens*. Smith et al. (2000) highlight the importance of cattle grazing for the continued occurrence of *R. minor* – the gaps created by cattle hooves allow germination of this species, and grazing animals additionally open up the sward by defoliation and trampling. Similarly, Ward (1990) recorded that *L. catharticum* did well in areas disturbed by grazing, but became much less frequent as the vegetation got taller and more dense, and Willems (1983) reports the loss of this species

upon cessation of grazing. Moles et al. (2005) in their study in Burren grasslands noted that "*…the continuing creation of small gaps* [by large grazing animals] *was important in maintaining species richness*." The amount of bare ground in the grasslands decreased in this study, leaving less space and opportunity for the colonisation or spread of less competitive species. A study in a dune grassland in the north of Ireland (Riley, 1984) focussed on the changes seen when grazers were introduced, at a high stocking density, to a previously ungrazed (for 14 years) area. Interestingly, they found that species such as *Euphrasia* agg. and *L. catharticum* increased, as did *Trifolium repens* (although they ascribe the increase in the latter to increased nutrient levels from cattle dung). Willems (1983) records the loss of *T. pratense* from chalk grassland in a grazing exclusion study in England.

Conversely, some species were found to have increased significantly in the absence of grazers, namely *Potentilla erecta* and *Pteridium aquilinum*. The significant increase in bracken is of some concern because, although this is a native species, it is also invasive. It was found at all twelve study sites, and the influence of cessation of grazing on its occurrence is noteworthy. Pakeman and Marrs (1992) state that areas dominated by bracken are generally species poor, both floristically and in terms of their fauna, and that its spread can lead to the loss of habitats of high conservation value. Marrs et al. (2000) hypothesise that bracken-dominated communities may occur in mid-successional positions, for example between grassland and woodland. Thus the possible future spread of bracken, particularly in the grassland sites, in the Burren is worrying. The increase of *P. erecta* inside the fenced exclosures is unexpected – a study on the effects of grazing management on the flora of turloughs found that this species was positively affected by grazing (Moran et al., 2008).

The reasons for the loss or decrease of certain species may include the rapid and dramatic build up of litter, and the relative expansion of competitive grass species. Bates (1988) reported a substantial build-up of litter inside the upper fenced 'Bonham' exclosure in the Burren National Park. Willems (1983), Morris (1990), Bullock and Pakeman (1997 - though this study is on heathlands), Moles et al. (2005) and Moran et al. (2008) all cite litter build-up as having a potentially negative impact on plant diversity. Willems notes that when litter accumulates there can be a change in microclimate – light measurements above the vegetation and at ground level (i.e. under the vegetation and litter) showed large differences, and these were "*clearly correlated with the variation in litter density*". Jacquemyn et al. (2003) found that after four years of grazing exclusion the percentage light penetration to the soil surface was almost zero, compared to a rate of 30% in grazed plots. Morris (1990) describes the changes in microclimate as 'considerable', with lower temperatures and higher humidities at ground level in ungrazed grassland swards. Williams et al. (2009), writing about the Burren winterages in particular, state that if they are not grazed litter builds up and smothers "*many of the light-dependent herbs*". This leads firstly to shifts in species abundances, and then to the loss

of species. The loss of four species has been documented in this study, over a period of just 24 months.

Many authors, including Willems (1983), During and Willems (1984), Dunford (2002), Moles et al. (2005) and Moran et al. (2008), mention that more aggressive grass species can come to dominate in the absence of grazing, causing a reduction in forb species. This was echoed here, with a significant increase in total cover of grasses, and with species such as *Festuca ovina/rubra, Arrhenatherum elatius* and *Anthoxanthum odoratum* doing particularly well.

(c) Scrub

It proved very difficult to elucidate patterns from the changes seen in the scrub vegetation. Even splitting the scrub into its grass-dominated and woody species-dominated portions did not produce detectable or measureable changes. This habitat is so heterogeneous in nature that considerably longer timeframes will probably be needed for the study of changes in its vegetation. One of the few discernable changes found was the increase in the amount of litter. This was significant in both the grassy and the woody quadrats, and mirrors findings from the grassland sites. Studies on changes in hazel scrub in the Burren (Bates, 1988, Byrne, 2001, Moles et al., 2005, Deenihan et al., 2009) have all documented measurable changes, but have all run for longer time periods (between six and 16 years). It is most likely the case that similar changes (e.g. expansion of hazel, build-up of litter and probable loss of plant species diversity) will be noted within the current grazing exclosures given a longer time period. In a study involving the cessation of goat grazing on the Canary Islands, Fernandez-Lugo et al. (2009) failed to demonstrate an effect during a four-year study. They attribute this to a low and irregular grazing pressure, and also to climatic variability, and both of these factors may be important here also.

Conclusions

The exclusion of grazing animals from woodlands and grasslands had dramatic and rapid effects. In woodlands the amount of bare ground decreased, and the cover and diversity of herb-layer plants increased. The grasslands showed a remarkable build-up of litter, and diversity and species richness dropped. Some species were lost altogether from grassland sites. All of these findings are in broad concurrence with findings from elsewhere.

Changes were seen in scrub sites, but they were too variable to form clear patterns, even with the splitting of the quadrats into ‘woody’ and ‘grassy’ groups. Longer timeframes are clearly needed in order to monitor changes in heterogeneous scrub communities.

Chapter Four:

Snail community structure in a limestone landscape – its make-up, variability and relationship with habitat

Figure 58 *Helicella itala* adult in grassland in the Burren, top and side views.

Introduction

Molluscs are an important group of invertebrates in many terrestrial ecosystems (Chatfield, 1976, Kerney and Cameron, 1979, Barker, 2001). Their low mobility, small size and sensitivity to environmental changes help to make them good habitat-quality indicators (Killeen, 2010). Terrestrial snails have been well-studied taxonomically and are reasonably easy to identify. Additionally, their shells are persistent and they are easily preserved, facilitating collection and study. The distribution of mollusc species in Ireland is quite well documented (for example: Kerney, 1999, Byrne et al., 2009). However, terrestrial mollusc ecology and community structure have not been well-studied (exceptions include some wetland species which are protected under the EU Habitats Directive (EEC, 1992), e.g. *Vertigo geyeri*). In contrast, there are a number of international works which deal in detail with molluscan ecology, some of which are discussed below.

This chapter details the snail fauna of woodland, scrub and grassland habitats in the Burren and assesses the communities of each of the chosen habitats. Drivers of variation are also investigated.

The Irish molluscan fauna

The most recently published checklist states that there are 163 native and naturalised taxa of non-marine molluscs in Ireland (Anderson, 2005). In 2009 a 'Red List' of non-marine mollusc species of conservation concern in Ireland was published by the National Parks and Wildlife Service (NPWS) (Byrne et al., 2009). In this, the total number of non-marine mollusc species listed for Ireland is 177, of which 150 are deemed to be native – i.e. they have established population(s) in the wild. Of these, 32 are species of slug, from ten genera (Anderson, 2005, Moorkens and Killeen, 2009). The habitat requirements of slugs, and many traits relating to morphology, reproduction and physiology, are detailed in the databases in Moorkens and Killeen. There is no up-to-date identification key for slugs in Britain and Ireland, the most recent being Cameron et al. (1983). However, Moorkens and Killeen (2009) state that one is in preparation by Dr Roy Anderson.

Almost 80,000 molluscan records from Ireland were used to create the 'Red List', and all of the 150 species of native non-marine molluscs found in Ireland were evaluated. This involved their conservation status being assessed using International Union for the Conservation of Nature (IUCN) criteria (IUCN, 2001, IUCN, 2003). In addition, expert judgement and opinion was employed, in particular where data were lacking. Of the 150 species, two are thought to be extinct in Ireland, five are critically endangered, 14 are endangered, 26 are vulnerable and six are near threatened. This amounts to 53 species out of the total of 150.

Some species of mollusc have populations of "*significant international worth*" in Ireland (Byrne et al., 2009). One such species is *Leiostyla anglica*. This species is almost endemic to Britain and

Ireland, having only small and isolated populations elsewhere in north-west Europe (Kerney, 1999, Byrne et al., 2009). Ireland holds at least one-fifth of the global population of this species. The 'Red List' notes that it is declining in Ireland. Another species which is nearly endemic to Britain and Ireland is *Acicula fusca*. This tiny snail is probably under-recorded, but is nonetheless undergoing a significant decline across its range (Kerney, 1999, Byrne et al., 2009, Killeen, 2010).

The molluscan fauna of Ireland is relatively depauperate compared to neighbouring countries, and is made up of species which either survived the last glaciation, or have made their way back into Ireland since then (Cameron, 2003, Cameron et al., 2009). Some species which have quite strict habitat affinities in Britain and elsewhere are found in a much wider variety of habitats in Ireland (Kerney and Cameron, 1979, Tattersfield, 1993, Kerney, 1999). For example, *Leiostyla anglica* and *Acicula fusca* are both more or less limited to old woodlands in Britain (Wardhaugh, 2011), whereas in Ireland they are also found in woodlands of more recent origin, scrub and even grasslands (Tattersfield, 1993). Some species which are common and widespread in Ireland, and which are not obviously limited to wetter habitats, are elsewhere described as 'hygrophiles' (species which inhabit moist or marshy places) - for example, *Carychium tridentatum* (Kappes et al., 2006) and *Cochlicopa* cf. *lubrica*. It is likely that the year-round mild and moist conditions (Adam et al., 1977, Webb and Scannell, 1983, Mooney and O'Connell, 1990), and the relatively constant and high humidity levels are important factors in explaining the wider niches, along with the increased niche-availability due to the depauperate fauna (Heslop Harrison, 1951a). For these reasons, the categorisation of habitat affinities for the mollusc species in Ireland can be challenging.

Ecological studies on molluscs in Ireland

There have been relatively few detailed ecological studies of terrestrial molluscs (excluding wetland species) in Ireland in the past 50 years (Bishop, 1977, Tattersfield, 1993, Speight et al., 2000, Moorkens and Gaynor, 2003, Platts et al., 2003, Gittenberger et al., 2006). Two other studies deserve a mention - Henry (1914), in a paper titled 'Woods and trees of Ireland', listed six mollusc species as occurring only in old woods in Ireland. O'Donovan (1987), in a PhD based in the Burren, included a chapter on the snail species *Helicella itala* as it was deemed to be "*the most conspicuous and probably dominant invertebrate*" in Burren grasslands. The study was based in an area of *Sesleria caerulea*-dominated grassland in the Burren National Park. The opening paragraph states that *H. itala* was found "*almost to the exclusion of other molluscs in open grassland*" – a statement which illustrates how a large, conspicuous species such as this can overshadow the multitude of tiny species which may be more abundant and widespread. She investigated the population structure and food preferences of *H. itala*, as well as the effects of its grazing on biomass and nutrient turnover. She concluded that *H. itala* has a biennial life cycle (confirmed in Falkner et al., 2001), and that population decreases seen in summer (mainly in the smallest size classes) were due to a combination of low rainfall and maximum sunshine hours. The snail

exhibited clear food preferences, and she found that the returns of nitrogen and phosphorus to the soil in snail faeces may be important, particularly as the system may be nutrient-constrained.

Ecological studies outside of Ireland

Outside Ireland there have been many studies where mollusc species and communities were related to particular habitats and environmental conditions. For example, Nekola (2010) surveyed a large number of acid sites in North America (processing approximately half a million individual molluscs) and discovered that approximately 10% of the fauna of North America can be said to favour acidic (i.e. low pH) sites. Latitude and moisture level were two of the main drivers of the variation that he found between these sites. In a series of publications, Horsak (Horsak and Hajek, 2003, Horsak, 2006, Horsak et al., 2007) examined the molluscan fauna of fens, and related this to the vegetation, and to soil and water chemistry properties. He found that, at least for fens, sites were classified similarly (using ordination techniques) whether mollusc or vegetation species data were used (Horsak and Hajek, 2003). He also confirmed that the variation in mollusc communities between sites could be explained by mineral richness (levels of calcium, magnesium, iron and potassium), as well as pH and conductivity. In his 2006 paper, he outlined how pH is correlated with species richness only in mid-pH ranges – at very base-rich sites mollusc species richness drops off.

Many studies relate mollusc diversity to gradients such as pH and mineral richness, but few have looked at gradients across habitats – e.g. from open to wooded vegetation. An exception is Davies (1999), who investigated the molluscan fauna across a woodland-grassland boundary. Davies noted that "*there have been few substantive studies across environmental boundaries*", and thus that the understanding of how communities relate to one another or overlap is quite speculative. He found that although mollusc communities do respond to changes in vegetation, their response is not always directly related to that of the vegetation. Barker and Mayhill (1999) relate patterns of diversity in molluscs in New Zealand to habitat. They found that sites with different vegetation types had different snail species assemblages. In woodlands, they found species richness correlated with floristic diversity and the pH of the litter. Ondina and Mato (2001) investigated the influence of three vegetation types on snail communities in northern Spain. They too found different communities associated with each type, and were able to assign certain mollusc species to certain vegetation communities, based on the frequency of their occurrence. The altitudinal patterns of molluscan communities in the south of France were examined by Aubry et al. (2005), who found that, in general, species density and species richness decrease with increasing altitude. Hoffmann et al. (2011) investigated the land snail faunas in the Altai mountains in Russia along a climatic gradient. They found that snail species were sorted along the gradients – few occurred ubiquitously, and they found that a few species may be indicators of vegetation types.

Two important reference works dealing with molluscs and how they relate to their habitats and environment are Boycott (1934) and Falkner et al. (2001). Boycott is, at this stage, dated, but is still a valuable starting point. Falkner et al. (2001) produced a database containing information on the distribution and macrohabitat and microhabitat preferences of mollusc species found in Ireland, Britain and north-west Europe, along with morphological details, reproductive traits, tolerances and food types. This resource can be queried to allow, for example, species lists from geographic areas/habitats/specific environmental conditions to be created. Findings from the field can then be compared to these lists of 'expected' species.

Studies of the malacofauna of woodlands, grasslands and scrub

In addition to the works mentioned above, a number of studies have been carried out focussing on particular habitats. A variety of authors have investigated molluscan faunas in woodlands (a selection of recent studies would include: Gardenfors et al., 1995, Suominen, 1999, Cameron and Pokryszko, 2004, Martin and Sommer, 2004b, Schilthuizen et al., 2005, Cameron et al., 2006, Kappes et al., 2006, Kiss and Magnin, 2006, Sulikowska-Drozd and Horsak, 2007, Gotmark et al., 2008, Horsak et al., 2010). Schilthuizen et al. (2005) and Cameron et al. (2006) were based in calcareous or karst woodlands. Schilthuizen et al. looked at a series of pairs of primary and secondary forest sites on limestone hills in Borneo. There are large numbers of endemic species in this area, and while diversities were not found to differ between primary and secondary forests, the community composition was altered, with fewer, or less frequent, endemics in secondary sites. Cameron et al. investigated the snail faunas of calcareous woods in southern England, and found them to be species rich, but relatively uniform.

With respect to the molluscan faunas of grasslands, much work has been carried out in recent years in central Europe (mainly Switzerland and Romania) by Baur and colleagues (e.g. Niemela and Baur, 1998, Baur et al., 2006, Baur et al., 2007, Boschi and Baur, 2007a, Boschi and Baur, 2007b, Boschi and Baur, 2008, Stoll et al., 2009). Among the more relevant to the current study are the works centring on the nutrient-poor calcareous grasslands of the Swiss Jura mountains by Boschi and Baur. Effects of management intensity, species of grazer and past management on molluscan communities have all been investigated. Overall, low intensity grazing regimes were found to be more beneficial for molluscs than higher grazing pressures. Interestingly, no effect of species of grazer was found. Past land use was found to have a strong influence on the molluscan community, and plant species richness was generally found not to be correlated with molluscan species richness.

The molluscan communities of grasslands, both managed and abandoned, have also been studied by Magnin (see Magnin et al., 1995, Magnin and Tatoni, 1995, Labaune and Magnin, 2001, Labaune and Magnin, 2002). Their findings reveal that grazing levels which lead to a homogeneous

short sward cause a reduction in snail diversity and abundance, and that habitat structure is more important that vegetation species composition in determining the molluscan community.

Three studies were found which looked at the malacofaunas of scrub habitats – Cameron and Cook (1998), Barker and Mayhill (1999) and Cameron et al. (2003b). Cameron and Cook investigated forest and scrub faunas in northern Madeira and found high numbers of endemic species. In a study encompassing a number of vegetation types, including many scrub study sites, Barker and Mayhill aimed to elucidate relationships between mollusc assemblages and their habitats. They found that sites with differing vegetation types had different snail species, and that these differences were driven by a number of factors (e.g. canopy tree species, floristic diversity, altitude, litter mass, etc.). Finally, Cameron et al. (2003b) surveyed a square kilometre of maquis habitat in Crete, with a view to comparing results with those of some other studies using similar methodologies. The Cretan scrub was found to be modestly species rich, with high densities of molluscs, and homogeneous on a local scale. None of these studies, however, are directly referrable to the current work in hazel scrub.

Some essential requirements

Molluscs, unlike many other terrestrial invertebrates, are reliant to a large degree on moisture for their day-to-day survival (Asami, 1993). They have a wet skin, and lose water constantly when they move due to the production of mucus (Kerney and Cameron, 1979). To avoid drying out many species are active mostly at night or during wet weather, and when conditions are unsuitable they may become inactive. Humidity (of soil and/or air) and microclimate are thus of great importance to snails and slugs (Kerney, 1999, Kiss and Magnin, 2006, Cejka and Hamerlik, 2009, Kuczynska and Moorkens, 2010). For most species, optimum conditions exist when humidity is high and relatively constant, not falling low for long (Kerney and Cameron, 1979).

Ondina and Mato (2001) point out that woodlands are good mollusc habitats due to their effectiveness as temperature and humidity buffers (see also Packham et al., 1992), in addition to the wealth of microhabitats they provide. It is essentially only those species which can withstand greater variations in temperature, light intensity and humidity which can survive in open habitats (e.g. grasslands). Dickinson et al. (1964), in a study on flora and microclimate in the Burren, found that within woodlands there was much less light, it was cooler, and there was higher relative humidity during the day, compared to conditions in open habitats. Similarly, MacHattie and McCormack (1961) compared conditions on two ridges in Canada; one wooded and one which had been cleared. They found that on the wooded ridge the minimum air temperature was 2^{o}C higher, and that evaporation was at least half that on the cleared ridge. Thus exposure to different and perhaps critical levels of drying will be significant aspects of the gradient 'grassland – scrub – woodland' which is under study here. Degree of shade tolerance and humidity requirements (or tolerance of desiccation) are inter-linked in this context.

Many attempts have been made to assign mollusc species to groups such as specialists or generalists, shade-lovers or open-ground species, wetland or dry-land species, etc. (e.g. Boycott, 1934, Davies, 1999, Falkner et al., 2001, Ondina and Mato, 2001, Kappes et al., 2006, Boschi and Baur, 2007). Some of the results are contradictory, placing the same species in different categories. This is not surprising due to the complexity and overlap of the ecological needs and tolerances of different species in different habitats and/or geographic locations. Kerney (1999) gives the example of *Ashfordia granulata*, a species which is relatively common in open habitats in western parts of Britain, but which is restricted to sheltered, more humid habitats in the south-east. He proposes that higher general levels of humidity in western Britain may be responsible for the scarcity of some xerophilic (i.e. of warm dry environments) species, e.g. *Pupilla muscorum* and *Vallonia costata*, in apparently suitable habitats there.

One of the other major factors known to dictate the occurrence and diversity of molluscs is the availability of calcium (Anderson, 1977, Martin and Sommer, 2004a, Nekola, 2010). This is an extremely important macronutrient for land snails (Dallinger et al., 2001, Cernohorsky et al., 2010), being used in shell construction and reproduction. One way to approximate the calcium present in a habitat is by using pH values as a proxy, as these have been found to be highly correlated (e.g. Sjors and Gunnarsson, 2002, Martin and Sommer, 2004a, Kappes et al., 2006, Cernohorsky et al., 2010). It is generally accepted that more calcareous sites support more molluscs than less calcareous ones (in fens and woodlands for example: Gardenfors et al., 1995, Kappes et al., 2006, Cernohorsky et al., 2010).

Aims of this chapter

This study aims to document the terrestrial snail communities present in woodland, scrub and grassland in the Burren region in the west of Ireland. Notable species and rarities are highlighted and discussed, as are species that are common elsewhere but were not found during this study. This project also aims to ascertain how distinct the snail communities in the three chosen habitats are from one another, and to what extent they relate to the plant communities and other habitat variables recorded.

Methods

Study area and study design

The study area for this survey was the Burren, a karstic region in the west of Ireland. This area is located mainly in north Co. Clare, and extends into adjacent areas of similar terrain in Co. Galway (see Chapter One). The Burren is famous as one of the most biologically interesting and biodiverse areas in Ireland (Webb and Scannell, 1983, Osborne and Jeffrey, 2003, Viney, 2003). However, detailed studies on the molluscan fauna of the region have been few. Those that do exist are largely non-systematic and/or unpublished. Geology, climate and other details on the region are provided in Chapter One.

This study concentrated on three habitat types: woodland, scrub and grassland. These habitats were chosen because they form part of a dynamic continuum which is of great interest and current relevance due to recent increases in scrub (mostly hazel) encroachment in the area (Dunford and Feehan, 2001, O'Donovan, 2001, The Heritage Council, 2006). Woodland in the Burren is dominated by hazel, a multi-stemmed shrub or small tree. Woodland sites have a closed canopy which is >5m tall, and possess a typical woodland ground flora. The scrub is also hazel-dominated, but hazel cover is patchy, and the bushes are <5m tall (Fossitt, 2000, Day et al., 2003), and more usually <3m tall. Hazel scrub is a very heterogeneous habitat, with some areas dominated by woody plants and others dominated by herbaceous plants. The scrub was split into 'woody' and 'grassy' sub-categories in some of the analyses to allow further elucidation of patterns (refer to Chapter One for rationale). The grasslands included in the study were semi-natural and generally species rich.

A network of study sites was selected - four in each of woodland, scrub and grassland (Chapter Two). At each of the sites, two 20 x 20m plots were marked out (see experimental design section, Chapter Two). Inside each plot was a grid of five fixed 2 x 2m quadrats, used for vegetation sampling. Mollusc samples were taken immediately adjacent to each of these (see below).

Field and laboratory methods

Sampling was carried out in October and November of 2006. Autumn is a good time of year to sample for molluscs as the weather is likely to be suitable – damp but not yet too cold (Cook, 2001). It also ensues the peak reproductive period of many mollusc species (see Chapter Five), thus ensuring that there should be many individuals present and maximising the chances of a more complete species inventory.

In the field, snails were quantitatively sampled using 25 x 25cm quadrats. Ten of these were collected from each site (giving a total of 120 samples). Within each quadrat all vegetation (field

and ground layer), litter and loose surface soil were removed and bagged (Cameron, 1982). Studies have shown that the collection of quantitative litter samples (and later sorting in a lab) provides more comprehensive results than direct searching alone (Oggier et al., 1998, Cameron and Pokryszko, 2005). Further, it is less destructive than the removal of soil and yields almost as complete a result (Oggier et al., 1998, Moorkens, 2003). Care was taken while sampling not to unduly shake or otherwise disturb overhead vegetation, in order to try to avoid inadvertently including arboreal species.

Samples were dried in the lab and weighed (to provide an estimate of phytomass and available litter habitat). Phytomass in this case is taken as the ground vegetation (vascular plants and bryophytes), litter (dead plant material), and also any mollusc specimens present (alive or dead). The samples were then hand-sieved into four size fractions (<0.5mm, 0.5-1mm, 1-5mm, >5mm). The <0.5mm fraction was discarded, as this contained only dust and shell fragments. The >5mm fraction was inspected for the presence of large snails, and then also discarded. The two middle fractions were carefully sorted through and searched by eye for snails, which were removed using soft forceps, counted and identified. A fully labelled reference collection of all species identified was made. In this chapter it is the data from the >1mm size fraction which are used.

Data collected

Slugs

This study deals only with terrestrial snails - slugs were not included. They were excluded because the sampling, storing and identification methods required are quite different to those employed in the study of shelled molluscs. Additionally, their activity is dependent on weather conditions to a much larger degree than for shelled molluscs. As an example, du Feu (2010) searched for slugs two nights in a row on the Isle of Skye, in the same place, at the same time. He writes that the "*only difference in the events was in the weather condition - it was raining on the first night, and dry on the second*." Eight species, with a mean abundance of 4.75, were recorded on the first night, while only six species, with a mean abundance of 3.16, were found on the second.

Adult, immature or dead?

All specimens were recorded as being 'adult', 'immature' or 'dead'. Specimens were listed as 'dead' if the shell was empty, and it was obvious that the animal had been dead for some time. This was ascertained by examining the shell for bleaching, damage, loss of colour and shell structure. Some shells were empty but appeared fresh – these could not be categorised with certainty as dead. As a result, some 'recently dead' specimens may have been counted in the 'alive' category. 'Dead' specimens were not further subdivided into adult and immature. The distinction between alive and dead is important, because in lime-rich areas shells may persist for many years in a subfossil condition (Cameron, 2003). It is thus important that they be separated from the main dataset, as

long-dead shells do not constitute evidence that a species is still present at a site (Kerney, 1999). Cernohorsky et al. (2010) in a study aimed at investigating the effects on results of including only living, or living and dead, specimens found that there was 'differential preservation' of shells among sites with differing soil chemistries. This lead to distortion of estimates of species richness and abundance, pointing to the importance of distinguishing between fresh and long-dead shells.

Immature specimens can sometimes be difficult to differentiate from adults of the same species – e.g. both *Columella* species (Paul, 1975a). If the shell had a lip and/or teeth, then it was identified as an adult (Cameron, 2003). However, adults of many species have neither, and some specimens required further examination of a number of more subtle characteristics. These include size (the size of the specimen is compared to the size of adults for that species given in reference books) and number of whorls (juveniles have fewer whorls than adults).

Species identification and nomenclature issues

Species were identified using Kerney and Cameron (1979) and Cameron (2003). Additionally, two sources of reference material were accessed: one, a privately held collection in Ireland, and the second, the various collections held at the Royal Belgian Institute of Natural Sciences (RBINS) at the Natural History Museum in Brussels (two ten-day visits were made in 2007). Nomenclature follows Anderson (2005).

A number of potential determination problems arose during the course of the labwork, pertaining especially to the identification of juveniles of some species, and also to dead or damaged specimens. All of these issues were resolved either by referral to an expert, or by comparison with verified reference collections. Identifications were 'quality-controlled' by random checking of specimens by an expert.

Among the most common issues arising were difficulties in telling apart the juveniles of some closely related species:

- *Cochlicopa* cf. *lubrica* and *C.* cf. *lubricella*
- *Columella aspera* and *C. edentula*
- *Oxychilus alliarius* and *O. cellarius*
- *Vitrea contracta* and *V. crystallina*

It is not uncommon for such issues to be encountered – for example, Valovirta and Vaisanen (1986).

Anderson (2005) stated that the "*taxonomy of* Cochlicopa *in Europe is difficult and confused*" and noted specifically that telling *C. lubrica* and *C. lubricella* apart in the field is challenging. He recommended that they be listed as *C.* cf. *lubrica* and *C.* cf. *lubricella*. A similar situation exists regarding the genus *Euconulus*. Hence, the *Euconulus* species found during this survey is listed as

E. cf. *fulvus*. Anderson (2005) also noted that *Vallonia excentrica* may comprise two paraphyletic taxa and it was recommended that the species be listed as *Vallonia* cf. *excentrica*.

Molecular studies have confirmed the assertion that *Balea heydeni* and *B. perversa* are distinct species (Gittenberger et al., 2006). Gittenberger et al. reported that although *B. heydeni* was known to occur in Europe, it had, since its description in 1881, been either "*completely overlooked or regarded as a synonym*" of *B. perversa*. It has become clear that *B. heydeni* is common in Ireland, while *B. perversa* is rare and declining (Gittenberger et al., 2006, Byrne et al., 2009). Specimens found during this study were checked by experts, and confirmed as *Balea heydeni*.

Other data collected

Detailed data were collected on the vegetation and soils at the twelve study sites (see Chapters Two and Three for details), along with a number of relevant environmental parameters (see Table 32 for a summary). The grid reference was recorded at each site, and thus records from this survey could be compared with existing molluscan records. All records will be submitted to the Irish Molluscan Recorder, to the National Biodiversity Data Centre (NBDC) and to NPWS.

Data analysis

To measure the extent to which the suites of species from the three habitats were different, the Sørensen coefficient (S_s) was calculated (Kent and Coker, 1992). Values range from 0 (no species in common) to 100 (species lists exactly the same).

$$S_s = \frac{2a}{2a + b + c}$$

a = number of species common to both lists
b = number of species in first list
c = number of species in second list

Differences between sites in the mean number of snails and the mean number of snail species were tested using one-way ANOVA where data were normal, with approximately equal variances. These were followed by a post hoc Fisher's LSD (Least Significant Difference) test to establish exactly which pairs were different (Dytham, 2003). Where data were non-normal, or where variances differed significantly, and transformations were unsuccessful, Kruskal-Wallis tests were used. These were followed by pairwise comparisons using the Mann-Whitney U test (Dytham, 2003). These tests were carried out in Minitab 13.1 (Minitab Inc, 2000). Correction for multiple comparisons was carried out following the Bonferroni method (Dytham, 2003).

Table 32 Habitat variables recorded at the twelve study sites.

Category	Variable	Level at which data collected*
Soil-related	▪ pH	All at plot level
	▪ Soil depth (cm)	
	• % LOI **	
	• Total P (μg/ml) **	
	• $CaCO_3$ (g/ml) **	
	▪ Texture (% sand/silt/clay) **	
Other physical/ environmental	▪ Dry weight of litter sample (g)	Quadrat (moll)
	▪ Slope (degrees)	Plot
	▪ Grazing level (4-point scale: no grazing, light, moderate or heavy grazing)	Plot
	▪ Altitude (m above sea level)	Site
	▪ Exposure (4-point scale: sheltered, moderately exposed, exposed, very exposed)	Site
Vegetation-related	▪ Vegetation height (m)	Quadrat (veg)
	▪ % covers:	Quadrat (veg)
	- grass, sedge, fern, bare earth, bare rock, herb layer, low woody (see Chapter Three)	
	- litter (veg)***	Quadrat (veg)
	- litter (moll)***	Quadrat (moll)
Derived variables	▪ Plant species count	Quadrat (veg)
	▪ Snail species count	Quadrat (moll)
	▪ Number of individual snails	Quadrat (moll)

* Plot = 20 x 20m, two at each of the twelve sites; Quadrat (moll) = 25 x 25cm, five in each plot, ten at each of the twelve sites; Quadrat (veg) = 2 x 2m, five in each plot, ten at each of the twelve sites; Site = one record made at each of the twelve study sites.

** These four soil parameters were measured by an undergraduate student (Kirrane, 2008) – see Chapter Two and Appendix 3 for more details.

*** Percentage cover of litter was measured in the vegetation and the mollusc quadrats. While the results are correlated, they were not exactly the same, and so both are used in analyses. (Investigated using scatterplot and Spearman's rank coefficient [$r = 0.647$, $p>0.0001$, one-tailed]).

Non-metric Multidimensional Scaling (NMS) was performed in PC-ORD 5 (McCune and Mefford, 2006), as was the outlier analyses associated with these ordinations. NMS was chosen as it is generally accepted as being one of the most robust forms of ordinations for detecting ecological patterns, and it is capable of dealing with non-normal and community data (McCune and Grace, 2002, Perrin et al., 2006b, Nekola, 2010). Species data were also loaded in the second matrix as this is one of the most useful ways in which to represent it in an ordination (see Chapter Two). Spearman's rank correlation coefficients were calculated between the most influential variables and the scores from the ordination axes using Data Desk 6 (Data Description Inc., 1996). Further details of these methods have been provided in Chapter Two. Correction for multiple tests used the Dunn-Sidak method (Quinn and Keough, 2002). Spearman's rank correlation coefficients were also used to investigate which of the measured variables might be correlated with snail abundance and/or richness.

Results

Data overview

[The results in this chapter are based on data from the >1mm size fraction, unless otherwise stated.]

The total number of individual snails collected was 1,572. There was a mean number of 13.1 snails per 25 x 25cm quadrat (Figure 59). Only 3.7, on average, (or 28.0%) were live adults. This meant that immature and dead specimens together made up 72.0% of the sample. Five percent of the sample was composed of fragments or unidentifiable shells. Of the total of 120, seven of the quadrats did not contain any snails, alive or dead, while 100 quadrats (or 83.3%) contained adult snails.

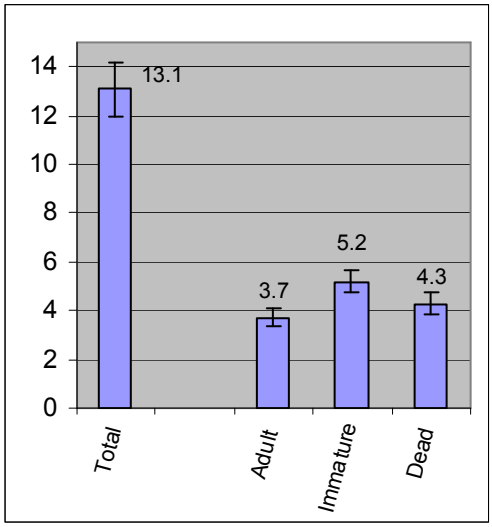


Figure 59 The mean number of snails per quadrat (+/- standard error) across the entire dataset, along with a breakdown into average numbers of adults, immatures and dead specimens.

A total of 29 species were identified (Table 33). The most common species overall were *Trochulus hispidus, Nesovitrea hammonis, Aegopinella pura* and *A. nitidula*, each with >100 individuals (or between 7.2 and 12.3% of the sample each). Together these species make up 36.3% of the total snails sampled. Members of the genus *Cochlicopa* were also very prevalent in the sample (20.0%). The most common species, by habitat, were *A. nitidula, T. hispidus, Balea heydeni* and *A. pura* in woodlands, *T. hispidus, Acanthinula aculeata* and *N. hammonis* in scrub, and *N. hammonis, Cochlicopa* cf. *lubrica* and *Vertigo pygmaea* in grasslands. For both *Cochlicopa* and *Vitrea,* many juveniles were indeterminable. As this could lead to under- or over-estimation of the numbers of individuals in each of the two pairs of species, the data on juveniles are presented separately, and these species are grouped separately at the bottom of Table 33.

Table 33 Snail species recorded (>1mm; data for adults, immature and dead combined).

