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Biological communities and environmental controls in a seasonal wetland habitat

A thesis submitted for the degree of Doctor of Philosophy

November 2016

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Declaration

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Summary

In a context of global biodiversity decline, ponds have been identified as biologically rich habitats, and temporary ponds can support distinct communities of rare species. Some pond habitats, including dune slacks, are conserved under the EU Habitats Directive, and their conservation status must be assessed once every six years by signatory states. Dune slacks are an example of a habitat which is periodically disturbed and experiences habitat heterogeneity, with both a dry and a flooded phase annually. The objective of this research was to determine whether the underlying conditions of dune slacks allow their biological assemblages to respond differently to environmental conditions.

I investigated the degree of cross congruence displayed by plants, snails and water beetles in dune slacks. I also tested the ability of the methods used under Article 17 of the Habitats Directive to determine whether a habitat assessment based on plants could identify specific snail and water beetle assemblages of conservation interest. I found that plants, snails and water beetles do not show congruent patterns of diversity or species composition, and that the habitat assessment did not identify sites where snails and beetles of conservation interest occurred. This is the first time that the structure and functions assessment used in compliance with Article 17 of the Habitats Directive has been tested to determine whether it functions as a broad indicator of habitat condition, and I showed that in a disturbed, heterogeneous habitat, cross-congruence among taxa should not be assumed, even in the absence of human disturbance.

I also examined the relationships between environmental variables and the composition of plants, snails and water beetles in dune slack sites. Both species and trait composition were used in the analysis which revealed that all three of the selected taxa responded to the presence of livestock, but the response could only be detected by examining the snail and beetle assemblages through their trait composition rather than their species composition. Through this, I demonstrated the importance of considering species traits in conservation ecology, both in designing conservation assessment protocols and in predicting potential responses for different taxa.

The hydrology and hydrochemistry of six dune slacks were characterised, constituting the first consistent study of hydrological functioning of dune slacks at multiple sites in Ireland. I also examined the hydrology and water chemistry of dune slacks under two different management regimes: non –intensive pasture and golf courses. I found that the maximum water level in dune slacks and the range of water fluctuation were greater in dune slacks managed as pasture than in dune slacks associated with golf courses. I also found evidence that denitrification was likely to be occurring below ground in dune slacks and that the response of groundwater to rainfall is very similar in some dune slacks. Finally, I explored the relationship of assemblages of plants and snails with water chemistry and water levels in the dune slacks where they occur. I found that snail communities were related to groundwater alkalinity and surface water soluble phosphorus. This demonstrates that groundwater as well as surface water conditions are relevant to invertebrates of wetlands.

I found that dune slacks provide habitat for a range of rare invertebrate species of wetlands and freshwater habitats as well as having a diverse flora. The results presented here demonstrate the need to consider new methods to assess the condition of habitats which experience such heterogeneous conditions. Suggestions are made for further research in the area and I made recommendations for management and assessment of dune slacks and wetlands of conservation interest.

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A list of specific contributors to the thesis is provided below.

List of main contributors to Chapters:

Chapter	**Name**	**Contribution**
1	Aoife Delaney	Writing
	Jane Stout	Structure and comments on draft chapter
2	Aoife Delaney	Concept/experimental design, data collection, sample processing and identification, statistical analysis, writing
	Jane Stout	Concept/experimental design, comments on draft chapter
	Shona Baker and Zeina Faris	Assistance in processing biological samples
	Maria Long, Jo Denyer and Garth Foster	Identification of voucher specimens
	Jesko Zimmerman	Comments on draft Chapter
3	Aoife Delaney	Concept/experimental design, data collection, sample processing and identification, statistical analysis, writing
	Jane Stout	Concept/experimental design, comments on draft chapter
	Zeina Faris	Assistance with habitat digitisation
4	Aoife Delaney	Concept/experimental design, data collection, sample processing and identification, statistical analysis, writing
	Jane Stout	Comments on draft chapter
	Catherine Coxon	Concept/experimental design, assistance with fieldwork, comments on draft chapter

	Pete Coxon and Laura Healy	Assistance with fieldwork, described and analysed sediment samples
	Mark Kavanagh	Assistance and guidance in carrying out analysis of water chemistry
	Andrew Jackson	Assisted with development of a statistical method to assess the response to of water levels to rainfall
	Jesko Zimmerman	Comments on draft Chapter
5	Aoife Delaney	Concept/experimental design, data collection, sample processing and identification, statistical analysis, writing
	Jane Stout	Concept/experimental design, comments on draft chapter
	Catherine Coxon	Concept/experimental design, assistance with fieldwork
	Mark Kavanagh	Assistance and guidance in carrying out analysis of water chemistry
	Shona Baker and Zeina Faris	Assistance in processing biological samples
	Maria Long, Jo Denyer and Garth Foster	Identification of voucher specimens
6	Aoife Delaney	Concept/experimental design, data collection, sample processing and identification, statistical analysis, writing
	Catherine Coxon	Concept/experimental design, comments on final draft
	Jane Stout	Concept/experimental design, comments on draft chapter

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1 Introduction

1.1 Temporary water bodies

Global biodiversity decline has been associated with reductions in ecosystem productivity (Liang *et al.*, 2016) and consequent ecosystem service provision (Cardinale *et al.*, 2012), across many different habitat types. In the last 15 years, there has been an increased focus on the ecology of temporary water bodies, such as ponds, in Europe, with growing awareness of the importance of such habitats as providers of ecosystem services and in preserving biodiversity (De Meester *et al.*, 2005; Céréghino *et al.*, 2008). De Meester *et al.* (2005) listed several characteristics which make ponds suitable for use as model systems where ecological theories can be tested: they are numerous and widespread, allowing for replication over wide geographic areas; they have well defined boundaries outside of which the habitat is very different; and for aquatic species, ponds can be considered oases in an otherwise unsuitable environment. Because ponds are small habitats with well-defined boundaries, relatively simple and low cost sampling procedures can prove effective. Ponds can be very biologically heterogeneous, and it is partly this variation which contributes to their importance as reservoirs of biodiversity (De Meester *et al.*, 2005). However, such idiosyncratic variation can make it difficult to discern explanatory variables in patterns of diversity (Hassall, Hollinshead and Hull, 2011). Dune slacks are a specialised subset of ponds, with many common features, so they offer excellent potential to study the effects of selected environmental variables on diversity in a relatively consistent habitat.

1.2 Dune slacks

Coastal sand dunes are found all over the world, and are widespread on the coast of Europe (Figure 1.1). Fixed dunes provide the bulk of the dune area, and at some locations they are interspersed with wet inter-dunal valleys, or dune slacks. Dune slacks are sheltered seasonal wetlands where the water table is close to the ground surface. Annual winter flooding of the slacks is common, in contrast to the exposed, free draining dune ridges, and they provide habitat for species which could not otherwise persist in sand dune habitats.

Figure 1.1 Range of dune slacks in the European Union (blue squares) according to the Article 17 Consultation Habitats Map (http://discomap.eea.europa.eu).

There are two natural ways in which dune slacks form. Primary slacks are relict beaches cut off from the sea by an aggressively forming dune ridge, and secondary slacks form when winds scour a dune system, removing sand from un-vegetated parts of the fixed dunes. Erosion can persist until the wet sand at the water table is exposed, leaving a depression or in some cases a large flat deflation plain.

1.3 Dune slack hydrology

Figure 1.2 A primary dune slack at Bull Island in August 2013 (left) and April 2014 (right).

A fluctuating, shallow water table and seasonal flooding set dune slacks apart from other sand dune habitats (Figure 1.2). The main supply of water to dune slacks is fresh, nutrient-poor groundwater, which is derived from rain that falls on the dune system and percolates into the sand. Groundwater in the sand dunes travels from areas of high to low elevation, so the position of the dune slack in the larger sand dune system affects its hydrological characteristics (Figure 1.3). Flow-through slacks occur where the groundwater rises above the level of the dune slack on one side and travels down the gradient to a point where it infiltrates back into the sand dune system. Alternatively, dune slacks may receive water from their surrounding dune ridges and lose it to evaporation. Dune slacks that are very close to the landward boundary of the dune system are more likely to have an influence of groundwater from outside the sand dune system. Inputs from inland may occur as surface water if drains, streams or rivers travel through the dune system before exiting to the sea. Water can travel downwards from these surface waterbodies to the groundwater as they travel through the sand (Rhymes *et al.*, 2014). Some slacks do not flood but maintain damp conditions because the water table is close to the surface.

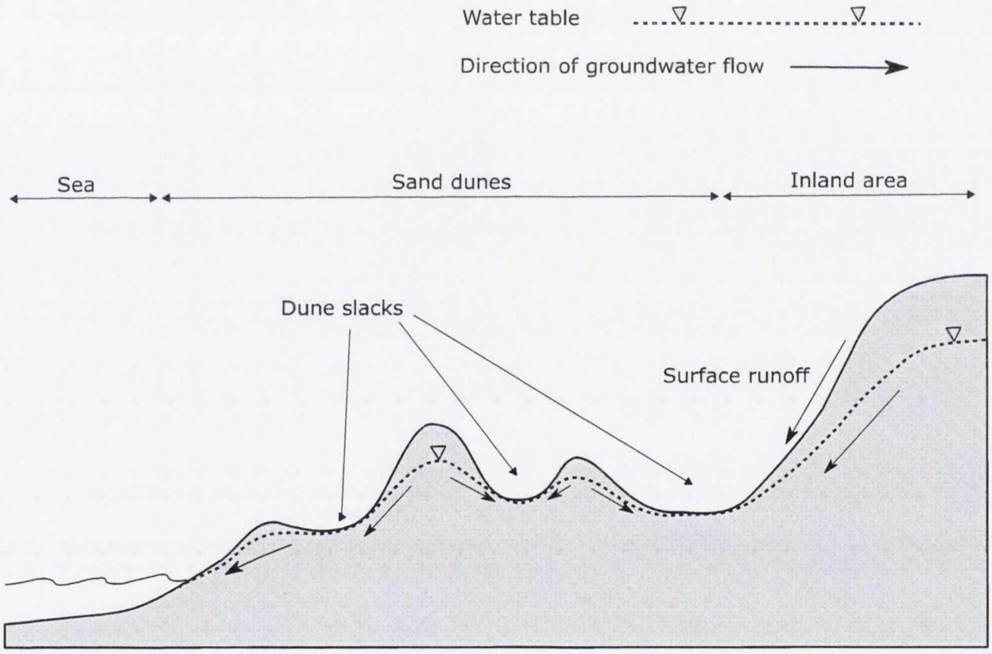

Figure 1.3 Simplified diagram showing groundwater moving through a sand dune system with dune slacks. Adapted from Davy *et al.* (2006).

Most Irish sand dunes contain calcium carbonate either due to the parent material of the sand or from shell particles, and as groundwater flows through the dunes it becomes rich in calcium (Curtis 1991). Dune slacks are naturally poor in nutrients, but water travels through sand quickly, and this makes the groundwater body vulnerable to contamination (Fenton *et al.*, 2011). Potential sources of contamination include domestic waste water from houses and campsites as well as agricultural waste; including silage leachate and run-off from farm yards and fertilised fields which enter the sand dune system through drains or in groundwater. Activities within the sand dune system are most likely to result in contamination, but at sites which receive an input of water from inland, the pollution sources can be outside of the sand dune system (Rhymes *et al.*, 2014).

1.4 Biological communities of dune slacks

European dune slacks typically contain a calcareous wetland flora with a low nutrient requirement. Sedges (*Carex nigra*, *C. flacca*) and grasses (*Festuca rubra*, *Agrostis stolonifera*, *Holcus lanatus*) are interspersed with broadleaved herbs (*Hydrocotyle vulgaris*, *Potentilla anserina*, *Mentha aquatica*, *Lotus corniculatus*) and there is often a rich cover of bryophytes (*Calliergonella cuspidata*, *Bryum pseudotriquetrum*, *Campylium stellatum*). In areas experiencing some nutrient enrichment, *Iris pseudacorus* and *Phragmites australis* may occur. Rare plants associated with dune slacks include *Pyrola rotundifolia* and *Petalophyllum ralfsii* (Rodwell, Pigott and Joint Nature Conservation Committee (Great Britain), 2000).

Several studies in the UK have commented on the links between dune slack invertebrate communities and those of other wetlands. Duffey (1968) found that most dune slack spiders were species typical of freshwater marsh, and Eyre and Luff (2005) found that dune slacks supported a distinct community of ground beetles in northern England, with the most common species noted being associated with wet grassland habitats. In a review of published and unpublished literature, 462 invertebrates species strongly associated with sand dunes in Wales were identified, and of these 50 were most commonly found in dune slacks, the greatest number primarily associated with any habitat other than bare sand (Howe, Knight and Clee, 2010). These studies were carried out during the dry summer season.

While investigations of vegetation and terrestrial invertebrates have shown that they have a characteristic flora and fauna, aquatic invertebrates of dune slacks have not been comprehensively studied in Europe or elsewhere. However, research has been carried out on aquatic invertebrates of temporary fresh water bodies such as turloughs, Mediterranean temporary ponds and ponds in agricultural landscapes. Turloughs, which are seasonal lakes of karst landscapes common in the west of Ireland, have been found to support a diverse macroinvertebrate community (O'Connor *et al.* 2004; Lott & Bilton 1991) including rare and restricted species particularly associated with sites that dry up completely in summer (Porst and Irvine, 2009b). In a network of Mediterranean temporary ponds, diversity both within ponds and between them was found to be high, and the suite of species found changed over the course of the flood period (Florencio *et al.*, 2009). A survey of ponds in agricultural land in the UK found that temporary ponds supported fewer species than permanent and semi-permanent ponds, but that there was a distinct set of species which was associated with the temporary habitat, and temporary and semi-permanent ponds had a tendency to include more rare species (Collinson *et al.*, 1995).

Dune slacks also provide habitat for amphibians, including the rare natterjack toad *Bufo calamita*, and provide forage for waders in Britain and Ireland (Jones, 1973; Beebee, 2002).

To understand the biological communities in dune-slacks, they need to be properly sampled. The aim of sampling is to obtain a representative sample of a biological population within the constraints of available resources. Sampling should be informed by the purpose of the survey, so for a study which will compare populations across space, the sampling protocol should be consistent across all sites to reduce the impact of sampling bias and should ensure a quantitative result for statistical analysis. If the effects of dominance, evenness and community composition are important, a measure of abundance should be incorporated (Maurer & McGill 2011, Kent 2011).

Comparing the diversity of biological organisms in different locations is a fundamental aspect of community ecology. The simplest approach is to count species. This is useful as it yields a number for analysis and can be replicated across different sites. However, it does not provide us with any information on composition, so two sites which both contain ten species will get the same score, even if the species are all evenly distributed at one site, whereas at the other 90% of the area is taken up by a single species. Measures such as Simpson's and Shannon diversity indices are sensitive to the abundance of different species, so that a site where species are more evenly distributed scores more highly than a site with a small number of highly abundant species and many low-abundance species. Diversity indices are more informative than species richness alone, but by collapsing information regarding a large number of species into a single number for each site, we still lose a lot of information. Importantly, we can no longer discriminate between sites which are equally diverse but contain totally different sets of species (Maurer & McGill 2011).

The concept of diversity partitioning was developed to explore species turnover along a gradient (Whittaker, 1972; Lande, 1996).This approach divides total diversity (gamma diversity) into average diversity within habitat patches (alpha diversity) and the diversity between habitat patches (beta-diversity). For example, in a set of dune slacks within a sand dune system, the gamma diversity for the dune slack habitat is the diversity calculated from surveys of all of the individual dune slacks put together. Alpha diversity is the average diversity within each dune slack, and beta diversity is the difference between alpha diversity and gamma diversity. If the dune slacks contain very similar species, alpha diversity will represent a large proportion of gamma diversity, while high turnover between dune slacks will result in beta diversity occupying a large portion of gamma diversity.

Multivariate methods such as ordination techniques allow us to compare communities by identifying sites which contain similar and different species. They are particularly useful for investigating environmental gradients which alter the composition of a habitat but do not change the overall number of species which occur in it (Kent 2011). An informative approach for identifying and explaining differences in diversity is to combine analyses of species richness, diversity and composition.

Methods to accurately estimate the number and types of species in a habitat can be labour intensive and time consuming. There is also a large skill and knowledge requirement for species identification. As a result, the costs of comprehensive surveying for large scale national and international conservation and monitoring schemes (e.g. see section 1.7) are prohibitive. An alternative method for assessing the condition of a habitat is to monitor a subset of species which are likely to be representative of the habitat as a whole, and which can be considered indicator species. To perform well as an indicator, a taxon should respond to environmental variation in a similar way to co-occurring species (Westgate *et al.*, 2016). It should be easy and inexpensive to sample and taxonomically well-described to facilitate identification (Pearson, 1994). It is also important to consider the habitat characteristics when choosing an indicator taxon, for example taxa with smaller body-sizes are better predictors of diversity at small grain sizes than larger taxa (Wolters *et al.* 2006). Plants of dune slacks are well studied and they are known to be sensitive to changes in hydrological functioning (Lammerts *et al.*, 1999; Lammerts, Maas and Grootjans, 2001). Snails and water beetles are strongly linked to the wetland habitat, their body size is suitable for a small habitat and they are sensitive to environmental variation (Foster *et al.*, 1992; Menetrey *et al.*, 2005). Thus they may be suitable additional indicators for dune slack habitats. These three taxa (plants, snails and water beetles) differ in their trophic level, mobility and response to disturbance, and so facilitate a comparison of complementary species in a naturally disturbed habitat.

Using species as indicators or surrogates in this way assumes cross-congruence; the diversity or composition of many taxa are linked, so that changes to the diversity or composition of the broader biological community can be determined by surveying the indicator species alone (Westgate *et al.*, 2016). Cross congruence has been shown to occur in nature and is very influential in conservation planning and policy (Howard *et al.*, 1998a; Gioria *et al.*, 2010), but there are situations when the composition and diversity of biological assemblages diverge. The scale of a habitat, degree of heterogeneity and history of human disturbance all affect the likelihood that cross congruence will be observed (Hess *et al.*, 2006; Ekroos *et al.*, 2013; Rooney and Azeria, 2015).

1.5 Environmental influences on dune slack communities

Plant communities of dune slacks are sensitive to changes in the nutrient status, pH, water level and flood duration (Grootjans *et al.*, 1991). Pollution of groundwater and lowering the water table in the Netherlands have been demonstrated to result in the vegetation of dune slacks undergoing rapid succession to vegetation types typical of mesotrophic or acidic conditions (Grootjans *et al.*, 1991). It is difficult to separate changes due to desiccation and nutrient enrichment, or determine the degree to which dune slacks are vulnerable to small changes in water chemistry, because much of the hydroecological work carried out to date has focused on highly contaminated dune slacks where water has been abstracted on a large scale (Davy *et al.*, 2010). Recent investigations, however, have demonstrated that farming adjacent to dune systems can cause groundwater pollution which is sufficient to alter the character of vegetation affected (Rhymes *et al.*, 2014).

Within temporary ponds, morphology of the pond, habitat heterogeneity, shading and productivity have been linked to differences in macroinvertebrate communities in Ireland and elsewhere in Europe, although there are inconsistencies between studies seeking to identify the main environmental factors affecting pond diversity (Porst & Irvine 2009; O'Connor *et al.* 2004; Florencio *et al.* 2013; Hassall *et al.* 2011; Briers & Biggs 2005). Desiccation is a major disturbance in an aquatic environment and exerts a strong selective pressure on the species associated with temporary ponds. Different species may have adapted to fluctuating water levels by having a broad tolerance of changing conditions or they may avoid unsuitable conditions through dormancy or migration (Collinson *et al.*, 1995).

Water chemistry also exerts selective pressure; diversity of both invertebrates and plants has been shown to increase with pH in ponds in the UK, indicating that more acidic ponds are less diverse (Biggs *et al.*, 2005). The effect of nutrient load varies among taxa so that in some cases eutrophic or oligotrophic conditions have fewer species (Hassall, Hollinshead and Hull, 2011), while in a study of turloughs, increasing corixid (a family of aquatic Hemiptera) diversity was associated with nutrient enrichment (Reynolds 2003). In temporary Mediterranean ponds of the Donana, Spain, Florencio *et al.* (2013) found that that environmental variables such as plant diversity, conductivity and water depth had a strong influence on macroinvertebrate diversity. Heavy grazing and trampling by livestock were found to have a negative effect on a rare assemblage of aquatic invertebrates associated with mossy turlough margins in particular (Bilton, 1988).

There is evidence that stochastic and selective pressures act simultaneously on temporary ponds (Jeffries, 2010; Florencio *et al.*, 2013), so that while many species may colonise the ponds, environmental factors within the ponds filter out poorly-adapted species. Stochastic distributions are associated with mobile taxa which can move between suitable patches of habitat. They are influenced by proximity or connectedness to other water bodies and by the dispersal abilities of different taxa (Bossuyt, Honnay and Hermy, 2003; Briers and Biggs, 2005).

1.6 Using functional traits to characterise ecological communities

Functional traits mediate the response of a species to its environmental conditions as well as dictating its effect on other species (Diaz and Cabido, 2001). The role of species traits in ecosystem functioning and in response to environmental conditions has been observed both in plants and invertebrates (Lavorel and Garnier, 2002; Poff *et al.*, 2006). The total diversity of traits in a community can be expressed as a single metric (Petchey and Gaston, 2006) or the abundance of different traits in the community can be related to environmental gradients (Chevene, Doleadec and Chessel, 1994). Linking the trait composition of a community or assemblage to specific environmental conditions provides a mechanistic insight into the pressures affecting different taxonomic groups, and is therefore particularly useful when comparing the responses of different assemblages to environmental variables (Diaz and Cabido, 2001). They are of particular value in habitat assessment because functional trait composition can have a stronger response to anthropogenic disturbance in freshwater habitats than species composition, and also because they function when applied at the species, genus or family level (Menezes, Baird and Soares, 2010). Although considering communities in terms of traits has proved to be useful, there are factors which can reduce the power of trait based analysis. A weak response to environmental variables is more likely if the traits chosen are strongly conserved within phylogenetic groups (Poff *et al.*, 2006) and the impact of a specific environmental variable is likely to be greater on some traits than others (Statzner, Dolédec and Hugueny, 2004). Caution should be also used when comparing communities on the basis of information from trait databases because they do not take into account habitat-specific phenotypic trait variation. Another reason why traits might fail to show as a response to environmental variation is the inclusion of disparate taxa which respond differently to change, so it is advised to choose groups of similar species for analysis (Usseglio-Polatera *et al.*, 2000).

1.7 Legislative framework

Because of their unstable sandy substrate, coastal dunes are unsuitable for many modern farming practices, and they have avoided the large scale drainage, reseeding and agrochemical application common in lowland Ireland and Europe. As traditionally managed habitats, they continue to provide habitat for a range of species which have become uncommon elsewhere.

The conservation value of sand dune habitats has been recognised under the EU Habitats Directive and they are designated as 2190 Humid dune slacks (Council Directive 92/43/EEC). The ultimate aim of the Habitats Directive is that all of the habitats and species of community interest achieve favourable conservation status (Evans and Arvela, 2011). In compliance with Article 17 of the Habitats Directive, the conservation status of Annex I habitats is assessed every six years by signatory states and reported to the European Commission. Conservation status is assessed under three parameters: area, structure and functions and future prospects. Recommendations for the assessing structure and functions include the use of indicator species (Evans and Arvela, 2011). Guidance regarding typical species is provided in the Interpretation manual for European Union habitats (European Commission, 2013) and individual countries are encouraged to develop their own list of typical species which are associated with the habitat when it is in good condition. A list of negative indicator species which are associated with habitat degradation should also be compiled. The abundance of these positive and negative species form a major component of the habitat structure and functions assessment (Evans and Arvela, 2011).

According to the guidelines for reporting under Article 17 (Evans & Arvela, 2011), animal species should be included in the assessment of coastal dune habitats. However, the typical species listed for Ireland, the UK (Common standards monitoring guidance, 27 Oct 2016), France and Portugal do not contain any animal species. Typical species for Denmark are not available, but the remaining countries in the Atlantic biogeographical region (Germany, the Netherlands and Belgium) have included some bird species and the natterjack toad (European topic centre on biological diversity, accessed 23 October 2016).

Dune slacks identified as protected areas under the Habitats Directive are also protected as groundwater dependent terrestrial ecosystems (GWDTEs) under the EU Water Framework Directive (Council Directive 2000/60/EC). Both of these pieces of legislation give protection to the groundwater bodies which feed dune slacks. However, implementation of the Water Framework Directive in Ireland has to date focussed on larger aquifers, and has not included sand dune features. While threats to the groundwater which feeds dune slacks can be inferred from the presence of drains, farmyards or camp sites within the dune boundaries, there has been no wide-scale monitoring of sand dune aquifers.

1.8 Research objectives

Dune slacks act as a refuge for wetland species which are now rare in lowland agricultural areas of Ireland. Their dual protection under the Habitats Directive and the Water Framework Directive is a reflection of their conservation value. However, by primarily assessing their current habitat condition based on plant indicator species, important changes in their value as a habitat for other taxa could be lost. There is also insufficient information regarding their hydrological functioning in

Ireland to determine the effects of human activities on their water levels and water chemistry. This study seeks to provide information supporting improved conservation outcomes for dune slacks through improved understanding of their biological communities, hydrology and water chemistry.

To determine whether plants are suitable indicator species in dune slack habitats, I compared the species richness, diversity and composition of plants, snails and water beetles in a large-scale national survey of Irish dune slacks (Chapter 2). I also carried out a habitat assessment of each dune slack in accordance with the guidance for assessing dune slacks under Article 17 of the Habitats Directive. I then compared the species richness, diversity and composition of snail and water beetles in the sites that passed and failed the habitat assessment to determine whether particular invertebrate assemblages were associated with habitats in good condition according to the assessment. All plant and invertebrate data were submitted to the National Parks and Wildlife Service and the National Biodiversity Data Centre.

Much of current conservation activity is focussed on the effects of natural environmental pressures on ecosystems, as well as reducing the impact of human activities on diverse habitats and rare species. However, it is difficult to characterise the effects of environmental drivers on biological assemblages which are characterised by high beta diversity, or species turnover between sites. In Chapter 3, functional traits of plants, snails and water beetles found in the large-scale national survey were used, in conjunction with species composition, to investigate the environmental factors which structure biological communities in dune slacks.

Hydrology and hydrochemistry have been shown to be major drivers of dune slack condition in continental Europe, but little is known about the hydrological functioning of dune slacks in Ireland. The majority of Irish dune slacks are located in conservation areas, but some are in golf courses which are excluded from the conservation network. In Chapter 4, I conducted detailed surveys in six sites in north-western Ireland to investigate the response of groundwater in dune slacks to rainfall. I also characterised the groundwater chemistry at each site with particular reference to indications that denitrification was taking place. Finally, I examined the relationship between groundwater chemistry and hydrology under management in conservation areas and as golf courses.

The penultimate chapter sought to connect the hydrology and water chemistry of dune slacks with their biological functioning. The diversity and composition of snail and plant assemblages found in dune slacks were compared to hydrological factors and water chemistry. The relationships of ground and surface water chemistry to plants and snails were examined separately.

In the final chapter, I discussed the main findings of this work in relation to the relevant literature, made suggestions for further research in the area and made recommendations for management and assessment of dune slacks and wetlands of conservation interest.

2 Do principles of cross congruence apply in a naturally disturbed habitat?

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2.1 Introduction

Increased awareness of the decline in biological diversity has stimulated many scientists to increase their efforts to quantify and monitor the Earth's biodiversity (Chapin *et al.*, 2000). However, often the resources available to scientists do not allow exhaustive studies of all the living things within systems of interest (Heino, 2010). An achievable alternative is the use of surrogates or indicators of biodiversity to infer the conservation status of a wide range of organisms in a habitat or area (Landres *et al.*, 1988). Indicator species have a long history in habitat assessment (Peterken, 1974; Ward and Evans, 1976) and were incorporated into international conservation policy as part of the EU Habitats Directive (Council Directive 92/43/EEC). Often the most familiar and easily surveyed groups, for which we have good records over space and time, are chosen as indicators, for example, birds, mammals and flowering plants (Sutherland *et al.*, 2004).

The use of indicator species to predict the diversity and distribution of other species is strongly reliant on theories of cross-taxon congruence, or the tendency of different taxa to have broadly similar diversity patterns across space. Large-scale comparative studies of diversity have demonstrated patterns of cross-congruence for either species richness or species composition, supporting the use of indicator species especially in regions of the world where diversity is poorly described (Howard *et al.*, 1998b; Lund and Rahbek, 2002; Wolters *et al.*, 2006). There is, however, a growing body of data which indicates that while cross-congruence is a common feature of ecological systems, relationships between diversity of different taxa are frequently weak. This undermines the effectiveness of indicator species in conservation assessments (Heino *et al.*, 2009; Westgate *et al.*, 2014).

