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Woodland vegetation change through space and time: impacts of large herbivores

Submitted for degree of Doctor of Philosophy in Botany

2014

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Summary

Semi-natural woodlands are a globally important ecosystem. The functioning of these woodlands are being impacted through a range of anthropogenic activities, which induce vegetation changes, including climate change, invasive species, fire, logging, agriculture and overgrazing. Wild large herbivores, especially deer, have dramatically increased their range across Western Europe in recent decades, with major impacts on woodland ecosystems. The ecological consequences of these high deer populations include: impacts on growth and survival of many herbs, shrubs and tree species; modified patterns of vegetation dynamics; impacts, at cascading levels, on insects, birds and mammals; reduced plant cover and diversity; altered nutrient and carbon cycles; and redirection of succession to shift future overstorey composition. Woodland ecosystem dynamics are often long-term processes, which are usually studied either empirically at short-term (within a decade) or historically at long-term (within centuries and millennia) scales. Being able to investigate medium and long-term vegetation community data across several decades, as in this study, allows for increased understanding of the ecosystem.

This thesis assessed the effects of time and large herbivores on the plant communities of temperate oak woodlands, with a goal of improving or feeding into management practices for biodiversity conservation areas. Specific objectives relating to large herbivore impact have been addressed: the impact of varying grazing levels on ground flora and tree regeneration, the long-term effects of large herbivore removal, cross-taxon surrogacies, and the effects of time and habitat on tree regeneration.

This thesis utilised an existing network of long-term experimental research plots, distributed among oak woods in three National Parks in Ireland: Killarney National Park, Co. Kerry, Wicklow Mountains National Park, Co. Wicklow, and Glenveagh National Park, Co. Donegal. The experimental plots ranged in size and age, including long-term deer exclosures, newly established controls, and a set of unfenced permanent plots. Data collected in 2010 and 2011 were combined with long-term survey data. Combinations of multi- and uni-variate statistical methods were employed in the analysis of data, including ordinations, ANOVA-based models, Procrustes techniques, correlations, and linear mixed-effects models.

The research presented in this thesis, in the context of previous studies, has shown that management practices must be diversified in space and time, in order to achieve site specific conservation objectives such as maintained species richness, tree regeneration, and heterogeneity within the woodland landscape. Large herbivore grazing levels have a range of impacts on vegetation and its structure: a general homogenisation of temperate oak woodlands is likely with total large herbivore removal. Results also suggest that the relationships within and between taxa may be altered, when comparing large herbivore exclosures with grazed areas. Without continued long-term monitoring projects, such as the ones detailed here, the true drivers of change may not be identified and the conservation of woodland will suffer.

On the basis of these findings, it can be recommended that where woodland conservation and regeneration are desired, low grazing impacts, but not zero grazing, should be maintained. Large-scale, long-term fencing of oak woodlands should be replaced by large herbivore management programmes, in order to ensure the conservation of diverse native woodland ecosystems. It is recommended that more taxonomic groups be included in biological assessment for management and conservation when stressors to ecosystem functioning, such as grazing, are present. Also, managers of protected area should use research findings, such as those presented in this thesis, to adapt management practices in order to promote woodland regeneration. Management should specifically focus on large herbivore impacts and quantifying tree regeneration change through time. Further research should focus on the continued monitoring of experimental plots; methods of assessment of large herbivore impacts; management objectives for large herbivore populations; the effects of grazing on the interactions among taxonomic groups; incorporating stakeholder perceptions; and translating research into policy and practice.

Acknowledgements

Foremost, I would like to acknowledge the support of my supervisors Daniel L. Kelly and Fraser J.G. Mitchell. Thanks to both of you for the opportunity to do this project and for the encouragement, helpful comments, and lab time, it was very much appreciated.

I want to extent my gratitude to the PLANFORBIO research group, in particular, Linda, Anke, and Aisling, for your support and advice with design, identification, and write-up. This project involved several collaborations, and I want to thank: Helen Armstrong and Richard Thompson (Forestry Commission Scotland); Lauren Fuller, Conor Graham, and Mark Wilson (University College Cork); and, John Cross, Kathryn Freeman, Paudie O'Leary (RIP), and the Managers and Rangers of Killarney, Wicklow Mountains, and Glenveagh National Parks (National Parks and Wildlife Service).

Several people helped me with field work, especially Aoife, Alex, Emily, and Stevie. I am grateful for your assistance and enthusiasm (even when it was lashing rain or thick with midges!).

The Botany Department is an enjoyable and encouraging environment in which to complete a research degree, and I'd like to thank everyone who has passed through in the last three years, in particular Karen who showed me the ropes when I arrived. The BiodiversityInOurLives initiatives were a fantastic distraction from data analysis and great way to socialise with such good friends and colleagues; thanks to Aoife, Dara, Eileen, Shane, Jesko, Erin Jo, and Susannah for that.

I want to thank the late Maximilian von Sternburg, fellow student and friend, for his name, his musings on life, and his love for having the craic. You left us too soon.

For support, encouragement and love, I thank my mother Linda, my sister Libby, and my grandparents Ed (Bud) and Karen Rubesch. I also wish to thanks Anne and Anthony for their continued support.

Love to Aoife for all her support throughout the last three years. You always helped me out when I needed it, no matter how mundane the task. I can't describe how thankful I am for you.

The last three years have, at times, been fantastic, horrible, inspiring, and tiring. I am truly grateful to have been in a position to pursue research of the natural world, I feel very lucky.

Go n-éirí an bóthar leat is do chosán cóngair,
Miles
17/05/2013

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Chapter 1:

General introduction

1 General introduction

1.1 Thesis context

Woodlands (synonymous with 'forests' in this thesis) are a globally important ecosystem (Klenner et al., 2009), covering approximately 25% of the earth's land area (excluding the Antarctic and Greenland), and supporting the majority of terrestrial biodiversity (Matthews et al., 2000). The greatest loss of global woodland cover between 2000 and 2005 is attributed to the boreal biome (Hansen et al., 2010). Temperate woodlands have the least cover of all the biomes and, as a percentage of loss over the period 2000-2005, they are second highest among all biomes (Hansen et al., 2010). Temperate broadleaved woodlands have declined drastically during the last millennia and have been identified as a habitat of conservation priority (Hannah et al., 1995).

The functioning of these temperate woodlands is being impacted through a range of anthropogenically induced vegetation changes (Rackham, 2008), including climate change (e.g. Munson et al., 2012, Rackham, 2008), invasive species (e.g. Santos et al., 2011, Mack et al., 2000, Rackham, 2008), fire (Hansen et al., 2010), logging (Hansen et al., 2010), agriculture (Matthews et al., 2000) and overgrazing (e.g. Côté et al., 2004, Rackham, 2008). The threat of overgrazing has been acknowledged in a European Union report as among the most important anthropogenic impacts associated with the decline in forest biodiversity (Slingenberg et al., 2009).

1.2 Impact of large herbivores on woodland ecosystem

Large wild herbivores, such as deer, have been increasing their range globally in recent decades and are now considered by many to be at unsustainably high levels in temperate woodlands (e.g. Côté et al., 2004, Apollonio et al., 2010). This has been shown to drive change in an ecosystem (Côté et al., 2004, Fuller and Gill, 2001) with cascading effects on a range of biotic and abiotic components such as invertebrates (Allombert et al., 2005, Bugalho et al., 2011, Pollard and Cooke, 1994), birds (McShea and Rappole, 2000), small mammals (Bush et al., 2012, Buesching et al., 2011), vegetation (Côté et al., 2004), soil (Mofidi et al., 2012), terrestrial carbon storage (Tanentzap and Coomes, 2012) and ecosystem functioning (Rooney and Waller, 2003).

Impacts should not, however, be seen with simplistically negative connotations, as many impacts associated with large herbivores may play integral roles in woodland survival, such as importance for tree regeneration (e.g. Vera, 2000), maintaining vegetation heterogeneity in the habitat (Kelly, 2000, Perrin et al., 2011), and maintaining habitats suitable for a wide range of taxa (e.g. Stewart, 2001, Oxbrough et al., 2005, Díaz, 2006, McShea and Rappole, 2000).

1.3 Ireland's semi-natural woodlands and large herbivores

At a European scale, 45% of the land area is forested, although only ~26% of this (4% excluding the Russian Federation) is classified as natural (undisturbed by man) and 70% (87% excluding the Russian Federation) as semi-natural (Forest Europe et al., 2011). Ireland has comparatively low land-area of semi-natural woodland relative to the European context, at less than 2% cover (Perrin et al., 2008). A national survey of semi-natural woodland communities identified four main woodland groups in Ireland (Perrin et al., 2008), including: *Quercus petraea-Luzula sylvatica* woodland groups; *Fraxinus excelsior-Hedera helix* woodland groups; *Alnus glutinosa-Filipendula ulmaria* woodland groups and *Betula pubescens-Molinia caerulea* woodland groups. Of the semi-natural woodlands found in Ireland, Oak woods (dominated by *Q. petraea*) are the most common (see Perrin et al., 2008). In suitable areas containing representative old sessile oak with *Ilex aquifolium* (holly) and *Blechnum spicant* (hard fern), sites are protected as Special Areas of Conservation (SAC) under the European Union's Habitats Directive (E.U., 1992).

Wild large herbivores in Ireland consist mostly of several species of deer, although no native deer species have survived from the last glacial cold stage to present day. Ireland was once home not only to the red deer (*Cervus elaphus*) but also the giant Irish deer (*Megaloceros giganteus*) and reindeer (*Rangifer tarandus*) (Woodman et al., 1997). New evidence suggests that red deer were re-introduced in the Neolithic period (Carden et al., 2012) after a period of extinction, while Japanese sika deer (*Cervus nippon nippon*) were introduced in the 19th century A.D. The most common woodland deer species now found in Ireland, red deer and sika deer, have increased in range by 565% and 353% respectively, between 1978 and 2008 (Carden et al., 2010). These two deer species have hybridised (Abernethy, 1994) in some areas, including Co. Wicklow, but have remained separate in others, such as Co. Kerry and Co. Donegal. Other introduced herbivores such as domestic cattle, sheep, pigs and goats have had a long history in the Irish landscape (Carden et al., 2012, Woodman et al., 1997, Mitchell and Ryan, 2003), indicating that large herbivore grazing, at varying intensities, has been a part of Irish woodland ecosystems for thousands of years. Goats

(*Capra hircus*), which were formerly domestic animals, are now locally abundant in a feral state in several areas of Ireland. In the recent past, high sheep grazing levels had major impacts on native woodlands in upland areas (Pollock et al., 2005, Milne and Hartley, 2001); however, since changes to the EU Common Agriculture Policy headage-based financial support in the 1990s, sheep grazing in woodland has declined across Europe (Hester et al., 2000).

1.4 Research rationale

Oak woods, dominated by *Q. petraea*, are the most common semi-natural woodland type in Ireland and are nationally and internationally important (Perrin et al., 2008, NPWS, 2008). This makes oak wood habitats an ideal choice for the study of large wild herbivore impacts, as the results are applicable over a wide area, across Ireland and Western Europe. Woodland ecosystem dynamics are long-term processes, which are usually studied either empirically at short-term (within a decade) or historically at long-term (within centuries and millennia) scales. Being able to investigate long-term vegetation community data allows for increased understanding of the ecosystem (Silvertown et al., 2010) and has become an increasingly important tool for biodiversity research (Magurran et al., 2010).

Although the results of the long-term data collection in Irish woodlands have been partially reported from a few individual exclosures (Bleasdale and Conaghan, 1996, Perrin et al., 2006, Perrin et al., 2011, Kelly, 2000), there is now a need to unify the analysis of long-term exclosure data in order to examine trends at wider temporal and spatial scales. Long-term data collection is vital to the understanding of woodland systems; without it we may be unaware of the difference between minor fluctuations and significant trends (Magnuson, 1990). This type of long-term monitoring can provide powerful insights into how large herbivores, e.g. deer, drive change in plant communities (Côté et al., 2004).

Woodland tree regeneration is vital to the long-term conservation and management of the woodland habitat. Much tree regeneration research is focused on one or two components of the woodland, usually under canopy or in gaps within the canopy (e.g. Perrin et al., 2006, Palmer et al., 2004). There is a need to study regeneration at the wider landscape scale by assessing a range of woodland and adjacent habitats surveyed together through time.

Large herbivores alter the woodland ecosystem in a variety of ways (see **section 1.2**). The implication of changing deer densities, in a range of different landscapes, has been identified as one of the 100 ecological questions for conservation policy in the U.K. (Sutherland et al., 2006). Experiments using exclosure and control areas, through time, can increase the understanding of large herbivore impacts (Côté et al., 2004). There is a need to identify appropriate large herbivore grazing regimes for a variety of conservation aims (e.g. Hester et al., 2000, Perrin et al., 2011, Kirby, 2001, Purser et al., 2009), as detailed knowledge regarding the impacts of grazing on biodiversity is required for the implementation of management strategies at the ecosystem and landscape scale (e.g. Mysterud, 2006).

1.5 Research aim

The overall aim of this research is to assess the effects of time and large herbivores on the woodland community, with the goal of improving or feeding into management practices in protected biodiversity conservation areas. Specific objectives, questions and hypotheses are set out for each chapter as follows:

Chapter 2 aims to investigate the differences in vegetation composition, structure and regeneration between grazed and ungrazed sites, and among different levels of grazing. It is hypothesised that low grazing intensities will be most appropriate for the conservation of both vascular plants and bryophytes. Addressing these aims will facilitate the formulation of long-term grazing management of wild herbivores in temperate oak woodland with a view to maintaining their conservation value.

The objective of **Chapter 3** is to investigate the changes in structure and composition occurring through time with the exclusion of large herbivores, using empirical vegetation data collected over a period of ~40 years. The responses of vascular plants to this removal and the potential homogenisation of temperate woodland vegetation through time will be assessed. This research will have implications for the management of large herbivores and the conservation of temperate woodland habitats.

The objective of **Chapter 4** is to investigate the potential surrogacy among taxonomic groups in temperate semi-natural oak woodlands, and to assess whether spiders and vegetation have similar responses to large herbivore grazing. The findings will have implications for the surveying and monitoring of biodiversity in woodlands, and also for the use of taxonomic indicator groups.

Chapter 5 sets out to assess changes in woodland regeneration in the medium-term (20 years). This study investigates the effects of habitat type and time on quantity of tree regeneration, and the change in regenerating tree species composition through time, within a range of woodland and adjacent habitat types. Learning more about underlying mechanisms behind tree regeneration is required in order to deliver more effective conservation management.

Chapter 6 provides a general conclusion and synthesis of the thesis. An overview of the main findings, their implications for management, and a list of recommendations is detailed.

1.6 Thesis contributors

This thesis has utilised a combination of primary data collection and the collation and analysis of existing long-term data sets. For **Chapters 2**, **3, 4** and **5**, field data were collected by the thesis author through 2010 and 2011. The multi-taxonomic data collection for **Chapter 4** involved field data collection by the thesis author (vegetation, TCD), Dr Linda Coote (vegetation, TCD), Ms Lauren Fuller (spiders, UCC), and Mr Rob Deady (spiders, UCC). Dr Conor Graham (UCC) collated the bird species richness data for analysis input. Lab based species identification was completed by the thesis author, with assistance from Ms Aisling Walsh and Prof Daniel L. Kelly. All data analysis was conducted by the thesis author, with advice from those acknowledged in each chapter. All chapters have been written by the thesis author, with comments incorporated from both supervisors (Profs Daniel L. Kelly and Fraser J.G. Mitchell), and the anonymous reviewers of **Chapters 2** and **3**. Prior to this thesis being submitted, the cross-taxonomic study (**Chapter 4**) has not been commented on by the co-authors. Additional contributions, made by individuals not named as co-authors at the beginning of each chapter, are noted in the acknowledgement section at the end of each chapter.

In addition to the data presented in this thesis, multi-authored manuscripts focused on the response of woodland ground flora to climate change (De Frenne et al., 2013) and the impact of grazing on the spider communities of yew and oak woods in Ireland (Fuller et al., 2014), have incorporated specific data collected by the thesis author.

Chapter 2:

Impacts of wild herbivores on the plant community, structure, and regeneration of ancient oak woodlands

To be submitted as:

Newman, M., Mitchell, F.J.G., and Kelly, D.L. Impacts of wild herbivores on the plant community, structure, and regeneration of ancient oak woodlands. To be submitted to Basic and applied Ecology.

2 Impacts of wild herbivores on the plant community, structure, and regeneration of ancient oak woodlands

2.1 Abstract

Wild large herbivores, especially deer, have dramatically increased their range across western Europe in recent decades, with a cascading impact on woodland ecosystems. This study investigates the differences in vegetation composition, structure and regeneration among different levels of grazing impact, and hypothesises that low grazing intensities will be most appropriate for optimal biodiversity of woodland flora.

Plant community composition differed among grazing impact levels, most strongly between absent and medium-high levels. With increasing impact levels of grazing, a decrease in the cover of bramble (*Rubus fruticosus* agg.), climbers, and vegetation structure between 50 and 200cm was found. With the same gradient of grazing, an increase in cover of forbs and bryophytes was detected, in conjunction with an increase in the species richness of graminoids, bryophytes and total vegetation (vascular plants and bryophytes together).

It is recommended that where woodland biodiversity conservation and tree regeneration are both desired, low grazing impacts, but not zero grazing, should be maintained in order to achieve a balance between the promotion of regeneration and maintenance of both vascular plant and bryophyte communities. Management practices should be diversified in space and time in order to achieve the overall conservation objectives.

2.2 Introduction

Large wild herbivores, such as deer, have been increasing their range globally in recent decades and are now considered by many to be at unsustainably high levels in temperate woodlands (e.g. Côté et al., 2004, Apollonio et al., 2010). The ecological impacts of these high deer populations can be summarised as: impacting the growth and survival of many herbs, shrubs, and tree species; modifying patterns of vegetation dynamics; impacting, at cascading levels, on insects, birds and mammals; reducing plant cover and diversity; changing nutrient and carbon cycles; and redirection of succession to shift future overstorey composition (Côté et al., 2004). Grazing, as a driver of disturbance, has been used in the early description of the intermediate disturbance hypothesis (Grime, 1973) to argue that an intermediate level of grazing will produce the most species rich plant community. However, this theory remains controversial (e.g. Fox, 2013).

The role, impact and ecology of herbivores has been studied globally (e.g. Danell et al., 2006, Tanentzap et al., 2009b, Tanentzap et al., 2011), at a European level (Vera, 2000, Allombert et al., 2005, van Uytvanck and Hoffmann, 2009, Pisanu et al., 2012, Kuijper et al., 2010a), and in Ireland (Mitchell, 1990, Perrin et al., 2006, Carden et al., 2010). While much research has been carried out on the relative impacts of domestic herbivore stocking rates (e.g. Cesa and Paruelo, 2011, Hester et al., 1996, Papachristou and Platis, 2011), less information is available regarding levels of wild herbivore impact. The reasons for this may be two-fold: 1) difficulties in creating 'controlled' environments at varying grazing levels, and 2) difficulties in assessing wild herbivore density and impact. In addition to this, few studies investigate the full spectrum of vegetation, with most focusing on vascular plants only and neglecting bryophytes. This can misrepresent the impacts of grazing on biodiversity when lower plants comprise a significant element of the woodland flora.

Fenced grazing exclosures provide an opportunity to investigate the impact of no large herbivore grazing on floristic biodiversity compared to the prevailing grazing regime that continues outside the exclosure. This approach to quantifying grazing and browsing impacts has been deployed throughout many temperate woodland ecosystems (Perrin et al., 2011, Collard et al., 2010, Hester et al., 2000, Buesching et al., 2011). While exclosure fences can be maintained for decades to ensure the zero grazing treatment, herbivore populations outside the exclosures can fluctuate and thus the "control" to the treatment can be temporally variable. Detailed long-term data on herbivore population dynamics in temperate woodlands are extremely rare so despite the limitations of the exclosure approach it is a widely adopted technique to assess the impact of large herbivores. Even when herbivore population dynamics are recorded, their application to other systems is invariably invalid due to large spatial and temporal differences in the herbivore carrying capacity in temperate woodland ecosystems. This challenge is further compounded when woodland forms part of a mosaic in the landscape with other more open habitats. One approach to accommodate this is the application of the 'woodland grazing toolbox' which assesses relative herbivore populations through vegetation damage assessment (Armstrong et al., 2011). It thus appears that qualitative herbivore grazing impact levels such as high, medium, and low are more applicable than quantitative assessment of populations.

Wild large herbivores in Ireland consist mostly of several species of deer, the populations of which have expanded in recent decades, making it an ideal location for the investigation of herbivore impacts. Most abundant are the red deer (*Cervus elaphus*) and the Japanese Sika deer (*Cervus nippon nippon*) of the uplands, and the western-Eurasian fallow deer (*Dama*

dama) of the lowlands. Although red deer are usually considered to be the only native deer species in Ireland, recent studies have identified the introduction of red deer from Britain during the Neolithic period (Carden et al., 2012). The two upland deer species have hybridised (Abernethy, 1994) in some areas, including Co. Wicklow, but have remained separate in others, such as Co. Kerry and Co. Donegal. The range of these upland deer in Ireland has increased dramatically in the period between 1978 and 2008, with an estimated increase greater than 5-fold for red deer and 3-fold for Sika deer (Carden et al., 2010). Goats (*Capra hircus*), which were formerly domestic animals, are now locally abundant feral animals in several areas of Ireland. In the recent past, high sheep (*Ovis aries*) grazing levels in woods contributed to herbivory. However, with changes to the EU Common Agriculture Policy headage-based financial support in the 1990s, sheep grazing in woodland declined across Europe (Hester et al., 2000).

It is common practice in many protected woodland areas to cull or exclude (through fencing) wild and domestic herbivores in order to maintain desired ecosystems or promote conservation. Fencing and culling programmes are often costly (both ecologically and monetarily (Hayward and Kerley, 2009)), and total exclusion of wild herbivores may not be desired; however optimal culling quotas can be difficult to estimate (e.g. Koh et al., 2010, Swanson et al., 2008). There is now a major need to investigate the impacts of grazing levels in temperate woodland (Perrin et al., 2006, Pellerin et al., 2010, Hester et al., 2000).

Of the ancient semi-natural woodland types found in Ireland, Oak woods are the most common (see Perrin et al., 2008), making this habitat an ideal choice for the study of large wild herbivore impacts, as the results are applicable over a wide area, across Ireland and western Europe. This research aims to investigate the differences in vegetation composition, structure and regeneration between grazed and ungrazed sites, and among different levels of grazing impact.

We test the hypothesis that low grazing impact levels will be most appropriate for optimal biodiversity of woodland flora. Addressing this will facilitate the formulation of long-term wild herbivore grazing management in temperate oak woodland with a view to maintaining their conservation value.

2.3 Methods

2.3.1 Study sites

The study sites are located within protected semi-natural oak woodlands in three National Parks in Ireland (between 52°0'-55°3 N and 6°18'-9°35'W). The three sites are roughly equidistant from each other (Fig. 2.1). Ireland's temperate climate is heavily influenced by the Atlantic Ocean and the Gulf Stream in particular, ensuring a climate of relatively cool summers and mild winters. Mean annual rainfall (between 1961-1990) at the 3 study sites was in excess of 1600mm, while the mean daily min of the coldest month and the mean daily max of the warmest month were 2.8°C and 16.1°C, respectively (available from www.met.ie). The eastern half of the country is drier than the west; however, the coastal distribution of mountains means that the oceanic conditions are still found in eastern counties (e.g. Wicklow and Antrim) (Ratcliffe, 1968). The combination of woodland composition and climatic conditions found at these sites supports the classification of these old oak woodlands as temperate rainforest, using the criteria of Alaback (1991).

In addition to national designations, these woodlands are protected as Special Areas of Conservation (SAC) under the European Union's Habitats Directive (E.U., 1992) as they contain representative areas of old sessile oak with *Ilex aquifolium* (holly) and *Blechnum spicant* (hard fern) (EU code 91A0). The semi-natural woodlands at the three study locations are similar in maturity, with a relatively even-age structure dominated by sessile oak (*Quercus petraea*) in the canopy, holly (*Ilex aquifolium*) as a scanty understorey, and a field layer dominated by bilberry (*Vaccinium myrtillus*) and grasses (mainly *Agrostis capillaris, Holcus mollis*) and woodrush (*Luzula sylvatica).* This woodland vegetation belongs to the Blechno-Quercetum Association (Kelly and Moore, 1975, Braun-Blanquet and Tüxen, 1952), corresponding to the *Quercus petraea-Luzula sylvatica* woodland group (Perrin et al., 2008).

The National Parks in Killarney, Glenveagh and the Wicklow Mountains, each cover an area greater than 10,000ha (Table 2.1), and are a mosaic of habitats, including blanket bog, heath, lakes, rivers, exposed rock, and woodlands. Both Glenveagh National Park (GNP) and the Wicklow Mountains National Parks (WMNP) have ~100ha of semi-natural woodlands, while Killarney National Parks (KNP) encompasses 1,220ha, the largest expanse of this habitat in Ireland. Parts of all three Parks were formerly private estates, transferred to the state between 1932 and 1975. All three Parks are bordered by agricultural landuses. As a result of the GNP's history as a sporting estate, 45km of mostly intact strained deer fence encloses the park (Telford, 1977). In addition, deer fences were erected to enclose a large proportion of the GNP woodland in 1975 (Bleasdale and Conaghan, 1996).