	Total number	**% of occurrences in Woodland**	**% of occurrences in Scrub**	**% of occurrences in Grassland**
Trochulus hispidus	**181**	37	54.1	8.9
Nesovitrea hammonis	**137**	7.3	44.5	48.2
Aegopinella pura	**111**	44.1	40.6	15.3
Aegopinella nitidula	**106**	87.7	12.3	0
Acanthinula aculeata	**89**	20.2	68.6	11.2
Lauria cylindracea	**55**	61.8	12.7	25.5
Balea heydeni	**50**	100	0	0
Columella edentula	**46**	32.6	58.7	8.7
Vertigo pygmaea	**43**	0	34.9	65.1
Leiostyla anglica	**37**	86.5	13.5	0
Carychium tridentatum	**26**	46.2	53.8	0
Vertigo substriata	**26**	0	65.4	34.6
Columella aspera	**23**	13.0	56.5	30.4
Euconulus cf. *fulvus*	**16**	43.8	56.2	0
Clausilia bidentata	**13**	92.3	7.7	0
Helicella itala	**12**	0	66.7	33.3
Vitrina pellucida	**12**	16.7	16.7	66.6
Oxychilus cellarius	**9**	100	0	0
Punctum pygmaeum	**4**	25	50	25
Carychium minimum[+]	**2**	0	50	50
Discus rotundatus	**2**	100	0	0
Cepaea nemoralis[++]	**1**	100	0	0
Vallonia costata[+]	**1**	0	0	100
Vallonia cf. *excentrica*[+]	**1**	0	0	100
Vertigo pusilla[+]	**1**	100	0	0
Cochlicopa cf. *lubrica**	**72**	19.4	27.8	52.8
Cochlicopa cf. *lubricella**	**34**	38.2	50	11.8
Cochlicopa indet.*	**189**	22.2	38.6	10.5
*Vitrea contracta***	**56**	12.5	51.8	35.7
*Vitrea crystallina***	**78**	44.9	41	14.1
Vitrea indet.**	**38**	26.3	63.2	10.5
No. species per habitat		**25**	**24**	**21**

[+] Found only as dead specimens.

[++] Found only as a single immature specimen.

* There were a very large number of *Cochlicopa* immatures in the samples which were not identifiable to species. To avoid the numbers for the individual *Cochlicopa* species being over- or under-estimated, the figures for indeterminable immatures are presented separately.

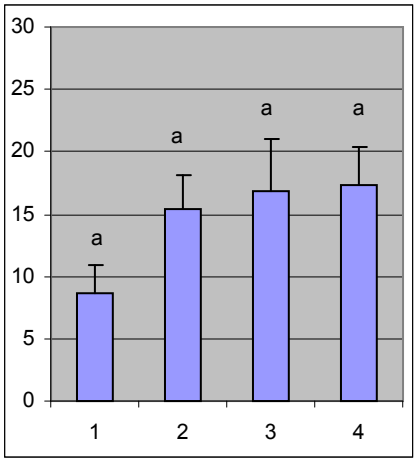
** The same approach was taken with any species where the proportion of indeterminable shells was >15% of the total count of determined specimens. Using this criteria, *Vitrea* spp were treated in the same way.

Numbers of snails in each habitat type

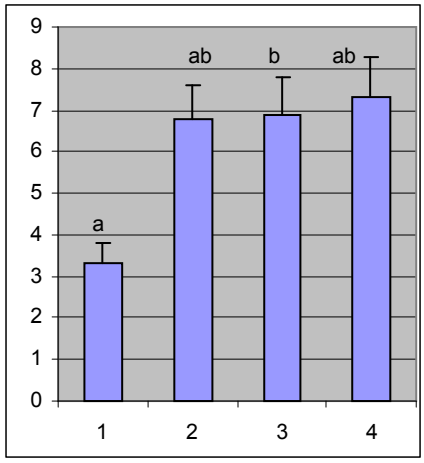
The average number of individual snails per quadrat at each site (calculated by pooling the ten quadrats) is shown in Figure 60. Quadrats from fenced and control plots at each site were pooled as they were found not to differ significantly [Scheirer-Ray-Hare test, $p>0.05$ (Dytham, 2003)]. (Note that no differences were expected as this was the first year of the experiment and samples were collected within one to three months of the erection of the fences.)

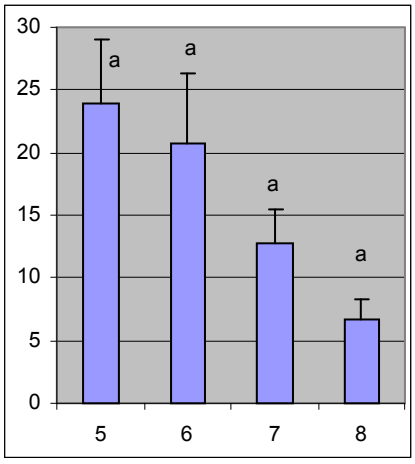
The grassland sites had lower numbers of snails when compared with woodlands and scrub. The variability within the data was also apparent, especially in the scrub and grassland sites, with one grassland site in particular being anomalous. In order to investigate whether there were statistically significant differences among average numbers of snails at each site, a Kruskal-Wallis test was carried out. The mean number of snails differed between sites ($p<0.001$), and therefore a series of pairwise Mann-Whitney U tests were used to ascertain which pairs of sites were significantly different (within each habitat type) (see Appendix 6 for full results). Labels on each bar in Figure 60 show the results of the pairwise comparisons within each of the three habitat types.

Patterns in the mean number of species and mean number of individuals per quadrat between sites were similar (Figure 61). The woodland snail fauna was at least as diverse as the scrub fauna, even though the absolute number of snails was slightly less. Grasslands tended to support fewer species and individuals than woodlands or scrub. Again, a Kruskal-Wallis test was used to check if there were statistically significant differences among the average numbers of species (the results were significant, $p<0.001$) and the results were further analysed using pairwise Mann-Whitney U tests to find out which pairs of sites were significantly different (Appendix 6 shows full results, and see labels on bars in Figure 61).

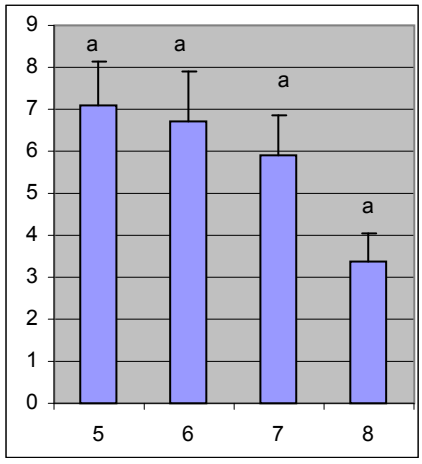


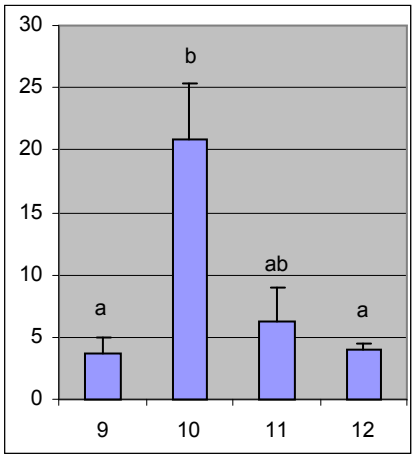
WOODLAND
1 – Ballyclery
2 – Glen-columbkille
3 – Glenquin
4 – Gortlecka





SCRUB
5 – Carran
6 – Knockans
7 – Rannagh
8 – Roo





GRASSLAND
9 – Caher
10 – Gregan
11 – Kilcorkan
12 – Slieve Carran

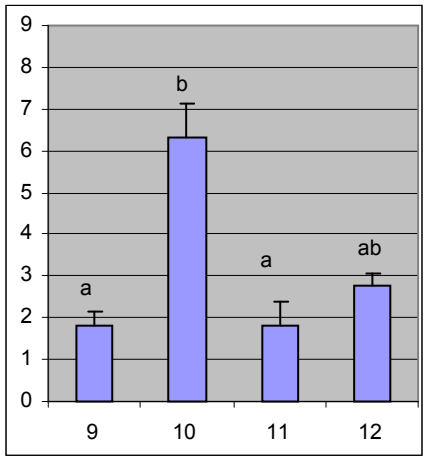


Figure 60
Average number of individual snails per quadrat at each of the twelve study sites (grouped by habitat type, +/- S.E.). [Sites that do not have significantly different numbers of snails WITHIN habitat types have the same letter.]

Figure 61
Average number of snail species per quadrat at each of the twelve study sites (grouped by habitat type, +/- S.E.). [Sites that do not have significantly different numbers of species WITHIN habitat types have the same letter.]

The results were pooled to assess differences among habitat types, both in terms of numbers of snails and numbers of species recorded (Figure 62 and Figure 63). One-way ANOVA analysis revealed significant differences ($p=0.015$ and $p<0.001$, for numbers of individuals and numbers of species respectively), and Fisher's LSD test was used to assess which of the habitats were significantly different in each case. The results indicate that the numbers of snails, and snail species, in grasslands are significantly different from those in both the woodlands and the scrub. The numbers for woodland and scrub habitats did not differ significantly from one another.

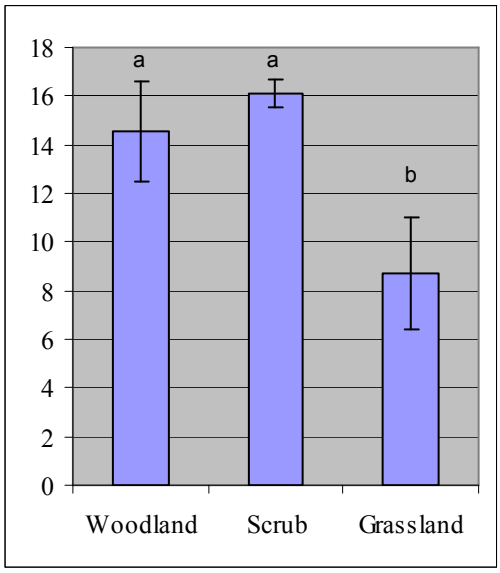


Figure 62 Average number of individual snails per quadrat in each of the three habitat types.

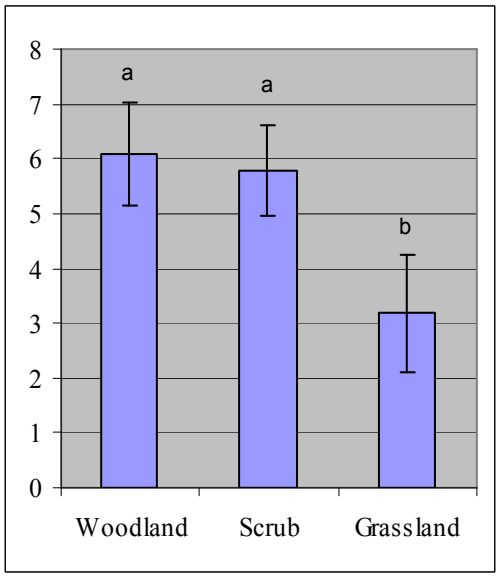


Figure 63 Average number of snail species per quadrat in each of the three habitat types.

Sørensen coefficient of similarity

The degree of similarity of the suite of species from each of the habitat types was assessed by calculating the Sørensen coefficient (Table 34). The list of species presented in Table 33 was used for the calculation, with the data converted to presence/absence. Woodland and grassland habitats were less similar than either woodland and scrub, or scrub and grassland. However, overall, the similarities were relatively low, indicating a degree of distinctiveness between communities.

Table 34 Sørensen coefficient for each combination of habitat types.

	Woodland	**Scrub**	**Woodland**	**Grassland**	**Scrub**	**Grassland**
Total occurrences:	25	24	25	21	24	21
No. joint occurrences:	20		15		19	
Sørensen coefficient	**0.45**		**0.39**		**0.46**	

Rare/threatened species, and notable absences

New 10km-square records

All mollusc records made during this survey were cross-checked with records held at the NBDC, RIMD (the Republic of Ireland Molluscan Database) and Moorkens (2001) (the latter has records for the Burren that have not yet been submitted to the central databases). A total of 38 new 10km-square records for 18 species were identified during this survey.

Rare/threatened species

The 'Red List' of non-marine mollusc species in Ireland (Byrne et al., 2009) lists species in a number of categories relating to how threatened they are. During this study, one species from the 'endangered' category was recorded, and three from both the 'vulnerable' and the 'near threatened' lists (Table 35). One of these species, *Vertigo pusilla*, is listed in Northern Ireland as being 'regionally extinct'.

Table 35 Snail species recorded which are on the 'Red List' for non-marine molluscs in Ireland. (Data from both size fractions included – i.e. 0.5-1mm and >1mm.)

'Red List' Category	Species name	Number of specimens
Endangered	*Vertigo pusilla*	1 (dead specimen only)
Vulnerable	*Acicula fusca*	16
Vulnerable	*Helicella itala*	12
Vulnerable	*Leiostyla anglica*	37
Near threatened	*Acanthinula aculeata*	89
Near threatened	*Vertigo pygmaea*	56
Near threatened	*Vertigo substriata*	46

Expected species and notable absences

The checklist of non-marine molluscs (Anderson, 2005) lists 163 native and naturalised taxa in Ireland, and the more recent 'Red List' (Byrne et al., 2009) lists 177, with 150 of these being native species. Of this 150, approximately 70 are terrestrial molluscs of mainly dry habitats (for the purposes of this study, I have excluded species of wetlands, and also slugs) (data derived from: Kerney, 1999, Falkner et al., 2001). This is the species-pool from which the species found during this study would be expected to come. Using the database of macro-habitat preferences provided in Falkner et al. (2001), and the distributional information available in Kerney (1999), the list was further curtailed to create a suite of 'expected species' for the chosen habitat types within the study area (Table 36).

Two additional species which are thought to need much wetter conditions were found during this survey: *Carychium minimum* and *Vertigo substriata*. They were not included in the list below as they were not expected for the habitat types under study, based on the available information (Paul,

1975b, Kerney and Cameron, 1979, Tattersfield, 1993, Kerney, 1999, Cameron, 2003, Cameron et al., 2006, Byrne et al., 2009).

Among the list of expected species (Table 36), those marked with an asterisk are synanthropic, or highly associated with man. Four out of the seven of these species on the list were not recorded during this study. Furthermore, *Cepaea nemoralis* was recorded as one immature specimen only, and *Discus rotundatus* was found only twice (one adult, one immature). Only *Oxychilus cellarius* occurred in moderate numbers (nine individuals). Species such as *Cepaea* spp, *Cornu aspersum, Discus rotundatus* and *Trochulus striolatus* are, generally speaking, very common species across Ireland. It was fully expected that they would be common in the dataset.

Table 36 'Expected species' for this study, derived from Kerney (1999), Falkner et al. (2001) and Byrne et al. (2009). Species in the left hand column arranged in decreasing order of abundance.

'Expected species' - found	**'Expected species' - not found**
Cochlicopa cf. *lubrica*	*Cecilioides acicula*
Trochulus hispidus	*Cepaea hortensis**
Nesovitrea hammonis	*Cornu aspersum**
Aegopinella pura	*Merdigera obscura*
Aegopinella nitidula	*Oxychilus alliarius**
Cochlicopa cf. *lubricella*	*Pupilla muscorum*
Vitrea crystallina	*Pyramidula pusilla*
Acanthinula aculeata	*Spermodea lamellata*
Vitrea contracta	*Trochulus striolatus**
Lauria cylindracea	*Zenobiella subrufescens*
Balea heydeni	
Columella edentula	
Vertigo pygmaea	
Leiostyla anglica	
Carychium tridentatum	
Columella aspera	
Acicula fusca	
Euconulus cf. *fulvus*	
Clausilia bidentata	
Helicella itala	
Vitrina pellucida	
*Oxychilus cellarius**	
Punctum pygmaeum	
*Discus rotundatus**	
*Cepaea nemoralis**	
*Vallonia costata***	
Vallonia cf. *excentrica***	
*Vertigo pusilla***	

*species which tend to show a high association with man – i.e. synanthropic species.

** found as single dead specimens only

Of the other species which were expected but not recorded, most occur in a limited range of habitat types. However, higher numbers of the two *Vallonia* species, *V. costata* and *V.* cf. *excentrica*, were expected. There was one dead specimen of each in the dataset. Both of these species would have been expected to be relatively common in the grassland sites.

Community structure in relation to habitat

Habitat affinities

In order to identify habitat affinities, species confined (or largely confined) to one of the three habitats were identified (Table 37). To facilitate comparison, information provided in Falkner et al. (2001) regarding shade and humidity requirements for the species recorded during this survey is presented in Table 38.

Table 37 Habitat preferences of the snail species recorded. Scrub was split into 'woody' and 'grassy'. A cut-off point of 50% cover of shrubs in the vegetation quadrats was used to make the split. Only those species with ≥10 adult individuals in the >1mm dataset are included.

	n	% frequency - Woodland (n=40)	% frequency - Woody Scrub (n=22)	% frequency - Grassy Scrub (n=18)	% frequency - Grassland (n=40)
Only/mainly woodland					
Balea heydeni	10	100	0	0	0
Aegopinella nitidula	21	95	5	0	0
Leiostyla anglica	21	86	14	0	0
Only/mainly woodland & woody scrub					
Columella edentula	12	50	50	0	0
Acanthinula aculeata	51	27	59	2	12
Vitrea crystallina	26	54	31	11	4
Mainly scrub					
Trochulus hispidus	30	13	60	20	7
Mainly grassland & grassy scrub					
Vertigo pygmaea	27	0	7	33	60
Preference not obvious					
Aegopinella pura	31	42	19	10	29
Cochlicopa cf. *lubrica*	59	17	20	9	54
Cochlicopa cf. *lubricella*	26	35	38	12	15
Lauria cylindracea	14	64	0	0	36
Nesovitrea hammonis	40	8	35	20	37
Vertigo substriata	16	0	38	12	50
Vitrea contracta	24	8	33	13	46

Table 38 Shade/light and humidity preferences of the snail species recorded during this survey, from Falkner et al. (2001). Data were not available in Falkner et al. (2001) for *Balea heydeni* as it is a recently re-discovered species.

[A 'fuzzy coding' system is used by Falkner et al. It describes the degree of association between a species and a variable. It enables "*incorporation of diverse kinds of ecological and biological information*" and provides much flexibility (Falkner et al., 2001). '0', or a blank cell, means 'no association', '1' signifies a 'minor association', '2' – 'moderate association' and '3' – maximum association.]

[Photophilic: growing or functioning best in strong light. Hygrophilic: growing or functioning best in moist or humid conditions. Euryhygromic: capable of using a wide spectrum of humidity graduations between xerotolerant and hygrophilous]

	Deep shade	Light shade	Photophilic
Carychium minimum	3		
Carychium tridentatum	3		
Discus rotundatus	3		
Leiostyla anglica	3		
Nesovitrea hammonis	3		
Oxychilus cellarius	3		
Punctum pygmaeum	3		
Vitrea contracta	3		
Vitrea crystallina	3		
Acanthinula aculeata	3	1	
Aegopinella nitidula	3	1	
Cochlicopa cf. *lubrica*	3	1	
Euconulus cf. *fulvus*	3	1	
Columella aspera	2	1	
Lauria cylindracea	2	1	
Aegopinella pura	2	2	
Clausilia bidentata	2	2	
Columella edentula	2	2	
Trochulus hispidus	2	2	
Vertigo pusilla	2	2	
Vertigo substriata	2	2	
Vitrina pellucida	1	2	
Cepaea nemoralis	1	2	1
Helicella itala	1	2	1
Vertigo pygmaea	1	2	1
Cochlicopa cf. *lubricella*		3	
Vallonia costata		2	3
Vallonia cf. *excentrica*		1	3

	Hygrophilic	Euryhygromic	Dry tolerant
Carychium minimum	3		
Leiostyla anglica	3		
Oxychilus cellarius	3		
Cochlicopa cf. *lubrica*	3	1	
Vertigo substriata	2	1	
Vitrea crystallina	2	1	
Aegopinella nitidula	2	2	
Carychium tridentatum	2	2	
Lauria cylindracea	2	2	
Vitrina pellucida	2	2	
Cepaea nemoralis	1	2	
Vallonia cf. *excentrica*	1	2	
Vitrea contracta	1	2	
Columella edentula	1	3	
Euconulus cf. *fulvus*	1	3	
Nesovitrea hammonis	1	3	
Punctum pygmaeum	1	3	
Acanthinula aculeata	1	3	1
Aegopinella pura	1	3	1
Discus rotundatus	1	3	1
Clausilia bidentata		3	
Columella aspera		3	
Trochulus hispidus		3	
Vallonia costata		3	
Vertigo pusilla		3	
Vertigo pygmaea		3	
Cochlicopa cf. *lubricella*		2	1
Helicella itala		1	2

Snail community structure in woodlands, scrub and grasslands

The snail community structure was investigated further using a series of NMS ordinations. Before analysis, species which were uncommon in the dataset (occurring in ≤3 quadrats; McCune and Grace, 2002) were deleted (=7), as were quadrats which did not have any snails (=20). This resulted in a main matrix consisting of 18 species and 100 quadrats. The second matrix consisted of 21 measured variables and three derived variables (Table 32) and the data for the 18 snail species.

Clear trends and patterns were observed, and these were repeatable over multiple runs, but the analysis had quite a high stress value (22.19, steady over four runs), and this should be borne in mind when interpreting the results. Values of between 10 and 20 are considered acceptable in ecology, and allow reasonable confidence. McCune and Grace (2002) warn, however, that values of 35-40 mean that points are essentially arranged at random in an ordination. Perrin et al. (2006b) report a stress of 23.54 but, having a large dataset, they believe that this still "*indicates a good solution*". Although this current dataset is not large (particularly in terms of number of species), the consistency of the patterns observed allows a reasonable degree of confidence in interpreting the results. Spearman's rank correlations were calculated between all variables which plotted on the NMS ordinations (i.e. those with a r^2-value of ≥0.2) and their axis scores (Table 39).

A 3-dimensional solution was recommended and all axis combinations are shown (Figure 64, Figure 65 and Figure 66). Overall, the ordination captured 59% of the variation in the distance matrix ($r^2 = 0.589$). Axis 3 accounted for 26% of this, axis 1 - 18%, and axis 2 - 15%. The quadrats clustered broadly into groups according to habitat type. The overall dispersion of points across the ordination diagrams is large, indicating that the data are well spread along all axes. This implies that no sudden boundaries exist between the faunas of the habitat types, rather that they grade into one another.

The largest proportion of the variation in the ordination was explained by axis 3. Snail species diversity and vegetation height were strongly negatively correlated with this axis, while the occurrence of the species *Vertigo pygmaea* and cover of sedges were strongly positively correlated with it. This suggests a separation of woodland and grassland quadrats, though the ordinations showed that the separation is not clear-cut.

Cover of field, grass and sedge layers were negatively correlated with axis 1. Plant species diversity was also negatively correlated with this axis, and vegetation height was positively related. Thus grassland quadrats were mainly positioned on the lower end of this axis. *Cochlicopa* cf. *lubrica* was also strongly negatively associated with axis 1, and *Aegopinella nitidula* was positively correlated, again highlighting the split between woody-dominated and grass-dominated habitats. Both measures of amount of litter were positively correlated with this axis.

Trochulus hispidus was strongly negatively correlated with axis 2, and is associated with the positioning of the scrub quadrats at the lower end of this axis. *Aegopinella nitidula* was positively correlated. The Spearman's rank correlation coefficient calculations also revealed a weak negative correlation between axis 2 and plant species diversity.

Table 39 Spearman's rank correlations between influential variables and axis scores. Statistically significant correlations are indicated: * p≤0.05, ** p≤0.01, *** p≤0.001. Those in bold are still significant following correction for multiple tests (Dunn-Sidak).

	Axis 1	**Axis 2**	**Axis 3**
Vegetation height	**0.397*** **	0.120	**-0.479*** **
Cover of field layer	**-0.43*** **	-0.087	**0.386*** **
Cover of grasses	**-0.464*** **	-0.092	**0.332*** **
Cover of sedges	**-0.356*** **	-0.158	**0.489*** **
Litter (veg)	0.264**	0.183	**-0.38*** **
Litter (moll)	**0.358*** **	0.02	-0.307**
Mollusc Species Diversity	-0.068	-0.148	**-0.578*** **
Plant Species Diversity	**-0.38*** **	-0.217*	0.315**
Aegopinella nitidula	**0.461*** **	**0.342*** **	-0.018
Cochlicopa cf. *lubrica*	**-0.689*** **	0.164	-0.123
Trochulus hispidus	0.253*	**-0.564*** **	0.054
Vertigo pygmaea	-0.091	0.102	**0.604*** **

Figure 64, Figure 65 and Figure 66. NMS ordinations of snail quadrat data. Each point represents a quadrat, and lines indicate correlations with measured variables – the length of the line indicates the relative strength of the correlation. (Explanations of the abbreviations used are provided below each ordination.)

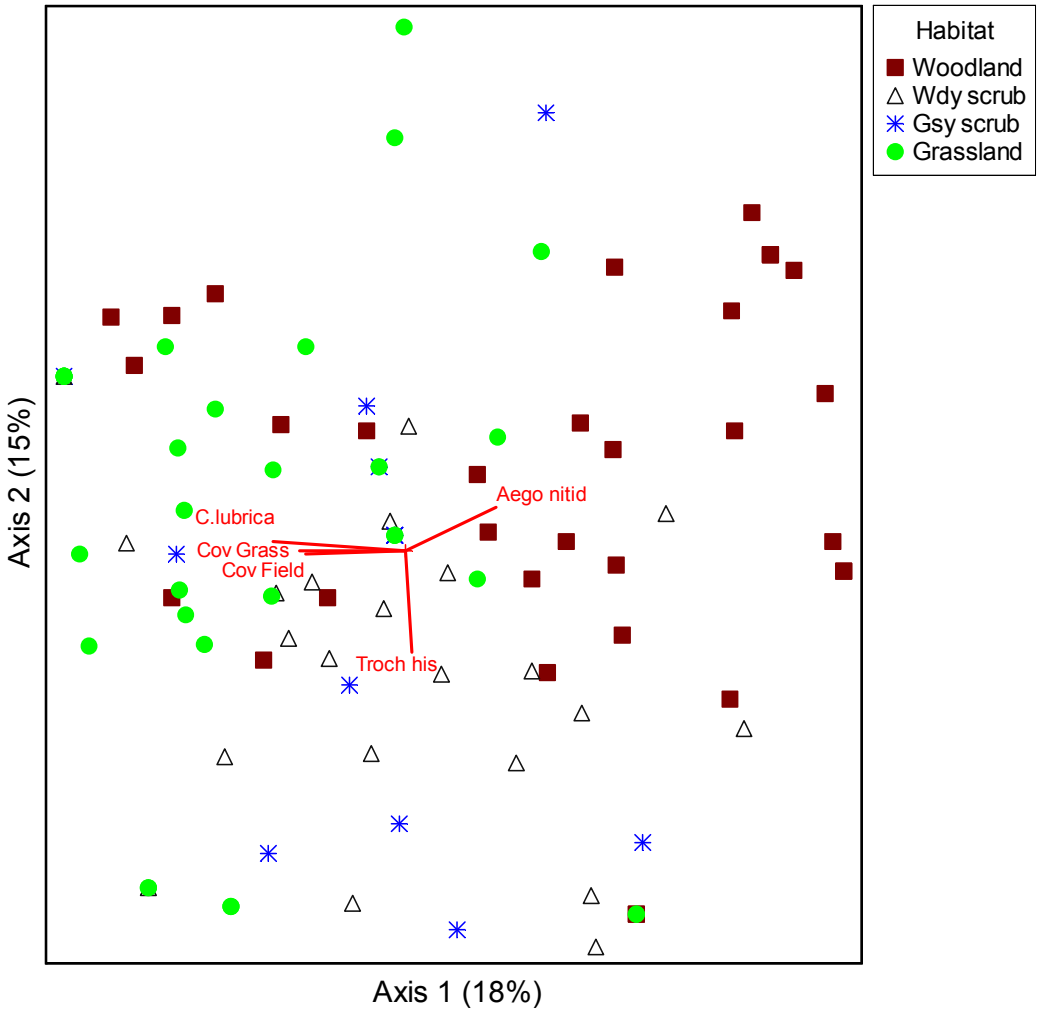


Figure 64 NMS ordination of snail samples: axis 1 and axis 2. 33% of the variation in the distance matrix is explained by this combination of axes.

C. lubrica = *Cochlicopa* cf. *lubrica*
Cov Grass = % cover of grasses
Cov Field = % cover of field layer
Troch his = *Trochulus hispidus*
Aego nitid = *Aegopinella nitidula*

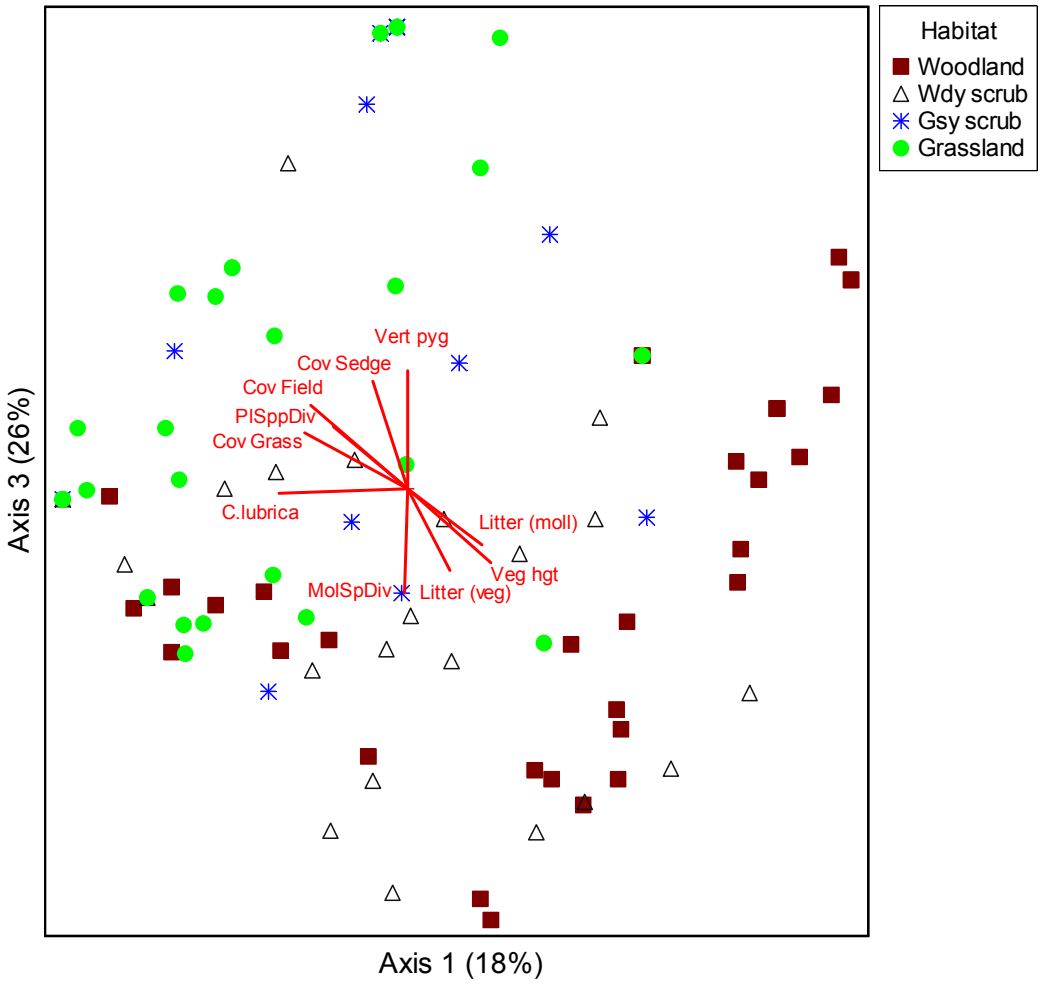


Figure 65 NMS ordination of snail samples: axis 1 and axis 3. 44% of the variation in the distance matrix is explained by this combination of axes.

Vert pyg = *Vertigo pygmaea*
Cov Sedge = % cover of sedges
Cov Field = % cover of field layer
PlSppDiv = plant species diversity (i.e. number of plant species per quadrat)
Cov Grass = % cover of grasses
C. lubrica = *Cochlicopa* cf. *lubrica*
MolSpDiv = mollusc species diversity
Litter (veg) = % cover of litter recorded in vegetation quadrats
Litter (moll) = % cover of litter recorded in snail quadrats
Veg hgt = height of vegetation

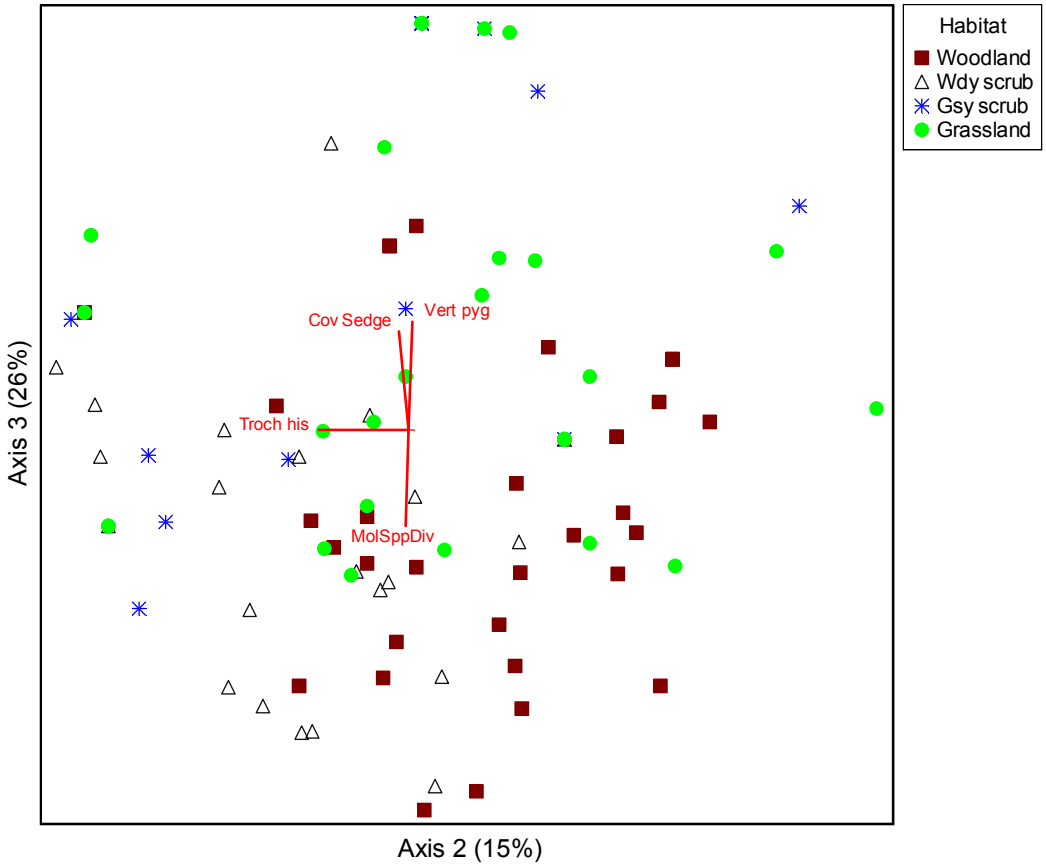


Figure 66 NMS ordination of snail samples: axis 2 and axis 3. 41% of the variation in the distance matrix is explained by this combination of axes.