In response, efforts have been made to identify factors which explain variation in cross-taxon congruence. Observed cross-congruence may be inflated in heterogeneous habitats as species diversity increases with habitat diversity (Ekroos *et al.*, 2013) and taxa which are very strongly associated with a particular habitat type are likely to be more congruent than generalist species (Prendergast, 1997). Therefore indicator species are most effective if they are applied within a specific habitat. The choice of indicator species should take habitat characteristics into account, for example cross-congruence tends to be weaker at smaller scales (Hess *et al.*, 2006), but this can be offset to some degree by using taxa with small body-sizes in habitats characterised by small patches (Wolters *et al.*, 2006). Strong cross-taxon congruence in aquatic systems has been observed in locations with little alteration due to human activities (Heino, 2010), which suggests that carefully chosen indicator species typical of undisturbed habitats may function well as surrogates for other taxa. This was demonstrated in a survey of wetlands where cross-congruence was weaker in systems with a history of human disturbance than in undisturbed sites, and individual species varied in their response to stress gradients (Rooney and Bayley, 2012). As a result, the choice of indicator taxon could strongly influence the ability of a habitat assessment to detect the effects of disturbances on other taxa.

Despite the body of research available to support decision-making in conservation, there is a history of non-evidence based conservation policies (Sutherland *et al.*, 2004). In many cases, financial expediency may take precedence over scientific research findings, reducing the value of interventions (Legg and Nagy, 2006). This has led to calls for monitoring schemes to assess the efficacy of conservation programs (Ferraro and Pattanayak, 2006).

The EU Habitats Directive combines interventions, such as setting up protected areas, with a monitoring programme. Part of this monitoring employs indicator species to assess the outcomes of conservation management on the structure and functions of habitats of conservation interest listed on Annex I of the Habitats Directive (Evans and Arvela, 2011). Plant-based indicator species lists are developed specifically for application in individual habitats. The listed species are strongly associated with the habitats and EU member states may suggest species which reflect the variant of habitat in their region (European Commission 2013). However, the monitoring system depends on indicator species from a narrow taxonomic range (vascular plants and bryophytes). Plants have been shown to correlate well with diversity of other taxonomic groups (Koch *et al.*, 2013), but some habitats in Europe are subjected to periodic natural disturbance events such as wild fire and flooding. If taxa respond differently to these natural disturbances, then using plant species as indicators of overall habitat condition may lead to important changes to the ecosystem being overlooked.

2.1.1 Aims

Using dune slacks as a model habitat, we assessed the degree of cross-taxon congruence among taxa with contrasting biological and habitat requirements in the context of frequent natural disturbance. Dune slacks are seasonally flooded depressions in sand dune systems ranging in size from a few square metres to several hectares (Grootjans and Stuyfzand, 1998; Delaney *et al.*, 2013). The annual flooding and desiccation events act as disturbances in the habitat, and the presence of a dry phase and an aquatic phase means that the habitat experiences temporal heterogeneity. Differences in weather conditions result in interannual variation as well as seasonal variation. They are also listed on Annex I of the EU Habitats Directive as 2190 Humid Dune Slacks (Council Directive 92/43/EEC), and their conservation status in signatory states to the Habitats Directive is assessed once every six years using a list of plants as indicator species.

The three taxa chosen for this study were plants (vascular plants and bryophytes), snails and water beetles. Vascular plants and bryophytes were chosen as these are currently used to assess habitat condition in dune slacks in accordance with the Habitats Directive. Water beetles and snails were chosen because they have small body size, are well described and can be identified to species, and are diverse groups which are sensitive to environmental changes (Bilton *et al.*, 2006). Both have been demonstrated to exhibit cross-taxon congruence in ponds (Bilton *et al.*, 2006; Gioria *et al.*, 2010) and they are commonly found in temporary waterbodies in Britain and Ireland (Reynolds, 1985; Nicolet *et al.*, 2004). However, because of differences in dispersal and lifecycles, water beetles and snails are likely to differ in their responses to flooding and desiccation.

Specifically, we tested three hypotheses:

1: species richness and diversity of all three taxa are positively correlated;

2: there is a relationship between the compositions of all three taxa such that they vary predictably in relation to each other;

3: the diversity and composition of snails and beetles are different in sites which passed and failed the habitat assessment.

2.2 Methods

2.2.1 Site selection

To do this, twenty-four dune slacks were selected across Ireland using pre-existing habitat maps (Ryle *et al.*, 2004; Delaney *et al.*, 2013) (Figure 2.1). Dune slacks were organised into six size classes (Appendix I). One slack from each size class was chosen in each of four areas: counties Donegal, Mayo, Kerry, and the east coast from Dublin to Wexford, which are the locations where most dune slacks are found in Ireland (Delaney *et al.* 2013). To ensure independence, only one slack was selected from any sand dune system. Dune slacks with permanent pools are rare in Ireland and were excluded from the site selection process as they are likely to have considerable ecological differences from seasonally flooded dune slacks and do not experience the annual disturbance of desiccation.

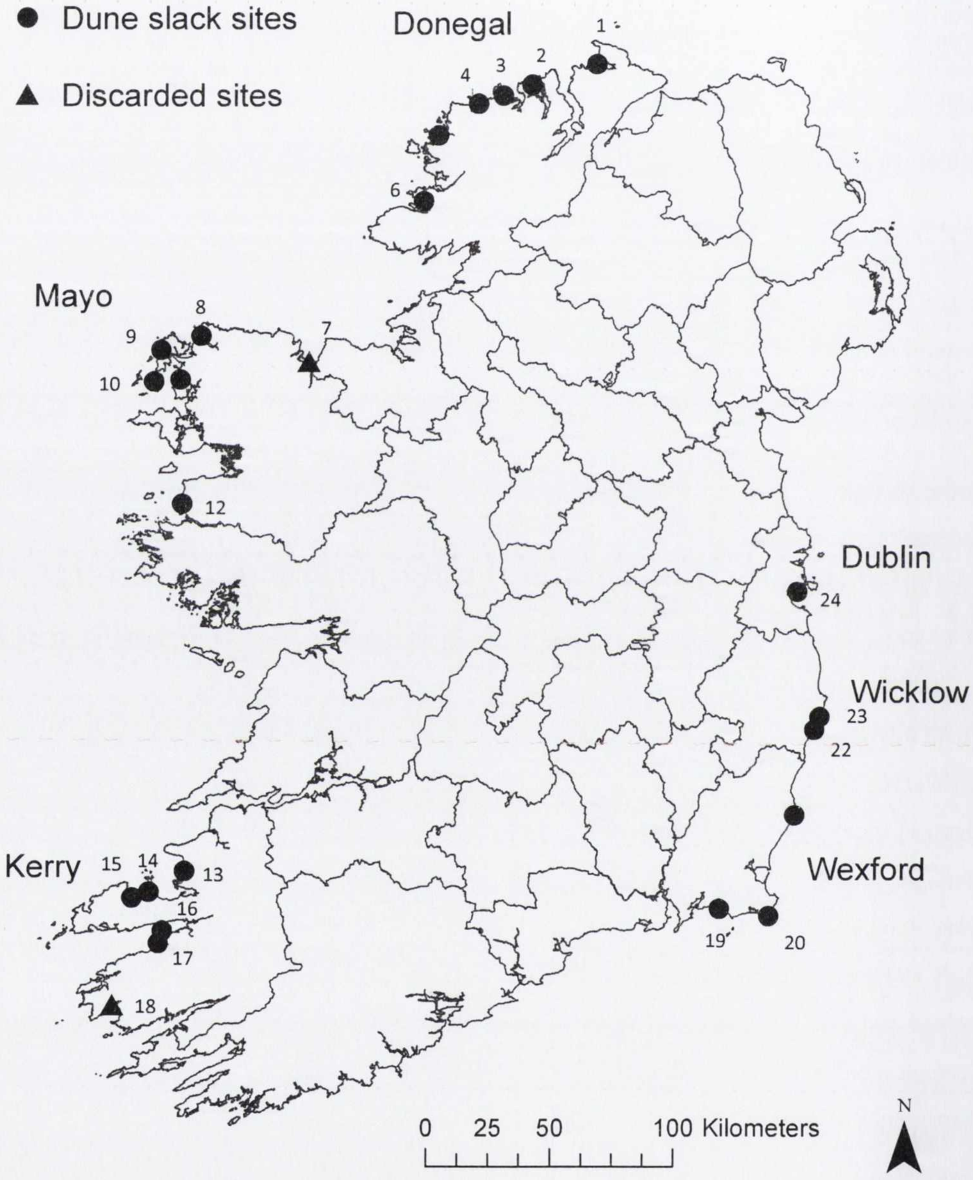

Figure 2.1 Dune slack sites included in this research. Reasons for discarding sites are given in section 2.3.

Table 2.1 Number of plant species and beetle and snail individuals recorded at sites. Blank fields represent sites for which records were not taken.

No.	Site	Code	Region	Area (ha)	Plant species	Snail individuals	Beetle individuals
1	Isle of Doagh	IOD	Donegal	6.85	40	30	2
2	Glenree	GRE	Donegal	1.54	44	35	4
3	Dunfanaghy	DFY	Donegal	0.82	31	226	2
4	Fortown	FTN	Donegal	3.15	50	22	3
5	Kincasslagh	KLH	Donegal	0.44	40	10	0
6	Sheskinmore	SKR	Donegal	0.27	37	76	71
7	Bartragh	BTR	Mayo	0.90			
8	Carrowteigue	CTG	Mayo	4.80	59	18	9
9	Termoncarragh	TMC	Mayo	0.27	31	27	3
10	Aghleam	AGM	Mayo	6.60	49	7	
11	Doolough	DLH	Mayo	0.44	32	22	2
12	Doaghtry	DTY	Mayo	1.77	38	13	0
13	Banna	BNA	Kerry	2.26	23	97	34
14	Castlegregory	CGY	Kerry	6.96	43	20	9
15	Fermoyle	FML	Kerry	0.23	38	59	2
16	Inch	INH	Kerry	4.09	35	19	0
17	Rossbehy	RBY	Kerry	0.42	33	2	
18	Waterville	WVL	Kerry	0.54			
19	Ballyteigue	BTG	East	0.34	31	5	
20	Carnsore	CSE	East	0.95	33	1	
21	Cahore	CHR	East	1.48	18	337	121
22	Mizen Head	MZN	East	3.28	22	0	
23	Brittas Bay	BTS	East	0.20	26	1	
24	Bull Island	BID	East	8.00	25	151	36

2.2.2 Vegetation survey

Vascular plants and bryophytes were recorded in 4m x 4m quadrats from June to September 2015. Quadrats were positioned using stratified random sampling: if several vegetation communities including reed bed, fresh water marsh, *Salix repens* dunes and intermediate slack/edge communities occurred in a single slack, at least one quadrat was placed in each microhabitat. A minimum of three quadrats were recorded in each dune slack, with additional quadrats recorded until the number of new vascular plant species recorded in each new quadrat was equal to one or zero (n = 3-9). The percentage cover of each species present was estimated to the nearest 5% unless it occupied less than 5% of the relevé, in which case it was estimated to 0.1, 0.3, 0.5, 0.7, 1 or 3 %. All plants were recorded digitally in the field using *Turboveg for Windows 2.120* (Hennekens and Schaminée, 2001) and nomenclature followed the Ireland2008v2 species list.

2.2.3 Invertebrate surveys

Sites were visited once during the dry phase from July to September 2014 and twice during the flooded phase in March and April 2015 to record snails. During the dry phase, snails were sampled by removing all material above the soil surface (including leaf litter, vegetation and loose soil) within a 25 cm X 25 cm quadrat adjacent to each vegetation quadrat. Water beetles were not surveyed during the dry phase as they do not remain in the habitat when water is not present (Reynolds 2003). During the flooded phase, all loose material was collected from within a high-sided 23 cm x 27 cm quadrat using a 0.5mm mesh net. This process was repeated at nine points within each dune slack, with an even distribution between the deeper and shallower parts of the dune slack. The material collected was dried and molluscs were isolated by sieving through a 0.5mm sieve (Long *et al.* 2012). All individuals which had more than three complete whorls and a developed mouth were treated as adults and identified to species following Cameron (2008). Juveniles could not be identified reliably for all species, and so were not considered during the analysis. Nomenclature followed Anderson (2005).

Two visits were made to each site to record water beetles during the flooded phase, one in March and one in April 2015. In accordance with O'Connor *et al.*, 2004, a high sided quadrat measuring 40cm x 35cm was placed adjacent to each of the aquatic snail quadrats. Loose material was collected with a 0.5 mm net and placed in a tray where the beetles were removed and stored in alcohol for identification. Identification was carried out using Foster and Friday (2011), Foster *et al.* (2014) and Friday (1988).

No samples of snails or beetles were taken at sites which were not flooded when they were visited in March or April.

2.2.4 Quantifying diversity

The number of samples recorded for each site varied due to differences in plant species richness and flood regime. Species – area curves approached the asymptote for plants at most sites, but beetle and snails were sparsely distributed at some sites, and 56% to 40% of sites respectively were under-sampled. To reduce the impact of variability in sample completeness, Hill numbers corresponding to species richness (H_0) and diversity (inverse Simpson's concentration: H2) were calculated from standardised samples (Chao *et al.* 2014). Inverse Simpson concentration is a useful measure of diversity and is complementary to species richness because it is highly sensitive to dominance (Jost *et al.* 2011). Standardisation was achieved by first estimating the coverage of the sample (the likelihood that any individual taken from the total species pool at a site will belong to one of the species included in the sample) at each site based on relative abundance (Chao and Jost, 2012). The species richness or diversity was then rarefied or extrapolated to correspond to 50% coverage to facilitate comparisons between sites. Fifty percent is the minimum coverage required for an accurate comparison between groups, and does not require extrapolating beyond the threshold for accuracy (extrapolation to twice the number of samples actually recorded) (Chao and Lee, 1992). Species richness and diversity calculations were carried out using the iNEXT package for R (R Development Core Team 2008, Chao *et al.* 2014). Estimated species richness represents a minimum value, whereas the metric corresponding to Simpson's diversity is relatively unbiased (Chao *et al.* 2014). Beetles occurred at very low density in some of the dune slacks, and at sites where four or fewer beetles were present the diversity index calculations are likely to be very approximate.

2.2.5 Data analysis

All data analysis was carried out in R (R Development Core Team 2008) with the aid of the data analysis package vegan (Oksanen *et al.* 2016).

Correlation analysis was used to test whether species richness and diversity of plants, snails and water beetles were related in dune slack sites. Sample sizes were uneven and the data distribution was non-normal so the non-parametric Kendall rank order correlation was used (Dytham 2003).

The compositions of quadrats were visualised with non-metric multidimensional scaling (NMS) which is a reliable method for zero-rich data (Kent, 2011). NMS was carried out on species records for snails and plants. Beetles were sparsely distributed and many species occurred only once within the dataset. To compensate, NMS was carried out on the beetle genera present in quadrats. This is reasonable since water beetle species within genera play ecologically similar roles (Tachet *et al.* 2010). The mean number of each species/genus recorded per quadrat at each site was calculated and log-transformed ($\log_{10}(x + 1)$) to reduce the influence of extreme values (McCune & Grace 2002), and species/genera which only occurred once in the dataset were removed. Any site which was left with no species or a single species was also removed. NMS was then carried out. Procrustean rotation was used to assess how similar the NMS plots for plants, snails and water beetles were. PROTEST, a permutational test, was used to test the significance of similarities between the plots.

2.2.6 Conservation assessment based on plant communities

The structure and functions part of the 2190 Humid Dune Slacks Annex I habitat assessment was carried out using the vegetation quadrat data in accordance with Delaney *et al.* (2013) (Appendix II). The assessment includes an assessment of bare sand cover in all dune slacks within the dune system, and this could not be included in our analysis of a single slack in each dune system. The median diversity of snails and beetles were compared at sites which failed and passed the habitat assessment using the non-parametric Mann-Whitney U statistic. PERMANOVA analyses were carried out to compare the distributions of plants, snails and water beetle species in sites which passed and failed the 2190 Humid Dune Slacks habitat assessment (distance measure: Bray Curtis, 1000 permutations).

2.3 Results

Snails and plants were collected at 22 sites and water beetles were collected at 16 sites because six of the sites failed to flood during the monitoring year (Table 2.1, Figure 2.1). Two sites were excluded from the project either because they did not prove to contain dune slack habitat (Waterville) or because they were inaccessible for much of the year (Bartragh). Plants were the most species rich group with 195 species followed by snails (33 species) and water beetles (23 species). Abundance of beetles and snails collected at each site was very variable. Six of the snail species recorded are listed as Vulnerable according to the Irish Red List for snails, and two are Near Threatened (Byrne *et al.*, 2009). The beetles recorded include one Vulnerable and one Near Threatened species (Foster, Nelson and O Connor, 2009). All of the plant species found were of least concern according to the Irish red lists for vascular plants and bryophytes (Curtis and McGough, 1988; Lockhart, Hodgetts and Holyoak, 2012). Full lists of plant, snail and beetle species are provided in Appendices III - V.

There was no significant correlation between estimated richness (H_o) and diversity (H_2) of plant, snail and beetle communities within a site (Table 2.2, Figure 2.2). The procrustean rotation plots for plant, snail and beetle ordinations (Figure 2.3) shows that that there is considerable distance between the locations of sites in the three ordination plots when they are at the optimal or closest matching rotation and no evidence for cross-congruence was detected (Table 2.2).

Table 2.2 Correlation tests for relationships between estimated species richness, diversity and composition of snails, plants and beetles.

Test	Subjects	Z-score	Tau	P value
Kendall rank correlation of estimated species richness (H_0)	Plants and snails	-0.33	-0.05	0.74
	Plants and beetles	0.62	0.13	0.54
	Snails and beetles	-0.24	0.05	-0.81
Kendall rank correlation of estimated diversity (H_2)	Plants and snails	-0.76	-0.11	0.45
	Plants and beetles	0.37	0.08	0.71
	Snails and beetles	-0.25	0.05	0.80

Test	Subjects	Sum of squares	Procrustes correlation	P value
Procrustes correlation of NMS plots	Plant and snail	0.85	0.39	0.13
	Plant and beetle	0.74	0.51	0.23
	Snail and beetle	0.80	0.45	0.39

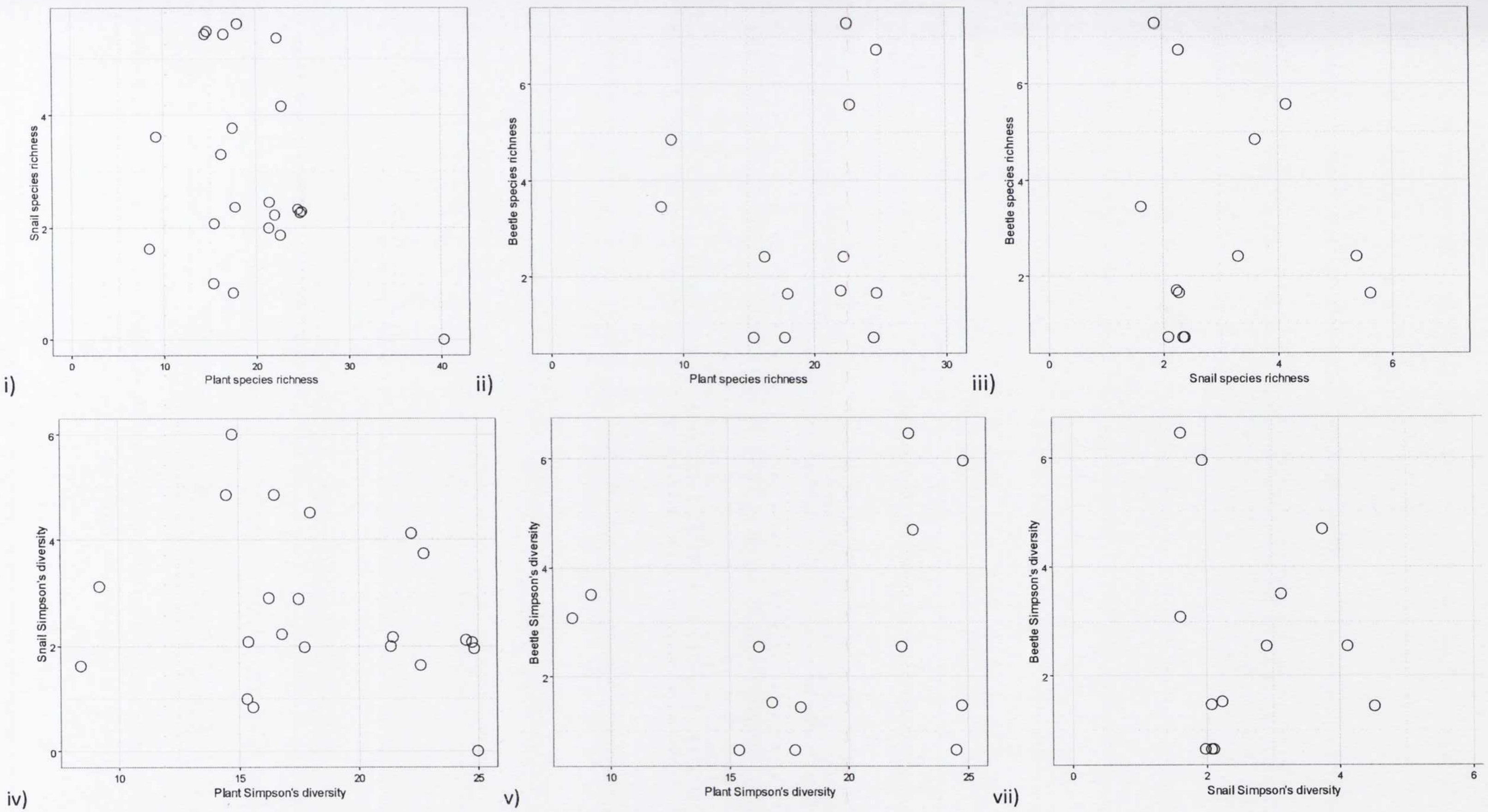

Figure 2.2 Relationship between richness (i-iii) and diversity (iv-vi) of plants, snails and beetles.

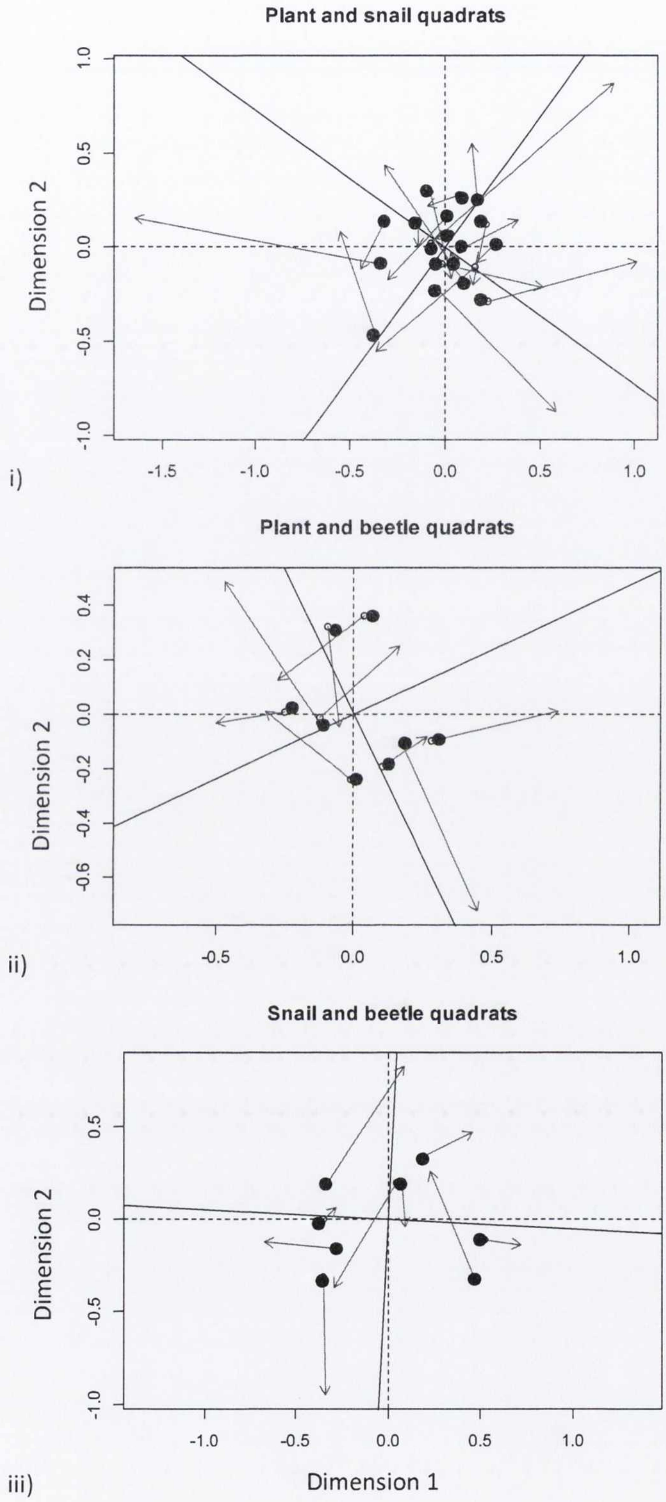

Figure 2.3 Superimposed ordination plots of snail and plant communities at the sites surveyed. The dots represent plant communities in (2.3i, 2.3ii) and snail communities (2.3iii). The length of the arrow indicates the degree of difference between locations of plots in ordination space at the most similar configuration.

Twelve sites passed and 10 sites failed the habitat assessment based on vascular plants. No significant difference was detected in the estimated species richness (H_o) or diversity (H_2) of snail or beetle species recorded at sites which passed and failed the assessment (Table 2.3, Figure 2.4). The species compositions of snails (F= 0.67, p = 0.79) and beetles (F = 1.55, p = 0.17) did not differ significantly at sites which passed and failed the habitat assessment.

Table 2.3 Results of the Mann-Whitney U test to determine whether there is a significant difference in estimated species richness (H_o) or diversity (H_2) of snail or beetles recorded at sites which passed and failed the assessment.

	Mann-Whitney U statistic	P-value
Snail species richness	0.61	> 0.05
Snail Simpson's diversity	0.62	> 0.05
Beetle species richness	0.17	> 0.05
Beetle Simpson's diversity	0.17	> 0.05

Species listed as Vulnerable and Near threated on the Irish Red Lists for snails and water beetles were found both in sites which passed and failed the habitat assessment (Table 2.4).

Table 2.4 Occurrence of species listed as Vulnerable and Near threatened according to the Irish Red Lists for snails and beetles in sites that passed and failed the habitat assessment.

Taxonomic group	Irish Red List status	Sites which passed	Sites which passed
Snail	Vulnerable	10	6
	Near threatened	10	4
Water beetle	Vulnerable	1	0
	Near threatened	0	1

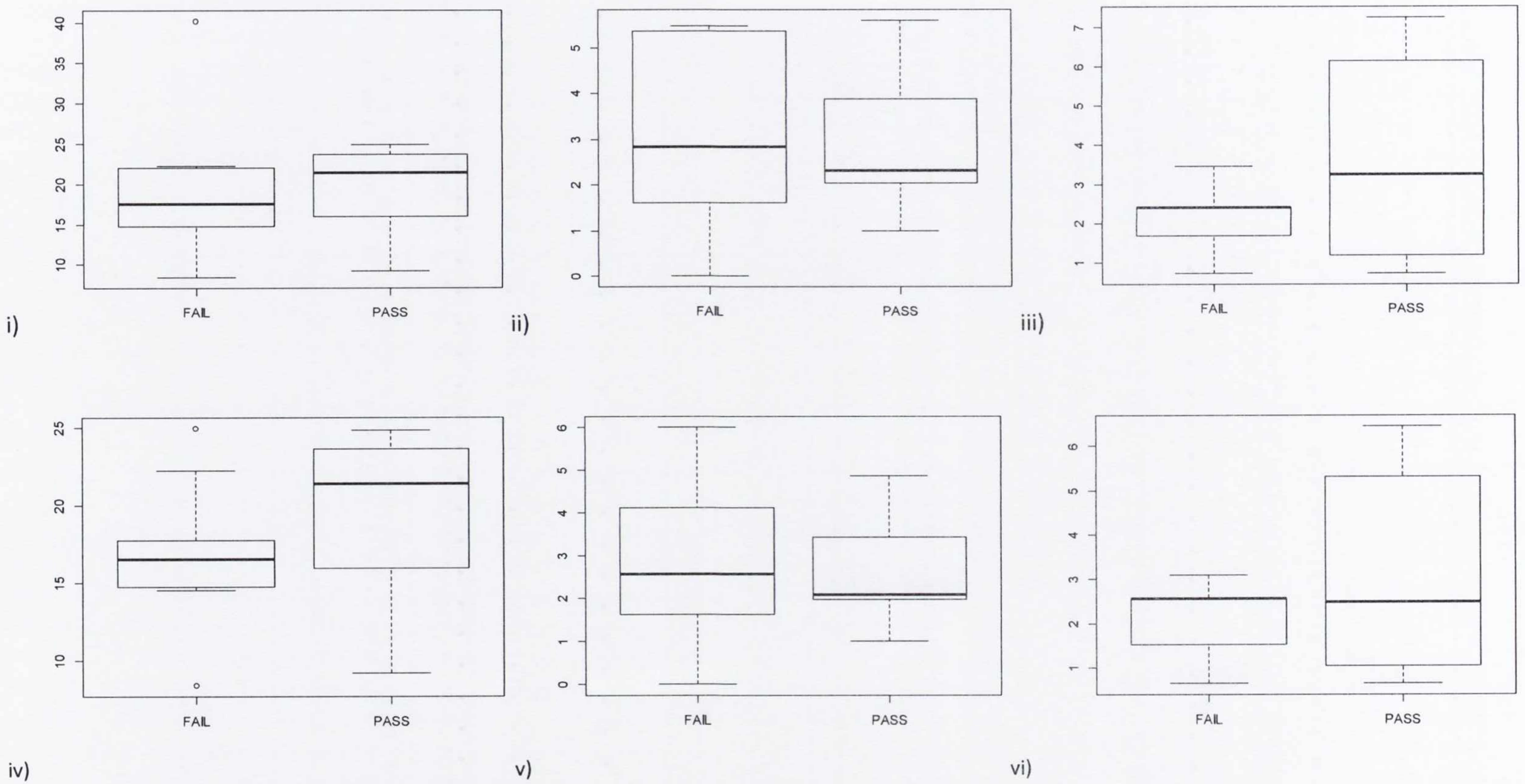

Figure 2.4 Estimated species richness (H_0) for i) plants, ii) snails and iii) water beetles and estimated Simpson's diversity (H_2) for iv) plants, vi) snails and vi) water beetles in sites which passed and failed the conservation assessment.

