Ephemeral wetlands of dune slacks; how do their environmental relations structure their patterning?

A thesis presented in fulfilment of the requirements for

Masters of Science

In

Ecology

At Massey University, Palmerston North, New Zealand.

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2015

Abstract

Coastal dunes are found throughout New Zealand, and within these dunes are the ephemeral dune slack wetlands, which are classified as rare ecosystems. They are temporary environments, which become inundated during the wetter periods of the year. Dune slacks support a distinct biota of turf species, many of which are threatened and in need of protection.

Turf species are found in these ephemeral wetlands, to which their geographic distribution is primarily limited. 15 out of 33 potential wetland sites were sampled across New Zealand, and sites were chosen based on the presence of 3 or more ephemeral wetland species, so distribution and patterning of these wetland turf species could be investigated. The environmental variables thought to structure the distribution of these species were also examined. Ephemeral wetlands of dune slacks occur in three main zones throughout New Zealand. This is despite the occurrence of dune fields throughout the country.

Nutrients are thought to be added to the wetlands when fresh sand from the foredunes comes in and buries these turf species; thus the ability to survive burial delays the eventual succession of these dune slack sites. The turf species were tested to determine which environmental factors influence their growth in glasshouse experiments. Plant growth rates were assessed in response to burial X nutrient addition, to waterlogging X shade tolerance, and the impact of tamping on these species was also briefly assessed. The results show these species need access to a water table, which therefore has to be close to, or above the surface. However they are adapted to burial, with the experimental addition of nutrients allowing them to grow through partial levels of burial. They are not well adapted to low light situations, suggesting that they are poor competitors.

Turf species appear to be early successional species, as they occur in sites with low total species' numbers, and few exotics, they are poor competitors and are easily shaded out from a site. The main indicator of wetland decline appears to be the presence or absence of other (non-turf) species.

Ephemeral dune slack wetlands are a dynamic ecosystem. Management solutions need to be active and address these issues in order to maintain these sites and their flora. They contain threatened flora in need of protection, and a suite of unique environmental variables worthy of further study.

Acknowledgements

This research was funded by the George Mason Charitable trust, Heseltine bursary and Horizons Regional Council, Palmerston North.

Thanks to the Allan Herbaria, The Auckland Museum, Te Papa and the Massey Herbarium for providing previous collection locations of the turf species, to assist in site selection. Also thanks go to Horizons Regional council for helping me with maps for all possible sites.

For site access and help in the field I would like to thank the Taranaki Regional Council and Horizons Regional Council. Also thanks to the Department of Conservation in Kaitaia, Great Barrier Island, Farewell Spit and Invercargill for help contacting land owners and granting site access. I would also like to thank the O'Shea's who gave access to their farm on Great Barrier Island, Chris Petyt who came out on the farewell spit and assisted with field work, David Havell for assistance locating the KareKare and Whatipu sites, the Sextons for access to their property in Himatangi.

A humongous thanks goes to Jill Rapson, for her continued support throughout this process and her endless patience. As well as suggesting this project in the first place. Also thanks to Jill for giving up her valuable time to help in collecting the experimental plants and hauling buckets of sand out from the dunes into the ute.

I would like to thank my awesome assistants Dominic van den Heuvel and Alana Bensemann for keeping me sane throughout my fieldwork, and putting up with me for extended periods of time, (after being bribed with free travel around New Zealand). I would also like to thank Bex Ingram for her continued assistance in the glasshouse, couldn't have done it without you, on those awful Friday mornings. Thanks to Cleland Wallace for creating my tamping tools, and PGU for glasshouse space. Thanks go out to Massey University staff and students for collecting all my yoghurt pottles. Cheers to Pierce McNie for your statistics help, and big thanks goes out to the Department of Ecology post grad computer room occupants for keeping me sane, proof reading and continual coffee breaks throughout the writing process.

Lastly big thanks go out to Steven King for his continued support throughout this whole process, for putting up with stressed out me and for his assistance with all the proof reading and all the little things. And thanks to my Family couldn’t have done it without you guys.

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Chapter 1

Introduction

A typical, small ephemeral wetland, Omaui, Invercargill

What is an ephemeral dune slack wetland?

Dunes are constructed from sand which has been deposited by wind (Johnson & Rogers, 2003). Coastal dunelands are widespread throughout New Zealand (Hilton et al., 2000). The largest areas of coastal dunes occur along the Northland and Manawatu coasts (Hilton et al., 2000). Originally, distinctive vegetation occurred throughout the New Zealand dunelands (Sykes & Wilson, 1991); unfortunately this has been easily destroyed by human activities (such as release of introduced species), leading to dune destabilisation.

Ephemeral dune slack wetlands are short lived seasonally wet depressions within the dunes. “Dune slacks are a distinctive but little known coastal habitat” (Sykes & Wilson, 1987). They are formed by wind-powered deflation of the dune surface (Hesp & Martinez, 2007), the depth of these erosion events being limited by the position of the water table, as damp sand does not ablate (Johnson & Rogers, 2003). The substrate of a dune slack is sand, and drainage is good; however ponding occurs when the water table is high. Most ephemeral wetlands are flat-bottomed and shallow when ponded (Johnson & Rogers, 2003). After wind events form these slacks, new niches develop and plant communities flourish (Hesp & Martinez, 2007). Dune systems contain vegetated wetland hollows or dune slacks, of various sizes and origins (Johnson & Rogers, 2003).

Ephemeral wetlands within the dune slacks were well represented when Cockayne (1911) toured the New Zealand’s duneland in 1909. Despite the current occurrence of duneland elsewhere, the distribution of dune slack wetlands throughout New Zealand is restricted to three main latitudinal zones: the northern North Island, central New Zealand and the southern South Island. The distribution of these dune slacks and their associated species will be further examined here for New Zealand as a whole.

How are ephemeral wetlands and their species distributed throughout New Zealand?

Dune slack environments are possibly the most hostile lowland environments, supporting a limited number of plant species (Esler, 1970). Short-statured plants often exist in sites of climatic extremes, such as dune slacks (Rogers & Wiser, 2010). In New Zealand, ephemeral dune wetlands contain turf species. Turf vegetation can be defined as commonly under 5cm tall, consisting mainly of herbaceous, vascular plants, which are prostrate and tightly interlaced, and form a dense group

(Johnson & Rogers, 2003). I selected species which are known to be pioneering species of dune slack wetlands, and all 10 known species that fit this description were the focal species for this thesis.

Turf communities of dune slacks are best developed where there is a modest level of disturbance (Johnson & Rogers, 2003), thus inferring that they represent an early successional state. Regional distinctiveness in sites is common, and turf vegetation has been seen to cover a majority of the depression within a wetland (pers. obs.) suggesting it is harder for weedy species to invade these habitats. A national survey of the distribution of dune slack wetlands and their associated species will be conducted to examine their distributions.

What patterns of environment and communities are found in wetlands?

Ephemeral wetlands are a distinct class of wetland and comprise possibly the most dynamic type, in terms of seasonal extremes both in water-table fluctuation, and in environmental variables (Johnson & Rogers, 2003). This situation may explain why New Zealand dune slacks are colonised by small turf species which have distinct distribution patterns amongst the species themselves (Esler, 1969). The predominant factors which influence duneland vegetation can be divided into two groups: topographical gradients (height above water table), and recurring disturbances (Hesp & Martinez, 2007).

Zonation of turf species is usually apparent, reflecting the wet/dry gradient of their habitat or the distribution limits of particular turf species (Esler, 1969; Johnson & Rogers, 2003). Probably submergence and drought in relation to micro-topography are the main environmental influences on slacks (Sykes & Wilson, 1990). Small topographic changes can cause a considerable difference in vegetation patterns (Sykes & Wilson, 1987). Ability to survive sand burial is of crucial importance to these dune species (Sykes & Wilson, 1990). The dunelands of New Zealand have a noteworthy morphological diversity in response to sediment supply, climate and topography (Hilton et al., 2000). Here I aim to determine what is behind species' patterning; whether it is environmental or species based. The approach will involve testing the individual species' 'tolerances' to assess the influence of these environmental dynamics on the growth of these species.\

Understanding the dynamics of ephemeral wetlands?

Formation of dune slack wetlands begins with damage or disturbance to the foredune vegetation (Murphy et al.,in press). As succession progresses in these sites the percentage covers of both sand and stones decrease while vegetation height increases and the water table increases in distance from the surface (Murphy et al.,in press). The species richness of an ephemeral wetland site is seen to increase initially as succession progresses but decreases later, favouring species tolerant of a much drier environment (Murphy et al.,in press), generally exotics. The inferred successional sequence is that these ephemeral wetland sites go from open wetland habitat, to turved wetland to rushland, similar to what was proposed by Esler (1969). However the rate of succession will be slower when the wetlands are isolated from each other (Singers, 1997). I will assess the appropriateness of this interpretation.

Understanding ephemeral wetlands and their conservation?

New Zealand has many diverse ecosystems (Williams *et al.*, 2007). They are often small due to being environmentally extreme habitats. Some species of ephemeral wetlands are rare due to human land use change and habitat loss (Sykes & Wilson, 1987). Human invasion of New Zealand has had a substantial impact on our dunelands today, due to widespread disturbance following European settlement (Hilton, et al., 2000).