Vert pyg = *Vertigo pygmaea*
Cov Sedge = % cover of sedges
Troch his = *Trochulus hispidus*
MolSppDiv = mollusc species diversity

Richness and abundance – correlated factors

Spearman's rank correlation coefficients were calculated between the vegetation and environmental factors recorded and snail abundance and richness (Table 40). For convenience, the factors recorded were separated into four categories: vegetation-related, litter-related, soil-related and 'other'. The litter-related variables, along with % LOI (loss-on-ignition) and % sand/silt/clay, were among the most strongly correlated variables when all habitats were combined.

Table 40 Spearman's rank correlation coefficients between the abundance and richness of snails and recorded variables.

			WOODLANDS		SCRUB		GRASSLANDS			ALL HABITATS COMBINED	
	Variable (range, median)	**n**	**Abundance**	**Richness**	**Abundance**	**Richness**	**Abundance**	**Richness**	**n**	**Abundance**	**Richness**
Vegetation -related	Cover of grasses (0-80, 20)	40	0.037	0.059	-0.211	-0.204	0.419 **	0.459 **	120	-0.104	-0.126
	Cover of herbs (0.5-100, 50)	40	0.048	0.165	-0.316 *	-0.318 *	0.204	0.247	120	-0.159	-0.178
	Cover of sedges (0-35, 3)	40	-0.008	0.01	-0.464 **	-0.464 **	-0.394 *	-0.409 **	120	-0.34 ***	**-0.366** ++
	Cover of ferns (0-70, 0.1)	40	-0.281	-0.347 *	0.344 *	0.347 *	0.151	0.192	120	0.077	0.067
	Cover of low woody plants (0-80, 7.5)	40	-0.32 *	-0.348 *	0.075	0.091	-0.293	-0.401 *	120	0.073	0.079
	Cover of bare earth (0-70, 1)	40	-0.43 **	-0.417 **	-0.107	-0.158	-0.269	-0.38 *	120	-0.166	-0.21 *
	Cover of bare rock (0-55, 0.75)	40	-0.199	-0.309	0.12	0.111	-0.114	-0.134	120	0.094	0.085
	Vegetation height (0.22-8, 1.25)	40	0.25	0.225	0.289	0.318 *	0.453 **	0.456 **	120	0.259 **	0.289 **
	Number of plant species (3-49, 23)	40	-0.01	0.057	0.185	-0.186	-0.061	-0.113	120	-0.108	-0.141
Litter -related	Cover of litter (2 x 2m plant quadrat) (1-75, 20)	40	0.38 *	0.358 *	0.223	0.189	0.421 **	0.517 ***	120	0.289 **	0.323 ***
	Cover of litter (25 x 25cm snail quadrat) (1-95, 40)	40	-0.221	-0.248	0.558 ***	0.539 ***	0.342 *	0.433 **	120	0.26 **	0.299 ***
	Dry weight of sample (27-230, 81)	40	0.372 *	0.339 *	**0.617** ++	**0.585** ++	0.347 *	0.398 *	120	**0.465** ++	**0.469** ++
Soil -related	pH (6.04-7.35, 6.76)	8	-0.69	-0.79 *	0.214	0.253	0.095	-0.299	24	-0.063	-0.241
	Soil depth (3.0-18.7, 8.1)	8	-0.18	-0.139	-0.66	-0.712 *	-0.368	-0.253	24	-0.574 **	-0.615 **
	% LOI (19.0-85.7, 31.1)	8	0.81 *	0.671	0.667	0.675	0.762 *	0.575	24	**0.733** ++	**0.711** ++
	Total P (98.9-412.4, 167.4)	8	-0.238	-0.371	-0.167	-0.193	-0.286	0.048	24	-0.305	-0.321
	$CaCO_3$ (0-0.059, 0.025)	8	0.476	0.287	0.431	0.455	-0.347	-0.584	24	0.232	0.129
	% sand (40-86, 70.5)	8	-0.359	-0.06	0.587	0.515	0.548	0.755 *	24	0.372	0.514 **
	% silt (1-48, 16)	8	0.228	0.006	-0.898 **	-0.891 **	-0.599	-0.825 **	24	-0.554 **	-0.662 ***
	% clay (6-24, 14)	8	0.554	0.358	0.446	0.476	0.229	0.43	24	0.525 **	0.551**
Other physical/ environmental	Slope (0-16, 3)	8	-0.086	-0.21	0.639	0.698 *	-0.485	-0.299	24	-0.115	-0.156
	Grazing level (4-point scale) [+] (1-3, 2)	8	--	--	--	--	--	--	24	-0.091	-0.237
	Altitude [+] (13-187, 71)	4	--	--	--	--	--	--	12	0.343	0.413
	Exposure (4-point scale) [+] (1-4, 1)	4	--	--	--	--	--	--	12	0.039	0.156

Statistically significant correlations are indicated: * p≤0.05, ** p≤0.01, *** p≤0.001, ++ p≤0.0001. Those in bold are still significant following correction for multiple tests (Dunn-Sidak).

[+] r-values are not presented for these variables either because the number of replicates is too small, or, in the case of 'grazing level', it is recorded on a four-point scale and thus the number of datapoints is low.

Discussion

Snail species recorded

A total of 29 species of non-marine terrestrial snail was recorded, which constitutes approximately 80% of the suite of 'expected' species. There were, on average, 13 snails per quadrat. About 40% of the specimens collected were immatures, with the remainder being split between live adults and long-dead, empty shells. The most common species found are all frequent and widespread in Ireland (e.g. *Cochlicopa* spp, *Trochulus hispidus, Nesovitrea hammonis, Aegopinella nitidula*, *A. pura, Vitrea* spp, etc.). The patterns for snail abundance and species richness were similar for all sites – i.e. sites with the highest numbers of snails also tended to have the highest numbers of species of snails. This concurs with findings elsewhere – e.g. Barker and Mayhill (1999) found that sites in New Zealand with high abundances of molluscs, were also species rich, and Liew et al. (2008) found a positive correlation between abundance of micromolluscs and species diversity in Malaysia.

Overall, grasslands supported significantly fewer snails (and also species of snails) than either woodlands or scrub (which had similar numbers). It is well known that woodlands are prime habitats for terrestrial molluscs (e.g. Kerney and Cameron, 1979, Ondina and Mato, 2001). They act as 'climate-buffers' – reducing daily and seasonal variations in temperature, humidity and light intensity. Most molluscs need relatively high and constant humidity and moisture in their environments, and thus molluscan abundance and diversity is maximised in habitats which can provide for this need. Another reason why woodlands are "*undoubtedly the richest of all habitats*" (Kerney and Cameron, 1979) for molluscs is that, as in much of Europe, in Ireland they were the main land cover through much of the postglacial period (Mitchell and Ryan, 1997) and indeed they also represent one of the predominant vegetation types before the development of agriculture (Cameron et al., 2006), and thus many of our mollusc species are adapted to woodland conditions. It is interesting that the scrub habitat in the Burren is at least as rich in snails as the woodlands.

The Sørensen coefficients of similarity showed that the suites of species found in woodlands and grasslands were less similar to each other, compared with those in woodlands and scrub, or scrub and grasslands, although the difference was not large (39%, 45% and 46% respectively). Given the heterogeneous nature of the scrub habitat in the Burren, being composed of grassy and woody elements, it is not surprising that there is a large degree of overlap between it and the other two habitats.

During this study 38 new 10km-square records were made. Species which the highest number of new records were: *Columella edentula* (four new records), and *Acicula fusca, Aegopinella pura, Euconulus* cf. *fulvus* and *Vertigo substriata* (three new records each).

Rare and threatened species

A number of rare and threatened species (one endangered, three vulnerable and three near threatened; Byrne et al., 2009) were recorded during this survey, and of particular importance is *Vertigo pusilla*. This very rare species was found at one of the woodland sites (one dead shell only). The species is typically found near sheltered walls in woodland, or in fixed dunes where it tends to favour rather dry microhabitats (Kerney and Cameron, 1979, Cameron, 2003, Byrne et al., 2009). There has been a 58% decline in its distribution in Ireland since 1980 and it is listed as 'endangered' in the 'Red List' (Byrne et al., 2009). This means that it is facing an extremely high risk of extinction in the country (IUCN, 2001). Elsewhere in Europe it is described as being "*widespread, but local, becoming rare northwards*" (Kerney and Cameron, 1979). It is not known whether this species still occurs alive at this woodland site. Six other species from the 'Red List' were found, some in large numbers (e.g. *Acanthinula aculeata*). Collectively, these species highlight the importance of the Burren for land snails.

Helicella itala has seen a 60% decline in distribution in Ireland in the last 30 years, mainly due to changes in agriculture in the midlands (Byrne et al., 2009). It is one of the largest, and also one of the most recognizable of the Burren molluscs, being very visible with its striped colour pattern and its prominent position, high up on the vegetation in many grasslands. Thus it might be expected to be among the most common species (cf. O'Donovan, 1987), but this was not found to be the case. Even in the grasslands, it made up only 1.2% of the numbers of individual snails in the samples collected.

Notable species

In addition to the rare and threatened species mentioned above, the presence of a number of species was notable – mainly because they do not typically occur in the type of habitats surveyed, but also due to unexpected co-occurrences with other species. An example was *Carychium minimum* (68 individuals recorded in 2006, includes 0.5-1mm size fraction). This species is noted as occupying "*wet places, such as marshes or very moist woods*" by Kerney and Cameron (1979). It has also been described as 'obligatory hygrophile' (Paul, 1975b), and Kerney (1999) writes that it is "*common in wet places generally*", and that it is "*much commoner in woods in oceanic areas (especially in Ireland) than in eastern Britain…*". It was recorded mostly from grasslands in this study (65 out of the 68 occurrences).

Vertigo substriata is another species which is more usually associated with wet areas. Both Kerney and Cameron (1979) and Cameron (2003) state that it is a species of damp or wet places. Byrne et al. (2009) writes that it is "*recorded principally from transition mires, but also occupies wet woodland*". Only Kerney (1999) mentions that "*more rarely, it is found in ground litter in ordinary woodland*". In this study 46 individuals were recorded in 2006, 15 from grassland sites and 31 from scrub sites. There were no records from woodland sites.

A number of other species recorded during the survey are known to prefer relatively wet conditions (see Falkner et al., 2001, and summary in Table 38) – *Cochlicopa* cf. *lubrica, Leiostyla anglica, Oxychilus cellarius* and *Vitrea crystallina*. Each of these species (except *O. cellarius*) was common in the dataset. This provides an indication of the relative dampness and humidity of many habitats in the extreme west of Ireland. As noted in the climate section in Chapter One, the weather in the west of Ireland is generally equable (mild winters and cool summers), with few extremes, and rainfall occurs year-round. In the Burren region it is quite high - approximately 1,500mm/yr. This facilitates the occurrence of moisture-demanding species in more open habitats, compared with areas with drier or more variable climates. It may also mean, however, that xerophilic species are less common (Kerney, 1999).

Kerney (1999) states that *Columella aspera* and *C. edentula* are "*only rather rarely associated*", and Killeen (1992) reports that he never found the two species living together "*in precisely the same habitat*" (during his work on an atlas of molluscs in Suffolk). In this study, they were found together at seven of the twelve study sites. *C. edentula* is known to be a catholic species – it is found in woods, marshes, and grasslands; a wide variety of moderately damp places (Kerney and Cameron, 1979). *C. aspera*, however, tends to favour drier, less calcareous habitats; is usually more of an upland species; and is often found in woodlands, both coniferous and deciduous (Kerney and Cameron, 1979). It is thus somewhat surprising to find it to be relatively widespread in the Burren, and often in association with *C. edentula.*

Vitrea contracta is a catholic species, favouring drier habitats than *V. crystallina* (Kerney and Cameron, 1979), but the two species are known to often be associated (Kerney and Cameron, 1979, Kerney, 1999, Cameron, 2003). Given the habitat preferences of the two species, one might expect to find *V. contracta* more plentifully in the grassland study sites, and this was indeed the case. *V. crystallina* was found more commonly in the woodlands. Interestingly, both species did well in the scrub.

'Missing' species

There are exceptionally few records of those snail species which are typically abundant in disturbed habitats, or which are linked closely with the presence of man – e.g. *Cepaea* spp, *Cornu aspersum, Discus rotundatus* and *Trochulus striolatus*. *C. asperum* is one of the largest and most common snails in Ireland, and is found in a range of habitats. Its total absence from the dataset is surprising. The almost complete absence of *D. rotundatus* is also perplexing. Bishop (1977) records *D. rotundatus* as the most widespread and abundant species in the acid woodlands of west Cork and Kerry, and Cameron (1982) found it the second most abundant species at a hazel woods in England. Moorkens (2001) found the species in the Burren in the Caher river valley, near Mullaghmore and also at Slieve Carran (no abundance values are given). The maps of the National

Biodiversity Data Centre show a small number of records for the species in the Burren (ten in total, with no habitat details provided; National Biodiversity Data Centre, 2011). However, the species being uncommon in an area with seemingly suitable habitat is not without precedent. Kerney (1972), while mapping non-marine molluscs in south-west Ireland, writes of *D. rotundatus*: "*A so-called 'ubiquitous' species, surprisingly hard to find in some 10km-squares with otherwise rich faunas*." Overall, the absence, or low numbers, of synanthropic species leads to the conclusion that the snail fauna of the Burren is a remarkably 'natural' one.

The other 'missing' species are mostly species which have quite specific habitat requirements. *Cecilioides acicula* is a subterranean species, which is often hard to find. *Pupilla muscorum* is a species of dry, exposed, stony or sandy places. Both *Spermodea lamellata* and *Zenobiella subrufescens* prefer old deciduous woodlands. *S. lamellata* requires deep, stable leaf litter (Byrne et al., 2009). It has been recorded in the Burren in recent years (Caher valley, Mullaghmore and Slieve Carran; Moorkens, 2001), however. *Merdigera obscura* is described in the 'Red List' (Byrne et al., 2009) as a habitat specialist – it is found on calcareous escarpments and woodlands, and is not common in the region. *Pyramidula pusilla* is found on exposed limestone rocks and walls.

The xerophilic element of the snail fauna recorded for the Burren during this study was poor. Species such as *Pupilla muscorum, Vallonia costata* and *V.* cf. *excentrica* were all-but absent from the dataset (only a single dead specimen of each of the two latter species was recorded). It may be, as discussed above with regard to moisture-demanding species, that the climate has a part to play – humidity levels, even in grasslands, are likely to be relatively constant and high year-round, thus possibly reducing the suitability for xerophilic species. Another issue is that the grasslands are not very heavily grazed, and the timing of the grazing may be important too - winter grazing means that the grasslands are at their most lush in summer time. Long, dense grassland vegetation is not suitable habitat for xerophilic species.

Habitat affinities

The task of identifying habitat affinities for mollusc species in Ireland is made difficult by the relatively depauperate fauna (meaning wider realised niches, cf. Heslop Harrison, 1951a, Heslop Harrison, 1951b, Adam et al., 1977), and also by the extreme oceanic climate (again influencing the niche/ habitat occupied by individual species). However, definite trends were seen, with some species being all but limited to woodland (e.g. *Balea heydeni* and *Aegopinella nitidula*) or grassland habitats (e.g. *Vertigo pygmaea*).

The ecology of *Balea heydeni* is not yet well-understood because of its only very recent distinction from *B. perversa* in Britain and Ireland (Gittenberger et al., 2006). At present, the ecology of both species is thought to be similar. Members of the genus *Balea* are known mostly from trees, rocks

and walls, and they are rarely found on the ground (Boycott, 1934, Gittenberger et al., 2006). Gittenberger et al. state that they favour areas that are "*invariably dry, usually away from the ground ... and inhabited by few (or no) other molluscs.*" In this study, this species was linked strongly to wooded habitats, but it was found in the presence of other snails in five out of the eight quadrats in which it occurred.

Aegopinella nitidula is listed in Kerney and Cameron (1979) and Cameron (2003) as being a species of moderately moist places such as woodlands and rough grasslands. In Kerney (1999) it is described as a "*catholic species, found under ground litter in a wide variety of sheltered places*". It was found mainly in woodlands in this study (95% of occurrences, with the other 5% being in woody scrub). All other records for this species in the Burren were examined, but few give specific habitat details and so comparison was not possible (Moorkens, 2001, National Biodiversity Data Centre, 2011).

Vertigo pygmaea is well known as a species which thrives in grassland habitats, particularly in calcareous areas (Kerney and Cameron, 1979), and while it is occasionally found in wetter habitats (e.g. marshes) it does not tolerate shade and so is not found in wooded areas (Kerney and Cameron, 1979, Kerney, 1999). It is not surprising, therefore, that it was not found in the woodlands at the study sites, and only very occasionally in woody scrub areas.

Henry (1914) listed six species which he believed were limited to old woods in Ireland (the modern name is given in brackets if different).

- *Zonitoides excavatus*
- **Sphaeradium edentulum (Columella edentula)*
- *Achanthinula lamellata (Spermodea lamellata)*
- *Hygromia fusca (Zenobiella subrufescens)*
- **Pupa anglica (Leiostyla anglica)*
- **Acicula lineata (*probably = *Acicula fusca)*

Three of these species have been found during this survey (denoted with *). *Columella edentula* and *Leiostyla anglica* were indeed found to be limited to woody habitats in this survey. The third species, *Acicula fusca*, was found in all three habitat types.

The species which showed woodland affinities in the current dataset are species which have among the highest associations with 'deep shade' and being 'hygrophilic' - i.e. growing or functioning best in moist or humid conditions (Falkner et al., 2001) (summary provided in Table 38). Similarly, *Vertigo pygmaea* is among the species with the lowest shade requirements.

Community structure - differences between habitats

The quadrats grouped together broadly by habitat type on the NMS ordinations, indicating that patterns exist in the snail community data. The scrub habitat appears to have a distinct fauna. Overall, the boundaries between the communities of the three habitat types were not sharp, however - rather, the snail communities of all three habitat types grade into one another.

A number of variables were shown to be associated with the variation seen, including cover of grasses, sedges, and field layer, and vegetation height. The first three are associated with grassland quadrats for the most part, and the latter with woodlands. Species diversity, of both plants and snails, were also important variables associated with the spread of the data points. Plant species diversity was positively related to quadrats from grassland sites, and snail species diversity was correlated with woodland and scrub quadrats. Four species emerged as being correlated with the distribution of the snail quadrats in the ordination space: *Aegopinella nitidula* (related to the position of the majority of the woodland quadrats), *Trochulus hispidus* (strongly related to the scrub quadrats) and *Cochlicopa* cf. *lubrica* and *Vertigo pygmaea* (both linked with the grassland quadrats, though there was much spread and variability in these). *A. nitidula, T. hispidus* and *V. pygmaea* had already been noted as being characteristic of woodland, scrub and grassland habitats respectively in the study area (Table 37).

Correlates of richness and abundance

A total of 24 variables were assessed for their influence on snail species richness and abundance by calculating Spearman's rank correlation coefficients. They were grouped into vegetation-related, litter-related, soil-related and 'other' factors.

Vegetation-related factors

Correlation analysis revealed that the cover of sedges was strongly negatively correlated with both species richness and abundance of snails when all habitats were analysed together. When separated by habitat, it was clear that this factor had little influence on snail populations in woodland habitats (probably because of the low cover of sedges in this habitat), but it had a strong effect in both scrub and grasslands. Interestingly, in the grassland sites the cover of grasses was positively correlated with abundance and richness. Grasslands (and grassy habitats, such as the grassy scrub quadrats) with higher amounts of grasses are likely to have denser swards, and therefore may be better at holding moisture. Also, due to their usually more prolific growth, the amounts of associated phytomass and litter build-up may be larger. Grasslands with higher proportions of sedges may be more open and less dense, making them less optimal mollusc habitats. Vegetation height was moderately positively correlated with the snail fauna of the grasslands (and with richness in scrub). It is possible that this too is linked with the vigour of the grass growth in some grassland quadrats.

The amount of bare earth present in a quadrat was negatively correlated with snail abundance and richness in woodlands, and to a lesser extent, with richness in grasslands (amounts of bare earth were small in general in the scrub and grassland areas). Molluscs need the food and shelter which is provided by plant, bryophyte and litter cover, and so it is not surprising that bare earth would be a poor micro-habitat for them.

No correlation was found between the number of plant species and either the abundance or richness of snails. This is unsurprising given the importance of litter and habitat structure and heterogeneity for molluscs (Labaune and Magnin, 2001). Baur et al. (1996) and Niemela and Baur (1998) similarly found that plant diversity was a poor indicator for snail diversity (both studies based in calcareous grasslands in Switzerland). Baur et al. (2007) found no significant correlation between plant species richness and the number of snail species recorded at one of their alpine grassland study sites in Romania (Fagaras Mountains). They did, however, have conflicting results at another site (Bucegi Mountains) where they found a positive correlation between plant species richness and the number of snail species. They conclude, in light of these contradictory findings, that plant richness may not be directly influencing the snail diversity – rather they may both be responding to the same or similar environmental conditions at the second site. On the other hand, Barker and Mayhill (1999) report that mollusc species richness was strongly associated with vegetation diversity in a study of terrestrial mollusc communities in the north-east of New Zealand.

Litter

All three measures of litter employed in this survey resulted in significant positive correlations with snail abundance and richness. The strongest correlations were found in scrub. Many authors have documented the importance of litter as a habitat for molluscs, and reported positive correlations between litter and mollusc species number (e.g. Bishop, 1977, Kerney and Cameron, 1979, Barker and Mayhill, 1999, Ondina and Mato, 2001, Kappes et al., 2006). Kerney and Cameron (1979) remark on the fact that the heavier the litter, the higher the humidity and the longer that this can be kept high. Kappes et al. (2006) note that if litter is sufficiently thick, it in fact provides a vertical gradient within which is found a range of humidity, light, chemical and aerobic conditions. Barker and Mayhill (1999) spell out the significance of litter as molluscan habitat: "*Litter is a highly complex, three-dimensional, horizontally stratified habitat which from the snail's viewpoint is probably subdivided into many subunits: newly fallen leaves at the top of the litter; fragmented leaves, twigs, and decomposed litter further down; and wet litter and finely particulate humus above ground level. To these subunits can be added the interstices in bark and logs*." Bishop (1977) says that while the vegetation communities at his study sites in acid woodlands in south-west Ireland were driven by the make-up of the soil, the snail communities were best explained by the composition of the litter.

Soil-related factors

Soil properties and soil chemistry are well known to influence the malacological faunas of a habitat (e.g. Ondina et al., 1998, 2004, Kappes et al., 2006). In this study, pH, soil depth, % LOI, and soil texture (% sand/silt/clay) were found to be correlated with snail richness or abundance.

pH

No overall relationship was found between soil pH and snail richness or abundance. There was a weakly significant negative correlation with richness in woodlands - but as the number of sample points was small (n=8), too much emphasis should not be placed on this trend. Martin and Sommer (2004a) failed to find a significant relationship between soil pH and the numbers of individuals and species in a study involving a large number of grasslands in Germany. They postulated that the management practices carried out in grasslands affect the snail populations to a larger degree than differences in pH. However, many authors have demonstrated the relationship of increasing molluscan richness with increasing pH in woodlands (e.g. Wareborn, 1970, Cameron, 1973, Walden, 1981, Gardenfors et al., 1995, Millar and Waite, 2002, Kappes et al., 2006). It is possible that the pH range in this study (6.0-7.4, median: 6.8) was too narrow for a trend to emerge, and the number of replicates per habitat is low. It is possible also that measurement of the pH of the litter (rather than the soil) might have revealed a relationship. Nekola (2010) wrote "*one of the principle global trends identified in land-snail ecology is the strong positive correlation between individual abundance, species richness and the pH of the organic litter in which land-snail communities reside*." Other authors, too, found that the pH of the litter is the best determinant of species richness in molluscs (e.g. Skeldon et al., 2007, Gotmark et al., 2008). Both van Straalen and Verhoef (1997) and Hobbie (2005) showed that soil pH and litter pH can be different, and the former note that pH can also vary noticeably with depth, quoting the example of one of their study sites in which this was particularly obvious because an acid pine needle litter layer was developing over a calcareous sediment.

Soil depth

Snail richness and abundance were found to be significantly negatively correlated with soil depth, when all habitat types were combined (there was also a significant negative relationship between soil depth and richness in scrub habitats). The reason for this relationship is not clear, but it may be that areas with shallower soils tend to support more heterogeneous vegetation types (they may be more patchy) and therefore they may support a more diverse vegetation structure and more microhabitats.

% Loss-on-ignition

The % LOI of the soils was very strongly positively correlated with both the richness and abundance of snails across all habitats. Soils with high % LOI have a high organic matter content, and this may mean that they have a structure favoured by snails (a friable, crumbly, well-aerated

soil, with plenty of air pockets is likely to be preferred by many species). Additionally, the high organic matter content means that moisture would be retained well (Kappes et al., 2006), a factor which is clearly beneficial for molluscs. Finally, as snails feed largely on decaying vegetation, the availability of this as a food source in soils with a high organic matter content may also be a factor (Kappes et al., 2006). Kappes et al. also report that the presence of coarse woody debris in litter in woodlands strongly positively influences molluscan occurrences. High organic matter content and the occurrence of coarse woody debris near the soil surface may be analogous – the enhanced structural heterogeneity providing a number of advantages for molluscs in each case.

Soil texture (% sand/silt/clay)

Soil texture, measured here as the percentage of sand, silt and clay, appeared to influence both snail abundance and richness. Percent silt showed the strongest patterns (strongly negatively correlated with snail occurrences, particularly in scrub habitats), while percent clay was also influential (positively correlated, when all habitats were combined). Patterns were least evident in woodland sites. Ondina et al. (2004) similarly found soil texture to be an important explanatory factor in snail community composition – in fact they believe that texture is the most important edaphic factor after amount of calcium and pH. In a study encompassing a range of habitats (woodlands, scrub, grasslands and cultivated areas) in Spain, Outeiro et al. (1993) also found relationships between snails and soil texture, with the amount of clay being important. They suggest that soil texture is influential because snails generally have a limited capacity for burrowing into soil, yet many species need to do this both for refuge and egg-laying, and the soil texture will have a bearing on this. The advantages and disadvantages of different textures for different species are not well understood, however, with a link between species size and the influence of soil texture being postulated (Outeiro et al., 1993).

Other factors

In general, strong relationships were not found between the remaining variables (slope, grazing level, altitude and exposure) and the abundance and richness of snails.

Conclusions

This study has provided a detailed documentation of the snail fauna of the woodland, scrub and grassland habitats of the Burren region in the west of Ireland. Rare and threatened species were recorded, and some species which are usually common were found to be absent or very rare. Some species showed strong habitat affinities, and these reflected the published accounts for these species. The snail communities of grasslands, scrub and woodlands in the Burren were shown to be fairly distinct, with factors such as vegetation height and covers of field layer, grasses and sedges all being important explanatory variables for community make-up. Analysis revealed that amount of litter, soil texture, % LOI, and the covers of grasses and sedges were the most significantly correlated variables with snail abundance and species richness.

Many studies have looked at land snail richness and abundance in relation to large scale factors (e.g. climate, altitude and geology), but few have looked at environmental factors on smaller scales (Menez, 2007). Even fewer have taken the fine scale, multi-faceted approach used here, and applied it across a number of habitat types. Information such as this helps greatly in furthering our understanding of the status and distribution of land snails in Ireland. The findings are important in leading the way towards a better understanding of the requirements of land snails, and also in pointing the way for the best direction of future studies (e.g. investigating further the influence of soil texture).

Chapter Five:

Investigations into population structure, and assessment of some common methodologies in malacology

Introduction

Population structure

Studies on molluscan population structure, in terms of the numbers of adult, immature and dead specimens, are few. Those that do exist tend to focus on a small number of species – for example, pest species (crop pests, and hosts for parasites such as liver fluke) and protected, mainly wetland, species – e.g. *Vertigo* spp (Killeen, 2001, Killeen, 2005). Examples which focus on land snails include the work of Cameron (1982) on a number of common species in a hazel woodland in England, and the unpublished work of O'Donovan (1987) on *Helicella itala* in the Burren.

Reproductive biology

The majority of the snail species found during this survey lay eggs – only *Lauria cylindracea* is ovo-viviparous, where the eggs hatch inside the mother (Falkner et al., 2001). Data for the recently re-discovered *Balea heydeni* were not available, though the closely-related *B. perversa* is also ovo-viviparous. Snails usually lay their eggs in clutches, with larger species having clutches of up to 200 eggs (Cameron, 2003). Most of the species in this study have smaller clutches, typically consisting of <10 eggs (Falkner et al., 2001). Clutches are typically laid in soils, or in cracks in wood, and most hatch within six weeks (Kerney and Cameron, 1979). Mortality of juveniles is generally high. Breeding seasons are extended and highly variable, though most species have peaks in spring, summer or autumn (Cameron, 2003). Development in land snails is direct – there is no metamorphosis, and young snails grow by adding whorls to their shell (Kerney and Cameron, 1979).

The database of Falkner et al. (2001), which covers all non-marine mollusc species occurring in north-west Europe, contains information on habitat requirements, food preferences and body metrics, as well as on many aspects of reproductive biology, including number of eggs, duration of egg development, main reproductive period and age at reproductive maturity. It is drawn on heavily in this chapter.

Some issues in population studies

The ability of some species to remain as immatures until favourable conditions occur is a confounding factor when trying to interpret findings relating to population structure (Dr Evelyn Moorkens, pers. comm.). Although a particular species may have a peak of reproductive activity, it is also possible that juveniles of that species will be present at any time of the year (Killeen, 2001, Cameron, 2003, Killeen, 2005). Many species breed opportunistically when suitable conditions prevail. Additionally, as many of the snail species are small, short-lived animals with rapid growth, they may undergo large seasonal fluctuations. Thus, for reliable data on population structure, repeated sampling is the ideal – both across the seasons, and over a number of years.

A common problem in population studies is the fact that immature specimens can be challenging to identify. Immature shells are often lacking in key characters and few identifications keys deal adequately with them. Problems are compounded if the specimens are very small and/or very young. In his work on *Vertigo geyeri*, a rare wetland snail, Killeen (2001) comments on the difficulties in telling the juveniles of some closely related species apart, and notes that in some cases it is not possible. His work demonstrates, however, that valuable information can still be gleaned from such data – e.g. the overall ratio of juveniles to adults.

Another issue in population investigations is how to deal with apparently empty or dead shells. Dead shells are usually damaged, worn or otherwise spoiled, and may lack many of the characters normally used for identification (e.g. colour pattern, shell striations, etc.). Additionally, they may persist for many years (Cameron, 2003), especially in lime-rich areas, and as such they may not constitute a valid part of a species list for a site (Kerney, 1999).

The processing, sorting and identification of immature and/or dead snail specimens is time-consuming, and generally more challenging than dealing with adult specimens. The importance of recording and identifying them is assessed in this chapter.

Sieve mesh size

A survey of the literature revealed that in a majority of malacological studies a 0.5mm sieve mesh was used for processing terrestrial snail samples, but there were exceptions (e.g. 1mm in Chatfield, 1977, and 2mm in Menez, 2001). The use of a 0.5mm mesh means that many tiny shells will be included in a sample, a majority of which are likely to be juveniles. Considering the amount of extra work involved in processing and identifying these, the question of whether to include (and identify) them is therefore an important one, and is dealt with in this chapter.

Aims

This chapter aims to detail the population make-up of the land snails in selected habitats in the Burren, in terms of the numbers of adult, immature and dead individuals. Additionally, two aspects of the methodologies commonly employed in sampling terrestrial snails are assessed. Firstly, the value of recording and/or identifying all immature and dead specimens is investigated. Secondly, an assessment of the effects of sieve mesh size on results is carried out.

Methods

As detailed in Chapter Four, all snail specimens found during this study were recorded as 'adult', 'immature' or 'dead'. Specimens were recorded as dead if the shell was empty, and had obviously been so for some time (i.e. it was bleached and/or damaged). Shells which were empty but appeared fresh could not always be categorised with certainty as dead, and so some 'recently dead' specimens may have been counted in the 'alive' category. Dead specimens were not divided into adult and immature. Immature specimens were often challenging to differentiate from adults of the same species. As quoted in Cameron (2003), "*If the shell has a lip and/or teeth, then it is an adult. But: Adults of many species have neither*.". Specimens which lacked teeth and/or a lip needed more careful examination, and features such as size and number of whorls were important in helping to assign them correctly.

Snails were processed by hand in the laboratory using a series of sieves in order to separate them by size (size fractions: <0.5mm, 0.5-1mm, 1-5mm, >5mm). The smallest fraction contained only dust and shell fragments and was discarded. The snails processed from the two fractions larger than 1mm form the basis of the data presented in Chapter Four. The snails found in the 0.5-1mm fraction were processed and identified separately, with a view to assessing whether the extra effort involved in their separation and identification was worthwhile, in terms of the numbers of snails recorded, the species found, and the proportions of these relative to the data from the >1mm size fraction. In the 0.5-1mm size fraction only the adults were identified to species due to the difficulties inherent in identifying such small specimens.

Results

Population structure

Patterns in population structure

Of the 1,572 individual snail shells collected (in the >1mm size fraction) approximately 28% were adults, 40% were immature and 33% were dead specimens (see Chapter Four).

The population make-up of the species recorded, in terms of numbers of adult, immature and dead specimens, is given in Table 41, and for the most common species in Figure 67. Species with fewer than 15 individuals were not included in Figure 67 as patterns would have been difficult to detect with such low numbers. The category 'adult' was the most commonly recorded category for only four species (see left hand side of graph). The middle group, which was by far the largest, consisted of those species for whom most specimens were immature, and the final group (two species) had more dead individuals than live.

Table 41 Numbers of snail specimens >1mm of each species in the categories, 'adult', 'immature' and 'dead'.