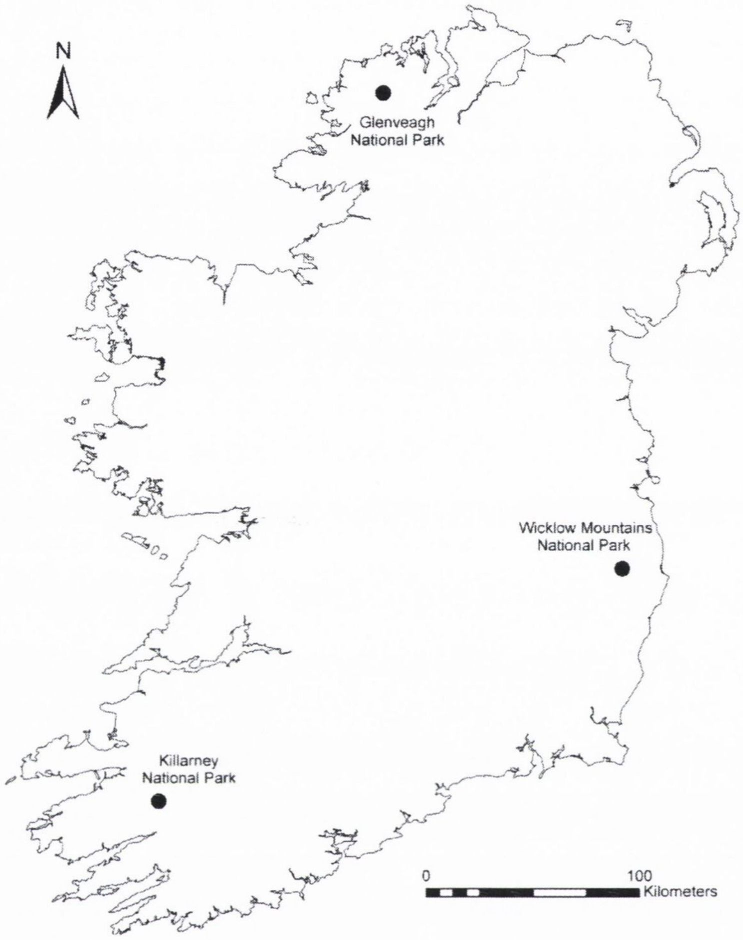

Fig. 2.1 Location map of Ireland showing study sites

2.3.2 Large herbivore community

Detailed quantitative data on the large herbivore communities at the three study sites are largely non-existent. Where quantitative data have been collected, translation into herbivore density is often meaningless as the landscape is highly fragmented. Large herbivores can move freely in and out of the most National Parks, but may also be forced to use specific woodland areas due to large woodland exclosures. This in turn can lead to highly localised impacts on the vegetation of these areas. The available information on the composition and historical changes to the herbivore communities is presented here. However, the data for large herbivore population estimates must be viewed with caution.

Large herbivores currently found in WMNP include red deer, Sika deer, their hybrid, and feral goats. It is likely that the wild deer population of the Wicklow uplands died out in the 18th century and was repopulated from escapes of red and Sika deer from the Powerscourt Estate in the 1920's (Nolan and Walsh, 2005, NPWS, 2005b). Numbers of deer have slightly increased since the establishment of WMNP (Nolan and Walsh, 2005). The principal herd of feral goats, estimated at ~150 in 2005, is found in the wooded valley where the study plots of this research are located (NPWS, 2005b).

Red deer, Sika deer, and feral goats make up the large herbivore community within KNP. The only long-established population of red deer in Ireland is found there, while Sika were introduced to the area in 1865 (NPWS, 2005a, Larner, 1977). Larner (1977) details the Sika deer present in KNP in the early 1970's and estimates the population to be between 850 and 1,250. The hybridisation between the species found in WMNP does not occur here. The estimated population of red and Sika deer in 2005 was ~1000 individuals per species. Herds of feral goats are described as being at 'unsustainable levels' within the Park (NPWS, 2005a), but no census data are available.

Red deer were introduced to GNP for sporting purposes, through various translocations from Scotland, England, and other areas of Ireland, between the 1890's and late 1940's (Whitehead, 1960). When the park was purchased by the state in 1975, there were 700 red deer within the fence (GNP, unpublished data). Annual red deer census results from 1981-2005 indicate a slow decline in the numbers in the park (from 538 to 270), with a peak population of 1004 recorded in 1986 (GNP, unpublished data). A large herd of feral goats grazed the woodlands of the park in the late 19th and early 20th century (GNP, unpublished data). Unwanted domestic goats are released into GNP from time to time but are removed (GNP, unpublished data).

Domestic sheep grazing has been a feature of all three study sites in the past, with damage being noted at all three sites (NPWS, 2005b, NPWS, 2005a)(GNP, unpublished data). Domestic sheep were once a major grazer in certain areas of the KNP, with 1,000 trespassing domestic sheep reported to be common in areas in the late 20th century (NPWS, 2005a). In GNP domestic sheep grazing was commonly practiced in the 19th century, before the creation of the sporting estate. However, sheep numbers in the National Park have decreased dramatically in the past decade and sheep grazing is now mainly confined to non-wooded upland areas (NPWS, 2005b, NPWS, 2005a)(GNP, unpublished data), with no sheep in wooded areas seen by the authors in 2010 and 2011 field seasons. Where domestic livestock grazing has declined, wild large herbivores communities may be increasing their dominance; a trend occurring across Europe in recent decades (Austrheim et al., 2011, Prins and Gordon, 2008).

Although the large herbivores described from the study sites are referred to collectively as 'grazers', it is acknowledged that the feeding behaviours of these herbivores are on a continuum from roughage eaters to intermediate eaters (between roughage and selected browsing) (e.g. Hofmann, 1989, van Wieren, 1996). These broad and flexible categories may be highly dependent on food availability and preferential species.

In the absence of more comprehensive data on contemporary herbivore densities, it was decided to use the 'woodland grazing toolbox' as a proxy (see section 2.3.4).

Table 2.1 Site and exclosure details

National Park	Park size (ha)	Area of oak woods (ha)	Exclosure code	Exclosure established	Exclosure size (m^2)	Distance to control (m)
Wicklow	17000	106	P3	1970	400	3
			P9	1970	400	3
Killarney	10000	1220	C1	1969	1090	3
			C2	1974	956	3
			C3	1974	260	5
			C4	1974	400	5
			TX	1972	5560	20
Glenveagh	16000	100	DBE	1988	~26000[a]	10
			SCE	1975	~27000[a]	2100

[a]Large area of exclosure extended into non-woodland habitat, wooded area ~11000m^2

2.3.3 Experimental design

Deer fences were erected in the three study locations between 1969 and 1975 (one additional fence was erected in 1988) (Table 2.1) in order to study the long-term effects of excluding grazing mammals. These exclosures were established in representative areas of the woodland. Baseline and interim surveys of these exclosures are analysed in **Chapter 3**.

Their results indicate that, while the exclosures were heterogeneous at point of fencing, after ~40 years of large herbivore removal, they had developed highly similar floristic compositions. These fenced exclosures used graded wire in order to exclude large (deer, feral goats, and sheep) and medium (hares) woodland herbivores. The exclosures (ungrazed plots) range in size from 260 to 27,000m^2. The current research has utilised this existing network of exclosures by establishing paired controls (grazed plots) in 2010. The controls were located beside the existing exclosures in areas with comparable topography and mature canopy cover. All control plots were within 20m of existing exclosures, with the exception of the SCE control (Table 2.1). This plot was located over 2km away from the exclosure as no suitable woodland was available directly outside the exclosure. The canopy openness of all plots was measured using the canopy scope method of Brown et al. (2000), and a mean openness (±SE) of 23±2% was recorded (M. Newman, unpublished data). The predominant soil type at the sites are podzols, with a mean pH (±SE) of 4.13±0.08 (top 10cm) (M. Newman, unpublished data). The study sites are in upland terrain, although the woodland study plots ranged in altitude between 35 and 175 m a.s.l. A total of 9 paired grazed and ungrazed plots were used in the experiment: 5 in Killarney National Park, 2 in Glenveagh National Park, and 2 in Wicklow Mountains National Park.

2.3.4 Data collection

Field surveys were conducted by the lead author between June-September in 2010 and 2011. Vascular plant ground flora (vegetation <2m in height) cover was recorded for each species within 1m^2 relevés to the nearest 5%. Approximations for cover values below 5% were recorded as 3% (cover 1-5%) and 0.5% (cover <1%). The abundance of non-epiphytic bryophytes (mosses and liverworts) was recorded for each species in a nested 25x25cm relevé, placed in the centre of each 1m^2 relevé. The structural composition of the plots was assessed in the field through the estimation of total vegetation cover (i.e. % of vegetation) in each of the following structure height classes: 0-5cm, >5-25cm, >25-50cm, >50-100cm, and >100-200cm. Regenerating tree species were divided into two categories: a) seedlings (<25cm in height), and b) saplings (≥ 25cm in height, but with a DBH of less than 3.2cm at 1.3m). Numbers of individual seedlings and saplings of each species, and their cover, were recorded within the 1m^2 relevés. Plant life-forms were categorised, by summing species cover values, into: graminoids – grasses, rushes, and sedges (Stace, 2010); forbs – herbs excluding graminoids and ferns; ferns; shrubs – woody plants that are not trees (Stace, 2010) or climbers; bramble – *Rubus fruticosus* agg.; climbers – *Lonicera periclymenum* and *Hedera helix*; and bryophytes – mosses and liverworts. The cover and species richness of the different life-form groups and of vascular plants, mosses, liverworts, bryophytes, and total vegetation (vascular plants and bryophytes) were subsequently calculated from the species data.

Restricted random sampling was used, whereby random numbers were used to place relevés within plots. Ten relevés were selected at random from each plot. Nomenclature follows Stace (2010) for vascular plants, Smith (2004) for mosses, and Paton (1999) for liverworts.

Adequate density data are not available for the large herbivore communities here. These may in any case not be an adequate metric for grazing impact assessment (see **Section 6.3.1**), as the mosaic of habitats in the study sites confound the importance of certain fragments within the complex (Kirby et al., 1994). Assessment of large herbivore populations has largely been based on density estimates through a variety of techniques including direct counts (Putman et al., 2011b), indirect methods such as faecal pellet surveys (e.g. Swanson et al., 2008), and indices such as hunter observations and bag numbers (Putman et al., 2011b). However, the accuracy of these methods may vary considerably and population changes may be difficult to detect (Daniels, 2006, Smart et al., 2003). In fragmented woodland landscapes it may be increasingly difficult to achieve accurate large herbivore population surveys through total count methods, as these techniques are largely limited to open areas (Putman et al., 2011b); deer may remain undetected or be double counted as they move into open areas. Although absolute deer densities are often the method used to assess large herbivores, they are unlikely to be good predictors of impact, as many factors influence what an impact level can be (Putman et al., 2011a). Therefore, the assessment of grazing intensity was completed using the online 'woodland grazing toolbox', developed by the Forestry Commission Scotland (2012). This toolbox qualitatively categorises the current grazing impact pressure (within the last 12 months) using the assessment criteria of ground disturbance, bark stripping, swards (grass, rush, and low herb vegetation), preferentially browsed species, tree seedlings and saplings, epicormic shoots, and basal shoots on trees. The approach was developed for adaptive management systems where re-surveys are compared to originals and a set of objectives are defined. Three grazing impact levels were derived by averaging the results of the assessment criteria for each plot: a) grazing absent (9 exclosed plots), b) low grazing (5 plots), and c) medium-high grazing (4 plots).

The toolbox was also used to assess the historic or long-term (last 20+ years) herbivore impacts at each of the plots. To determine the long-term impact, the assessment used criteria such as: forb and grass indicator species, dominance of bryophytes, height of the sward, presence of preferentially browsed species, degree of understorey development, and browseline prominence. The assessment indicated high levels of historic herbivore impact at all control plots, excluding P3 (W1) in Wicklow, which indicated low historic grazing impacts; this is likely due to the influence of a regional road located 10m from these plots.

2.3.5 Data analysis

Formal statistical analyses were carried out using a two-tiered approach. First, a comparison of grazed and ungrazed plots was conducted. This was followed by the comparison of responses to the three grazing impact levels (absent, low, and medium-high).

Species composition was examined with a non-metric multidimensional scaling (NMS) ordination using the averaged species abundance data for each plot in PC-ORD 6.08 (McCune and Mefford, 2011). NMS was used to view the relationships among treatments by reducing the dimensionality of the data space (McCune and Grace, 2002). The ordination was run using the Sørenson (Bray-Curtis) distance matrix, with a maximum of 500 iterations (250 with real data and 250 with randomised data), an orthogonal rotation, and a Monte Carlo randomisation test, for a data matrix of 18 plots and 93 plant species.

In order to test for differences in species composition and abundance between grazed and ungrazed plots, and among the three grazing impact levels, a permutational multivariate analysis of variance (PerMANOVA) (Anderson, 2001a) was conducted. This procedure provides a multivariate equivalent to the *F*-ratio calculated through any symmetric distance or dissimilarity matrix, with a *p*-value based on permutations (Anderson, 2001a). The tests were performed in PERMANOVA+ 1.0.3, an add-on function to PRIMER 6.1.13 (PRIMER-E, 2009). For the grazed vs. ungrazed comparison, a randomised complete block design was used, where groups were defined by each pair of grazed and ungrazed plots, and treatment (grazed or ungrazed) was a fixed factor. For the comparison among grazing impact levels, a randomised design with grazing impact level as fixed factor and geographical location (national park) as random factor was employed. For both tests the Sørenson (Bray-Curtis) distance matrix was used on a total of 9999 unrestricted permutations of raw data, with type III (partial) sums of squares. A pair-wise comparison of grazing impact level was conducted to highlight the community composition differences among the three grazing impact levels. A Monte Carlo randomisation test was also carried out with the procedure. The Monte Carlo results may be of greater importance when the number of permutations is small (<100), and this *p*-value should be preferred over the permutation *p*-value, as a general rule, because it can provide a more accurate test (Anderson et al., 2008).

Initially, univariate analysis on the various vegetation cover and species richness variables was carried out, where the pairs of grazed/ungrazed plots were treated as the lowest level and blocked by geographical location. However, blocking was not significant as no interaction effect was found between geographic location and pairs of plots, therefore, pseudoreplication was addressed and the design could be simplified. The paired t-test design was used to test significant differences as it is highly suitable for this simplified type of comparison. Paired t-tests and required transformations (log(base)) were carried out in R (R Core Team, 2012).

In order to investigate differences among grazing impact levels for the vegetation variables, a General Linear Model (GLM) was performed in SPSS version 19 (SPSS, 2010). Initially, geographic location was added as a random factor; however this was not found to have a significant effect and was removed from the model. Where significant differences were found among the three grazing impact levels, post-hoc analysis using Tukey Honestly Significantly Difference (HSD) comparison technique (Hsu, 1996) was carried out. Transformations of the vegetation variables followed those carried out for the paired t-test analysis.

2.4 Results

2.4.1 Community composition

The most suitable ordination solution for average species abundance in grazed and ungrazed plots was a 2-dimentional solution with a final stress of 12.78. Stress can be described as the discrepancy from the fitted curve (Zuur et al., 2007), where the closer the point lies to the line, the lower the stress (McCune and Grace, 2002). This stress level is well within the recommended cut off of 20 (McCune and Grace, 2002). The ordination shows a degree of overlap between grazed and ungrazed plots (Fig. 2.2), with the main overlap between absent and low grazing impact levels, while plots with medium-high grazing impact levels are somewhat separate. Plots where grazing is absent are characterised by *Sorbus aucuparia, Rubus fruticosus* agg., *Ilex aquifolium*, while low grazing plots are characterised by *Luzula sylvatica* and *Eurhynchium striatum*. The characteristic species of medium-high grazing plots are *Oxalis acetosella*, *Rhytidiadelphus loreus*, *Agrostis capillaris*, and *Thuidium tamariscinum*.

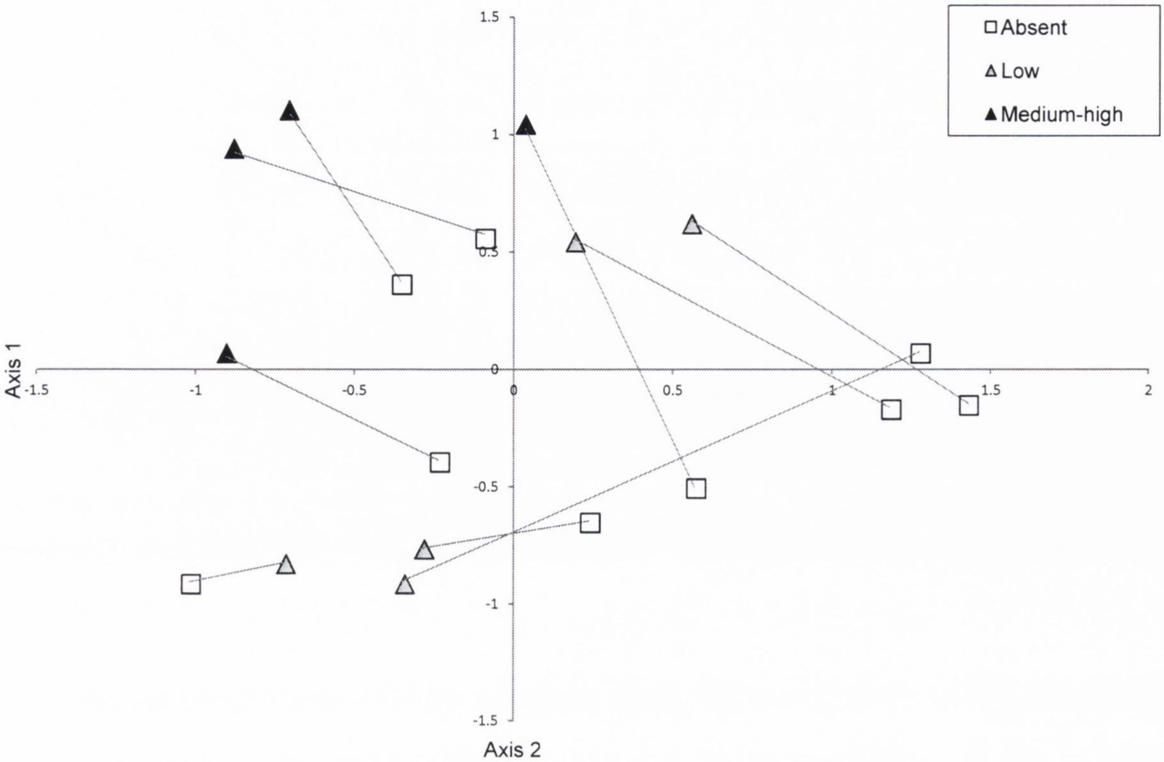

Fig. 2.2 NMS ordination of plots showing grazing impact levels. Open squares = ungrazed plots, filled triangles (grey) = low grazing impact plots, filled triangles (black) = medium-high grazing impact plots. Vectors show pairing of plots. Final stress was 12.78, Monte Carlo Randomisation test results for axis 1 and 2 were 0.036 and 0.004, and instability was ≤0.00001. The r^2 of Axes 1 and 2 were 39.1% and 45.5%, respectively.

The results of the multivariate PerMANOVA indicate a significant difference in vegetation community composition between treatments (grazed and ungrazed) ($F_{1,8}$= 4.95, *p*(perm)<0.001) and paired plots ($F_{8,8}$= 2.65, *p*(perm)<0.001), using the averaged species abundance data matrix. Vegetation community composition was also found to be significantly different among the three grazing impact levels ($F_{2,3}$ =2.6, *p*(perm)<0.009). Although geographical locations (parks) were significantly different from each other ($F_{2,10}$= 3.03, *p*(perm)<0.001), there was no interaction between park and grazing impact level ($F_{3,10}$= 0.84, *p*(perm)=0.674).

The pair-wise comparison indicates a significant difference between the absent and medium-high grazing impact levels (Table 2.2); one other noteworthy comparison was a near significant difference between low and medium-high levels of grazing impact. As a general rule, when the number of unique permutations is <100, the Monte Carlo p-value may provide a better test (Anderson et al., 2008). In this case, the difference between the pair-wise tests which produced <100 unique permutations, are still not significant using the Monte Carlo p-values.

Table 2.2 PerMANOVA results – Pair-wise comparison of grazing impact levels

Grazing impact levels	*T*-stat	*P* (perm)	Unique perms	*P* (MC)	Average similarity
Absent vs. Low	1.4805	0.196	30	0.2017	31.582
Absent vs. Med-high	1.8187	**0.0175***	360	**0.0489***	19.868
Low vs. Med-high	1.7595	0.0693	30	0.1207	29.31

*significant difference at $p<0.05$, *P* (perm) = probability of rejecting H_0 based on permutations, Unique perms = number of unique permutations out of 9999, *P* (MC) = p-value for the Monte Carlo randomisation test.

2.4.2 Life-form, structure height class, and tree regeneration

The cover and species richness of certain life-form groups differed significantly between grazed and ungrazed plots, and also among grazing impact levels (Table 2.3). Graminoid species richness was higher in grazed plots, but when the different grazing impact levels were examined it was only significantly higher than no grazing at medium-high grazing impact levels. Forb cover was significantly higher at medium-high grazing impact levels, compared to both low and absent. Bramble (*Rubus fruticosus* agg.) cover, and climber cover (*Hedera helix* and *Lonicera periclymenum*) were both significantly higher in ungrazed plots.

Total bryophyte cover was higher in grazed than ungrazed plots, but only significantly higher than absent grazing at medium-high grazing impact levels. There were also more species of bryophytes in grazed compared to ungrazed plots, but again this was only significantly higher than absent grazing at medium-high grazing levels. Moss cover and species richness was significantly higher in grazed plots and significantly higher than absent grazing at medium-high grazing impact levels. Total vegetation species richness was significantly higher in grazed plots compared to ungrazed plots.

Vegetation structure height classes differed significantly at the higher categories (50-200cm) (Table 2.3). The vegetation stratum between >50-100cm had greater cover in ungrazed plots, differing significantly between absent and medium-high grazing impact levels. The stratum above this (>100-200cm) also had greater cover in ungrazed plots, where cover significantly differed among all three grazing impact levels with higher values at lower grazing levels.

Tree seedling cover was significantly greater at low grazing when compared to both absent and medium-high grazing impact levels (Table 2.4). The number of seedlings was greater in grazed plots, specifically at low grazing levels. Sapling cover was greater in ungrazed plots, and at low and absent grazing level when compared to medium high. Sapling species richness was greater at low and absent grazing impact levels when compared to medium-high. The number of individual saplings was greater in ungrazed plots, and at low and absent grazing impact levels when compared to medium high.

Table 2.3 Life-form composition and structure height classes in grazed vs. ungrazed plots (averaged data ±SE) compared using paired t-tests, and grazing impact level (averaged data ±SE) compared using GLM post-hoc test. Significant differences are highlighted in bold.

	Cover %					**Species Richness**				
	Ungrazed	Grazed	Absent	Low	Med-High	Ungrazed	Grazed	Absent	Low	Med-High
n	9	9	9-5	5-4	9-4	9	9	9-5	5-4	9-4
Life-forms										
Total vascular	48.9±8.2	41.2±5.4	48.9±8.2	50.1±5.6	30±7.1	12.0±2.0	13.9±1.1	12.0±2.0	12.6±1.6	15.5±1.2
Graminoid	8.2±2.7	13.6±2.9	8.2±2.7	13.8±4.7	13.3±3.6	1.8±0.6	**3.3±0.7***	**1.8±0.6^{A}**	2.2±0.8	**4.8±1^{B}**
Forb	^{L}0.9±0.6	^{L}2.4±0.9	**^{L}0.9±0.6^{A}**	**^{L}0.5±0.2^{A}**	**^{L}4.7±1.1^{B}**	1.4±0.7	1.7±0.4	1.4±0.7	0.8±0.2	2.8±0.3
Fern	6.8±2.4	5.7±1.3	6.8±2.4	6.4±2	4.9±1.5	2.2±0.6	2.9±0.3	2.2±0.6	3±0.4	2.8±0.5
Shrub	7.2±2.7	8.5±3.5	7.2±2.7	11.3±5.2	4.9±4.4	1.0±0.3	1.2±0.3	1.0±0.3	1.2±0.4	1.3±0.5
Bramble^{L}	**2.9±2.0**	**0.3±0.2***	2.9±2.0	0.4±0.4	0.1±0.05	N/A	N/A	N/A	N/A	N/A
Climber	**^{L}5.1±1.7**	**^{L}1.5±0.6***	**^{L}5.1±1.7^{A}**	^{L}2.4±0.8	**^{L}0.2±0.1^{B}**	1.1±0.7	1.1±0.3	1.1±0.7	1.4±0.2	0.8±0.5
Bryophyte	**14.9±5.3**	**36.5±7.3***	**14.9±5.3^{A}**	25±8.8	**51±8^{B}**	6.6±1.3	**11.3±2.3***	**6.6±1.3^{A}**	**7.6±2.5^{A}**	**16±2.7^{B}**
Moss	**14.3±5.1**	**34.5±6.9***	**14.3±5.1^{A}**	24.5±8.4	**46.9±8.4^{B}**	5.7±1.1	**8.9±1.4***	**5.7±1.1^{A}**	6.8±2	**11.5±1.2^{B}**
Liverwort^{L}	0.6±0.3	2.1±0.8	**0.6±0.3^{A}**	**0.5±0.5^{A}**	**4.1±1^{B}**	0.9±0.3	2.4±1.0	**0.9±0.3^{A}**	**0.8±0.6^{A}**	**4.5±1.7^{B}**
Total vegetation	58.4±11	74.2±7.1	58.4±11	69.4±10	80.2±10.9	18.6±2.9	**25.2±2.9***	18.6±2.9	20.2±3.7	31.5±1.7
Structure classes										
0-5cm	5.2±1.5	5.9±1.0	5.2±1.5	4.9±1.3	7.2±1.3					
>5-25cm	8.8±1.5	15.8±2.7	8.8±1.5	17.4±3.2	13.8±5					
>25-50cm	11.8±3.7	10.3±2.8	11.8±3.7	14.7±3.8	4.9±2.5					
>50-100cm^{L}	**8.9±2.8**	**2.4±1.2****	**8.9±2.8^{A}**	4±1.8	**0.4±0.2^{B}**					
>100-200cm^{L}	**11.2±2.1**	**2.5±1.0****	**11.2±2.1^{A}**	**4±1.6^{B}**	**0.6±0.5^{C}**					

*significant at $p<0.05$; **significant at $p<0.01$; ^{L}log (base) transformed for analysis. All data displayed in table are un-transformed. Superscript letters indicate significant post-hoc differences among grazing impact levels ($p<0.05$); same letters are not significantly different.