New Zealand's dune slack wetlands are classified as nationally rare ecosystems (Williams et al., 2007). The term 'rare' signifies a system which is small in size even if widespread geographically (Williams et al., 2007). Many aspects of ephemeral wetlands of dune slack impact on their conservation (Johnson & Rogers, 2003). Sedimentation also impacts these systems with sand blowing into the dune slacks and burying the turf species, whilst increasing the distance to the water table (Johnson & Rogers, 2003). Grazing of turf species by rabbits is common due to the turves' location within the duneland (Johnson & Rogers, 2003). The influence of nutrient addition on the growth of these species will be further assessed.

Disturbance of these sites can be by grazing from hooved animals (Johnson & Rogers, 2003). Human foot and vehicle traffic also impact these systems, breaking up the turf itself and damaging the individual species (Johnson & Rogers, 2003). A flow-on effect of trampling of these systems is that it may provide microsites suitable for the establishment and germination of weedy species (Johnson & Rogers, 2003). The impact of trampling on these species will be examined.

Aims of thesis

New Zealand's wetland turf communities may be of high global significance as there appear to be no similar ecosystems in the northern hemisphere, which are instead dominated by taller plants (Johnson & Rogers, 2003). New Zealand turf species and their coastal ecosystems receive little protection or management (Rogers & Wiser, 2010), and as part of improving mangement, there is a need for a national inventory survey of ephemeral wetlands in New Zealand (Johnson & Rogers, 2003). This thesis examines the wetland systems of dunes and their turf inhabitants in depth by conducting a national survey and small experimental investigations into environmental preferences, to further the knowledge of both these systems as a whole and the individual species which inhabit them.

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Chapter 2

The distribution patterns of rare ephemeral dune wetlands and their turf species

Farewell Spit ephemeral wetland, prominently featuring *Eleocharis neozelandica.*

Abstract

Question: Where are the ephemeral wetlands of dune slacks and their turf species located throughout New Zealand? How do these distributions compare to previously known turf species' distribution patterns? Does species composition of a wetland differ with differing environmental variables? How do traits vary with environmental parameters?

Location: New Zealand.

Methods: Ephemeral dune wetlands were identified as being dish-shaped depressions in dune fields, which have standing water at some period of the year. Environmental information on each wetland was recorded, including the distance to the water table. Vegetation was sampled by running two transect lines at right angles to each other through the wetland. 25x25cm quadrats were regularly spaced along the transect lines and used to record species' presence, vegetation cover and maximum vegetation standing height, as well as micro-topography. Plant traits were also measured for the turf specialists (leaf length and thickness from 2-4 random quadrats per site, not necessarily on a transect). An NMDS was conducted based on the presence/absence data of each species at each site, and the proportion of each species per site for the turf specialist species.

Results: The most geographically widespread species was *Isolepis basilaris,* even though it was considered the most threatened species seen. *Gunnera dentata*, the southern boundary of which was previously thought to be West Coast of the South Island, was found throughout the sites at the bottom of the South Island, as well as up to Patea in the North Island. From the NMDS a latitudinal gradient across the North and South Island sites can be seen. The Farewell Spit sites group with the North Island sites based on species' composition.

Conclusions: The distribution ranges for *Gunnera dentata* and *Isolepis basilaris* have been extended. Dune slack sites occur in only 3 main zones throughout NZ, despite the occurrence of dune fields elsewhere, such as Wanganui, Westland, Taranaki, and Fiordland. Species' dispersal out of these zones is probably difficult. Dune slacks are unique ecosystems that rank highly on the conservation agenda, due to possession of rare or threatened species. Transient wetlands such as ephemeral wetlands have a large ecological value. Plant community descriptions provide a sound basis for assessment of slack sites and therefore their future conservation decisions.

Keywords

Rare species, turf, distribution, dune slack, ephemeral wetland, national survey.

Introduction

Coastal dunes are found worldwide. They form where there are large quantities of sand and strong offshore winds which shift this sand onshore (Packham & Willis, 1997). Dunes are naturally dynamic and slowly move inland from the coastline blown by on-shore winds (Singers, 1997). Coastal dunes provide habitats for plants which can tolerate moving substrate, strong desiccating winds and a greatly changing environment (Esler, 1970). Only few native species flourish in these harsh environments (Esler, 1970).

Windblown sand gives rise to many different landforms, including foredunes, rear dunes, dune slacks and dune wetlands. Within the New Zealand dune sequence, wetland hollows can be found of various sizes (Johnson & Rogers, 2003). The term "slack" is derived from a Norse word "Slakki" which means a small depression between two stretches of raised ground (Ranwell, 1959). The first detailed description of a New Zealand dune slack was conducted in 1987 by Sykes & Wilson (1987). They found that primary slacks develop behind new dune ridges and they are often inhabited by these native turf species (Esler, 1969).

One of the most stable-looking of these environments is the dune wetland, but even this is dynamic, being wet in winter and dry in summer. The ephemeral dune wetlands found throughout New Zealand are temporary environments, which can become inundated with fresh water during the wetter periods of the year (Singers, 1997), thus temporarily submerging these dune slack plants. These wetlands support a very distinctive and species-rich biota (Johnson & Rogers, 2003), and host a flora of specialist species which are minute in size. Short-statured plants often exist in sites of climatic extremes, such as dune wetlands (Rogers & Wiser, 2010). Due to their stature and ground-hugging nature these species are here referred to as turf species. Little is known about these turf species, or their distribution throughout New Zealand (Esler, 1969). The effects on submergence of these turf species will be looked at further in chapter 4.

Since European settlers arrived, the native dune vegetation has been slowly destroyed by invasive species and land clearing (Sykes & Wilson, 1991). In order to promote conservation of the few remaining sites which remain undamaged by land use change and human impact, the composition of these sites needs to be understood in order to maintain their diversity, thus ensuring the survival of these species (Roxburgh et al.,1994). Therefore a nationwide survey was conducted to determine the distribution of these specialist dune slack species and the differences within these slack habitats. Documented locations of turf species were used to establish possible wetland sites, and ground truthing was used to identify dune wetland sites.

Methods

Study sites

Wetlands were sampled throughout New Zealand, in the North and South Islands, as well as Stewart and Great Barrier Islands (Fig. 1). Wetlands were identified as being dish-shaped depressions in dune fields. Sites were selected with the help of local botanical knowledge. Since the focus here is on ephemeral wetland turf species, I required a minimum of three turf species (Fig. 1) to be present in order for the site to be sampled, allowing me to see species' interactions within sites as well as species' distribution. This information was sourced from DOC records, herbaria specimens and local botanical knowledge. Most sites visited fit the general description of a dune slack wetland, being in a dune depression hollow. Points of interest (POI) sites were areas of wetland which had less than 3 turf species, or they were areas which were not wetlands but still had some species of interest present. They were sampled briefly.

In the South Island 15 possible sites were identified for examination; however due to the use of selection criteria (i.e., wetland having a minimum of 3 turf species) only 8 sites were surveyed. In Northland 8 possible sites were found; however many of these sites were highly invaded by macrophytic vegetation, and/or were going through successional changes, with large quantities of jointed wire (*Apodasmia similis*) rush present, and so only 4 wetland sites were sampled. Great Barrier Island was similar. Of the 10 possible sites found only one met the minimum requirement of 3 or more turf species. Lastly along the Manawatu coast many sites are known to be present as this is a highly studied area, and so a representative site from each of Himatangi and Foxton was chosen.

Figure 1: Location of sampling sites. Spit sites = Farewell Spit sites 1-3. Ste = Stewart Island sites. POI is a point of interest site not wetland sites

Sampling was conducted in summer (January – March) 2014. I measured:

- The slope of the site
- Distance to the sea
- Height above sea level
- Surrounding species' composition
- Surrounding dune height

General percentage covers (estimates) were recorded per wetland for:

- Live vegetation cover (as shadow)
- Standing water
- Bare sand
- Rock cover
- Litter (dead plant material)
- Anthropogenic rubbish
- Faecal matter

The distance to the water table was measured in the centre of each wetland along the transect line by digging a hole into the zone of damp sand, and leaving it for an hour to fill in with water, before the distance from the sand's surface to the standing water was recorded (Fig 2a).

Along all the transect lines I measured the micro-topography of the site. This was done at regularly spaced intervals (of 1m) from end to end of the wetland, using a 1m long builder’s level (Fig 2b). The distance to the water table and the micro-topography data of each site was then used to calculate the quadrat’s distance to the watertable by adding or subtracting the rises and falls of the sand to the distance to water table measurement.

Figure 2a: Image of hole dug in sand to locate the water table.

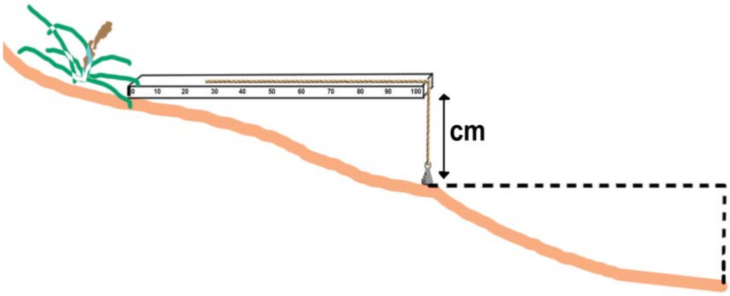


Figure 2b: How the microtopography was measured.