	ADULTS	IMMATURE	DEAD
Acanthinula aculeata	51	26	12
Aegopinella nitidula	21	56	29
Aegopinella pura	31	34	46
Balea heydeni	10	24	16
Carychium minimum	0	0	2
Carychium tridentatum	7	4	15
Cepaea nemoralis	0	1	0
Clausilia bidentata	3	5	5
Cochlicopa cf. *lubrica*	59	0	13
Cochlicopa cf. *lubricella*	26	0	8
Columella aspera	5	12	6
Columella edentula	12	27	7
Discus rotundatus	1	1	0
Euconulus cf. *fulvus*	1	9	6
Helicella itala	2	3	7
Lauria cylindracea	14	27	14
Leiostyla anglica	21	8	8
Nesovitrea hammonis	40	53	44
Oxychilus cellarius	2	2	5
Punctum pygmaeum	3	0	1
Trochulus hispidus	30	91	60
Vallonia costata	0	0	1
Vallonia cf. *excentrica*	0	0	1
Vertigo pusilla	0	0	1
Vertigo pygmaea	27	10	6
Vertigo substriata	16	1	9
Vitrea contracta	24	25	7
Vitrea crystallina	26	31	21
Vitrina pellucida	6	4	2
Aegopinella indet.	0	0	14
Carychium indet.	1	0	0
Cochlicopa indet.	0	157	32
Columella indet.	2	0	0
Oxychilus indet.	0	8	4
Vitrea indet.	0	0	38

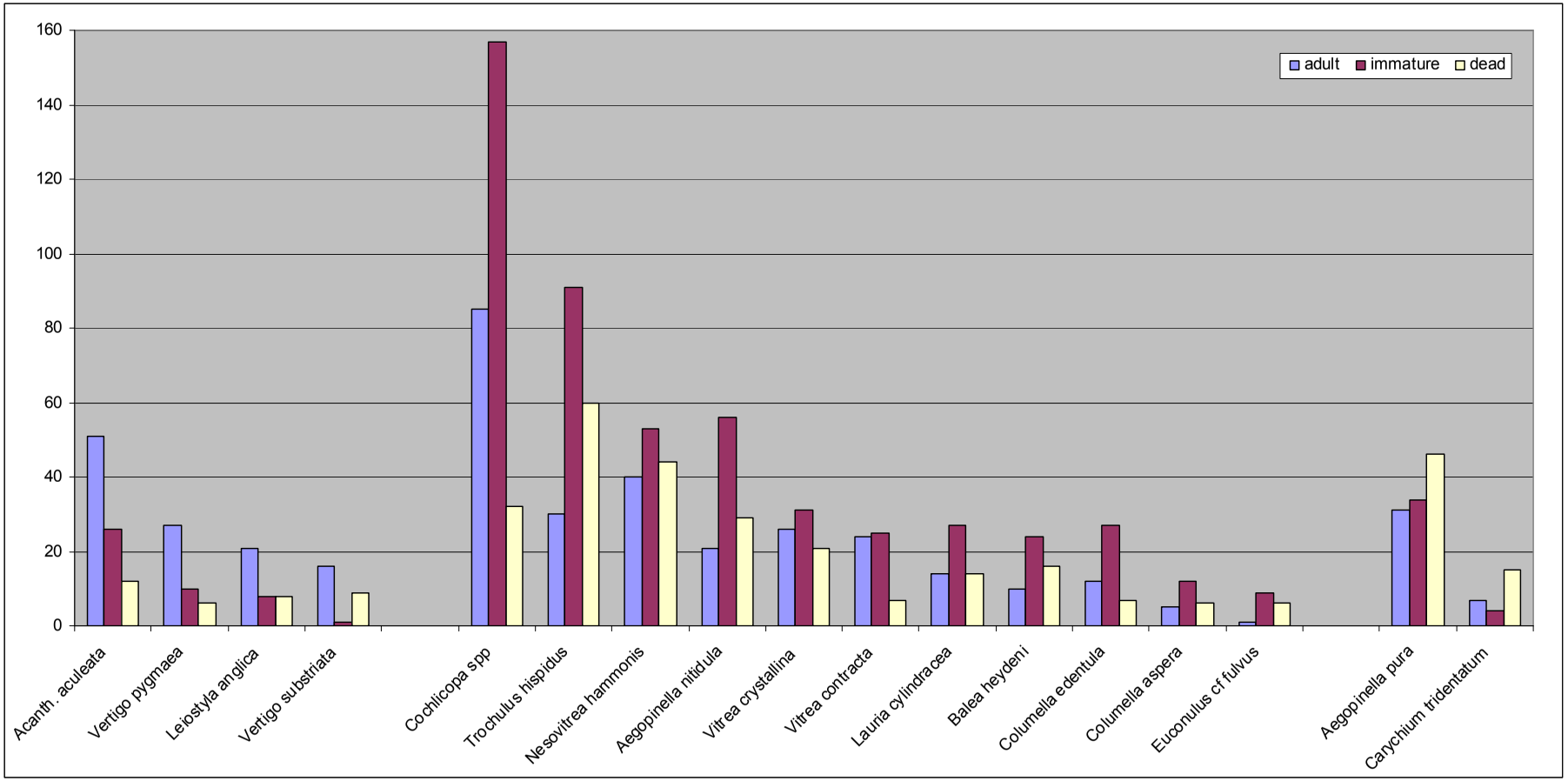


Figure 67 Numbers of adult, immature and dead snail specimens >1mm, for the most common species in the dataset. (Those species whose populations had a majority of adults are on the left hand side of the graph, those with more dead specimens are on the right hand side, and in the middle are those with mainly juveniles.)

Note: *Cochlicopa* cf. *lubrica* and *C.* cf. *lubricella* have been merged for this analysis due to the difficulty of identifying immatures to species level.

Data on body size was obtained (Table 42) in order to check if there was any relationship between it and the population make-up. Of those species in the smallest size category (<2.5mm maximum adult size), only four occurred in numbers large enough to be included in Figure 67. Three of these had a majority of adults specimens, and the fourth, *Carychium tridentatum*, occurred most often as dead specimens. The largest species (of those presented in Figure 67) are *Cochlicopa* spp, *Trochulus hispidus, Aegopinella nitidula* and *Balea heydeni*, all of which were found most often as immatures. (The remainder of the middle portion of Figure 67 was composed of medium-sized species.)

Some reproductive traits were examined to investigate why most species have such a high proportion of juveniles present. The first trait looked at was 'number of eggs produced'. Falkner et al. (2001) wrote that only *Trochulus hispidus* and *Aegopinella nitidula* (from the group of species included in Figure 67) produce medium to large (10-100) numbers of eggs. All of the remaining species produce <10 eggs per clutch.

The second element investigated was 'reproductive period' (Table 43). This is defined in Falkner et al. (2001) as the "*time of the year (in two month periods) of oviposition*" (i.e. egg-laying). All molluscan sampling for this project was carried out in October and November. Many of the most common species found in this survey have their main reproductive period around (or just before) then. The species in the first group in Figure 67 are mainly reproductively active earlier in the season.

Inclusion of immature and/or dead specimens

The number of specimens available for analysis in the current dataset (>1mm, 2006 data), when all three categories (adult, immature, dead) are included, is 1,572. This would drop by 72% to 440 individuals if the immature and dead specimens were excluded.

The most common species from the full dataset were compared with those from a dataset from which the immature and dead specimens had been removed (Table 44). Three out of the four species which were present most commonly as adults in the dataset (see Figure 67) move up in the rankings substantially (*Acanthinula aculeata, Vertigo pygmaea* and *Leiostyla anglica*). For example, *A. aculeata* becomes the second most common snail overall when only adults are considered, but it is not in the top five when immature and dead specimens are included. In the case of grasslands and scrub, the lists of the most common species change relatively little, but the woodland lists look quite different, with only one species in common.

Table 42 Maximum body size for the snail species recorded in this survey (data from: Falkner et al., 2001).

[A 'fuzzy coding' system is used. It describes the degree of association between a species and a variable – in this case, maximum body size. It enables "*incorporation of diverse kinds of ecological and biological information*" and provides much flexibility (Falkner et al., 2001). A blank cell means 'no association', '1' signifies a 'minor association', '2' – 'moderate association' and '3' – maximum association.]

	<2.5mm	**2.5 - 5.0mm**	**5 - 15mm**	**>15mm**
Acanthinula aculeata	3			
Carychium minimum	3			
Carychium tridentatum	3			
Punctum pygmaeum	3			
Vallonia cf. *excentrica*	3			
Vertigo pusilla	3			
Vertigo pygmaea	3			
Vertigo substriata	3			
Acicula fusca	2	2		
Columella aspera	2	2		
Vallonia costata	2	2		
Vitrea contracta	2	2		
Aegopinella pura		3		
Columella edentula		3		
Euconulus cf. *fulvus*		3		
Lauria cylindracea		3		
Leiostyla anglica		3		
Nesovitrea hammonis		3		
Vitrea crystallina		3		
Cochlicopa cf. *lubricella*		3	1	
Vitrina pellucida		3	1	
*Balea heydeni**		1	3	
Aegopinella nitidula			3	
Clausilia bidentata			3	
Cochlicopa cf. *lubrica*			3	
Discus rotundatus			3	
Oxychilus cellarius			3	
Trochulus hispidus			3	
Helicella itala			2	2
Cepaea nemoralis				3

* As this is a recently discovered species, data were not available in Falkner et al. (2001). They were modified instead from Gittenberger et al. (2006).

Table 43 Reproductive period(s) for each of the snail species presented in Figure 67* (data from: Falkner et al., 2001). For clarity, the most likely periods for each species are shaded.

[A 'fuzzy coding' system is used. It describes the degree of association between a species and a variable – in this case, main reproductive period. It enables "*incorporation of diverse kinds of ecological and biological information*" and provides much flexibility (Falkner et al., 2001). A blank cell, means 'no association', '1' signifies a 'minor association', '2' – 'moderate association' and '3' – maximum association.]

	Jan/Feb	Mar/April	May/Jun	July/Aug	Sept/Oct	Nov/Dec
Aegopinella pura				1	2	1
Nesovitrea hammonis				1	2	1
Vitrea contracta				1	2	1
Vitrea crystallina				1	2	1
Aegopinella nitidula		1	1	1	3	1
Euconulus cf. *fulvus*		1	1	1	2	1
Cochlicopa cf. *lubricella*			2	1	2	
Cochlicopa cf. *lubrica*		1	2	1	2	1
Trochulus hispidus		1	2	1	2	1
Leiostyla anglica		2	2		2	1
Lauria cylindracea		2	3	1	2	
Acanthinula aculeata			2	2	1	
Carychium tridentatum		1	2	2	1	1
Columella aspera			2	2		
Vertigo pygmaea		1	2			
Vertigo substriata		1	2			
Columella edentula			3			

* As *Balea heydeni* is a recently discovered species, data pertaining to it was not available in Falkner et al. (2001). Thus this species is not included here.

Table 44 The most common species overall (and in each of the habitat types separately) using all data combined, or adults-only dataset.

	Adults, immatures and dead combined	Adults only
OVERALL	*Cochlicopa* spp	*Cochlicopa* cf. *lubrica*
	Trochulus hispidus	*Acanthinula aculeata*
	Nesovitrea hammonis	*Nesovitrea hammonis*
	Aegopinella pura	
	Aegopinella nitidula	
BY HABITAT		
Woodland	*Aegopinella nitidula*	*Aegopinella nitidula*
	Trochulus hispidus	*Leiostyla anglica*
	Balea heydeni	*Acanthinula aculeata*
	Aegopinella pura	*Vitrea crystallina*
Scrub	*Trochulus hispidus*	*Acanthinula aculeata*
	Acanthinula aculeata	*Trochulus hispidus*
	Nesovitrea hammonis	*Nesovitrea hammonis*
Grassland	*Nesovitrea hammonis*	*Cochlicopa* cf. *lubrica*
	Cochlicopa cf. *lubrica*	*Vertigo pygmaea*
	Vertigo pygmaea	*Nesovitrea hammonis*

Snails in the 0.5-1mm size fraction

There were 3,726 individual snails in the 0.5-1mm samples. The majority of these were immature (53%), with 20% adults and 27% dead. There were an average of 31.1 snails per quadrat in this fraction, with approximately 6.3, 16.4 and 8.4 in the adult, immature and dead categories respectively (Figure 68).

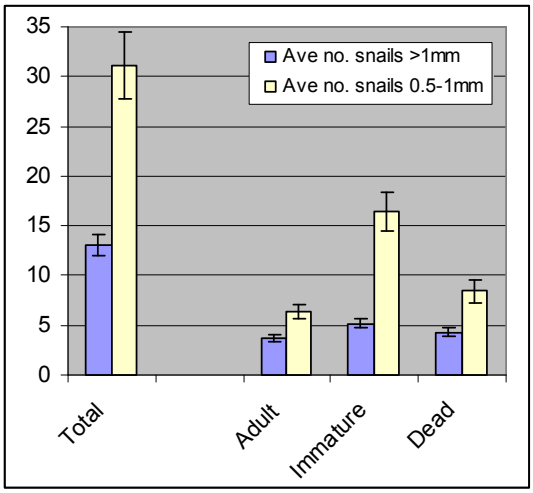


Figure 68 The average number of snails per quadrat (+/- standard error) from the >1mm (data from Chapter Four) and 0.5-1mm size fractions.

Only the adults were identified from this size fraction and six species were recorded (Table 45). One of these species was a new addition to the list and was found at nine of the twelve sites: *Acicula fusca*. (This species is listed as 'Vulnerable' in the 'Red List' for Irish non-marine molluscs (Byrne et al., 2009).) The number of species per site ranged from one to four, and two of the sites had only one species (the newly recorded species *Acicula fusca*). There were ten quadrats which did not contain snails, and 32 of the quadrats had no adult snails (total number of quadrats = 120).

The average number of snails per quadrat in each of the twelve study sites, in both the 0.5-1mm and >1mm size categories, is shown in Figure 69. The same data are presented in Figure 70 showing the breakdown between 'adult', 'immature' and 'dead' specimens. It is clear that the large proportion of immature specimens is the main source of the increased numbers in the 0.5-1mm size fraction (although the site Carran has a very large number of dead specimens in this size fraction).

Table 45 Snail species (adults only) identified from the 0.5-1mm size fraction, and the numbers from the >1mm data (from Chapter Four) for comparison.

Species name	No. of adult individuals (0.5-1mm)	No. of adult individuals (>1mm)
Carychium tridentatum	503	7
Punctum pygmaeum	138	3
Carychium minimum	66	0
Vertigo substriata	20	16
Acicula fusca	16	0
Vertigo pygmaea	13	27
Total	**756**	**53**

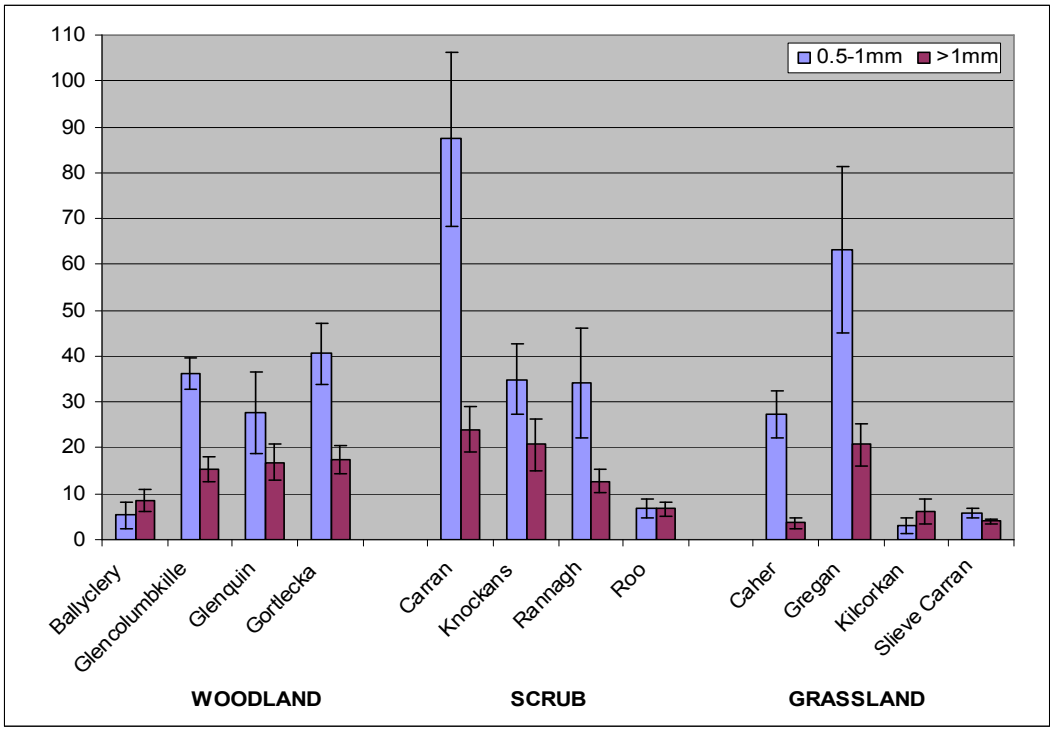


Figure 69 Total number of snail specimens at each of the study sites in two different size fractions, with adult, immature and dead categories amalgamated.

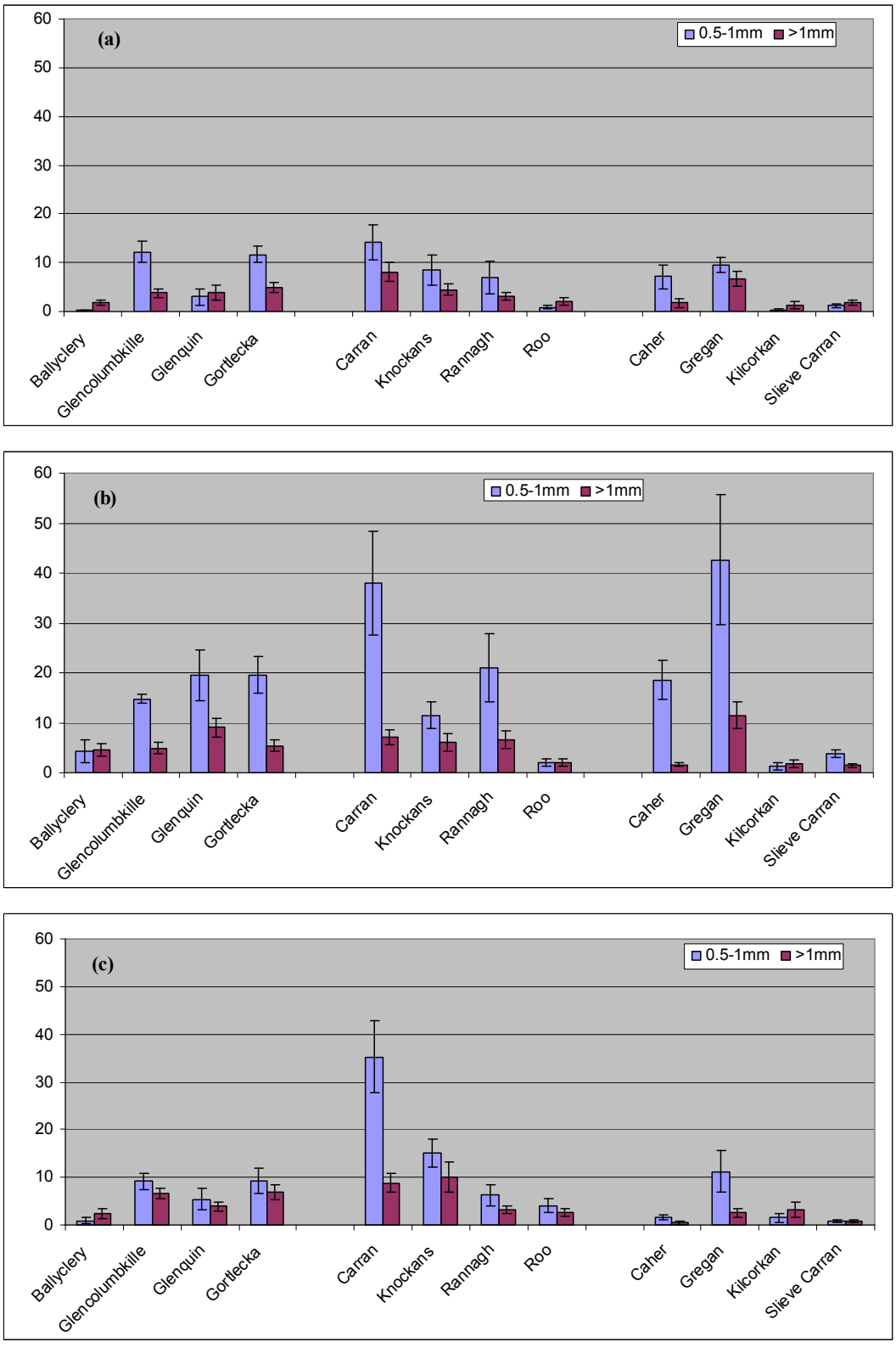


Figure 70 Number of snail specimens at each of the study sites in both size fractions, split between (a) adults, (b) immatures and (c) dead specimens.

Discussion

The population make-up

One-third of the snail specimens recorded in the >1mm size fraction of the samples were dead. It appears that the proportion of dead specimens can vary widely: Cameron (1982) found just under half of the specimens which he collected in a hazel woodland in England were dead, whereas Schilthuizen et al. (2005) found that >99% of the 16,278 snails they collected in forests in Borneo were dead. Having such a high proportion of dead shells may not very surprising – snails are generally short-lived (most smaller species live for less than one year), but their shells can be very long-lasting. This can result, in certain situations, in a seemingly disproportionate amount of dead shells.

Cameron (1982) notes that "*adults often make up only a small proportion of the total population*". Here, they consisted of 28%. Cernohorsky et al. (2010) found 24% adults, from a sample of >21,000 molluscs from fens in the Czech republic. The majority of species were most common in this dataset as juveniles/immatures, and 40% of the total number of snail specimens were immatures. The majority of the indeterminable specimens were found in the immature or dead categories, highlighting the difficulties inherent in the identification of young and/or dead specimens.

Of the most common species, some smaller ones occurred in the dataset mainly as adults, and it is most likely that detection of immatures was difficult due to their tiny size. Additionally, many of the tiny immatures would have passed through the 1mm sieve mesh. Two of the more common species had more dead specimens than live ones in the dataset: *Aegopinella pura* and *Carychium tridentatum*. In the case of *C. tridentatum*, it is most likely that its tiny size (1.8-2mm high, and 0.8-0.9mm wide: Kerney and Cameron, 1979) protects it from being crushed, due to the fact that it does not contain large airspaces, allowing the shells to persist for longer. This is likely to at least partly account for its proportionately large occurrence as dead shells in the samples.

Reproductive period (time of egg-laying) and reproductive output (measured as number of eggs produced per clutch) may both be influential on the high proportions of juveniles found in the samples. Reproductive output was low (<10 eggs per clutch) for all but two species – *Trochulus hispidus* and *Aegopinella nitidula*. Interestingly, these two species had the highest numbers of immature specimens, apart from the taxon *Cochlicopa* indet. Almost all of the species from amongst those which had a majority of immatures in the samples have their main reproductive period in September and October – just before or during the sampling period. This is likely to have played a part in the large numbers of immature specimens found for many species.

As well as being generally smaller, the species found mostly as adults tended to have breeding times earlier in the year. This means that there was a higher chance of finding them as adults later in the year, at the time of sampling. It should be borne in mind, however, that molluscs are opportunistic breeders, and may take advantage of suitable conditions to breed at any time of the year, complicating the picture.

Recording immature and/or dead individuals

If dead and/or immature specimens had not been included in this study, it would have vastly decreased the size of the dataset (from 1,572 to 440). Some species would have been missed because they did not have any live adults, but these were all species which occurred in low numbers (*Carychium minimum* [2x dead], *Cepaea nemoralis* [1x immature], *Vallonia costata* [1x dead], *V.* cf. *excentrica* [1x dead] and *Vertigo pusilla* [1x dead]). The species which were recorded as dead specimens only may no longer occur at the sites in question, so their inclusion in species lists for those sites is of dubious value. Thus the use of an adults-only dataset would have generated an overall species list broadly equivalent to that generated by the full dataset.

The lists of the most common species (from the full dataset, and the adults-only one) were not very different in the case of grasslands and scrub, but there were substantial shifts in woodlands, and when all the data were pooled. Species which occurred mostly as adults had moved up the rankings (e.g. *Acanthinula aculeata*) and species which had high proportions of immatures or dead specimens had moved down (e.g. *Trochulus hispidus*). In this case, the use of either a full, or an adults-only, dataset resulted in somewhat different species lists.

The inclusion of records of immature and dead specimens in a dataset carries risks, however. If there has been a recent reproductive event for one (or a few) snail species, there can be high numbers of immatures, leading to skewed results. Similarly, the inclusion of dead shells can result in bias – as mentioned already, the shells of tiny species such as *Carychium* spp can withstand crushing better than those of larger species, thus outlasting them in many instances. Further, species which no longer occur at a site may still be present as very old shells (particularly at more calcareous locations, Kerney, 1999). Their inclusion gives a false impression of the suite of species present, and distorts species counts and community assemblage data. (However, in some studies, their inclusion may be advantageous – e.g. "*As soil collection often yields empty shells that could have belonged to individuals from previous years…, it provides a fairly accurate long-term record of a habitat's species composition. As such, this additional sampling strategy has facilitated more accurate characterizations of micromollusc assemblages.*" (Liew et al., 2008).) Timing of sampling may result in bias also – e.g. Cameron (1982) report that they recorded a larger than average number of dead shells at the end of winter, and also in September, and O'Donovan (1987) found that a much higher number of empty shells of *Helicella itala* were recorded in September, compared to other sampling times.

However, the distinction between live and dead shells is always important to make. Cernohorsky et al. (2010) investigated what effects including only living, or living and dead, specimens would have on their results. They found 'differential preservation' of shells among sites (particularly those with different soil chemistries), leading to distortion of richness and abundance estimates. These differences can be due to shell thickness or chemical composition, and also to morphology. They therefore stress the importance of distinguishing between fresh and long-dead shells.

Based on the findings here, it is concluded that data on immature and dead snails are of great importance. Individual specimens should be assigned to one of these categories, and the data should be separated and used in various combinations for analyses. Their use depends on the question being asked. For example, dead specimens are necessary if one is interested in the historical fauna of a site, or if one is interested in changes in the molluscan fauna over time. If one is investigating how changes in management are affecting snails, investigations into the population structure, focussing on numbers of immatures may be appropriate. The identification to species level of all immature and dead specimens in a sample, however, should only be undertaken where that level of detail is specifically required.

Influence of sieve mesh size

There were more than double the number of snails in the 0.5-1mm fraction compared to the >1mm one. However, a higher proportion of these were immature. A breakdown of the average number of snails per quadrat at each of the study sites (into adult, immature and dead) showed that it is the difference in numbers of immature specimens between the two size fractions that causes the largest portion of the discrepancy. The huge numbers of immatures recorded from some of the sites in particular highlight the issue of skewing if immature specimens are included in results.

All adults in this size fraction were identified to species, resulting in the addition of one new species to the dataset: *Acicula fusca*. This threatened species was present at nine of the twelve study sites, but due to its tiny size it went completely undetected when using the >1mm sieve mesh. Other species were very common in the smaller size fraction, but were recorded only in very small numbers in the larger one (e.g. *Carychium tridentatum*: 503 adult individuals in the 0.5-1mm fraction, 7 in the >1mm). It is clear that species such as *Carychium tridentatum, Punctum pygmaeum*, *C. minimum* and *Acicula fusca* are all grossly under-estimated if only the >1mm dataset is used. The two *Vertigo* species found were also underestimated, but less so. Thus if it is important to have confidence that smaller species are not being missed, or grossly underestimated, the use of a 0.5mm sieve mesh is recommended. However, the time involved in processing and identifying the large numbers of smaller snails is difficult to justify. It may be better, in some situations, to accept that certain species will be under-recorded when using a 1mm sieve and use the time gained by having less lab work to collect more samples.

Conclusions

The population structure, in terms of the ratios of adult, immature and dead specimens, of the snail fauna of three habitat types in the Burren in the west of Ireland was investigated. The majority of species were recorded more often as immatures, rather than as adults or dead specimens. This possibly reflects the fact that sampling occurred not long after the peak reproductive period of many of the species recorded. Those that were recorded as adults most frequently were small in size, and/or had their peak breeding periods earlier in the year.

Two aspects of the methodology involved in the sampling and study of land snails were investigated. The importance of recording all snail specimens as either adult, immature or dead was illustrated. Significant extra work and expertise is involved if all immature and dead specimens are also to be identified. The additional information gained by this would need to outweigh the extra time and effort, and this depends on the research question.

With regard to sieve mesh size, it was concluded that the decision whether to use a 0.5 or 1mm mesh depends again on the aim of the study in question. Using a 1mm sieve results in the possibility of missing some species (in this case, one widespread species was missed), and in hugely underestimating the abundances of some other of the smallest species. The numbers of species involved was low, however, and this fact needs to be weighed against the considerable benefits of the time gained by a reduced work load in the lab.

Chapter Six:

The effects of cessation of grazing on snail communities – results from woodland, scrub and grassland habitats in the Burren region, western Ireland

Figure 71 Difference between outside (left hand side) and inside the fence at a grassland experimental site. (Fence erected late summer 2006, photo taken April 2010.)

Introduction

This chapter presents the findings of an experimental study in which large grazers are completely excluded (using fenced exclosures) from a network of sites in the Burren region in western Ireland. The aim is to investigate how snail species and communities respond to lack of grazing (and trampling) pressure. The three habitat types were chosen so as to represent one of the main successional gradients that exists in the region: calcareous grassland → hazel scrub → hazel woodland. Data presented here come from surveys carried out between 2006 (when the fences were first erected) and 2008. This work forms the beginning of what is hoped to be a longer-term monitoring project.

Changes in farming, changes in biodiversity

As in many parts of Europe (MacDonald et al., 2000, Strijker, 2005, Schmitt and Rakosy, 2007), in the west of Ireland farming is increasingly being concentrated in more productive areas, leaving marginal lands to be slowly abandoned (The Heritage Council, 2010). This is happening for a number of reasons, including the perceived benefits of 'economies of scale', as well as due to a lack of manpower (the numbers of farmers in Ireland has been falling for a number of years) and issues with accessibility for vehicles (Tasser and Tappeiner, 2002) (refer to the 'Changes in farming' section in Chapter One for more details). These changes in land use will undoubtedly bring changes for biodiversity, but it is as yet unclear whether they will be positive, negative or mixed. It is highly likely that the effects will vary considerably between habitats and between taxa (Baur et al., 2007). Many habitats (and this is especially true in Ireland) are maintained by the activities of man – e.g. grasslands in areas that would otherwise be forested - and so their suites of species are, to a large extent, reliant on continued management. These areas are likely to experience the greatest and most rapid changes if management ceases or changes.

In the Burren in particular, where farming practices are unique (refer to Chapter One), a dramatic change in the landscape has accompanied the changes in farming over the past few decades – the spread of hazel scrub. One of the main facets of the change in management thought responsible is a lessening of grazing pressure. Other changes caused by reduced levels of grazing include the build-up of plant litter (particularly in abandoned or little-used grasslands), the decrease of some flowering herb species and a general increase in competitive grass species. With regard to vegetation, decreases in diversity when large grazing animals are removed have been documented experimentally as part of this project (Chapter Three). It is well accepted that, given enough time, much of Ireland would revert to tree cover if land management were to cease altogether (Heslop Harrison, 1951a - quoting R. Tüxen, Tansley, 1965a, Cross, 1998, Feehan, 2003), and this would happen to a large part of the Burren too (Ivimey-Cook and Procter, 1966). Indeed, the Burren has been shown to have had extensive tree cover in the past (Watts, 1984, Feeser and O'Connell, 2009).

This process would take time, and it is one of the aims of this project to document the initial stages of the process of abandonment and to detail the responses of snail communities to the changes.

Grazing exclosures, differing management and successional gradients

Experimental studies

There have been very few experimental studies which focus on the effects of the cessation of grazing (by large herbivores) on mollusc communities using exclosures (those sourced are: Morris, 1968, and Ausden et al., 2005 - both studies were based in the UK, and Suominen, 1999 - based in Fennoscandia). Molluscs formed only a small part of Morris' study, which ran over two to three years. A species list is provided for grazed and ungrazed chalk grassland sites, but the numbers of molluscs found are too small to be very informative. The most substantive element of the results was that fewer mollusc individuals were found in the grazed sites, compared to the ungrazed. (This pattern of larger numbers of individuals in the ungrazed sites is repeated for 18 of the 22 groups of invertebrates examined in Morris' study.) Ausden et al. (2005) found, using experimental exclosures in fen habitats, that there were negative impacts of light cattle grazing on mollusc densities after a four-year study. In one of the only published studies, to our knowledge, that looks at the effects of large grazers on molluscs in wooded habitats, Suominen (1999) documented higher densities of snails in ungrazed areas of boreal forests in Fennoscandia, compared to plots grazed by either moose or reindeer. This was assessed at a series of study sites, with exclosures/fencing ranging in age from ten to over 50 years old.

Non-experimental studies of management effects

Some studies have looked at mollusc community responses to grazing using non-experimental methods – e.g. comparing areas with different managements or management histories. Boyd (1960) studied an area of machair grassland on the Scottish island of Tiree, in which a fence had been erected twelve years previously. There had been no grazing (by large herbivores at least) at one side of the fence since then. He found five species of mollusc on the ungrazed side of the fence and only two on the grazed side (total numbers of molluscs were broadly similar). The numbers of molluscs found were too small to draw strong overall conclusions, but one finding in particular was striking - the complete absence of one species (*Oxychilus alliarius*) from the grazed grassland, compared to 25 individuals in the ungrazed area.

Chapell et al. (1971), working in an area of chalk grassland in England, aimed to assess the effects of trampling pressure (due to human and vehicular traffic) on plant communities and on a range of animal groups. They chose three sets of study sites – (1) rank vegetation with accumulations of litter and occasional scrub, (2) short grass, low amounts of litter, some trampling, but no soil damage evident, and (3) heavily trampled grassland with some formation of ruts – regularly used by vehicles as well as pedestrians. They found that there were significantly less molluscs in the

most heavily trampled zone in comparison to the other two zones (which did not differ significantly). Overall, they noted an increase in xerophilic mollusc species, but a decrease in most other species in the areas with the highest trampling pressure. The findings were similar for both soil arthropods and earthworms.

Working on chalk grasslands in Britain, Ruesink (1995) found that 'open-country' snails were more common in grazed sites, but that heavy grazing resulted in low overall mollusc diversity. Labaune and Magnin (2002) found that large sheep-grazed areas, consisting of homogeneous short grass cover, supported fewer mollusc species than other more heterogeneous areas, in a Mediterranean mountainous landscape. Baur et al. (2007) had inconclusive findings – in one alpine grassland site in Romania he found that areas grazed heavily by sheep had lower molluscan species richness than sites which were grazed only intermittently and lightly by wild grazing animals, but he found the opposite at another site. In a study looking at changes over an 80-year period, Tattersfield (1993) could find no difference in species richness between grazed and ungrazed (or lightly grazed) areas in a coastal site in the west of Ireland, though the habitat types were different (grazed scrub and ungrazed cliff ledges).