2.4 Discussion

The plants collected included species of wetlands and sandy places typical of dune slacks in the UK and Ireland (Fossitt, 2000; Rodwell, Pigott and Joint Nature Conservation Committee (Great Britain), 2000). Eight of the snail species recorded are aquatic snails which must either recolonise during the flooded period (Figuerola and Green, 2002; Van Leeuwen *et al.*, 2013) or persist through the dry period in a resistant state or as eggs (Chapius 2011; Gold 1975). There are no published records of large scale surveys of aquatic species in temperate dune slacks, and the number of coleopteran and gastropod species recorded in other temporary water bodies can be highly variable. In comparison to surveys of other temporary freshwaters in Ireland and Britain, dune slacks appear to be relatively poor in water beetle species (Nicolet 2004; Collinson *et al.* 1995; Porst 2009).

In contrast to other investigations of cross-congruence between plants and invertebrates in Ireland and mainland Europe, (Gioria *et al.* 2010, Koch *et al.* 2013) we found no evidence of cross-congruence in either estimated diversity or composition between the three taxonomic groups considered. We removed some of the factors associated with reduced cross-congruence by using invertebrates with a small body size, conducting the research in a specific habitat type and selecting sites within a conservation network to minimise the likelihood of human impacts (Prendergast 1997; Wolters *et al.* 2006; Rooney and Bayley 2012), so the most likely reason for divergent patterns of diversity is the natural disturbance of periodic flooding. This is likely to relate to differences in biological requirements of the three taxonomic groups. For plants, for example, the fluctuating water table is a requirement rather than a disturbance (Davy *et al.* 2006) whereas for beetles, desiccation of the habitat is a major disturbance and dune slacks must be recolonised each flood season. The relationship between species traits and environmental conditions is investigated in Chapter 3.

One consequence of the lack of cross-congruence among plants, snails and water beetles is the poor performance of the habitat assessment in differentiating between snail and beetle assemblages on the basis of their diversity or composition. There is no reference list of invertebrates associated with ideal conditions in dune slacks, but species classified as Vulnerable on the Irish red lists were found at six of the ten sites which failed the habitat assessment. Although these are not necessarily dune slack specialists, two of these were aquatic species and four were wetland species (Foster *et al.* 2009; Byrne *et al.* 2009), so they are likely to be particularly associated with the humid conditions in dune slacks rather than the sand dune habitat as a whole. Because many of the species of conservation interest occurred at sites which failed the conservation assessment, they may be subjected to conservation measures which are not designed to protect them (e.g.: NPWS, 2014).

The presence of eight snail species and two water beetle species listed as Near Threatened or Vulnerable on Irish red lists (Appendices IV and V) indicates that dune slacks provide important habitat for invertebrates whose populations are in decline in Ireland. The Irish populations of two of the species recorded here are of international significance (*Vertigo angustior, Leiostyla anglica*). Many of the species on the Irish Red List were formerly found throughout Ireland but are now most commonly found in coastal locations (Byrne *et al.* 2009, Foster *et al.* 2009). This suggests that the protection of coastal habitats including sand dunes under the Habitats Directive has provided a refuge for species which would not otherwise be restricted to coastal areas. Sand dune systems are therefore important conservation features not just for their typical flora and fauna, but also for species which have declined due to human activities in areas affected by conventional agriculture and urbanisation.

Most of the dune slacks visited flooded, which has been shown to be important in important maintaining their calcareous wetland character elsewhere in Europe (Grootjans *et al.* 1991). Six sites did not flood in the winter of 2014/2015, despite the fact that rainfall in 2014 exceeded the annual average of the preceding 30 years (Table 2.5). Four of these were on the east coast of Ireland which receives less rainwater input than the west coast (Met Eireann website http://met.ie accessed September 2016) and experiences greater pressure on water resources due to urban and tourist developments (Ryle *et al.* 2009, Delaney *et al.* 2013). Three of the six sites which were not observed to have flooded in 2014/2015 passed the conservation assessment.

Table 2.5 Annual rainfall (mm) recorded at weather stations in counties Donegal, Belmullet, Tralee and Malahide.

Weather station	30 year average annual rainfall	2014 total rainfall
Kincasslagh, Co. Donegal	1325.8	1451.6
Belmullet, Co. Mayo	1234.3	1275.2
Tralee, Co. Kerry	1618.6	1832.9
Malahide, Co. Dublin	695.1	872.8

Drying out is a major threat to European Dune slacks (Grootjans and Stuyfzand 1998), but a plant-based assessment was not sensitive enough to highlight slacks which do not flood annually.

2.5 Conclusions

Because plant, snail and water beetle species are not cross-congruent in dune slacks, managing the habitat to protect or restore a specific plant community will not necessarily protect the snails and water beetles found there. This could lead to a decline in some macroinvertebrate species of conservation interest if inappropriate conservation measures are applied. Further, the current monitoring system failed to identify sites which no longer flood on an annual basis and no longer reliably provide habitat for aquatic species. To ensure that dune slacks continue to provide habitat for a diverse range of macroinvertebrates, a larger number of taxa should be included in the habitat assessment and site visits should be made during both the dry and wet seasons.

3 Relationships between environmental variables and plants, snails and water beetles in dune slacks

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3.1 Introduction

Functional traits govern the response of a species to its environment (Diaz & Cabido 2001; Lavorel *et al.* 2013), and thus particular environmental conditions may support a suite of individuals with a particular set of traits. Environmental disturbance, or changes in those environmental conditions, can change the trait composition of a biological community. For example, grazing in Scottish grasslands has been linked to increased representation of rosette growth forms in plants (Pakeman, 2004). Functional traits vary between taxonomic groups and species (Moretti *et al.*, 2013), and so taxa may respond differently to the same disturbance event (De Szalay and Resh, 2000). In the case of a major disturbance such as flooding, response traits such as flood resistance or mobility will determine whether a species can survive *in situ*. Therefore, if a habitat experiences repeated major disturbances, variation in functional traits can result in different taxonomic assemblages existing in a habitat at different successional stages, subject to different community assembly processes.

The set of species that is present at any location is the result of processes of community assembly and these are governed by interacting biotic and abiotic forces. The ability of a species to tolerate certain environmental conditions determines whether it can become established in a given habitat or is effectively filtered out (Keddy, 1992). However, since the set of species which can tolerate the environmental conditions in a habitat are likely to interact with each other, biotic interactions can affect the assemblage at any given time. For example, interspecific competition can lead to exclusion, where the weaker competitor is unable to remain in the habitat, or coexistence via mechanisms such as niche differentiation/niche partitioning (MacArthur and Levins, 1967; Connor and Simberloff, 1979). For species which react in a similar way to environmental stimuli and can be considered ecologically equivalent, colonisation and establishment may be governed by neutral processes (Hubbell, 2005).

There is growing evidence that neutral and deterministic processes act in concert during community assembly (Ejrnæs, Bruun and Graae, 2006; Stokes and Archer, 2010). Successional stage influences the relative importance of neutral and deterministic processes, so that several similar species may initially colonise a habitat-patch, but over time species may be lost to the system through competitive interactions (Cadotte, 2007; Jabot, Etienne and Chave, 2008). As well as the potential for coexistence of similar species, this implies that in a meta-community containing a large number of species trait composition may be similar among habitat patches despite high species turnover. As a result, where both biotic interactions and chance events play an important role in determining community composition within habitat patches in a meta-community, the influence of environmental pressures may be most evident in trait composition rather than species composition

(Leibold *et al.*, 2004). Functional traits, therefore, offer a way to detect responses to environmental stimuli which are otherwise difficult to detect due to the interactions of community assembly processes.

The purpose of this research was to determine whether taxonomic groups with different characteristics responded in a similar manner to environmental variables in a habitat which undergoes periodic disturbance. Dune slacks were used as a model habitat as they undergo annual flooding and drying (Chapter 1.2) and support species with a range of morphological and ecological characteristics. I used plants, snails and water beetles as taxa with differing functional traits.

Typical dune slack flora is composed of primarily hygrophilous species (Rodwell *et al.* 2000; Grootjans & Stuyfzand 1998). The vegetation is stable and a calcareous wetland community can persist for decades with little variation (Adema *et al.*, 2002). Plant communities are likely to be influenced by a history of strong habitat filtering leading to a restricted set of functional traits, and interspecific competition, which would favour community differentiation at the species level. Snails are reliant on passive dispersal to move between isolated patches of suitable habitat (Van Leeuwen *et al.*, 2013), but some species have developed adaptations such as desiccation resistance and resistant states (Den Hartog and De Wolf, 1962; Havel *et al.*, 2014). Wetland snails must tolerate a wide range of conditions and some are both highly tolerant of flooding and capable of surviving for months in dry periods (Falkner, 2001). Both land and freshwater snails occur in dune slacks. Given their varied life-history traits, a range of community assembly processes is likely to affect them, and species may respond differently to environmental pressures. A small number of beetle species can produce eggs which will tolerate desiccation (Wissinger & Gallagher 1999), but for the most part water beetles cannot persist in the dune slack during the dry period, so recolonisation occurs during each flood period (Wissinger, 1997). As a result, they are likely to be heavily influenced by neutral processes. However, in a review of wetland insect communities, Batzer and Wissinger (1996) found that a high density of water beetles in temporary waterbodies commonly led to competitive interactions.

As well as flooding and desiccation, water chemistry, hydroperiod, management (grazing) and connectedness to other water bodies are likely to act as environmental filters (Chapter 1.5).

3.1.1 Aims

Because of the differing impacts of flooding, plants, snails and water beetles can be expected to exist at different successional stages in dune slacks with different community assembly processes affecting each group. Plants, which tolerate both wet and dry phases, are likely to be present at a later successional stage than water beetles which migrate and recolonise annually. As a result, the effects of environmental filtering are more likely to be visible in the distribution of plant species and water beetle traits. Snails of wetlands include both species tolerant of disturbance and species which effectively exploit passive migration, and effects of environmental variables may be detected at the species or trait level. I investigated the influence of environmental variables on snails, plants and water beetles by testing the following hypotheses:

1. Selected environmental factors are correlated with species compositions of plants, snails and water beetles found in dune slacks

2: Selected environmental factors are correlated with trait compositions of plants, snails and water beetles found in dune slacks

3: Environmental variables which are related to plant, snail and beetle assemblages in dune slacks correlate with species richness and diversity (or abundance, in the case of beetles).

3.2 Methods

3.2.1 Study sites

Sites were chosen as described in chapter 1.

3.2.2 Field survey

Data were collected as described in Chapter 2.

3.2.3 Diversity indices

Diversity indices were calculated as described in Chapter 2.

3.2.4 Environmental factors

The environmental factors recorded in the field could broadly be placed in the following groups: dune slack morphology, surface water chemistry, management and landscape context (Table 3.1), and these have been found to affect diversity in temporary ponds (Florencio *et al.* 2013; Porst 2006; Gioria *et al.* 2010; De Meester *et al.* 2005, Bilton 1988). Schäfer *et al.* (2006) showed that the impact of surrounding water bodies and habitat affected assemblages of water beetle at intermediate distances (100m - 3000m) in Sweden. Abundance, diversity and composition were related to landscape factors at different scales, but all three were associated with water bodies and habitat (forestry) within 500m, and so in this study the influence of water bodies and intensively managed habitats were mapped to a distance of 500m. Environmental factors were recorded in the field and remotely by analysing habitat maps and aerial photographs using GIS. Surface water samples were collected in the field and returned to the lab where pH, alkalinity, conductivity and total phosphorus were analysed as described in Chapter 4.2. Selection of environmental variables for analysis followed Zuur *et al.* (2007). Environmental variables were subjectively placed in related groups and compared using scatter plots and correlation. Independence between binary and continuous variables was tested using a Mann-Whitney U test for difference. Within groups, the variables which could be recorded most accurately (i.e. field recordings versus aerial photography) were selected over other variables with which they were correlated. When correlated variables had been removed from within related groups, variance inflation factors (VIFs) were calculated using the usdm package in R. Any variable which was had a high correlation value with the remaining variables (correlation threshold = 0.5) or a high VIF (greater than 4) was excluded at this point (Zuur *et al.* 2007).

Table 3.1 Environmental factors included in the analysis.

Variable name	Details	Included/removed
Dune slack area (m^2)	Total area of selected dune slack	Included
Depth (cm)	Average depth of water in the four deepest quadrats	Included
Connectivity (presence/absence)	Connection to other fresh surface water such as a stream or drain	Included
pH	Surface water pH	Included
Total phosphorus (mg l^{-1})	Total phosphorus in surface water (proxy for nutrient status).	Included
Conductivity ($\mu S\ cm^{-1}$)	Surface water conductivity	Included
Livestock (present/absent)	Including sheep, cattle and horses	Included
Freshwater (ha)	Area of freshwater habitats (including wetlands and dune slacks) within 500m of the edge of the dune slack.	Included
Intensive (ha)	Area of intensively managed land within a 500m radius of the dune slack centre.	Included
Flooded area (ha)	Area containing standing water	Included
Flood period	0: no flooding, 1: flooded in March, 2: flooded in March and April	Removed
Alkalinity (mg l^{-1})	Surface water alkalinity	Removed
Height of vegetation (cm)	Median vegetation height	Removed
Total dune area (ha)	Total area of the sand dune system	Removed
Total dune slack area (ha)	Total area of dune slacks in the sand dune system	Removed
Distance (m)	Distance from dune slack to the land ward edge of the sand dune system.	Removed

3.2.5 Impacts of environmental factors on species distributions

The species compositions of plant and snail quadrats were visualised with non-metric multidimensional scaling (NMS) as described in Chapter 2. Environmental variables were checked for extreme values and $\log_{10}$ transformed if extreme values were present. Environmental variables were then fitted to the ordination and the degree of correlation between each environmental variable and the species distribution in ordination space (NMS axis scores) was calculated and tested for significance using permutations. Ordinations were carried out in R (R Core team 2013) using the vegan package (Oksanen *et al.* 2016). Beetles were not included in this analysis because fewer than five individuals were recorded at ten out of the 16 sites that flooded, and these data were not considered robust enough to generate a community comparison based on species.

3.2.6 Impacts of environmental factors on trait distributions

Traits relating to dispersal, trophic level, life-cycle length and morphology were included. These traits are phylogenetically labile (Poff *et al.* 2006) and are related to conditions in dune slacks (short hydroperiod, isolation from other freshwater). Plant data were available as averages of measured traits from EcoFlora (Fitter and Peat, 1994) and LEDA (Kleyer *et al.*, 2008) databases accessed via TR8 (Bocci 2015) in R in July 2016. The trait information contained in EcoFlora and Leda relate to British and north-west European records and so these were selected in preference to other databases. The plant traits selected were maximum height, leaf dry matter content, leaf mass and seed mass (Table3.2).

Table 3.2 Plant traits selected for analysis.

Trait		Source	Range
Maximum height (cm)	h_max	EcoFlora	5.0 - 1000
Leaf dry matter content (mg/g)	leaf_dmc	EcoFlora	83.3 – 438.8
Leaf mass (mg)	leaf mass	Leda	0.1 – 6.8
Seed mass (mg)	seed mass	Leda	0.2 – 38.1

Traits for beetles and snails were available as fuzzy-coded data, allowing for variation within the species or genus to be taken into account in the analysis. The traits for beetles were provided to genus level (Tachet *et al.* 2010), while data were available for each species of snail (Falkner *et al.* 2001). In general, snail species within genera share similar traits, for example all three of the *Vallonia* species recorded scored identically in 14 of the 16 trait categories analysed, and so the difference in taxonomic resolution of trait information is expected to have a small impact on the analysis. Trait categories which were very similar ecologically and those which were poorly represented within the sample were combined into a single trait category and given a score equal to the highest value for the combined categories (Tables 3.3 and 3.4). Ecological traits such as flood tolerance were not considered as these were derived from a wide variety of sources and are often generated from known habitat associations so their use in an analysis of drivers of species distributions would be circular (Bis and Usseglio-Polatera 2004, Hill *et al.* 1999). Because the trait data were taken from existing databases, the trait values used should be considered typical of the genus or species and do not take local conditions into account.

Table 3.3 Snail traits selected for analysis.

Trait	Category	Value	Adaptations	Average site score (s.d)
Maximum body size	Small	< 2.5 mm	None	1.3 (0.9)
	Medium	2.5 – 5 mm	None	0.6 (0.8)
	Large	5 - 15 mm	None	1.0 (0.8)
	Extra large	> 15 mm	None	0.9 (0.9)
Main reproductive period	Filling	November to February	Combination of two categories	0.4 (0.3)
	Emptying	March to June	Combination of two categories	2.1 (0.5)
	Dry	June to October	Combination of two categories	1.8 (0.4)
Longevity	Shortest	< 1 year	None	0.4 (0.6)
	Short	1 – 2 years	None	2.5 (0.9)
	Long	2 – 5 years	None	0.5 (0.6)
	Longest	> 5 years	None	0.2 (0.6)
Food type	Detritus	Detritus, dead plants, deciduous leaf litter	Combination of three categories	2.5 (0.3)
	Fungi and Lichen	Fungi, epilithic lichen	Combination of two categories	0.1 (0.23)
	Pleuston	Water surface	None	0.1 (0.1)
	Herbivore	Algae, mosses, higher plants	Combination of three categories	1.3 (0.5)
	Carnivore	Carnivorous/ saprophagous	None	0.2 (0.4)

Table 3.4 Selected beetle traits. Life cycle of over a year and locomotion by crawling were removed before NMS was carried out.

Trait	Category	Value	Adaptations	Average site score (s.d)
Max size	Small	0.25 – 0.5cm	None	2.2 (0.1)
	Medium	0.5-1 cm	None	2.1 (0.8)
	Large	1 – 2 cm	None	0.4 (0.5)
Lifecycle duration	Months	< Year	None	0.9 (0.2)
	Year +	> Year	None	3.0 (0)
Cycles/year	Univoltine	1	None	2.2 (0.7)
	Multivoltine	>1	None	1.7 (0.7)
Food	Detritus	Detritus, plant detritus	Combination of two categories	0.4 (0.3)
	Plants	Living macrophytes	None	2.4 (0.5)
	Carnivore	Living microinvertebrates, macroinvertebrates, vertebrates	Combination of three categories	1.6 (1.1)
Locomotion	Flier	Flier	None	1.0 (<0.1)
	Swimmer	Surface or full water swimmer	Combination of two categories	2.9 (<0.1)
	Crawler	Crawler	None	3.0 (0)

Relative abundances of plant and snail species and beetle genera per site were calculated. Relative abundances were multiplied by the trait values of each species/genus and summed to give the total score for each trait category at each site (i.e. community weighted mean).

The trait matrices were $\log_{10}$ transformed to remove extreme values and any trait with no variation, or which occurred less than twice in the dataset was deleted before proceeding, as were sites with fewer than two trait records. The trait distributions were visualised using NMS. Some of the trait data were not available for some plant and beetle species, and sites where 15% or more of the relative cover was occupied by species with incomplete trait data were removed. The trait categories available for vascular plants were not available for bryophytes due to their differing morphology so bryophytes were not included in the trait analysis.

The impacts of selected environmental drivers on estimated species richness (H_o) and Simpson's Diversity (H_2)of plants and snails were tested using univariate tree models with conditional inference using the "partykit" package (Hothorn and Zeileis 2015). The method of estimation is as described in chapter 2.2.4. Only variables which had a significant relationship (p= 0.06 – 0.1) or were strongly correlated ($r^2 > 0.3$) with species or trait distribution of each group in the NMS were used as explanatory variables in the tree models. Beetle and snail abundances were placed in two categories according to whether the total number of individuals exceeded the median value (abundant) or not (rare) and the relationship of environmental drivers with the abundance category of snails and beetles was tested.

Univariate tree models are non-parametric models which do not have assumptions regarding data distributions, can identify relationships which are not linear, and show interactions between variables. They can be used on continuous data (regression trees) or categorical data (classification trees) (De'ath & Fabricus, 2000). As a result, they offer the potential to use comparable methods to assess the impacts of environmental factors on disparate groups, in this case plant, snail and water beetle diversity and abundance. Both categorical and continuous independent variables can be used. This method works by using the factor which explains the largest portion of variance to split the dependent variable into two groups or "nodes" at a point which maximises the homogeneity within the nodes. The nodes are then further split based on the remaining factors. Permutations were used to assess whether the differences in dependent variable between nodes were statistically significant. Splitting will cease when there are no remaining factors with a significant effect on the dependent variable (Hothorn *et al.* 2006). At each split, the p-value for the split is given along with the values and number of samples accounted for each node identified. If no independent variable is shown to have a significant effect on the dependent variable, then no nodes are generated. Abundance of beetles at some sites was very low so the estimated species richness and diversity were not sufficiently robust to be used in this form of analysis and only abundance of beetles was used.

3.3 Results

As described in section 2.4, snail and plant species were recorded at 22 sites and water beetles were surveyed at 16 sites.

3.3.1 Environmental variables

The environmental factors which were retained for analysis of drivers of species and trait diversity and composition were: pH, total phosphorus, conductivity, connectivity of the target dune slack with other freshwater sources, area of the target dune slack, presence of freshwater within 500m of the edge of the dune slack, the area of intensively managed land within a radius of 500m from the centre of the dune slack, presence or absence of livestock and floodwater depth (Table 3.1).

There were differences in the averages of several variables for sites where vegetation, beetles and snails were recorded because beetles and snails were not recorded at all of the sites (Table 2.1, Table 3.5). Almost a third of sites had some connection with other freshwater, and livestock were present at over half of the sites (Table 3.6). All three taxonomic groups were sampled at sites which flooded (Table 3.7). Median pH in standing water was 7.75.

Table 3.5 Mean values for environmental variables recorded at each site where plants, snails and beetles were recorded (the latter were not recorded at all sites). Standard deviation is shown in brackets.

Variable	Plants	Snails	Beetles
Dune slack area (ha)	2.55 (2.54)	2.58 (2.62)	3.25(2.79)
Freshwater within 500m (ha)	2.12 (5.91)	2.30(6.02)	2.69 (6.62)
Intensively managed land within 500m (ha)	5.62 (6.34)	5.02 (5.88)	5.62 (4.68)
Water depth (cm)	17.88 (13.29)	19.66 (12.31)	23.21 (6.99)

Table 3.6 Number of sites where plants, snails and beetles were recorded with connecting waterbodies and livestock.

Variable	Plants	Snails	Beetles
Connectivity (presence)	8	8	7
Livestock (presence)	13	13	9

Table 3.7 Mean values for environmental variables recorded in surface water. Standard deviation is shown in brackets.

Variable	Value
Total phosphorus (mg l^{-1})	0.064 (0.12)
Conductivity (µS cm^{-1})	622.33 (214.72)

Depth was strongly correlated with flood period (tau = 0.67, $p < 0.05$). Water depth was selected over flood period because flood period could only be gauged by the presence of flood water on two occasions during the aquatic period, whereas water depth could be measured in the field. Dune slack area was strongly correlated with flooded area (tau = 0.65, $p < 0.05$), total sand dune area (tau = 0.33, $p < 0.05$) and total area of dune slacks within the sand dune system (tau = 0.54, $p < 0.05$); and total area of the sand dune system was correlated with the distance to the landward boundary of the sand dune system (tau = 0.31, $p = 0.05$). Consequently, sand dune area, distance to the edge of the sand dune system and total area of dune slacks in the sand dune system were all removed from the analysis. Sites where livestock were recorded had significantly shorter vegetation than those with no livestock (median livestock = 20.0cm, no livestock = 9.5 cm, U = 87.5, $p = 0.03$). Presence of grazing livestock was included in the analysis rather than vegetation height, as it was independent of the vegetation composition. Alkalinity was removed because it was identified as having a VIF greater than 4.

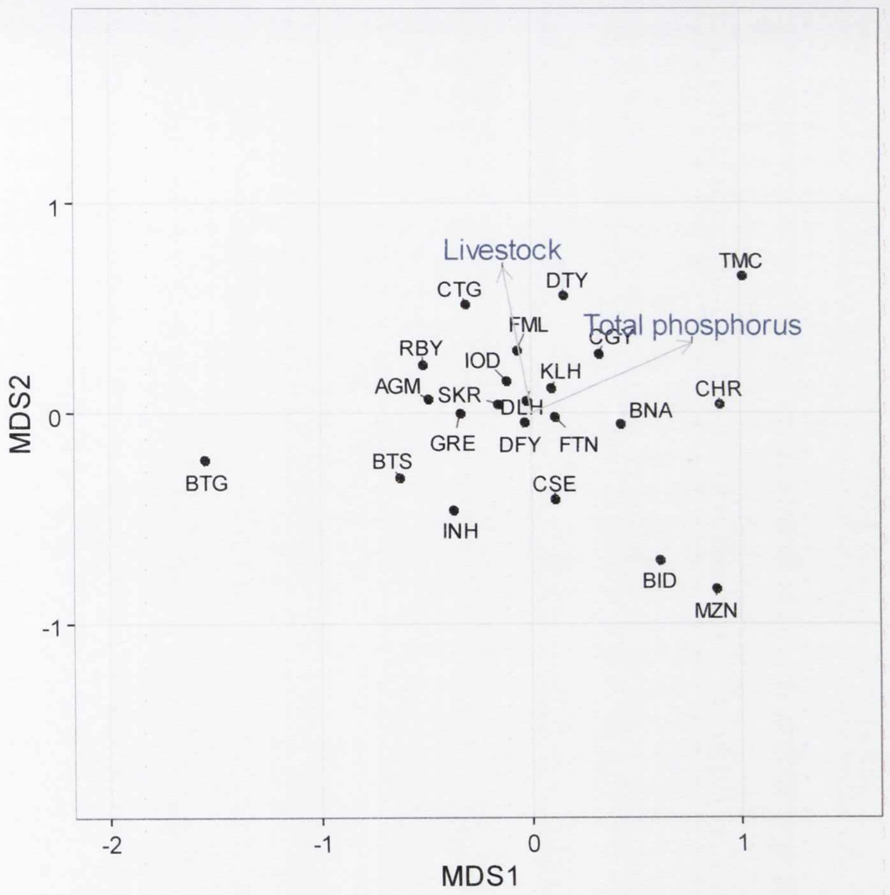
3.3.2 Traits

One site was removed from both the beetle and plant NMS analyses linking traits to environmental variables because trait data were lacking for species which accounted for more than 15% of the total abundance. Two trait categories were removed from the ordination linking environmental factors to trait distributions because all of the species scored equally for these categories, so they did not add information to the ordination (life cycle duration of a year or more and locomotion by crawling).

Maximum height for plant species recorded in dune slacks ranged from 5 to 1000cm, leaf dry matter content was between 83.3 and 428.8 mg/g, leaf mass was between 0.1 and 6.8 milligrams and seed mass was between 0.2 and 38.1 mg (Table 3.2). For snails, the average trait score per site shows that most snails were in the smallest category (Table 3.3). Most of the snails found have their main reproductive period between March and June, and most of them live between one and two years. Detritus was the most common food type, followed by plants and algae. Most of the beetles collected were in the small or medium category, and all are recorded as being commonly long-lived (Table 3.4). Most of the genera recorded have a single reproductive cycle per year, and are most frequently plant eaters. They have been most often observed as crawlers and swimmers rather than fliers.

3.3.3 Species distributions and environmental drivers

The NMS exploring plant species distribution in relation to environmental variables showed that the variables which had the strongest relationship with species distribution in vegetation were total phosphorus content of surface water ($r^2 = 0.71$, p=0.001) and presence of livestock ($r^2 = 0.5$, p=0.005) (Figure 3.1) There was no significant relationship between plant species distributions and other environmental variables. No significant relationship was detected between the distribution of snail species and environmental variables.