The vegetation of each wetland was sampled by running two transect lines at right angles to each other through the wetland. Additional perpendicular lines along the long axis of the wetland were used if the wetland was of particular interest (contained species listed as rare or threatened, Table 1) or if a larger wetland (i.e., greater than 45m long). 25x25cm quadrats were regularly spaced along the transect lines at 1-2m intervals depending on the size of the wetland, giving 11-50 quadrats per wetland. These quadrats were used to record species' presence and absence, as well as the percentages of vegetation cover (by estimating the shadow cast by live vegetation at solar zenith) and maximum vegetation standing height.

For areas within the wetland that had the largest number of focal species, 4 25x25cm quadrats (of areas of interest) were used to assess individual turf species' microhabitats and traits; these were randomly placed. These individual quadrats had their percent covers of live vegetation, standing water, bare sand, rock cover, litter (dead plant material), anthropogenic rubbish, and faecal matter recorded. For all focal turf species present, leaf thicknesses using a micrometer, and leaf length were also recorded. Plant traits were measured to determine if differences in environmental parameters had an effect on the individual plants/species themselves. These interest quadrats were also used in areas which were not identified as wetlands (POIs), but had species of interest, to sample the other habitats that these species occur in and to assess whether their individual traits were similar throughout differing habitats. Plant traits, and percent covers were measured here as well as height above sea level, distance to the sea, surrounding vegetation and dune height. 2-4 quadrats were used to assess POI sites.

Statistical methods

The floristic composition of each site was assessed by determining the number of native, non-native and focal species present at a site. The environmental information for each sampled site was also looked at to determine if any particular variable impacted species' composition of a site. Plant trait data (both leaf length and thickness), were averaged for each species at each site to see if the trait data varied with differing environmental parameters.

To assess if species' patterning existed within sites or locations an NMDS (non-metric multi-dimensional scaling) ordination was conducted in R [3.0.2] (R Foundation for Statistical Computing, Vienna, AT, USA), using the Vegan package (Oksanen et al, 2013) to assess the relatedness of the surveyed sites based on the presence/absence data per quadrat for all the wetland sites, (presented in Figure 6). The reverse ordination of the species was also conducted (Figure 6E). In order to incorporate non wetland species into the ordinations the wetland species data needed to be in the same format i.e.: presence/absence. Environmental variable (latitude) was then fitted to the NMDS surface using procedure Ordisurf by Jari Oksanen in the Vegan package (Oksanen et al., 2013) in R (3.0.2), to investigate correlates of species' patterns. NMDS used presence/absence data, which gives the most critical information, being whether a species is present or absent in a site. Other surfaces were based on the Native (excluding ephemeral): Ephemeral species ratio of each site and on the Native (all): Exotic species ratio to see whether any of these descriptors of community composition influenced the sites' positioning or grouping within the NMDS.

Micro-topography was also measured (Fig 2b) along the longitudinal transects of all wetland sites, of which 4 representative sites are graphed, to depict the typical shape of the wetlands. The average water table preference for each turf species was calculated using the distance to the water table plus the micro-topography data for each quadrat a species was found in.

Results

Floristic composition

Total flora from all wetlands sampled throughout New Zealand consisted of 44 species [Appendix 1]. Six of these species are at risk or threatened according to de Lange et al. (2012; Table 1). Twelve of the 44 species were exotic; the remaining were native species. The species which is most widespread geographically is *Isolepis basilaris*. The next most common species found throughout the wetlands sampled, in descending frequency are: *Isolepis cernua*, *Myriophyllum votschii*, *Lilaeopsis orbicularis*, *Selliera rotundifolia*, *Eleocharis neozelandica*, *Limosella lineata* and *Selliera radicans* (Table 3).

Selliera radicans
(Sel rad)

Ranunculus acaulis
(Ran aca)

Limosella lineata
(Lim lin)

Selliera rotundifolia
(Sel rot)

Lilaeopsis orbicularis
(Lil orb)

Gunnera dentata
(Gun den)

Myriophyllum votschii
(Myr vot)

Isolepis basilaris
(Iso bas)

Isolepis cernua
(Iso cer)

Eleocharis neozelandica (the brown stems) (Ele neo)

Figure 3: Images of ephemeral dune wetland turf species. All photos of species were taken from experimental plants in the glasshouse except for both *Isolepis species* and *Eleocharis neozelandica* which were taken in Omaui (Invercargill). The abbreviations are the three letter codes for each of these species, as used in the results.

Table 1: Rare or uncommon species recorded in coastal wetlands or turves throughout New Zealand. Classifications are from de Lange *et al.* (2012) and distributions are from the NZ Plant Conservation Network, as well as incorporating locations sampled. Locations are mapped in Figure 1. DP = Data poor, EF = Extreme fluctuations, RR = Range restricted, Sp = Sparse.

Classification	**Criteria**	**New Zealand distribution**	**Locations sampled**
Nationally Vulnerable			
Isolepis basilaris	EF, RR, Sp	Endemic, Hawkes Bay to Southland.	Farewell Spit, Stewart Island, Pouto, Great Barrier Island, Karekare, Patea, Himatangi, Foxton.
Declining			
Eleocharis neozelandica	DP, EF	Endemic, North Island, and Farewell Spit.	Omaui, Farewell Spit, Pouto, Patea, Himatangi.
Selliera rotundifolia	RR	Endemic, North Island only. Whanganui south to Paekakariki.	Himatangi, Foxton.
Coprosma acerosa	DP	Endemic, North, South, Stewart and Chatham Islands	Omaui, Farewell Spit, Stewart Island, Karekare
Naturally Uncommon			
Craspedia robusta var. pedicellata	RR, Sp	Endemic, distributed throughout New Zealand	Farewell Spit, Stewart Island
Pimelea lyallii	RR, Sp	Endemic, Confined to Stewart Island coastline	Stewart Island
Natives (not threatened)			
Gunnera dentata		Endemic, mostly found West Coast and central NZ.	Omaui, Waipapa, Stewart Island, Patea.
Isolepis cernua		Indigenous. Found throughout New Zealand.	Omaui, Waipapa, Stewart Island, Pouto, Great Barrier Island, Karekare, Himatangi, Foxton.
Lilaeopsis orbicularis		Endemic, found throughout New Zealand	Waipapa, Pouto, Great Barrier Island, Karekare, Himatangi, Foxton.
Limosella lineata		Endemic, South, North, Stewart, Great Barrier, Three Kings Island.	Farewell Spit, Stewart Island, Pouto, Great Barrier Island.
Myriophyllum votschii		Endemic, North, South, Stewart and Chatham Islands.	Omaui, Waipapa, Farewll Spit, Pouto, Great Barrier Island, Himatangi.
Ranunculus acaulis		Indigenous, South, North, Stewart, Chatham and Auckland Islands.	Waipapa, Stewart Island, Patea, Foxton.
Selliera radicans		Endemic. North, South, Stewart, Chatham, Three Kings Island.	Omaui, Waipapa, Farewell Spit, Karekare, Patea.

Species' distribution

Eleocharis neozelandica was found in less than half of the surveyed sites; it was however found in Omaui at the bottom of the South Island, which extends its known distribution (Table 1). *Selliera rotundifolia* was found where expected, in the sites along the Manawatu coast only. The other interesting species' distribution seen for the non-threatened species was for *Gunnera dentata* which was previously known only from the west coast of the South Island and the central North Island New Zealand, but was found all through the bottom of the South Island sites as well as in Patea (Table 1).

A. Waipapa site 2; Typical ephemeral wetland, situated in a dune slack.

B. Awana, (GBI); ephemeral wetland plants found growing by a stream running through a cow paddock.

C. Awana, (GBI); *Limosella lineata* growing in pugged cow pat substrate.

D. Omaui, Invercargill; ephemeral wetland site on rocky cliff top.

E. Patea, Taranaki; site bordered by farm land on one side and extreme cliff scarp on the other.

F. Mason's Bay Stewart Island POI 2; creek running through ephemeral wetland (plants growing in flowing water).

Figure 4: A typical ephemeral wetland where the wet area is fully surrounded by dunes (A) as well as other interesting ephemeral sites that differed from expected (B-F).

Typical ephemeral wetland sites were bowl- or dish-shaped depressions (Fig. 4a), located within the dunes themselves. These accounted for 11 of the 15 wetland sites that I surveyed and therefore I assume this is the standard for these sites and, as such, the ‘normal’ habitat for these turf species. Sites that differed from the norm (Fig. 4B-F) included Awana (Great Barrier Island), Mason's Bay, Stewart Island, Omaui in Invercargill and Patea in Taranaki. The Awana site was found in a cow paddock with a small stream running through it, 1014m from the sea, with no sand dunes on site. Ephemeral wetlands were found on the edges of rocky cliff faces (Fig. 4D,E) and around stream sites. Both Omaui and Patea were located on rocky cliff faces with steep drops to the ocean on one side and dunes on the other. Mason's Bay Stewart Island POI 2 also differed from the ‘norm’, due to its presence of flowing water (Table 2b). As it did not fit the description of a dune slack site, it was measured as a POI site, due to its multiple small disjoint patches of turf species present.