In work based in nutrient-poor Swiss mountain grasslands Boschi and Baur (2007b) found that sites with low grazing intensity supported more molluscs than sites with higher grazing intensity. They found that while the intensity of the grazing affects the molluscs present, the species of livestock used to graze a site does not (Boschi and Baur, 2007a). Boschi and Baur also found that past shrub cover had a negative effect on the total number of snail species (Boschi and Baur, 2008). Cameron et al. (2003a), however, found that the protected species *Vertigo angustior* could be lost from a site if the species of grazer changed (specifically, if the change was from cattle to sheep).

Other invertebrate groups

Investigations into the impacts of grazing on other invertebrate groups have unsurprisingly found mixed results. For example, McFerran et al. (1994a) found that there were higher numbers of species of ground beetles in heathlands in Northern Ireland with higher grazing intensities, and Marini et al. (2009) found greater diversity of orthopterans (bugs) in managed (mown) and early-stage abandoned meadows (three to five years since last cut), compared to sites at a later stage of abandonment. However, many studies found that high intensity grazing causes a decrease in invertebrate diversity (e.g. Dennis et al., 1998 - three groups each of small insects and arachnids, Kruess and Tscharntke, 2002a - two groups of bugs, beetles and wasps, Kruess and Tscharntke, 2002b - looking at grasshoppers, butterflies, bees and wasps, Dumont et al., 2009 - butterflies and grasshoppers). In his 1960 study (mentioned above), Boyd found large differences between adjacent grazed and ungrazed grassland for almost all invertebrate species, but the differences were not always in the same direction. Ants, harvestmen and some bugs and beetles were more common in the grazed areas, while spiders, one species of grasshopper and some other beetles were most

common in the ungrazed plots. In a study in the Beara Peninsula, south-west Ireland, Woodcock et al. (2004) found that cattle grazing was one of a number of factors which affected ground beetle community structure, although it did not have a significant effect on abundance, richness or diversity. Putman et al. (1989) found marked differences between the ground invertebrate faunas of grazed and ungrazed woodland plots. Almost all beetles were more common in the grazed plots, as were ants and spiders. Flies and harvestmen were more abundant in the ungrazed areas.

In an unpublished work, Byrne (2001) investigated the abundance and species richness of several invertebrate taxa, with a particular focus on ground-dwelling coleoptera (beetles) and araneae (spiders), in two fenced exclosures in the Burren National Park. When these were compared with the findings from nearby control areas the results showed large variability, but significantly more species and individuals of most groups were found within the fenced plots.

In a series of articles looking at many aspects of diversity on a farm in southern Ireland, the complexity of the relationship between management regimes and invertebrate success was highlighted (Good, 2001, Speight, 2001, Speight and Good, 2001a, 2001b, Speight and Good, 2005). The timing of certain management operations was found to have significant effects on some invertebrate groups (including odonata – damselflies and dragonflies, and syrphidae - hoverflies), often by interfering with certain stages in their life cycle. Brown et al. (1990) found species richness and abundance of leaf miners to be directly related to grazing intensity, and also noted the importance of the timing of certain management events. He recorded that species responded in different ways to the timing and intensity of grazing in particular. Morris (1990), too, noted that timing, duration and seasonality of management have important effects on invertebrates. Invertebrate groups such as molluscs may be particularly susceptible to the timing of certain types of management due to their limited mobility.

Successional studies

Studies which focus on sites at different stages along a succession continuum, or along stages of abandonment, are very relevant to the type of study being conducted here. Such studies (involving molluscs) include: Cameron and Morgan-Huws (1975), Magnin and Tatoni (1995) and Baur et al. (2006). Cameron and Morgan-Huws studied ten grassland sites in Britain, at a range of stages of early succession – sites which had been invaded by woody species were not included, but sites with tall non-woody vegetation were. They found a decrease in xerophilic mollusc species, and an increase in shade-loving species, with advancing successional stage. They also note that grazing does not need to have ceased for long before large changes in the molluscan fauna are seen. Magnin and Tatoni (1995), in their study of abandoned cultivation terraces in the south of France, noted that once a cover of 50% of woody species is reached in an area that is undergoing succession, the occurrence of woodland mollusc communities is facilitated. (Interestingly, Ward (1990) found a similar pattern relating to plants – i.e. once a cover of approximately 50% is

reached, the shading, and therefore altering, of the field layer became significant.) Magnin and Tatoni found that plant and mollusc communities had similar dynamic patterns during succession, and state that gastropods seem to have a relatively passive role in driving the changes in vegetation. Finally, Baur et al. (2006) studied four different habitat types (extensive hay meadows, abandoned hay meadows, birch forest, mature forest), which exist along a successional gradient. They found that the mature forests held the most mollusc species, and that open-land species decreased with successional stage (however, it should be noted that the overall numbers of molluscs recorded in the survey were small).

Overall, the picture that emerges is that heavy grazing in grasslands is not favourable for molluscs, but neither is abandonment, especially for xerophilic or open-land species.

Aims of this chapter

- Present results from grazing exclusion experiment carried out in the Burren region between 2006 and 2008;
- Illustrate how snail species and communities respond to lack of grazing;
- Document responses from within each of the three habitat types (woodland, scrub, grassland).

Methods

Field and laboratory methods

As detailed in Chapter Two, twelve study sites were chosen in the Burren region of north Co. Clare and south Co. Galway, with four sites each of hazel woodland, hazel scrub and semi-natural calcareous grassland. At each site a fenced exclosure (20 x 20m) was erected in 2006, and an unfenced control plot was established nearby. Each plot contained five fixed 2 x 2m vegetation quadrats arranged in a grid formation. A detailed account of the molluscan sampling methods used is provided in Chapter Four, and summarised here. Snails were sampled using 25 x 25cm quadrats which were placed adjacent to the vegetation quadrats. The location of samples from 2006 had been noted so as to avoid re-sampling the same area. Within the 25 x 25cm quadrat all vegetation, litter and loose surface soil was removed and bagged. This was then dried in the lab, weighed, and sieved into four size fractions (<0.5mm, 0.5-1mm, 1-5mm, >5mm). The smallest fraction was discarded, the 0.5-1mm fraction was stored (it does not form part of the analysis here), and the others were carefully sorted through, and the snails removed. These were counted and identified. Slugs were not included in this study (see Chapter Four for rationale).

Use of control plot data

Separating the data into the fenced- and control-plot portions allows us to investigate whether any changes in the numbers of snails recorded in 2008 reflect changes brought about by the experimental exclusion of grazers, or whether they may reflect other between-year variables (e.g. differences in weather conditions or natural population variations). If values in the controls stay approximately the same, this indicates that there is little background or yearly variation. If there is considerable change, however, then the extent and nature of this background variation needs to be factored into the interpretation of any changes seen in the fenced exclosures. If the change is both substantial and consistent, then other factors must also be considered to be acting on the snail populations.

Data collected

All live adult snail specimens were identified, to species level in almost all cases. Samples which were long-dead (bleached and damaged shells) and those which were immature were noted as such (see Chapter Five for more details on this). These specimens were counted, but not identified to species. The decision to work mainly with the adults from this dataset was based on the fact that the inclusion of juveniles carries the risk of the results being skewed by recent large, opportunistic breeding events in some species. Notes on nomenclature can be found in Chapter Four. Other variables recorded at the study sites are shown in Table 46.

Table 46 Environmental and floristic variables recorded at the twelve study sites.

Details	Level at which data collected*
Mean vegetation height (m)	Vegetation quadrat
Dry weight of litter sample (g)	Snail quadrat
% cover of litter	Recorded in both vegetation and snail quadrats
% cover: - grass, sedge, fern, bare earth	Vegetation quadrat
Plant species count	Vegetation quadrat
Mollusc species count	Snail quadrat
Number of mollusc individuals	Snail quadrat

* Snail quadrat = 25 x 25cm, Vegetation quadrat = 2 x 2m.

Weather

Many authors agree that the weather can have a large influence on the numbers of molluscs found during a survey (e.g. Kerney and Cameron, 1979, Cameron, 2003, Cook, 2001), and so details on the weather in the study region in 2006, 2007 and 2008 were obtained from Met Éireann, the Irish Meteorological Service (www.met.ie). This enabled important elements such as rainfall to be compared, and large deviations which might have affected snail numbers could be identified (cf.

Gardenfors et al., 1995). Data were obtained from the closest synoptic weather station, Shannon Airport, which is approximately 40km south of the Burren region.

Additionally, the weather on each day of surveying was noted, along with whether it had rained the previous day/night. For analysis, the conditions were recorded as one of three categories: 1 = wet/raining, 2 = recently raining (i.e. previous day or night, or earlier that day), 3 = dry. The numbers of snails recorded were plotted against these data, in order to ascertain if there was a noticeable increase in the numbers of snails collected on wet days.

It should be noted, however, that a large effect of weather is not expected. Shelled molluscs are less susceptible to changes in the weather than slugs. Also, the sampling method employed in this survey (i.e. the removal of material for later sorting) is much less affected by weather conditions than direct searching, for example.

Data analysis

The statistical significance of differences in numbers of snails in the categories 'adult', 'immature' and 'dead' between 2006 and 2008 were assessed using one-tailed paired t-tests in Minitab 13.1 (Minitab Inc, 2000), following the method outlined in Dytham (2003). Differences in the changes in numbers of snails (and number of snail species) between 2006 and 2008 were assessed using general linear ANOVA models, again in Minitab 13.1. Normality was checked using the Kolmogorov-Smirnov test and homogeneity of variances with the Levene's test (Dytham, 2003).

Non-metric Multidimensional Scaling (NMS) (PC-ORD 5: McCune and Mefford, 2006) was used to investigate which, if any, of the measured variables were influencing the snail communities. NMS is widely accepted as one of the best methods of ordinations when dealing with ecological data (McCune and Grace, 2002, Perrin et al., 2006b, Nekola, 2010). Outlier analysis was carried out beforehand. Successional vectors were used to illustrate the direction and relative magnitude of the changes seen in each pair of quadrats (i.e. the same quadrat between 2006 and 2008). Successional vectors are often used when samples are taken over time and they allow the trajectory of that quadrat to be visualised (McCune and Grace, 2002). Spearman's rank correlation coefficients were calculated between the most important of the measured variables and the ordination axis scores using Data Desk 6 (Data Description Inc., 1996). Their significance was assessed using the method outlined in Kent and Coker (1992). A more detailed explanation of these methods has been provided in Chapter Two. Correction for multiple tests used the Dunn-Sidak method (Quinn and Keough, 2002).

Results

[Data are from the >1mm size fraction and only live adults are included, except for Table 49 and Figure 72, which both present data on the immature and dead specimens also.]

Overall changes in species between 2006 and 2008

In 2008 25 snail species were recorded (Table 47). This is the same number as in 2006 (counting live adults only), but there were some differences between the lists. *Carychium minimum* and *Oxychilus alliarius* were new to the list in 2008 - but only one individual was recorded in each case. *C. minimum* was relatively common (66 individuals) in the <1mm size fraction in 2006, so its occurrence in the 2008 dataset is not surprising. *O. alliarius* is a new addition to the species list for the study sites. *Discus rotundatus* was not re-found in 2008. Only one adult and one immature had been recorded in 2006 (both from the same site).

Table 47 Snail species recorded in 2006 and 2008 (data from fenced and control plots merged), numbers of individuals of each species, and percentage change.

	No. individuals 2006	**No. individuals 2008**	**% change since 2006***
Columella aspera	5	19	↑ 280
Vitrina pellucida	6	18	↑ 200
Vertigo substriata	16	34	↑ 113
Columella edentula	12	25	↑ 108
Nesovitrea hammonis	40	73	↑ 83
Vertigo pygmaea	27	49	↑ 82
Aegopinella pura	31	53	↑ 71
Balea heydeni	10	16	↑ 60
Vitrea contracta	24	31	↑ 29
Vitrea crystallina	26	30	↑ 15
Lauria cylindracea	14	16	↑ 14
Cochlicopa cf. *lubrica*	59	66	↑ 12
Euconulus cf. *fulvus*	1	13	(↑ 1,200)
Helicella itala	2	4	(↑ 100)
Oxychilus cellarius	2	3	(↑ 50)
Acanthinula aculeata	51	33	↓ 35
Cochlicopa cf. *lubricella*	26	17	↓ 35
Leiostyla anglica	21	11	↓ 48
Trochulus hispidus	30	9	↓ 70
Aegopinella nitidula	21	4	↓ 81
Clausilia bidentata	3	2	(↓ 33)
Punctum pygmaeum	3	2	(↓ 33)
Carychium tridentatum	7	1	(↓ 86)
Carychium minimum		1	na
Oxychilus alliarius		1	na
Carychium indet.	1		na
Discus rotundatus	1		na
	439 individuals	**531 individuals**	**↑21**
	25 species	**25 species**	

* The % change for species for which low numbers of individuals were recorded in both years is given in brackets to denote that the results should be interpreted with caution.

Rare/notable species

In 2006 there were seven species recorded from the Irish 'Red List' for non-marine molluscs (Byrne et al., 2009), of which five were found in the >1mm adult portion of the sample. All five species were again found in 2008 (Table 48). The other two species found in 2006 were: *Vertigo pusilla* ('endangered', a single dead specimen) and *Acicula fusca* ('vulnerable', 16 specimens, all from the <1mm size fraction). *Vertigo pusilla* was again recorded in 2008 as a single dead individual, but from a different site. *Acicula fusca* was noted in small numbers in the 2008 >1mm sample, but as dead and immature specimens only.

Table 48 Numbers of 'Red List' snail species found in 2006 and 2008.

'Red List' Category	Species name	2006	2008
Vulnerable	*Helicella itala*	2	4
Vulnerable	*Leiostyla anglica*	21	11
Near threatened	*Acanthinula aculeata*	51	33
Near threatened	*Vertigo pygmaea*	27	49
Near threatened	*Vertigo substriata*	16	34

Changes in population structure

The total number of individual snails processed in 2008 (in the >1mm fraction) was 1,960. This was an increase of 25% on 2006. The average numbers of adults, immatures and dead specimens collected in both years in the fenced and control plots, along with the overall totals is presented in Table 49. The increases seen in the fenced plots suggest that the changing conditions suited at least some of the snail species during the time period of the study.

Table 49 Changes in the average numbers of snails per quadrat between study years in the fenced and control plots, with a breakdown into numbers of adult, immature and dead specimens.

		FENCED PLOTS			CONTROL PLOTS		
		Mean	S.E.	% change in mean	Mean	S.E.	% change in mean
Overall total	2006	14.10	2.27		12.10	2.59	
	2008	20.9	5.41	↑ 48.6%	11.8	2.46	↓ 3%
Adults	2006	3.8	0.6		3.6	0.9	
	2008	5.65	1.67	↑ 50.7%	3.2	0.7	↓ 11.1%
Immatures	2006	5.87	1.32		4.5	0.8	
	2008	9.93	3.18	↑ 69.3%	5.42	1.19	↑ 21.7%
Dead	2006	4.5	0.8		4.08	1.11	
	2008	5.3	1.0	↑ 19.5 %	3.2	0.8	↓ 22.9%

In order to see if any differences which may be habitat-specific could be identified, the data were further analysed by looking at each of the habitats separately (Figure 72). While no obvious pattern of change was evident for woodlands or scrub, a distinct pattern was seen in grasslands, with substantial increases in all categories (adult, immature, dead and total) from inside the fenced plots. There appear to have been increases in the control, but these were smaller and more variable. This strongly implies that the changes seen inside the exclosures are due to the experimental manipulation, rather than to any background or yearly variations. Due both to the small sample sizes (n=4), and also to the large variability between sites (resulting in large variances associated with the means), none of these changes were found to be statistically significant (assessed using paired t-tests).

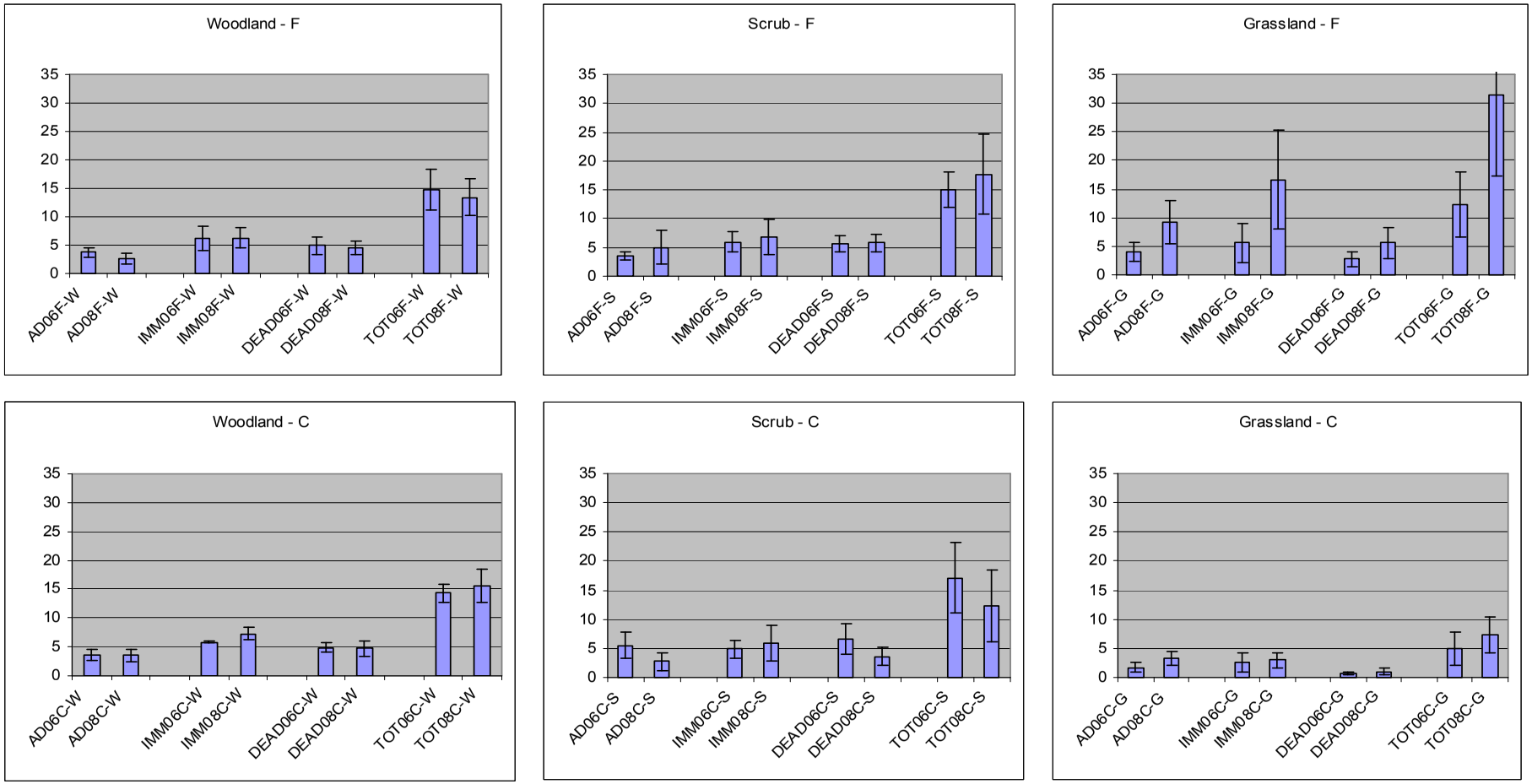


Figure 72 Mean numbers of snails per quadrat in fenced and control plots, for each of the three habitat types, in each of the two study years (+/- standard error). Abbreviations used: fenced plot [F] and control plot [C]; adult [AD], immature [IMM], dead [DEAD] and total [TOT]; study years - 2006 [06] and 2008 [08]; habitat type – woodland [W], scrub [S] and grassland [G].

Changes in abundance and species richness

To investigate further the influence of the exclusion of grazers on snail numbers, the changes (between 2006 and 2008) in numbers of individual snails, and also number of snail species, in the fenced and control plots were plotted side by side for each site (Figure 73 and Figure 74). A similar general pattern was seen for abundance and richness. The most obvious and consistent changes were the increases in the number of individual snails (and to a lesser extent, snail species) recorded at three of the grassland sites. One of the grassland sites (Caher) was anomalous, exhibiting a decrease in snail numbers inside the fenced plots. The data are pooled by habitat in Figure 75 and Figure 76, and mean number of adults from the fenced plots in 2006 is added in order that the scale of the changes can be related to original abundance/richness levels.

To investigate if the differences were statistically significant the data were analysed using an ANOVA general linear model. The variables inputted were equivalent to those used in the analysis of the vegetation data (Chapter Three): H = habitat, T = treatment, S = site (nested within habitat, and assigned as a random factor), and an interaction term H*T. The effect of year was accounted for by using 'changes in numbers of individuals' as the response variable, rather than simply using 'number of individuals' for each of the two years.

The results of the initial analysis for snail abundance, which included data from all sites, indicated that there was a significant interaction between 'habitat' and 'treatment' (Table 50), but post-hoc analysis (Tukey Simultaneous Tests) showed that there were no statistically significant differences between the changes found in the fenced and control plots *within* any of the habitats (the significant differences picked up by the ANOVA were between plots from different habitats). The analysis highlighted the large variability in the control plot in Carran and in the fenced plot in Gregan as problematic, and so the analysis was run again with data from these sites removed. No significant difference between fenced and control plots was found with this reduced dataset.

Table 50 Results from general linear model: mean changes in number of individual snails between 2006 and 2008 in quadrats in three habitat types, with fenced and control plots.
[H = habitat, S = site, T = treatment]

Source	DF	Seq SS	Adj MS	F	P
H	2	424.02	212.01	2.87	0.109
S(H)	9	664.65	73.85	2.90	0.004
T	1	158.70	158.70	6.23	0.014
H*T	2	175.85	87.93	3.45	0.035
Error	105	2674.25	25.47		
Total	119	4097.47			

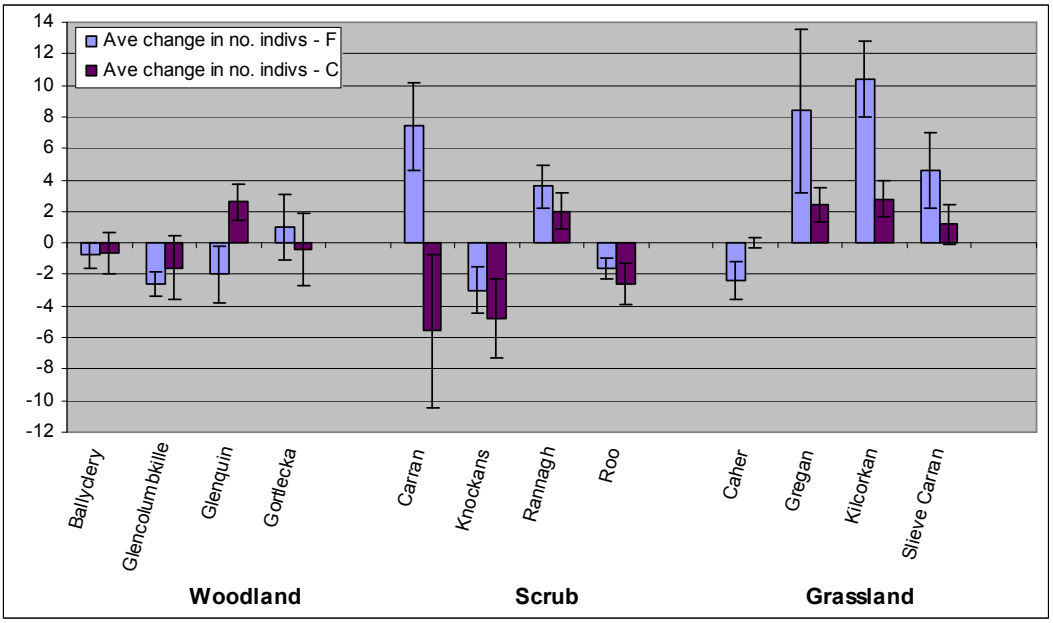


Figure 73 Changes in numbers of individual snails in fenced and control plots at each of the twelve study sites (average from five quadrats, +/- the standard error). [F = fenced plots, C = control plots.]

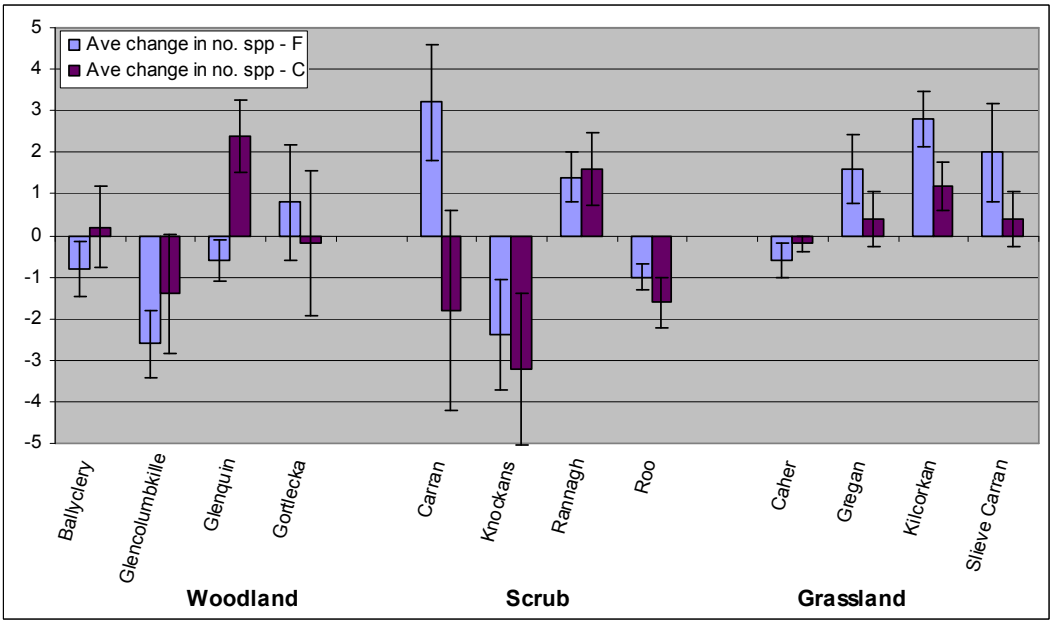


Figure 74 Changes in number of snail species in fenced and control plots at each of the twelve study sites (average from five quadrats, +/- the standard error). [F = fenced plots, C = control plots.]

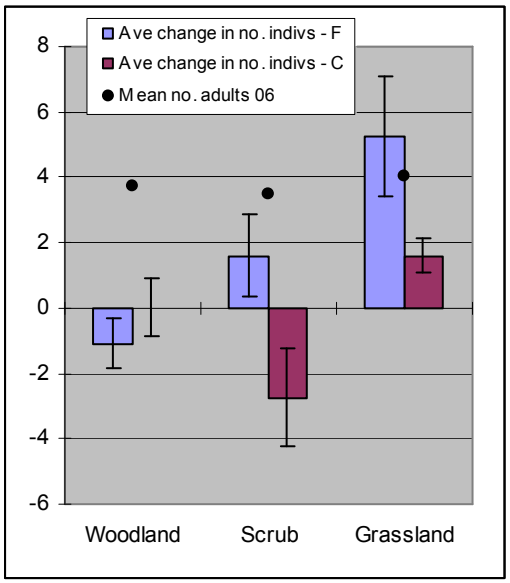


Figure 75 Changes in numbers of individual snails in fenced and control plots in each of the three habitats (average from 20 quadrats, +/- the standard error). [F = fenced plots, C = control plots.] Mean number of adults from the fenced plots in 2006 is added in order that the scale of the changes can be related to original abundance levels.

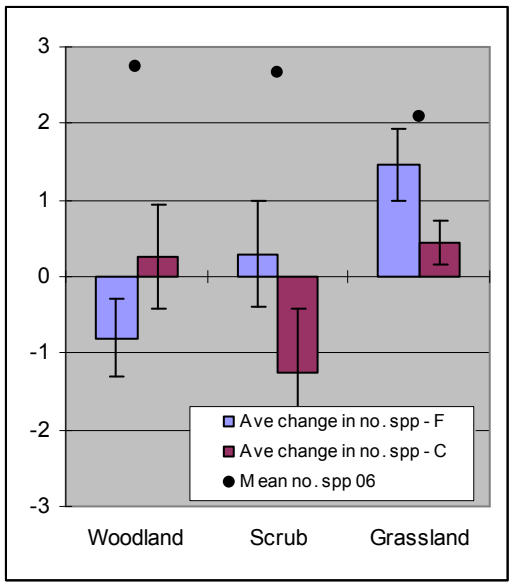


Figure 76 Changes in numbers of snail species in fenced and control plots in each of the three habitats (average from 20 quadrats, +/- the standard error). [F = fenced plots, C = control plots.] Mean number of species from the fenced plots in 2006 is added in order that the scale of the changes can be related to original richness levels.

The strong trend seen in three of the grassland sites (Figure 73) may have been masked by the variability in the other two habitats. In order to check if this were the case, the grassland sites were analysed in isolation. A statistically significant effect of treatment (i.e. fencing) was not found (Table 51).

Table 51 Results from general linear model: mean changes in number of individual snails between 2006 and 2008 in quadrats in grassland sites only, with fenced and control plots.
[S = site, T = treatment]

Source	DF	Seq SS	Adj MS	F	P
S	3	8.8404	2.9468	4.16	0.013
T	1	1.3649	1.3649	1.93	0.174
Error	35	24.8098	0.7089		
Total	39	35.0151			

The test for significant differences in species richness similarly indicated that there was a (borderline) significant interaction between 'habitat' and 'treatment' when data from all sites were included (Table 52), but post-hoc analysis revealed that the differences were again attributable to differences between plots in different habitats, rather than within habitat types. Once again, as Figure 74 showed a trend for three of the grassland sites which may have been masked by overall

variability, a further analysis was conducted using just the grassland data. A borderline significant difference was found between the fenced and control plots (Table 53). This result should be interpreted with some caution, however, in light of the variability of the dataset as a whole.

Table 52 Results from general linear model: mean changes in number of snail species between 2006 and 2008 in quadrats in three habitat types, with fenced and control plots.
[H = habitat, S = site, T = treatment]

Source	DF	Seq SS	Adj MS	F	P
H	2	47.617	23.808	1.13	0.366
S(H)	9	190.450	21.161	3.48	0.001
T	1	7.500	7.500	1.23	0.269
H*T	2	37.550	18.775	3.09	0.050
Error	105	638.350	6.080		
Total	119	921.467			

Table 53 Results from general linear model: mean changes in number of snail species between 2006 and 2008 in quadrats in three grassland sites only, with fenced and control plots.
[S = site, T = treatment]

Source	DF	Seq SS	Adj MS	F	P
S	3	29.900	9.967	4.06	0.014
T	1	10.000	10.000	4.07	0.051
Error	35	86.000	2.457		
Total	39	125.900			

Scrub is essentially composed of a mosaic of two very different vegetation types – (a) dense low woody vegetation and (b) open grassy vegetation. To check if any patterns in the scrub data could be elucidated, the quadrats were split into 'woody' and 'grassy' (Figure 77 and Figure 78). The distinction between the two was made based on the cover of woody species within a quadrat, with >50% woody cover meaning that a quadrat was classed as woody scrub. The graphs indicate that this split yielded no further clarity - there was still a very large amount of variability, with no trend emerging.

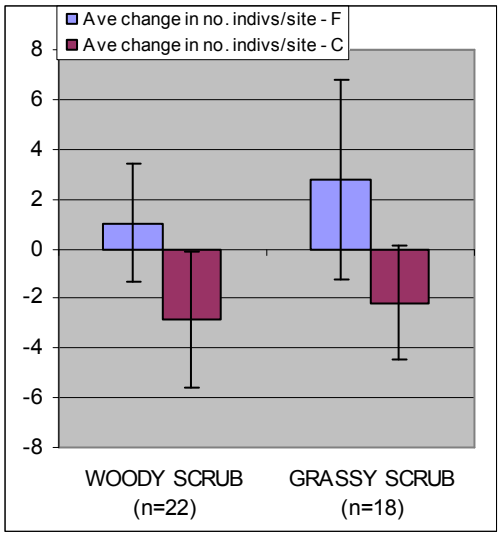


Figure 77 Average changes in numbers of individual snails recorded in the 'woody' scrub quadrats and the 'grassy' scrub quadrats, +/-standard error. [F = fenced plots, C = control plots.]

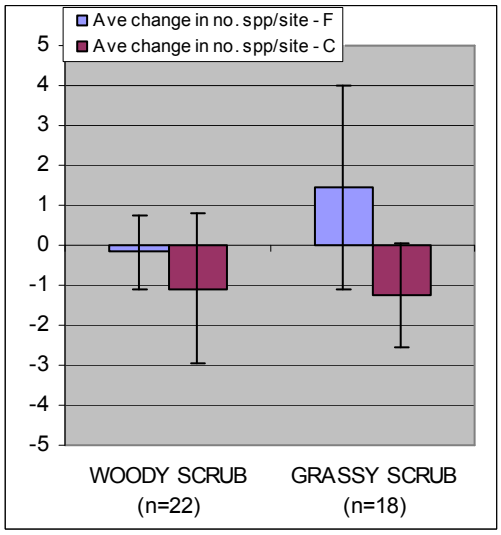


Figure 78 Average changes in numbers of snail species recorded in the 'woody' scrub quadrats and the 'grassy' scrub quadrats, +/-standard error. [F = fenced plots, C = control plots.]

Which species showed the greatest changes?

The numbers of individuals recorded for each species are presented in Table 54, Table 55 and Table 56, with scrub split into its 'woody' and 'grassy' components. In most cases species are present in numbers too small from which to discern strong patterns.

Table 54 Numbers of individuals of each snail species recorded in the woodland sites in 2006 and 2008. The larger changes are shaded, and control plots numbers are shown for comparison.

	Fenced plot		**Control plot**	
	2006	**2008**	**2006**	**2008**
Acanthinula aculeata	8	4	6	7
Aegopinella nitidula	11	4	9	0
Aegopinella pura	6	9	7	5
Balea heydeni	2	4	8	12
Carychium tridentatum	2	0	3	1
Clausilia bidentata	2	1	0	0
Cochlicopa cf. *lubrica*	5	6	5	2
Cochlicopa cf. *lubricella*	2	2	7	2
Columella aspera	0	2	0	1
Columella edentula	4	8	2	3
Discus rotundatus	1	0	0	0
Euconulus cf. *fulvus*	0	0	0	7
Lauria cylindracea	7	1	2	5
Leiostyla anglica	8	4	10	7
Nesovitrea hammonis	1	0	2	3
Oxychilus alliarius	0	0	0	1
Oxychilus cellarius	2	1	0	2
Punctum pygmaeum	1	0	0	0
Trochulus hispidus	3	1	1	2
Vitrea contracta	1	2	1	1
Vitrea crystallina	7	4	7	8
Vitrina pellucida	2	0	0	1
TOTAL	**75**	**53**	**70**	**70**

Table 55 Numbers of individuals of each snail species recorded in the scrub sites in 2006 and 2008, with data split between 'woody' and 'grassy' scrub quadrats. The larger changes are shaded and control plots numbers are shown for comparison.