Table 2.4 Percentage cover, species richness and number of individuals of tree regeneration in grazed vs. ungrazed plots (averaged data ±SE) compared using paired t-tests, and grazing impact level compared using GLM post-hoc test. Significant differences are highlighted in bold.

	Ungrazed	**Grazed**	**Absent**	**Low**	**Med-High**
n	9	9	9	5	4
			Cover (%)		
Seedling^L	1.4±0.4	3.5±1.3	**1.4±0.4^A**	**5.75±1.9^B**	**1.1±0.3^A**
Sapling^L	**11.1±2.7**	**2.3±1.0****	**11.1±2.7^A**	**4.02±1.4^A**	**0.1±0.1^B**
			Species Richness		
Seedling^L	2.8±0.6	3.0±0.4	2.8±0.6	3.2±0.7	2.8±0.3
Sapling	2.1±0.3	1.0±0.3	**2.1±0.3^A**	**1.6±0.4^A**	**0.3±0.3^B**
			Number of individuals		
Seedling^L	**15.9±6.7**	**70.0±24.3***	**15.9±6.7^A**	**104.2±36.2^B**	27.3±16.6
Sapling^L	**19.4±6.3**	**8.7±4.7***	**19.4±6.3^A**	**15.4±7.4^A**	**0.3±0.3^B**

*significant at $p<0.05$; **significant at $p<0.01$; ^{L}log (base) transformed for analysis. All data displayed in table are un-transformed. Superscript letters indicate significant post-hoc differences among grazing impact levels ($p<0.05$); same letters are not significantly different.

2.5 Discussion

It has been shown here that grazing impacts do not have a unified effect on vegetation community composition, life-forms, structure, or regenerating trees. Several of these vegetation variables were not affected by grazing, while others showed significant increases or decreases in species richness and cover. This finding is consistent with what would be expected through optimal foraging strategy of large herbivores (e.g. van Wieren, 1996, Mitchell, 1990, Tanentzap et al., 2009a, Bee et al., 2009).

2.5.1 Community composition

This research has illustrated the effects of grazing impact level on the vegetation communities of semi-natural oak woodlands. The overlap of absent and low grazing impact level plots in the ordination, combined with the results of the PerMANOVA, suggest a gradient in species composition and abundance running alongside a gradient of grazing impact levels. Deer grazing has been shown to alter plant community composition (Putman et al., 1989) through a shift in dominance from woodland specialists to generalists (Pellerin et al., 2010), increased ruderal plants (McEvoy et al., 2006), and a general simplification of the woodland ecosystem (Stockton et al., 2005).

2.5.2 Life-forms

Graminoid cover was greater when grazing was present, particularly at medium-high grazing impact levels. This trend has also been reported in British broadleaved woods (Kirby, 2001) and in northern USA grazed woodland plots (Rooney, 2009), as well as in more open habitats (McNaughton, 1984, Latham and Blackstock, 1998, Cesa and Paruelo, 2011). Tanentzap et al. (2009a) describe the order of palatability of woodland vegetation to deer as:

herbaceous dicots > graminoids > non-graminaceous monocots > woody plants > ferns. Graminoids were found to be the main summer food source for enclosed red deer in a heath habitat (Sherlock and Fairley, 1993). The increased abundance of graminoids in grazed areas may reflect the adaptation of this life-form to grazing pressure (McNaughton, 1984).

This study found forb cover to be greater at medium-high grazing impact levels, while others have found high grazing to reduce their cover, e.g. on islands of British Columbia, Canada (Stockton et al., 2005). Although no effect was detected for shrub cover and species richness in this study, Onaindia et al. (2004) have shown that shrub species, such as *Vaccinium myrtillus* and *Calluna vulgaris* were reduced in cover when grazing was present. Bramble (*Rubus fruticosus* agg.) had higher cover in ungrazed plots. Other studies have noted this trend of decreased cover/abundance of bramble when grazing pressure is present (Kirby and Thomas, 2000, McEvoy et al., 2006, Pellerin et al., 2010, Kirby, 2001) and increases in bramble with herbivore exclusion (Perrin et al., 2011). The work of Harmer et al. (2010) suggests that bramble can form a protective cover for tree regeneration, with varying effects depending on the species, a finding supported by Kelly (2002). On the other hand, van Uytvanck and Hoffman (2009) found that large thickets of bramble, occurring when grazing was absent, reduced the cover of some herb species.

The cover of climbers (*Hedera helix* and *Lonicera periclymenum*) was found in the present study to be greater in ungrazed plots. These findings are supported by those found for *Hedera helix* alone, where it disappeared from grazed woodlands in Belgium (van Uytvanck and Hoffmann, 2009) and where it increased greatly in deer fenced woodland areas in south-west Ireland (Perrin et al., 2011).

Bryophyte species richness and cover were greatest at medium-high grazing impact levels. This is probably due to the reduced competition with vascular ground flora when grazing is present (Mitchell and Kirby, 1990). Few studies have investigated the impact of grazing on bryophyte communities, and even fewer in temperate woodland ecosystems. However, it has been suggested that low levels of grazing may be most appropriate for the conservation of bryophytes in oak woods (Averis, 1990). The presence of herbivory from geese promoted bryophyte species richness in Arctic fens (Jasmin et al., 2008). Takala et al. (2012) likewise found that species richness of bryophytes in semi-natural grasslands was significantly higher in continuously cattle grazed sites compared to those that have been abandoned. Although it has been suggested that vascular plant diversity can be used as a surrogate for bryophytes (Pharo et al., 1999), the opposite has also been found when sheep habitat-preference and density was increased on St. Kilda Island (Virtanen and Crawley, 2010). This may be due, however, to the type of habitat preferred by sheep. The conflicting results previously found, and those reported here, highlight the difficulty in predicting diversity in different taxonomic groups using surrogates, and illustrate the importance of complete or representative survey design. Bryophytes may be very important in the woodland ecosystem; particularly in Ireland which has a relatively depauperate vascular plant flora in relation to that of Britain and Europe (Webb, 1983), with bryophytes and lichens making up an important component of the woodland flora (Kelly, 2006, Kelly and Moore, 1975).

Overall species richness (combined vascular plants and bryophytes) was higher in grazed areas. Although no significant difference was found between low and medium-high grazing impact levels, the average for overall species richness at plots with low grazing is intermediate between that with medium-high levels and no grazing. Vascular plant richness did not differ significantly with grazing in this study, a finding supported by research in the Atlantic oak woods of the Basque country (Onaindia et al., 2004). However, several studies have found differences, with either increases (McEvoy et al., 2006, Perrin et al., 2011) or decreases (Chaideftou et al., 2009, Stockton et al., 2005) in vascular species richness with the presence of grazing. These discrepancies may reflect the combined effects of woodland type, biogeography, herbivores present in the system, and grazing impact level.

2.5.3 Structural height class

The cover of vegetation between 50 and 200cm was greater where grazing impact was low or absent, likely due to the impact of grazing and browsing. Stockton et al. (2005) found that deer grazing presence had a significant negative effect on vegetation cover between 50-100cm, but also for the 0-50cm stratum. By contrast, in another North American study, the 0-50cm stratum was found to have greater cover in the absence of grazers (Collard et al., 2010).The structural differences found at different grazing impact levels may have implications for both the taxa covered in this study and for wider biodiversity. Vegetation structure is important for invertebrates (Woodcock and Pywell, 2010, Bromham et al., 1999, Baines et al., 1994, Oxbrough et al., 2005) and birds (e.g. Sweeney et al., 2010). If the quantity of vegetation within structural height classes can be taken as a surrogate for overall potential biomass, the results from this study are mirrored in others where overall biomass and cover per stratum are greater when large herbivores are absent (McNaughton, 1984, Rooney, 2009, van Uytvanck and Hoffmann, 2009).

2.5.4 Tree regeneration

Many studies have reported the impact of large herbivores on tree regeneration (e.g. Perrin et al., 2006, Pellerin et al., 2010, Tanentzap et al., 2011). With varying degrees of palatability to large herbivores, changes in tree species composition with grazing have been noted (Gill, 2006, Smit et al., 2006, Kuijper et al., 2010b). Research has shown that regeneration is particularly sensitive to deer presence (Gill and Morgan, 2010), and that grazing intensity can reduce overall tree regeneration (van Hees et al., 1996, Barkham, 1978, Latham and Blackstock, 1998, Kuijper et al., 2010b).

This study has shown that, when grazing impact levels were low, tree seedlings were more abundant in both cover and number of individuals than in either ungrazed or medium-high grazed plots. This was also reported by Pellerin et al. (2010) who showed that deer browsing activity was positively correlated with seedling numbers. The large number and cover of seedlings at sites subjected to low grazing did not however translate into large numbers and cover of saplings, likely due to the effects of deer browsing and shading (e.g. Kelly, 2002).

Saplings had greater cover and number of individuals in ungrazed plots compared to grazed ones, and low grazing showed better sapling survival then medium-high grazing impacts. This reduction in sapling survival when grazing is present has been previously noted (Tanentzap et al., 2009b, Takatsuki, 2009, Pellerin et al., 2010, Stockton et al., 2005, Linhart and Whelan, 1980); it has also been found that reducing deer numbers has a significant positive effect on sapling survival (Palmer et al., 2005, Hobbs, 2009). However, regeneration can occur at sites which are subjected to grazing (Pollock et al., 2005), as some species are more susceptible to browsing than others (Bobiec et al., 2011). Results presented here suggest that no grazing and low grazing are most favourable for the regeneration of tree seedlings and saplings, which is somewhat concurrent with the proposed hypothesis. Palmer et al. (2004) note that Atlantic oak woods have the potential to regenerate but, even with complete removal of large herbivores, regeneration is unlikely to be widespread under mature canopy due to the suppression of saplings by shade, a conclusion supported by Vera (2000). Kelly (2002) also concluded that successful oak regeneration may only be expected in unshaded or lightly shaded sites where grazing impact is low.

2.5.5 Management implications

Although high biodiversity is a common theme of natural area management, it may come at a cost to long-term woodland survival if a balance between tree regeneration and ecological richness is not met. Bryophytes add significantly to the plant species richness of woodlands, in particular ancient oak woods, but with a grazing impact level suited to high 'bryo-diversity' and cover, canopy regeneration is likely to be curtailed. In terms of wider woodland biodiversity, vegetation structure found in areas of low grazing may be more suitable to a wider range of flora and fauna than either absent or medium-high grazing impact levels. Low grazing impact resulted in significant increases to the cover and number of individual seedlings, when compared to other grazing levels and no grazing. However, low grazing impact did provide an intermediate level between absent and medium-high for many variables.

Several studies have encouraged the use of large herbivores to manage and enhance woodland ecosystems (Armstrong et al., 2011), with low and varied levels of grazing being recommended (van Uytvanck and Hoffmann, 2009, Kirby, 2001, Perrin et al., 2011). However, where grazing impact was high and a reduction in impact has been achieved, vegetation may be slow to recover (Tanentzap et al., 2012). The potential influence of herbivore predators is also worthy of investigation (e.g. Ripple and Beschta, 2004).

Hayward and Kerley (2009) state that, ultimately, long-term fencing for conservation purposes is an acknowledgement that we are failing to successfully coexist with biodiversity and that fences may be as much of a threat as what they are meant to exclude. Conservation of woodlands requires effective communication of management aims (Tanentzap et al., 2012), with management plans tailored to the woodland, the surrounding area (Austin et al., 2013), and the full range of large herbivores present (Palmer et al., 2004).

The density and impact of large herbivores is not constant over time in natural ecosystems (Vera, 2000) but the intervention of herbivore management tends to focus on targets that maintain consistent herbivore densities. This research has demonstrated that, in a temperate woodland ecosystem, grazing and browsing impacts do not have a unified effect on vegetation community composition, life-forms, structure, or tree regeneration. Consequently, when herbivore densities are being managed, the targets should be tailored to achieve specific aims dictated by the regenerative cycle of the ecosystem, for example, this may be to promote tree regeneration or enhance bryophyte biodiversity. However, the promotion of low grazing impact as optimal for conservation purposes may still be the most appropriate management option, if a balance between ground flora and tree regeneration is to be met.

2.6 Conclusions

The research presented in this study has explored the changes that are occurring to woodland vegetation composition, structure, and tree regeneration at differing grazing impact levels. Here, it was hypothesised that low grazing impact levels would be most appropriate for vegetation. It was found that vegetation life-form groups and tree regenerating do not all respond similarly to this impact level. However, in order to achieve a balance of tree regeneration and optimal biodiversity of flora, this level may still be appropriate. It could be expected that if a low grazing impact level was maintained, woodlands would exhibit increased cover in vegetation between 100-200cm, increased tree seedling cover and number of individuals, and increased sapling cover, species richness, and numbers of individuals. On the basis of these findings, it can be recommended that where woodland conservation and regeneration are desired, low grazing impacts, but not zero grazing, should be maintained. This is most likely to promote regeneration while also maintaining both vascular plant and bryophyte communities. Management practices must be diversified in space (i.e. site specific) and time in order to achieve the overall conservation objectives.

2.7 Acknowledgements

We are grateful to all those involved in the creation of these experimental exclosures and those who have seen to their maintenance down the years, especially Alan Craig and John Cross of the National Parks & Wildlife Service and to successive Managers and Rangers of in the National Parks. The authors would like to thank the BIOPLAN team, in particular Linda Coote, Anke Dietzsch, and Mark Wilson for their input on data analysis and earlier drafts, and Aisling Walsh for her input on species identification. This research has been funded by the Department of Agriculture, Food and the Marine under the National Development Plan 2007 – 2013.

Chapter 3:

Exclusion of large herbivores: long-term changes in plant community composition

Published as:

Newman, M., Mitchell, F.J.G., and Kelly, D.L. 2013. Exclusion of large herbivores: long-term changes in plant community composition. Forest Ecology & Management, DOI: http://dx.doi.org/10.1016/j.foreco.2013.09.010.

3 Exclusion of large herbivores: long-term changes in plant community composition

3.1 Abstract

Semi-natural woodlands are a globally important relict ecosystem for biodiversity, which are now threatened through a range of anthropogenically induced changes, including overgrazing by large herbivores. Fencing to conserve biodiversity is increasingly used as a management tool, so the long-term impacts of large herbivore removal requires investigation. The objective of this research is to investigate the effect of large herbivore exclusion on vegetation, through time, using empirical long-term vegetation data collected over ~40 years. The responses of ground flora communities to this removal will be assessed, and it is predicted that a change in woodland vegetation will occur through time. Plant community composition was surveyed in a network of 7 large-herbivore exclosures, within protected temperate oak woodland in Ireland, at intervals of up to 41 years. Ground flora species abundance was quantified and time since fencing was used to standardise the survey data, with three time groups being derived from this to assess beta diversity changes through time. With total removal of large herbivores from the oak woodland ecosystem, this study has identified significant changes in ground flora composition and abundance, and a general homogenisation of the vegetation community with increasing time since large herbivore removal. Large-scale long-term fencing of oak woodlands should be replaced by large herbivore management programmes, in order to ensure the conservation of diverse woodland ecosystems.

3.2 Introduction

Semi-natural woodlands are a globally important ecosystem (Klenner et al., 2009). At a European scale, 45% of the land area is forested, although only ~26% of this (4% excluding the Russian Federation) is classified as natural (undisturbed by man) and 70% (87% excluding the Russian Federation) as semi-natural (Forest Europe et al., 2011). The functioning of these woodland ecosystems are being impacted through a range of anthropogenically induced vegetation changes (Rackham, 2008), including climate change (e.g. Munson et al., 2012, Rackham, 2008), invasive species (e.g. Santos et al., 2011, Mack et al., 2000, Rackham, 2008), and overgrazing (e.g. Côté et al., 2004, Rackham, 2008). Large herbivore overabundance can impact greatly on the woodland ecosystem and has been shown to drive change in an ecosystem (Côté et al., 2004, Fuller and Gill, 2001) with cascading effects on a range of biotic and abiotic components such as invertebrates (Allombert et al., 2005, Bugalho et al., 2011, Pollard and Cooke, 1994), birds (McShea and Rappole, 2000), small mammals (Bush et al., 2012, Buesching et al., 2011), vegetation (Côté et al., 2004), soil (Mofidi et al., 2012), terrestrial carbon storage (Tanentzap and Coomes, 2012) and ecosystem functioning (Rooney and Waller, 2003). A European Union report stated that overgrazing is among the most important anthropogenic impacts associated with the decline in forest biodiversity (Slingenberg et al., 2009).

Woodland ecosystem dynamics are long-term processes, which are usually studied either empirically at short-term (within a decade) or historically at long-term (within centuries and millennia) scales. Being able to investigate long-term vegetation community data allows for improved understanding of the ecosystem (Silvertown et al., 2010) and has become an increasingly important tool for biodiversity research (Magurran et al., 2010). It is particularly useful for understanding the effects of anthropogenic impacts on plant communities, such as those caused by deer grazing, as it can also provide powerful insight into how deer drive changes within plant communities (Côté et al., 2004). The longer a study is, the more valuable it becomes, allowing for the detection of cumulative or slow-acting impacts (Silvertown et al., 2010). The impact of the removal of deer on aspects of tree regeneration has been covered extensively in temperate native woodlands (**Chapter 2**, Tanentzap et al., 2011, Bobiec et al., 2011, Perrin et al., 2006). However, there has been less focus on ground flora changes with deer removal, particularly over longer time-scales.

Fencing to conserve resources is not a new concept and is one which has developed dual purposes; keeping something out, and keeping something in (Hardin, 1968, Hayward and Kerley, 2009). Fencing for biodiversity conservation is a more contemporary concept, which may ultimately be an acknowledgement of our failure to successfully coexist with biodiversity (Hayward and Kerley, 2009). Long-term fencing to exclude large herbivores, in particular, has been adopted as a defence against over-grazing and has become a method used to implement conservation objectives such as tree regeneration (NPWS, 2005b, NPWS, 2005a). However, initial costs of fencing are high, fences may not be totally effective, maintenance will be required, and there may be a reduction of tourism value in the area (Pérez and Pacheco, 2006). Also, it has been noted that only short-term fencing to achieve management aims may be appropriate (Hester et al., 2000).

Ireland has comparatively low land area of semi-natural woodland relative to the European context, at less than 2% cover, of which oak dominated woods are among the most common (Perrin et al., 2008). Much of these woods have been found to be grazed by large herbivores such as deer and feral goats (Perrin et al., 2008). Although no native deer species have survived from the last glacial cold stage to present day, Ireland was once home not only to the red deer (*Cervus elaphus*) but also the giant Irish deer (*Megaloceros giganteus*) and reindeer (*Rangifer tarandus*) (Woodman et al., 1997). New evidence suggests that red deer were re-introduced in the Neolithic period (Carden et al., 2012) after a period of extinction, while Japanese sika deer (*Cervus nippon nippon*) have been introduced in more recent times. The most common woodland deer species now found in Ireland, red deer and sika deer, have increased in range by 565% and 353%, respectively between 1978 and 2008 (Carden et al., 2010). Other herbivores such as wild boar (*Sus scrofa*), and domestic cattle, sheep, pigs and goats have had a long history in the Irish landscape (Carden et al., 2012, Woodman et al., 1997, Mitchell and Ryan, 2003). This indicates that large herbivore grazing, at varying intensities, has been a part of Irish woodlands for thousands of years (Mitchell, 2005).

The combination of low cover of semi-natural oak woodland habitat and recent dramatic increases in wild herbivores makes Ireland an ideal location to study the management option of long-term herbivore removal, as the conservation status of this oak habitat has been designated as unfavourable (NPWS, 2008). This unfavourable status was given because the structure and functions (including features such as typical species, low-branched trees, and many ferns, mosses, lichens, and evergreen shrubs) necessary for the long-term maintenance of semi-natural oak woodland did not exist and were likely not to exist for the foreseeable future (NPWS, 2008). Although the results of the long-term data used here have already been partially reported from a few individual exclosures (Bleasdale and Conaghan, 1996, Perrin et al., 2006, Perrin et al., 2011, Kelly, 2000), this study is unique as it is the first to unify the analysis of long-term exclosure data in order to examine trends at a wider temporal and spatial scale.

The objective of this research is to investigate the effect of large herbivore exclusion on vegetation, through time, using empirical long-term vegetation data collected over ~40 years. The responses of ground flora communities to this removal will be assessed, and it is predicted that a change in woodland vegetation will occur through time.

3.3 Materials and Methods

3.3.1 Study Sites

The study sites are located within protected ancient oak woodlands in three National Parks in Ireland: Killarney National Park, Co. Kerry; Glenveagh National Park, Co Donegal; and

Wicklow Mountains National Park, Co. Wicklow, located between 52°0'-55°3' N and 6°18'-9°35'W (Fig. 3.1). In addition to national designations, these woodlands are protected as Special Areas of Conservation (SAC) under the European Union's Habitats Directive (E.U., 1992) as they contain representative areas of old sessile oak with *Ilex aquifolium* (holly) and *Blechnum spicant* (hard fern) (Annex 1 EU code 91A0) (nomenclature follows Stace (2010)).

Quantitative data on the large herbivore communities at the three study sites at the time of fencing is largely non-existent. Where quantitative data have been collected, translation into herbivore density is often meaningless (c.f. Putman et al., 2011a, Putman et al., 2011b) as the landscape is highly fragmented, large herbivores can move freely in and out of the National Parks, and large woodland exclosures displace deer habitat. A qualitative assessment of historical grazing levels (20+ years) (as detailed by Forestry Commission Scotland, 2013), adjacent to the long-term fenced plots used in this study, indicated high levels of historic herbivore impact at all control plots, excluding one plot, which indicated low historic grazing impacts; likely due to the influence of a regional road (single carriageway with two lanes) located 10m from the plot (**Chapter 2**). High historic grazing levels were identified using indicators such as: vegetation forming a low sword; dominance of grasses and bryophytes; absent or limited understorey; and a prominent browseline (Forestry Commission Scotland, 2013). Areas with low historic grazing levels were characterised by indicators including: dense *Vaccinium myrtillus*; frequent *Rubus fruticosus* agg. and *Lonicera periclymenum*; and an understorey of tree species with low growing branches (Forestry Commission Scotland, 2013).

A detailed paired comparison of the vegetation between long-term fenced plots and adjacent contemporary control (grazed) areas is described in **Chapter 2**.

Mean annual rainfall (between 1961-1990) at the 3 study sites was in excess of 1600mm, while the mean daily min of the coldest month and the mean daily max of the warmest month were 2.8°C and 16.1°C, respectively (available from www.met.ie). The eastern half of the country is drier than the west; however, the coastal distribution of mountains results in oceanic conditions still being found in eastern counties (e.g. Wicklow and Antrim) (Ratcliffe, 1968). The predominant soil type at the sites is podzolic, with a current (2011) log mean pH (±SE) of 3.96±0.1 (top 10cm) (M. Newman, unpublished data). The study sites are in upland areas, although the woodland study plots ranged in altitude between 35 and 175m above sea level.