Sites differed substantially in all environmental factors except substrate and water presence (Table 2a &b). Sites were found from 1m through to 1014m from the sea; however a majority of sites were around the 200-300m mark, with the average distance to the sea for the wetland sites being 363m, while for the POI sites this was 333m (Table 2b). The average height above sea level was similar across all sites studied. The average wetland length was 30m; however Himatangi was 100m long. The distance to the water table of these wetlands ranged from 13.5cm – 69cm below ground, with the mean of 35cm in wetland sites and 36cm in POI sites. The average percent plant cover in a site was 63% with the highest being 90% in Karekare, and the lowest at 30% seen at both Spit 1 and Stewart Island 1. Only 2 sites had standing water, Omaui and Whatipu POI 1, and both of these were low percentages. Flowing water was only found at Awana and Stewart Island POI 2 (Table 2a: Fig. 4). The average cover of bare sand seen across wetland sites was 28% while the POI averages were nearly double. Rock cover was rare, with the highest cover being 10% at Stewart Island 3. Percent faeces, litter and rubbish were low to zero across all sites surveyed (Table 2a &b).

Table 2a: Environmental information for each sampled site. NM means not measured. Sites are in North to South order. Site name abbreviations in Figure 1.

Sites	Total spp. Nº	Number of quadrats sampled	Wetland length (m)	Latitude (as southing) & Longitude (as northing) in degrees	Dist. to sea (m)	Height above sea level (m)	Distance to water table (cm)	Estimated surrounding dune height (m)	Plant cover (%)	Standing water (%)	Flowing water (%)	Bare sand (%)	Rock cover (%)	Faeces (%)	Litter (%)	Rubbish (%)
Awana	9	49	33	-36.20 & 175.48	1014	2	47	No dunes	50	0	10	20	0	19	1	0
Pouto	7	27	14	-36.32 & 174.03	250	14	30	25	50	0	0	50	0	0	0	0
Karekare	7	48	43	-37.00 & 174.48	300	6	21	4	90	0	0	7	2	0	1	0
Patea	14	35	23	-39.76 & 174.47	1 (10m vertical dist)	15	13.5	5.5	70	5	0	20	3	0	2	0
Himatangi	16	89	100	-40.39 & 175.23	194	3	27	9	65	0	0	30	0	0	5	0
Foxton	15	58	29	-40.45 & 175.22	244	11	21	20	70	5	0	25	0	0	0	0
Spit 3	15	40	34	-40.52 &172.92	276	6	25	2	70	0	0	25	0	0	5	0
Spit 2	11	38	23	-40.52 &172.91	152	3	45	5	75	0	0	13	0	0	2	0
Spit 1	5	41	15	-40.52 &172.86	386	6	44	15	30	0	0	70	0	0	0	0
Omaui	18	22	34	-46.51 & 168.26	600	43	36	5	80	1	0	0	8	2	9	0
Waipapa 1	10	19	19	-46.66 & 168.85	275	10	52	9	60	0	0	30	0	0	7	0
Waipapa 2	11	19	21	-46.66 & 168.85	280	10	30	9	60	0	0	26	0	3	4	10
Ste Is 1	10	26	17	-46.92 & 167.77	382	20	43	2	30	0	0	67	0	0	3	0
Ste Is 2	15	29	24	-46.95 & 167.73	192	10	69	6	75	0	0	20	0	0	5	0
Ste Is 3	19	35	22	-46.96 & 167.71	542	6	22	4	70	0	0	18	10	0	2	0
Averages	12	38	30		363	11	35	9	63	0.7	0.7	28	2	2	3	0.7

Table 2b: Environmental information for each sampled POI site. Sites are in North to South order. Site name abbreviations in Figure 1.

Whatipu POI	7	4		-37.05 & 174.49	70	9	NM	4	55	4	0	40	0	0	1	0
Waipapa POI	8	2		-46.66 &168.85	300	6	44	2.5	70	0	0	27	0	0	3	0
Ste Is POI 1	7	2		-46.93 & 167.76	295	15	42	2	30	0	0	66	0	0	4	0
Ste Is POI 2	7	4		-46.92 & 167.76	550	19	10	10	50	0	40	10	0	0	0	0
Ste Is POI 3	7	2		-46.93 & 167.77	560	17	48	30	5	0	0	95	0	0	0	0
Ste Is POI 4	7	2		-46.93 & 167.77	225	9	NM	5	40	0	0	59	0	0	1	0
POI Averages	7.17	2.67			333.33	12.50	36.00	8.92	41.67	0.67	6.67	49.50	0.00	0.00	1.50	0.00

Regarding the total species' numbers, there is an average of 5 turf species present in a site (Table 3), compared to POI sites which had an average of 4 turf species present. *Gunnera dentata* was mostly found in South Island sites, as was *Selliera radicans.* All 3 Farewell Spit sites had similar species composition as did all 3 Stewart Island sites.

Both Waipapa 1 and Waipapa 2 had few native species that weren't turf species, and a relatively small proportion of weedy exotic species present. The Manawatu sites (Himatangi, Foxton and Patea) had an even distribution of natives, turf species and exotics. Some sites such as Ste 2 had a high proportion of exotics (Fig. 5). Pouto had no native species present that weren't turf species, and only 1 exotic species (Fig 5). There was an overall high proportion of non-turf species (both natives and exotics) present within all sampled sites.

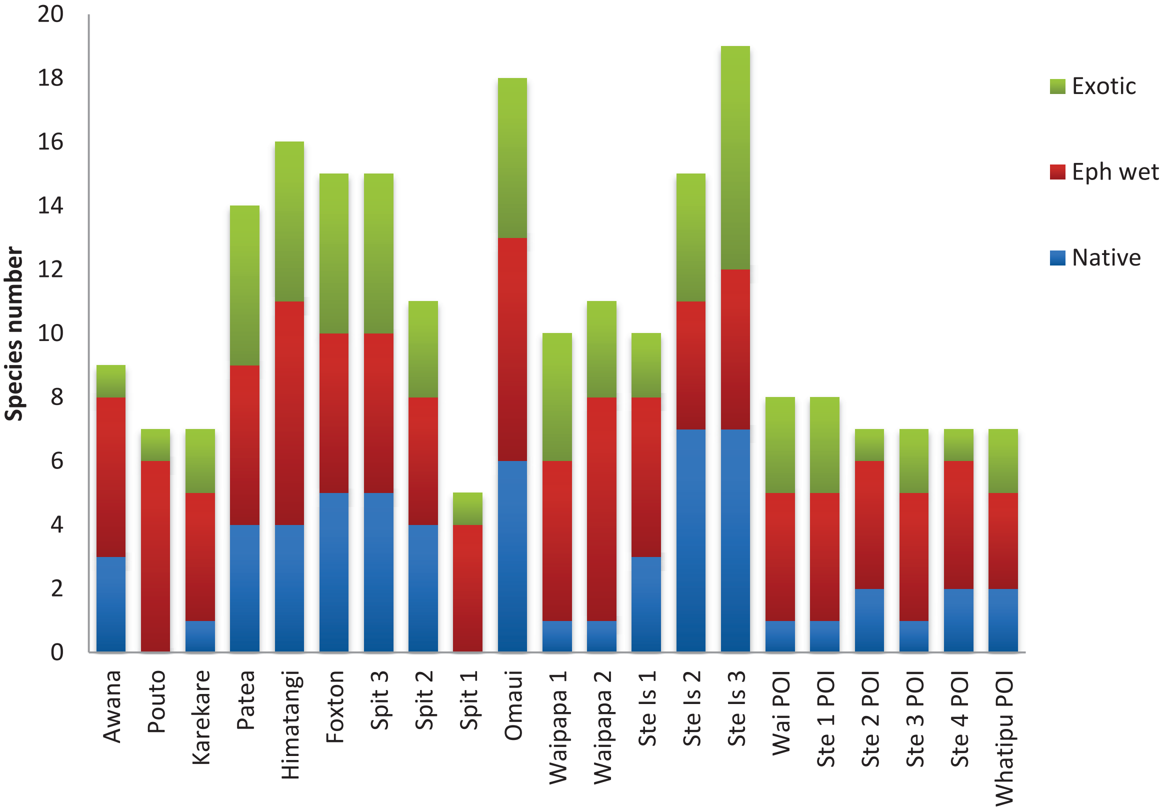


Figure 5: Proportions of native non-turf species, exotic species and native ephemeral wetland turf species at each site organised from north to south within each of the standard and POI site types.

Table 3: Turf species' occurrence at each site ('x' shows presence). Species abbreviations as in Fig3.

	Ele neo	*Gun den*	*Iso bas*	*Iso cer*	*Lil orb*	*Lim lin*	*Myr vot*	*Ran aca*	*Sel rot*	*Sel rad*	*Total*
Awana			X	X	X	X	X				5
Pouto	X		X	X	X	X	X				6
Karekare			X	X	X					X	4
Patea	X	X	X		X			X		X	6
Himatangi	X		X	X	X		X	X	X		7
Foxton			X	X	X			X	X		5
Spit 3	X		X			X	X			X	5
Spit 2	X		X				X			X	4
Spit 1	X		X			X	X				4
Omaui	X	X	X	X			X	X		X	7
Waipapa1		X		X	X			X		X	5
Waipapa2		X	X	X	X		X	X		X	7
Ste Is 1		X	X	X		X		X			5
Ste Is 2		X	X	X		X					4
Ste Is 3		X	X	X		X		X			5
Wai POI		X		X				X		X	4
Ste 1 POI		X	X	X				X			4
Ste 2 POI		X	X	X		X					4
Ste 3 POI			X	X	X	X					4
Ste 4 POI				X	X	X		X			4
Whatipu POI	X		X		X						3

On average these turf species' leaf lengths are all approximately 2cm tall and under. *Gunnera dentata* and *Lilaeopsis orbicularis* at Waipapa 2 was very elongated compared with the lengths seen in all the other sites. All leaf lengths were far larger in Awana.