	'Woody' quadrats				**'Grassy' quadrats**			
	Fenced plot		**Control plot**		**Fenced plot**		**Control plot**	
	2006	**2008**	**2006**	**2008**	**2006**	**2008**	**2006**	**2008**
Acanthinula aculeata	6	8	24	4	1	1	0	3
Aegopinella nitidula	0	0	1	0	0	0	0	0
Aegopinella pura	2	9	4	6	0	3	3	1
Cary indet.	1	0	0	0	0	0	0	0
Carychium tridentatum	1	0	1	0	0	0	0	0
Clausilia bidentata	0	0	0	0	0	0	1	1
Cochlicopa cf. *lubrica*	2	5	10	1	2	2	3	1
Cochlicopa cf. *lubricella*	5	4	5	6	0	0	3	0
Columella aspera	1	2	3	2	0	0	0	1
Columella edentula	6	7	0	5	0	0	0	2
Euconulus cf. *fulvus*	0	5	1	0	0	0	0	1
Helicella itala	0	0	1	0	1	1	0	0
Lauria cylindracea	0	2	0	0	0	1	0	0
Leiostyla anglica	2	0	1	0	0	0	0	0
Nesovitrea hammonis	6	14	8	3	5	4	3	7
Punctum pygmaeum	1	0	0	0	0	0	0	0
Trochulus hispidus	7	2	11	1	3	2	3	0
Vertigo pygmaea	1	0	1	1	4	3	5	2
Vertigo substriata	3	0	3	1	0	1	2	0
Vitrea contracta	2	10	6	4	2	7	1	0
Vitrea crystallina	3	7	5	1	2	0	1	0
Vitrina pellucida	0	0	0	1	0	1	0	0
TOTAL	**49**	**75**	**85**	**36**	**20**	**26**	**25**	**19**

Table 56 Numbers of individuals of each snail species recorded in the grassland sites in 2006 and 2008. The larger changes are shaded and control plots numbers are shown for comparison.

	Fenced plot		Control plot	
	2006	**2008**	**2006**	**2008**
Acanthinula aculeata	6	4	0	2
Aegopinella pura	7	18	2	2
Carychium minimum	0	0	0	1
Cochlicopa cf. *lubrica*	23	32	9	17
Cochlicopa cf. *lubricella*	1	0	3	3
Columella aspera	0	10	1	1
Helicella itala	0	3	0	0
Lauria cylindracea	3	7	2	0
Nesovitrea hammonis	10	34	5	8
Punctum pygmaeum	0	0	1	2
Trochulus hispidus	0	1	2	0
Vertigo pygmaea	11	20	5	23
Vertigo substriata	5	27	3	5
Vitrea contracta	9	7	2	0
Vitrea crystallina	1	10	0	0
Vitrina pellucida	4	12	0	3
TOTAL	**80**	**185**	**35**	**67**

Within the grasslands, *Columella aspera* appeared for the first time in the fenced plots in three of the sites in 2008, indicating that the altered habitat conditions in the ungrazed plots are favourable to this species. There was a large gain for *Nesovitrea hammonis* at one of the grassland sites (3→24 individuals). There were contradictory changes in the species *Vertigo pygmaea* – it was lost at one grassland site (ten individuals in 2006, zero in 2008), and increased substantially at another (1→13 individuals across four quadrats). Small gains were made at the other two grassland sites. *Vertigo substriata* increased at one grassland site (4→25 individuals). *Vitrea crystallina* appeared at one grassland site for the first time (seven individuals, across all five quadrats). Perhaps surprisingly, there was a lack of patterns which manifested across all grassland sites, apart from the success of *Columella aspera*. However, the general trend was for a small but consistent increase in snail numbers and species, across three of the four sites. The anomalous site, Caher, had so few snails that it was quite difficult to draw conclusions from the data.

Weather during the study period

According to data available from the Irish Meteorological Service 2006 was a warmer, sunnier and wetter year than average across the country. (All meteorological records are compared to 30-year averages [1961-1990].) However, at the nearest synoptic station to the study sites, Shannon Airport, only 44% of the normal amount of rain fell during the summer months (June/July/August). In contrast, in the autumn (September-November) there was 33% more rain than average. The temperature was 1.2^{o}C and 1.3^{o}C higher for summer and autumn respectively, and there was 28% and 25% more sunshine than normal. The year 2007 was the warmest on record in places in

Ireland, and was sunnier than normal, but with an exceptionally wet summer and a very dry autumn. However, at Shannon Airport synoptic station the rainfall was close to normal for the year as a whole, the temperature was 1.1°C higher than average and there was about 10% more sunshine than expected. Shannon Airport had its wettest year on record in 2008, with the summer being particularly wet (rainfall up 92% on normal figures). Temperatures were close to average and sunshine also.

To highlight the most relevant points (from the Shannon meteorological station):

- 2006: summer - much drier than normal (only 44% of expected rainfall), autumn - quite wet (33% more rainfall than average)
- 2007: summer and autumn - rainfall close to normal
- 2008: summer - exceptionally wet (92% more rainfall), autumn - quite wet (↑ 24%).

To provide more localised weather-related information, the weather was recorded (using broad descriptive categories) on each survey day. In order to check if more snails were recorded on wet days, the numbers of snails recorded per quadrat in 2006 were plotted against the weather categories (Figure 79). The number of samples taken on 'dry' days were few compared to those taken on 'wet' or 'recently wet' days, making comparisons difficult. However, it is clear that the numbers of snails collected on wet days are not markedly larger than those on dry days.

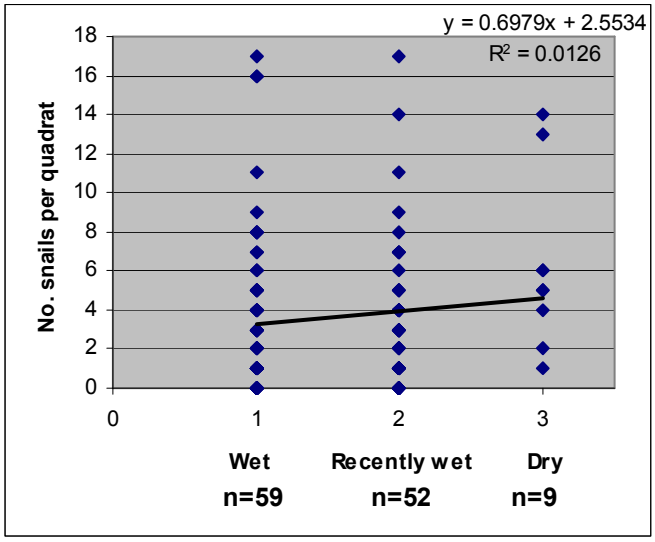


Figure 79 Weather (recorded using the broad general categories 'wet', 'recently wet' and 'dry') on each survey day in 2006, and number of snails recorded per quadrat.

Influence of measured variables

As there was a high amount of variability in the data relating to the snail assemblages of woodlands and scrub, with no clear patterns emerging, the remaining analyses were restricted to the grassland communities.

The data were analysed in NMS to ascertain which, if any, of the measured variables (see Table 46) were influencing the changes seen in the snail fauna of the grasslands. The 'successional vectors' function was used to illustrate the direction and relative magnitude of the changes seen in individual quadrats. Only three of the four grassland sites were included in the analysis - one (Caher) lacked enough data points for inclusion. Quadrats were only included if snails had been recorded in both years due to the fact that NMS does not accept empty rows. This resulted in the exclusion of one pair of quadrats (from Kilcorkan). Additionally, although the analysis was conducted initially with both control and fenced plot data, only data from the fenced plots are presented here – inclusion of control data in the ordinations showing successional vectors would have greatly decreased clarity and interpretability. Species which were uncommon in the dataset were deleted (=5). This resulted in a main matrix consisting of 11 species, and 28 quadrats (14 pairs). Outlier analysis did not reveal any species or quadrat outliers. The final stress of the NMS solution was 15.178, which is within the acceptable range (McCune and Grace, 2002). However, the analysis returned quite a high instability value: 0.00361 (steady over four runs). McCune and Grace (2002) recommend striving for an instability value of <0.0001, but state that 0.001 is acceptable if the stress is low. While the instability value here is larger than ideal, the low stress and the consistency of the ordination outputs mitigate against this, and render the findings acceptable. Other authors have made similar decisions – e.g. Regan et al. (2007) reported an instability value of 0.0046 for their ordination of turlough vegetation.

A 3-dimensional solution was recommended and the ordination captured almost 76% of the variation in the distance matrix ($r^2 = 0.755$). Axis 1 was responsible for explaining 30%, with axes 2 and 3 both holding 23% of the variation each. The NMS solution is presented using two plots – axis 1 v 3 and 1 v 2 (Figure 80). The 28 grassland quadrats are coded by survey year, and are overlaid by the most influential variables from the second matrix (cut-off: r^2=0.2) (McCune and Grace, 2002). Spearman's rank correlation coefficients were calculated between the overlaid variables and the ordination scores (Table 57).

Most of the quadrats sampled in 2006 are at the bottom right hand side of both ordinations, i.e. at the upper end of axis 1 and the lower end of axes 2 and 3. This suggests that they are characterised by more bare earth, shorter vegetation, less litter and lower numbers of snails than the 2008 quadrats, generally speaking. There is more spread in the quadrats recorded in the second year of study.

Table 57 Spearman rank correlation coefficients for ordination scores, habitat variables and numbers of snail individuals. Those in bold are still significant following correction for multiple tests (Dunn-Sidak).

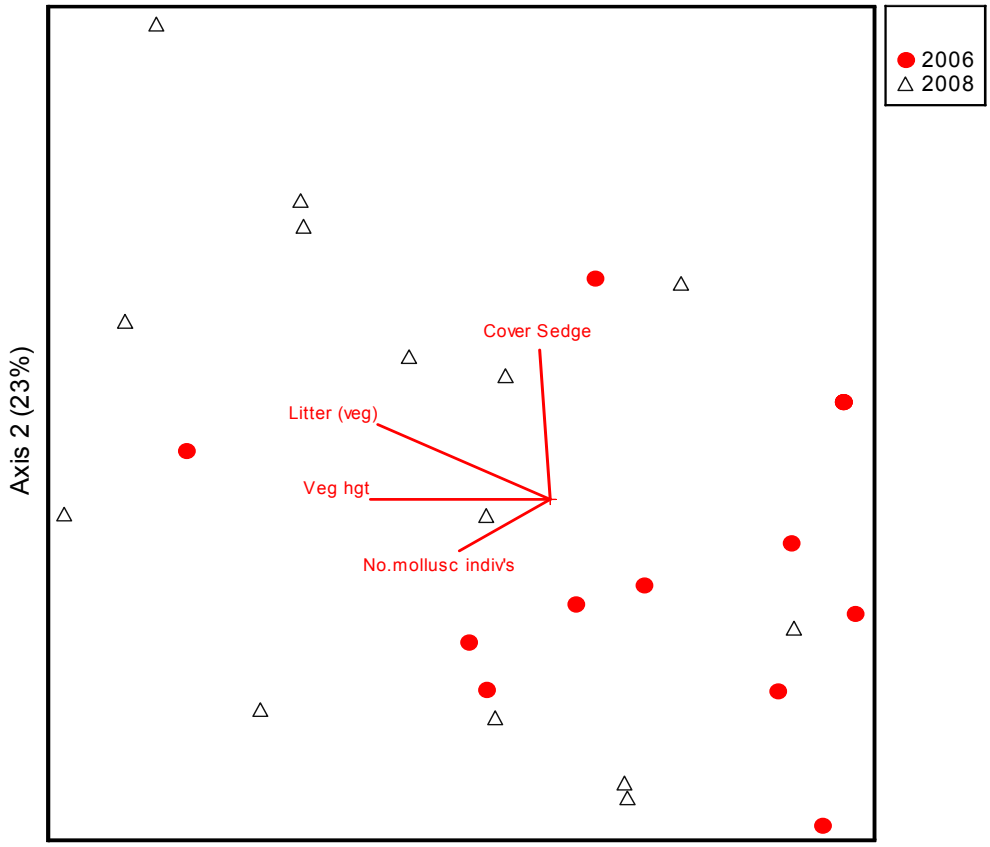
	Axis 1	Axis 2	Axis 3	Cover of sedges	Litter (from vegetation quadrat)	Vegetation height	No. individ-ual snails
Cover of sedges	0.12	0.536**	0.193	-	-	-	-
Litter (from vegetation quadrat)	**-0.591*****	0.294	0.425*	0.012	-	-	-
Vegetation height	**-0.651*****	0.005	0.151	-0.407*	**0.736*****	-	-
No. individual snails	-0.539**	-0.311	0.225	**-0.633*****	0.301	**0.671*****	-
Cover of bare earth	**0.601*****	-0.139	-0.441*	0.165	**-0.763*****	**-0.805*****	-0.549**

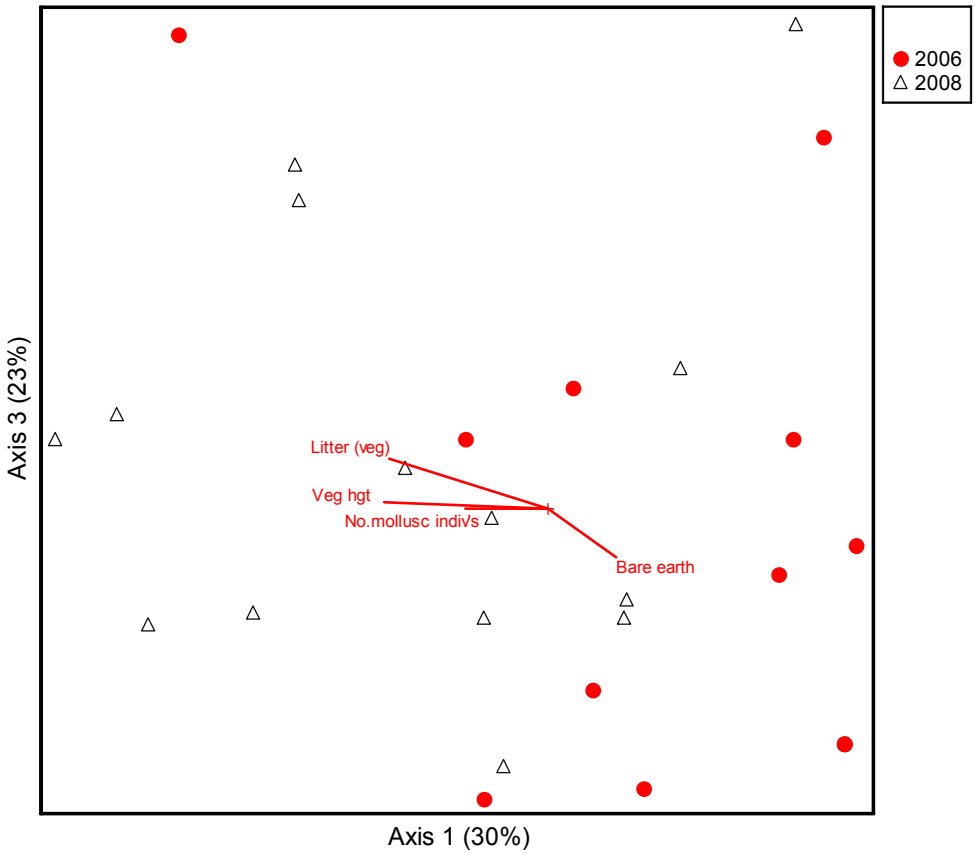
Statistically significant correlations are indicated: * p≤0.05, ** p≤0.01, *** p≤0.001.

An overview of the spread of all of the grassland quadrats within the ordination space is provided in Figure 80, but in order to see how individual quadrats have changed over time, the next three figures (Figure 81, Figure 82 and Figure 83) present pairs of quadrats linked by successional vectors for each site. They are presented separately by site for ease of interpretation. Each pair represents the same quadrat, sampled in 2006 and 2008. Only axis 1 v axis 2 is presented in each case, for the sake of brevity and clarity.

Quadrats show the largest and the most uniform changes at Slieve Carran (Figure 81). The direction and slope of most of the vectors matched well with the overlaid variable, cover of litter. There was one anomalous quadrat which moved in the opposite direction. At Gregan (Figure 82), three of the five quadrat pairs showed a similar relationship with amount of litter, though it was less strong (as indicated by the shorter successional vectors). The change seen in one quadrat was parallel to the variable 'number of molluscs', and there was again one quadrat going against the trend. For Kilcorkan (Figure 83) only one quadrat seemed strongly related to cover of litter, and the changes in the other three pairs were in a similar direction to the variable 'number of mollusc individuals'.

Figure 80 (Next page) NMS ordinations – axis 1 v 3 and 1 v 2. Each point corresponds to a quadrat. Figures in brackets on axis labels are the percentage of the variation in the distance matrix which is explained by this axis. The most influential variables from the second matrix are overlaid.
Cover Sedge = % cover of sedge layer, Litter (veg) = % cover of litter layer (measured in vegetation quadrat), Veg hgt = mean height of vegetation, No. mollusc indiv's = total number of snails recorded per quadrat


2006
2008
Axis 2 (23%)
Cover Sedge
Litter (veg)
Veg hgt
No.mollusc indiv's


2006
2008
Axis 3 (23%)
Litter (veg)
Veg hgt
No.mollusc indiv's
Bare earth
Axis 1 (30%)

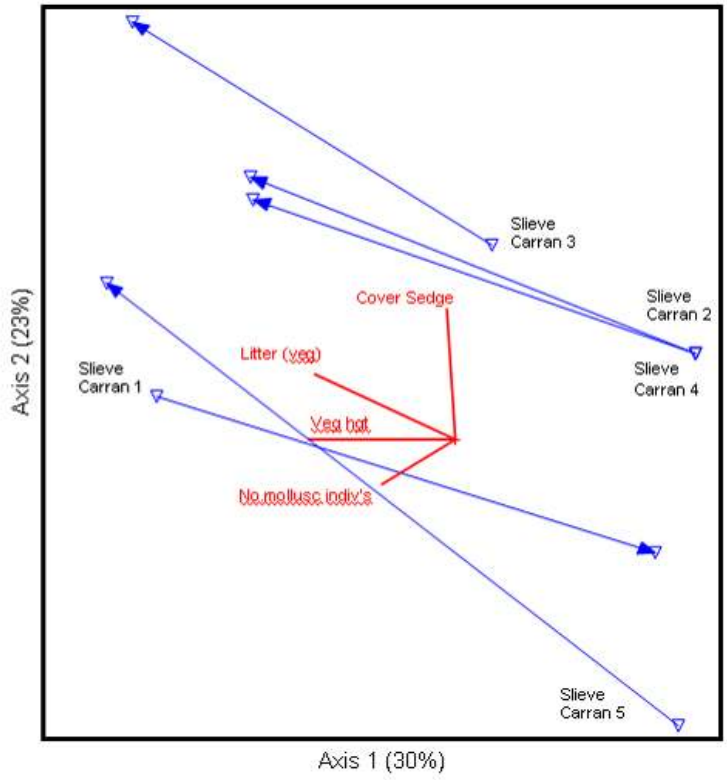


Figure 81 NMS with successional vectors for the grassland site, Slieve Carran (as Figure 80 but with data points from the other grassland sites removed).

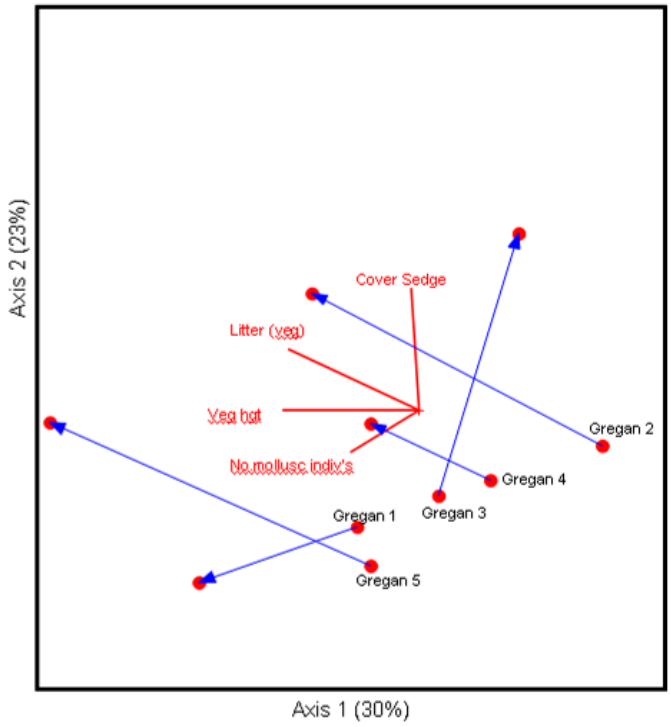


Figure 82 NMS with successional vectors for the grassland site, Gregan (as Figure 80 but with data points from the other grassland sites removed).

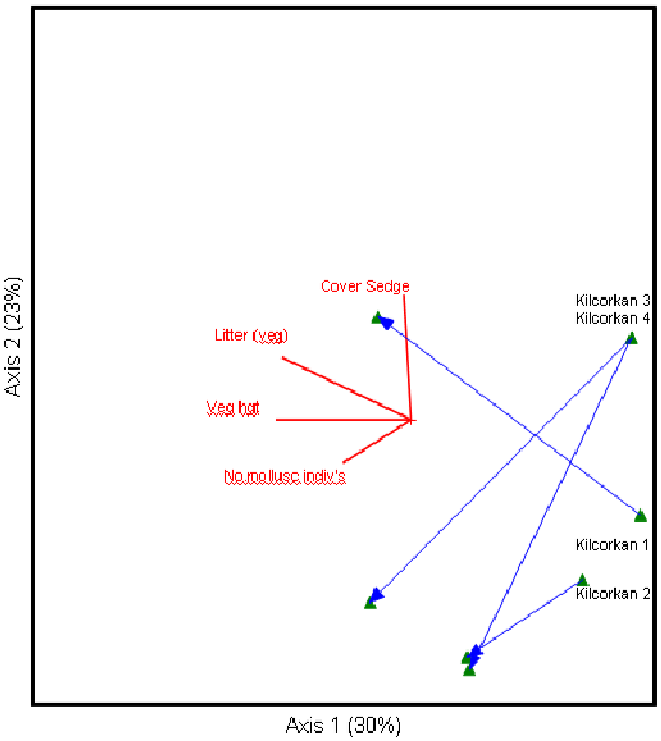


Figure 83 NMS with successional vectors for the grassland site, Kilcorkan (as Figure 80 but with data points from the other grassland sites removed).

Discussion

Species recorded

A total of 25 species of snail (live adults, >1mm size) was recorded from samples in both 2006 and 2008. This masks a small turnover between the study years - two species were lost and two were gained. In each of these cases only one specimen was recorded, i.e. these species were very rare in the dataset. Many snail species increased in number between 2006 and 2008. The largest gains occurred for *Columella aspera, C. edentula, Nesovitrea hammonis, Vertigo pygmaea, V. substriata* and *Vitrina pellucida,* all of which increased by over 75% compared to the 2006 figures. These figures are remarkable, given that these data are not split between fenced and control plots. Species which have decreased (again, fenced and control plots pooled) include *Aegopinella nitidula, Trochulus hispidus* and *Leiostyla anglica* (decreases of ~50% or more).

The five 'Red List' species which were found in 2006, were again recorded in 2008. Two of these species had decreased strongly in numbers (*Leiostyla anglica* and *Acanthinula aculeata*), and three had increased (*Helicella itala, Vertigo pygmaea* and *V. substriata*). A single dead individual of the rare *V. pusilla* was found at one of the woodland sites. A single (dead) individual was also found in the 2006 samples, from a different, but nearby (+/- 1km) woodland. While the recording of dead snail shells gives no indication as to whether the species is currently present in an area, it is encouraging, in conservation terms, to have found shells at two neighbouring sites.

Effects of weather

The overall weather patterns during the years of this study showed some deviations from normal. The survey period, autumn, was wetter than average in each of the study years. This means that weather conditions were not hugely different between 2006 and 2008, and are thus broadly comparable.

The weather was described using broad descriptive categories on each day of surveying, and it was shown that wet days did not yield substantially more snails from the samples. It may be that weather conditions were homogeneous enough over the study period so as to not to have had a noticeable effect, but it is more likely that the survey methodology (i.e. collecting samples for later processing) is robust to the effects of differing weather conditions on snail sampling.

Changes in population structure and abundance

The total number of snails recorded in 2008 (>1mm; includes adults, immatures and dead shells) was 1,960, compared to 1,572 in 2006 (an increase of 25%). When this is separated into the fenced and control plot portions, it can be seen that most of this increase comes from within the fenced plots (an increase of 49% in the fenced plots, and a decrease of 3% in the controls; overall changes

in mean number of snails per quadrat, see Table 49). This suggests that the experimental treatment (i.e. fencing out large grazing animals) has had a substantial positive influence on the abundance of snails.

Across all habitats, adults were up 51% in the fenced plots, and down 11% in the controls. This indicates a strong and real increase in adult numbers inside the exclosures. This in turn indicates that conditions are suitable for the successful expansion of the populations of at least certain snail species. Changes in the proportions of live adult specimens found in a survey gives a measure of the 'health' of a population. Increases in these figures give a strong signal that conditions (in this case, brought about by the cessation of grazing) are favourable for at least some of the snail species. The number of immature specimens recorded increased by 69% inside the fence, and by 22% outside the fence. Again, the magnitude of this change is convincing. An increase in juveniles can be more complicated to relate to successful population expansion, however, due to high mortality rates.

The dead shell data are a little harder to interpret: an increase of 20% was documented in the fenced plots, and a decrease of 23% in the control plots. A considerable change in the proportion of dead shells can be informative - an increase suggests that at least some species are not coping well with the changes being experienced. The more detailed breakdown of the dead shell data provided in Figure 72 illustrates that, for the most part, the numbers of dead shells stays relatively constant, apart from an increase in the grassland fenced plots, and a decrease in the scrub control plots. The increase in the grassland sites may indicate that some species are not as tolerant of the new conditions as others.

In the woodlands, no large or consistent changes in snail abundance or population structure were apparent – in either the fenced or the control plots. The scrub showed more variation, but again no consistent patterns were observed. In the grasslands, however, a noticeable and recurring pattern of increasing numbers of snails can be seen for all groups (i.e. adult, immature, dead and total) from within the fenced plots. This strongly suggests that the changes are due primarily to the experimental manipulation, rather than to any background or yearly variations. This is perhaps not surprising, given the amount of structural change seen – e.g. the litter build-up documented in the vegetation study (Chapter Three). There was also a small but consistent increase in snail numbers in the controls. This indicates that some background factor (possibly weather conditions) is also acting favourably on the snail communities. However, the increase in the fenced plots is large by comparison. The largest proportion of the increased numbers comes from the immature category, though there is much variability.

Habitat-specific changes in abundance and richness

Changes in abundance and richness (between 2006 and 2008) were compared for fenced plots and control plots across all sites, and no differences were found within habitats.

Examination of the raw data (see Figure 72, Figure 73 and Figure 74, for example) suggested that there were increases in snail abundance and species richness at three of the four grassland sites. The fourth site, Caher, showed an anomalous pattern – the number of snails decreased within the fenced plot. In the case of abundance, analysis failed to confirm the changes seen as significant, most likely due to the high levels of variability between quadrats. However, there was a borderline significant result for species richness. Overall, while the increase in numbers of snails in ungrazed grassland is variable, there was a definite trend, and these findings concur with those of Boyd (1960), Morris (1968), Chappell et al. (1971) and Labaune and Magnin (2002). Ausden et al. (2005) also found that in fens, the exclusion of cattle caused an increase in the number of molluscs. The reason for the decrease in one of the sites is not clear, but snail numbers recorded there were very low, and so the effects of noise, or (ecologically) meaningless variation, may have been amplified at this site.

The findings from the woodland sites were so variable as to defy recognition of a trend, but, if anything, they hinted at a decrease in snail numbers. The sole study located which looked at the effects of the exclusion of grazers on molluscs in woodlands (Suominen, 1999) found a strong and consistent increase in molluscs in ungrazed plots. It should be noted, however, that the woodland type was different (pine/birch woods), as were the species of grazers (moose and reindeer). Furthermore, the exclosures in that study were standing for between ten and 50-60 years. Thus it is likely that the current study is at too early a stage to show measurable results.

The scrub data were even more variable, and separation into ‘woody’ and ‘grassy’ parts failed to reveal any consistency of response to the experimental treatment. Again, it is likely that it is too early to measure change in this habitat type, which is very heterogeneous. Delays in detecting differences have been reported in other studies – e.g. Brown et al. (1990) wrote that some unmanaged habitats may take years before showing detectable signs of change.

In the case of both abundance and richness, the average values from 2006 were calculated and plotted for each of the three habitats. This was in order to investigate if habitats with higher initial values might change more. There did not appear to be a relationship.

Species-specific changes

Grasslands

In order to ascertain which, if any, of the species were driving the overall changes seen in the grasslands, the species data were looked at in detail. There was a lack of trends which manifested across all sites. The strongest pattern found was the increase of *Columella aspera* - it appeared for the first time at three of the grassland sites in 2008. (Interestingly, it also appeared in both the fenced and control plots of the woodlands for the first time, though in very low numbers.) Of the studies reviewed, none mentioned *C. aspera* specifically as a species which responds either quickly or strongly to the removal of grazing in grasslands. However, it is noted in Kerney (1999) as a species which is found in uncultivated grassland, as well as other habitats such as coniferous and deciduous woods and in marshes (in general, in more base-poor areas than *C. edentula*). It may be that this species is well suited to the rougher vegetation which is now growing inside the fenced exclosures after two years without grazing. The taxon '*Columella* spp' is reported in Suominen (1999) as being borderline significantly ($p<0.1$) more common in ungrazed than in grazed woodland sites.

Other species which showed increases in at least one of the grassland sites were *Nesovitrea hammonis* (found also by both Chappell et al., 1971, and Cameron and Morgan-Huws, 1975, to be more abundant in longer grassland vegetation), *Vertigo pygmaea, V. substriata* and *Vitrea crystallina*. However *V. pygmaea* also declined at one of the sites, and so exhibited a contradictory response. Chappell et al. (1971) found that this species had an optimum occurrence in areas with moderate disturbance, and Cameron and Morgan-Huws (1975) found it to increase in abundance with increased grazing/shorter vegetation. It is expected that this species will decline in the longer-term in the absence of grazing, given that it is not a shade-tolerant species (Falkner et al., 2001).

Other species (from those recorded in this survey) which are not shade-tolerant include *Cochlicopa* cf. *lubricella, Helicella itala* and *Vitrina pellucida* (see Chapter Four). It is highly likely that all of these species will be put under pressure in the medium-term within the fenced grassland and grassy scrub plots due to the increased litter build-up and taller, denser vegetation. Two of these (*Helicella itala* and *V. pygmaea*) are species of conservation concern. Therefore an overall increase in snail abundance may come at the cost of losing some of the open-land species. The overall proportion of species recorded during this survey which could be classed as xerophilic (i.e. adapted to dry conditions, such as those found in open or heavily grazed grasslands) was low. Species such as *Pupilla muscorum, Vallonia* cf. *excentrica* and *V. costata* were absent (apart from one dead individual of each of the latter two species). This may indicate that the climate dictates that the grasslands in the Burren are not dry enough, but it is also very likely that they are not that heavily grazed. The timing of grazing is likely to be a factor also, with the Burren grasslands being winter-

grazed in general. This means that in summer and autumn, when snails are most active, the grasslands are at their most lush.

Interestingly, even though there was a significant increase in the numbers of snails recorded, there were few new species recorded within the grassland plots (*Columella aspera* was the main exception, and *Helicella itala* adults also appeared for the first time inside the fence in 2008). Colonisation of new areas is curtailed somewhat by the limited mobility of land snails in general, and indeed the timeframe for this study was short, however, colonisation is facilitated in the Burren in particular by the small scale mosaic-like nature of the vegetation.

Woodlands

Overall, the numbers of snails in the fenced plots decreased in woodlands (from 75 in 2006 to 53 in 2008), while in the control plots the numbers did not change (70 individuals recorded in both years). However, this decrease masks a large variability between sites. Patterns for individual species, similarly, are not strong. One of the more marked was a decrease for *Lauria cylindracea*. *Aegopinella nitidula* decreased inside the fenced plot, but this was mirrored by a similar decrease in the control plot. This suggests that it was not the lack of large herbivore grazing which caused the decrease. Souminen (1999) found significantly higher numbers for three of the taxa which occur in this dataset (*Columella* spp., *Vitrina pellucida* and *Euconulus* sp.) in ungrazed plots, compared to grazed ones. A longer timeframe for study will be needed in order to see if comparable results will be found here.

Scrub

The scrub data were split into their 'woody' and 'grassy' components in an attempt to tease out possible patterns for individual species. Again, however, the variability in the data precluded any strong conclusions being drawn. Changes in the woody scrub included increases for *Nesovitrea hammonis, Euconulus* cf. *fulvus* and *Aegopinella pura*. One of the big losers was *Trochulus hispidus*, which decreased in both the fenced and control plots – indicating again that factors such as weather conditions may be acting on some species. There were surprisingly few obvious changes in the grassy scrub quadrats. It might have been expected that as the grassland sites exhibited the strongest and most consistent patterns of change, that similar changes might have been evident here also. It is possible that the grassy areas within scrub habitats are already quite rank (i.e. they already consist of tall, dense grassy habitats), and so the changes due to exclusion of grazers were less dramatic than in the grassland sites.

Influence of measured variables on changes in grassland snail communities

In order to examine the relationships between the snail assemblages, the measured variables, and the changes seen, pairs of grassland quadrats from 2006 and 2008 were analysed using NMS. Successional vectors were used to join up the pairs, and thus to visualise the direction and relative

distance they had 'moved' in the ordination space. The results showed that most of the quadrats from within the fenced plots in 2006 were associated with lower vegetation height, lower cover of litter, higher cover of bare earth and lower numbers of snails than the 2008 quadrats. The 2008 quadrats were, however, more spread out over the ordination space by comparison, indicating greater heterogeneity of composition. It should be noted that the control quadrats were also analysed, and no such patterns were observed.

Using successional vectors allowed the changes in the snail communities to be related to the overlaid variables. Most quadrats had, broadly speaking, moved from right to left on the ordination diagram – i.e. they were now associated with higher litter levels, taller vegetation and lower amounts of bare earth. Four pairs of quadrats had vectors more-or-less aligned with the variable 'number of molluscs'. This is not an explanatory variable and the factor(s) driving the changes are not known. This unknown factor(s) is likely to be especially important at the site Kilcorkan, where three of the four quadrats have changed or 'moved' in this direction.