Code	Site
AGM	Aghleam
BID	Bull Island
BNA	Banna
BTG	Ballyteigue
BTS	Brittas Bay
CGY	Castlegregory
CHR	Cahore
CSE	Carnsore
CTG	Carrowteigue
DFY	Dunfanaghy
DLH	Doolough
DTY	Doaghtry
FML	Fermoyle
FTN	Fortown
GRE	Glenree
CTG	Carrowteigue
KLH	Kincasslagh
MZN	Mizen Head
RBY	Rossbehy
SKR	Sheskinmore
TMC	Termoncarragh
INH	Inch

Figure 3.1 NMS plot showing the location of sites according to their plant species distributions with environmental factors overlaid. Total phosphorus and livestock were significantly correlated with plant species distribution. The length of the arrow is proportional to the strength of the correlation.

3.3.4 Trait distributions and environmental variables

No environmental variables had a significant relationship with the plant traits chosen for analysis.

Presence of livestock was significantly related to the distribution of traits derived from the snail data (Livestock $r^2 = 0.38$, $p = 0.048$) (Figure 3.2). Total phosphorus in the surface water showed a strong correlation with the distribution of snail traits, but was not significant ($r^2= 0.44$, $p = 0.065$). Sites with livestock were associated with longer-lived snail species, and were characterised by herbivores and detritivores rather than carnivores. Sites with high phosphorus appeared to contain more medium-sized, short-lived species, although the relationship was not significant. The main reproductive period varied very little.

For beetles, the presence of livestock was also the only environmental variable related to trait distribution in sites ($r^2 = 0.53$, $p = 0.032$) (Figure 3.2). The area of the dune slack correlated strongly with the trait distribution, but this relationship was not significant (DS Area $r^2 = 0.45$, $p= 0.064$). Detritivores occurred frequently in sites with livestock, where there was a weaker link with medium-sized species, univoltine species and plant eaters. Large species tended to be associated with large sites. Smaller sites tended to be characterised by smaller, shorter–lived species, but this relationship was not significant.

3.3.5 Impact of environmental variables on species richness and diversity

Sites where livestock were recorded had significantly greater plant diversity when measured with Simpson's index (Figure 3.3) but were not more species rich. Total phosphorus did not affect species richness or diversity of plants. None of the selected environmental variables had a significant effect on the diversity, species richness or abundance of snails or abundance of beetles. Because tree models are not generated if significant relationships are not detected between independent and dependent variables, there are no test statistics to quote for the effects of total phosphorus on plants or snails, or for livestock or dune slack area on snails or water beetles.

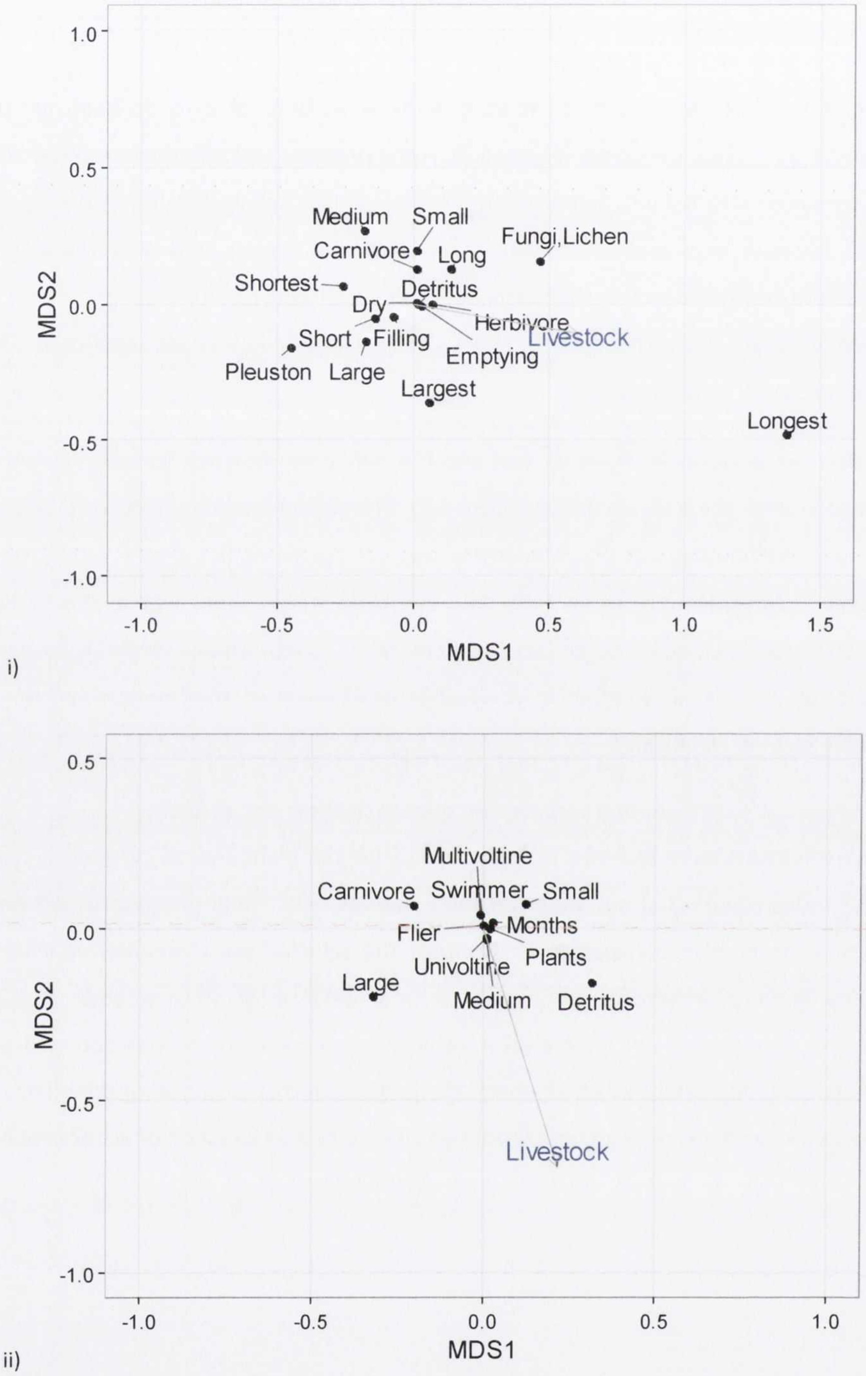


Figure 3.2 NMS plot showing the location of sites according to their i) snail and ii) beetle trait distributions with environmental factors overlaid. The length of the arrow is proportional to the strength of the correlation.

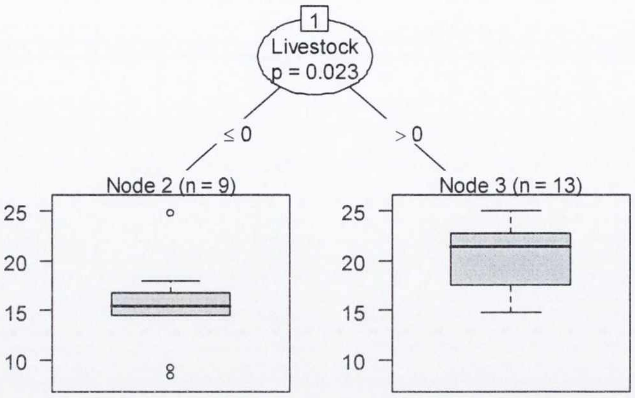


Figure 3.3 Impact of livestock on Simpson's diversity of plants in dune slacks. Sites without livestock (Node 2) were less diverse than sites with livestock (Node 3).

3.4 Discussion

The relationship between presence of livestock and trait distributions for snails and water beetles suggests that environmental filtering affects these two taxa. However, no relationship was detected in the species distributions. It is likely that there is high turnover of snail and beetle species between sites, but the strong environmental filters affecting dune slacks means that there is a large component of functional overlap, despite dissimilarity in species composition. Difficulty in linking environmental drivers with species diversity in aquatic macroinvertebrates has been found in other disturbed habitats: Bischof *et al.* (2013) found that environmental gradients explained an unexpectedly small proportion of invertebrate diversity in seasonal ponds in Minnesota, and this could relate to high diversity between habitat patches and co-existence of species with similar traits. Grazing also affected plant distributions, but the impact was only visible at the species level, not at the trait level. The impact of environmental filtering on the composition of plant species suggests that interspecific competition in plants has resulted in a limited set of species which can reliably be found in different dune slacks throughout Ireland, so both habitat filtering and niche differentiation are likely to be occurring. Niche differentiation at the species level has also been observed in dune slack vegetation in west Wales (Wilson and Gitay, 1995; Bossuyt, Honnay and Hermy, 2005) as well as other stable vegetation communities (Maire *et al.*, 2012). Traits relating to dispersal and competition did not affect the distribution of plants recorded. This could indicate that the specific traits studied did not represent the most important factor governing plant community assembly. Plant height and seed mass in particular have been shown to be inconsistent in their response to environmental gradients (Garnier *et al.*, 2007). Alternatively, the result could be due to the use of values obtained from a database of traits. Phenotypic variability was not taken into account so the values listed in databases may not be good representation of plants *in situ*.

Sites with no livestock contained more carnivores. This is likely to relate to the fact that sites without livestock had taller grass, and habitats with long grass and greater structural complexity are associated with greater complexity in the invertebrate assemblages which occupy them (McAbendroth *et al.*, 2005; Florencio *et al.*, 2013).

Although total phosphorus was not related to plant species richness or diversity, it did correlate with plant composition and this suggests that as total phosphorus increases, some plant species are lost from the system and others are gained, resulting in a compositional shift. Experiments on dune slack flora have indicated that phosphorus limitation is secondary to nitrogen limitation (Lammerts and Grootjans, 1997), and other studies have shown that the response is dependent on the ratio of nitrogen to phosphorus (Verhoeven, Koerselman and Meuleman, 1996). A study of turloughs indicated that while nitrogen and phosphorus concentration did not correlate within sites, raised phosphorus tended to occur in sites where raised nitrogen also occurred (Cunha Pereira *et al.*, 2010). If this relationship holds in dune slacks, the detection of an effect of phosphorus on plant species composition may be due to some simultaneous enrichment with nitrogen and phosphorus.

In contrast to findings elsewhere (Florencio *et al.* 2009; Curreli *et al.* 2013; Porst 2006), water depth, which was strongly correlated with flood period, was not related to any of the taxonomic groups assessed. The response to water depth or flooding was probably reduced because there were no permanent ponds included in this research.

Conductivity and pH were not significantly related to any of the communities, despite having been identified as an important driver for plants and invertebrate community composition and species richness elsewhere (Nicolet *et al.*, 2004; Hassall, Hollinshead and Hull, 2011; Florencio *et al.*, 2013). This is likely due to the fact that there was a very narrow range of pH and conductivity recorded during this project in comparison to other surveys of temporary ponds. In effect, all of the plant communities included here had some tolerance of calcium as they all occurred within calcium-rich sand dune systems. Where conductivity has been recorded as an important driver of macroinvertebrate communities (Florencio *et al.*, 2013) the variance of conductivity has been far greater than recorded in this study.

Connectedness to freshwater, area of freshwater within 500m and intensively managed land within 500m were not related to species or trait distributions. The influence of nearby land under intensive management may be reduced because all of the sites were immediately surrounded by sand dune habitats managed for conservation and the fixed dunes effectively act as a buffer. A larger radius may have been needed to detect a relationship. Connectivity and proximity to freshwater was expected to promote water beetle diversity by providing source populations, but no such effect was observed. Distance to other waterbodies has been noted as a factor elsewhere (Sanderson, Eyre and Rushton, 2005; Florencio *et al.*, 2013), but only for a specific distance range in each case. Other factors such as grazing may have over-ridden the importance of source populations. The total area of dune slacks in the system was removed due to correlation with dune slack area, and this may have made it more difficult to detect the impact of connectivity. Alternatively, I may not have tested the relationship with other freshwater bodies at the correct scale.

While the presence of livestock affected all three taxonomic groups studied, they did not all respond in the same way. Grazing is associated with the typical diverse dune slack community of plants, and reduced grazing results in a compositional shift and reduced plant diversity. These effects, as well as that of phosphorus, are likely to be taken into account in the current habitat assessment protocol based on plant species (Delaney *et al.* 2013). The presence of livestock also exerts pressure on the assemblages of snails and water beetles in dune slacks, but there is no indication that snail or beetle assemblages are less diverse or have less conservation value in sites without livestock. The potential for ungrazed sites to provide habitat for species of conservation interest is illustrated by the fact that species listed as vulnerable or near threatened were found at 18 sites, of which 7 were not grazed. Indeed, dune slacks without livestock may provide an important resource for wetland invertebrates; three species were exclusively found at sites with no livestock: the snail *Aplexa hypnorum* (vulnerable) and the water beetles species *Dryops similaris* (near threatened) and *Enochrus halophilus* (vulnerable) (Foster *et al.* 2009). *Dryops similaris* and *Enochrus halophilus* were each recorded only once.

All of the surveying for this research was undertaken between June 2014 and May 2015. Plant species are stable across time-spans of many years in dune slacks in the absence of major changes to the environment (Adema *et al.*, 2002) and surveying plants during a single year is unlikely to have had a major impact on the results. Plants which may have been overlooked due to surveying in mid to late summer include the rare liverwort *Petalophyllum ralfsii* and *Chara* species. The composition of invertebrate species varies from month to month and year to year, so the conclusions of this research would be more robust if invertebrate sampling had taken place over a longer period. Increasing the survey period would also have resulted in a larger dataset, and this would have strengthened the analysis, especially in relation to water beetles. Nevertheless, the impact of inter-annual variation and small species number at some sites is likely to have been mitigated by the use of traits rather than species to detect the effects of environmental filtering, and the effect of livestock we found on snail and water beetle composition remains valid. Assessing the macroinvertebrate assemblage in ponds on the basis of a single visit and using a species richness estimator is an established practice (Oertli *et al.*, 2005). Because the methods used were economical and could be achieved within a relatively narrow time window, the results provide insight into the potential investment and rewards which would be achieved by expanding the current habitat assessment protocol to include macroinvertebrates. Further analyses which would support these findings include calculating functional divergence (Mason *et al.*, 2005) to explore the degree of similarity and complementarity of traits in the three assemblages studied and using diversity partitioning to explore between-site and within-site diversity of plants, snails and water beetles.

3.5 Conclusions

Plants, snails and water beetles all responded to the presence of livestock, but the response of plants was not the same as that of snails or water beetles. Dune slacks which do not contain livestock contain invertebrate species of conservation interest and increase the overall diversity of dune slack species. While plant species could be a good surrogate to detect grazing pressure, they would not differentiate between the conservation value of sites in terms of their snail and beetle assemblages. In an ecosystem which experiences natural periodic disturbances, indicator species should include representatives of more than one taxon and they should be complementary to represent the varied functional traits of different taxonomic groups.

By using traits as a tool to assess the response of snails and water beetles to environmental variables, I was able to detect a response to environmental variables which would have been obscure if the species data were used alone. I was also able to show which traits were most closely related to the main driver in dune slacks. Trait analysis is therefore particularly useful as a means of analysing biological assemblages which are likely to exhibit high beta-diversity, including those which are subjected to repeated disturbances.

4 Characteristics of ground and surface water in dune slacks in Co. Donegal under differing management regimes.

To be submitted for publication as Aoife Delaney, Jane Stout, Andrew Jackson, Pete Coxon, Catherine Coxon "Characteristics of ground and surface water in dune slacks in Co. Donegal under differing management regimes." Target journal: Science of the Total Environment

4.1 Introduction

The Water Framework Directive (2000/60/EC) is the main legislative basis for the maintenance of ground and surface water quality within the European Union. Among other objectives, the WFD requires that groundwater-dependent terrestrial ecosystems (GWDTEs) are not at risk of degradation due to the quantity or quality of the water supplying them. Although they are GWDTEs, dune slacks are usually associated with small, local aquifers which are not among the groundwater bodies identified in Ireland for the Water Framework Directive (Kimberley and Coxon, 2013), so the status of their groundwater in Ireland is still not well understood. Because dune slacks are both GWDTEs and Annex I habitats, the Water Framework Directive works in conjunction with the Habitats Directive (92/43/EEC) to ensure that the hydrological requirements of biological communities in dune slacks are met.

Dune slacks are typically freshwater habitats which are cut off from the sea. Schlufters, dune slacks which have a connection with seawater and are strongly affected by tidal fluctuations (Verwaest *et al.* 2005), were not the main focus of this research. A primary requirement of biological organisms living in dune slack habitats is a fluctuating water table which is close to the surface all year (Grootjans and Stuyfzand, 1998). Water levels are heavily dependent on precipitation within the larger sand dune system, and this is particularly true of barrier islands and spits (Carretero and Kruse, 2012; Röper *et al.*, 2012). The water table varies depending on the season and from year to year (Curreli *et al.*, 2013; Martens *et al.*, 2013), but a period of inundation during late winter and spring is a normal feature (Grootjans *et al.*, 2002; Davy *et al.*, 2006). Water levels in dune slacks which are located near the landward boundary of sand dune systems are maintained partly by groundwater inputs from land inshore, while those located in the main dune area are more sensitive to changes in the water table in response to precipitation within the dune system (Davy *et al.*, 2006). Frequency and duration of flooding, and maximum and minimum annual water levels have been shown to have a strong influence on the vegetation of dune slacks (Noest, 1994; Curreli *et al.*, 2013; Martens *et al.*, 2013), and these can be affected by human activities such as water abstraction and drainage.

Vegetation typical of dune slacks is supported by inflow of calcium-rich water. Studies of Dutch dune systems have shown that for calcium rich groundwater to enter the dune slack, the water table must be high enough to travel through dune sands with a calcium carbonate content above 0.3% before exfiltrating into the dune slacks (Grootjans and Stuyfzand, 1998). Reduction in the water level below the level of the dune slack in winter results in acidification as rainwater leaches calcium from the sand which is not replaced by inflowing calcium rich water. This in turn leads to a loss of the typical dune slack flora. Large fluctuations in rainfall have been observed to result in reduced water levels and subsequent dune slack acidification, although this may have been compounded by historic water abstraction (Grootjans *et al.*, 1991).

Nutrients also play an important role in maintaining the dune slack habitat (Lammerts and Grootjans, 1997). Nitrogen is a particularly important determinant of dune slack vegetation composition, and phosphorus can also affect vegetation if nitrogen levels increase. Nutrient enrichment leads to the loss of broad-leaved herb species and a shift towards species poor vegetation dominated by grasses and dwarf shrubs (Lammerts *et al.*, 1999).

Groundwater in dune slacks is vulnerable to contamination as a result of anthropogenic activities within the sand dune system including diffuse agricultural inputs and point source contamination from domestic waste water (Reddy *et al.*, 2015). Groundwater travelling into the sand dune system from intensively farmed adjacent lands can also transport nutrients into the system. The amount of groundwater that enters a sand dune system is likely to depend on local topography and the aquifer characteristics (permeability and porosity) of the adjacent bedrock and sediments, and this may influence the degree of contamination of the sand dune aquifer. For example, Rhymes *et al.* (2014) studied groundwater inputs of nitrogen to a dune system in north Wales from adjacent sandy pasture land, and Jones *et al.* (2006) noted inputs from limestone springs to a dune system in south Wales. While some influence of exogenous groundwater is anticipated in bay or hind-dune systems (Jones *et al.*, 2006), the importance of exogenous groundwater inputs in dune systems is likely to vary depending on the underlying bedrock or sediment permeability and the topography of the landscape surrounding the dune system (Soulsby *et al.* 1997).

Under suitable conditions, natural processes such as denitrification attenuate the nitrate content of groundwater. During denitrification, heterotrophic microbes consume nitrate in groundwater and release nitrogen gas to the atmosphere (Buss *et al.*, 2005). In addition to nitrate, requirements for denitrification include dissolved organic carbon, anaerobic conditions and presence of denitrifying bacteria (Burford and Bremner, 1975; Starr and Gillham, 1993). Denitrification occurs as part of a sequence of oxidation-reduction reactions which release reduced forms of iron (dissolved ferrous iron, Fe^{2+}) and manganese (Mn^{2+}). Very low nitrate content along with raised dissolved iron and manganese are signs that denitrification might be occurring (Chapelle *et al.*, 2009). Nitrate can also be processed via dissimilatory nitrate reduction to ammonium (DNRA). Because the end product is ammonium, DNRA causes a build-up of bioavailable nitrogen. DNRA is more tolerant of water level fluctuations than denitrification and occurs under strongly reducing conditions where nitrate is low in relation to carbon (Pett-Ridge, Silver and Firestone, 2006; Roberts *et al.*, 2014). Phosphorus in groundwater is also subjected to natural processes which reduce its effects on vegetation. Phosphorus can be immobilised by adsorption to mineral surfaces or by forming chemical complexes. In sediments rich in calcium carbonate, phosphorus and calcium can combine to form insoluble compounds which precipitate out of solution (Reddy *et al.*, 2015).

In the past, much research on dune slack hydrology and hydrochemistry focussed on sand dune systems of barrier Islands and spits or slacks which had a history of considerable anthropogenic impacts through contamination or abstraction of groundwater (Lammerts & Grootjans 1997; Grootjans *et al.* 1996; Bakker *et al.* 2006; Soulsby *et al.* 1997). However, many dune slacks are exposed to groundwater influences from outside of the dune system while also being less degraded than dune slacks close to urban areas on the Dutch and Belgian coasts. More recent studies have focussed on sites which have an input of exogenous groundwater but also have lower impacts than those described on the Dutch coast (Jones *et al.*, 2006; Röper *et al.*, 2012; Robins and Stratford, 2013; Rhymes *et al.*, 2014). These have tended to be intensive studies of dune slacks within individual sites and have provided insight into site-specific groundwater conditions rather than producing generalizable results. There is a lack of research using comparable methods to assess groundwater conditions in dune slacks with common management practices.

4.1.1 Aims

This was the first comparative study of dune slack hydrology and hydrochemistry in Ireland. It examined the groundwater conditions in dune slacks in northwest Ireland with three main aims; (a) To compare the relationship between groundwater levels and rainfall at six sites in northwest Donegal; (b) To characterise the hydrochemistry of ground and surface water and determine whether there are chemical indications of denitrification; and (c) to compare groundwater chemistry and hydrology of two major land uses for sand dunes in Ireland: non-intensive pasture and golf courses.

4.2 Methods

4.2.1 Site Descriptions

Six sites were selected in Co. Donegal, northwest Ireland (Table 4.1, Figure 4.1) with the aid of NPWS habitat maps (Delaney *et al.*, 2013) and digital aerial photography (ESRI World Maps in ArcMap 10.1). All of the dune slacks were located in sand dune systems at least 3 km apart and with no shared groundwater body (Figure 4.1). The sand dune system was defined as the total area of continuous sandy substrate surrounding the dune slack, and it could include machair plains, ephemeral foredunes and areas of windblown sand over low coastal hills (climbing dunes).

Sites were separated by a maximum distance of 72 km to limit variation in weather conditions and atmospheric nitrogen inputs. The mean annual rainfall recorded at Malin Head between 1985 and 2015 was 1088mm and mean temperature is consistently between 9 and 10 °C (Met Eireann website http://met.ie accessed September 2016). Less than 2kg ha $^{-1}$ of atmospheric nitrogen is deposited annually in northwest Ireland, which is low in comparison to other coastal temperate regions of Europe (Simpson *et al.* 2011).

None of the dune slacks was predominantly a barrier island or sand spit. All of the slacks selected were between 0.2 and 1.0 ha in size. The dune slacks were between 2.3 m and 11.6m above Ordnance datum (a.O.D.) (Table 4.1). The tallest dunes at the six sites were between 10 and 40 metres a.O.D..

Table 4.1 Sites used in this study.

Site name	**Abbreviation**	**Management**	**Area (ha)**	**Slack elevation (m)**	**Dune system height (m)**	**Distance to sea (m)**
Ballyliffin	BFN	Golf club	0.2	9.3	30-39	840
Ballyness	BNS	Pasture	0.93	2.5	10-20	262
Dunfanaghy	DFY	Golf Club	0.33	2.3	10-20	90
Kincasslagh	KLH	Pasture	0.44	11.6	30-39	168
Lough Nagreany	LNY	Pasture	0.26	3.1	10-20	187
Rosapenna	RPA	Golf club	0.63	4.9	30-39	433

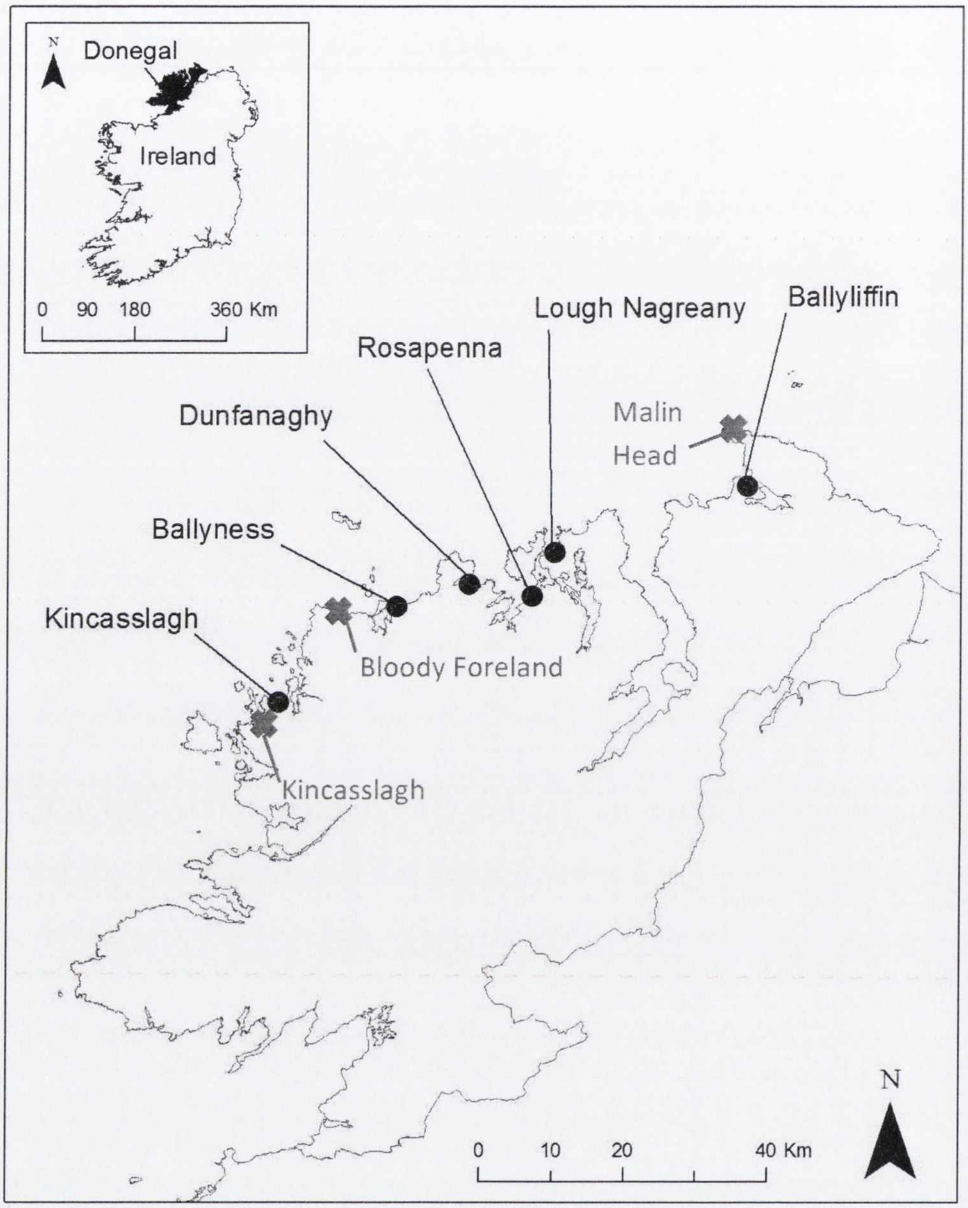


Figure 4.1 Black dots indicate the locations of sites selected for monitoring water levels and water chemistry. Rainfall stations are shown as grey crosses. The inset map shows the location of County Donegal in northwest Ireland.

The most common bedrock types were quartzites, granites and schists with occasional marble. All sites were associated with poor aquifers with unproductive bedrock or with unproductive bedrock except for some local zones, and they were all in areas of highly vulnerable groundwater with the exception of Kincasslagh, where the groundwater was extremely vulnerable (Geological Survey of Ireland Groundwater Data Viewer, http://spatial.dcenr.gov.ie/GeologicalSurvey/Groundwater/index.html accessed (20 September

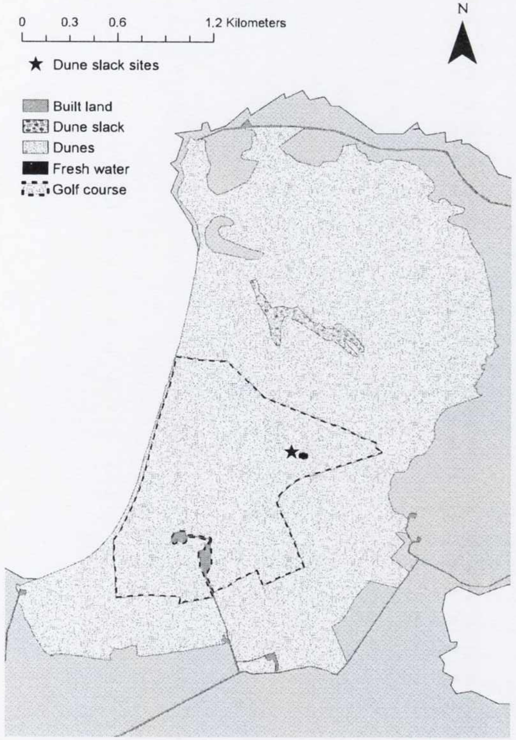
2016). Sand dunes in the west of Ireland are generally composed of sand rich in shell fragments high in calcium carbonate (Curtis 1991), and the flora of all of the sites conformed to a calcium-rich dune habitat.