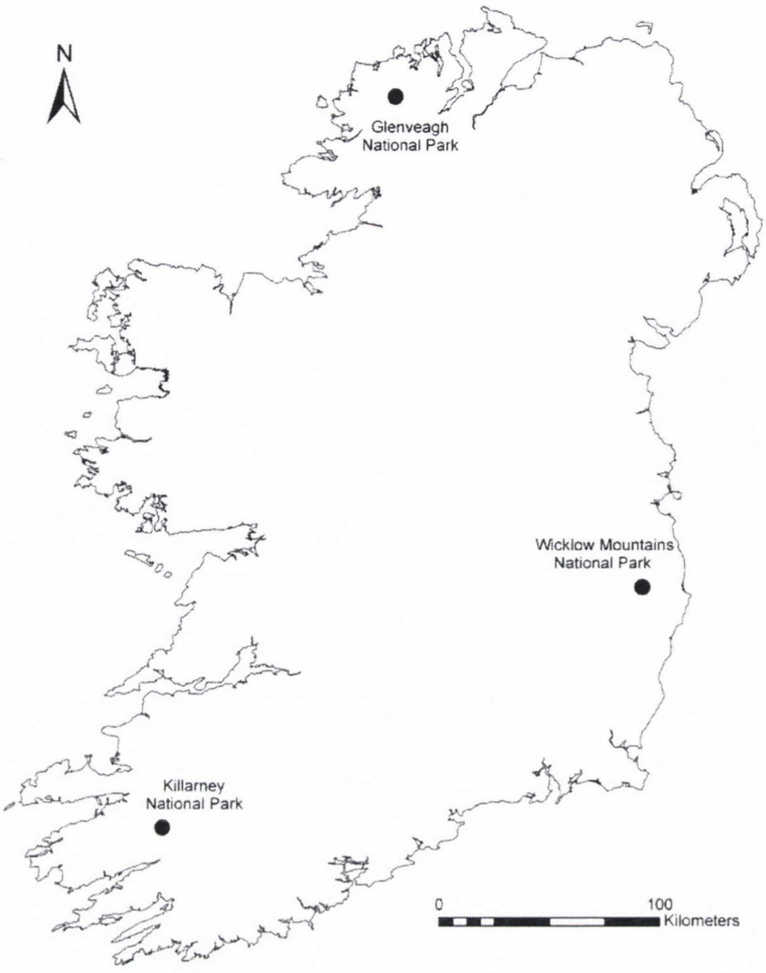

Fig. 3.1 Map of Ireland showing study sites

3.3.2 Experimental design, data collection and standardisation

The data used for this study were collected over a 41 year period (1969-2011) from within seven deer exclosures established in the three National Parks between 1969 and 1988 (Table 3.1). Historic data are only available from within the exclosure and, consequently, there are no control data available. The cover of each vascular plant species (excluding tree species), occurring as part of the woodland ground flora (i.e. ≤2m in height), was sub-sampled in varying sizes of sub-plot with varying degrees of replication (Table 3.2). The cover of species within a plot were averaged over the sub-plot replicate records. Species cover was collected using the Braun-Blanquet, Domin, and percent scales (Kent, 2010). In order for meaningful comparisons to be made, all cover data were converted to percent using the Domin 2.6 (Currall, 1987) method from values recorded in Domin scale, and the median percent value of each of the ranges in Braun-Blanquet scale. The Domin 2.6 conversion uses a simple function (cover = (Domin score)$^{2.6}$/4) to provide a closer approximation to the functional relationship between Domin scores and percent cover over the entire Domin range (Currall, 1987).

As there is variation in the year in which the exclosures were established and surveyed, a standardisation variable of time since fencing (years) has been used. This has been used to sequentially order sample point by time since fencing instead of year of survey, resulting in 33 sample points (Table 3.2).

Table 3.1 Study exclosures

Exclosure code	Exclosure size (m^2)	Year fenced	National Park
K1	1090	1969	Killarney
K2	5560	1972	Killarney
W1	400	1970	Wicklow
W2	400	1970	Wicklow
W3	400	1970	Wicklow
G1	~26000[a]	1988	Glenveagh
G2	~27000[a]	1975	Glenveagh

[a] Large area of exclosure extended into non-woodland habitat, wooded area ~11000 m^2. First letter of exclosure code indicated National Park location.

Table 3.2 Plots surveyed, survey year, time since fencing and time group, and replication

Survey plot	Year surveyed	TSF	Time group	Sub-plot replication
G1-1[a]	1996	8	1	1x4m^2
G1-2[a]	1996	8	1	1x200m^2
G1-3[a]	1996	8	1	1x4m^2
G1[a]	2011	23	2	20x1m^2
G2-1[b]	1987	12	1	1x24m^2
G2-1[b]	1996	21	2	1x24m^2
G2-2[b]	1996	21	2	1x4m^2
G2[b]	2011	36	3	20x1m^2
K1	1969	0	1	9x1m^2
K1	1974	5	1	10x1m^2
K1	1980	11	1	15x1m^2
K1	1985	16	2	15x1m^2
K1	1993	24	2	15x1m^2
K1	1997	28	2	15x1m^2
K1	2001	32	3	20x1m^2
K1	2010	41	3	20x1m^2
K2	1972	0	1	10x8m^2
K2	1973	1	1	10x8m^2
K2	1981	9	1	10x8m^2
K2	1988	16	2	10x8m^2
K2	1994	22	2	10x8m^2
K2	2007	35	3	12x1m^2
K2	2011	39	3	20x1m^2
W1	1976	6	1	50x1m^2
W1	1980	10	1	50x1m^2
W1	2002	32	3	50x1m^2
W1	2010	40	3	20x1m^2
W2	1976	6	1	50x1m^2
W2	1980	10	1	50x1m^2
W2	2002	32	3	50x1m^2
W2	2010	40	3	20x1m^2
W3	1967	6	1	50x1m^2
W3	1980	10	1	50x1m^2

TSF = Time since fencing; [a]plot located within G1 exclosure ,[b]plot located within G2 exclosure; . First letter of exclosure code indicated National Park location.

3.3.3 Data Analysis

Species composition of each sample point was analysed using a non-metric multidimensional scaling (NMS) ordination of averaged species abundance data in PC-ORD 6.08 (McCune and Mefford, 2011). This ordination technique was used to view the relationships among plots through time by reducing the dimensionality of the data space (McCune and Grace, 2002). The ordination was run using the Sørensen (Bray-Curtis) distance matrix, with a maximum of 500 iterations (250 with real data and 250 with randomised data), an orthogonal rotation, and a Monte Carlo randomisation test, for a data matrix of 33 plots and 55 plant species.

In order to test for a significant difference in vegetation composition over time, a permutational multivariate analysis of variance (PerMANOVA) (Anderson, 2001a) was conducted. This procedure provides a multivariate equivalent to the *F*-ratio, calculated through a distance or dissimilarity matrix by partitioning the total sum of squares and expectations of mean squares, according to the nature of the experimental design (Anderson, 2001a, Anderson et al., 2008). A *p*-value, based on permutations, is then calculated (Anderson, 2001b, Anderson and ter Braak, 2003). The test was performed in PERMANOVA+ 1.0.3, an add-on function to PRIMER 6.1.13 (PRIMER-E, 2009). This test was carried out with time since fencing (TSF) as a continuous co-variable and site (National Park) as a random factor in a crossed design, using a Sørenson (Bray-Curtis) distance matrix on a total of 9999 permutation of residuals under a reduced model, with type III (partial) sums of squares.

Average multiple-site dissimilarity measures were used to assess changes to vegetation community turnover and nestedness through time. In order to compare changes in diversity through time, the data points were divided into three a-priori age groups. These groups were delimited by gaps in the frequency histogram of survey points on a time since fencing scale. The three natural groups in the data represent the time since fencing groups of: time 1 (0-12 years, *n*=16), time 2 (16-28 years, *n*=8), and time 3 (32-41 years, *n*=9). Sørensen and Simpson, with their many variations, are some of the most used measures of beta diversity (Baselga, 2010). Issues relating to the dependence of beta diversity measures on species richness (see Anderson et al., 2011) are not a concern here, as preliminary analysis indicated that species richness varies little between time groups. Here, the multi-site dissimilarity measures (based on Baselga, 2010) of Simpsons beta (β_{SIM} - species turnover) and Sørensen beta ($\beta_{SØR}$ - species turnover and nestedness – subsets of the same species occurring among sites) are used to highlight dissimilarities in species turnover and nestedness among time groups. The Sørensen (Bray-Curtis) matrix calculated for the ordination analysis has also been used to compare species abundance and time groups. This measure is similar to $\beta_{SØR}$ but also takes plant abundance into account. The β_{SIM} and $\beta_{SØR}$ diversity measures were calculated using the ecodist package (Goslee and Urban, 2007) in R (R Core Team, 2012), and the Sørensen (Bray-Curtis) measure was calculated in PC-ORD 6.08 (McCune and Mefford, 2011).

Differences among the time groups and diversity measures were analysed using a General Linear Model (GLM), with time group as a fixed factor and site (National Park) as a random factor, with a Tukey HSD post-hoc comparison test (Hsu, 1996) in SPSS (2010). To ensure comparability between time groups in the analysis and compliance with the assumptions of GLM, the Levene's test of homogeneity was carried out in SPSS (2010). Log_{10} transformations were carried out where necessary.

To analyse the contribution of individual species abundances to differences between time groups, a similarity percentage routine (SIMPER) was carried out in PRIMER 6.1.13 (PRIMER-E, 2009). The Sørenson (Bray-Curtis) distance matrix was used to decompose dissimilarities within and between time groups (Clarke and Gorley, 2006). A two way crossed design using time group and site was used to allow for the selection of species which contribute to the different times occurring in all Parks.

3.4 Results

3.4.1 Community composition, diversity, and heterogeneity

The NMS output sample points exhibit some grouping by site (National Park) but, with time, all points move towards the centre of ordination space (Fig. 3.2 A). This is the same trend with plots which are connected through resurvey and time; they move closer together with increased time. Plots recorded closer to the time of fencing (i.e. low TSF) exhibit the widest dispersion, with the vast majority of the plots recorded within the first 12 years of fencing positioned on the periphery of the ordination. As the TSF increases, plots move towards the centre of ordination space, exhibiting some separation by site. The trajectory of resurveyed plots through time illustrates that, with resurvey through time, plots do not all go in the same direction but mostly trend towards a similar end point (Fig. 3.2 B). Plots at the periphery of the ordination are characterised by *Oxalis acetosella, Blechnum spicant*, *Anthoxanthum odoratum* and *Agrostis capillaris,* while plots at the centre are characterised by *Luzula sylvatica, Rubus fruticosus* agg., *Lonicera periclymenum and Vaccinium myrtillus.* Analysis of the plant community composition and time since fencing (TSF), using PerMANOVA, indicates that community composition differs significantly with TSF (p<0.0001), among sites (p<0.0001), and also with the interaction between TSF and site (p=0.0021). When species presence/absence was tested instead of abundance with PerMANOVA, community composition differed significantly with TSF (p=0.01) and site (p=0.001), but the interaction effect was not significant.

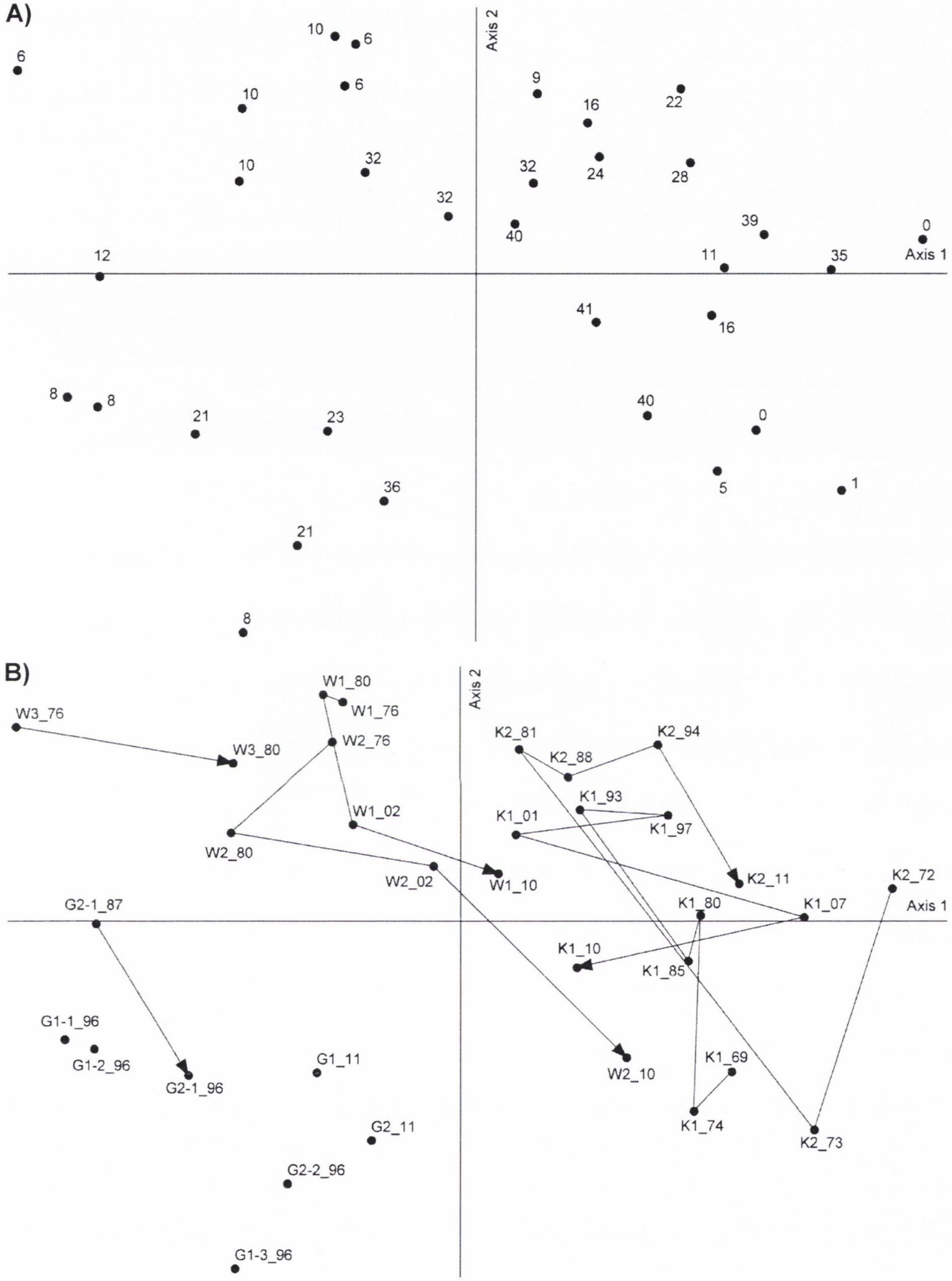

Fig. 3.2. NMS ordinations of average species abundance per plot, displaying A) time since fencing (TSF) in years, and B) plot code with survey year, and successional vectors. Successional vectors link the trajectory of plots through time; plots without vectors are once off survey plots. The most suitable ordination was a 2-dimensional solution, with a final stress was 15.78 and an instability of <0.00001. The r^2 of Axis 1 and 2 were 52.8% and 21.2%.

The beta diversity results show a similar pattern to the ordination, where an increase in community composition similarity is seen through time (Fig. 3.3). Sørensen's distance indicated that plots from the three time groups were not significantly different, but there is a decreasing trend with time towards similarity in terms of species turnover and nestedness, however, the interaction between time group and site was significant (*p*=0.001). Sørensen's beta diversity (β_{SOR}) shows that all three time groups are significantly different from each other, with an increase in similarity among plots with time. Simpson's beta diversity (β_{SIM}) indicated that plots from times 2 and 3 are significantly more similar to each other than to time 1, in terms of species turnover.

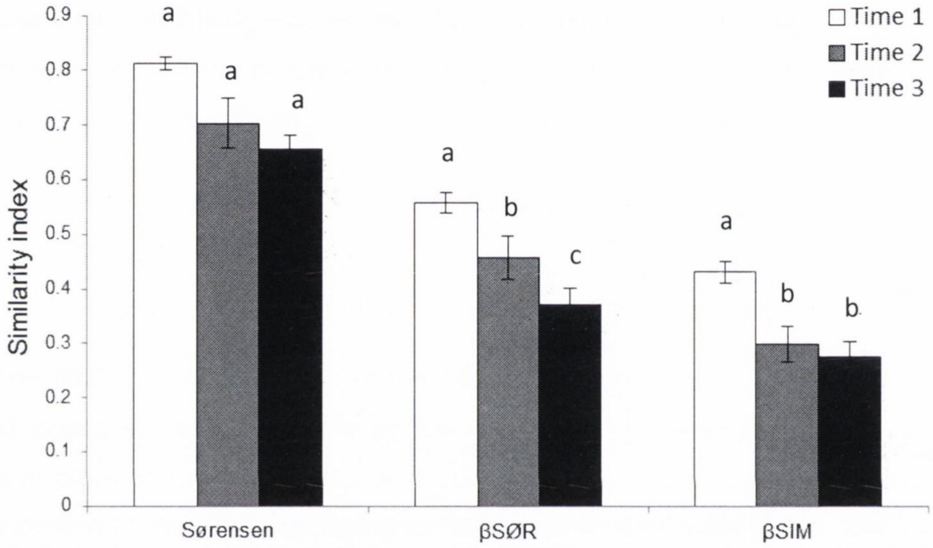

Fig. 3.3. Comparison of average dissimilarity measures (±se) among time groups, where 0=complete similarity and 1=complete dissimilarity. Significant difference (Tukey post-hoc, p<0.05) between lowercase letters. Time 1=0-12 (n=16) years, time 2=16-28 years (n=8), and time 3=32-41 years (n=9).

3.4.2 Species abundance changes

Analysis of species abundance dissimilarities over time has highlighted some characteristic differences between the time groups (Table 3.3). Group dissimilarity is greatest between times 1 and 3, while times 2 and 3 are most similar. The abundance of *Luzula sylvatica* and *Pteridium aquilinum* are important species contributing to the dissimilarity between each time group comparison, while the abundance of *Luzula sylvatica* and *Vaccinium myrtillus* contribute greatest to group dissimilarities in each comparison.

Table 3.3. Time group dissimilarity and species abundance dissimilarities between time groups. Time 1=0-12 (n=16) years, time 2=16-28 years (n=8), and time 3=32-41 years (n=9)

Time group Comparison	Mean group dissimilarity	Species	Mean abundance (%) per time group		Contribution to dissimilarity (%)
1 vs 2	65.4		1	2	
		Luzula sylvatica	17.74	18.31	39.31
		Hedera helix	0.17	3.03	7.56
		Pteridium aquilinum	9.51	1.95	5.92
1 vs 3	69.64		1	3	
		Vaccinium myrtillus	16.84	13.68	17.56
		Luzula sylvatica	17.74	21.74	17.16
		Pteridium aquilinum	9.51	4.99	8.84
2 vs 3	52.55		2	3	
		Luzula sylvatica	18.31	21.74	40.25
		Vaccinium myrtillus	6.09	13.68	23.64
		Pteridium aquilinum	1.95	4.99	6.76

3.5 Discussion

The results of this study have shown that species abundance and assemblages change with time since large herbivores exclusion. A homogenisation of the ground flora is seen when comparing time groups, with the abundance of four key species accounting for the differences between these time groups.

Plant community composition and abundance was shown to change with time since large herbivore exclusion. Although the composition and abundance of species is changing at all sites, with TSF, not all sites are responding in the same way. This may be explained visually by studying the ordination plot (Fig. 3.2B). It is clear that vegetation plots are moving in ordination space through time, and also that the plots from some sites are moving more than others. Although the direction of movement in ordination space differs, plots trend towards the centre with increased TSF. Analysis of the species presence/absence matrix gave similar results to the analysis of species abundance. However, all sites responded in a similar way, indicating that species turnover is happening in the same way at all sites. The species which characterise plots at the centre of the ordination space (*Luzula sylvatica, Rubus fruticosus* agg., *Lonicera periclymenum and Vaccinium myrtillus*) may do so because of their sensitivity to large herbivore browsing/grazing, which is discussed in more detail later.

The role played by large herbivores in maintaining the heterogeneity of an ecosystem has been previously noted (Hester et al., 2000, Vera, 2000), and changes in temperate woodland vegetation composition with time following removal of grazing have been identified (Putman et al., 1989, Price et al., 2010). Time lags in the response of species density to time since large herbivore removal have been noted, with 14 years being the time before a significant difference was detected (Price et al., 2010), a trend reiterated by a study of deer reductions in New Zealand woodlands (Tanentzap et al., 2012). These general vegetation changes have been described as the recovery and development of tall-growing browse-sensitive species after 12 (Anderson and Katz, 1993) and 32 (Perrin et al., 2011) years. However, after 8 years of deer exclusion, Webster *et al.* (2005) found no recovery of browse-sensitive species, illustrating the different conclusions which can be drawn depending on the time scale of such experiments and highlighting the value of long-term datasets. Having datasets which extend for multiple decades, as the one presented here, allows the tracking of vegetation change and the identification of trends on a larger temporal scale. A potential drawback of working with long-term datasets is that experimental design principles, which are paramount now, may not have been as important decades ago. In this case, control plots were not established when the experiment began. It could be argued that the wider landscape is changing in the same way over time as in the exclosures, however, a comparison of these exclosures with contemporary adjacent controls has shown that significant differences, in the vegetation composition and cover, are present between exclosures (ungrazed) and control (grazed) plots (**Chapter 2**).

Using beta diversity as a proxy for plot dissimilarity, an increase in vegetation composition homogenisation is seen with increased time since fencing. This indicates that woodland vegetation is becoming more similar with time when large herbivores are excluded, possibly due to increased dominance of certain species when grazing disturbance is removed.

The beta diversity measures illustrated that homogenisation of the ground flora was occurring through increasing time groups. More specifically, a reduction in turnover (β_{SOR}) of plant species among plots at each increasing time group. From the time group analysis it appears that turnover and species abundance is not significantly different among the groups, although the decreasing trend with increasing time group can also be seen here. The proportion of species shared among plots within a time group (β_{SIM}), decreased significantly between 16 and 41 years since fencing, compared to recently fenced plots (0-12 years). This is an important issue for biodiversity conservation as the results indicate a potential reduction in the number of plant species found in areas where large herbivore grazing has been removed for long periods (e.g. >12 years). An increase in community homogeneity was also noted in previous studies on some of the Killarney research sites. Species richness and Simpson's diversity index in the K2 plot peaked after 10 years of exclusion, trending downwards thereafter, with the mean number of vascular plant species and total number of angiosperm herbs falling below what they were prior to fencing, after 26 years (Kelly, 2000).

Looking at 32 years of deer exclusion data for the K1 plot, Perrin *et al.* (2011) noted that there appeared to be an initial increase in species diversity, followed by a long-term decline. It is clear that changes are occurring in the vegetation with increasing time since fencing, but what species are driving this change? Of the four key species identified as the greatest contributors to species abundance difference between the time groups, two species (*Luzula sylvatica* and *Pteridium aquilinum)* contribute to the differences between all the group comparisons. The mean abundance of *L. sylvativa* was shown to increase with time, a finding supported by other studies of the plots in Killarney National Park after 26 years (Kelly, 2000) and 32 years (Perrin et al., 2011) of exclusion. The dominance of *L. sylvatica* following cessation of grazing was also noted by Mitchell and Kirby (1990). This species may not respond to large herbivore removal in the same way as other graminoids because reductions in graminoids were noted after 16 years in woodland exclosures in Wisconsin (Rooney, 2009) and after 22 years in England (Putman et al., 1989). The decline was also noted in the Scottish uplands after 9 years of large herbivore removal (Miller et al., 2010). The increased abundance of graminoids in grazed areas may reflect the adaptation of this life-form to grazing pressure (McNaughton, 1984), as graminoids have been identified as the main summer food source for enclosed red deer (Sherlock and Fairley, 1993). The increasing dominance of *L. sylvatica* with large herbivore removal may be due to its sensitivity to grazing (Kirby, 2001, Rodwell, 1991). This species may also be out-competing other graminoids, as indicated by the reduction in graminoid species richness seen when these long-term plots were compared to grazed areas (**Chapter 2**).

The abundance of the climber *Hedera helix* L. was shown to be one the main differentiating species between time group 1 and 2, with an increasing cover when large herbivores were removed. This increase is likely due to the absence of herbivores, as this species can be considered grazing sensitive. This finding is supported by an increase in frequency of *Hedera helix* with time since fencing in an English woodland (Putman et al., 1989), and also by the decreased cover of climbers (*Hedera helix* and *Lonicera periclymenum*) noted when exclosed plots were compared with grazed plots in Ireland (**Chapter 2**). Few shrub species were recorded in this study; however, *Vaccinium myrtillus* has been identified as an important species differentiating species composition through time, showing a reduction in abundance from time 1 to 2, with a subsequent rebound with increased time since fencing. This initial reduction may be counterintuitive as previous studies described the species as browse sensitive and noted increased abundance when grazing was absent (Perrin et al., 2011, Onaindia et al., 2004). The abundance of the fern, *Pteridium aquilinum,* shows a similar trend as *Vaccinium myrtillus,* where a decline from time 1 to 2 was followed by a slight rebound in time 3. *P. aquilinum,* the only fern species recorded from a long-term woodland deer exclosure, showed a decreasing trend in frequency after 22 years (Putman et al., 1989). Ferns may be negatively impacted by large herbivore exclusion as a declining trend in overall fern abundance was noted after 32 years of deer exclusion by Perrin *et al.* (2011), while the loss of the locally frequent (Page, 1997) Tunbridge filmy-fern (*Hymenophyllum tunbrigense*) was recorded after 26 years of herbivore exclusion in Killarney (Kelly, 2000). This may be a result of increased competition from rebounding browse sensitive plant species.