Overall, eight out of the 14 pairs of quadrats had successional vectors which were parallel (or nearly so) to the variable 'cover of litter'. This illustrates how important this particular change (i.e. the dramatic increase in the amount of plant litter inside the fenced exclosures) has been for the snails. Litter is advantageous to many mollusc species because it provides moisture, food and shelter. Morris (1990) documented rapid responses in grassland invertebrates to the "*accumulation of living biomass, increased architecture in the vegetation and changed microclimate*" upon cessation of grazing management. Ausden et al. (2005) found that on introduction of cattle grazing to fens, there was a reduction in litter, and a reduction in mollusc densities. Labaune and Magnin (2002) point out that in tightly-grazed grasslands, there are a reduced number of niches for molluscs – especially the shade-loving molluscs and litter-feeders.

Conclusions

Have changes been documented? Were they as expected?

Snail abundance increased inside the fenced plots, with grasslands showing the largest and most consistent changes (though these were not statistically significant due to the large variability among quadrats and among sites). The woodland and scrub faunas did not change in an obvious way. Few species exhibited trends across all sites, the exception being *Columella aspera*, which appeared to do well in many sites following the cessation of grazing. It was thought that species typical of open land (e.g. *Vertigo pygmaea* and *Vitrina pellucida*) might disappear quickly once grazing ceased. This has not been documented, and may take a number of years to occur. The build-up of litter was found to be one of the most important variables associated with the increase in snail numbers.

What do the findings mean for the future of snails in areas where grazing ceases (or decreases)?

The findings imply that the cessation of grazing has a fast and measurable impact on snail communities in grassland habitats (also found by Cameron and Morgan-Huws, 1975). While few species were lost or gained, many species changed in abundance. No consistent changes were documented in woodlands or scrub in the timeframe of this study. Changes may happen over a longer timespan – only continued monitoring of the study sites will confirm or refute this.

In general, the build-up of litter and increased vegetation height caused by the removal of grazing animals from grasslands has been shown to favour snail abundance. As the grasslands slowly become more scrubby, and perhaps ultimately revert to woodland, its snail communities will continue to change. Continued detailed study of these and other similar plots will be needed to document these changes.

Chapter Seven:

Synthesis and conclusions

Summary and synthesis

One of the main aims of this thesis was to document the plant and snail communities found in a range of habitats in the Burren region in the west of Ireland. The habitats chosen were woodland, scrub and grassland, as these exist along a successional continuum. Scrub encroachment is a big issue for many land owners and managers in the area, with hazel being the most significant species involved. Thus the woodland and scrub habitats selected for study were hazel-dominated, and all of the grasslands had hazel scrub nearby.

The second principal aim of this work was to investigate the short-term changes in plant and snail communities following cessation of grazing by large herbivores. This was achieved through the setting-up of a network of twelve fenced exclosures (ten in north Co. Clare and two in south Co. Galway). These excluded all large grazing animals, which, in the case of the study sites chosen, were mainly cattle and feral goats. The plant and snail communities were sampled intensively at the beginning of the project in 2006, and again in 2008, and any changes were analysed.

Additional work with the molluscan data included an examination of the population structure and an assessment of methodological issues.

In this chapter I summarise the findings of the work and draw some general conclusions. As part of this, I make reference to the ancillary projects which complemented this work, and I present one final analysis in which the plant and mollusc data are integrated. The limitations of the project are discussed, along with its relevance to other areas. I conclude by suggesting some directions for future research.

The vegetation and land snail communities of woodlands, scrub and grasslands in the Burren

The flora of the Burren is renowned and has been well-studied, but the vegetation communities are less well understood. Existing works on this subject were reviewed. The findings of this study indicate that, unsurprisingly, the vegetation of woodlands and grasslands differ substantially, with soil fertility as well as light penetration being important in the separation. Interestingly, the scrub vegetation differed floristically from both woodland and grassland. Further, it could be split into two distinct subsets – ‘woody’ and ‘grassy’. These elements formed distinct entities which were related to the woodland and grassland vegetation communities respectively, but were distinct from either. This points to the importance of scrub as a habitat type in itself.

The flora of the study sites was found to be very rich – at one site alone over 10% of the total native flora of Ireland was found within the two 20 x 20m plots. The grasslands were more species rich and more diverse than the woodlands, and while the scrub held more species than the

grasslands, it was found to be less diverse (Simpson's Diversity Index). A large number of rare or notable species were encountered, including many 'Burren specialities', and also a suite of species which are regarded as putative old woodland indicators. Although cover of woodland and scrub is likely to have been very low in the Burren in the past (in the 19th century in particular), the occurrence of so many indicator species suggests that there may have been at least some degree of continuity of woody cover. Another possibility is that grikes in the limestone pavement act as areas of refuge for woodland plants (from grazers and harsh conditions like wind), and so may have allowed the survival of an altered woodland flora in times when woody cover was absent. The similarities between woodland and grike floras have been demonstrated by Dickinson et al. (1964).

Within the woodlands, the canopy species was found to be the most important driver of the variability in the overall vegetation composition – quadrats with the same species in the canopy plotted together, even if they were from different sites. The grassland sites, in contrast, were separated distinctly by site, indicating that each had a subtly different flora. Soil factors (such as depth, texture and % LOI) were most important (among the measured variables) in explaining the variation. The scrub samples separated clearly into their 'woody' and 'grassy' components. Similar factors to those seen in the analysis of the overall vegetation dataset emerged as important in explaining the variation in vegetation composition seen between the two groups – light penetration, vegetation height and fertility foremost among them.

A total of 30 species of snail was recorded from the twelve study sites, which was approximately 75% of the suite of 'expected' species and ~45% of the total land snail fauna of Ireland. Approximately half of the specimens were immature, with adults and dead (i.e. long-dead) specimens making up the rest of the sample. Some species were limited to one habitat type – e.g. the species *Aegopinella nitidula, Balea heydeni* and *Leiostyla anglica* were only found in woodlands or in woody scrub quadrats. The only species strongly linked to grasslands (and grassy scrub) was *Vertigo pygmaea*. Seven species listed on Ireland's 'Red List' for non-marine molluscs were found, some of which were common (e.g. *Acanthinula aculeata*) and/or widespread (e.g. *Acicula fusca*) in the dataset.

The woodlands and scrub had higher abundances of snails, and were more species rich, than the grasslands. The amount of litter in a quadrat was an important factor correlated with snail species richness. Interestingly, plant species richness was not correlated with snail richness. A surprising finding was that cover of sedges is negatively related to snail abundance and richness, whereas cover of grasses is positively correlated with these. A denser, and therefore more moist and litter-rich, sward is thought to be the explanation of the difference between sedge-rich and grass-rich swards. Soil texture was found to be influential on snail communities also, with higher amounts of sand and clay appearing to be beneficial, and higher proportions of silt having a negative impact.

There were only two alien species found during the vascular plant surveys, and the snail fauna was surprisingly lacking in synanthropic species – both results indicate that quite 'natural' communities exist, consisting of mostly native species. This is an encouraging finding from a conservation point of view.

The short-term effects of the cessation of grazing on vegetation and snail communities

The changes in the vegetation brought about by the cessation of grazing were rapid and dramatic in the grasslands in this study. Many plant species declined in abundance and several flowering plant species were lost (*Cerastium fontanum, Euphrasia* agg., *Linum catharticum, Odontites vernus* and *Rhinanthus minor*, all of which are small herbs and therophytes (annuals), except *C. fontanum*). This suite of species reflects on a small scale a major trend identified by Preston et al. (2002b) when analysing changes in the British flora between 1930 and 1999. They found that a disproportionate number of small plants of open habitats which are not nutrient-rich had been lost. There was a huge build-up of litter at the grassland sites during the period of this study, and cover of grasses increased significantly. Both diversity and species richness of plants decreased, with the only species increasing substantially being *Potentilla erecta* and *Pteridium aquilinum*. The success of the invasive (though native) species, bracken, is particularly worrying from a conservation point of view (Pakeman and Marrs, 1992, Marrs et al., 2000).

The woodlands presented contrasting findings to the grasslands, with plant diversity increasing significantly. Species richness increased also, although the change was not statistically significant. The amount of bare earth decreased dramatically, and the cover of field layer plants increased in parallel. These findings may indicate that there is a heavy grazing or trampling pressure on Burren woodlands. Several other studies have shown, however, that increases in diversity in woodland habitats following changes in management may be transitory, followed by subsequent decreases over longer time periods.

There was little detectable pattern of change in the scrub vegetation, most likely due to the heterogeneity and variability of the habitat itself. Among the only changes measured were in relation to the amount of litter, which increased significantly, and cover of field layer plants, which also increased.

A large change was seen in the snail communities in the grasslands following the exclusion of grazers. In this case, however, abundance and species richness increased. The changes were linked with the litter build-up, and the denser, taller vegetation within the fenced plots. Few individual species showed strong trends (except for *Columella aspera*, which appeared for the first time at three of the grassland sites), with the pattern instead being a small and variable, but relatively consistent, increase across all species. The snail communities showed little appreciable changes in

the woodlands and scrub during the timespan of this survey. Again, the period of 24 months may not have been long enough for measurable changes to manifest themselves.

Population structure and common methodologies in malacology

Some of the difficulties involved in sorting and identifying young or dead snail specimens were outlined. The snail populations at the study sites were shown to be composed mainly of juveniles, although some species were present more often as adults (mainly smaller species, or species with a peak in breeding early in the year) or as dead specimens (two species only, one of which is tiny and therefore relatively resistant to crushing, meaning that its shells tends to persist in the soil). The inclusion of dead and immature individuals in the dataset added six species to the list, but they were all species which occurred in very low numbers (≤2). The relative abundances of species was shifted, however, if only adults were included.

The advantages of using a sieve mesh size as low as 0.5mm were shown by the large numbers of snails found in this size fraction (more than double that found in the >1mm size fractions) and, in particular, by the demonstration that a number of species (in this case six) were under-estimated when sampling using a 1mm sieve mesh (four of these grossly so). However, this needs to be weighed against the benefits gained in terms of time involved in lab work to process and identify the samples. The aims of individual studies will dictate which method is best.

Soils

The results of the soil analyses are presented in full in Appendix 3. In summary, % LOI varied from 19 to 86% across all twelve study sites. Three of the grassland sites had the lowest % LOI figures, but the fourth site, Gregan, had the highest. The soils varied in texture, with most being composed mainly of sand, with smaller proportions of silt and clay. The silt was the most variable portion. The weight of $CaCO_3$/ml in the soil was measured for the ten sites which had pH >6.5. It ranged from 0.009 to 0.059, with the woodland sites generally having the highest levels. The measurements of total P were relatively homogeneous across all sites apart from one (the woodland Glenquin). With this outlier removed, values ranged from 98.9 to 246.3µg/ml.

Ancillary projects

Ancillary projects covering ants, anthill vegetation, lichens and bryophytes were carried out at the study sites during the course of this project (Chapter Two). These projects were carried out largely by undergraduate or postgraduate students, under the supervision of Dr Daniel L Kelly and Maria Long. Ants were searched for at all of the study sites. None were found in the woodlands, seven species were recorded from the scrub sites, and six from the grasslands. The vegetation associated with anthills was investigated at five sites and results are to be submitted for publication (Howard-Williams et al., in prep.). The epiphytic lichen flora of hazel in woodlands and scrub was surveyed, resulting in the recording of 47 species. Distinct communities were shown to exist in scrub and

woodland, with scrub being more diverse. Bryophytes were also surveyed and a total of 55 species were found. Again, results indicated relatively distinct floras for each of the habitat types.

Anomalous sites

Through the questionnaire responses (Chapter Two) it was discovered that there had been an attempt at reclamation at the grassland site, Kilcorkan, approximately 30 years ago. This was a cause for concern. Data were revisited to see if any obvious effects could be found. In Chapter Three, the ordination of the grassland sites revealed that Kilcorkan quadrats were characterised by high proportions of 'R' species (sensu Grime et al., 1988) and also by high Ellenberg 'light' scores. This was the grassland site with the lowest average number of plant species per quadrat, but it was not exceptionally low (Kilcorkan - 24.2, Slieve Carran - 25.1, Gregan - 28.7, Caher - 41.1). Overall, this site does not appear obviously different to the others, and the only evident effect of the past disturbances was the higher than average proportion of 'R' species. This may indicate that there is good potential for recovery or restoration following disturbance in Burren grasslands, and indeed this has been shown to be true in other similar areas of calcareous grasslands (e.g. in the alvar grasslands of western Estonia: Partel et al., 1998).

Snails were much more abundant, as well as more species rich, at Gregan, compared to the other grassland sites. The NMS vegetation ordinations in Chapter Three showed that Gregan separated quite distinctly from the other grassland sites, and was characterised by higher % LOI values, a higher percentage of sand in the soil, higher Ellenberg 'fertility' values and taller vegetation. Gregan hosted a number of typically moisture-loving vascular plants (in particular, *Filipendula ulmaria* and *Geum rivale* were common), which were otherwise uncommon in this study. Degree of wetness (using Ellenberg scores) was included in analyses, but did not emerge as a significant factor. What may be more important is the fact that the vegetation at Gregan was more dense and lush than at the other grassland sites (pers. obs.) and that this impacted favourably on the snail fauna (through moisture retention, shelter and increased food availability). Gregan had by far the lowest cover of sedges of any of the grasslands sites, a variable which was found to be negatively correlated with snail abundance and richness (see Chapter Four). It had the highest cover of grasses. Its soil characteristics (high % LOI, high % sand and high fertility) may also have contributed to the differences seen in the vegetation.

Integration of vascular plant and molluscan data

In order to investigate whether using both the vegetation and snail data together added significantly to our understanding of the factors influencing community make-up at ecosystem level, an NMS ordination was carried out with both datasets included. The molluscan data came from the >1mm size fraction, adults only; both datasets were from 2006 (Figure 84). Methods follow those used in earlier chapters.

There was a clear separation of the habitat types, with 'woody' and 'grassy' scrub also separating well. In total, 88% of the variation seen in the data was explained by the ordination solution: 79% on axis 1 and 9% on axis 2. The final stress was 15.1, which is within acceptable limits, but there was a relatively high final instability (0.003). However, there was consistency in the ordination solutions provided in multiple runs of NMS and the solution can be accepted albeit with some caution.

The factors which emerge as important are broadly similar to those found when the ordination was carried out using only the vegetation data (refer to Chapter Three). The differences are subtle, and include the fact that the various measures of litter used (cover from snail and vegetation quadrats, as well as dry weight) increase in importance. The variation between quadrats is still dominated by differences in vegetation height, fertility, light penetration, species richness and cover of the field layer. None of the overlaid variables plotted in parallel with axis 2. By reducing r^2 to 0.1, however, the following variables plotted, and all were moderately significantly correlated with axis 2 (verified by Spearman's rank correlation analysis): % LOI, % clay, snail species richness, Grime's 'S' value and grazing level. All except 'S' were negatively correlated with axis 2. This axis represents only 9% of the variation seen in the data and so interpretation of explanatory variables should be treated with caution.

The positioning of the four habitat groups in this ordination is almost linear, running parallel to the axis which explains the majority of the variation, and this strongly supports the idea that woodlands, scrub and grasslands (as habitats) exist along a continuum, in the Burren region at least.

It should be noted that there are many more species of plant than snail, and so it may be the case that the snail data are somewhat swamped, and therefore patterns may be obscured.

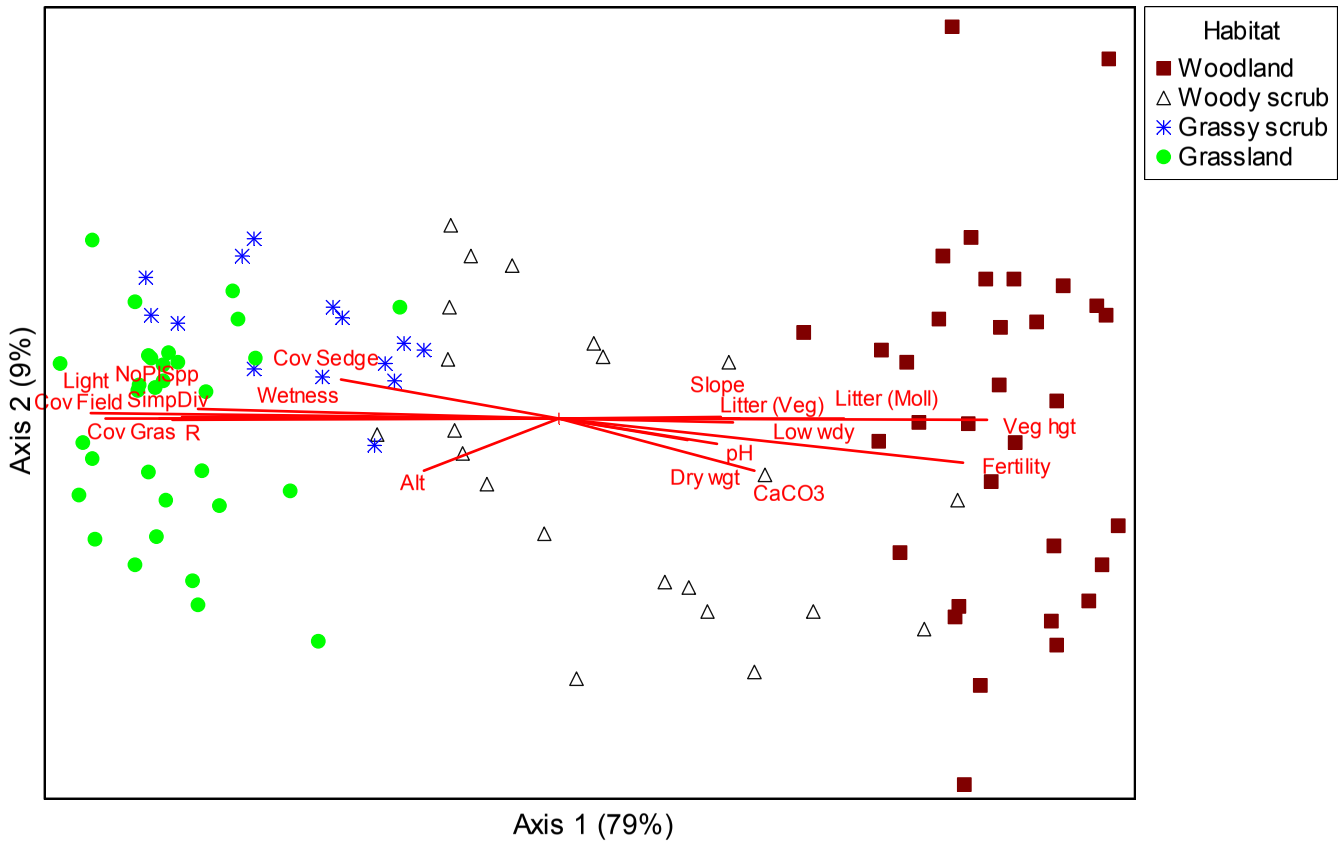


Figure 84 NMS ordination using combined plant and mollusc data from 2006. Each point corresponds to a quadrat and the most influential variables from the second matrix are overlaid. This solution explains 88% of the variation in the distance matrix.

Veg hgt = height of vegetation, Fertility = average 'Ellenberg score' for fertility, Litter (moll) = % cover of litter recorded in snail quadrats, Low wdy = cover of all species which are woody, but which are not trees or shrubs, Litter (veg) = % cover of litter recorded in vegetation quadrats, $CaCO_3$ = % calcium carbonate ($gCaCO_3$/ml) of the soil, Slope = slope of the site, pH = pH of the soil, Dry wgt = weight of litter removed and dried, Alt = altitude, Cover Sedges = cover of all sedges, Wetness = average 'Ellenberg score' for wetness, NoPlSpp = number of plant species per quadrat, SimpDiv = Simpson's Diversity Index score for vegetation, R = Grime's 'R' category: ruderals, Cover Grass = % cover of grasses, Cover Field = % cover of herb layer, Light = average 'Ellenberg score' for light.

Relevance of the research

Methodological limitations and considerations

Choosing replicates in the real world

The issues highlighted in the 'Anomalous sites' section above illustrate some of the problems involved in selecting replicate sites for ecological studies. In the real world (rather than in controlled lab, or even experimental farm, situations) it can be very difficult to choose sites which can act as replicates. I aimed to choose twelve sites with similar geologies, soils, topographies, species of grazer, etc. In reality some compromises had to be made, the main one being that not all sites have only cattle and feral goats as the main large grazer (there are donkeys, sheep and horses at some sites, see Chapter Two).

Analyses have shown, however, that the four individual woodland sites show substantial overlap in vegetation composition, as do the four individual scrub sites, validating the choices made. The grassland sites, however, showed greater distinctness. Each of the four grasslands clustered separately in NMS ordinations (Chapter Three), indicating differences in vegetation composition. An element of variability such as this is probably inevitable in real-life ecological studies.

Grazing pressure results from the questionnaire

Data were collected on grazing pressure through the questionnaire administered to all landowners/ managers (Chapter Two). Although carefully designed to elicit the relevant information, without being too intrusive, the questionnaire yielded surprising results for grazing pressure (measured as the number of cattle per hectare for each site). In particular, the high grazing pressures stated for Knockans (2.97 cattle/ha) and Carran (3.3 cattle/ha) didn't seem to tally with personal observations. Although the calculations used for grazing pressure were relatively crude, large discrepancies were not expected. Not withstanding these concerns, the questionnaire results were used in analyses but have not been relied upon heavily in the interpretation of results.

Levels of grazing pressure

The current project used grazing exclosures to investigate the effects of the cessation of grazing on vascular plants and snails. In reality, however, grazing as a land management rarely ceases altogether, especially over large land areas. Thus the use of exclosures which completely exclude grazers could be seen as a rather crude tool (e.g. Morris, 1990, Watkinson et al., 2001). However, given the lack of grazing research in limestone habitats in Ireland, a baseline study of the changes which occur in what is arguably the simplest scenario – i.e. complete cessation of grazing - was thought to form a valuable starting-point for this field of research. As pointed out by Morris (1990), dealing with invertebrates, "*It is clear that even in the very simple change from continuous, intensive grazing to complete absence of management, the effects on the invertebrate core*

community are complex and dynamic." Further to this, grazing levels in the chosen habitats were generally relatively low (in comparison to those, for example, in intensive agricultural grasslands). Thus the scope for manipulating levels is more limited than it would be in an intensive management situation. See 'Future research' section below for more on grazing levels.

The inclusion of scrub as a habitat type to study

When choosing which habitats to include in this project, a number of key decisions had to be made, many concerning scrub. This is not a well-studied habitat (see Chapter One) – and for good reason! It is heterogeneous, variable, often ecotonal, and added to this, scrub is often logistically difficult to survey in. Most ecologists have tended to ignore it – as evidenced by its lack of inclusion in many vegetation categorisation schemes. Given all of the above warning signs, it is perhaps not surprising that significant results pertaining to changes, either for plants or snails, were not found. So one might ask if we made the right decision to study scrub in the first place. I believe that we were fully justified in including scrub as one of the three study habitats. It has proven to hold distinct plant, snail, bryophyte and lichen communities. It is more species rich than either of the other habitats in terms of vascular plants, and supports a higher abundance of snails than either. It is a habitat which has long been overlooked, and presumed less diverse than others, without adequate investigation. The serious (conservation, economic and cultural) issue of encroachment of hazel scrub in the Burren needs to be tackled with the benefit of as much scientific ecological information as possible, in order to best inform future management decisions.

I have demonstrated that some of the communities of plants and animals that live in hazel scrub in the Burren are distinct (i.e. distinct from those found in either grasslands or woodlands), and learning the effects of changing management practices (such as cessation of grazing) on these will be of the utmost importance. That we did not find measurable results during this study is perhaps disappointing, but the work of others (Byrne, 2001, Moles et al., 2005) from scrub in the Burren suggest that changes will indeed manifest themselves in the medium- to long-term. Harmer et al. (2001) found, for example, in a study looking at vegetation change (from grassland to woodland) over 100 years, that the transition from a suite of light-demanding species to one of shade-tolerant species took between ten and 40 years.

Use of inferential statistics on a dataset which includes subsamples

By necessity, many ecological field experiments which take place in the real world (rather than on experimental farms or plots, for example) have much inherent variability, and further, they often lack replication. This latter deficiency may be due to insufficient resources, logistical issues or issues relating to permission. This current study is unusual in offering replication of the experimental units (the study plots) for each of the three habitat types. Samples (the quadrats) were taken from within each of the experimental units to allow a picture of the vegetation, and its variability, to be gained for each plot. Data from these samples are pooled in some cases, but

entered as separate entities for other analyses – e.g. the NMS ordinations. While this procedure (inputting all quadrat data to an NMS) is commonplace, the consequent use of inferential statistics on the data may not be satisfactory, an issue which came to light only in the final stages of the write-up of this study.

The quadrats are essentially arranged in groups of five in this study (refer to experimental design, Chapter Two), and so the members of each of these groups cannot be taken to be independent from each other. Using NMS analysis to investigate *patterns* in the dataset as a whole for an experimental design such as this one is valid, whereas using inferential statistics (used in this study to link environmental drivers to the variation seen in the vegetation data) is of questionable validity, and depending on the hypothesis being tested, may amount to pseudoreplication (cf. Hurlbert, 1984).

An ideal design would be one in which the treatments are assigned randomly (or in a stratified random manner) to plots, and both control and treated plots are interspersed spatially. In field ecology, however, costs and logistics tend to make such an experimental design impractical. To have the same number of samples as were taken in this study (i.e. 120 quadrats), one would have needed 60 separate small fenced exclosures - the difficulties in trying to achieve this are clear.

A more suitable approach to allow the use of inferential statistics on the data might have involved the pooling of the quadrat data for each plot (by getting a mean cover for each species, or mean value for each variable), and then testing the resultant plot data. There would then have been 24 sets of data points - four replicates for both fenced and control plots, for each of the three habitats.

Relevance, implications and practical applications of the research

A ready-made long-term monitoring network

With land abandonment a major threat to ecosystems throughout Europe (e.g. Strijker, 2005, Baur et al., 2006, Enyedi et al., 2008, Marriott et al., 2009), the cessation of existing management regimes is likely to have a huge impact on plant and animal communities. The use of long-term experiments is one of the most effective ways of documenting and understanding these changes. This network of twelve fenced exclosures, and their associated control plots, will be an important resource, now and in the future. As a study of three distinct but related habitats, with balanced replication of each, they enable the study of ecological change on a number of scales – quadrat, site, habitat and landscape. In this regard, the network is unique in Ireland. Already, detailed baseline information has been gathered on vascular plants, bryophytes and snails, and lichens and ants too have been surveyed.

Scrub – a new view

One of the most significant outputs of this project has perhaps been the information regarding scrub as a habitat in its own right. It provides a fresh look at this often ignored vegetation type, and sheds light on its biodiversity value and also its relationships to other habitats. As mentioned above, it has been shown to be a diverse and speciose habitat for a number of taxa, and it is definitely more than simply a mixture of woodland and grassland species – it holds distinct communities of plants and animals, different from both. This challenges the commonly held view that the biodiversity of the Burren is to be found largely in open habitats such as limestone pavement and semi-natural grasslands.

Scrub – an ongoing threat?

This project, running over 24 months, failed to document changes in plant or snail communities in scrub as a result of the exclusion of large grazing animals. As noted above, it is likely that the timeframe was too short in order to detect differences, especially given the heterogeneity of the scrub itself. Other workers in the Burren have seen changes over the medium term (10-16 years) (Byrne, 2001, Moles et al., 2005), and work commissioned by The Heritage Council (2006) has shown that the rate of spread of hazel is increasing. Control of hazel scrub on farms was one of the main focus areas of the BurrenLIFE project, and forms a part of the work of the current Burren Farming for Conservation Programme (BurrenLIFE, 2010a, 2010b). Thus if monitoring of the study sites set up during this project is continued as planned, it is likely to yield valuable information on the dynamics and timeframes of scrub encroachment, and also details on the ecological implications for plant, snail and other communities.

The information gathered on the value of scrub itself as a habitat for both plants and animals reiterates the view that scrub control and management should be targeted at newer, actively encroaching areas, rather than at well-established or older stands. This is broadly the approach which is currently taken by BurrenLIFE and the Burren Farming for Conservation Programme, two of the main farm management projects operating in the area, and among the main sources of advice for farmers on the management of their lands in the Burren.

New molluscan records and ecological information

While the broad scale distribution of land snails in Ireland is well-known, the records backing up the distribution maps are few. The necessity for a survey such as this one was highlighted by the fact that there were 38 new 10km-square records for the area. Needless to say, there is also a dearth of ecological studies on molluscs in Ireland, and this applies to Ireland as a whole, not just to the Burren region. The ecological data gathered here, such as habitat preference, influential environmental factors, population structure and the changes seen after cessation of grazing, all serve to further our knowledge of molluscan ecology in general.

Relevance to broader landscape change issues

Although the results of the current study come from fenced exclosures at twelve specific locations, the findings are relevant to the whole of the Burren region, and indeed beyond. The applicability is greatly enhanced by the replication of the study plots at the habitat scale.

This study found that changes occur rapidly in grasslands upon cessation of grazing. This was true for both groups studied – plants and land snails. This means that grasslands may be more vulnerable to change, at least in the short-term, following changes in land management than other habitats like woodlands and areas of scrub. This information may be useful in helping to prioritise conservation efforts, especially where resources are limited.

While differences were found for both plants and land snails, the nature of the changes observed were different – the richness and diversity of *plants* in grasslands was reduced when grazing stopped, whereas the abundance and diversity of *land snails* increased. These apparently contradictory trends highlight the complexity of the issue. Different facets of diversity can require very different conditions, and this must be borne in mind by land managers. In most cases, a uniform management strategy is not sufficient to adequately cater for the needs of a variety of plants and animals. For example, while grazing is recommended as a management tool, large areas which are continuously and heavily grazed are less likely to support a wide variety of plants and animals than are areas with a more varied regime. Structural heterogeneity, often present in less intensively managed but still actively grazed areas, is likely to allow for a range of suitable conditions, such that a greater diversity of species can be accommodated.

In this study, some sites were found to be quite different from others, *within* habitat types (e.g. Gregan had much higher numbers of snails than the other grassland sites). This suggests that, firstly, replication is indispensible, even in large scale landscape studies where it may be costly and logistically tricky, and secondly, that site-to-site variation further complicates the issue of recommending management prescriptions. Local knowledge, and in particular, that of the person who is or has been farming the land, is crucial in the formulation of management recommendations – no-one knows better the individual idiosyncrasies of an area of land than the person who farms it.

Reversibility of changes

It is expected that within the fenced plots erected during this study the vegetation will become rank and eventually scrubby. Should it be necessary to reverse these changes it is most likely that grazing would be resumed. As already noted, the past disturbance at the Kilcorkan site, along with its current species-richness, is suggestive of good restoration potential in Burren grasslands. It is likely, however, that in areas where the scrub has reached a certain height (1 - 1.5m), grazing alone may not be sufficient for restoration. It is worth noting also that if changes are quantitative rather than qualitative (i.e. changes in abundance rather than the loss or gain of species), the changes may

be more easily reversed. However, even where species are lost, there is likely to be better than average recolonisation potential due to the mosaic-like nature of the vegetation and habitat patches in the Burren.

Future research

Tracking medium- and long-term changes in the study plots

The most immediate and pressing future research which is recommended on the basis of the work carried out here is a continuation of the monitoring of plant and snail communities at the study plots. There is little doubt that changes will continue to occur, and the detailed documentation of these will be of great value. For example, bracken has been shown to thrive in the absence of grazing in the short-term, but what about the medium- or long-term? And while a significant decrease in the snail species of open ground within the exclosures (e.g. *Vertigo pygmaea*) was not documented during this survey, it is likely that changes will occur in the future (Dr Evelyn Moorkens, pers. comm.). But how soon? And of what magnitude? An increase in plant species was seen in woodlands, but other work suggests that this may be a short-term effect only. Will this indeed prove to be the case in the Burren?

The extent and speed with which hazel expands in the scrub and grassland plots will be of great use in informing management decisions for hazel management in the Burren. It is this latter information which has perhaps the broadest applicability. It would be of great interest, and also practical use, to link the results of this study with spatial data which already exists relating to the expansion of hazel scrub (and the consequent loss of other habitats).

Utilising the long-term monitoring network

The permanent network of exclosures set up as part of this study should be capitalised upon in the future by being utilised for a number of monitoring studies. The potential amount of work based in the study plots would of course have to be balanced against the potential damage (e.g. by trampling, removal of material/samples) caused by survey work.

Expansion of the invertebrate work to include other groups, in particular, would be very desirable. A cross-section of guilds would be ideal – e.g. a group of flying insects (e.g. diptera, syrphidae), a group of ground-dwelling invertebrates (e.g. coleoptera) and perhaps a soil-dwelling group (e.g. mites). Work on soil mites in the Burren has already taken place (Rodríguez Tuñón, unpublished), and so comparisons would be facilitated.

Grazing intensities/timing

The current study excluded large grazers completely, and so compared a situation of 'grazing' with 'no grazing'. However, it is often important to elucidate the effects of different grazing levels. In the case of the Burren habitats studied here, however, grazing levels are generally low, reducing

(but not eliminating) the possibilities for manipulation of levels. Another aspect which could usefully be investigated in the Burren is seasonality or timing of grazing. Work has shown that seasonality can have a large impact on the effects of grazers on vegetation (e.g. Mitchell and Kirby, 1990, Hester et al., 1996, Mitchell et al., 1996, Hester et al., 2000, Hennessy et al., 2006). In Burren grasslands in particular, where the season of grazing is of extra importance (winter grazing removes enough of the productivity, while being less damaging to flowering herbs) (Bacon, 1990, Dunford, 2002), subtle changes in the timing of the grazing could have large effects on the plant (and animal) communities.

The species of grazer, and combinations of species, could also be investigated. Sheep were much more prevalent in the region in times past (see Chapter One), and it is accepted that mixed grazing by cattle and sheep can have conservation benefits. There is much scope for research in this area.

Vertigo pusilla

The rare mollusc species, *Vertigo pusilla*, was found during this survey – a single dead shell at each of two nearby woodland sites. A dedicated search for this species should be undertaken in order to ascertain if it occurs alive in the area. If it were found, it would constitute only the sixth known site for the species in Ireland.

Litter pH

As noted above (Discussion, Chapter Four), measuring the pH of the soil may not be adequate for mollusc survey work because many authors have found that the pH of the litter is strongly linked with molluscan abundance and diversity, and that this is not necessarily equivalent to the pH of the soil. It is suggested that future work on molluscan ecology should include a measure of litter pH, in addition to soil pH.

Concluding remarks

Many changes have occurred in Irish agriculture in recent decades. The knock-on effects of some of these changes can be seen in the Burren, the most dramatic example being the expansion in hazel scrub. This has been attributed mainly (though not exclusively) to changes in grazing practices. As part of this project a network of exclosures for the investigation of the effects of cessation of grazing on biodiversity was set up. The studies conducted have provided detailed and wide-ranging baseline data. The work of monitoring the changes in these exclosures has also begun, with short-term changes identified after just 24 months. The findings of this project lead to a number of practical conclusions and recommendations, but the information gathered at each re-survey in the future will increase in value as time passes.