Table 4: Average values for species' leaf length (cm) at each site. Species' name abbreviations as per Fig 3.The figure in brackets is the number of samples used to calculate these value.

	Ele neo mean	*Ele neo Std dev*	*Gun den mean*	*Gun den Std dev*	*Iso bas mean*	*Iso bas Std dev*	*Iso Cer mean*	*Iso cer Std dev*	*lil orb mean*	*Lil orb Std dev*	*Lim lin mean*	*Lim lin Std dev*	*Ran aca mean*	*Ran aca Std dev*	*Sel rot mean*	*Sel rot Std dev*	*Sel rad mean*	*Sel rad Std dev*
Awana					3.3 (23)	1.1	3.4 (10)	1	5.1 (8)	0.5	1.8 (25)	0.3						
Pouto	1.6 (10)	0.4			1.9 (15)	0.7			1.8 (10)	0.3	1.1 (10)	0.4						
Karekare					2.8 (20)	1.6			2.3 (5)	0.2							0.6 (3)	0.2
Patea	1.9 (5)	0.2	1.5 (1)	0	2.7 (5)	0.6			2.8 (5)	0.5	0.7 (5)	0.2					0.7 (1)	0
Himatangi					1.2 (28)	0.4			0.9 (33)	0.2	0.5 (35)	0.3			0.4 (8)	0.0		
Foxton					1.2 (25)	0.5			1.1 (5)	0.3			0.5 (3)	0	0.4 (6)	0		
Spit 3	0.7 (10)	0.2			0.8 (10)	0.2					0.5 (10)	0.3						
Spit 2	1.2 (20)	0.4			1.1 (20)	0.3					0.7 (5)	0.2						
Spit 1	1.1 (10)	0.2			1.2 (10)	0.4					0.9 (5)	0.1						
Omaui			0.5 (2)	0.1													0.4 (2)	0.6
Waipapa 1			0.5 (2)	0.8			1.5 (7)	0.3			0.7 (1)	0	2.1 (2)	1.9			1 (1)	0
Waipapa 2			4 (1)	0					8.5 (2)	0.5			2.5 (2)	0.5			0.7 (2)	1
Ste Is 1			0.4 (1)	0	2.4 (5)	1.6					1.4 (5)	0.3	0.5 (1)	0				
Ste Is 2			3 (1)	0	1.8 (5)	0.4	0.9 (5)	0.3										
Ste Is 3			0.7 (1)	0			0.6 (5)	0.1			0.6 (5)	0.1	2.7 (1)	0				
Av.	1.3		1.5		1.9		1.7		3.1		1		1.6		0.4		0.7	

Leaves were much thicker at Patea for *Selliera radicans* and *Gunnera denata*. *Lilaeopsis orbicularis* leaves were thicker at both Patea and Pouto 1.2 (std dev 0), 1.2mm (std dev 0.1) compared to the average of 0.7mm. *Selliera rotundifolia* had thicker leaves (std dev 0.3) compared to its close relative *Selliera radicans* 0.6mm difference between the averages.

Table 5: Average leaf thicknesses (mm) for each species' at each wetland site. Species name abbreviations as per Fig 3. The figure in brackets is the number of samples used to calculate these value.

	Ele neo mean	***Ele neo Std dev***	***Gun den mean***	***Gun den Std dev***	***Iso bas mean***	***Iso bas Std dev***	***Iso Cer mean***	***Iso cer Std dev***	***lil orb mean***	***Lil orb Std dev***	***Lim lin mean***	***Lim lin Std dev***	***Ran aca mean***	***Ran aca Std dev***	***Sel rad mean***	***Sel rad Std dev***	***Sel rot mean***	***Sel rot Std dev***
Awana					0.6 (5)	0.5	0.2 (2)	0.03	0.6 (3)	0.09	2 (5)	0.6						
Pouto	1.3 (2)	0.2			1.1 (3)	0.4			1.2 (2)	0.1	0.6 (2)	0.01						
Karekare					1 (4)	0.5			0.7 (1)	0					1.4 (3)	0.04		
Patea	1.5 (1)	0	2.4 (1)	0	1.2 (1)	0			1.2 (1)	0	1.1 (1)	0			2.6 (1)	0		
Himatangi					0.6 (6)	0.5			0.6 (8)	0.5							2.4 (8)	0.3
Foxton					0.3 (5)	0			0.4 (1)	0			0.8 (3)	0.4			2.3 (6)	0
Spit 3	0.4 (2)	0			0.3 (2)	0.2					0.6 (2)	0						
Spit 2	0.5 (4)	0.4			0.1 (4)	0.5					0.1 (1)	0						
Spit 1	0.1 (2)	0			1.3 (2)	0.1					0.2 (1)	0						
Omaui	0.2 (2)	0	1.6 (2)	0.4			0.9 (1)	0							1.8 (2)	0.6		
Waipapa			0.9 (2)	0.5			0.2 (1)	0	0.3 (1)	0	1.5 (1)	0	0.7 (2)	0.4	1.4 (1)	0		
Wapapa 1			1.2 (1)	0					0.3 (2)	0			1.4 (2)	0.5	1.9 (2)	0.4		
Ste Is 1			0.3 (1)	0	1.1 (1)	0					1.3 (1)	0	0.4 (1)	0				
Ste Is 2			0.7 (1)	0	0.2 (1)	0	0.7 (1)	0										
Ste Is 3			1.1 (1)	0			0.2 (1)	0			1.2 (1)	0	1.2 (1)	0				
Av.	0.7		1.2		0.7		0.5		0.7		0.9		0.9		1.8		2.4	

The ordination of the surveyed sites per quadrat (Fig 6) is based on the species' presence and absence (species' list in Appendix 1) of each site. Fig 6 grades the sites between North and South Island sites, (Fig. 6b.) with the Farewell Spit sites being floristically grouped with the North Island sites. The sites which diverged from this split based on species' composition are Himatangi, Spit 2 and Spit 3. The ordisurf based on the Native: Ephemeral ratio (Fig 6c) suggests that the presence of more native (but non turf) species tends to equate to more turf species present in a site.

Figure 6a:

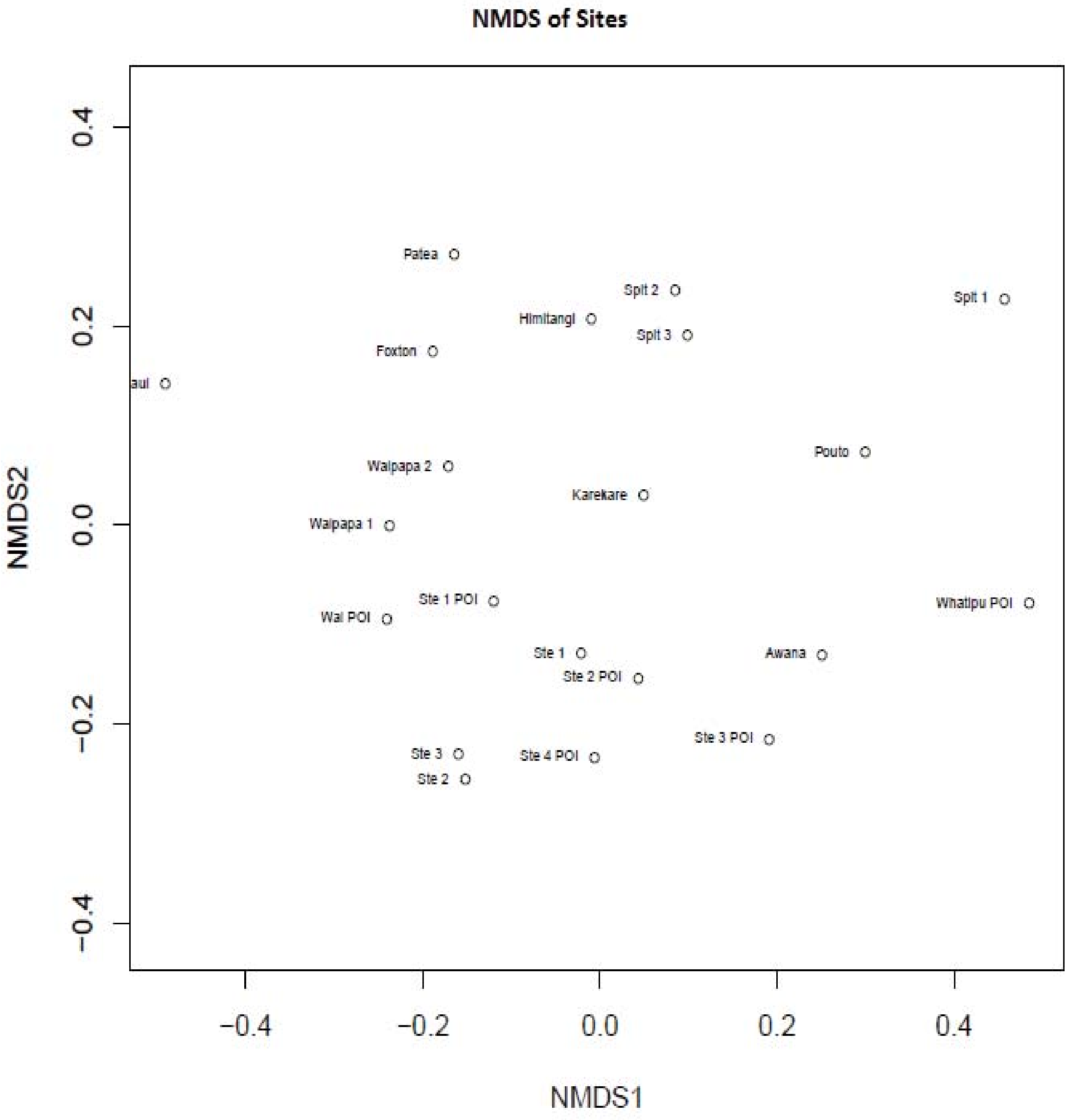

NMDS of Sites
Patea
Spit 2
Spit 1
Himitangi
Spit 3
Foxton
aul
Waipapa 2
Pouto
Karekare
Waipapa 1
Site 1 POI
Wai POI
Whatipu POI
Site 1
Awana
Site 2 POI
Site 3 POI
Site 3
Site 4 POI
Site 2
NMDS2
0.4
0.2
0.0
−0.2
−0.4
−0.4
−0.2
0.0
0.2
0.4
NMDS1

Figure 6b:

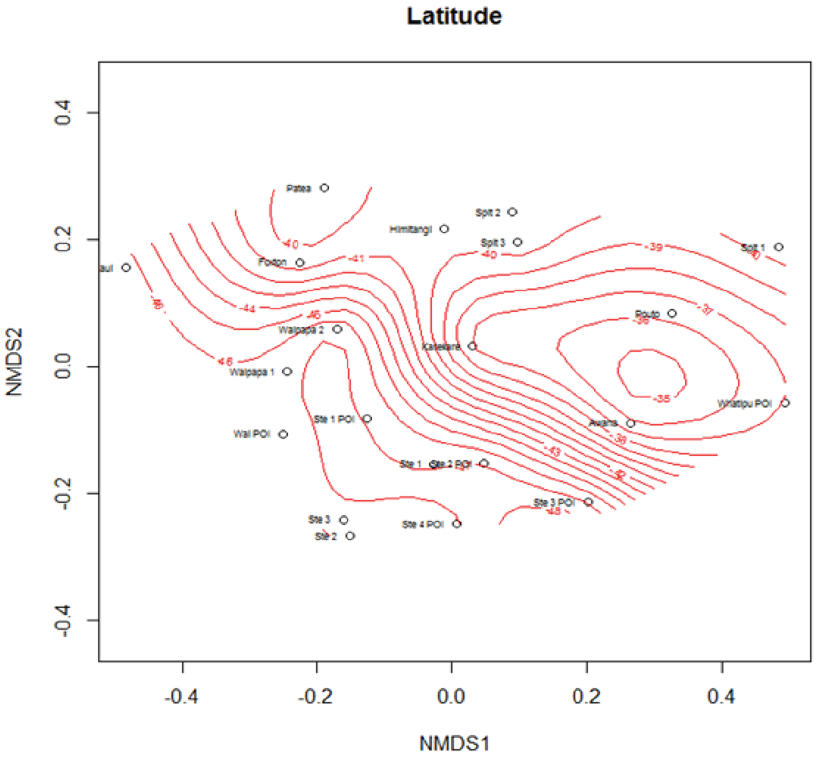


Figure 6c:

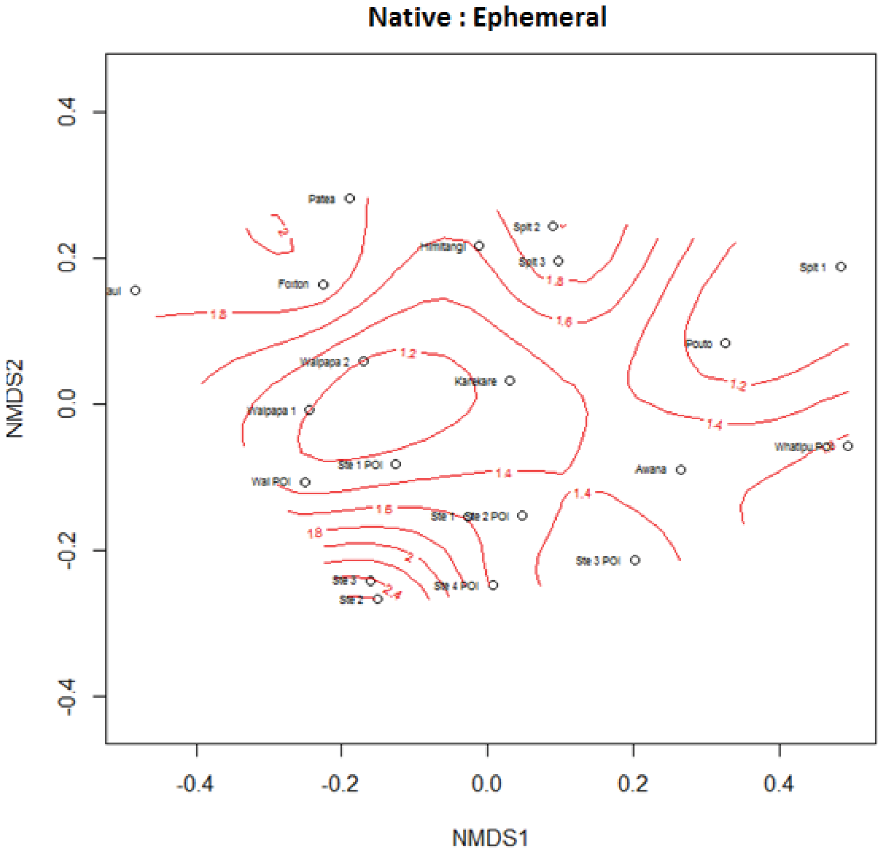


Figure 6d:

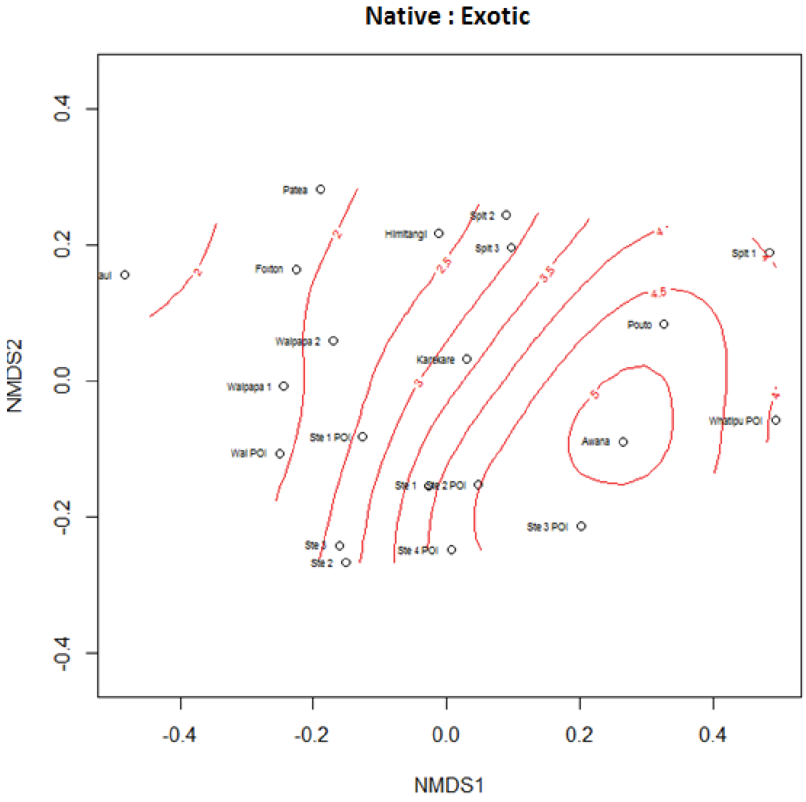


Figure 6e:

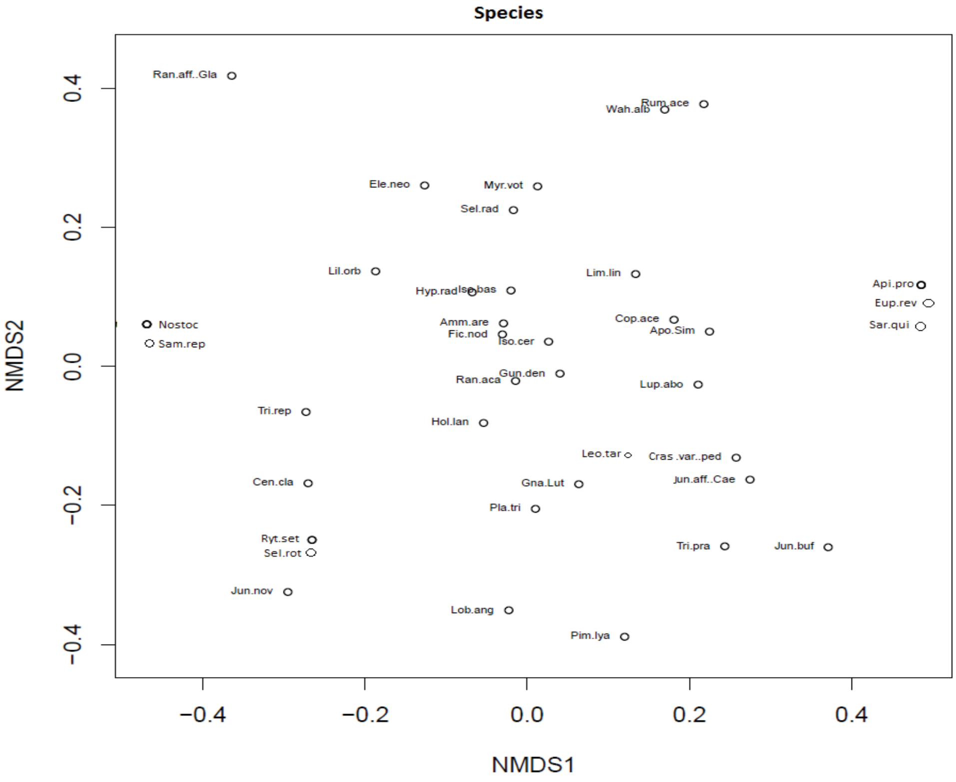


Figure 6: NMDS (a) of sites, (b) with fitted ordisurfs for latitude (contour units are degrees south of the equator)the northern sites are in the upper right and the southern sites are in the lower left, (c) the native: ephemeral species ratio (more ephemeral species are in the upper right and fewer ephemeral species are in the lower left) (d) the native: exotic ratio (which has a patchy distribution) and (e) the reverse species ordination (species abbreviations in appendix 1).

The ordination of the surveyed sites was based on what proportion of quadrats within a site had each species (Fig 7a). As with the ordination based on species' presence and absence (Fig 6A) there again appears to be a split between the North and South Island sites, with the Farewell Spit sites being grouped with the North Island ones. The turf species are grouped together (Fig 7b) showing they tend to occur together; however there is a separation between *Selliera radicans* and *Selliera rotundifolia.* The other species which commonly co-occur with the turf species are *Ammophila arenaria*, *Ficinia nodosa, Leodonton taraxacoides* and *Hypochaeris radicata. Gunnera dentata* and *Ranunculus acaulis* are central, suggesting they are very widespread and widely differentiated from the other ephemeral wetland species. *Coprosma acerosa* and *Pimelea lyalii* are some of the species which are not associated with the ephemeral wetland species. Although there is a strong latitudinal gradient along with a wet/dry gradient seen in these ordinations, there is no clear sign of patterning based on what I consider to be community types.

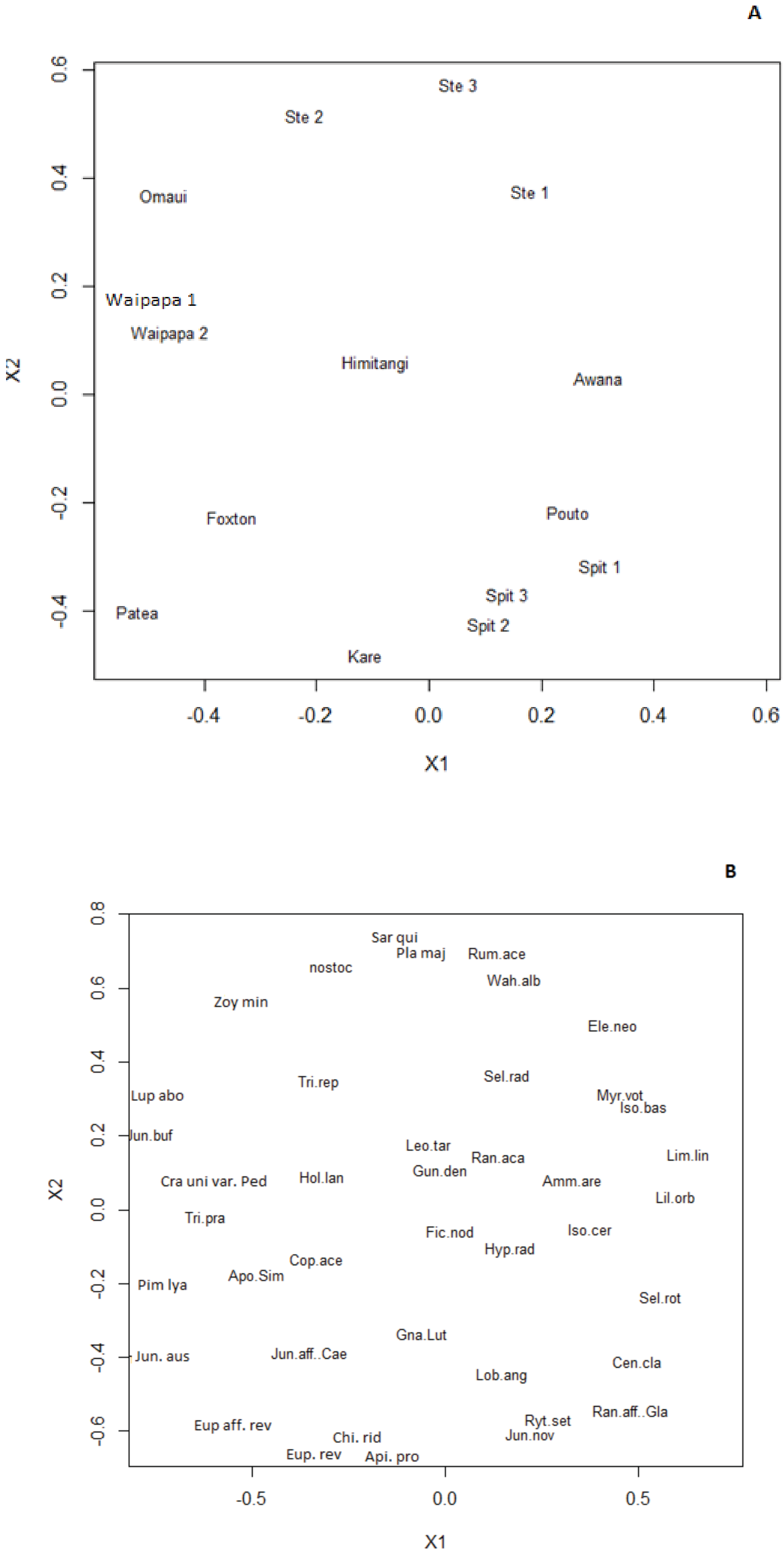
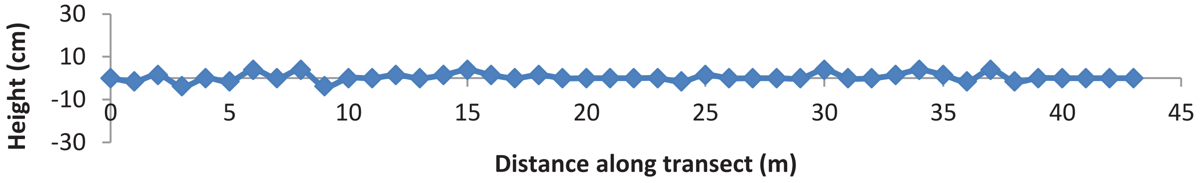


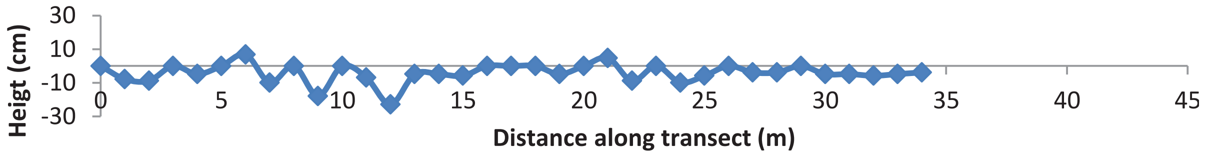
Figure 7: NMDS of sites (a) and species (b) based on the proportion of quadrats each species occupies, focusing on non-POI sites. X1 =axis1. Species' full names in Appendix 1.

The shape of these wetland sites was terrace/bowl shaped, with only small differences seen in the micro-topography across the sites (Fig 8). Karekare (a) is a relatively flat site with a few mounds which are above the water table. Omaui's (Fig. 8b) was often below the watertable; however this particular wetland site can be seen to have many changes in micro-topography of the surface providing many different microhabitats for the ephemeral species (Table 3). The micro-topography for Farewell Spit site 1 (fig 8c) again is relatively flat with a steep rise towards the end of the wetland. The landscape of Spit site 2 starts at a low point (Fig. 8d), stays constant across most of the transect and ending in a steady increase in ground height, suggesting an almost terrace like shape to the wetland.