Three sites were under pasture within Special Areas of Conservation (SACs) designated under the EU Habitats Directive (92/43/EEC). Sand dune habitats in SACs are subjected to restricted management practices designed to maintain their low nutrient status and high floral diversity; application of agrochemicals is restricted and stocking densities are regulated (National Parks and Wildlife Service Notifiable actions https://www.npws.ie/farmers-and-landowners/notifiable-actions/listed-habitats-and-species accessed 20 October 2016). The remaining sites were in ungrazed and unmown areas within or beside golf courses. The golf courses in this study are links courses which are a matrix of intensively managed grasslands in the teeing-off areas, greens and fairways along with typical sand dune vegetation in "rough" areas. The dune slacks selected were located in the rough or in unmanaged land adjacent to the golf course. Non-intensive pasture and golf courses are common land uses on sand dunes in the west of Ireland (Ryle *et al.* 2009). None of the dune slacks was known to have a history of intensive management techniques such as reseeding or direct application of agrochemicals. The information regarding land management practices within the dune slacks was provided voluntarily by the landowners, and some details may have been withheld. None of the farmers reported using agrochemicals or abstracting water.

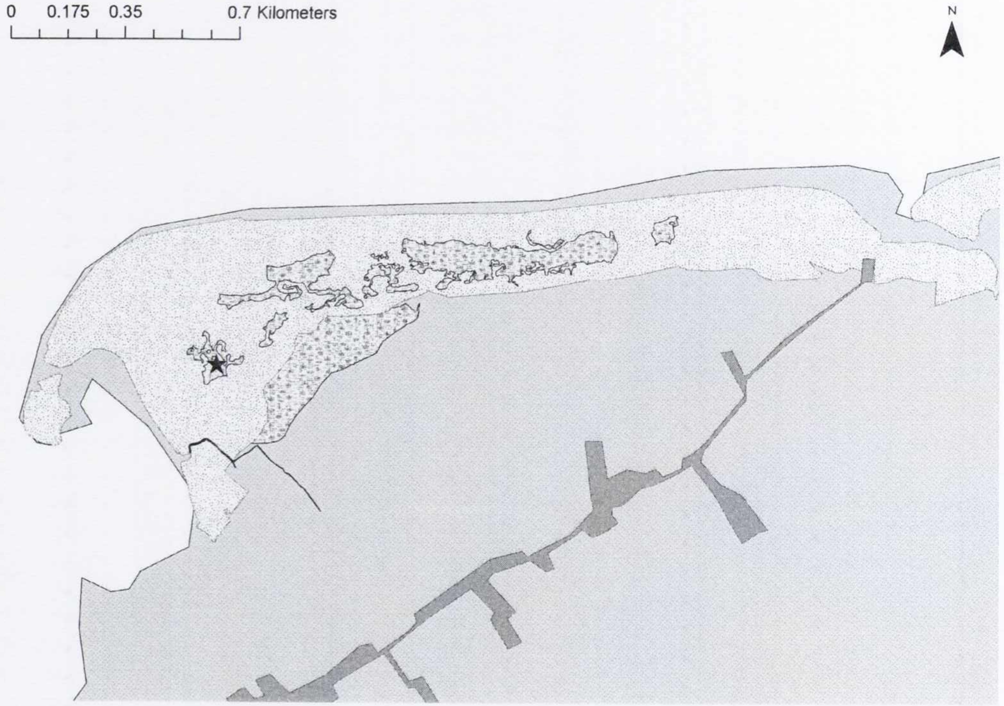
4.2.1.1 Ballyliffin

Sand dunes cover an area of 580 hectares at Ballyliffin (Figure 4.2). Machair plains are present in the south and east and the central area has dune hills over 10 m high. The dunes rise over a hill reaching 70m in the north.

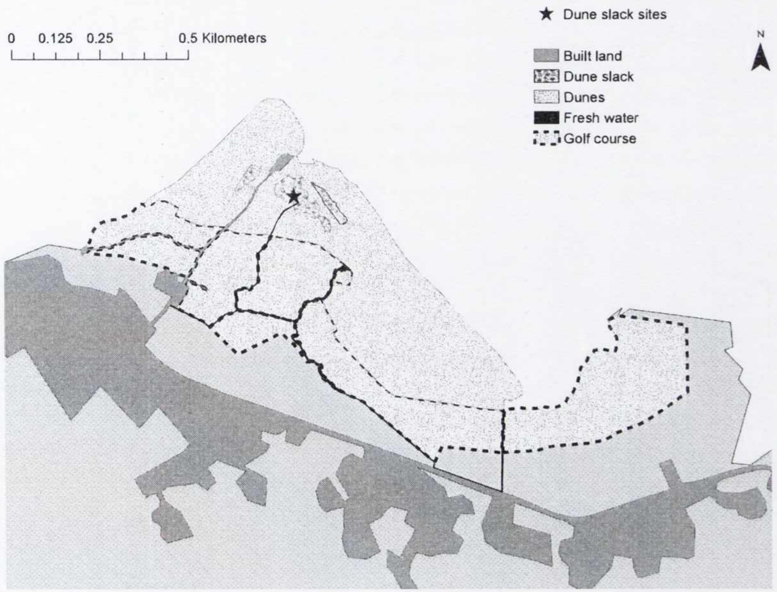
Golf courses occupy 142.6 ha and the remainder is managed as pasture for sheep and cattle. The golf club uses liquid fertiliser derived from seaweed as well as ammonium sulphate and iron sulphate. Fertiliser is applied up to seven times per year on the greens which occupy a small part of the golf course, and once a year on the fairways which are maintained as tightly mown grasslands. A pesticide targeting crane fly larvae and fever fly is applied once a year and herbicide targeting broadleaved herbs is applied to the greens and fairways twice a year. Approximately half of the area within the golf course is unmanaged, and supports species rich calcareous sand dune vegetation. These areas do not directly receive any fertilisers or pesticides. Water is pumped from boreholes during wet periods to prevent flooding of playable areas, and groundwater is used for irrigation during dry periods. Frequency of irrigation is low, and during years with more rainfall than average no irrigation is carried out. A network of channels drains the farmed area and exits into the sea to the south of the sand dunes. The dune slack selected is within the golf course, and is adjacent to an artificial pond which intersects the water table.



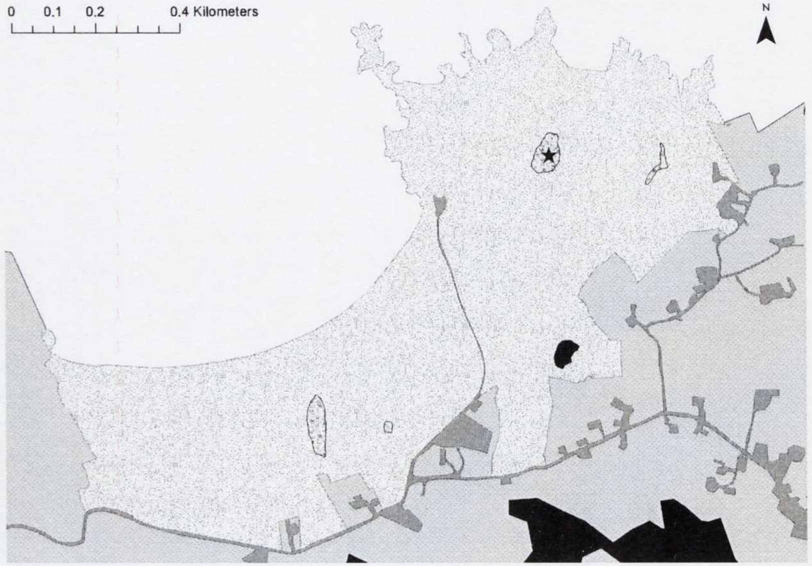
Ballyliffin



Ballyness



Dunfanaghy



Kincasslagh

Lough Nagreany

Rosapenna

Figure 4.2 The six selected dune slacks and the dune systems where they are found.

4.2.1.2 Ballyness

The dune system at Ballyness extends over 99.1 ha and dune slacks occupy 17 ha at this site (Figure 4.2). The land is managed as non-intensive pasture for cattle and sheep, although the main dune ridge has been fenced so animals cannot access it. Several drains from the steep hill on the landward side of the dune system terminate in the sand dunes. In many cases, these only contain water after heavy rainfall. There are no dwellings within the sand dune system.

4.2.1.3 Dunfanaghy

The dune system at Dunfanaghy covers an area of 61.9 ha (Figure 4.2). Of this, 30.9 hectares are managed as a golf course, 4.8 ha are used as pasture for sheep, and the remainder is not managed. The dune slack selected in Dunfanaghy is in unmanaged dunes outside the boundary of the golf club. The majority of the land within the golf course boundary is intensively managed. The golf club occasionally abstracts a small amount of groundwater for irrigation, but more water is removed from the course through drainage. Waste water generated at the clubhouse is treated in a septic tank near the western edge of the dune system. The golf club maintains drains which connect to streams running from the hills inland, and one of the drains terminates directly into the selected dune slack. A liquid seaweed fertiliser is applied to playable areas. The dune system lies close to a main road and associated housing developments (Figure 4.2) which are backed by hills.

4.2.1.4 Kincasslagh.

Sand dunes extend over 85 ha at Kincasslagh, and are managed as extensive pasture (Figure 4.2). The site is managed as commonage, and there is no indication of fertiliser application. A small number of private dwellings have been built (Figure 4.2) within the sand dune system. The slack selected is located in climbing dunes on a rocky headland where bedrock is close to the surface.

4.2.1.5 Lough Nagreany

The dune system at Lough Nagreany is 53.7 ha in size, and is backed by hills up to 70m high on the landward side (Figure 4.2). There are two streams that run through the site and these have led to the development of freshwater marsh within the dune system, and during wet periods a temporary stream conducts water from the adjacent hillside into the sand dune system, where it infiltrates into the soil. There is an area of machair in the west of the site and in the east the dunes rise over a low hill reaching 40m. The central part of the system is made up of ridges and slacks. The system is managed as pasture for cattle and sheep. There was no evidence of fertiliser use on the site during the period of the survey, but fields adjacent to the machair appear to have been managed more intensively and are likely to be fertilised.

4.2.1.6 Rosapenna

The sand dune system at Rosapenna is 568.4 ha in extent, of which 305.9 ha are managed as golf courses (Figure 4.2). Approximately half of the area within the golf course is unmanaged "rough". The selected dune slack is in unmanaged land within the golf club. Inorganic fertiliser containing nitrogen and phosphorus is applied on the mown areas once a year, and more frequently in the most intensively managed areas. Pesticides and herbicides are applied once a year on the mown areas to control invertebrate larvae and broadleaved herbs. Irrigation is carried out infrequently and the wells which serve the golf course and clubhouse are located in the northern part of the dune system 1.5 – 2 km north of the dune slack included in this project. The clubhouse is connected to the mains sewerage system. Housing estates and ribbon developments have been built near the roads on the flat land at the edges of the dune system, many of which may originally have been part of the machair plain. Although the sewerage arrangements are not clear, it is likely that the houses built along the road approximately 500m from the dune system are now or were in the past serviced by septic tanks. A stream runs through the southern edge of the dune system to the sea.

4.2.2 Site investigation and instrumentation

Two 25mm-diameter high density polyethylene (HDPE) piezometers were inserted at each site using a Cobra TT percussion drill (Atlas Copco, Stockholm). The wells were inserted to a depth of 3 - 3.5 m with a 1 m perforated section at the base of each for ingress of groundwater. One metre of well casing remained above the surface to permit access to the groundwater when the dune slacks were flooded. Bentonite clay was placed around the edges of the well to prevent infiltration of surface water at the bore hole. The wells were capped to prevent entry of rainfall or contaminants. One piezometer (well 1) was placed within the seasonally flooded part of the dune slack and one at the edge (well 2, Figure 4.3). The position of the piezometers was recorded using a differential GPS.

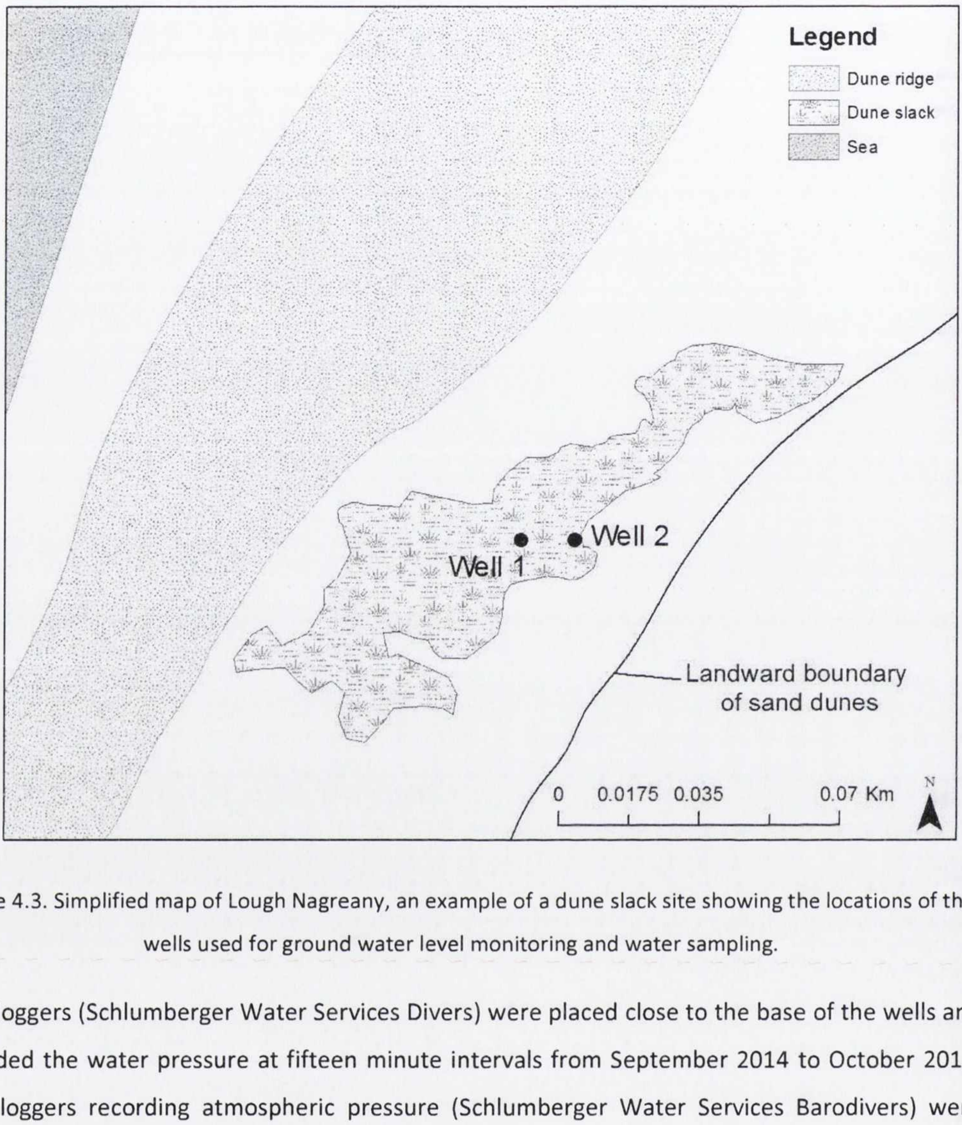


Figure 4.3. Simplified map of Lough Nagreany, an example of a dune slack site showing the locations of the wells used for ground water level monitoring and water sampling.

Data loggers (Schlumberger Water Services Divers) were placed close to the base of the wells and recorded the water pressure at fifteen minute intervals from September 2014 to October 2015. Data loggers recording atmospheric pressure (Schlumberger Water Services Barodivers) were installed above the water at two sites to allow conversion of water pressure to water depth in the wells. Disturbance of the dataloggers due to human and animal activity (including downloading data) could be detected in the logger data as sudden, extreme fluctuations in water levels and divergence between the water levels recorded in the two wells at each site. Disturbance events accounted for less than 0.1% of the data recorded and were removed from the dataset before analysis. The wells at the centre of the site (well 1) were less affected by disturbance than wells at the edge of dune slacks. Because there was a strong correlation between the water levels recorded within sites (Kendall's tau 0.89 to 0.98), data from the less disturbed well (well 1 at each site) was used in the data analysis.

A 3 m sediment core was extracted at a location between the pair of piezometers at each site. Field observations regarding sediment type and stratification were made and sediment samples were returned to the lab. Samples were dried in an oven at 60°C for 48 hours and then divided using a rotary cone sampler to ensure that the samples used in each analysis were representative. The proportion of organic material was determined using loss on ignition following Bengtsson & Enell (1986). Particle analysis followed Sperazza *et al.* (2004), Eshel *et al.*, 2004 and Gray *et al.* (2010). The dried material was disaggregated using sodium hexametaphosphate (50g/l) and passed through sieves with mesh sizes of 8mm, 4mm, 2mm and 1mm to separate coarse sand and pebbles. Material which passed through the sieves was placed in a Malvern Mastersizer laser granulometer to determine the proportions of clay, silt and fine sand. Sediment samples were described using the Wentworth size classes (Wentworth 1922).

Effective rainfall was calculated by subtracting actual evapotranspiration rates from actual rainfall. Precipitation, potential transpiration and actual transpiration data recorded at Malin Head, Co. Donegal, in 2014 and 2015 for well drained soils were obtained from Met Eireann (Met Eireann website http://met.ie accessed September 2016). Soil moisture deficits used to derive actual evapotranspiration rates were calculated using the FAO Penman-Monteith Equation (Schulte *et al.* 2005). In freely draining dune soils where water movement is vertical rather than lateral, effective rainfall is expected to approximate to groundwater recharge; Misstear *et al.* (2009) propose a recharge coefficient of 80-90% in such situations.

Rainfall data were also available for Bloody Foreland rainfall station near Dunfanaghy and Kincasslagh rainfall station (Figure 4.1), but no information regarding evapotranspiration rates for these stations was available. Rainfall from Malin Head was compared to that at Bloody Foreland and Kincasslagh to assess how similar rainfall patterns were over the total study area. Rainfall data were not normally distributed so these were compared to rainfall data for Malin Head using Kendall rank correlation. Correlations showed that daily rainfall in Malin Head was significantly correlated with rainfall at Kincasslagh (tau =0.5, p <0.005) and Bloody Foreland (tau =0.5, p <0.005), but the correlations were stronger for weekly (Kincasslagh tau =0.7, p <0.005, Bloody Foreland tau =0.69, p <0.005) and monthly data (Kincasslagh tau =0.85, p <0.005, Bloody Foreland tau =0.78, p <0.005). Water levels at all of the sites were compared to effective rainfall at Malin Head. The comparison of rainfall patterns for Malin Head, Kincasslagh and Bloody Foreland showed rainfall is sufficiently similar across the region to justify using effective rainfall calculated at Malin Head for all of the sites.

4.2.3 Water chemistry

Water samples were taken from all of the accessible wells in October 2014, January 2015, April 2015 and July 2015 using a peristatic pump. As a result of annual flooding, wells could not be accessed at two of the six sites in January 2015, and only the wells at the edge could be accessed at the rest of the sites. Three well-volumes were pumped from the wells to remove standing water from the wells before samples were collected. If surface water was present samples were taken from an area of undisturbed water near the centre of the slack using a weighted 5 l container.

The most time-sensitive tests were for soluble reactive phosphorus, ammonium, nitrite, pH and alkalinity and these were conducted as soon as possible, but because of travel time between the sites and the lab, the maximum time between sampling and testing was three days after collection. Analysis of ammonium, nitrite, chloride sulphate and nitrate were not carried out in January.

Anion concentrations (chloride, sulphate and nitrate) were measured using a Dionex ICS-1500 ion chromatography system with an attached AS40 automated sampler. Ammonium and nitrite were analysed using a Lachat QuickChem QC8500 automated ion flow injection analyser. Cations (calcium, iron, potassium, magnesium, manganese and sodium) were quantified using a Varian Liberty AX inductively coupled plasma atomic emission spectrophotometer (ICP-OES). All of these analyses were carried out on filtered samples. Filtration was carried out in the field using a Whatman 0.45µm mixed cellulose ester membrane filter. Methods used followed Rice (2012).

Phosphorus content was measured by colourimetry using a Hach DR5000 UV/visible spectrophotometer. Samples for soluble reactive phosphorus (SRP) were filtered in the field and total phosphorus was derived from unfiltered samples after acidic persulphate digestion. Methods followed Murphy & Riley (1962) with adaptations according to Eisenreich *et al.* (1975). pH and alkalinity of unfiltered water were assessed in the lab using a pH and conductivity meter (Jenway 4330) and titration with 0.01 M sulphuric acid to pH 4.5.

4.2.4 Quality control

Three replicate samples were taken in the field for analysis of soluble reactive phosphorus and total phosphorus. The samples collected for pH and alkalinity, anions, cations and nitrite and ammonium were divided into three replicates during preparation for analysis in the laboratory. Commercially bought reference standards for used for calibration purposes and these standards were cross referenced with internal laboratory quality control solutions run every 10 samples. An Environment Canada analytical reference water (Ontario-99, Lot No. 1109) was also used to verify the accuracy of analysis for anions and cations. The results of chemical analysis of reference samples were within 5% of the expected value, meeting the criterion for reliability.

Ion balance errors were calculated according to Lloyd & Heathcote (1985). The ionic content of 85% of the samples was balanced to within 5%, indicating that they were within the acceptable limits. There was a 5 – 10% difference in the balance of anions and cations for four of the 46 samples, indicating that they should be used with caution. Error exceeded 10% in three of the water samples: well 1 in Dunfanaghy in October 2014 and June 2015 and at well 1 at Kincasslagh in October 2015. These were retained in the dataset for comment, but caution should be used when interpreting the results.

4.2.5 Data analysis

Mean daily water levels and weekly (7 days) and monthly (30 days) moving average water levels for a period of 423 days from the 4th of September 2014 were calculated and compared with mean effective rainfall for the corresponding time periods following Jones *et al*. (2006). Correlation coefficients for water levels and rainfall were calculated for lag periods of zero to seven days for daily water levels, up to 30 days for weekly water levels and up to 240 days for monthly water levels. The greatest correlation coefficient indicated the lag period after which water level showed the maximum response to rainfall. Rainfall data were not normally distributed so Kendall rank correlation was used.

Mann-Whitney U tests were carried out to compare number of flood days, water level range, maximum and minimum in pasture sites and golf courses. Median total and soluble reactive phosphorus, dissolved inorganic nitrogen, ammonium, nitrate and nitrite in groundwater at pasture sites were also compared with golf course sites using the Mann-Whitney U test for difference. Water samples from the wells at the edge of the dune slacks (well 2) were used in these analyses because they were sampled more frequently and ion balances showed that the data were more reliable in well 2 at Kincasslagh and Dunfanaghy. The information from the wells in the centre of the sites was retained for comment and to aid interpretation, but was not included in statistical analysis.

4.3 Results

4.3.1 Sediment

All of the sites show evidence of organic material near the soil surface. In most cases, this was composed of poorly decomposed organic layer between 3 and 40 cm deep, but at Kincasslagh organic matter at the surface was present only as humic mottling in yellow sand. Distinct dark layers containing organic matter were visible in the sediment cores at Ballyness, Lough Nagreany and Ballyliffin. The maximum organic matter content of samples taken from the sediment core at these sites was 8.9 %, 2.6% and 2.6% respectively (Appendix VI). There were no organic layers visible in the cores taken at the other sites, and samples from Rosapenna, Kincasslagh or Dunfanaghy had a maximum organic matter content of 1.9%. The soil and subsoil at all of the sites was dominated by medium and fine sand. With the exception of Lough Nagreany, the deepest sediment samples which corresponded to the depth of the piezometer screen were characterised by over 75% medium and fine sand in varying proportions. At Lough Nagreany the deepest sample from the core was dominated by large particles over 2mm in diameter.

4.3.2 Water levels

All of the sites flooded during the monitoring period except for Ballyliffin (Table 4.2). Kincasslagh had the most flooded days (233 days) and Ballyness had the deepest flood water (115.58 cm). Water levels fell below one metre below ground at Kincasslagh and Lough Nagreany.

Table 4.2 Hydrological characteristics of sites during the monitoring period. Minimum and maximum values are based on daily data means and shown with reference to ground level.

Site	Abbreviation	Minimum (cm)	Maximum (cm)	Range (cm)	No. days flooded
Ballyliffin	BFN	-99.85	-52.63	47.22	0
Ballyness	BNS	-83.26	115.58	198.85	187
Dunfanaghy	DFY	-65.92	45.23	111.15	185
Kincasslagh	KLH	-145.78	68.42	214.21	233
Lough Nagreany	LNY	-111.87	59.88	171.75	167
Rosapenna	RPA	-63.72	19.41	83.13	131

In 2014 1213mm of rainfall was recorded at Malin Head, 106% of the average value recorded in 30 years between 1985 and 2015. In 2015, 1484 mm of rain fell: 126 % of the 30 year average rainfall. Between 04 Sept 2014 and 04 Sept 2015, 1329 mm of rain fell.

The weekly and monthly moving averages for rainfall at the three rainfall stations were more strongly correlated than the daily averages and are therefore more reliable estimates of rainfall across the region. Effective rainfall was greatest between November 2014 and March 2015, but large effective rainfall events occurred throughout the year (Figure 4.4). The water level peaked in January at Ballyness, Dunfanaghy and Lough Nagreany, in March at Kincasslagh and in May at Ballyliffin and Rosapenna (Figure 4.4).