3.6 Conclusion

With total removal of large herbivores from the oak woodland ecosystem, this study has described significant changes in ground flora composition and abundance, and a general homogenisation of the vegetation community with increasing time since large herbivore removal. In temperate oak woodlands which have evolved with large herbivores, complete removal of herbivores may cause more long-term damage (e.g. reduction in vegetation community heterogeneity) then it would prevent. Removal is undesirable other than for short-term objectives to be completed (Hester et al., 2000), because large herbivores perform integral ecosystem functions, such as disturbance and driving succession through selective herbivory, within woodlands (c.f. Vera, 2000). Short-term fencing, directed at increasing tree regeneration or biodiversity maintenance for example, could still be used with the knowledge that community homogenisation may take place after 12 years. It can therefore be concluded that the findings of this research, combined with those of others (e.g. Perrin et al., 2011, Kelly, 2000), suggest a general homogenisation of temperate oak woodlands will occur with total large herbivore removal. It is recommended that large-scale long-term fencing of oak woodlands be replaced by large herbivore management programmes, in order to ensure the conservation of diverse native woodland ecosystems. These management programmes should be implemented through adaptive management where large herbivore impacts are monitored and adjusted, through localised culling, to achieve specific long-term management objectives such as landscape-level heterogeneity.

3.7 Acknowledgements

We are grateful to all those involved in the creation of these experimental exclosures, especially Mr Michael Neff, Mr Dan Kelleher, and the late Professor Bill Watts. We also thank those who have seen to the maintenance of these exclosures down the years, particularly the successive managers and rangers of the National Parks, and to all those who carried out the fieldwork. For support of this present study, we are grateful in particular to: Dr

Kathryn Freeman, the late Mr Paudie O'Leary, and Mr Patrick Dawson of Killarney National Park; Mr Dave Duggan and Mr Pat Warner of Glenveagh National Park; and Mr Wesley Atkinson and Mr Damian Clarke of Wicklow Mountains National Park. The authors would like to thank the BIOPLAN team, in particular Dr Anke Dietzsch for her input into analysis and Dr Linda Coote for her input into analysis and comments on earlier drafts. We would also like to thank the National Parks & Wildlife Service for access to sites and, for support at successive stages of this study, in particular, Dr Alan Craig and Dr John Cross. We would also like to thank the anonymous reviewers for improving this manuscript with their detailed and helpful comments. This research has been funded by the Department of Agriculture, Food and the Marine under the National Development Plan 2007 – 2013.

Chapter 4:

Can taxonomic surrogacy be used when grazing stressors are present: a case study of temperate oak woodland vegetation and spiders.

To be submitted as:

Newman, M., Fuller, L., Coote, L., Dietzsch, Mitchell, F.J.G., Kelly, D.L. Can taxonomic surrogacy be used when grazing stressors are present: a case study of temperate oak woodland vegetation and spiders. To be submitted to Ecological Indicators.

4 Can taxonomic surrogacy be used when grazing stressors are present: a case study of temperate oak woodland vegetation and spiders

4.1 Abstract

Taxonomic surrogacy has been widely used in ecology as a shortcut to monitor and address conservation problems. Here, the aim is to evaluate the usefulness of within and between taxa surrogacy for the ecological assessment of temperate woodlands exposed to grazing.

A case study of vegetation and ground spider assemblages in semi-natural temperate oak woods was used to test the effect of large herbivore grazing on within-taxa and between-taxon surrogacies. Six year old deer exclosures were used, with paired vegetation plots and spider transects surveyed to assess the community composition, species richness, and cover/relative abundances in both exclosures and grazed areas.

Result from the case study indicated that correlations testing surrogacies within vegetation and spider group categories displayed difference relationships in exclosure and grazed areas. Relationships of community surrogacy between vegetation and spider were found within exclosures, but not in grazed areas. Species indicator values were higher in exclosures for both vegetation and spiders, with only one species (the spider *Monocephalus fuscipes*) identified as an indicator for both grazed and ungrazed communities.

The usefulness of within and between taxa surrogacy for the ecological assessment of areas exposed to stressors, such as varying intensities of grazing, needs to be carefully considered. The presence of a stressor or factor of disturbance can alter the relationship among and between taxa. It is recommended that a full evaluation of the factors potentially impacting the taxonomic communities, and their relationships, be included in any proposals of surrogacy for the assessment and management of ecological systems.

4.2 Introduction

4.2.1 Terminology and use

Taxonomic surrogacy has been widely used in ecology as a shortcut to monitor and address conservation problems (Caro and O'Doherty, 1999). There has been some confusion and synonymy in the literature regarding the description of surrogate and congruent relationships. Caro and O'Doherty (1999) provide clarification on the three main uses of surrogacy: flagship species, umbrella species and indicator species. The use of flagship species has mainly been for public and political attention, while umbrella species have primarily been used to determine a desired habitat or size of protected area (Caro and O'Doherty, 1999, Western, 1987, Wilcox, 1984, Bifolchi and Lodé, 2005). Indicator species are defined by Landres et al (1988) as "organisms whose characteristics (e.g., presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest". The use of specie congruence in the literature appears to be associated with cross- and multi-taxonomic relationships (e.g. Heino, 2010, Buse and Griebeler, 2012) and is considered a synonym of surrogate relationships here.

It is a major challenge to identify, with confidence, reliable surrogate indicator taxa (Lund and Rahbek, 2002), in order for them to be useful for biological assessments in conservation biology (Caro and O'Doherty, 1999). Indicator species may bear no direct or simple cause and effect relationship to the taxonomic group of interest (Landres et al., 1988). Several approaches have been taken for biodiversity assessments including: species-specific surrogacies (Carrascal et al., 2012, Carignan and Villard, 2002, Hoare et al., 2013), surrogacies at higher taxonomic levels (Bertrand et al., 2006, Bevilacqua et al., 2012), life-form group surrogacies (Pharo et al., 1999), and cross-taxonomic surrogacies (Negi and Gadgil, 2002, Christopher and Cameron, 2012, Coote et al., 2013).

Taxonomic surrogacies can be made across a wide range of scales, e.g. from the surrogacies between soil micro-organisms and soil macro-fauna (Keith et al., 2012) to relationships between deer and vegetation (e.g. Chapter 2, Côté et al., 2004). Issues of scale need to be taken into account when assessing surrogate relationships between and among taxa (c.f. Lindenmayer and Fischer, 2003), as it is unlikely that relationships between taxa at different scales are reliable or homogeneous across landscapes.

4.2.2 Stressors, disturbances and surrogacies

Nieme and McDonald (2004) warn that the use of ecological surrogacies requires clear objectives, spatial and temporal scale recognition, assessment of statistical variability, coupled with economic and social indicators, and linkages with specific stressors. It is possible that factors of stress and disturbance alter the assemblages of species and in-turn impact on the relationships among and between taxa (Ficetola et al., 2007). Surrogacy and relationships between taxonomic variables can be altered for many reasons including: habitat fragmentation and loss, alien species invasion, changing management regimes, climate change, grazing, and all the possible interactions between these factors.

The specific stressor of interest here is large herbivore grazing. Grazing as a driver of disturbance was used in early descriptions of the intermediate disturbance hypothesis (Grime, 1973) and has been show to drive change in an ecosystem (Côté et al., 2004) with cascading effects on a range of biotic and abiotic components such as invertebrates (Allombert et al., 2005, Bugalho et al., 2011, Pollard and Cooke, 1994, Hoffmann, 2000), birds (McShea and Rappole, 2000), small mammals (Bush et al., 2012, Buesching et al., 2011), vegetation (Chapter 2, Chapter 3, Côté et al., 2004), soil (Mofidi et al., 2012), terrestrial carbon storage (Tanentzap and Coomes, 2012) and ecosystem functioning (Rooney and Waller, 2003). This results in a potentially unique situation in every habitat, as stressors will impact on the physical environment and the communities of species present. Although several studies have noted the impact of grazing on taxonomic surrogacies, these are mostly confined to agricultural systems (e.g. Debinski et al., 2011, Keith et al., 2012, Oertli et al., 2005, Sauberer et al., 2004), tropical habitats (e.g. Williams-Linera et al., 2005, Baldissera et al., 2004), and plantation forests (e.g. Coote et al., 2013, Irwin et al., 2014, Smith et al., 2008). Few studies have investigated these potential impacts in semi-natural temperate woodlands.

4.2.3 Surrogacies in temperate woodlands

Semi-natural woodlands are globally important ecosystems (Klenner et al., 2009) and these resources require assessment and monitoring to ensure effective conservation and management. Temperate broadleaved woodland has declined drastically during the last millennia and has been identified as a habitat of conservation priority (Hannah et al., 1995). The limited peer-reviewed studies focusing on species surrogacy in temperate woodlands have assessed both within-taxa and between-taxa relationships over several taxonomic groups.

Within-taxa surrogacy relationships were assessed for plants by Norden et al. (2007) in oak rich temperate woodlands in southern Sweden. They found that significant correlative relationships were found between lichen indicator species and the number of red list plant species. It was also found that red list lichens were correlated to total lichen species richness, and that plant indicator species were useful surrogates for total bryophyte species richness (Norden et al., 2007). In a study of saproxylic beetle surrogacy in a range of temperate woodland types in France and Belgium, Sebek et al. (2012) showed that, in general, surrogacy did not vary significantly across wide environmental gradients. However, they did find that the number of rare species and the species richness of single beetle families were weakly surrogated with total beetle richness. Within taxa surrogacy potential has also been tested for woodpeckers as surrogates for wider forest bird communities in temperate Polish forests (Mikusiński et al., 2001). A positive relationship between woodpecker species richness and a) the number of total bird species, b) the number of forest specialist birds, and c) the number of forest generalist birds, was found (Mikusiński et al., 2001). Mikusiński et al. (2001) recommend that in regions of Europe where bird data are not available, species such as woodpeckers be used as surrogates for assessing forest bird diversity at landscape scales. However, this recommendation may not be as widely applicable as stated, as the fragmented temperate forest and woodland in Western Europe contain less forest specialist species, and these relationships may not exist.

Between or cross taxonomic studies of surrogacy in temperate woodlands have also focused on a range of scales and taxa. Amphibian, reptile, grasshopper, vascular plant, and moss species richness were all significantly correlated with each other in a study conducted in temperate woodland in southwest Germany (Buse and Griebeler, 2012). However, when these relationships were tested for validation using data collected from an adjacent area, several of the significant correlations were not found. This difference in findings between sites may highlight site effects and potential variances in ecosystem drivers. Cross taxonomic relationship s have also been noted between large herbivores, such as deer, and plants (Chapter 2, Chapter 3, Pellerin et al., 2010, Perrin et al., 2011). The presence of deer has been shown to affect the abundance and frequency of plant species such as Bramble (*Rubus fruticosus* agg.) (**Chapter 2**).

4.2.4 Research rationale and aims

An understanding of taxonomic relationships is necessary for efficient biological assessment and for the development of effective conservation measures, as focusing biological surveys and management on a small number of species has potential to be both time efficient and effective (Mikusiński et al., 2001, Ficetola et al., 2007). However, the impact of disturbing and threatening processes on the relationships between and among taxa has seldom been tested (Ficetola et al., 2007). From a review of the literature relating to this in temperate woodland, the following knowledge gaps have been identified:

1. The impact of grazing on relationships within and between taxa in temperate woodlands
2. The usefulness of surrogacy for ecological assessment in temperate woodlands

Ireland is a suitable location to investigate the effect of grazing on taxonomic surrogacies, as populations and ranges of wild large herbivores, specifically deer, have greatly expanded in recent decades (Carden et al., 2010).

The objective of this research is to investigate surrogacy among and between taxonomic groups in temperate semi-natural oak woodlands, and to assess whether spiders and vegetation have similar responses to wild herbivore grazing. Through the use of a case study of vegetation and ground-dwelling spider responses to large herbivore grazing in the temperate oak woodland community, this objective will be fulfilled by testing the specific hypothesis: within and between taxa surrogacy relationships are significantly impacted by large herbivore grazing. The findings of this study will have implications for the surveying and monitoring of biodiversity in temperate woodlands, the use of taxonomic indicator groups, and for implementation into management practices.

4.3 Case study: spiders and vegetation surrogacies in the temperate oak woodlands of Killarney National Park, Ireland

4.3.1 Methods

Study area

The study area, Ullauns wood, is located within Killarney National Park in an upland area in the southwest of Ireland (Fig. 4.1). The park is protected as a Special Area of Conservation (SAC) under the European Union's Habitats Directive (E.U., 1992), and also as a Biosphere Reserve by the United Nations Educational, Scientific and Cultural Organisation (UNESCO). The south-west of Ireland has a strongly oceanic climate, heavily influenced by its proximity to the Atlantic Ocean and the Gulf Stream. Mean annual rainfall at the nearest weather station (between 1981-2010) was in excess of 2000mm, while the mean daily minimum temperature of the coldest month and mean daily maximum temperature of the warmest month were 3.9°C and 17.9°C respectively (Valentia observatory, data available from met.ie). The study plots are located between 75-200m above sea level. The large herbivores present in the study area consist of red deer (*Cervus elaphus*), the Asian sika deer (*Cervus nippon nippon*), and feral goats (*Capra hircus*). Domestic sheep were once a significant grazer in the area but populations almost completely disappeared with changing agricultural fiscal aid in the 1990's. The semi-natural woodlands in the study area have a relatively even-age structure dominated by sessile oak (*Quercus petraea*) in the canopy, holly (*Ilex aquifolium*) and downy birch (*Betula pubescens*) as a scanty understorey, a field layer dominated by grasses (mainly *Agrostis capillaris)* and wood rush (*Luzula sylvatica),* with *Thuidium tamariscinum*, *Isothecium myosuroides*, and *Rhytidiadelphus loreus* as the dominant bryophytes. This woodland vegetation has been previously described (Kelly, 1981) and belongs to the Blechno-Quercetum Association (White and Doyle, 1982, Kelly and Moore, 1975, Braun-Blanquet and Tüxen, 1952), equating to the WN1 Irish habitat classification (Fossitt, 2000) and the *Quercus petraea-Luzula sylvatica* woodland group (Perrin et al., 2008), and matches the W17 classification of British plant communities (Rodwell, 1991). The soils of the study area are podzolic with a log average pH of 4.09 (range: 3.66-4.63) (Newman, unpublished data).

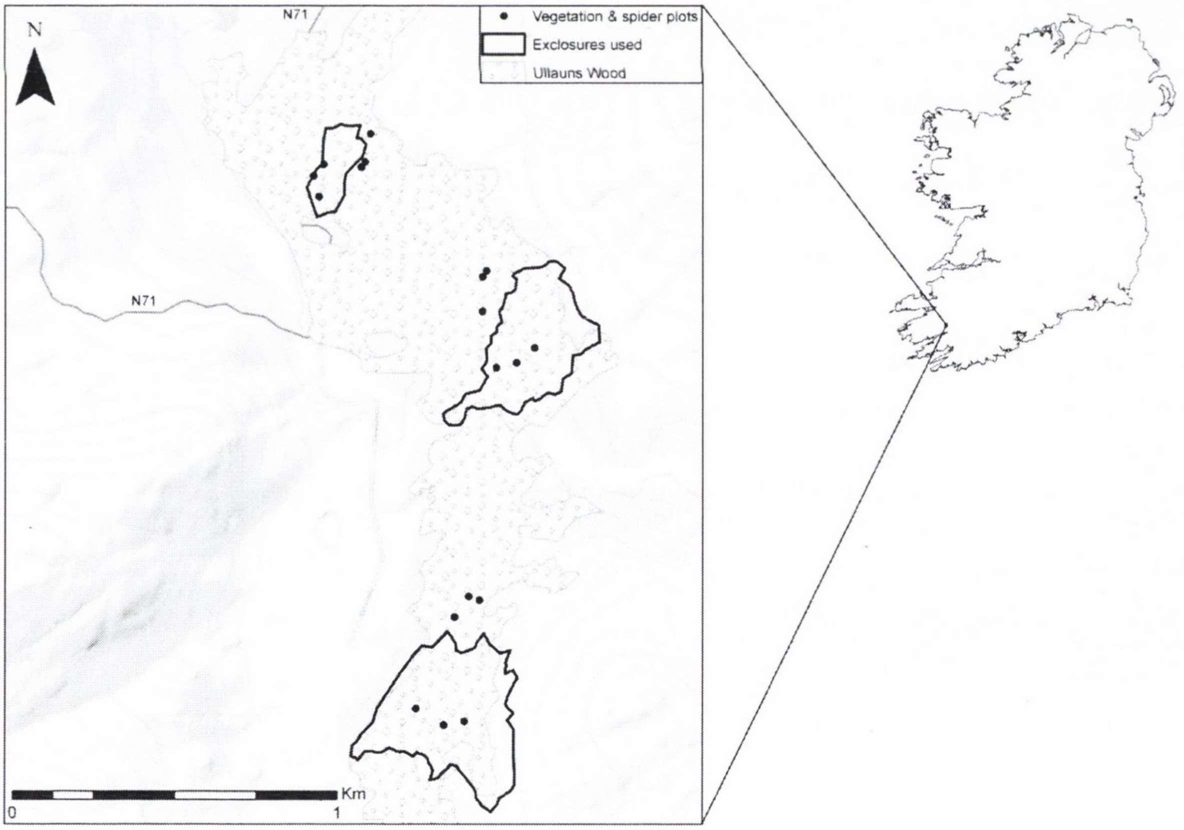

Fig. 4.1 Site location map showing the exclosures in Ullauns wood and survey plots, with insert of Ireland.

Experimental Design

Eleven fenced deer exclosures were established in Ullauns wood in 2005, with corridors left between them to allow the movement of deer through the area. Three exclosures were selected for the study: NORTH (2.9ha), MID (10.8ha), and SOUTH (15.2ha) (Fig. 4.1). The corridors between the exclosures were used for locating grazed plots. The approximate unexclosed woodland areas were 5ha, 10ha, and 3.9ha corresponding to the NORTH, MID and SOUTH, respectively. Three 10x10m plots were established in each exclosure and grazed area, with a total of 9 plots within exclosures and 9 plots in grazed areas. Plots were placed a minimum of 25m apart from each other, the edge of the woodland, any large areas of open space, and the exclosure fences.

Data Collection

All field data were collected in the summer of 2011, 6 years after the establishment of the exclosures. At the plot level, percentage cover of each vascular plant and bryophyte species in the ground-flora, was estimated to the nearest 5%. For cover value below 5%, two cover-abundance units were distinguished: 3% (for cover of 1–5%) and 0.5% (for cover <1%). Nomenclature follows: Stace (2010) for vascular plants; Smith (2004) for mosses; and Paton (1999) for Liverworts. The degree of affinity of different plant species for woodlands was assessed using the criteria set out in French et al. (2008) and Coote et al. (2012). These categories were described as: WA1- species not generally associated with woodlands, WA2 – species commonly found both in woodlands and in open habitats, WA3 – typical woodland species.

Ground-dwelling spiders were sampled using pitfall traps. The traps consisted of plastic cups (approximately 9cm high with a diameter of 7cm), sunken to just below ground level, with drainage slits 1cm from the top to allow water to escape and prevent flooding. The traps were filled to 3cm with a killing agent (ethylene glycol). Each plot contained a pitfall transect of 5 traps. The contents of each pitfall trap were collected four times, in three week blocks, from May to August 2011, resulting in a total of 84 trapping days. The trap contents were transferred into bottles and stored in 70% ethanol, until sorting and identification to species (using Roberts, 1993), with nomenclature following Platnick (2012). The data from each collection and trap were added together to give a total abundance of each spider species per plot, which was converted to relative abundance. The spider species richness and relative abundance data were categorised into feeding guilds and habitat preferences. Feeding guilds were split into web-spinning and cursorial (not web-spinning), and habitat preferences were defined as follows: woodland specialist (including woodland and shade associated species), open habitat specialist, and habitat generalist (following Nolan, 2008). It should be noted that it was not possible for this study to identify fully the nature of the taxonomic relationship for the entire suite of web building spiders, as pitfall traps do not effectively sample these spiders from higher layers of vegetation (Standen, 2000).

Data Analysis

As the focus of the research was to identify potential differences in taxonomic surrogacy between exclosures and grazed areas, the data were split and analysis was carried out on the two treatments separately. For analysis of the differences between vegetation and spider communities with grazing impacts, see **Chapter 2** and Fuller et al. (2014).

In order to investigate possible relationships between the ground spider and vegetation community composition, a procrustes analysis was conducted. This technique can measure the association of plots between multivariate distance matrices (Peres-Neto and Jackson, 2001). As an input to the analysis, spatial ordination results were used. The non-metric multi-dimensional scaling (NMS) ordinations, of both the ground spider species relative abundance and vegetation cover, were carried out using PC-ORD v.6.08 (McCune and Mefford, 2011), using 500 runs and unrotated scoring. The procrustes analysis was carried out using the protest function in the vegan package (Oksanen et al., 2012), with 9999 permutations, in R (R Core Team, 2012).

To investigate potential surrogacy between vegetation and spider species richness variables, correlations were conducted on data for 9 plots within exclosures and 9 plots in grazed areas. Although the variables were continuous, the Spearman's rank correlation technique was used as parametric statistical assumptions were not met. The cor.test function in R (R Core Team, 2012) was used to test for significant correlation coefficients with a Bonferroni correction used to account for multiple comparisons. Only significant Bonferroni corrected correlations are presented.

In order to investigate potential differences between species indicating the vegetation and spider communities of exclosed and grazed woodlands, the Indicator Species Analysis in PC-ORD v.6.08 (McCune and Mefford, 2011) was used. This analysis calculated the percent of perfect indication (indicator value) for vegetation and spider species, in both exclosures and grazed areas, based on a combination of relative abundance and relative frequency for each specie, using the methods of Dufrene and Legendre (1997). The 5 species with the greatest indicator value were selected for each group.

4.3.2 Results

Taxa overview

A summary of the different taxonomic groups illustrates the similarity of average species richness per plot in exclosures and grazed areas (Table 4.1). The biggest difference is seen between species richness of ground-spiders in exclosures and grazed area, with a higher average richness found in exclosures. A detailed study of the differences in the ground-spider community between grazed and ungrazed areas has been completed (Fuller et al., 2014). Whereas, the impact of grazing on the species richness of vegetation has been investigated in **Chapter 2**.

Table 4.1 Total and average species richness (±SE) for vegetation and spiders in exclosures and grazed areas.

	Total species richness			**Average (±SE) species richness**	
	All plots	Exclosure	Grazed	Exclosure	Grazed
n	*18*	*9*	*9*	*9*	*9*
Vegetation	123	94	99	39.2±2.5	40.6±2.3
Spiders	59	48	38	17.4±1.5	13.7±1.5

Community relationships

The most suitable ordination solution for both spider and plant taxonomic community composition was 2 dimensions, with diagnostics of the ordinations shown in Table 4.2. The stress levels of the vegetation and spider ordinations are all within the recommended level to allow for interpretation of the results (McCune and Grace, 2002, Zuur et al., 2007). Results from the Procrustes analysis revealed a significant correlation in the symmetric rotation of vegetation community cover and ground spider community relative abundance within exclosures (r=0.66, *p*=0.03) (Fig. 4.2). In grazed areas, however, the correlation in the symmetric procrustes rotation was not significant (r=0.33, p=0.74).

Table 4.2 Diagnostics from NMS ordinations

Community	**Stress**	**Instability**	**r^2 axis 1**	**r^2 axis 2**
Vegetation in exclosures	6.6	<0.00001	48.2%	38.2%
Spiders in exclosures	5.1	<0.00001	27.6%	51.3%
Vegetation in grazed areas	6.6	<0.00001	53.5%	29%
Spiders in grazed areas	11.9	<0.00001	44.6%	30.7%

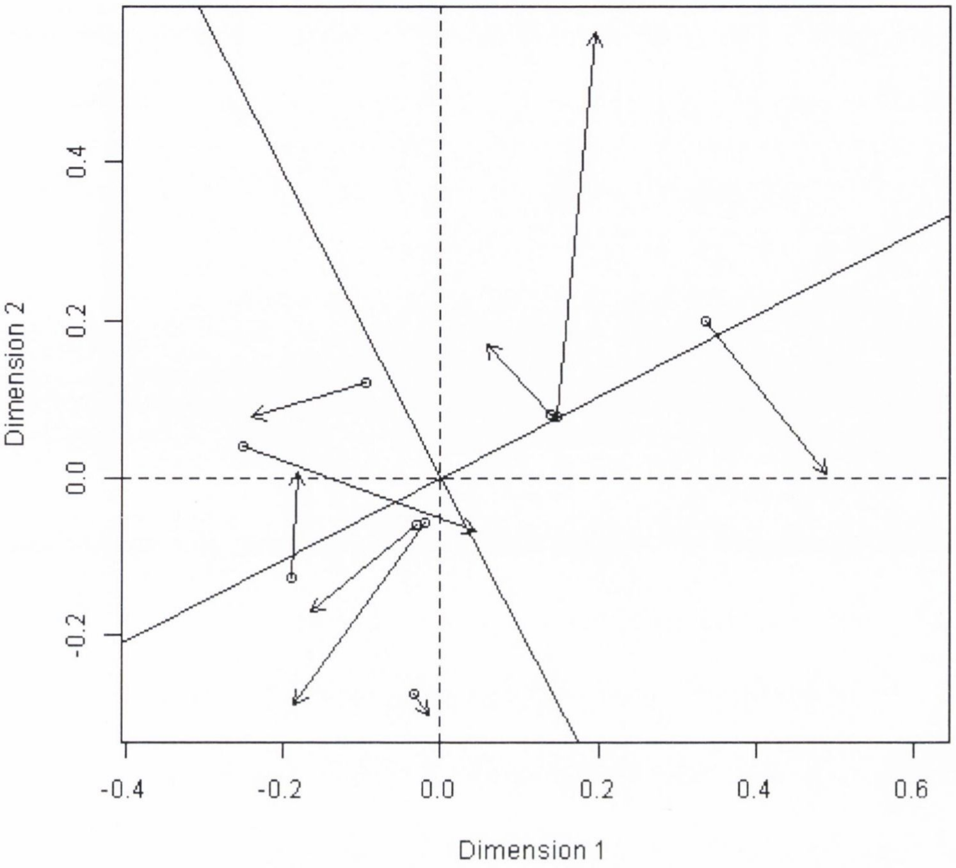

Fig. 4.2 Procrustes symmetric rotation of vegetation species abundance (open circles) and spider relative abundance (arrow trajectory) in exclosures. Broken line axes = vegetation ordination; solid line axes = ground spider ordination.