Conclusions:

- Cessation of grazing by large herbivores has significant impacts on biodiversity.
- These impacts are complex, however, and vary depending on the habitat and the taxa being studied.
- Cessation of grazing in Burren semi-natural grasslands leads to a quick and dramatic decrease in vascular plant diversity, with the almost immediate loss of certain sensitive species.
- Snail numbers and diversity, however, benefit from the increased grass cover and denser litter in ungrazed grasslands.
- In woodland habitats, plant diversity increases on removal of grazers. This is likely to be a short-term effect, and longer-term study is required to assess the effects satisfactorily. Snails did not appear to be affected in the short-term.
- The effects of the removal of grazers from scrub on plant and/or snail communities are less clear-cut. A longer timescale will be needed to assess and quantify the rates of change, although significant litter build-up was documented.

Recommendations:

- Grazing should continue in grasslands and scrubby areas to prevent the loss of plant diversity. The practice of winter grazing, at moderate stocking levels, is likely to suit the Burren habitats best, but may not be enough to prevent the encroachment of hazel scrub.
- Many snail species in grasslands benefit from high litter levels and dense grassy swards. Thus heavy grazing levels resulting in close-cropped uniform swards are not recommended.
- While the removal of grazing animals from woodlands was followed by an increase in plant diversity in this study, longer-term work is needed to fully assess the impact of grazers in this habitat. Based on other studies, moderate stocking levels are likely to be best.
- This network of experimental plots must continue to be re-surveyed in order to maximise its value.
- Additional studies should be set up, especially on little-worked groups such as some invertebrates. Follow-up studies on bryophytes and lichens are also highly desirable.
- Work on molluscs should be expanded – there is ample opportunity to expand studies experimentally. For example, the effects of snails as grazers themselves could be investigated.
- Continued liaison with farmers and land managers is essential, both for continuation of survey work, and also for any planned management for biodiversity conservation.

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APPENDIX 1: Common and scientific names of some species referred to frequently in the text

Table 1 Common and scientific names of some species referred to frequently in the text. Common names from Scannell and Synnott (1987), except Wilson's honeysuckle from Stace (1997).

Common name	Scientific name	Comment
Ash	*Fraxinus excelsior*	
Beech	*Fagus sylvatica*	
Blackthorn	*Prunus spinosa*	
Bracken	*Pteridium aquilinum*	
Bramble	*Rubus fruticosus* agg.	Also locally known as 'briar'
Buckthorn	*Rhamnus cathartica*	
Downy birch	*Betula pubescens*	'Birch' used in text as only one species recorded during study
Eared willow	*Salix aurita*	'Willow' used in text as only one species recorded during study
Elm	*Ulmus* sp.	
Guelder-rose	*Viburnum opulus*	
Hawthorn	*Crataegus monogyna*	
Hazel	*Corylus avellana*	
Holly	*Ilex aquifolium*	
Ivy	*Hedera helix*	
Juniper	*Juniperus communis*	
Oak	*Quercus* sp.	
Pine	*Pinus* sp.	
Rowan/Mountain ash	*Sorbus aucuparia*	
Spindle	*Euonymus europaeus*	
Wilson's honeysuckle	*Lonicera nitida*	

APPENDIX 2: Management questionnaire

Site name: _____

Respondent's name: _____

1. How long have you owned/leased/managed this land?

2. What types of animals do you currently have grazing the land on which the exclosure stands?

Stock species	Breed	Numbers	Months in which land is grazed
Cattle (sucklers, bulls, calves, etc.)			
Sheep			
Horses			
Goats - domesticated			
Donkeys			
Other			

3. How much land do these animals have access to at the same time? (approx no. hectares/acres)

Habitat type	Area (ha/acres)
Woodland	
Scrub	
Grassland (rough)	
Grassland (good quality)	
Creg (limestone pavement)	
Other	
Total	

4. How much time do you think they spend proportionately in the habitat type that the exclosure is in?

Habitat type	Time (proportion of their total time on the land – e.g. little, half, most, etc.)
Woodland	
Scrub	
Grassland (rough)	
Creg (limestone pavement)	
Other	
Total	

5. What other wild animals graze the land?

Wild/feral herbivore species	Numbers (high, low, occasional, rare, etc.)
Goats – feral	
Red/Sika/Fallow deer	
Deer species	
Rabbits	
Hares	
Other	

6. What other management is carried out in the area where the exclosure is? (e.g. hay, silage, burning, wood harvesting, left fallow/abandoned)
7. Where are the animals fed? What are they fed? When are they fed?
8. How different was the management regime 10 years ago? (i.e. what types animals, which months, what areas have access to?)
9. How different was the regime 30 years ago? (i.e. what types animals, which months, what areas have access to?)
10. Can you tell me anything about management >30 yrs ago?
11. Do you know if the patch of land that has the exclosure was woody/scrubby/open 10 years ago?
12. How about 30 years ago?
13. How far back can you confirm that it was woody/scrubby/open?
14. Was there ever an attempt to 'improve' or clear the land?
15. Was it ever re-seeded?
16. Was fertiliser ever applied? (provide details)
17. Have you ever carried out any other management practices (such as ragwort pulling, supplementary feeding, etc.)…?
18. Who else could I ask these questions to? Who would know about the habitats and/or grazing/management regimes in the past?

APPENDIX 3: Methods and results of soil laboratory analyses.

All soil analyses were carried out by Maria Kirrane (refer to full report - Kirrane, 2008), under the supervision of Siobhan McNamee.

Methods are based largely on those used in practical/laboratory classes in the Botany Department of Trinity College Dublin (developed by Prof. D.W. Jeffrey, Dr Francis Brearley and technician Siobhan McNamee, and modified from methods published in: Dean, 1974, Bowman, 1989, U.S. Department of Agriculture - Natural Resources Conservation Service, 2008, among others).

METHODS

A separate sample was taken from each of the fenced and control plots at the twelve study sites, so there were 24 samples in total. For all analyses except soil texture two replicates were carried out for each plot, giving 48 results in each case.

Loss-on-ignition (% LOI)

Four grammes of soil from each sample were weighed out and placed in a furnace at 105°C for two hours to remove moisture in preparation for loss-on-ignition analysis. This ensured that any loss in weight would be due to organic content and not moisture. Six grammes of soil were used from the more peaty sites (Carran, Rannagh, Roo and Gregan, determined from visual observation). Forty-eight crucibles were placed in the oven and after two hours the soil samples and crucibles were removed and placed in a desiccator containing silica gel which prevents absorption of atmospheric moisture.

After the samples had been cooled, 1g of each was weighed into a previously weighed crucible. Two grammes of soil were used for the four sites mentioned above, as these, being more peaty, could potentially lose a larger amount of weight. Weights were taken to four decimal places for optimum accuracy. The samples in the crucibles were then placed in the furnace. The temperature of the furnace was set at 150°C for a half-hour, 180°C for one hour, 200°C for a half-hour, 220°C for a half-hour, 240°C for a half-hour, 300°C for one hour and 550°C for five hours. The slow rise to the highest temperature ensures that the samples are not turned to ash by a sudden increase to a very high temperature. The samples were then left to cool overnight and placed in a desiccator. The crucibles and soils were reweighed and the loss in soil weight following ignition was then determined. Percentage loss-on-ignition was calculated and the bulk density was derived using the method described by Jeffrey (1970).

Textural Analysis (% sand/silt/clay)

Fifty grammes of air-dried soil from each sample were weighed out. As loss-on-ignition analysis found all twelve sites to have an organic content of greater than 12%, this was destroyed with hydrogen peroxide to ensure accuracy when measuring sand, silt and clay. The 50g samples were placed in 400ml glass beakers and covered with distilled water. Twenty millilitres of hydrogen peroxide were added and the mixture was warmed gently until the reaction subsided. More hydrogen peroxide was added as necessary until all organic matter had been destroyed. The soil was then transferred to a 1 litre graduated cylinder. Four hundred millilitres of room temperature tap water and 25ml of 5% Calgon solution were added. This solution was dispersed using a plunger mixer and then made up to 1 litre with room temperature tap water. The solutions were then stirred for 1 minute using the plunger mixer. The solutions were left to settle for 4 minutes 28 seconds, after which time a hydrometer was inserted and read after 20 seconds (A). The solutions were then left for a further five hours, after which the hydrometer was inserted and a second reading (B) taken. A blank sample with tap water and Calgon solution was also measured and the reading was subtracted from the other samples to account for any effect of the Calgon. The percentage of sand, silt and clay was determined using the following formulae:

Clay	=	B x 100/50
Silt + Clay	=	A x 100/50
Silt	=	(Silt + Clay) - Clay
Sand	=	100 – (Silt + Clay)

When the percentage composition of each soil had been calculated the soil texture was then determined using the textural triangle which is based on the USDA (United States Department of Agriculture) guide for classification of soil texture (Figure 1). This system divides soils into twelve textural classes based on their proportions of sand, silt and clay.

Calcium carbonate ($CaCO_3$)

The percentage of calcium carbonate was determined only for soils with a pH of greater than 6.5. This excluded two sites: Roo and Slieve Carran. One gramme of dry soil from each sample was weighed into a 100ml beaker. Twenty millilitres of 1N hydrochloric acid was slowly added to each sample. The beaker was covered with a watch glass and left to stand for one hour, swirling occasionally. A 5ml aliquot of supernatant was pipetted into a 50ml conical flask and titrated with 1N sodium hydroxide using phenol red as an indicator. Five millilitres of the original acid was titrated as a blank. The concentration of calcium carbonate was determined by subtracting the actual titre from the blank titre and multiplying this number by 20. The volume of $CaCO_3$ in the soils was expressed by multiplying the weight in grammes by the bulk density derived from loss-on-ignition.

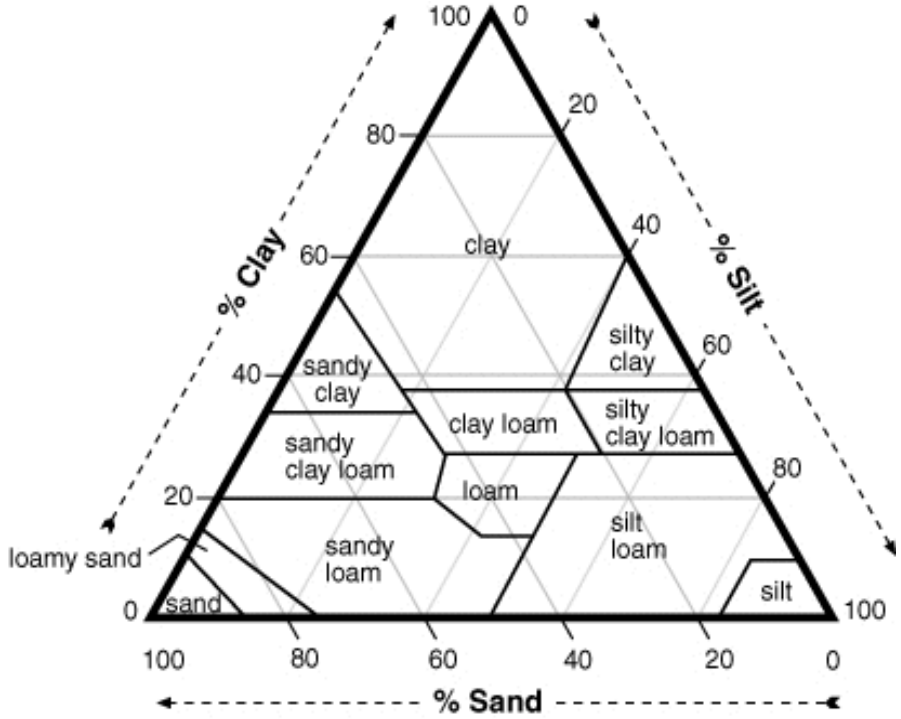

Figure 1. USDA classification of soil texture based on percentage sand, silt and clay (source: University of Minnesota).

Total Phosphorus (Total P)

Two grammes of soil from each sample was furnaced to 500°C, using the same increments as for % LOI, to remove organic content. This soil was then placed into 100ml conical flasks. Fifty millilitres of 1M sulphuric acid were added to the flasks and they were placed in a water bath at 90°C for one hour. The flasks were then left to cool and the contents filtered into 100ml volumetric flasks. The solutions were made up to 100ml using distilled water.

A set of standards was also prepared to produce a straight line curve from which the phosphorus concentration for the samples could be derived. The standards were prepared from a stock solution of 1000mg/L of PO_4-P diluted with distilled water to produce solutions of 1.00mg/L, 0.75mg/L, 0.50mg/L, 0.25mg/L and 0.00mg/L. Five millilitres of each solution were pipetted into test-tubes. One millilitre of colour development reagent, which had been prepared using 25ml of 3.6N H_2SO_4, 25ml of Antimony Potassium Oxide Tartrate solution, 25ml of Ammonium Molybdate solution and 0.2g of Ascorbic acid, were also added. The test-tubes were covered with parafilm, inverted to mix the contents and left for 15 minutes to develop. The absorbance of each standard at 882nm was determined on a Hitachi U-1100 Spectrophotometer which had been set to 3 to take 1.5ml sips of solution.

To determine the phosphorus concentration of the samples 0.25ml of the diluted filtrate was pipetted into a test-tube with 4.75ml of distilled water. One millilitre of colour development reagent, which had been prepared using the same method as for the standards but with 13ml of 3.6N H_2SO_4, was also added. The samples were then left to develop for the same time as the standards and absorbance was determined on the spectrophotometer in the same way as before. If the absorbance of any sample was found to be higher than that of the highest standard then the sample was tested again this time using 0.10ml of filtrate and 4.90ml of distilled water.

The concentration of phosphorus in mg/l in the samples was determined using the standard curve, for the 0.25 dilutions the answer was multiplied by 20 and for the 0.10 dilutions the answer was multiplied by 50. To calculate the concentration per kg the following equation was used:

$$mg\ kg^{-1} = (\ mg\ l^{-1} \times 50 \times 20)/\text{soil dry weight.}$$

The weight of phosphorus per unit volume was determined by multiplying the weight in mg by the bulk density as derived from loss-on-ignition.

RESULTS

Data from Kirrane (2008).

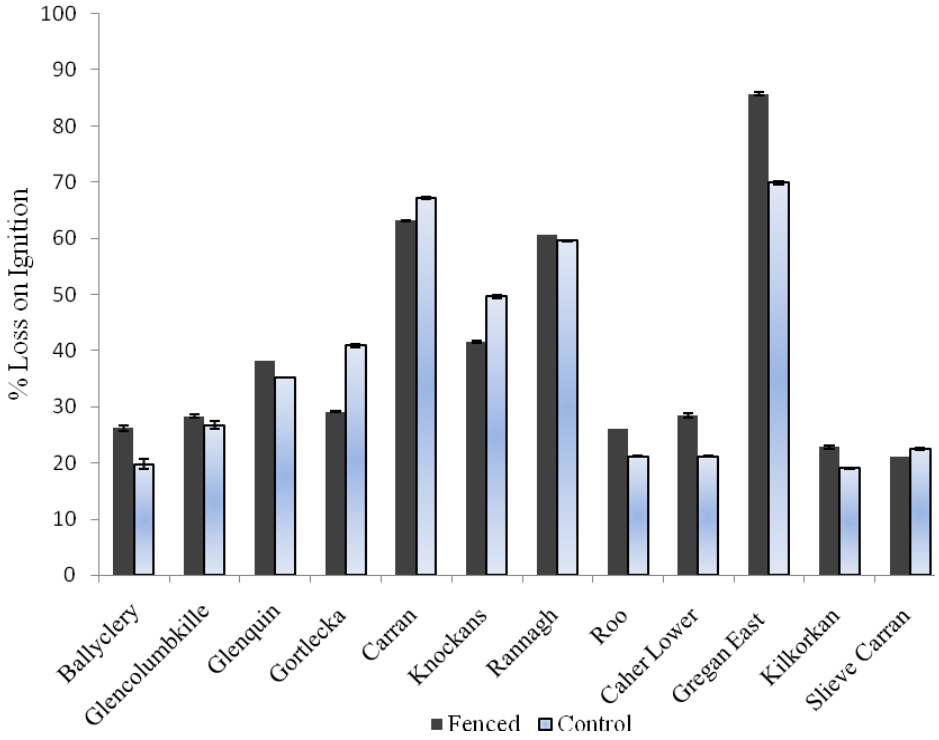

Figure A. Percentage LOI for soils from each of the twelve sites, within both control and fenced plots.

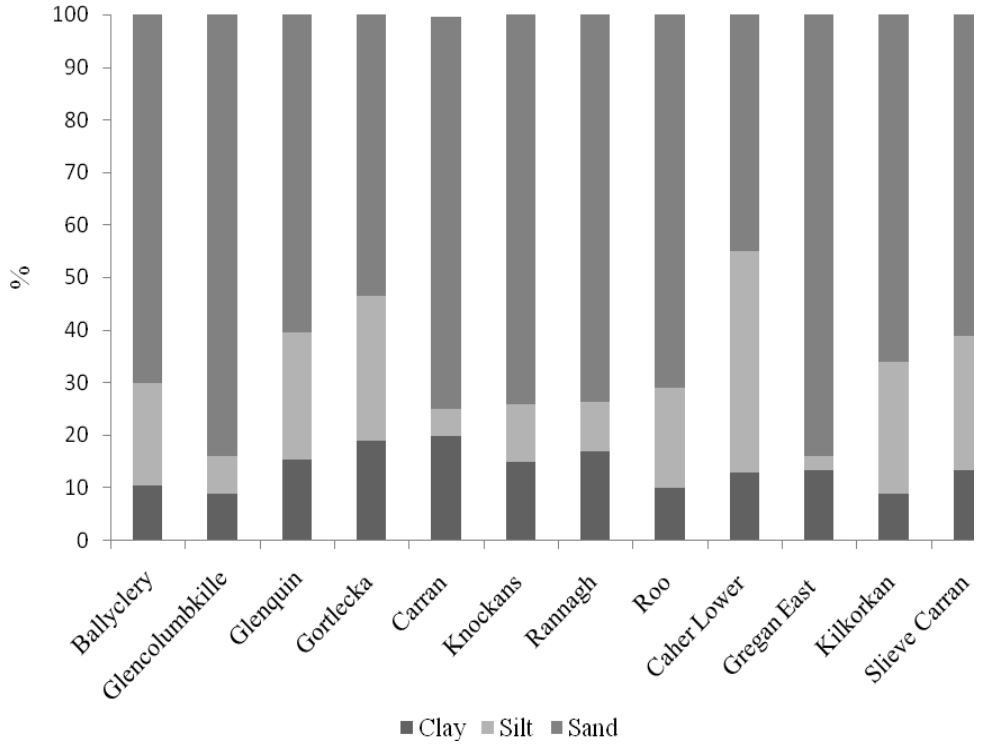

Figure B. Proportion of sand, silt and clay composition of soils for each of the twelve sites. Proportions given are an average from each pair of fenced and control plots.

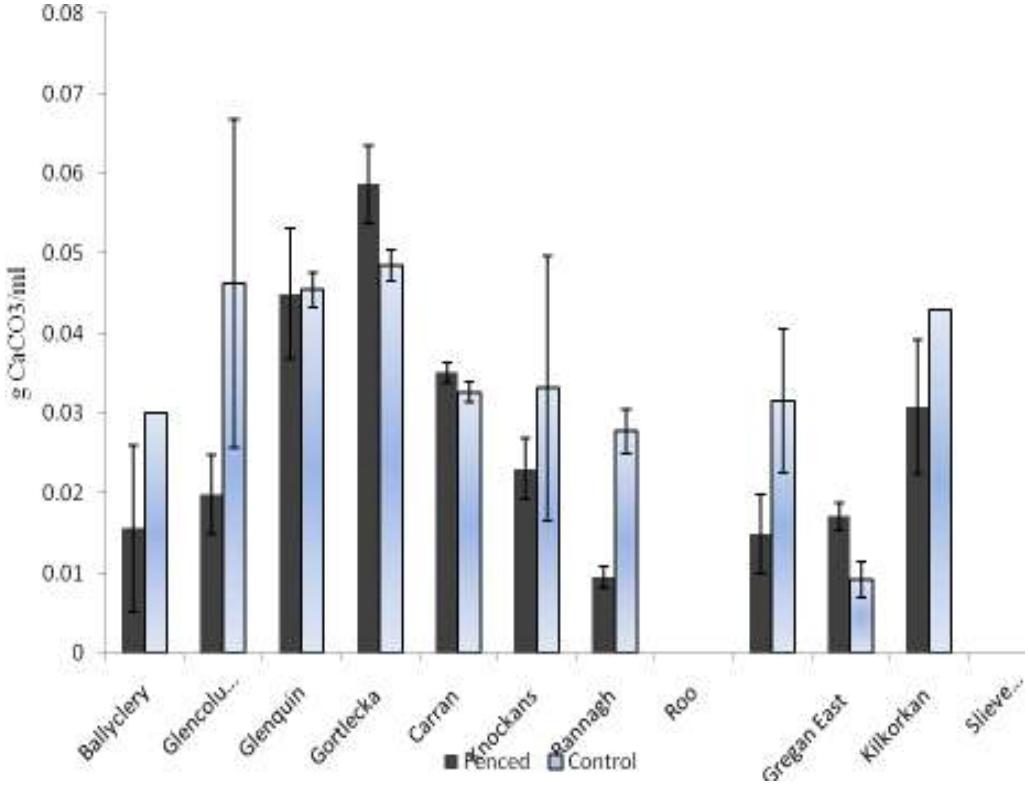

Figure C. Weight of $CaCO_3$ per unit volume of soil from each of the twelve sites (figure taken as zero for soils with pH <6.5).

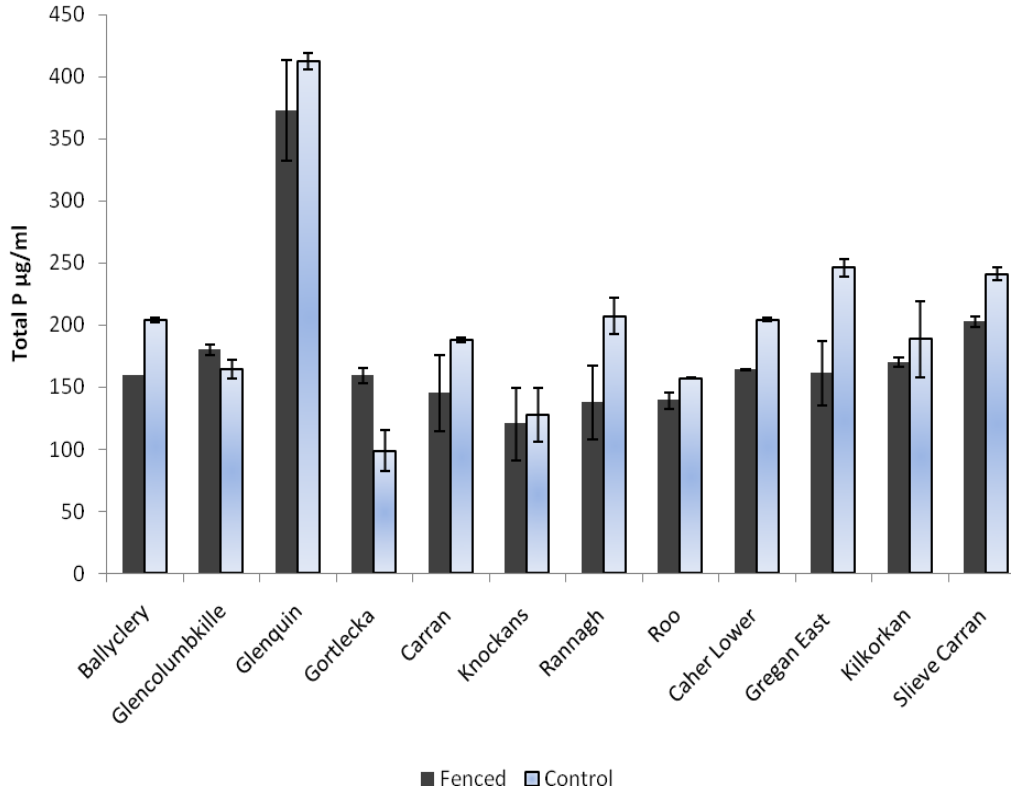

Figure D. Weight of Total P per unit volume measured from each of the sites, for both fenced and control plots.

APPENDIX 4: Lichen species found at each woodland & scrub site.

Data from Campbell (2008).

Ballyclery (woodland)

Anisomeridium polypori
Arthonia cinnabarina
Arthonia didyma
Arthonia elegans
Arthonia impolita
Arthopyrenia punctiformis
Arthopyrenia ranunculospora
Bacidia laurocerasi
Eopyrenula avellanae
Graphina anguina
Graphis elegans
Graphis scripta
Lecanora chlarotera
Lecanora confusa
Mycoporum quercus
Opegrapha atra
Opegrapha herbarum
Opegrapha vulgata
Pertusaria leioplaca
Porina aenea
Pyrenula chlorospila
Pyrenula macrospora
Tomasellia gelatinosa

Glencolumbkille (woodland)

Anisomeridium biforme
Arthonia cinnabarina
Arthonia elegans
Arthonia impolita
Arthopyrenia punctiformis
Graphina anguina
Graphis scripta
Lecanora chlarotera
Lecanora confusa
Lepraria lobificans
Normandina pulchella
Opegrapha herbarum
Opegrapha vulgata
Eopyrenula avellanae
Pertusaria leioplaca
Phaeographis smithii
Porina aenea
Pyrenula chlorospila
Pyrenula macrospora
Thelotrema lepadinum

Glenquin (woodland)

Arthonia elegans
Arthonia ilicina
Arthonia impolita
Arthopyrenia punctiformis
Bacidia laurocerasi
Eopyrenula avellanae
Graphina anguina
Graphis elegans
Graphis scripta
Lecanora chlarotera
Lecanora confusa
Lepraria lobificans
Leptogium lichenoides
Lobaria pulmonaria
Normandina pulchella
Opegrapha vulgata
Parmelia sulcata
Pertusaria leioplaca
Phaeographis smithii
Porina aenea
Pyrenula macrospora
Pyrenula chlorospila
Sticta fuliginosa
Sticta limbata
Tomasellia gelatinosa

Gortlecka (woodland)

Acrocordia gemmata
Anisomeridium biforme
Arthonia cinnabarina
Arthonia elegans
Arthopyrenia punctiformis
Bacidia laurocerasi
Arthonia ilicina
Degelia plumbea
Graphina anguina
Graphis scripta
Lepraria lobificans
Normandina pulchella
Opegrapha herbarum
Opegrapha vulgata
Pertusaria leioplaca
Phaeographis smithii
Pyrenula chlorospila
Pyrenula macrospora
Sticta fuliginosa
Sticta sylvatica
Thelotrema lepadinum
Tomasellia gelatinosa

Carran (scrub)

Anisomeridium biforme
Arthonia cinnabarina
Arthonia didyma
Arthonia elegans
Arthonia impolita
Arthonia radiata
Arthopyrenia lapponica
Arthopyrenia punctiformis
Arthopyrenia ranunculospora
Bacidia laurocerasi
Degelia plumbea
Graphina anguina
Graphis scripta
Lecanora chlarotera
Lecanora confusa
Lecidella elaeochroma
Normandina pulchella
Opegrapha herbarum
Opegrapha vulgata
Eopyrenula avellanae
Pertusaria leioplaca
Phaeographis dendritica
Phaeographis smithii
Physcia aipolia
Porina aenea
Pyrenula macrospora
Tomasellia gelatinosa

Knockans (scrub)

Anisomeridium biforme
Anisomeridium polypori
Arthonia cinnabarina
Arthonia didyma
Arthonia elegans
Arthonia radiata
Arthopyrenia lapponica
Arthopyrenia punctiformis
Arthopyrenia ranunculospora
Bacidia arceutina
Bacidia laurocerasi
Dimerella pineti
Eopyrenula avellanae
Graphina anguina
Graphis elegans
Graphis scripta
Lecanora chlarotera
Lecanora confusa
Normandina pulchella
Opegrapha atra
Opegrapha herbarum
Opegrapha vulgata
Pertusaria leioplaca
Phaeographis dendritica
Phaeographis smithii
Porina aenea
Pyrenula chlorospila
Pyrenula macrospora
Tomasellia gelatinosa

Rannagh (scrub)

Anisomeridium biforme
Arthonia cinnabarina
Arthonia didyma
Arthonia elegans
Arthonia impolita
Arthonia punctiformis
Arthonia radiata
Arthopyrenia lapponica
Arthopyrenia punctiformis
Arthopyrenia ranunculospora
Bacidia laurocerasi
Graphina anguina
Graphis scripta
Lecanora chlarotera
Mycoporum quercus
Normandina pulchella
Opegrapha herbarum
Opegrapha vulgata
Pertusaria leioplaca
Phaeographis smithii
Porina aenea
Tomasellia gelatinosa

Roo (scrub)

Anisomeridium biforme
Arthonia cinnabarina
Arthonia didyma
Arthonia elegans
Arthonia ilicina
Arthonia impolita
Arthonia punctiformis
Arthonia radiata
Arthopyrenia punctiformis
Arthopyrenia ranunculospora
Bacidia laurocerasi
Caloplaca ferruginea
Eopyrenula avellanae
Graphina anguina
Graphis elegans
Graphis scripta
Lecanora chlarotera
Lecanora confusa
Lecidella elaeochroma
Mycoporum quercus
Opegrapha atra
Opegrapha herbarum
Opegrapha vulgata
Pannaria rubiginosa
Pertusaria leioplaca
Phaeographis dendritica
Phaeographis smithii
Physcia adscendens
Porina aenea
Pyrenula chlorospila
Pyrenula macrospora
Tomasellia gelatinosa
Xanthoria parietina

APPENDIX 5: Bryophyte species recorded at each site.

Data from Walsh (2009a) and Lu (2009).

Table 1 Number of occurrences of bryophyte species in each of the three habitat types, and overall frequency. (A = Acrocarp, P = Pleurocarp and L = Liverwort).

	Species name	Grassland n = 24	Scrub n = 24	Woodland n = 24	Total occurrences n = 72	% Frequency
P	*Ctenidium molluscum*	10	20	23	53	74
P	*Thuidium tamariscinum*	12	16	23	51	71
P	*Pseudoscleropodium purum*	21	20	5	46	64
P	*Calliergonella cuspidata*	22	14	4	40	56
A	*Plagiomnium undulatum*	10	10	18	38	53
P	*Brachythecium rutabulum*	16	11	5	32	44
P	*Loeskeobryum brevirostre*	7	16	8	31	43
P	*Rhytidiadelphus squarrosus*	18	10	3	31	43
P	*Eurhynchium striatum*	0	7	23	30	42
P	*Rhytidiadelphus triquetrus*	4	13	11	28	39
P	*Kindbergia praelonga*	4	7	13	24	33
P	*Thamnobryum alopecurum*	0	2	20	22	31
A	*Tortella tortuosa*	3	8	9	20	28
A	*Fissidens dubius*	2	6	11	19	26
P	*Hylocomium splendens*	4	15	0	19	26
A	*Breutelia chrysocoma*	5	10	3	18	25
P	*Isothecium alopecuroides*	0	4	14	18	25
P	*Neckera complanata*	0	6	12	18	25
A	*Plagiomnium elatum*	6	7	3	16	22
L	*Lophocolea bidentata*	5	8	0	13	18
A	*Fissidens taxifolius*	2	2	8	12	17
L	*Scapania aspera*	2	4	5	11	15
P	*Neckera crispa*	1	1	8	10	14
P	*Oxyrrhynchium hians*	5	1	4	10	14
L	*Plagiochila porelloides*	1	0	8	9	13
L	*Frullania tamarisci*	3	3	2	8	11
P	*Hypnum jutlandicum*	2	4	2	8	11
A	*Dicranum scoparium*	3	4	0	7	10
L	*Frullania dilatata*	0	4	2	6	8
P	*Homalothecium sericeum*	0	3	3	6	8
A	*Dicranum bonjeanii*	2	3	0	5	7
L	*Radula complanata*	0	1	4	5	7
P	*Cirriphyllum piliferum*	2	2	1	5	7
A	*Rhizomnium punctatum*	0	0	4	4	6
A	*Ulota phyllantha*	0	1	3	4	6
L	*Lejeunea patens*	1	0	3	4	6
P	*Hypnum cupressiforme*	1	1	2	4	6
A	*Ditrichum flexicaule*	0	1	2	3	4
L	*Metzgeria furcata*	0	0	3	3	4
L	*Plagiochila asplenioides*	0	0	3	3	4
P	*Campyliadelphus chrysophyllus*	2	1	0	3	4
P	*Hypnum lacunosum*	1	1	1	3	4
A	*Pohlia melanodon*	1	0	1	2	3
A	*Pohlia wahlenbergii*	0	2	0	2	3
A	*Ulota crispa*	0	0	2	2	3
A	*Ulota bruchii*	0	2	0	2	3
A	*Weissia sp.*	0	2	0	2	3
L	*Lejeunea* sp. (other)	0	0	2	2	3
A	*Ceratodon purpureus*	0	1	0	1	1
A	*Didymodon rigidulus*	1	0	0	1	1
L	*Porella arboris-vitae*	1	0	0	1	1
L	*Saccogyna viticulosa*	0	0	1	1	1
P	*Climacium dendroides*	0	0	1	1	1
P	*Hypnum andoi*	0	0	1	1	1
P	*Isothecium myosuroides*	0	0	1	1	1

APPENDIX 6: Results of Mann-Whitney U tests for differences among average numbers of snails at each site.

Table 1 Post hoc pairwise comparisons of the average number of snail individuals found at each site, within habitat types (Mann-Whitney U test). Those which are significant following correction for multiple comparisons (Bonferroni method) are in bold. ('ns' denotes those which were not significant before correction for multiple comparisons.)

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11
Site 1											
Site 2	ns										
Site 3	ns	ns									
Site 4	0.0255	ns	ns								
Site 5											
Site 6					ns						
Site 7					ns	ns					
Site 8					0.0057	ns	ns				
Site 9											
Site 10									**0.0007**		
Site 11									ns	0.0078	
Site 12									ns	**0.0012**	ns

Table 2 Post hoc pairwise comparisons of the average number of snail species found at each site, within habitat types (Mann-Whitney U test). Those which are significant following correction for multiple comparisons (Bonferroni method) are in bold. ('ns' denotes those which were not significant before correction for multiple comparisons.)

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11
Site 1											
Site 2	0.0083										
Site 3	**0.0012**	ns									
Site 4	0.004	ns	ns								
Site 5											
Site 6					ns						
Site 7					ns	ns					
Site 8					0.0069	0.0397	ns				
Site 9											
Site 10									**0.002**		
Site 11									ns	**0.002**	
Site 12									0.0363	0.0066	ns