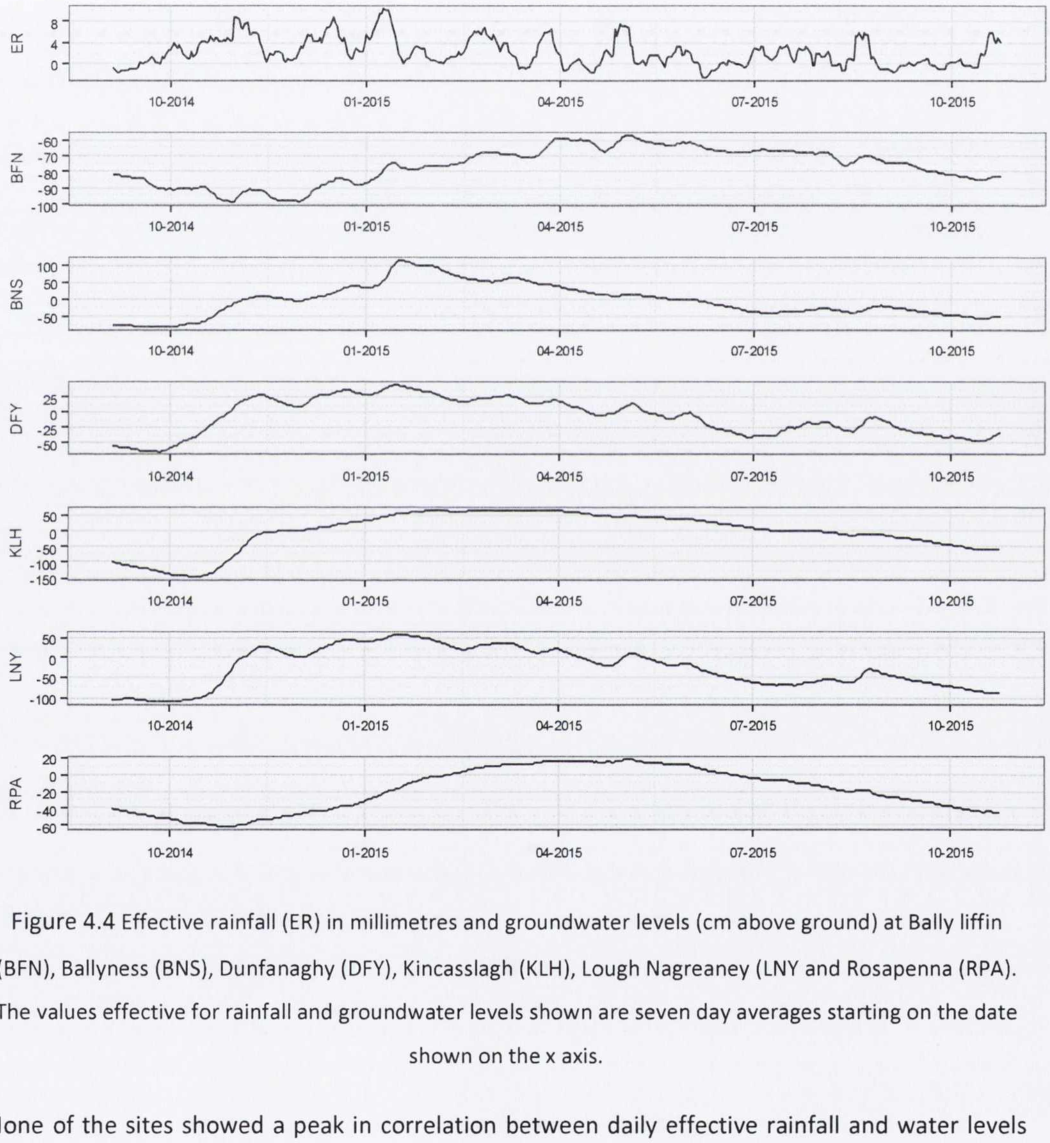
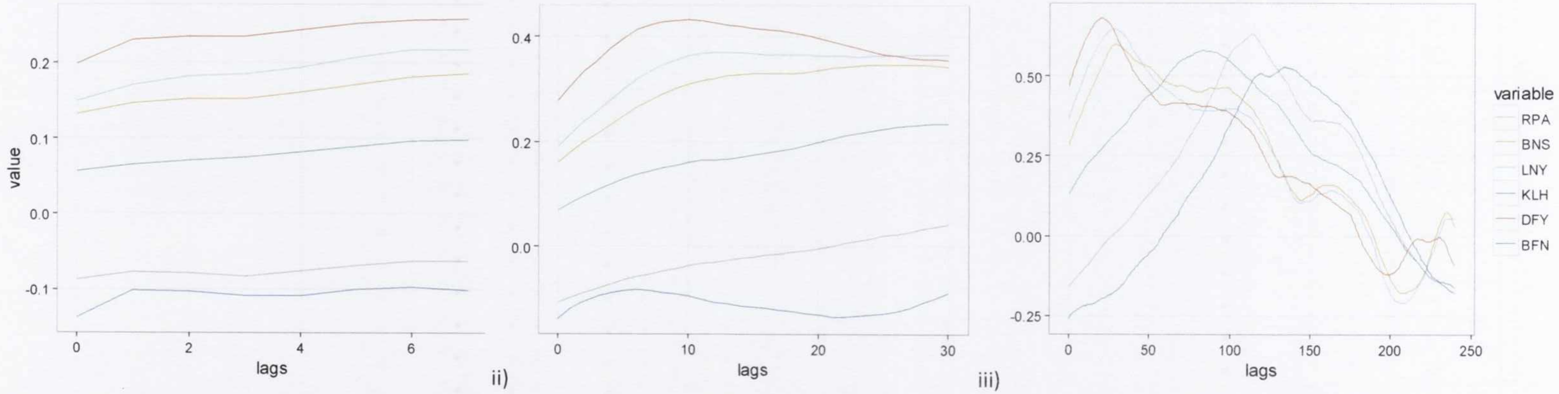


Figure 4.4 Effective rainfall (ER) in millimetres and groundwater levels (cm above ground) at Bally liffin (BFN), Ballyness (BNS), Dunfanaghy (DFY), Kincasslagh (KLH), Lough Nagreaney (LNY and Rosapenna (RPA). The values effective for rainfall and groundwater levels shown are seven day averages starting on the date shown on the x axis.

None of the sites showed a peak in correlation between daily effective rainfall and water levels within seven days (Figure 4.5i). For the seven day moving average (Figure 4.5ii), only the correlation between rainfall and water levels at Dunfanaghy peaked within 30 days (peak at lag = 11 days, tau = 43, $p < 0.005$). At Ballyness and Lough Nagreany the increase in correlation between the seven-day moving averages for water levels and rainfall appeared to even off after 10 days. The highest correlation between water levels and rainfall were observed when a thirty day moving average was applied to the data (Figure 4.5iii). Dunfanaghy, Lough Nagreany and Ballyness showed a peak response to rainfall after a lag of 30 days or fewer (Table 4.3), and all of these sites showed smaller roughly corresponding peaks or shoulders at lags of 50 – 100 days and 125 – 175 days. After 200 days there is an apparent increase in the correlation between rainfall and water levels again, but Kendall's tau is close to zero. The response time at Dunfanaghy always anticipated those at Lough Nagreany and Ballyness by around 10 days. The correlation between rainfall and lagged water levels is markedly different at Kincasslagh, Rosapenna and Ballyliffin. All of these sites show a peak correlation after a longer time lag (84 to 136 days) and while none of them has a second peak, they all have a break in their slope from a relatively shallow decline in correlation to a steep decline after a lag of about 175 days. This change in slope is most marked at Rosapenna where the graph has a distinct shoulder from 150 days.

Table 4.3 Lag periods for the peak correlation between thirty day moving averages for effective rainfall and water level change with the test statistic (Kendall's tau) and *p* value.

Site	Lag (days)	*tau*	P-value
Ballyliffin	136	0.53	> 0.005
Ballyness	30	0.59	> 0.005
Dunfanaghy	21	0.68	> 0.005
Kincasslagh	84	0.58	> 0.005
Lough Nagreany	30	0.65	> 0.005
Rosapenna	115	0.63	> 0.005



i) ii) iii)

Figure 4.5. Correlation between water level change and rainfall for i) daily, ii) seven day and iii) 30 day moving average values.

4.3.3 Water chemistry

Most of the samples are rich in calcium in comparison to sodium (Table 4.4). The samples from well 1 and the surface water at Dunfanaghy had higher sodium and chloride than the samples from other sites. The samples from well 2 at the same site had similar sodium and chloride content to wells at other sites. Mean alkalinity was below 200 mg l^{-1} $CaCO_3$ in surface water at all sites but greater than 200mg $CaCO_3$ in all of the wells. Mean groundwater alkalinity ranged from 202.21 mg l^{-1} $CaCO_3$ in well 2 at Dunfanaghy to 386.20 mg l^{-1} $CaCO_3$ at well 1 in Ballyness (Table 4.4). Mean pH was greater in surface water than in the wells at all sites except Rosapenna, where surface water pH was intermediate between the mean pH recorded in well 1 and well 2. It was lowest in well 2 at Lough Nagreany and greatest in well 2 at Dunfanaghy.

Table 4.4 Mean alkalinity, pH and major ions recorded in ground and surface water samples.

Site location	Alkalinity (mg l^{-1})	pH	Chloride (mg l^{-1})	Sulphate – sulphur (mg l^{-1})	Calcium (mg l^{-1})	Magnesium (mg l^{-1})	Sodium (mg l^{-1})	K (mg l^{-1})
BFN 1	232.54	7.59	37.07	4.18	79.85	13.72	23.29	2.30
BFN 2	220.59	7.64	37.19	2.95	76.51	12.31	24.51	1.18
BNS 1	386.20	7.12	47.62	0.30	140.77	11.52	25.63	1.75
BNS 2	293.92	7.40	45.17	1.84	108.24	9.69	27.36	2.89
DFY 1	312.88	7.22	743.86	40.68	167.64	60.08	595.53	22.19
DFY 2	202.21	7.68	28.10	2.56	73.16	6.16	20.20	1.29
KLG 1	280.45	7.57	51.80	2.94	89.49	7.94	31.62	2.58
KLG 2	243.25	7.54	69.19	3.40	95.75	8.29	38.15	2.50
LNY 1	299.05	7.11	45.71	0.26	111.97	7.83	31.49	1.15
LNY 2	314.49	7.02	46.63	0.32	119.31	8.14	32.37	1.38
RPA 1	203.30	7.65	32.80	3.02	71.57	7.03	26.96	0.79
RPA 2	241.07	7.48	44.10	1.72	98.48	6.40	20.66	1.31
BNS surface	145.78	8.08	55.14	1.05	59.08	6.54	35.92	3.38
DFY surface	234.80	8.20	378.27	10.53	95.16	36.11	241.25	10.02
KLG surface	193.95	8.13	81.10	1.53	80.75	8.22	43.73	2.28
LNY surface	194.25	8.10	66.94	1.52	72.29	6.26	34.70	1.58
RPA surface	201.72	7.57	37.78	0.75	81.46	6.67	22.52	0.67

Dissolved inorganic nitrogen (DIN - the sum of nitrite, nitrate and ammonium) content was greater in the groundwater than in the surface water at all of the sites except for Rosapenna in June 2015 (Table 4.5).

Table 4.5 Dissolved inorganic nitrogen content of ground and surface water samples in October 2014, March 2015 and June 2015.

	Dissolved inorganic nitrogen (DIN) (mg l^{-1})		
Location	October 2014	March 2015	June 2015
BFN 1	0.199	1.536	0.737
BFN 2	0.480	0.600	0.310
BNS 1	0.022		0.028
BNS 2	0.128	0.133	0.189
DFY 1	0.168	0.084	0.178
DFY 2	0.943	0.736	0.870
KLG 1	0.276		0.305
KLG 2	0.105	0.824	0.325
LNY 1	0.314	0.205	0.263
LNY 2	0.469	0.443	0.506
RPA 1	0.722	0.117	0.070
RPA 2	0.020	0.040	0.024
BNS surface		0.006	
DFY surface		0.006	
KLG surface		0.005	0.149
LNY surface		0.008	
RPA surface		0.013	0.116

In some cases there was considerable within-site variability in DIN, for example at Dunfanaghy, as well as between sampling times and between sites. The wells at Rosapenna and Ballyness contained the lowest recorded content of dissolved inorganic nitrogen. Nitrate was responsible for most of the dissolved inorganic nitrogen content at Kincasslagh, Ballyliffin and well 2 at Dunfanaghy (Table 4.6). Ammonium was the main constituent of dissolved inorganic nitrogen at Lough Nagreany, Ballyness and well 1 at Dunfanaghy. Nitrate content varied greatly between months and ammonium remained relatively stable in comparison (Table 4.6). Nitrite was only found in three samples and always at very low levels, with a maximum of 0.02 mg l^{-1}.

Table 4.6 Range of ammonium, nitrite and nitrate content of ground and surface water samples. Levels below the detection limit are shown as <0.005 for nitrite and ammonium and <0.02 for nitrate.

Location	Nitrite-N (mg l^{-1})		Nitrate-N (mg l^{-1})		Ammonia-N (mg l^{-1})	
	Min	Max	Min	Max	Min	Max
BFN 1	<0.005	<0.005	0.193	1.531	0.005	0.075
BFN 2	<0.005	<0.005	0.206	0.548	0.020	0.102
BNS 1	<0.005	<0.005	<0.02	<0.02	0.022	0.026
BNS 2	<0.005	<0.005	<0.02	<0.02	0.128	0.187
DFY 1	0.003	0.015	<0.02	<0.02	0.080	0.165
DFY 2	<0.005	0.010	0.711	0.924	0.005	0.156
KLG 1	<0.005	0.006	0.188	0.238	0.031	0.116
KLG 2	<0.005	<0.005	0.102	0.821	<0.005	0.050
LNY 1	<0.005	0.005	<0.02	<0.02	0.205	0.313
LNY 2	<0.005	<0.005	<0.02	<0.02	0.443	0.504
RPA 1	<0.005	<0.005	<0.02	0.715	<0.005	0.068
RPA 2	<0.005	<0.005	<0.02	<0.02	0.020	0.040
BNS surface	<0.005	<0.005	<0.02	<0.02	0.006	0.006
DFY surface	<0.005	<0.005	<0.02	<0.02	0.006	0.006
KLG surface	<0.005	<0.005	<0.02	<0.02	0.005	0.147
LNY surface	<0.005	<0.005	<0.02	<0.02	0.008	0.008
RPA surface	<0.005	<0.005	<0.02	<0.02	0.013	0.116

Mean total phosphorus ranged from 0.015 mg l^{-1} to 0.288 mg l^{-1}, and mean was below 0.1 mg l^{-1} in ten of the 12 wells (Table 4.7). In surface water mean total phosphorus was between 0.013 mg l^{-1} and 0.04 mg l^{-1}. Mean soluble reactive phosphorus was between 0.004 mg $l^{-1}$and 0.059 mg l^{-1} in groundwater, and from below the detection limit to 0.003 mg l^{-1} in surface water.

Table 4.7 Mean, maximum and minimum content of total phosphorus (TP) and soluble reactive phosphorus (SRP) in ground and surface water. Values below the detection limit ares shown as <0.001.

Site	Mean TP (mg l^{-1})	Max TP (mg l^{-1})	Min TP (mg l^{-1})	Mean SRP (mg l^{-1})	Max SRP (mg l^{-1})	Min SRP (mg l^{-1})
BFN 1	0.068	0.086	0.056	0.059	0.064	0.055
BFN 2	0.050	0.054	0.045	0.054	0.055	0.052
BNS 1	0.064	0.076	0.051	0.022	0.040	0.003
BNS 2	0.021	0.032	0.007	0.005	0.010	0.003
DFY 1	0.288	0.380	0.236	0.014	0.034	0.004
DFY 2	0.050	0.066	0.037	0.020	0.037	0.008
KLG 1	0.102	0.105	0.098	0.004	0.004	0.004
KLG 2	0.040	0.063	0.023	0.010	0.011	0.001
LNY 1	0.064	0.090	0.045	0.054	0.070	0.024
LNY 2	0.022	0.024	0.019	0.026	0.033	0.021
RPA 1	0.015	0.018	0.012	0.007	0.012	0.001
RPA 2	0.075	0.079	0.069	0.047	0.052	0.037
BNS surface	0.040	0.057	0.031	0.001	0.003	<0.001
DFY surface	0.018	0.027	0.011	0.002	0.003	0.001
KLG surface	0.013	0.017	0.011	0.001	0.002	<0.001
LNY surface	0.013	0.015	0.011	0.001	0.001	<0.001
RPA surface	0.017	0.029	0.003	0.001	0.004	<0.001

The greatest dissolved iron content was found in well 1 at Dunfanaghy (Table 4.8), where it reached a maximum of 9.30 mg l^{-1} in March 2015. Dissolved iron occurred in concentrations greater than 0.1 mg l^{-1} in both wells at Ballyness, Lough Nagreany and well 2 at Rosapenna. Dissolved iron exceeding 0.1 mg l^{-1} was detected in the surface water at Kincasslagh and Rosapenna. Manganese concentrations greater than 0.05 mg l^{-1} were found in both wells at Lough Nagreany and Rosapenna, well 1 in Dunfanaghy and in well 2 at Ballyliffin. The surface water also contained more than 0.05 mg l^{-1} of Manganese (Mn^{2+}) at Rosapenna in July 2015.

Table 4.8. Minimum and maximum manganese and iron content (mg l^{-1}).

Location	Min Mn^{2+}	Max Mn^{2+}	Min Fe^{2+}	Max Fe^{2+}
BFN 1	0	0.017	0	0.014
BFN 2	0.052	0.074	0.003	0.026
BNS 1	0.034	0.052	0.365	1.318
BNS 2	0.028	0.041	0.075	0.922
DFY 1	0.071	0.089	1.363	9.299
DFY 2	0.008	0.019	0.002	0.032
KLG 1	0.001	0.018	0.01	0.025
KLG 2	0.003	0.018	0	0.026
LNY 1	0.06	0.07	0.16	1.25
LNY 2	0.11	0.12	0.021	0.137
RPA 1	0.01	0.07	0	0.017
RPA 2	0.06	0.08	0.111	0.17
BNS surface	0.017	0.017	0.023	0.023
DFY surface	0.022	0.022	0.022	0.022
KLG surface	0.017	0.026	0.019	0.101
LNY surface	0.017	0.017	0.023	0.023
RPA surface	0.028	0.113	0	1.017

4.3.4 Relationship with management

Maximum water height and the water level range (Figure 4.6) were greater in pasture sites than golf course sites ($U = 0$, $p = 0.05$), but there was no significant difference in lowest water level ($w = 8$, $p = 0.95$) or number of flood days ($w = 1$, $p = 0.1$).

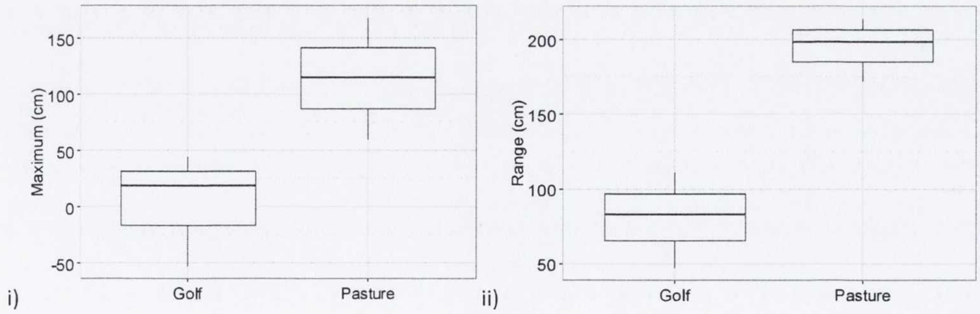


Figure 4.6 i) Maximum water level (cm) and ii) range (cm) in sites managed as golf course and pasture.

There was no significant relationship between dissolved inorganic nitrogen, ammonium, nitrate, nitrite or dissolved reactive phosphorus and management (Table 4.9). However, total phosphorus was significantly greater in groundwater samples from golf course sites than pasture sites (w = 9, p=0.05).

Table 4.9. Mann Whitney-U tests for difference in groundwater water chemistry and water levels depending on management (golf course vs. pasture). Asterisks indicate significant results.

Test	U statistic	P value
Minimum water level is greater in pasture than golf courses	5	0.65
Maximum water level is greater in pasture than golf courses	0	0.05*
Water level range is greater in pasture than golf courses	0	0.05*
No. flooded days is greater in pasture than golf courses	1	0.1
Dissolved inorganic nitrogen is greater in golf courses than pasture	6	0.35
Nitrate is greater in golf courses than pasture	7	0.18
Ammonium is greater in golf courses than pasture	3	0.8
Nitrite is greater in golf courses than pasture	4.5	1
Total phosphorus is greater in golf courses than pasture	9	0.05*
Soluble reactive phosphorus is greater in golf courses than pasture	8	1

4.4 Discussion

4.4.1 Water levels

Water levels at Lough Nagreany, Ballyness and Dunfanaghy had the earliest peak responses to effective rainfall observed, and these sites are all part of relatively low lying sand dune systems into which streams or drains from the surrounding landscape were observed to run (Table 4.1). The short lag between rainfall and water level response may be related to the swift delivery of water to low-lying parts of the sand dune system by streams originating outside of the sand dunes. Flow through rates for water in sandy substrates depend on the coarseness of the substrate, but have been measured at 3cm per hour (Tang and Shindo, 1999), although the water would take some additional time to infiltrate to the groundwater (Winter, 1999). The dune slack at Lough Nagreany is close to the boundary of the dune slack system (Figure 4.2), so water entering the system has a very short distance to travel to the dune slack.

All of the sites showed some increased correlation between rainfall and water levels at three to four months, which corresponds with a lag observed by Jones *et al.* (2006) in a dune system at Methyr Mawr Warren in South Wales. Jones *et al.* (2006) suggest that this likely corresponds to the period required for water to infiltrate through the sand dunes to a depth of 2m. The degree of variation between sites may relate to the differences in dune height and depth of sand above the water table. A final increase in the correlation between water levels and rainfall was observed at 125 to 175 days, and this may relate to groundwater flow originating outside of the dune slack. A similar time lag was observed at Methyr Mawr Warren (Jones *et al.*2006).

The speed of responses to rainfall at Rosapenna and Ballyliffin were very different from those at Lough Nagreany, Ballyness and Dunfanaghy. Part of the dune systems at Rosapenna and Ballyliffin act as an isthmus, joining a rocky promontory to the mainland (Figure 3). The elevation of the sand dunes is higher in comparison to the surrounding landscape than is the case at Lough Nagreany, Ballyness and Dunfanaghy (Table 4.2) and there are no drains terminating in the sand dune systems. A larger proportion of the change in water levels in these sites is likely to relate specifically to infiltration of rainfall which lands within the sand dune boundaries. The response to rainfall at Kincasslagh is intermediate between those observed Lough Nagreany, Ballyness and Dunfanaghy and at Rosapenna and Ballyliffin. The dune slack at Kincasslagh is located in a rocky basin in elevated position in the dune system and the area which could drain into it is relatively limited in comparison to Lough Nagreany, Ballyness and Dunfanaghy. There are rocky outcrops at the edges of the dune slack, and this may limit speed of water draining out of the slack.

Studies of dune slacks in Britain, the Netherlands and Argentina (Soulsby *et al.*, 1997a; Grootjans and Stuyfzand, 1998; Carretero and Kruse, 2012; Robins and Stratford, 2013) have recorded annual fluctuations of between 0.5m and 1 metre in groundwater underlying dune slacks. The variation in annual water level fluctuations between sites is very large in this study (Table 4.2), and this is likely to reflect multiple differences between the sites such as drainage and topography as discussed above. Management was significantly related to the maximum water level and also the annual range of water level fluctuation. Water is actively pumped or drained out of the sand dune systems at two of the three golf course sites (Ballyliffin and Dunfanaghy) after heavy rainfall, and this may have reduced the amount of water available for groundwater recharge during wet periods. This may have reduced maximum levels. If removal of water to prevent the course flooding is the dominant abstraction, and water abstraction for use in the clubhouses on the golf courses is steady, then the reduced maximum water levels could also explain the smaller water level range at golf course sites.

At Ballyliffin the dune slack did not flood at all, despite the fact that 2014 – 2015 was a wetter year than average in Co. Donegal. The absence of flooding has a major direct impact on wetland species of dune slacks, but there are also indirect effects. There was no evidence that denitrification was occurring at Ballyliffin, and this is likely to be linked to the drop in the water table and loss of anaerobic conditions. This means that if groundwater comes into contact with the dune slack it is more likely to affect the vegetation and cause a shift away from a typical dune slack community. Ballyliffin has less plant diversity and more dwarf shrubs than the other sites selected and this is likely to relate to drier, more nutrient rich conditions at the dune slack.

4.4.2 Water chemistry

Most of the sites were primarily underlain by non-calcareous bedrock, and this is normal over much of the west coast of Ireland. Coastal sand dunes are typically rich in shell matter in northwest Ireland, and the dominance of calcium and bicarbonate in water samples from all but one of the wells is likely to be due to the presence of calcium carbonate in the sand (Curtis 1991). Lough Nagreany was the site with the least alkaline water, and this is likely to be because it is located close to the landward boundary of the sand dune system and is influenced by water entering the dune slack which has not travelled through calcium rich substrate.

Nitrogen input occurs on all of the dune systems either through fertiliser application or from cattle or sheep urine and faeces, as well as potential inputs from surface and groundwater entering the dunes from the landward boundary at some sites. If no nitrate is detected in the groundwater, for example at Ballyness, it is likely that the nitrogen was taken up by vegetation before it reached the groundwater, or that nitrate processing is occurring below ground. Concentration of either or both reduced manganese (Mn^{2+}) and dissolved iron meet the criteria listed in Chapelle *et al.* (2009) which suggest denitrification is occurring at well 2 in Rosapenna, both wells in Lough Nagreany, well 1 in Dunfanaghy and well 1 in Ballyness on all site visits. At well 2 in Rosapenna and well 2 in Ballyness there were indications of oxidation-reduction reactions in July and March of 2015 but not in October of 2014. At Rosapenna 1, the absence of reduced manganese and dissolved iron in October coincided with the highest nitrate concentration and the lowest water levels. It is possible while water levels were low conditions were unfavourable for denitrification due to the exhaustion of available carbon in aerobic processes or aerobic conditions penetrating to the level of the well screen (Starr and Gillham, 1993). Denitrification may have ceased at Ballyness on October because all of the available nitrate had been consumed. At Rosapenna, Lough Nagreany, Dunfanaghy and on one occasion at Ballyness manganese and iron concentrations were not typical of any specific process, but it is possible several oxidation-reduction processes were occurring simultaneously due to small scale differences in soil conditions.

At Ballyliffin and Kincasslagh, concentrations of nitrate were higher and dissolved iron (Fe^{2+}) and manganese (Mn^{2+}) were lower than would be expected if denitrification were occurring according to the concentrations shown in Chapelle *et al.* (2009), so it is unlikely that denitrification is occurring. There was little organic material on the ground surface or in the sediment samples from Kincasslagh, so dissolved organic carbon may not have been sufficient to maintain denitrification. At well 2 in Dunfanaghy, nitrate content was consistently above 0.7 mg l^{-1} on every visit. Denitrification may not have been occurring there, or alternatively it may have had higher nitrogen inputs.

Dissimilatory nitrate reduction to ammonium (DNRA) could be at least partially responsible for raised ammonia levels at Lough Nagreany, well 2 in Ballyness and well 1 at Dunfanaghy. Alternatively, raised ammonium levels could indicate a local point source of contamination (Environmental Protection Agency, 2003).

Most surface water samples contained less dissolved inorganic nitrogen than the groundwater samples, which is likely to relate to uptake by plants. At Rosapenna the surface water sample from June contained more nitrogen than the ground water. This could be the result of spray from fertiliser application on adjacent parts of the golf course being blown into the dune slack.

The amount of dissolved inorganic nitrogen in most samples was low, but the samples taken at each site were very variable and all of the sites exceed the threshold for suspected contamination of groundwater on a least one occasion during the year (0.4 mg l^{-1}) (Davy *et al.* 2010). Dissolved inorganic nitrogen exceeded this level in all of the samples from well 2 at Dunfanaghy and on two occasions at each well in Ballyliffin. The dissolved inorganic nitrogen levels and nitrate content at Ballyliffin are comparable to a site with an established link to contamination in Wales (Rhymes *et al.* 2014), and well 2 at Lough Nagreany and well 2 at Dunfanaghy have similar, though slightly lower levels.

Differences in nitrate content within sites are likely to be a reflection of small scale differences in soil conditions and microbial activity, but more intense monitoring systems would be required to make reliable inferences on the processes responsible for variation within sites. The large difference in water chemistry between the wells at Dunfanaghy suggests that the two wells are influenced by water from different sources. Sea water intrusion is the most likely reason for the high sodium and chloride content at in the well at centre of the dune slack at Dunfanaghy.

Nitrogen content in ground and surface water samples did not reflect management differences and this is likely to be because nutrients from fertiliser or manure / urine are among a range influences on nutrient levels in the dune slacks such as presence of conditions promoting denitrification.

Although total phosphorus was significantly higher in groundwater at sites managed as golf courses, there was no difference in the soluble reactive phosphorus content. The additional phosphorus input to the site in the form of annual fertiliser additions may raise the total phosphorus content at golf course sites, although livestock also represent a source of phosphorus. Unlike nitrate, phosphorus is easily immobilised and may precipitate out of solution easily (Reddy & DeLaune, 2011). Soluble reactive phosphorus is likely to be taken up by plants once water comes to the surface (Cunha Pereira *et al.*, 2010). At both wells in Ballyliffin, Lough Nagreany well 1 and Rosapenna well 2, the mean soluble reactive phosphorus content of the groundwater exceeded the Irish groundwater threshold value for molybdate reactive phosphorus of 0.035 mgl^{-1} (European Communities Environmental Objectives (Groundwater) Regulations, 2010). At Ballyness well 1 and Dunfanaghy well 2, the maximum soluble reactive phosphorus concentration was above this groundwater threshold value (which is based on the Irish environmental quality standard for good status of rivers under the Water Framework Directive).

Surface water in northwest Ireland is vulnerable to elevated phosphorus in agricultural areas through a combination of poorly drained soils and occasional high volumes of rainfall. If a proportion of the groundwater in some dune slacks is attributable to the infiltration of surface water from surrounding agricultural fields, occasional peaks in phosphorus related to rainfall events may be expected (Schulte *et al.*, 2006). More frequent recordings of soluble reactive phosphorus in groundwater would be required to determine whether this is occurring. Alternatively, phosphorus may be entering the system from activities occurring within the sand dune system. Little has been published relating to phosphorus content in dune slacks (Davy *et al.* 2010), so it is difficult to compare these sites with groundwater in dunes elsewhere. For the dune slack standing waters, it may be appropriate to compare with total phosphorus thresholds for lakes, given that Cunha Pereira *et al.* (2010) have found this comparison appropriate for turlough temporary water bodies. The OECD (1982) boundary for mean total phosphorus between mesotrophic and eutrophic lakes is 0.035 mgl^{-1}: it can be noted that the mean total phosphorus in the Ballyness standing waters exceeds this threshold while the mean surface water values for the other four sites containing standing water are below the threshold. Comparisons with total phosphorus from dune slack standing waters elsewhere would be desirable but unfortunately data are lacking.

4.5 Conclusions

Most of the sites flooded for several months during winter. Golf courses were associated with a reduction in the maximum water level in the slacks and this has probably led to a reduction in the total flooded area in winter and the length of the flood period. Response to rainfall varies between sites, and low-lying sites appear to respond more quickly to rainfall events than more elevated sites. This is likely to reflect entry of water from the surrounding landscape into the groundwater of low-lying sand dunes, so sand dunes adjacent to farmed land may be at risk of groundwater contamination from agrichemicals. There was evidence for denitrification at several of the sites which flooded, indicating that the high water levels are helping to maintain the low nutrient status in the dune slacks.