Life-form surrogacy

Analysis of potential surrogate relationships between and among vegetation and spider variables produced several significant correlations within exclosures and grazed areas (Tables 4.3 and 4.4). Within vegetation variable surrogacies (Table 4.3), significant relationships were found in exclosures and grazed areas, however, only the positive relationship between total vegetation species richness and species richness of species commonly found both in woodlands and in open habitats was found in both exclosures and controls. Within spider variable surrogacies (Table 4.3), more significant relationships were found in grazed areas than exclosures, however, three species richness relationships were the same in both exclosures and grazed areas: web-building spiders and generalist spiders; web-building spiders and total spiders; and, generalist spiders and total spiders. No significant correlations were found between vegetation and spider variables in either exclosures or grazed areas.

Table 4.3 Vegetation life-form correlation coefficients in exclosures (unfilled) (n=9) and grazed areas (grey filled) (n=9). All significant Bonferroni corrected ($p<0.0033$) correlations shown.

WA1	.	.	.	.	0.92
.	**WA2**	.	.	0.86	0.95
0.89	.	**WA3**	.	.	.
0.9	.	.	**Total vascular**	.	.
.	.	.	.	**Bryophyte**	.
.	0.93	.	.	.	**Total veg**

WA1- species not generally associated with woodlands, WA2 – species commonly found both in woodlands and in open habitats, WA3 – typical woodland species, Total veg – total vegetation (vascular and bryophyte).

Table 4.4 Spider guild correlation coefficients in exclosures (unfilled) (n=9) and grazed areas (grey filled) (n=9). All significant Bonferroni corrected ($p<0.0033$) correlations shown.

Web building	.	.	.	0.86	0.98
.	**Cursorial**	.	.	.	.
0.91	.	**Woodland**	.	.	.
.	.	.	**Open**	.	.
0.86	0.86	.	.	**Generalist**	0.91
0.95	.	.	.	0.96	**Total**

Woodland - woodland specialist, Open – open habitat specialist.

Indicator species analysis

The identification of indicator species for vegetation and spider communities, in both exclosed and grazed areas (Table 4.5), has shown that only one species (the spider *Monocephalus fuscipes*) indicates both exclosed and grazed areas. The indicator values of the indicator species are higher in exclosures for both vegetation (U_{10}=-2.1, p=0.035) and spiders (U_{10}=-2.6, p=0.009). For vegetation, the indicator species within exclosures are a mix of grasses, forbs, and bryophytes, while in grazed areas, all the vegetation indicator species are bryophytes. For spiders, the indicator species are mostly web-building spiders with woodland associations for both exclosures and grazed areas.

Table 4.5 Vegetation and spider indicator species and indicator values for exclosures and grazed areas.

		Species	Indicator value %
Vegetation	Exclosure	*Luzula sylvativa*	80
		Hypnum jutlandicum	73
		Agrostis capillaris	70
		Scapania gracilis	69
		Potentilla erecta	65
	Grazed	*Isothecium myosuroides*	70
		Saccogyna viticulosa	60
		Dicranum scoparium	60
		Bazzania trilobata	50
		Mnium hornum	50
Spiders	Exclosure	*Robertus lividus*	80
		Pirata hygrophilous	70
		Tenuiphantes alacris	60
		Microneta viaria	58
		Monocephalus fuscipes	58
	Grazed	*Saaristoa abnormis*	48
		Tenuiphantes zimmermanni	45
		Trochosa terricola	44
		Diplocephalus latifrons	42
		Monocephalus fuscipes	35

4.4 Discussion

The results have revealed the complexity of the relationships between vegetation and spiders. However, it should be noted that explaining these complex interactions is not always possible, as direct and meaningful cause and effect relationships are not always present (Landres et al., 1988). Focus of this discussion will be on the data presented here and available literature on the relationships within and between taxonomic groups and the usefulness of surrogates in temperate broadleaved woodlands.

4.4.1 Impact of grazing on relationships within and between taxa

One taxon from a particular taxonomic group is often used as a surrogate for the greater group (e.g. Norden et al., 2007, Mikusiński et al., 2001), however, findings from this case study, where grazing stressors are incorporated, have shown contradictory results for this approach.

Variation in the response of within taxa surrogacy to grazing was seen in this study. Only one correlation, of a matrix of six vegetation variables, was significant in both exclosures and grazed areas, while within spider surrogacies were more frequent in grazed areas compared to ungrazed, and all relationships found in ungrazed areas were also found in grazed areas. This demonstrates the potential problems with using surrogates for biological assessment, particularly when ecosystem altering factors, such as grazing, are present. Reasons behind these differences in within taxonomic surrogacy responses may be explained by investigating the taxon links with large herbivore grazing impacts. Grazing, at certain intensities, can cause a greater diversity in vegetation composition and alters structure (**Chapter 3**, **Chapter 2**). There is evidence that ground dwelling spiders respond to the structural heterogeneity of the habitat (Oxbrough et al., 2005, Uetz, 1991, Stewart, 2001). However, a study of woodland invertebrates in Mediterranean oak woods found that although several orders of invertebrates were significantly affected by grazing, spiders were not (Bugalho et al., 2011). In some cases invertebrates may remain relatively unaffected by grazing as, although vegetation may be reduced by grazing, there is less disturbance of the litter layer, which is the key habitat requirement for ground dwelling spiders (Allombert et al., 2005).

Differences were also seen in the species identified as surrogate indicators of vegetation and spider communities for grazed and ungrazed woodlands. Vegetation indicators in ungrazed areas were dominated by graminoids, byrophytes, and an herb, while only bryophytes indicated grazed area. The dominance of bryophytes as indicators of the vegetation community in grazed areas is likely linked to the increase in species richness and cover of bryophytes shown to be associated with large herbivore grazing in **Chapter 2**.

Spider indicator species of ungrazed communities were more associated with vegetation structure requirements, such as high vegetation cover and structure (Nolan, 2008), features shown to be greater in exclosures (**Chapter 2**). Spider indicators of communities where grazing is active were mostly associated with low vegetation cover (Oxbrough et al., 2012, Oxbrough et al., 2010), bare ground (Nolan, 2008) and were found in areas of high bryophyte cover (Fuller et al., 2014). These vegetation habitat associations are in-line with those found in grazed areas (**Chapter 2**). The only common indicator species found in both grazed and ungrazed areas was a spider forest specialist (*Monocephalus fuscipes*) with ubiquitous habitat associations (Nolan, 2008), which may more easily be able to adapt to stressors.

The cross-taxonomic relationships between spider and vegetation communities in grazed and ungrazed treatments illustrated the community composition of the taxa responded differently to grazing pressure. This may be because large herbivore grazing alters vegetation community composition (Côté et al., 2004) through decreases in cover of bramble, climbers, and tree saplings (McEvoy et al., 2006, Perrin et al., 2011, Pellerin et al., 2010, Chapter 2) and the cover of vegetation between 50 and 200cm high (Stockton et al., 2005, Chapter 2). These changes in vegetation composition have been shown to have knock-on effects for invertebrate communities (Takada et al., 2008). A significant relationship between the community composition of ground-dwelling spiders and vegetation was also highlighted in a study of combined temperate broad-leaved woodlands and plantation forests (Irwin et al., 2014). However, results for individual woodland types were not available, and disturbance factors such as large herbivore grazing were not assessed.

Although several studies have investigated the impact of disturbance on cross-taxon surrogacy in temperate woodland, few if any have focused on the impact of large herbivore grazing. In a comparison of naturally recovering and restored temperate pine woodlands in Canada, surrogacies between vascular plants and lichens were only significant in naturally recovering forests (Anand et al., 2005). This may be due in part to the impact of fertilising and planting, which took place in restored woodlands. The surrogate relationship between birds and butterflies has been shown to change along a gradient of urbanisation of former temperate oak woodlands in California, resulting in no two taxa displaying similar relationships along the gradient (Blair, 1999). Although the study used a strong gradient, levels of urbanisation, it does illustrate the impacts of stressors on taxa relationships, and thus parallels can be found with the case study presented here. Amphibian, reptile, grasshopper, vascular plant, and moss species richness were found to be surrogate relationships in temperate woodlands in Germany, however, climatic parameters strongly correlated with richness in all taxonomic groups (Buse and Griebeler, 2012), indicating again that that stressors can alter ecological relationships. On a wider scale, interaction between climate change and grazing, and the potential effects for bird communities, can result in milder winter conditions resulting in increased grazing (Martin and Maron, 2012). This can in-turn alter the vegetation communities and impact the interactions between birds and plants (Martin and Maron, 2012).

4.4.2 Usefulness of surrogacy for ecological assessment

Taxonomic surrogacy often assumes that all species being tested respond in similar ways to threatening processes, while species-specific responses to the same source of disturbance have been shown to differ (Ficetola et al., 2007). Variation in response to a disturbance can greatly reduce the usefulness of a species for surrogacy in ecological assessment and management (Ficetola et al., 2007).

Habitat, scale and landscape context have also been shown to influence surrogacy in taxonomic species richness, however, few studies produce data allowing for the rigorous testing of differences in surrogacy strength between these factors (Ekroos et al., 2013). Care must be taken not to extrapolate beyond the scope of the data used to identify potential taxonomic surrogacies. As relationships between different taxonomic groups often appear to have no direct cause and effect relationship (Landres et al., 1988), extreme caution is required when surrogacies based on a limited number of taxa are used to assess the management of wider biological diversity (Rossi, 2011). A study of bird and butterfly surrogacy in UK montane habitats concluded that within the study mountain range, identified umbrella species remain relevant, however, the ability of these species to confer protection to other taxa may vary among taxa and geography (Betrus et al., 2005).

4.5 Conclusions

The usefulness of within and between taxa surrogacy for the ecological assessment of areas exposed to stressors, such as varying intensities of grazing, needs to be carefully considered. Results from the case study presented here, and the review of previous studies, have indicated that the presence of a stressor or factor of disturbance can alter the relationship among and between taxa. It is recommended that a full evaluation of the factors potentially impacting the taxonomic communities, and their relationships, be included in any proposals of surrogacy for the assessment and management of ecological systems.

4.6 Acknowledgements

The authors would like to thank the BIOPLAN team, in particular Ms Aisling Walsh, Mr Rob Deady, and Mr Alexandre Jéké for assistance in the field. A special thanks to Ms Aisling Walsh for assistance with bryophyte identification. We would also like to thank the management and rangers of Killarney National Park, in particular Mr Patrick Dawson, Dr Kathryn Freeman, and the late Paudie O'Leary, for access to the sites and assistance. This research has been funded by the Department of Agriculture, Food and the Marine under the National Development Plan 2007 – 2013.

Chapter 5:

How dependent is woodland regeneration on habitat type and time?

To be submitted as:

Newman, M., Mitchell, F.J.G., and Kelly, D.L. How dependant is woodland regeneration on habitat type and time? To be submitted to Journal of Vegetation Science.

5 How dependent is woodland regeneration on habitat type and time?

5.1 Abstract

Tree regeneration is essential for the continuity of woodland so it is a vital consideration in the conservation management of protected woodland habitats. This study investigates the effects of different habitats and the passage of time on the composition and quantity of tree regeneration.

This study was carried out in three ancient oak woodlands in Killarney National Park, Co. Kerry. A set of 37 permanent 4x4m plots was used to assess tree regeneration over 20 years in 4 woodland habitat types: under canopy, in gaps, at woodland edge, and in open areas. Regeneration was quantified within 3 categories: S1 seedlings ≤ one year old, S2 seedlings > one year old but < 25cm in height, and S3 saplings ≥ 25cm in height with a max diameter of 10cm at 1.3m. Data were analysed using linear mixed-effects models to detect effects of time and habitat, PerMANOVA to assess community change through time, and SIMPER to identify key species differences over the 20 years.

Time was a significant factor for older seedlings and saplings, whereas both time and habitat were significant for young seedlings. The composition of the regenerating tree species has not changed over the 20 years of this study, indicating changes in species quantity but not in turnover. The quantity of *Ilex aquifolium* seedlings (S2) contributed the most to differences in the composition between 1991 and 2011 in canopy, gap and edge plots, while *Betula pubescens* (S2) accounted for most difference in open plots. It is recommended that protected area managers use these findings to adapt management practices in order to promote woodland regeneration.

5.2 Introduction

Woodlands are mosaic ecosystems, with a pattern of gaps, juvenile stands, and mature stands, which go through successional changes over long time frames. The classic theory of succession to climax forest proposed by Clements (1916) has caused controversy and has been challenged repeatedly (e.g. Vera, 2000, Mitchell, 2005). This primary succession theory is based on a starting point of bare soil, a colonisation by low-growing plants, shrubs, followed by the introduction of tree species. This progresses until tree species dominate the habitat by eliminating the potential for other vegetation to dominate, known as climax vegetation (Clements, 1916). Regeneration within climax woodland has been seen to occur in gaps in the tree canopy (e.g. Watt, 1925, Yamamoto, 2000, Higgins, 2001), where sufficient light is allowed to reach the woodland floor and encourage the growth of regenerating saplings. Regeneration in old growth woodlands has been achieved, to varying degrees, through the creation of artificial gaps in the canopy (e.g. Kelly, 2002, d'Oliveira and Ribas, 2011). Large herbivores can greatly alter woodland tree regeneration through a wide range of direct and indirect processes including grazing, browsing, disturbance, and nutrient flow modifications (e.g. Vera, 2000, Hester et al., 2000, Côté et al., 2004, Harrison and Bardgett, 2004).

The woodland edge, i.e. the limit of a closed canopy of trees, can often be an abrupt transition from woodland to open area. In areas where intensive agriculture abuts semi-natural woodland, a clearly defined line often exists between the two land uses. This is sometimes confounded by the burning and removal of heathland and woodland vegetation during the extension of agriculture into woodland areas (e.g. Pacheco, 2012, Mwavu and Witkowski, 2008). Man-made structures, such as roads and pipelines also contribute to the definition of the edge. The suitability of land for woodland growth often causes a similar effect to woodland edges as that of land use, where abrupt changes in geology, topography, nutrients, temperature, exposure, and ground moisture inhibit the growth of woodland.

Open areas adjacent to established woodlands often consist of areas unsuitable for woodland development (e.g. too wet, insufficient soil, and unsuitable topography) and abandoned agriculture land. These are locations, when suitable conditions permit, where secondary succession from grassland or heathland to woodland can occur (e.g. Watt, 1924, Hester et al., 1991).

Woodland tree regeneration is vital to the long-term conservation and management of the woodland habitat. Much tree regeneration research is focused on one or two components of the woodland, usually under canopy or gap habitats, while this study views regeneration at the wider woodland scale by assessing a range of woodland and adjacent habitats surveyed together through time. Long-term and medium-term data collection is vital to the understanding of woodland systems, and without it we may be unaware of the difference between minor fluctuations and significant trends (Magnuson, 1990). Although the monitoring plots used here have been resurveyed at 5 year intervals for 20 year, this study reports the first formal analysis of this medium-term dataset.

The question posed is as follows: what is happening to woodland regeneration in the medium-term (20 years)? This study investigates the effects of habitat and time on quantity of tree regeneration, and the change in regenerating tree species composition through time, within a range of woodland and adjacent habitat types. In order to deliver effective conservation management an increased understanding of the underlying mechanisms behind tree regeneration is required.

5.3 Methods

5.3.1 Study Area

The study area, Killarney National Park, Co. Kerry, is located in a region of strong oceanic climate in the southwest of Ireland. The park is over 10,000 hectares in size, covering a range of habitats including uplands, peatlands, lakes, rivers, and woodlands. Native semi-natural woodlands cover approximately 1,400 hectares of the Park and range from between ~30m (at the lake margins) up to ~300m a.s.l (on Tomies Mountain). The Park is protected as a Special Area of Conservation (SAC) under the European Union's Habitats Directive (E.U., 1992), and also as a Biosphere Reserve under the United Nations Educational, Scientific and Cultural Organisation (UNESCO). This study will focus on the woodlands of Derrycunihy, Tomies, and Muckross.

Ireland as a whole has a temperate climate, influenced heavily by the Atlantic Ocean and the Gulf Stream. Mean annual rainfall at the nearest weather station (between 1981-2010) was in excess of 2000mm, while the mean daily min of the coldest month and mean daily max of the warmest month were 3.9°C and 17.9°C respectively (Valentia observatory, data available from www.met.ie).

The large herbivore population present in the study area consists of red deer (*Cervus elaphus*), the Asian sika deer (*Cervus nippon nippon*), and feral goats (*Capra hircus*). Domestic sheep were major grazers, in some of these woods, at the start of this study but populations were sharply reduced with changing agricultural fiscal aid in the 1990's.

The semi-natural woodlands in the study area have a relatively even-aged structure dominated by sessile oak (*Quercus petraea*) in the canopy, holly (*Ilex aquifolium*) and downy birch (*Betula pubescens*) as a scanty understorey, and a field layer dominated by grasses and woodrush (mainly *Agrostis capillaris* and *Luzula sylvatica).* This woodland vegetation belongs to the Blechno-Quercetum Association (Kelly and Moore, 1975, Braun-Blanquet and Tüxen, 1952), equating to the WN1 Irish habitat classification (Fossitt, 2000), the

Quercus petraea-Luzula sylvatica woodland group (Perrin et al., 2008), and matching the W17 classification of British plant communities (Rodwell, 1991).

There are several management issues threatening the park. The alien invasive woodland plant, rhododendron (*Rhododendron ponticum*), introduced in the early 19th century, is a serious threat and management concern in the park (Cross, 1981, NPWS, 2005a, Kelly, 2006). Overgrazing has been recognised as a serious issue since the 1960s (Kelly, 1981, Kelly, 2000, Perrin et al., 2006). Culling of red and sika deer is carried out when deemed necessary (NPWS, 2005a) and there are now substantial differences in grazing levels between different woodland areas. Uncontrolled fires in open and woodland edge habitats are also a serious threat to the park, particularly in spring (NPWS, 2005a, O'Sullivan and Kelly, 2006).

5.3.2 Study design

A monitoring scheme, established in 1991, has been used to record the vegetation changes within woodland and potential woodland habitats, through the use of an extensive network of permanent plots. There are now 87 permanent plots (37 used here) distributed throughout Killarney National Park in a variety of woodland habitat types (Table 5.1). These plots are 4x4m in size, are marked in each corner by a metal stake, and have been re-surveyed at 5 year intervals in 1991 (Hayes et al., 1991), 1996 (Higgins et al., 1996), 2001 (Higgins et al., 2001), 2006 (Casey et al., 2007, Hogan et al., 2008), and 2011. The replication of plots per habitat type is detailed in Table 5.2.

Table 5.1 Habitat type classification for the location of permanent plots within and outside of the woodlands

Habitat	**Details**
Canopy (C)	Under closed canopy
Gap (G)	In woodland gap – break in canopy equal to the width of canopy crown
Edge (E)	At woodland edge – merging with open non-wooded area
Open (O)	In open heathland/grassland (unwooded area at least 15m wide)

Table 5.2 Distribution of permanent monitoring plots established in 1991

Woodland	**Habitat type**				**Total**
	Canopy	Gap	Edge	Open	
Derrycunihy	3	3	3	3	12
Tomies	3	3	3	3	12
Muckross	4	3	3	3	13

5.3.3 Data collection

Regeneration was categorised into three classes: S1 - seedlings in the first year of growth with woody tissue absent; S2 - seedlings with woody stems and <25cm tall; and, S3 - saplings >25cm tall, with a maximum diameter of 10cm at 1.3m above ground level. The number of individuals in each class was recorded in each plot. Nomenclature followed that of Stace (2010). In addition to regenerating tree species, the tree canopy covering each plot was recorded in the percent scale by standing in the middle of the plot, looking upwards and visually estimating the amount of canopy obscuring the view of the sky

5.3.4 Data analysis

Several sample points were removed from the analysis due to plot relocation (an issue covered by Ross et al., 2010), fire damage, and missing data due to plot loss. Plots removed for specific analyses are detailed in Table 5.3.

Species composition of each plot was analysed using a non-metric multidimensional scaling (NMS) ordination of number of regenerating individuals of S1, S2, and S3 ,in PC-ORD 6.08 (McCune and Mefford, 2011). This ordination technique was used to view the relationships among plots through time by reducing the dimensionality of the data space (McCune and Grace, 2002). The ordination was run using the Sørensen (Bray-Curtis) distance matrix, with a maximum of 500 iterations (250 with real data and 250 with randomised data), for a data matrix of 71 plots and 29 regeneration specie categories.

As the quantity of S1 tree seedling can be highly variable from year to year (e.g. Perrin et al., 2006), S2 and S3 regeneration was the focus of analysis on community composition change. Differences in regenerating tree species composition between the first (1991) and last (2011) survey were analysed, for each habitat type using a permutational multivariate analysis of variance (PerMANOVA) (Anderson, 2001a). This procedure provides a multivariate equivalent to the *F*-ratio calculated through any symmetric distance or dissimilarity matrix, with a *p*-value based on permutations (Anderson, 2001a). The tests were performed in PERMANOVA+ 1.0.3, an add-on function to PRIMER 6.1.13 (PRIMER-E, 2009). An interaction model with time (1991 and 2011) as fixed factor and woodland as random factor was used. The Sørenson (Bray-Curtis) distance matrix was used on a total of 9999 unrestricted permutations of raw data, with type III (partial) sums of squares.

To analyse the contribution of individual regenerating tree species (of category S2 and S3) to the first and last survey (1991 and 2011), a similarity percentage routine (SIMPER) was carried out in PRIMER 6.1.13 (PRIMER-E, 2009). The Sørenson (Bray-Curtis) distance matrix was used to decompose similarities/dissimilarities within and between groups (Clarke and Gorley, 2006). A two way crossed design using time and woodland was used to allow for the selection of species which contribute to the different times in all woodlands only.

A linear mixed-effects model was used to test for an effect of time and habitat on the numbers of individual regenerating tree species occurring within the plots. Computations were performed using the lme function of the nlme package (Pinheiro et al., 2013), run using R (R Core Team, 2012). Two main factors (habitat type and time) and their interaction were included in the model. To account for the nested structure of the data, plot nested in woodland type was added to the model as a random factor. A correlation variance structure (corAR1) of time accounted for the resampling of plots over time. Log-transformations were used on response variables to improve residual variance and normality of the data.

Table 5.3 Plots removed from analyses

Analyses	No. of plots	Plots removed	Reason for removal
Ordination	3	TO3_11, DO1_96, ME3_11	The first two plots contained no data, the third plot was recently exposed to fire
Mixed effects model	3	MO3_06, ME3_06, ME3_11	First two were incorrectly placed, third plot recently exposed to fire
PerMANOVA and SIMPER	12	DC1_91, DC2_91, DC1_11, DC2_11, DG2_91, DG1_11, DG_2_11, TG1_11, DE2_11, DE3_11, DO1_91, MO1_91, T03_11	Plots contained no records for S2 or S3 species; therefore a similarity matrix could not be assembled of they were included.

Plot codes: T=Tomies, D=Derrycunnihy, M=Muckross, O=open, E=edge, C=canopy, G=gap, 1/2/3=replicate plot identifier, _91=1991, _96=1996, _06=2006, _11=2011.

5.4 Results

5.4.1 Regenerating species composition

A total of 13 regenerating tree species were recorded as either seedling (S1 and S2) or saplings (S3) over the 20 year timeframe (Table 5.4). Species richness, per habitat per year, ranged from 4 to 10 in total, with 2 species (*Pinus contorta* and *P. sylvatica*) recording only one individual over the 20 years (Table 5.4).

The differences in species assemblage and number of individuals, between habitats and over time are illustrated in Fig. 5.1 A-D. Although a general downward movement of plot through ordination space is seen between 1991 and 2011, results from the PerMANOVA community composition analysis indicate that there was no significant change in composition between 1991 and 2011, within any habitat. There was however a significant effect of woodland in gap plots ($F_{2,8} = 2.32$, $p<0.01$), indicating that gap plots were not following the same trajectory in all woodland sites. Following a pair-wise comparison of woodlands through time, it was revealed that gap plots in Muckross are significantly different from gap plots in other woodlands (Table 5.5).

Although no significant difference in S2 and S3 species composition was found between 1991 and 2011 in any habitat, differences in the numbers of individuals between the times can be seen (Table 5.6). *Ilex aquifolium* S2 contributed the highest average dissimilarity between the 1991-2011 for canopy, gap and edge plots, with an increase seen under canopy and a decrease seen in gaps. *Betula pubescens* S2 contributed the most to the difference in open plots, showing a decline over time. Other contributions to the differences over time include the number of individual *Quercus petraea* S2 and *Sorbus aucuparia* S2.

Table 5.4 Total number of individual regenerating tree species per habitat type over time. Year: 91=1991, 96=1996, 01=2001, 06=2006, and 11=2011.

		CANOPY					GAP					EDGE					OPEN				
Year/Species		91	96	01	06	11	91	96	01	06	11	91	96	01	06	11	91	96	01	06	11
n		*10*	*10*	*10*	*10*	*10*	*9*	*9*	*9*	*9*	*9*	*9*	*9*	*9*	*8*	*8*	*9*	*9*	*9*	*8*	*9*
Arbutus unedo	S1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Arbutus unedo	S2	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	-	1	-	-
Arbutus unedo	S3	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Betula pubescens	S1	80	5	4	-	1	59	13	84	60	41	65	22	4	5	5	195	21	8	269	6
Betula pubescens	S2	22	9	18	8	1	28	41	22	12	34	16	21	7	4	15	235	172	31	18	9
Betula pubescens	S3	-	-	20	64	18	1	2	34	-	5	-	-	-	-	11	-	42	69	25	23
Crataegus monogyna	S1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Crataegus monogyna	S2	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Fagus sylvatica	S1	1	-	-	-	-	5	1	1	-	-	-	-	-	-	-	2	-	-	-	-
Fagus sylvatica	S2	-	-	-	-	-	4	4	-	2	-	-	-	-	-	-	-	1	-	-	-
Fagus sylvatica	S3	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Fraxinus excelsior	S1	3	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fraxinus excelsior	S2	-	1	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-
Ilex aquifolium	S1	480	597	557	889	1259	144	111	33	36	46	58	69	27	11	47	32	13	7	4	6
Ilex aquifolium	S2	57	50	264	131	125	126	103	115	104	35	53	22	33	18	38	108	32	43	41	29
Ilex aquifolium	S3	-	-	35	79	97	-	27	93	58	50	4	6	5	3	5	3	53	18	26	6
Pinus contorta	S1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Pinus sylvestris	S1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Quercus petraea	S1	263	275	70	2	34	33	105	43	2	11	4	25	2	1	3	8	29	-	2	-
Quercus petraea	S2	45	16	130	4	27	5	9	36	8	4	2	12	23	2	2	1	4	3	13	1
Quercus petraea	S3	-	-	-	-	1	-	-	-	1	2	6	1	8	-	-	-	-	-	1	1
Rhododendron ponticum	S1	15	-	-	-	8	2	-	-	-	1	-	-	-	-	5	5	-	-	-	7
Rhododendron ponticum	S2	-	-	-	-	7	-	-	-	-	11	-	-	-	-	4	-	-	-	-	4
Rhododendron ponticum	S3	-	-	-	-	-	-	-	-	-	4	-	-	-	-	11	-	-	-	-	5
Salix cinerea	S1	-	-	-	-	-	-	-	-	-	-	-	9	-	-	-	1	-	-	-	-
Salix cinerea	S2	-	-	-	-	-	-	-	1	-	-	-	3	3	-	-	7	6	-	-	-
Salix cinerea	S3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	8	-	3
Sorbus aucuparia	S1	70	101	14	11	49	32	18	4	4	2	26	14	1	-	8	4	4	-	-	1
Sorbus aucuparia	S2	12	22	46	31	26	45	36	44	32	15	20	21	16	16	15	8	5	3	4	7
Sorbus aucuparia	S3	-	-	1	1	3	-	3	7	1	10	4	5	13	2	3	-	1	6	-	8
Taxus baccata	S1	21	61	9	3	9	19	2	2	-	1	1	-	-	-	-	1	-	-	-	-
Taxus baccata	S2	-	-	7	5	-	-	1	3	-	-	-	-	-	-	-	-	-	2	-	-
Species richness		8	6	5	6	7	7	8	7	6	9	5	6	6	4	6	10	6	7	4	6

S1=seedlings in the first year of growth; S2=seedlings >S1 but <S3; S3 = saplings >25cm tall, with a maximum diameter of 10cm at 1.3m above ground level.

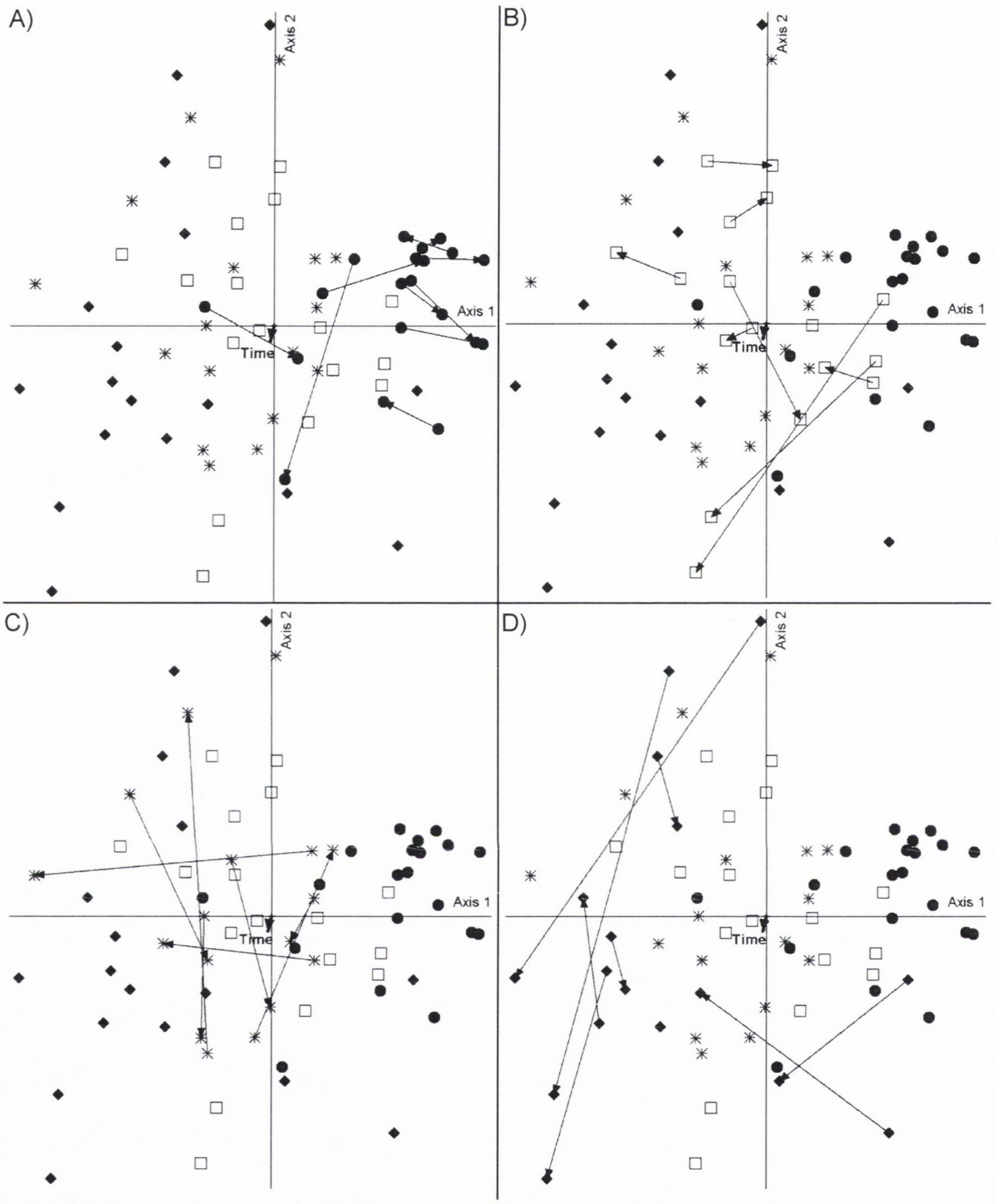

Fig 5.1 Ordination showing composition of seedling (S1 and S2) and saplings (S3) from 1991 and 2011 plots for each habitat type. Black circles = canopy plots, open squares = gap, black asterisk = edge, black diamonds = open. Successional trajectories show movement of plots through time (1991-2011), and A) shows movement of canopy plots, B) shows movement of gap plots, C) shows movement of edge plots, and D) shows movement of open plots. Recommended 2D solution with an R^2 for axes 1 and 2 of 32% and 28%, respectively, with final stress of 19.75%.

Table 5.5 Comparison of gap plots within woodlands

Woodland comparisons	**t-stat**	**P(perm)**
Derrycunihy vs. Tomies	1.1137	0.28
Derrycunihy vs. Muckross	1.3867	**0.03**
Tomies vs. Muckross	1.9268	**0.001**

Table 5.6 Species with the two highest contributing to dissimilarity between 1991 and 2011, per habitat

Habitat	**Species/category**	**Average no. of individuals**		**Average dissimilarity (%)**
		1991	2011	
Canopy	*n*	*8*	*8*	
	Ilex aquifolium/S2	7.13	15.63	27.15
	Quercus petraea/S2	5.63	3.38	17.20
Gap	*n*	*8*	*6*	
	Ilex aquifolium/S2	15.75	5.83	26.36
	Betula pubescens/S2	3.50	5.67	13.03
Edge	*n*	*10*	*7*	
	Ilex aquifolium/S2	5.30	5.43	29.78
	Sorbus aucuparia/S2	2.10	2.14	10.84
Open	*n*	*7*	*8*	
	Betula pubescens/S2	33.57	1.13	31.88
	Ilex aquifolium / S2	15.43	3.63	20.72

5.4.2 Regeneration quantity

The total quantity of regenerating tree species recoded from each habitat and survey can is detailed in Table 5.4. The most abundant species found in all habitats were *Betula pubescens*, *Ilex aquifolium*, *Quercus petraea*, and *Sorbus aucuparia*. Species with the greatest quantity within each regeneration category for each habitat were: *Ilex aquifolium* S1, S2, and S3 for canopy and gap plots; *Ilex aquifolium* S1 and S2 ,and *Sorbus aucuparia* S3 for edge plots; and *Betula pubescens* S1, S2, and S3 for open plots. Only four individuals of *Quercus petraea* S3 were recorded from all plots surveyed in 2011. Although some plots contained mature tree at the beginning of the study (1991), no additional mature trees (i.e. tree species >S3 category) have been recorded in any plot.

The linear mixed effect model showed that time was a significant factor for all regeneration categories, but habitat type was only important for S1 regeneration. Habitat, time and the interaction of habitat and time were all significant for S1 regeneration (Table 5.7). The average number of S1 individuals per habitat type suggests a fluctuation in canopy and open plots, while gap and edge plots show a general decline with time (Fig. 5.2 A). Time was the only significant factor found to drive change in the numbers of S2 and S3 regenerating individuals (Table 5.7). There appears to be an overall declining trend in number of individual S2 seedlings in open and gap plots over time (Fig. 5.2 B). An increasing trend in number of individuals with time is seen for regenerating S3 saplings in canopy and edge plots (Fig. 5.2 C).

Table 5.7 Summary statistics for the linear mixed effects model and the main fixed factors

Category	Main factors	DF num	DF den	F-ratio	*p*-value
S1 seedlings					
	Habitat	3	31	22.34	**<.0001**
	Time	4	129	7.83	**<.0001**
	Habitat*Time	12	129	2.02	**0.0276**
S2 seedlings					
	Habitat	3	31	0.96	0.4226
	Time	4	129	3.39	**0.0112**
	Habitat*Time	12	129	1.58	0.1037
S3 saplings					
	Habitat	3	31	0.63	0.6010
	Time	4	129	7.43	**<.0001**
	Habitat*Time	12	129	1.21	0.2840

DF num = degrees of freedom for the numerator; DF den = degrees of freedom for the denominator

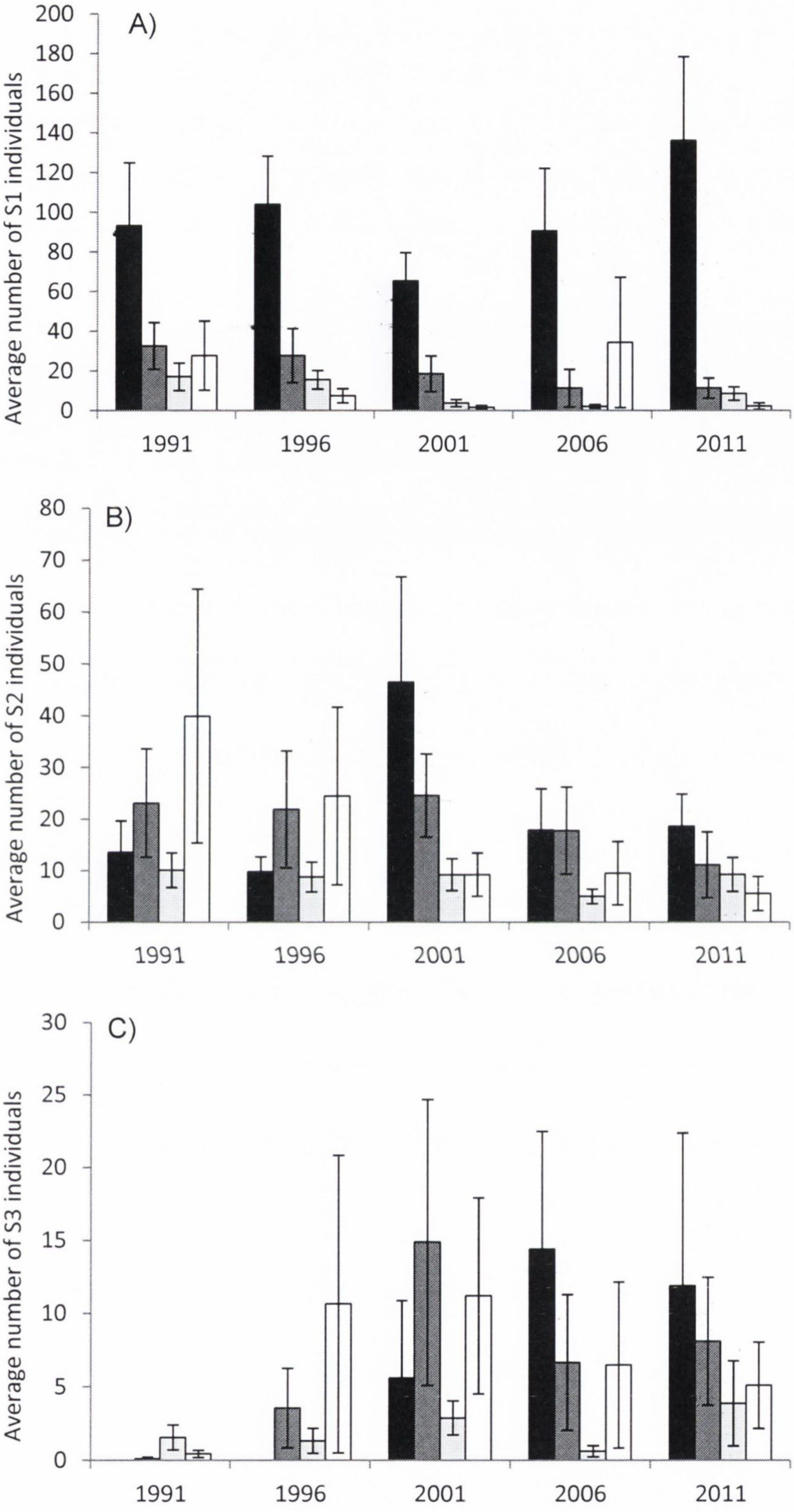

Fig. 5.2 Average number of individuals per 4x4m plot ±SE for S1 seedlings (A), S2 seedlings (B), and S3 saplings (C), through habitat and time. Black = canopy plots, dark grey = gap plots, light grey = edge plots, white = open plots

5.5 Discussion

Regeneration of tree species is key to the long-term sustainability of woodlands. Time and, to a lesser extent, habitat have been shown here to significantly affect the quantity and assemblage of regenerating tree species over 20 years. However, other factors that possibly interact with time and habitat, such as management and grazing pressure, were not included in the analysis due to lack of data, but are explored here.

5.5.1 Composition changes

No change in the species composition of regenerating seedlings (S2) and saplings (S3) was found over the 20 years of this study but the relative abundance changed markedly in some habitats. A similar result was recorded after 17 years in English lowland woods (Kirby et al., 1996). This suggests that although the numbers of individuals of regenerating tree species are changing through time, their overall species composition is not, indicating potential oscillations in dominance of species but no change in the species suite.

The difference of Muckross as compared to other sites may be explained by the intensive deer culling which has taken place in this peninsula woodland over the preceding 2 decades (P. O'Toole pers comm). The almost complete removal of large herbivores in these woods (specifically Sika deer) has likely resulted in a change in the plant communities, as shown from previous studies of large herbivore impacts in the area (**Chapter 2**, **Chapter 3**).

A further consideration for species composition changes in the future is the interaction between habitat and time, i.e. habitat change through time. There is an increasing trend in the average canopy tree cover in gap plots (Fig. 5.3) as lateral expansion of canopy from adjacent mature trees is likely filling the gap, and a possible decrease in cover of canopy plots. While edge and open plot appear to remain stable, future surveys may show significant changes to the canopy cover of all plots.

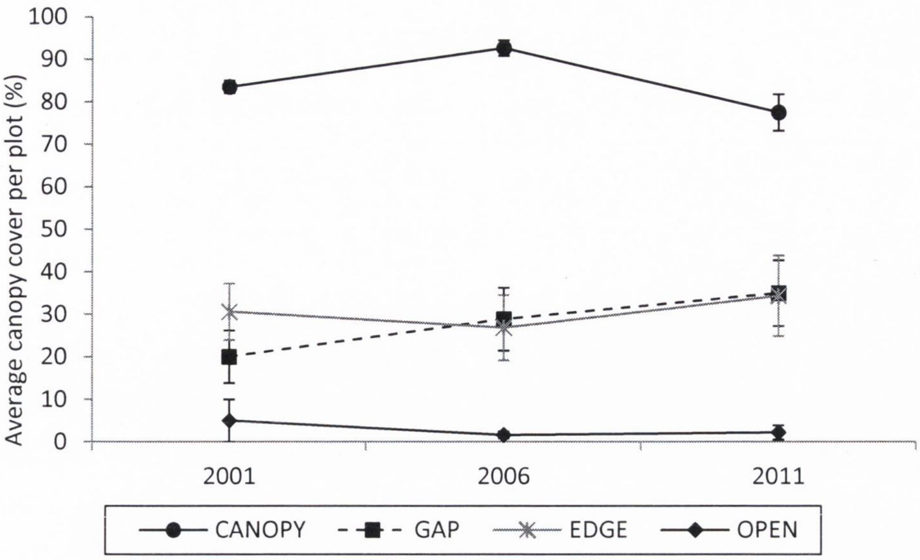

Fig. 5.3 Changes in average canopy cover (±SE) of canopy, gap, edge, and open plots, between 2001 and 2011 (data not available for earlier surveys).

There is a notable increase in the average quantity in canopy plots while a reduction was recorded in gap plots. Although the average quantity of *I. aquifolium* showed a decrease in open plots over the 20 years, it was not the contributing the most to the dissimilarity in time (see Table 5.5). In a study of in central Spain with similar experimental design as the one presented here (based on canopy, gap, edge and open permanent plots), *I. aquifolium* seedling regeneration was shown to be habitat dependent, with highest numbers under closed canopy and a complete absence in open grassland areas (Arrieta and Suárez, 2006). The results of their study differ from those presented here in that regeneration of *I. aquifolium* has been noted in open plots and also the quantity of seedlings and saplings is similar in both canopy and gap plots. These differences may be explained by climate and management issues such as large herbivore grazing in Killarney National Park. *I. aquifolium* seedlings (S1 and S2 categories tagether) have been shown to have significantly higher densities in areas subjected to large herbivore grazing compared to exclosures; however, *I. aquifolium* saplings were found at higher densities with exclosures (Perrin et al., 2006). This indicated that the success of regenerating *Ilex* is affected by grazing, which has been noted previously (Kirby et al., 1994).

In open habitat plots, the most distinguishing regenerating species category, between the first and last survey, was *Betula pubescens* S2. *B. pubescens* S1 and S3 categories also declined over this time period. The reduction of *B. pubescens* S2 regeneration through time may be linked to self-thinning, grazing pressure and preferential browsing. Self-thinning is unlikely as no *B. pubescens* individuals above S3 category were recorded. Several studies have shown that *Betula* regeneration can be altered by grazing (van Hees et al., 1996, Hester et al., 2000, Kelly, 2002, Hester et al., 1996). Kelly (2002) noted the dominance of *B. pubescens* in tree regeneration following the creation of an artificial gap within an deer exclosure in Tomies wood in Killarney.

5.5.2 Quantity of regeneration

The effect of time emerged as a significant factor in the changing quantity of all three regeneration categories. However, first year seedlings were also significantly affected by habitat type. First year tree seedlings (S1) have previously been shown to be highly variable from year to year, especially in mast-seeding species such as *Quercus petraea* (Kelly, 2002, Perrin et al., 2006), so the fluctuations seen here through time and habitat are expected. Older seedlings in open and gap plots showed a decreasing trend in quantity over time. This is likely linked to the combined effect of S2 mortality and growth into the next regeneration category (S3), a process that follows a classic population growth for a cohort (Silvertown and Charlesworth, 2001). However, the concern is that as S2 move on to S3, there may be little replacement of S2, resulting in a cessation of regeneration. This may be the case in open plot and gap plots, where the numbers of S2 (specifically *Betula pubescens*, *Ilex aquifolium*, *Sorbus aucuparia*) are reducing through time without marked increases in S3 categories. The increase in the quantity of S3 category regeneration with time is promising as it is these saplings which will potentially form the canopy of the future woodland. However, the average numbers of S3 individuals per plot are skewed due to inflated contributions from certain species all habitat types. The number of *Quercus petraea* saplings (S3) has remained low in all habitats with only one individual recorded from canopy plots, and a decline to zero seen in edge plots over the 20 years. A decline in the quantity of young oaks individuals was also recorded over 17 years in Wytham wood in England (Kirby et al., 1996).

Impacts of large herbivores must be considered here also, as previous research under canopies has shown that the number of seedlings is highest at grazed sites, particularly at medium-high grazing levels (Pellerin et al., 2010, **Chapter 2**), however this does not translate into number of saplings, which have been shown to be at greater quantities at ungrazed and low grazing level sites (Stockton et al., 2005, Takatsuki, 2009, **Chapter 2**).

5.6 Conclusion

This chapter has focused on investigating the effects of habitat and time on the quantity and composition of regenerating tree species over 20 years. This, in conjunction with other studies, has shown that time and habitat are significant factors for the number of individuals regenerating. The composition of the regenerating tree species has not been shown to change over the 20 years of this study, indicating change in species quantity but not in species turnover; however, one site had significantly different gap plots from the others, possibly due to a reduction in large herbivore. The overall increase in numbers of saplings (S3) is encouraging; however, this increase is modest for *Quercus petraea*. The quantity of *Ilex aquifolium* seedlings (S2) contributed the most to differences in the composition between 1991 and 2011 in canopy, gap and edge plots, while *Betula pubescens* (S2) accounted for most difference in open plots.

Long-term monitoring is vital to the understanding of tree regeneration and also in affording us the ability to identify areas where management practices should be altered. During 40 years of repeated observations in Denny Woods in the UK, a cessation in tree regeneration was identified and attributed to heavy browsing and grazing by wild and domestic large herbivores (Mountford et al., 1999). Without continued monitoring projects, such as the one detailed here, these drivers of change may not be identified and the conservation of woodland will suffer. It is recommended that protected area managers use these findings to adapt management practices in order to promote woodland regeneration.

5.7 Acknowledgements

The authors would like to thank Ms Emily Wallace for assistance in the field, Mr Alexandre Jéké for digitising a portion of the field-data sheets, and Dr Anke Dietzsch for advice on data analysis. We would also like to thank the Management and Rangers of Killarney National Park, in particular Mr Patrick Dawson, Mr Pascal Dower, Dr Kathryn Freeman, Mr Peter O'Toole, and the late Mr Paudie O'Leary, for access to the sites and assistance. This research has been part funded by the National Parks and Wildlife Service and part by COFORD through the Department of Agriculture, Food and the Marine under the National Development Plan 2007-2013.