5 Differences in sensitivity to water chemistry and hydrology among snail and plant communities in dune slacks.

To be submitted for publication as Delaney, A., Coxon, C., and Stout J.C. "Differences in sensitivity to water chemistry and hydrology among snail and plant communities in dune slacks" Target journal: Science of the Total Environment

5.1 Introduction

The vegetation type typical of dune slacks has been threatened in Europe due to human activities, and a considerable body of research in Belgium, the Netherlands and the UK has examined the complex interactions between groundwater, surface water and vegetation communities (Soulsby *et al.*, 1997a; Grootjans and Stuyfzand, 1998; Bossuyt, Honnay and Hermy, 2003; Curreli *et al.*, 2013). Throughout the literature, there is a consensus that maintaining a high water level is important to ensure that calcium rich water enters the dune slack and supports a calcicolous wetland plant community (Grootjans *et al.*, 1991; Sival, Mucher and van Delft, 1998). Fertilisation experiments have shown that nutrients also help to determine the vegetation type (Lammerts and Grootjans, 1997) and this has been borne out in the field (Malcolm and Soulsby, 2001; Rhymes *et al.*, 2014). For vegetation communities, nitrogen is the primary limiting factor, and increases are associated with a change from forb-rich herbaceous vegetation to vegetation dominated by grasses and dwarf shrubs. Phosphorus can also have an impact during the early successional stages or in conjunction with nitrogen, but is of secondary importance as a driver (Lammerts and Grootjans, 1997).

Macroinvertebrates are an intrinsic part of wetland ecosystems (Batzer *et al.* 2015), but have received relatively little attention in dune slacks habitat compared with vegetation. Studies of invertebrates in dune slacks tend to be part of larger investigations of sand dune invertebrates (e.g. Howe *et al.* 2010) or limited to specific species of conservation interest and are most frequently focussed on species associated with the dry phase (e.g. Gröning *et al.* 2007). This means that an important aspect of dune slack ecosystem functioning is poorly understood. For example, invertebrates play an important role in nutrient cycling as they consume plant matter, algae and detritus (Ohta *et al.* 2016, Porter *et al.* 1999). Furthermore, the role of surface water chemistry and hydrology in structuring macroinvertebrate assemblages is a major theme in aquatic ecology, but the potential role of groundwater is rarely considered (Stendera *et al.*, 2012). Therefore, there is little information available regarding the impacts of groundwater on invertebrates of groundwater dependent terrestrial ecosystems.

Currently, the habitat condition of dune slacks is assessed for the EU Habitats Directive (92/43/EEC) using a list of plant indicator species (European Commission 2007). Because we have very little information regarding the invertebrate assemblages associated with aquatic phase of dune slacks, or their relationship with ground and surface water conditions, it is possible that by using plants to indicate habitat condition we may fail to observe factors affecting the functioning of the dune slack during the aquatic phase.

5.1.1 Aims

To assess whether plants and macroinvertebrates have differing sensitivity to hydrology and hydrochemistry in dune slacks, we compared the water levels and water chemistry in six dune slacks in northwest Ireland with the diversity and composition of plants and snails found there. The relationships of plants and snails to groundwater and surface water were examined separately. Snails were chosen to represent macroinvertebrates because many species are known to occur in dune slacks (Kerney 1999), they are sensitive to environmental conditions (Hoverman *et al.*, 2011) and they have congruent distributions with other aquatic macroinvertebrates (Bilton *et al.*, 2006; Ruhí and Batzer, 2014). There were three main questions:

1. Do hydrological variables affect species diversity or composition of plants or snails in dune slacks?

2. Does groundwater chemistry affect species diversity or composition of plants or snails in dune slacks?

3. Does surface water chemistry affect species diversity or composition of plants or snails in dune slacks?

5.2 Methods

5.2.1 Site selection

Six sites were selected in Co. Donegal, as described in Chapter 4.

5.2.2 Collection of biological samples

Vegetation and snail samples were collected at each site as described in Chapter 2.

5.2.3 Hydrological monitoring

Hydrological monitoring and water chemistry analysis were carried out as described in Chapter 4.

5.2.4 Selection of hydrochemical and hydrological variables

The average daily water level in relation to the ground surface was calculated. Daily water levels were used to derive three values for each site: the minimum water level, number of days flooded and daily water level fluctuations (Table 5.1). Water level variables were derived from the data from the wells placed in the middle of the selected dune slacks. The water levels for each were subtracted from those of the following day to generate a differenced dataset. Mean daily fluctuation was calculated as the mean of the absolute values of the differenced dataset. The wells close to the slack centre were placed inside the flooded area, but at two sites they were found not have been located at the deepest point. At these sites (Rosapenna and Lough Nagreany) water may have remained in small depression for longer than was recorded in the wells. At Rosapenna, the difference in ground level height between the well and the deepest point was 8 cm, while at Lough Nagreany, the undulating ground surface resulted in some small depressions being 28.5 cm lower than the ground where the well was inserted.

Hydrochemical variables comprised dissolved inorganic nitrogen (sum of ammonium, nitrite and nitrate) soluble reactive phosphorus, total phosphorus, alkalinity, pH and conductivity as these have been shown to have an important impact on the composition of dune slacks plant communities (Grootjans and Stuyfzand 1998). Groundwater chemistry results presented here are the mean values for wells at the edge of the slacks. Wells in the centre of the slacks were sampled less frequently and differences in their chemical composition from those at the edge meant they could not be considered replicate samples, so they were excluded.

All of the sites which flooded contained water in January and March, after which point some sites dried out. To avoid the influence of seasonal changes in water chemistry in sites with longer flood periods, mean values for surface water samples from January and March were included in the analysis. Analysis of ammonium, nitrite, and nitrate were not carried out in January, so these and the DIN figures were derived from samples taken in March only. Ballyliffin did not flood during the course of the monitoring.

Table 5.1 Hydrochemical and hydrological variables included in the analysis

Variable	Abbreviation	Location	Description
Minimum water level	Minimum		Greatest depth below ground reached by the water table
Variability	Variability		Variance in the difference between the water level from day to day
Dissolved inorganic nitrogen	DIN	Ground	Dissolved inorganic nitrogen in groundwater
Soluble reactive phosphorus	SRP	Ground	Dissolved phosphorus in groundwater
Alkalinity	Alkalinity	Ground	Alkalinity in groundwater
Ammonium	Ammonium	Surface	Ammonium in surface water
Soluble reactive phosphorus	SRP	Surface	Dissolved phosphorus in surface water
Alkalinity	Alkalinity	Surface	Alkalinity in surface water

5.2.5 Testing for collinearity

Correlation and variance inflation factors (VIFs) were used to test for collinearity among the hydrochemical and hydrological variables following Zuur *et al.* (2007) (Appendix VII). Relationships between variables relating to surface water, ground water and water levels were tested separately. Variables which had a significant correlation or a VIF of 5 or greater were excluded from further analysis. When correlated variables had been excluded from surface water, groundwater and water level groups, VIFs were calculated for the remaining variables. Variables with a VIF greater than 5 were removed.

5.2.6 Biological composition

Average species abundances per quadrat were calculated for snails and plants at each site and entered into a species by site matrix. The similarity of species composition at different sites was examined separately for snails and plants using non-metric multidimensional scaling (NMS) as described in Chapter 2. Water chemistry and hydrological variables were fitted to the ordination and tested for correlation with species distributions using methods described in Chapter 3.

5.2.7 Diversity correlations

Quadrat data were used to generate species accumulation curves for snails and plants at each site. Species richness and Simpson's diversity for each site were then estimated by using extrapolation and rarefaction as described in Chapter 2 to reduce the influence of sampling bias. Snail richness and diversity were estimated for 80% coverage and plant richness and diversity were estimated for 90% coverage. Simpson's index was considered appropriate because it is influenced by dominance and so complements species richness (Chao *et al.*, 2014).

Diversity indices for plant and snail assemblages were compared with water chemistry and hydrological variables using Kendall's rank correlation. This non-parametric method was appropriate because the data contained outliers and the small sample sizes made it difficult to determine whether the data conformed to a specific distribution.

5.3 Results

A total of 90 plant species were found, with 14 to 45 species per site (Table 5.2). Between three and seven plant quadrats were recorded per site, and species accumulation curves levelled off, indicating that sites had been adequately sampled. Estimated species richness was very similar to observed species richness.

Table 5.2 Observed species richness and estimated species richness and diversity for vegetation.

Site	No. quadrats	Observed richness	Estimated richness	Estimated Simpson's diversity	Estimation method and coverage
Ballyliffin	3	14	16.6	12.1	Extrapolation to 90%
Ballyness	3	32	37.0	29.1	Rarefaction to 89%
Dunfanaghy	5	29	36.9	23.6	Extrapolation to 90%
Kincasslagh	6	30	40.0	29.4	Observation at 90%
Lough Nagreany	6	23	26.5	19.5	Rarefaction to 89%
Rosapenna	7	45	61.0	40.7	Extrapolation to 90%

Snail samples were less diverse with 19 snail species found in total, and five to ten species found per site (Table 5.3). Abundance was variable among snail samples and between seven and 234 individuals were found per site. A minimum of three and maximum of 46 quadrats were recorded. Species accumulation curves suggested that snails were under-sampled at three sites: Ballyliffin, Kincasslagh and Lough Nagreany. Estimation of species richness had a greater impact on diversity figures for snails than plants and changed the order in which sites ranked from most to least diverse. Ballyliffin was the site which had the fewest observed species with five snail species and 14 plant species.

Table 5.3 Observed abundance and species richness and estimated species richness and diversity for snails.

Site	No. quadrats	Abundance	Observed richness	Estimated richness	Estimated Simpson's diversity	Estimation method and coverage
Ballyliffin	3	8	5	5.6	4.3	Extrapolation to 79%
Ballyness	44	104	8	4.8	3.6	Rarefaction to 80%
Dunfanaghy	26	234	10	5.4	4.1	Rarefaction to 80%
Kincasslagh	44	35	7	4.7	3.1	Extrapolation to 80%
Lough Nagreany	46	71	7	2.5	1.9	Rarefaction to 80%
Rosapenna	46	39	8	5.5	3.6	Rarefaction to 80%

5.3.1 Water chemistry and hydrology

All of the water chemical analyses used in the data analysis were of acceptable quality according to the ion balance calculations and the results of tests for reference standards were as expected. Number of days flooded was removed from the analysis due to collinearity issues, as were conductivity, pH and total phosphorus in both ground and surface water (Appendix VII).

Ammonium was the only type of dissolved nitrogen detected in the surface water, and was recorded as 0.01 mg l^{-1} in all sites except Kincasslagh where it was below the detection limit (Table 5.4). In groundwater, mean dissolved inorganic nitrogen at each site ranged from 0.02 mg l^{-1} at Rosapenna to 0.82 mg l^{-1} at Ballyliffin. Alkalinity was consistently greater in groundwater than surface water. The water table was shallow all year round at all of the sites, never exceeding 134.6 cm below the ground surface. The mean day to day water level fluctuations ranged from 0.95 cm at Rosapenna to 2.2 cm at Dunfanaghy.

5.3.2 Biological composition

The NMS plots for snails and plants indicated that Ballyliffin was an outlier, and it was removed from the analysis. NMS was carried out on the snail and plant abundance data for the remaining five sites. For plants, the NMS plot indicates that Ballyness and Dunfanaghy are very closely related, and both are close to Rosapenna in ordination space (Figure 5.1). Kincasslagh and Lough Nagreany are relatively isolated. None of the water chemistry or hydrology variables were correlated with plant distributions (Appendix VIII). For snails, Ballyness and Lough Nagreany were the closest together on the NMS plot, and Rosapenna and Kincasslagh were also similar (Figure 5.2). Dunfanaghy was not closely related to any other site in comparison. Snail composition was only significantly related to groundwater alkalinity ($r^2 = 0.96$, $p = 0.04$) and soluble reactive phosphorus ($r^2 = 0.95$, $p = 0.05$) in surface water.

Table 5.4 Hydrological variables and mean values of groundwater chemistry for 2014 – 2015 and surface water chemistry. Surface water SRP and Alkalinity are means of values recorded in January and February 2015 and ammonium figures are from samples taken in March 2015. Surface water was not present at Ballyliffin.

	Minimum (cm)	Fluctuation (cm)	No. flooded days	DIN groundwater (mg l^{-1})	Alkalinity groundwater (mg l^{-1})	SRP groundwater (mg l^{-1})	Ammonium surface (mg l^{-1})	SRP surface (mg l^{-1})	Alkalinity surface (mg l^{-1})
Ballyliffin	-99.6	1	0	0.82	230.8	0.06			
Ballyness	-83.3	1.7	187	0.15	293.9	0.01	0.01	0.001	139.44
Dunfanaghy	-65.9	2.2	185	0.64	202.2	0.02	0.01	0.002	233.55
Kincasslagh	-145.8	1.3	233	0.41	243.3	0.01	0.00	0.000	174.07
Lough Nagreany	-111.9	2.2	167	0.36	314.5	0.03	0.01	0.001	192.46
Rosapenna	-63.7	1	131	0.02	241.1	0.05	0.01	0.000	192.20

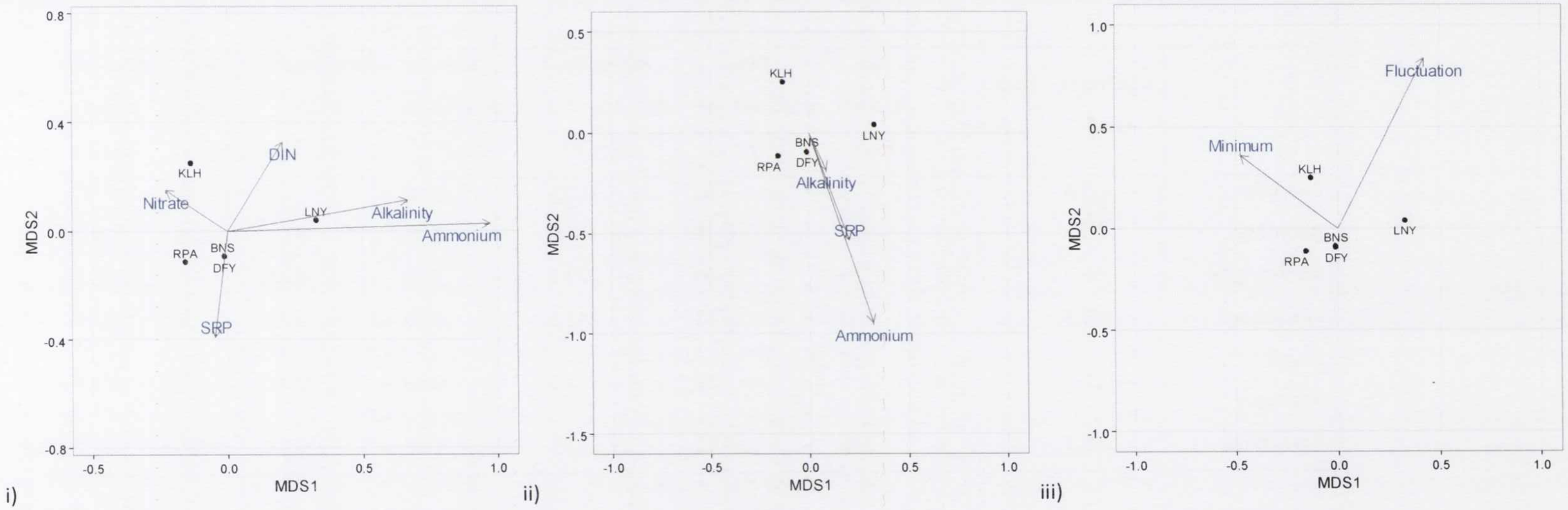


Figure 5.1. NMS plot showing vegetation communities with arrows indicating the strength of correlations with i) groundwater chemistry, ii) surface water chemistry and iii) hydrological variables. Dissolved inorganic nitrogen is abbreviated to DIN and soluble reactive phosphorus is abbreviated to SRP.

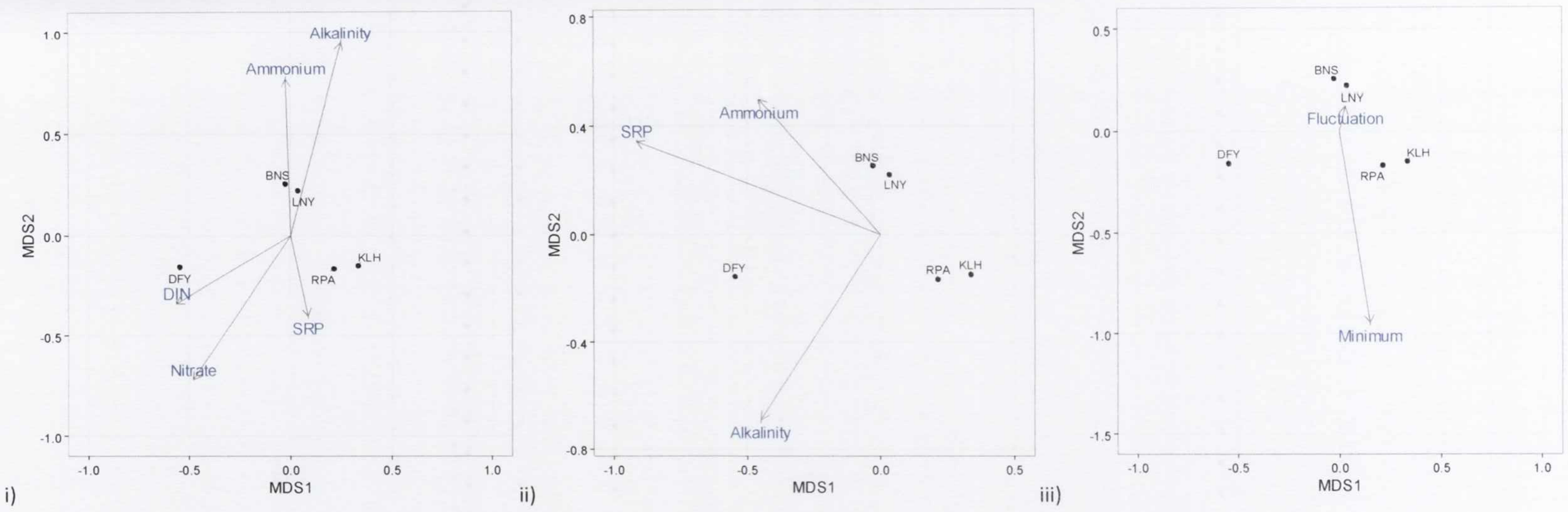


Figure 5.2 NMS plot showing snail assemblages with arrows indicating the strength of correlations with i) groundwater chemistry, ii) surface water chemistry and iii) hydrological variables. Dissolved inorganic nitrogen is abbreviated to DIN and soluble reactive phosphorus is abbreviated to SRP.

5.3.3 Species richness and diversity

None of the environmental variables were significantly related to the diversity of plants or snails (Appendix IX).

5.4 Discussion

The species richness of snails per site was greater than was found in a survey of other calcareous wetlands in Ireland (Porst and Irvine, 2009), but this is probably due to our inclusion of both terrestrial and aquatic snails. Plant species richness was very variable, with three times as many species recorded at the most species rich site than the least species rich site.

Snail composition was correlated with groundwater alkalinity rather than surface water alkalinity and there are two potential explanations for this. The main chemical which is responsible for high alkalinity in these sites is calcium carbonate (Chapter 4). Plants of calcium-rich habitats are less efficient at taking calcium up from soil water than other plants (Snaydon and Bradshaw, 1961; Clarkson, 1965) so even at relatively high alkalinity, the concentration of calcium in plant tissues may vary depending on the calcium content of the groundwater. The availability of calcium in plant matter is likely to be an important factor as the most common snail species at sites with high alkalinity in the groundwater were *Galba truncatula* and *Carychium minimum*, both of which most frequently eat decaying plant matter (Falkner *et al.* 2001). Secondly, when calcium-rich groundwater reaches the surface, calcium carbonate can precipitate out of solution and form a deposit on the surface of plants growing in the dune slack (Coxon, 1994). Grazing snails may take the calcium carbonate deposits up, supplementing the calcium in their diets. The difference in alkalinity between ground and surface water samples at sites included in this study suggests that calcium carbonate precipitation may have occurred. The presence of calcium in surface water has been found to influence invertebrate distributions and abundances (Heino, 2000), and soil calcium is also an important factor (Hotopp, 2002). A study of molluscs in fens in the Czech Republic and Slovakia found that calcium concentration in spring water was an important driver up to concentrations of 100 mg l^{-1} (Horsák and Hájek, 2003). The calcium concentration in groundwater in Donegal dune slacks recorded for this project ranged from 59.2 to 178.9 100 mg l^{-1}.

Low soluble reactive phosphorus in surface water was associated with lower abundance of snails, and this is in line with other studies of gastropods in wetlands and freshwater bodies (Costil and Clement 1996, Crowns *et al.* 1992). While phosphorus is of secondary importance in determining the vegetation of dune slacks (Lammerts and Grootjans, 1997) algal growth in lakes is generally phosphorus limited (Cunha Pereira *et al.*, 2010). The availability of phosphorus at some sites could promote algal growth, providing an additional food supply. *Cochlicopa lubrica*, *Cochlicopa lubricella* and *Carychium minimum* were common at sites where soluble reactive phosphorus is highest in surface water, and algae form a part of their diet (Falkner *et al.* 2001). However, Crowns *et al.* (1992) found that rare species tended to be associated with low nutrient, relatively species poor water bodies, so differences in phosphorus could have an impact on the value of the habitat for species of conservation interest. As a result, current monitoring methodologies may not be sufficient to detect changes affecting snail assemblages in dune slacks.

Nitrogen levels in ground and surface water were towards the lower end of the range in comparison to those recorded at sites in the UK (Malcolm and Soulsby, 2001; Jones *et al.*, 2006; Rhymes *et al.*, 2014). There is little information regarding phosphorus concentration in the groundwater or surface water of dune slacks, but both the ground and surface water concentrations of phosphorus were lower than observed in a survey of 71 temporary ponds in the UK (Nicolet *et al.*, 2004). The low nutrient levels may explain why none of the variables tested had an impact on plant distributions. At the sites in Donegal which flood, the differences between hydrochemical and hydrological variables present at different sites are not sufficient to structure the plant communities, but they do have an effect on snail composition. As a result, plant species may not act as effective surrogates for snail species in dune slacks.

Seasonal flooding is generally considered to be one of the most important factors affecting plant communities in dune slacks (Grootjans and Stuyfzand 1998), but was not shown to affect species richness or diversity at the sites studied here. Only one site failed to flood, and to evaluate the impacts of desiccation, a balanced design targeting sites which do and do not flood annually would be required. Because dune slacks are located within sand dunes, there is generally a diverse source of plants available to colonise the drier areas (Rodwell 2000), so even though there is likely to be an effect of desiccation, it may not be apparent in comparisons of species richness and diversity.

The number of sites used in this study was small and each site had an important impact on the overall findings, so including a larger number of sites would give more robust generalizable results. Nevertheless, this is the first time that invertebrate diversity has been examined in relation to ground and surface water conditions of dune slacks at different sites in a comparable manner, and should help to inform future investigations.

Although NMS can be used to examine the similarity of small numbers of samples (Dangles, Malmqvist and Laudon, 2004), the numbers of individuals in each sample was small in this case, and this reduces the reliability of the method (Forcino *et al.*, 2015). While principal components analysis is an alternative for smaller sample sizes, it is not recommended for use with zero-inflated data (Kent, 2011). Using Kendall's Tau was appropriate for this data set because it was small and contained extreme values, but an alternative approach would have been to use a robust generalised linear models for each taxonomic group, incorporating all of the environmental variables (Heritier *et al.* 2009) The use of a large number of explanatory variables would have been a drawback for this method, as generalised linear models is not normally intended for exploratory analysis, but to quantify a suspected relationship (Zuur *et al.* 2007). Given the small number of samples, only a very strong signal would have resulted in a significant result, so it is unlikely that using robust GLM would have yielded a different result.

5.5 Conclusions

This research indicates that snail composition is sensitive to some ground and surface water variables, and these are unlikely to be picked up in an assessment based on plant species. Widening the list of indicator species would enhance the habitat assessment protocol. The importance of groundwater to snail distributions shows that organisms which are associated with the surface of the dune slack and with surface water can be affected by groundwater chemistry in ways that cannot not be detected by examining surface water. The results presented here should be considered a preliminary examination of dune slack hydroecology demonstrating the potential benefits of a modified approach to conservation assessment.

6 General Discussion

There is a long history of research focussing on the effects of environmental drivers on natural habitats and their biological communities, but the effects of environmental pressures on different taxa which share periodically disturbed habitats have not been thoroughly investigated. Understanding diversity patterns in relation to major habitat disturbance is important because it helps to predict how environmental change will affect biological communities. This in turn provides scientific evidence to inform effective conservation policies, which are vital for maintaining biodiversity.

In this study, I compared patterns of diversity in contrasting taxonomic groups in a seasonally flooded wetland, explored the main drivers linked to diversity in each group and characterised the groundwater which causes periodic inundation and desiccation. Dune slacks were an ideal model habitat because they experience periodic disturbance through flooding, have consistent physical characteristics and generally experience low levels of anthropogenic pressure in Ireland. They are a widely distributed habitat of conservation interest and their flooding regime is similar to other natural habitats such as prairie pot-holes and vernal pools in North America (Euliss, Mushet and Johnson, 2002; Marty, 2005). In Chapter 2 I investigated the degree of cross congruence displayed by plants, snails and water beetles in dune slacks. I also tested the ability of the methods used under Article 17 of the Habitats Directive to determine whether a habitat assessment based on plants could identify specific snail and water beetle assemblages of conservation interest. I found that plants, snails and water beetles do not show congruent patterns of diversity or species composition, and that the habitat assessment did not identify sites where snails and beetles of conservation interest occurred. Chapter 3 examined the relationships between environmental variables and the composition of plants, snails and water beetles in dune slack sites. Both species and trait composition were used in the analysis which revealed that all three of the selected taxa responded to the presence of livestock, but the response could only be detected by examining the snail and beetle assemblages through their trait composition rather than their species composition. The hydrology and hydrochemistry of six dune slacks were characterised in Chapter 4, which constituted the first consistent study of hydrological functioning of dune slacks at multiple sites in Ireland. In this chapter, I also examined the hydrology and water chemistry of dune slacks under two different management regimes: non–intensive pasture and golf courses. This showed that the maximum water level in dune slacks and the range of water fluctuation were greater in dune slacks managed as pasture than in dune slacks associated with golf courses. I also found evidence that denitrification was likely to be occurring below ground in dune slacks and that the response of groundwater to rainfall may be related to local topography. Chapter 5 explored the relationship of assemblages of plants and snails with water chemistry and water levels in the dune slacks where they occur. I found that snail communities were related to groundwater alkalinity and surface water soluble phosphorus.

6.1 Conservation of biological communities in dune slacks

The dune slacks surveyed for this research contained diverse plant communities typical of the habitat (Rodwell, Pigott and Joint Nature Conservation Committee (Great Britain), 2000). There is very little information regarding dune slack invertebrates in the literature, but I found that snail abundance and diversity were high in relation to other temporary waterbodies (Nicolet *et al.*, 2004; Porst and Irvine, 2009a), though this may be partly due to having surveyed both during the wet and dry phases rather than focussing on one or the other. In common with other temporary pond habitats (Nicolet *et al.*, 2004), a large proportion of the species found were of conservation interest and this highlights the need to monitor the conservation status of temporary waterbodies including dune slacks in a comprehensive way.

The effectiveness of one approach to monitoring conservation status, i.e. using Annex I indicator species for assessing the wider community of organisms which use dune slacks, has not been investigated elsewhere. However, the species recommended for protection under Annexes II and IV of the Habitats Directive have proved to be potentially reliable umbrella species in conservation planning (Lund, 2002). This is likely to relate to the fact that Articles II and IV include a wide range of taxa, so the conservation sites chosen on the basis of these species would contain a range of environmental conditions suitable for a variety of taxonomic groups. The lack of cross congruence among different taxa in dune slacks has implications for conservation assessments: the plant communities that passed the assessment across my sites were not associated with particular snail or water beetle communities. Thus the conservation assessment did not identify habitat of exceptional conservation value for some taxonomic groups which depend on dune slacks.

6.2 Environmental factors affecting biological assemblages in dune slacks

Snails and beetles respond differently from plants to the presence of livestock, and this may be because they have a stronger relationship with the structure of vegetation than the identity of the plants. Light grazing is considered beneficial for dune slack plant communities because it increases diversity (Millett and Edmondson, 2013), a trend which is reflected in my findings, but it also reduced vegetation height. Greater structural complexity (McAbendroth *et al.*, 2005) and height of vegetation (Becerra Jurado *et al.*, 2009) have been associated with greater diversity of macroinvertebrates, and height of vegetation has been shown to affect the composition of macroinvertebrate communities (De Szalay and Resh, 2000). The role of plant functional diversity rather than plant species diversity in regulating the other trophic levels has been explored through the framework of response and effect traits (Lavorel and Garnier, 2002; Suding *et al.*, 2008; Lavorel *et al.*, 2013). This approach emphasizes the importance of biotic interactions in mediating the overall effects of environmental variables. For habitat management, using a response-effect framework to consider the wider implications of a management intervention such as introducing grazers to increase plant diversity could help to prevent unforeseen negative outcomes. To do so requires a thorough knowledge of the characteristic traits of organisms within the system and interactions between multiple stressors.