Chapter 6:

General conclusions and synthesis: impacts of large herbivore grazing in space and time

6 General conclusions and synthesis: impacts of large herbivore grazing in space and time

6.1 Overview

This thesis set out with the overall aim of assessing the effects of time and large herbivores on the woodland community, with the goal of improving or feeding into management practices in high conservation value areas. This was achieved through extensive fieldwork and data compilation of vascular plant, bryophyte, and tree regeneration records from three National Parks in Ireland. A combination of existing and newly established research plots were employed to investigate the impacts of large herbivores at varying grazing levels, the medium to long-term effects of large herbivore removal on ground-flora, the effect of grazing on cross-taxonomic surrogacies, and the effects of time and habitat type on tree regeneration.

Chapter 2 investigated differences in vegetation composition, structure and regeneration among varying levels of grazing, and hypothesised that low grazing would be most appropriate for conservation of overall plant diversity. It was found that low grazing impact levels, but not zero grazing, should be maintained in order to achieve a balance between the promotion of regeneration and maintenance of both vascular plant and bryophyte communities. **Chapter 3** assessed the effects of large herbivore removal, through time, on the community composition and diversity of oak woodland vegetation. There was a specific focus on woodland homogenisation and changes in species through time. The results suggested that general homogenisation of the plant communities of temperate oak woodlands will occur over time with total large herbivore removal. **Chapter 4** assessed the surrogacy relationships among and between taxonomic groups in temperate semi-natural oak woodlands using spider and vegetation data. It was found that relationships among and between taxa may be altered when large herbivore grazed pressure is present. **Chapter 5** focused on the effects of different habitats and of the passage of time on the composition and quantity of tree regeneration. The composition of the regenerating tree species did not change but relative abundance did change over the 20 years of the study, indicating changes in species quantity but not in turnover. The quantity of older seedlings and saplings varied significantly over time but not by habitat, whereas younger seedlings varies with habitat and time.

In this final chapter, a synthesis of the main research themes is presented, along with the implications of this research, suggested future research directions, and some concluding remarks.

6.2 Summary and synthesis

6.2.1 Large herbivore impacts

Large wild herbivores, such as deer, have been increasing their range globally in recent decades and are now considered by many to be at unsustainably high levels in temperate woodlands (e.g. Côté et al., 2004, Apollonio et al., 2010). The ecological impacts of these high deer populations can be summarised as: impacting the growth and survival of many herbs, shrubs, and tree species; modifying patterns of vegetation dynamics; impacts, at cascading levels, on insects, birds and mammals; reducing plant cover and diversity; changing nutrient and carbon cycles; and redirection of succession to shift future overstorey composition (Côté et al., 2004).

The impacts of large herbivores on vegetation, at varying grazing levels, were noted in this thesis. In **chapter 2** it was found that, with increasing levels of grazing, a decrease in the cover of bramble (*Rubus fruticosus* agg.), climbers, and vegetation structure between 50 and 200cm was found. With the same gradient of increasing grazing levels, an increase in cover of forbs and bryophytes was detected, in conjunction with an increase in the species richness of graminoids, bryophytes and total vegetation (vascular plants and bryophytes together). The cover and species richness of regenerating tree saplings were also negatively impacted by increases in grazing levels. A summary of these main results is displayed in Table 6.1. Tree regeneration was covered in more detail in **Chapter 5** and has been synthesised in **section 6.2.4**. Results from **Chapter 3** illustrated the impact of large herbivore removal, while **Chapter 4** detailed the effects of large herbivore grazing on the relationships among different taxonomic groups.

Table 6.1 Simplification (visualisation) of trends occurring in vegetation, with an increase in large herbivore impact

	Graminoids	Forbs	Bramble	Bryophytes	Total vegetation	Structure 50-200cm	Tree Seedlings	Tree Saplings
Cover		↑	↓	↑		↓	↷	↓
Species richness	↑			↑	↑			↓

6.2.2 Long-term changes and large herbivore removal

Woodland ecosystem dynamics are usually studied either empirically at short-term (within a decade) or historically at long-term (within centuries and millennia) scales. Being able to investigate long-term vegetation community data allows for increased understanding of the ecosystem (Silvertown et al., 2010) and has become an increasingly used for biodiversity research (Magurran et al., 2010). This thesis investigated the medium and long-term trends in vegetation associated with the impact of large herbivores.

In **Chapter 3** it was found that vegetation composition was at its most heterogeneous within the first 12 years after large herbivore fencing, and the changes to species composition within this time were at their greatest. Between 16 and 28 years of large herbivore removal, the vegetation community was becoming more similar, and the composition of plots between 32 and 41 years since large herbivore removal were most similar at all beta diversity measures used. The main result from **Chapter 3** is summarised in Fig. 6.1. **Chapter 2** described the impact of large herbivores after ~40 years, through the comparison of long-term deer exclosures with areas of varying large herbivore impact, and also identified a reduction in diversity with long-term large herbivore removal. **Chapter 5** investigated the changes in tree regeneration occurring over 20 years in grazed woodlands and identified the importance of habitat and possible links to changes in herbivore impact levels.

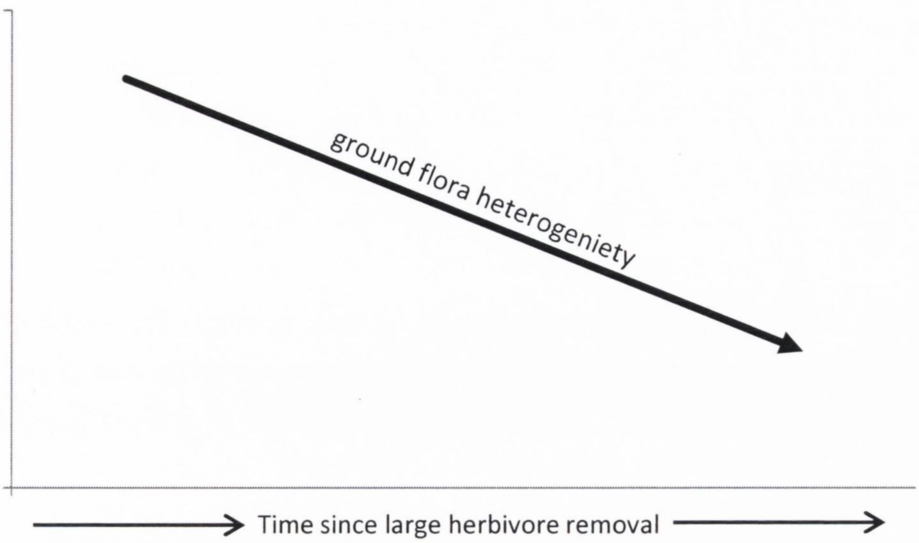

Fig. 6.1 Large herbivore removal - trends over time

6.2.3 Cross-taxon surrogacy and grazing

It is a major challenge to identify, with confidence, reliable surrogate indicator taxa (Lund and Rahbek, 2002) that have the potential to be useful in conservation biology (Caro and O'Doherty, 1999). Surrogacy and relationships among taxonomic variables can be altered for many reasons. The specific stressor of interest here is large herbivore grazing which has been shown to drive change in an ecosystem (Côté et al., 2004) with cascading effects on a range of biotic and abiotic components such as invertebrates (Allombert et al., 2005, Bugalho et al., 2011, Pollard and Cooke, 1994), birds (McShea and Rappole, 2000), small mammals (Bush et al., 2012, Buesching et al., 2011), vegetation (Côté et al., 2004), soil (Mofidi et al., 2012), terrestrial carbon storage (Tanentzap and Coomes, 2012) and ecosystem functioning (Rooney and Waller, 2003).

Multi-taxon surrogacies and their relationship to large herbivore grazing were covered in **Chapter 4**. This thesis has shown that community composition of vegetation and ground-dwelling spiders exhibit significant parallel responses in exclosures but not in grazed areas, which corroborates the findings of Côté et al. (2004). Results from the case study indicated that correlations testing surrogacies within vegetation and spider group categories displayed difference relationships in exclosure and grazed areas, this further highlights the knock on effect that important ecosystem drivers, e.g. grazing, have on taxonomic groups. These results indicate that cross taxon surrogacy should be approached with caution when such drivers are present. This is a difficult task and may defeat the purpose for why surrogates are chosen in the first place i.e. to save time and money.

6.2.4 Tree regeneration through space and time

Woodlands are mosaic ecosystems, with a pattern of gaps, juvenile stands, and mature stands, which go through successional changes over long time frames. The different habitat components of the woodland have been described in this thesis as: under canopy, gaps, woodland edges, and open areas outside of woodlands (**Chapter 5**). Regeneration within mature woodland has been seen to occur mostly in gaps in the tree canopy (e.g. Watt, 1925, Yamamoto, 2000, Higgins, 2001), where sufficient light is allowed to reach the woodland floor and encourage the growth of regenerating saplings. Regeneration in old growth woodlands has been achieved, to varying degrees, through the creation of artificial gaps in the canopy (e.g. Kelly, 2002, d'Oliveira and Ribas, 2011).

In **Chapter 5,** time was identified as a significant factor for changes to the quantity of older seedlings and saplings, whereas both time and habitat were significant for young seedlings. Promisingly, an overall trend of increase in the quantity of tree saplings was seen over time. However, the replacement of older seedlings appears to be in decline, and the number of *Q.petraea* saplings was <2 individuals in all habitat types in the 2011 survey. The composition of the regenerating tree species was shown not to have differed over the 20 years of the study, indicating changes in species quantity but not in turnover. The quantity of *Ilex aquifolium* seedlings contributed the most to differences in the composition between 1991 and 2011 in canopy, gap and edge plots, while *Betula pubescens* accounted for the greatest difference in open plots. A direct comparison of tree regeneration under canopy, between large herbivore exclosures and areas subjected to different levels of grazing, was completed in **Chapter 2**. Here, the quantity of individual regenerating tree species were found to be highest at absent and low grazing levels. Species richness of saplings was greater when large herbivores were removed, and the cover of seedlings and saplings was greater at low and absent grazing levels.

6.3 Research implications

6.3.1 Methodological considerations

Several environmental, structural, and vegetation recording methods were employed in this thesis. Although mostly standard and accepted methods were used, some are worthy of additional discussion, including large herbivore assessment and bryophyte sampling.

The assessment of large herbivore populations has largely been based on density estimates through a variety of techniques including direct counts (Putman et al., 2011b), indirect methods such as faecal pellet surveys (e.g. Swanson et al., 2008), and indices such as hunter observations and bag numbers (Putman et al., 2011b). However, the accuracy of these methods may vary considerably and population changes may be difficult to detect (Daniels, 2006, Smart et al., 2003). In fragmented woodland landscapes it may be increasingly difficult to achieve accurate large herbivore population surveys through total count methods, as these techniques are largely limited to open areas (Putman et al., 2011b); deer may remain undetected or be double counted as they move into open areas. Although absolute deer densities are often the method used to assess large herbivores, they are unlikely to be good predictors of impact, as many factors, such as habitat fragmentation and population structure, influence what an impact level can be (Putman et al., 2011a). In cases where management wishes to understand the impact of large herbivores on a conservation value (e.g. species richness, vegetation complexity, tree regeneration, specific species promotion), an assessment method which focuses on measuring these characteristics may be more appropriate than a broader density assessment. It may also be that reliable deer population data are not available in an area of conservation interest, as was the case for the study sites used in this thesis. Here, the use of a grazing level proxy, such as the 'Woodland Grazing Toolbox' (Forestry Commission Scotland, 2012, Armstrong et al., 2011) can provide the adequate qualitative data necessary to meet the research objectives. These methods were found to be highly useful in the research for this thesis as they provided estimated grazing intensities for both past and present woodland conditions.

Another methodological consideration is the inclusion of lower plants (in particular bryophytes and lichens) in woodland biodiversity surveys. As the woodland habitat covered in this thesis represents temperate rainforest (using the criteria set out by Alaback, 1991), conditions are ideal for high diversity of lower plants and epiphytes. Bryophytes and lichens contribute greatly to the species richness of Atlantic oak woodland flora (Kelly, 2006, Kelly and Moore, 1975, Rodwell, 1991, Dickinson and Thorp, 1968, Coppins, 2002). Data collection in this thesis was focused on ground flora (as this is the stratum of vegetation most likely to be directly impacted by large herbivores) and included the recording of both bryophyte and lichen records. However, the lichen flora of the woodland floor is poor and mostly confined to crustose saxicolous species, with only a few folious macro lichens being recorded. The saxicolous lichen communities were wholly dependent on exposed boulders; therefore, lichen records were removed from analysis. The inclusion of bryophytes added greatly to the total species richness of plots and also to the interpretation of the results; changes in bryophyte species richness and cover, with grazing impact levels, often showed opposing trends to those for vascular plants (**Chapter 2**, **Chapter 3**). The inclusion of bryophytes has added to the conservation knowledge of diversity within woodlands.

6.3.2 Management Implications

Woodland conservation management can benefit greatly from the use of quality long-term data. The longer a study is, the more valuable it may become (Silvertown et al., 2010). However, it is essential that collected field data must also be analysed and interpreted. The implications of the long-term findings of this thesis are important for management, as this is the first time the data have been collated and analysed at this scale. The comparison of vegetation subjected to varying grazing impact levels, with that of ungrazed areas (~40 year since large herbivore removal), demonstrates the responses of vegetation to large herbivore grazing (**Chapter 2**). These findings allow managers to set out specific targets focused on the promotion of vascular ground flora, bryophytes, or tree regeneration, by maintaining or altering grazing levels. The main changes attributed to long term large herbivore removal, from semi-natural oak woods, are a reduction in vascular ground flora heterogeneity and a reduction in bryophyte cover (**Chapter 3**). Short-term fencing, directed at increasing tree regeneration or biodiversity maintenance for example, could still be used with the knowledge that community homogenisation may take place.

The importance of multi-taxon survey designs was highlighted in **Chapter 5**. Species form one taxonomic group can sometimes be used to assess the diversity and abundance of other taxonomic groups. However, it is a major challenge to identify, with confidence, reliable surrogate indicator taxa (Lund and Rahbek, 2002), which have the potential to be useful in conservation biology (Caro and O'Doherty, 1999). These indicator species also require linkage with specific stressors (Niemi and McDonald, 2004), such as large herbivore grazing. Grazing has been identified as a stressor which can alter, and often reverse, the nature of the surrogacy relationships among vegetation, spiders and birds (**Chapter 5**). This is particularly relevant for nature conservation, where management aims are often developed with a focus on one particular group or species, and the wider biodiversity implications may not be considered. For example, a management aim focused on promotion of bryophyte diversity may increase grazing pressure, which in turn may reduce vertical structure of the vegetation and have negative knock-on effects on the bird and spider communities (**Chapter 2**, **chapter 5**).

Conducting research for the improvement of conservation area management can be theorised as being part of a continuous process cycle (Fig. 6.2). This process is based on continuous improvement through a consultation-research-policy-practice cycle and is often referred to as adaptive management (van Wilgen and Biggs, 2011, Wintle and Lindenmayer, 2008, Rogers and Biggs, 1999, Keith et al., 2011). With regard to large herbivore management, the inclusion of stakeholders in management processes has highlighted the importance of landscape-level collaborative management in achieving conservation objectives (Austin et al., 2013), although careful consideration is required when sharing responsibilities (Davies and White, 2012). Traditional land management practices can often play a part in conservation management, particularly where landscapes have evolved with herbivore grazing (Middleton, 2013).

Research into a wide variety of issues relating to large herbivore interaction with woodlands has been carried out (e.g. Côté et al., 2004), and now this needs to be translated into policy. Even within a small geographic area such as the UK and Ireland, a unified policy on the management of wild large herbivores may not be possible (Putman, 2010). Policies on large herbivore management are often made at a local (e.g. individual land owners) or regional (e.g. regional government agency) scale, resulting in a wide range of approaches. Fencing is a policy which has been put into practice in several National Parks in Ireland (NPWS, 2005b, NPWS, 2005a), however, the ecological and financial costs of this do not always return positives (e.g. Pérez and Pacheco, 2006, **Chapter 3**). For the effective management of wild large herbivores in the landscape, and for bridging the gaps between the stages of the continuous management process (Fig 6.2), communicating with policy makers, stakeholders, and the public may be as important as scientific findings (Tanentzap et al., 2012). The findings of this thesis now need to be fed into the management process through a set of clear recommendations.

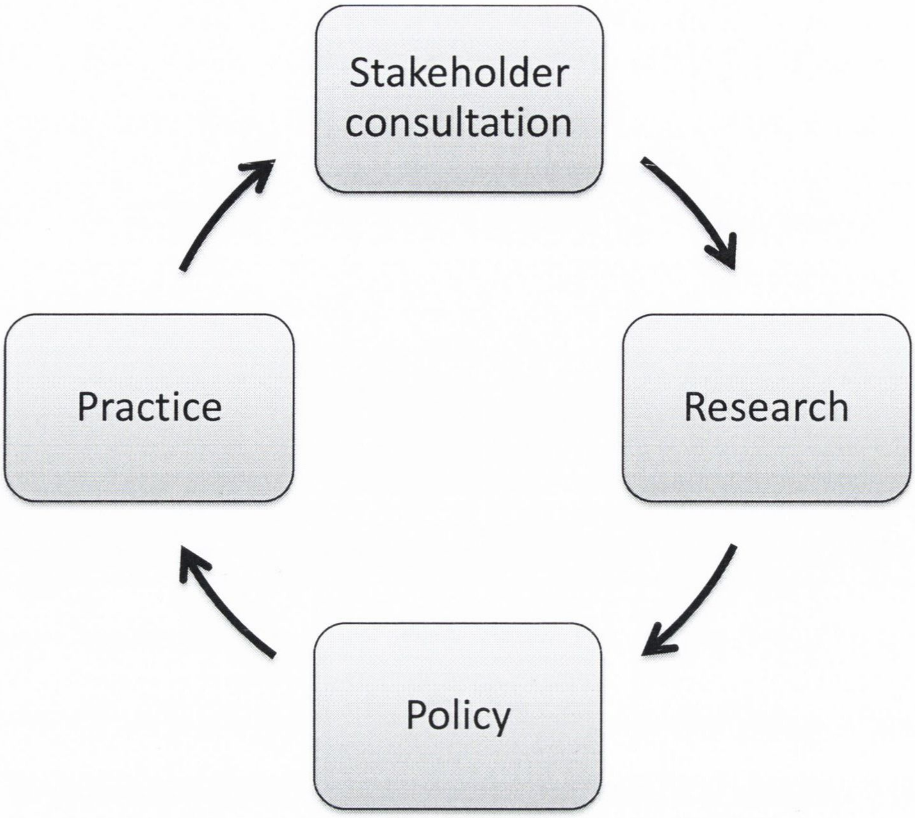

Fig. 6.2 Theorised management process where each stage feeds into the next for continuous improvement.

6.4 Recommendations

One of the goals of this thesis was to improve and enhance large herbivore management practices in protected oak woodland conservation areas. This body of work has combined extensive primary research with detailed reviews of these findings in the context of other classic and contemporary work. The following management recommendations can be endorsed:

- Where woodland conservation and regeneration are desired, low grazing impacts, but not zero grazing, should be maintained. This is most likely to promote regeneration while also maintaining both vascular plant and bryophyte communities. Management practices should be diversified in space and time in order to be adaptable to specific site conditions and achieve the overall conservation objectives.

- Assessment of large herbivore populations should be focused on a set of clearly defined conservation objectives. There are many assessment methods available but their usefulness depends on the specific objective of management.

- Large-scale long-term fencing of oak woodlands should be replaced by large herbivore management programmes, in order to ensure the conservation of diverse native woodland ecosystems. These programmes should be implemented using adaptive management, where large herbivore impacts are monitored and adjusted, through culling, to achieve specific long-term management objectives.

- Additional taxonomic groups should be included in the assessment of woodland biodiversity, for management and conservation purposes, particularly when stressors to ecosystem functioning, such as grazing, are present.

- Managers should implement long-term tree regeneration survey programmes, in a range of woodland habitat types, in order to understand long-term trends and to focus management to encourage regeneration in areas where woodland regeneration is desired.

- The continued monitoring and maintenance of the existing experimental plot network should be included in any long-term management plans for these protected areas. This will ensure that quality data is available to help inform management decisions in the future.

6.5 Limitations and future research

6.5.1 Limitations

As with all ecological studies, and scientific method in general, there are limitations to the research presented in this thesis. Ecological studies benefit greatly from an increase in true replication (Underwood, 2005) as the variation present in the 'real world' is often high, and can be difficult to account for in analyses. This thesis utilised every suitable experimental plot available in Irish semi-natural oak woodlands, however, lack of exclosure maintenance (resulting in derelict plots) and changes to management objectives, reduced the number of available plots. However, new exclosures have been added to the network (see **section 6.5.2**).

During this research, significant effort was expended on the scrutiny and digitisation of long-term survey records. Many of these records, dating back to 1969, were in the form of original field recording sheets. Although much time and effort was spent on this task, which could have been analysing additional datasets not included in this thesis, it has resulted in the first fully assembled digital database for a network of long-term woodland exclosure plots within National Parks in Ireland.

Unfortunately, there were limited data analysis options for **Chapter 3**. After attempts at linear and non-linear mixed effects modelling, residual data points displayed unacceptably heterogeneous patterns, voiding the significant effect of 'the time since fencing' continuous variable. After this, limited analysis techniques were available, without the violation of statistical assumptions.

Although all suitable experimental plots were utilised, this thesis, and most studies, would have benefited from larger number of independent experimental plots more widely distributed across the habitat, and a completed 'ready to use' electronic database of long-term survey results.

6.5.2 Future research

The issues and themes highlighted in this thesis present the opportunity for a wide variety of additional and continuation research. As all biological experimentation is essentially preliminary and requires progression (Underwood, 2005), it is recommended that future research focus on the following:

- Firstly, the continued monitoring, and maintenance, of the existing network of experimental plots is essential. Woodland dynamics are long-term processes, and datasets spanning multiple decades allow for the separation of short-term fluctuations from long-term trends within the woodland system. Three new large herbivore exclosure plots were established in Wicklow Mountains National Park during the duration of this thesis (winter 2012), but could not be surveyed for inclusion here. It is vital for future analysis and interpretation of vegetation change that baseline surveys are carried out for new exclosures.

- Deer impact assessment and management is a continuing and necessary stream for research focus. Future research should focus on guidelines for appropriate methods of assessment based on specific management objectives.

- Future research should further investigate the effects of large herbivore grazing on the relationships among different taxonomic groups. This research avenue, which was highlighted in this thesis, is of high interest to management and could be greatly expanded on. Future research should test the relationships among taxa on independent data sets, and also carry out surveys across a range of grazing impact levels in order to understand how surrogacy relationships are altered.

- Finally, the public's perception of woodlands and their management is in need of further investigation. Social science methods can be employed to help bridge the gap between the public, policy, and practice. Of particular interest is the public's perception of woodland conservation areas and policies of large herbivore management through culling. This can be a contentious issue as stakeholders often exhibit contrasting opinions. Future research should incorporate stakeholder perceptions into the study design, and focus on translating research findings into policy and practice.

6.6 Concluding remarks

Where wild large herbivores have co-evolved with the landscape, their presence in the ecosystem is of great importance (Vera, 2000, Kirby et al., 1994, Hester et al., 2000). However, through reduction of suitable natural habitats, loss of natural predators, and population expansion into former agriculture, large wild herbivores population levels have increased throughout Europe in recent decades (Carden et al., 2010, Austrheim et al., 2011). Large herbivores interact with vegetation through browsing and grazing, which can alter growth, succession, interactions among taxonomic groups and overall ecosystem functioning (e.g. Côté et al., 2004, Tanentzap and Coomes, 2012).

This thesis assessed the effect of time and large herbivores on the woodland community, with a goal of improving or feeding into management practices for protected biodiversity conservation areas. Specific objectives relating to large herbivore impact have been addressed: the long-term effect of large herbivore removal, multi-taxon surrogacies, and the effects of time and habitat on regeneration.

The research presented in this thesis, in the context of previous studies, has shown that management practices should be diversified in space and time in order to be adaptable to specific site conditions and achieve the overall conservation objectives. Large herbivore grazing levels have a range of impacts on vegetation and its structure, whereas a general homogenisation of temperate oak woodlands is likely with total large herbivore removal. Results also suggest that the relationships among taxa may be altered, and sometimes reversed, when comparing large herbivore exclosures with grazed areas. Without continued long-term monitoring projects, such as the ones detailed here, the true drivers of change may not be identified and the conservation of woodland will suffer.

On the basis of these findings, it can be recommended that where woodland conservation and regeneration are desired, low grazing impacts, but not zero grazing, should be maintained. Large-scale long-term fencing of oak woodlands should be replaced by large herbivore management programmes, in order to ensure the conservation of diverse native woodland ecosystems. It is recommended that more taxonomic groups be included in biological assessment for management and conservation when stressors to ecosystem functioning, such as grazing, are present. Also, Managers of protected area should use research findings, such as those presented in this thesis, to adapt management practices in order to promote woodland regeneration. Management should specifically focus on large herbivore impacts and quantifying tree regeneration change through time.

Further research should focus on the continued monitoring of experimental plots, the assessment methods and objectives for large herbivores, the effects of grazing on the interaction among taxonomic groups, incorporating stakeholder perceptions, and translating research into policy and practice.

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