Passive transport of snails by livestock could result in composition of snail species differing at grazed sites (Bohonak and Jenkins, 2003), although if this process was the main factor differentiating dune slack snail communities, diversity might be expected to be higher at sites with livestock as recruitment of snails would be faster. Higher species richness or diversity of snails at sites with livestock was not observed. Bilton (1988) suggested that trampling was responsible for the absence of the rare turlough-edge beetle assemblage, and trampling may play a similar role in dune slacks. The fact that habitat filtering processes affecting invertebrates could be discerned through their traits but not their species composition indicates that species turnover between habitats may be high even in very similar sites. If this is so it would not be possible to identify a suite of species reliably associated with particular conditions and it would be unlikely that cross-taxon congruence would be observed.

The contrasting effects of grazing on plant and aquatic macroinvertebrate communities helps to explain why habitats which passed the conservation assessment were not characterized by particular snail or beetle assemblages. The indicator species used in the habitat assessment are designed to identify a specific type of diverse dune slack plant community which is not associated with the factors that promote invertebrate diversity. Incorporating a wider range of taxa into the conservation assessment would provide a more comprehensive assessment of the ecological functioning of the habitat.

6.3 Groundwater of dune slacks

The speed of response to rainfall was variable in the sites surveyed, with three sites showing similar trends and the remaining three sites less similar in terms of their responses. A detailed analysis of the groundwater flow patterns and hydraulic gradients within the total catchment, including the area inland of the sand dunes where necessary, was not within the remit of this project but might help to explain patterns observed. Nevertheless, the results here suggest that sand dune systems which are low-lying in relation to the surrounding landscape may receive water from outside the sand dune boundary through surface run-off and drains leading into the dunes. Soulsby *et al.* (1997) documented a similar pattern in a dune site in northeastern Scotland, where the groundwater catchment area of a sand dune system included part of a plateau and ridge on the landward side of the dune system. The management activities inland of the sand dune system may also affect the groundwater quality, particularly at sites which have an input of water from agricultural areas or urban developments (Rhymes *et al.*, 2014), and especially if the bedrock underlying the dunes is fractured or permeable (Jones *et al.*, 2006). The interaction between topography and surrounding land use may help to explain why the amount of land under intensive management within 500 metres of the dune slack did not have a significant relationship with the plant communities: the groundwater is unlikely to be affected by agrochemicals unless the local topography causes water to travel from the surrounding landscape through the dune system. However, the proximity of the coast to uplands in the three counties which account for the largest area of sand dunes in Ireland (Donegal, Mayo and Kerry) suggests that many sites in Ireland may be vulnerable to contamination from impacts outside the sand dune system. This is also likely elsewhere in western Europe with hilly coastal regions, such as Western Scotland. Because the vegetation communities of most dune slacks are limited primarily by nitrogen rather than phosphorus, the evidence for denitrification found in dune slacks in Donegal suggests that even if nutrient inputs from outside the dune system do affect dune slacks, there is the potential for attenuation through natural processes. This may be one of the factors which has contributed to maintaining the low-nutrient characteristics of many dune slacks in western Ireland.

Soluble reactive phosphorus found in surface water at the dune slacks in Co. Donegal was low in comparison to the amount previously found in turloughs in the west of Ireland (Cunha Pereira *et al.*, 2010), and the amount of total phosphorus in the surface water was in the middle of the range for turloughs. The total phosphorus found in dune slacks in the national survey (Chapter 3) was far more variable than at the sites in Donegal, and at some sites it was comparatively very high. Raised phosphorus is likely to be related to land management practices within or outside of the sand dune system (Schulte *et al.*, 2006).

Both plant and snail community compositions showed a response to phosphorus in surface water. Dissolved reactive phosphorus contains phosphorus available to plants (Vanni, 2002). Because nitrogen has generally been associated with eutrophication of dune slacks, information about the amount of phosphorus in dune slacks is lacking elsewhere (Davy *et al.*, 2010). The influence of very low levels of dissolved reactive phosphorus in surface water on snail composition in Co. Donegal is surprising, but there is some indication that it might be reflect a genuine trend because total phosphorus had a strong (but non-significant) relationship with snail trait distribution in the national survey. This may be related to phosphorus supporting algal growth as algae form part of the diet of some snails. In Donegal, the small remaining quantity of soluble reactive phosphorus may be the remainder after algae have almost exhausted the supply (Cunha Pereira *et al.*, 2010).

6.4 Linking ecology and hydrology

Along with dune slacks in Scotland, the dune slacks of western Ireland form the north-western limit of the habitat in Europe. Differences in climate, atmospheric pollution and historic land-use differentiate the dune slacks across Europe, so observations made at one location may not be true elsewhere. For example, heavy rainfall in dune slacks which do not flood regularly has been shown to cause rapid decalcification in the Netherlands (Grootjans *et al.*, 1991), but in Ireland, machairs (a combination of dry and damp flat dune habitats) retain their calcareous character for long periods of time despite not flooding (Curtis, 1991). Understanding the hydrological and hydrochemical functioning of dune slacks and how groundwater relates to biological communities at the edge of their range is vital for the preservation of the range of the dune slack habitat in Europe.

There are difficulties associated with taking an integrated approach across disciplines; hydrological investigations generally focus on a small number of sites because they are expensive, complex and time consuming, but small samples limit the generalisability of results in ecological terms. Comparing results across multiple independent investigations can be complicated, for example where wells are dug to different depths, the age of the water sampled can be very different, so the water chemistry results are not comparable (Röper *et al.*, 2012). From an ecological point of view, some replication is required in the experimental design to detect the relationships between of environmental factors including hydrology and water chemistry and biological functioning. However, by spreading the resources across multiple sites, our capacity to understand the specific processes affecting hydrology at a site level is reduced. Where resources are limited a compromise must be struck between the usefulness of information we can obtain on the hydrological functioning within a site and the usefulness of the information we obtain to explain patterns and make predictions beyond the sample sites. By using a simple design replicated at six sites, we were able to show that while water levels in dune slacks are variable, there are some similar patterns visible at different sites, and we suggested that this appeared to be linked to topography. We also showed that there is evidence of denitrification occurring at some dune slacks. Both of these observations have implications for sand dune ecology and should provide a basis for future research.

6.5 Directions for future research

Although a large body of work has addressed cross-congruence, trait analysis and functional diversity, this is the first study to use these fundamental ecological theories to evaluate the effectiveness conservation under Article 17 of the Habitats Directive – the most influential conservation policy in Europe. It is also the first time that an integrated hydro-ecological approach has been applied across a range of dune slack sites in Ireland. As a result of this work, I have identified some key areas which require further investigation.

6.5.1 Disentangling the effects disturbance and habitat heterogeneity

I theorised that because dune slacks experience periodic natural disturbances and temporal habitat heterogeneity, the biological assemblages found in them may not display cross-taxon congruence. This proved to be the case, but I was not able to show whether the patterns of diversity in different taxonomic groups are due to the combination of heterogeneity and disturbance or whether they would occur in a system which experiences a short disturbance before returning to normal. The results are useful in the context of habitats which have two distinct phases, such as floodplains or marshes. A short-lived natural disturbance such as fire may have a different effect on cross-taxon congruence. Investigating the effects of short lived disturbances would help to define the mechanisms which undermine cross congruence.

6.5.2 Hydrological functioning

Our results suggested that there may be a predictable link between landscape topography and the speed of response to rainfall, and this is consistent with ingress of water from outside of the dune system. The conditions which promote ingress of water from the surrounding landscape could be developed on the basis of a project combining a detailed desk study with a field survey to establish the hydraulic gradient at sand dune sites. This approach combined with knowledge of local rainfall patterns would help to detect thresholds governing intermittent exogenous groundwater supply such as those observed by Jones et al. (2006).

6.5.3 Nutrient loads and denitrification in sand dunes

I detected evidence that denitrification is occurring in some sand dune sites, but was not able to estimate the rate of denitrification or the quantity of nitrogen that could enter the groundwater without resulting in a change in vegetation away from the typical dune slack flora. Ex-situ tests could determine denitrification activity under different nitrogen loads. By inoculating sterile sand samples with sand from different dune slacks, the presence of denitrifying microorganisms in different dunes could be assessed. The effects of differing quantities of organic material could be investigated by repeating the experiment with sand containing different quantities of organic carbon. By adjusting temperature and water levels, the effects of season on denitrification activity could be estimated.

6.6 Recommendations for conservation practice

1. The habitat assessment would be improved by including a wider range of taxa in the indicator species list for dune slacks. However, the use of multiple taxa involves increased cost and effort, so the additional species should be proven to add significantly to the assessment process (Wilson & Bayley, 2012). When investigating the most appropriate taxa to include, complementarity in resource use should be considered in order to maximize the effectiveness of indicator species. The use of functional types based on traits associated with specific habitat variations may be more practical than targeting specific species.

2. While the sites identified as being in good conservation status by the habitat assessment are capable of supporting diverse macroinvertebrate fauna, so are sites which failed the habitat assessment. The resources associated with macroinvertebrate diversity should be identified, especially those which promote the persistence of rare species. As well as ensuring the typical dune slack flora be maintained, the variations in dune slack habitat that are exploited by threatened and vulnerable invertebrate taxa should be conserved.

3. Adjacent land uses are likely to affect groundwater in sand dunes. If this proves to be the case, the factors which make a dune slack vulnerable to contamination should be identified and consideration given to working with landowners surrounding dune systems to minimise the likelihood of groundwater contamination.

6.7 Concluding remarks

The increasingly precarious position of much life on earth has been highlighted in the recent publication of the World Wildlife Fund's Living Planet Report (World Wildlife Fund 2016), a report that echoes themes in the academic literature (Díaz *et al.*, 2006; Cardinale *et al.*, 2012). Wetlands and their dependent taxa are among many that have suffered losses. Large-scale interventions to conserve habitats and species such as the Habitats Directive are to be welcomed but it is important to test them and ensure that the resources invested in conservation yield the best possible result. I found that like other seasonal wetlands, dune slacks are an important resource for invertebrates and they support many threatened species, but that current policies do not protect them and may lead to negative outcomes, for example through introduction of grazing to currently ungrazed dune slacks. If we wish to reverse, or even mitigate, losses in diversity, we must integrate advances in ecological theory into conservation policy and practice.

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8 Appendices

Appendix I. Size classes used during site selection

Size class	Area range (hectares)
1	0.20 – 0.29
2	0.30 – 0.49
3	0.50 – 0.99
4	1.00 – 2.99
5	3.00 – 5.99
6	6.00 – 8.00

Appendix II. Habitat assessment protocols according to Delaney *et al*. 2013.

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Monitoring stop data																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1a. Positive indicator species (√ if																
Anagallis tenella																
Bryum pseudotriquetrum																
Calliergon cuspidatum																
Campylium stellatum																
Carex arenaria																
Carex flacca																
Carex nigra																
Dactylorhizaspp.																
Epipactis palustris																
Equisetum spp.																
Galium palustre																
Hydrocotyle vulgaris																
Juncus articulatus																
Lotus corniculatus																
Mentha aquatica																
Potentilla anserina																
Prunella vulgaris																
Ranunculus flammula																
Sagina nodosa																
Salix repens ssp. *argentea*																
Agrostis stolonifera																
Festuca rubra																
1b. Number of positive indicator species at each stop																
2. Cover of bryophytes (Domin)																
3. Cover of *Salix repens* (%)																

Habitat assessment for the site			
Habitat assessment criteria	**Habitat assessment scores**	**Required to pass**	**Result (pass/fail)**
1a. Positive indicator species	**% frequency**	*At least four species present in more than 40% of stops and another two species present in more than 20% of stops*	
Anagallis tenella			
Bryum pseudotriquetrum			
Calliergon cuspidatum			
Campylium stellatum			
Carex arenaria			
Carex flacca			
Carex nigra			
Dactylorhizaspp.			
Epipactis palustris			
Equisetum spp.			
Galium palustre			
Hydrocotyle vulgaris			
Juncus articulatus			
Lotus corniculatus			
Mentha aquatica			
Potentilla anserina			
Prunella vulgaris			
Ranunculus flammula			
Sagina nodosa			
Salix repensssp. argentea			
Agrostis stolonifera			
Festuca rubra			
1b. Lowest number of positive indicator species in a monitoring stop		*At least three species present in every stop*	
2. Bryophytes	**% frequency**	*Present in more than 20% of stops*	
3. Cover of *Salix repens* (% of habitat[1])		*Less than 40%*	

Appendix II (*cont'd*).

4a. Negative indicator species (Domin)																
Arrhenatherum elatius																
Cirsium arvense																
Cirsium palustre																
Cirsium vulgare																
Lolium perenne																
Pteridium aquilinum																
Senecio jacobea																
Urtica dioica																
Other:																
4b. Highest Domin score at each stop																
5. Non-native species (Domin)																
Name of species:																
Name of species:																
6. Cover of scrub (Domin within 20m radius)																

4a. Negative indicator species	**% frequency**	**% of habitat[1]**	*No species present in more than 60% of stops and combined cover of negative indicators 5% or less and highest Domin score 5 or less*	
Arrhenatherum elatius				
Cirsium arvense				
Cirsium palustre				
Cirsium vulgare				
Lolium perenne				
Pteridium aquilinum				
Senecio jacobea				
Urtica dioica				
Other (specify)				
4b. Highest Domin score across all stops				
5. Non-native species	**% frequency**		*No species present in more than 20% of stops*	
Name of species:				
Name of species:				
6a. Cover of scrub (% frequency)			*Scrub present in no more than 40% of stops and combined cover of 5% or less*	
6b. Cover of scrub (% of habitat[1])				

Appendix III. Plant species recorded for the national survey

Species	No. sites	Species	No. sites	Species	No. sites	Species	No. sites
Achillea millefolium	2	*Capsella bursa-pastoris*	3	*Cynosurus cristatus*	6	*Euphrasia officinalis ag.*	10
Agrostis stolonifera	21	*Cardamine flexuosa*	1	*Dactylis glomerata*	1	*Eurhynchium striatum*	1
Aira caryophyllea	1	*Cardamine pratensis*	1	*Dactylorhiza fuchsii*	1	*Festuca rubra*	18
Alopecurus geniculatus	1	*Carex arenaria*	14	*Dactylorhiza incarnata*	1	*Filipendula ulmaria*	4
Amblystegium serpens	1	*Carex flacca*	19	*Dactylorhiza purpurella*	1	*Fissidens species*	1
Ammophila arenaria	2	*Carex hirta*	17	*Dactylorhiza species*	1	*Fissidens taxifolius*	2
Anagallis arvensis	1	*Carex hostiana*	3	*Danthonia decumbens*	8	*Fontinalis antipyretica*	2
Anagallis tenella	5	*Carex nigra*	1	*Daucus carota*	3	*Galium palustre*	8
Aneura pinguis	1	*Carex otrubae*	15	*Dicranum scoparium*	1	*Galium verum*	8
Anthoxanthum odoratum	5	*Carex panicea*	5	*Didymodon tophaceus*	1	*Geranium molle*	1
Anthyllis vulneraria	1	*Carex pulicaris*	2	*Ditrichum gracilis*	1	*Glaux maritima*	5
Apium nodiflorum	3	*Carex rostrata*	1	*Drepanocladus aduncus*	7	*Glyceria fluitans*	1
Arenaria serpyllifolia	2	*Carex species*	1	*Drepanocladus cossonii*	1	*Gnaphalium uliginosum*	2
Arrhenatherum elatius	1	*Carex vesicaria*	2	*Drepanocladus polycarpus*	1	*Helictotrichon pubescens*	1
Atriplex glabriuscula	1	*Carex viridula*	1	*Eleocharis palustris*	4	*Holcus lanatus*	10
Baldellia ranunculoides	1	*Centaurea nigra*	2	*Eleocharis quinqueflora*	1	*Helictotrichon pubescens*	1
Bellis perennis	3	*Centaurium erythraea*	2	*Eleocharis uniglumis*	2	*Holcus lanatus*	10
Bolboschoenus maritimus	1	*Cerastium fontanum*	6	*Elytrigia repens*	4	*Homalothecium lutescens*	9
Brachythecium rutabulum	2	*Ceratodon purpureus*	1	*Epilobium palustre*	1	*Hydrocotyle vulgaris*	17
Brachythecium species	9	*Cirsium arvense*	3	*Epipactis palustris*	8	*Hylocomium splendens*	5
Bryum pseudotriquetrum	5	*Cladonia rangiformis*	1	*Equisetum arvense*	2	*Hymenostylium recurvirostrum*	1
Bryum species	4	*Cladonia species*	1	*Equisetum palustre*	3	*Hypnum cupressiforme*	1
Calliergonella cuspidata	17	*Climacium dendroides*	4	*Equisetum species*	2	*Hypnum lacunosum*	3
Calystegia sepium	1	*Cratoneuron filicinum*	5	*Equisetum variegatum*	1	*Hypochaeris radicata*	6
Campylium stellatum	1	*Ctenidium molluscum*	2	*Equisetum x litorale*	1	*Iris pseudacorus*	1

Species	No. sites	Species	No. sites	Species	No. sites	Species	No. sites
Isolepis setacea	1	*Myosotis laxa*	3	*Rhytidiadelphus squarrosus*	14	*Trifolium repens*	15
Jasione montana	1	*Odontites vernus*	1	*Rhytidiadelphus triquetrus*	6	*Triglochin palustre*	1
Juncus acutiflorus	8	*Ononis repens*	3	*Riccardia chamedryfolia*	1	*Veronica arvensis*	1
Juncus acutus	3	*Ophioglossum vulgatum*	6	*Rorippa nasturtium-aquaticum*	1	*Veronica chamaedrys*	1
Juncus articulatus	11	*Parnassia palustris*	4	*Rosa spinosissima*	1	*Veronica scutellata*	2
Juncus bufonius	1	*Peltigera species*	2	*Rubus caesius*	1	*Vicia cracca*	8
Juncus bulbosus	1	*Persicaria maculosa*	2	*Rumex acetosa*	4	*Vicia sativa*	1
Juncus effusus	1	*Phragmites australis*	2	*Rumex crispus*	4	*Viola canina*	1
Juncus gerardii	4	*Pilosella officinarum*	1	*Rumex obtusifolius*	1	*Viola species*	1
Juncus maritimus	3	*Pinguicula vulgaris*	2	*Sagina apetala*	1	*Vulpia bromoides*	1
Jungermannia atrovirens	1	*Plagiochila asplenioides*	1	*Sagina nodosa*	5		
Kindbergia praelonga	1	*Plagiomnium elatum*	3	*Sagina procumbens*	1		
Lathyrus pratensis	2	*Plagiomnium undulatum*	9	*Salix cinerea s. cinerea*	5		
Leiocolea turbinata	1	*Plantago maritima*	2	*Salix repens*	12		
Leucanthemum vulgare	1	*Poa humilis*	18	*Samolus valerandi*	1		
Linum catharticum	8	*Plantago coronopus*	4	*Selaginella selaginoides*	1		
Leucanthemum vulgare	1	*Plantago lanceolata*	11	*Senecio aquaticus*	1		
Leontodon autumnalis	10	*Plantago major*	3	*Senecio jacobaea*			
Leontodon hispidus	3	*Plantago maritima*	2	*Senecio vulgaris*	1		
Leontodon saxatilis	12	*Poa humilis*	18	*Sonchus arvensis*	1		
Linum catharticum	8	*Poa pratensis*	3	*Stellaria media*	1		
Lolium perenne	4	*Polygonum aviculare*	1	*Stereocaulon species*	1		
Lophocolea bidentata	2	*Potentilla anglica*	7	*Succisa pratensis*	3		
Lotus corniculatus	18	*Potentilla anserina*	18	*Syntrichia ruralis*	1		
Lotus pedunculatus	1	*Prunella vulgaris*	12	*Taraxacum officinale ag.*	6		
Luzula campestris	4	*Ranunculus aquatilis*	1	*Thuidium tamariscinum*	3		
Lythrum salicaria	1	*Ranunculus flammula*	6	*Thymus polytrichus*	1		
Matricaria discoidea	1	*Ranunculus repens*	16	*Tortella flavovirens*	1		
Mentha aquatica	7	*Ranunculus species*	2	*Trifolium dubium*	1		
Molinia caerulea	1	*Rhinanthus minor*	5	*Trifolium pratense*	6		

Appendix IV. Snail species recorded during the national survey

Species	Red list status	No. sites
Aegopinella pura	Least concern	1
Anisus leucostoma	Least concern	1
Aplexa hypnorum	Vulnerable	2
Candidula intersecta	Least concern	3
Carychium minimum	Least concern	13
Carychium tridentatum	Least concern	2
Cepea nemoralis	Least concern	3
Cernuella virgata	Least concern	2
Cochlicella acuta	Least concern	2
Cochlicopa lubrica	Least concern	10
Cochlicopa lubricella	Least concern	10
Columella aspera	Least concern	1
Euconulus alderi	Least concern	2
Galba truncatula	Least concern	12
Gyraulus crista	Least concern	1
Helicella itala	Vulnerable	3
Lauria cylindracea	Least concern	1
Leiostyla anglica	Vulnerable	1
Lymnaea fusca	Least concern	1
Nesovitrea hammonis	Least concern	5
Oxyloma elegans	Least concern	1
Punctum pygmaeum	Least concern	9
Radix balthica	Least concern	3
Troculus hispidus	Least concern	1
Vallonia costata	Least concern	1
Vallonia excentrica	Least concern	6
Vallonia pulchella	Vulnerable	3
Vertigo antivertigo	Vulnerable	1
Vertigo angustior	Vulnerable	1
Vertigo pygmaea	Near threatened	5
Vertigo substriata	Near threatened	1
Vitrea contracta	Least concern	3
Vitrea crystallina	Least concern	1

Appendix V. Beetle species recorded during the national survey

Species	Red list status	No. sites
Agabus bipustulatus	Least concern	5
Agabus sturmii	Least concern	1
Cercyon tristis	Least concern	1
Colymbetes fuscus	Least concern	2
Dryops luridus	Least concern	2
Dryops similaris	Near threatened	1
Enochrus fuscipennis	Least concern	1
Enochrus halophilus	Vulnerable	1
Helophorus aequalis	Least concern	1
Helophorus brevipalpis	Least concern	2
Helophorus flavipes	Least concern	4
Helophorus grandis	Least concern	5
Helophorus minutus	Least concern	2
Helophorus obscurus	Least concern	1
Hydrobius fuscipes	Least concern	9
Hydroporus erythrocephalus	Least concern	1
Hydroporus memnonius	Least concern	4
Hydroporus nigrita	Least concern	2
Hydroporus planus	Least concern	10
Hydroporus pubescens	Least concern	6
Hydroporus striola	Least concern	5
Hydroporus tesselatus	Least concern	1
Hygrotus impressopunctatus	Least concern	4
Ilybus montanus	Least concern	1
Lymnebius truncatellus	Least concern	1

Appendix VI. Organic matter (%) in sediment samples

Site	Sample depth below ground (cm)	Organic content (%)
Ballyliffin	60-70	1.77
Ballyliffin	110-120	2.57
Ballyliffin	140-160	0.51
Ballyliffin	210-230	1.70
Ballyliffin	370-390	1.91
Ballyness	10-30	1.90
Ballyness	80-90	7.43
Ballyness	105-125	1.89
Ballyness	145-148	8.95
Ballyness	160-170	1.65
Ballyness	225-245	1.74
Ballyness	280-290	1.77
Dunfanaghy	60 - 70	0.90
Dunfanaghy	150-160	0.55
Dunfanaghy	230-250	0.75
Dunfanaghy	280-300	0.69
Lough Nagreany	230-245	0.57
Lough Nagreany	260 - 276	2.60
Lough Nagreany	280-290	1.36
Lough Nagreany	295-300	0.89
Kincasslagh	60-75	0.84
Kincasslagh	190-200	1.50
Kincasslagh	235-250	0.89
Kincasslagh	260-275	0.92
Rosapenna	50-60	1.54
Rosapenna	140-160	1.34
Rosapenna	270-280	1.89

Appendix VII. Variable selection

Variable	Location	Correlation/Collinearity	Included/removed from analysis
Minimum water level		None	Included
Number of days flooded		Collinearity	Removed
Daily fluctuation		None	Included
Dissolved inorganic nitrogen	Ground	None	Included
Soluble reactive phosphorus	Ground	None	Included
Total Phosphorus	Ground	Collinearity	Removed
Alkalinity	Ground	Correlated with groundwater conductivity	Included
Conductivity	Ground	Correlated with groundwater alkalinity	Removed
pH	Ground	Correlated with surface water dissolved inorganic nitrogen	Removed
Dissolved inorganic nitrogen	Surface	Correlated with surface water pH	Included
Ammonium	Surface	None	Included
Soluble reactive phosphorus	Surface	Correlated with surface water conductivity	Included
Total Phosphorus	Surface	Collinearity	Removed
Alkalinity	Surface	None	Included
Conductivity	Surface	Correlated with surface water soluble reactive phosphorus	Removed
pH	Surface	Correlated with surface water dissolved inorganic nitrogen	Removed

Appendix VIII. Correlations between water chemistry, hydrology and composition (NMS axes)

Assemblage	Diversity metric	Variable	R^2	p
Snail	Composition	Ammonia groundwater	0.59	0.34
Snail	Composition	Nitrate groundwater	0.75	0.4
Snail	Composition	DIN groundwater	0.43	0.63
Snail	Composition	Alkalinity groundwater	0.96	0.04 *
Snail	Composition	SRP groundwater	0.17	0.83
Snail	Composition	Ammonia surface	0.45	0.4
Snail	Composition	Alkalinity surface	0.68	0.33
Snail	Composition	SRP surface	0.95	0.05 *
Snail	Composition	Minimum surface	0.92	0.06
Snail	Composition	Fluctuation	0.01	0.98
Plant	Composition	Ammonia groundwater	0.95	0.13
Plant	Composition	Nitrate groundwater	0.07	1
Plant	Composition	DIN groundwater	0.15	0.87
Plant	Composition	Alkalinity groundwater	0.46	0.53
Plant	Composition	SRP groundwater	0.16	0.81
Plant	Composition	Ammonia surface	0.99	0.2
Plant	Composition	Alkalinity surface	0.04	0.91
Plant	Composition	SRP surface	0.33	0.72
Plant	Composition	Minimum surface	0.88	1
Plant	Composition	Fluctuation	0.1	0.98

Appendix IX. Correlations between water chemistry, hydrology and estimated species richness/diversity

Assemblage	Diversity metric	Variable	R^2	p
Snail	Species richness (est)	DIN groundwater	-0.07	1
Snail	Species richness (est)	Alkalinity groundwater	-0.07	1
Snail	Species richness (est)	SRP groundwater	-0.33	0.47
Snail	Species richness (est)	Ammonium surface	0.32	0.48
Snail	Species richness (est)	Alkalinity surface	0	1
Snail	Species richness (est)	SRP surface	0.11	0.80
Snail	Species richness (est)	Minimum water level	0.06	1
Snail	Species richness (est)	Fluctuation	-0.02	0.72
Snail	Simpson's diversity (est)	DIN groundwater	-0.33	0.47
Snail	Simpson's diversity (est)	Alkalinity groundwater	0.2	0.72
Snail	Simpson's diversity (est)	SRP groundwater	0.2	0.72
Snail	Simpson's diversity (est)	Ammonium surface	0.32	0.48
Snail	Simpson's diversity (est)	Alkalinity surface	0	1
Snail	Simpson's diversity (est)	SRP surface	0.53	0.21
Snail	Simpson's diversity (est)	Minimum water level	0.6	0.14
Snail	Simpson's diversity (est)	Fluctuation	0.07	1
Plants	Species richness (est)	DIN groundwater	-0.6	0.14
Plants	Species richness (est)	Alkalinity groundwater	-0.07	1
Plants	Species richness (est)	SRP groundwater	-0.33	0.47
Plants	Species richness (est)	Ammonium surface	-0.32	0.48
Plants	Species richness (est)	Alkalinity surface	-0.2	0.82
Plants	Species richness (est)	SRP surface	-0.53	0.21
Plants	Species richness (est)	Minimum water level	-0.07	1
Plants	Species richness (est)	Fluctuation	-0.33	0.47
Plants	Simpson's diversity (est)	DIN groundwater	-0.6	0.14
Plants	Simpson's diversity (est)	Alkalinity groundwater	-0.07	1
Plants	Simpson's diversity (est)	SRP groundwater	-0.33	0.47
Plants	Simpson's diversity (est)	Ammonium surface	-0.32	0.48
Plants	Simpson's diversity (est)	Alkalinity surface	-0.2	0.82
Plants	Simpson's diversity (est)	SRP surface	-0.53	0.21
Plants	Simpson's diversity (est)	Minimum water level	-0.07	1
Plants	Simpson's diversity (est)	Fluctuation	-0. 33	0.47