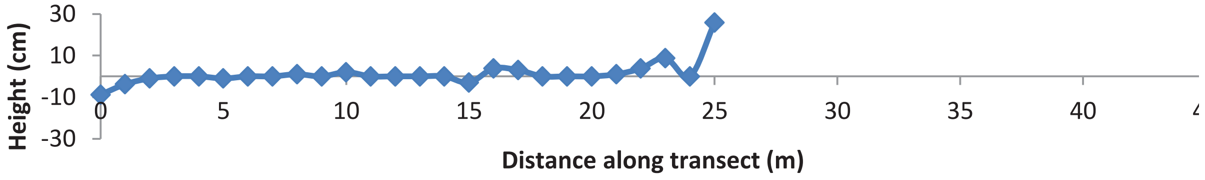
A. Karekare



B. Omaui



C. Spit 1



D. Spit 2

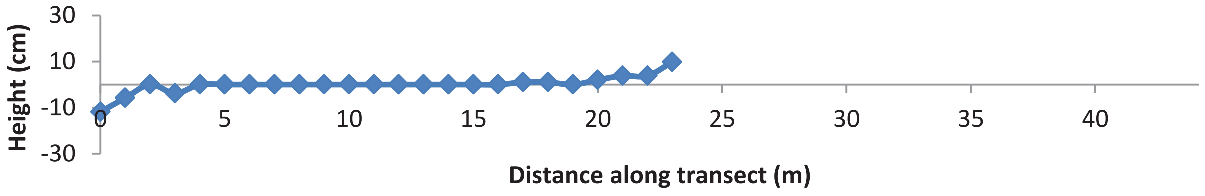


Figure 8: The micro-topography along the longitudinal transects of four of the surveyed sites. These sites were selected as they are representative samples of the surveyed sites. The 0 line is the water table line.

The average water table preferences for each species, seen across all wetland sites (Fig 9) identifys the species which have an inclination for the wetter parts of the wetland. These species are *Selliera rotundifolia* and *Ranunculus acaulis.* Both *Isolepis* species are tolerant of water tables which are 33-37cm from the surface, therefore the drier parts of the wetland (Fig 9). The most tolerant species of a dry environment is *Limosella lineata* although the majority of the species sit at an average water table of 30cm from the surface. Species water table preferences are discussed further in chapter 3.

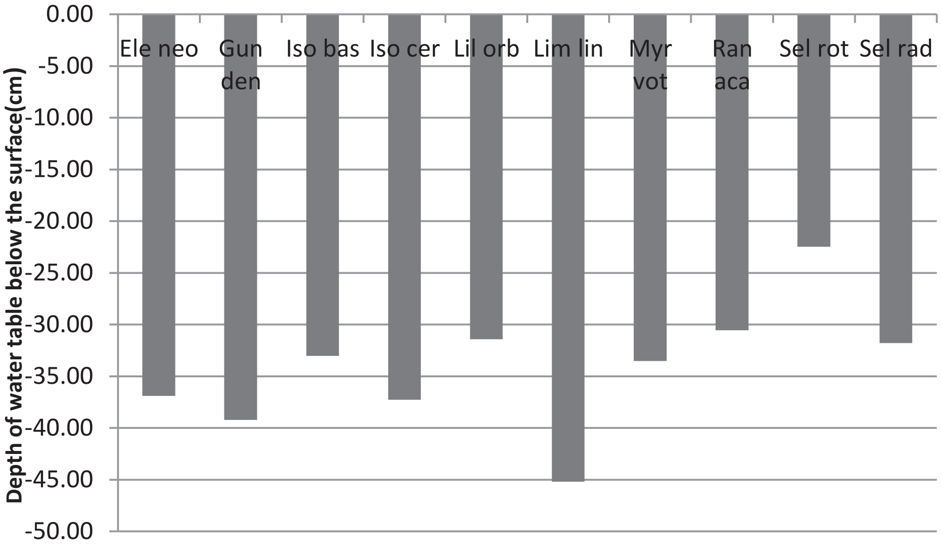


Figure 9: Average water table preference (distance from the surface) of each turf species across all sites at which the species occurs.

Discussion

This thesis aims to examine the within species interactions of these wetlands as well as the interactions of species with their associated environmental variables. Dune slack wetlands are distinct ecosystems, which contain many of New Zealand's rare turf species. Plant community descriptions provide a foundation for the assessment of slack sites and their future conservation decisions. This study of New Zealand wetlands and their species showed that *Isolepis basilaris* was the most widespread species throughout all the wetland sites surveyed, suggesting it may not be as rare or range-restricted as previously thought. This could be due to misidentification or lack of data, as it is an extremely small and inconspicuous species, and easily mistaken for its more common relative *Isolepis cernua. Gunnera dentata*'s southern boundary was thought to be the West Coast of the South Island; however this turf species was found as far south as Stewart Island (Table 3) signifying a greater range than expected.

The species associated with the drying out/invasion of wetland turf are *Apodasmia similis, Pimelea arenaria* and *Coprosma acerosa* (Fig 7b), as these are specialist shrubs of dunelands, and these are often associated with *Ammophila arenaria, Hypochaeris radicata, Trifolium pratense,* and *Leodonton taraxacoides*, which are weeds in such wetlands (Fig 7b).

Where are these wetlands distributed?

A strong latitudinal gradient along the North Island and South Island sites is demonstrated by the ordinations. Dune slack sites were found to occur within three main zones throughout New Zealand, being the northern North Island, the southern South Island, and central New Zealand, despite the occurrence of dune fields elsewhere throughout the country. The Waikato dunes are blown onto raised substrate whereas the Manawatu dunes are formed by the coast moving seaward with time (prograding) as a result of the sediment of the Manawatu and Rangitikei rivers (Cory Matthew, pers. obs.). However this is not the case for these surveyed sites as they are all founded on sand, it seems mobile dunefields alone can host ephemeral wetlands. Dunefields can be found in Northland, the Manawatu coast, Stewart Island, Great Barrier Island and the lower South Island.

Coastal duneland is predominantly found along the Northland and Manawatu coasts (Hilton et al., 2000), although ephemeral wetlands are rare in Northland. Ephemeral wetlands are also found on Farewell Spit and the bottom of the South Island as well as Stewart Island (Johnson & Rogers, 2003). Of these 33 wetland sites found throughout New Zealand, only 15 sites were found to have more than three turf species, and thus were investigated further. So most possible sites found throughout New Zealand were surveyed. The minimum of three species was rarely an issue as very occasionally did I find a wetland dominated by less than three of these focal turf species and if one was found it tended to be going through later successional stages (pers. obs.). Within the dunelands, the majority of rare taxa can be found in the expected three main latitudinal zones, the northern North Island, the southern South Island, and central New Zealand (Manawatu to Farewell Spit), the first two associated with zones of high endemism (Rogers & Walker, 2002). Therefore there is no surprise that a number of specialist species of ephemeral wetland turves are rare.

How rare are these systems?

The estimated area of duneland in New Zealand has declined significantly from 128 000ha to 52 000ha in the last 50 years, due to stabilisation and planting up of the dunes with pines (Hilton et al., 2000). Dune deflation hollows (dune slacks) are classified as rare ecosystems (Williams et al., 2007); this is due to their small size and geographically widespread nature. Wetlands are in general poorly understood and undervalued, and ephemeral dune wetlands with their distinctive turf vegetation have been almost completely overlooked. There is a strong need to increase the data set of these systems (Johnson & Rogers, 2003). Previously many dune slack sites were found in Northland and throughout this survey only one site meeting the selection criteria was found. Dune slack habitats could be drying up due to droughts seen in their regions, thus their numbers are in decline.

How do wetlands differ from each other?

New Zealand's dunelands show a large diversity in physical characteristics in response to both local and regional environmental variations (Hilton et al., 2000). The sites which I studied differed in total area, with the largest sites being in the North Island (Himatangi), and the majority of the smaller sites occuring in the South Island.

The floristic composition of each site was similar throughout New Zealand (Figure 5, 6, 7) including the species of exotics that were present. Weedy species grow in all niches within an ecosystem (Williams & West, 2000). The majority of the wetlands surveyed had more native (non-turf species) than exotics present (Fig 5). Stewart Island 3 had the highest proportion of exotic species present of all the wetland sites (Fig 5). The highest total species number of all sites was 18 (Stewart Island 3), with the least being 5 species in Farewell Spit 1 (4 turf species and 1 exotic present).

Awana, which was not in close proximity to duneland (Table 2a), differed from the other wetland sites only slightly in species' composition. Instead of being surrounded by *Apodasmia similis* and/or *Ammophila arenaria*, this site was surrounded by agricultural grasses and was grazed. Both Awana and Waipapa 1 had faeces present (Table 2a) within the site; this correlated with an increased leaf length (Table 4), perhaps due to high nutrient levels compared to other sites. This correlation will be further investigated in Chapter 4 via the impact of nutrient addition to these turf species and their growth.

What are the individual habitat and environmental ranges of these species?

Many aspects of these dune slack systems contribute to their importance. Despite their scattered occurrence throughout New Zealand, they contain diverse communities of plant species, and are often the sole habitat for threatened species, such as some of the turf species within the dune slack environment (Johnson & Rogers, 2003).

Zonations of plants along a water gradient are one of the best-studied patterns in plant ecology (Bakker et al., 2007). Community structure and species' patterning differed across all sites, but I cannot confidently attribute this to water table. Here I only measured water table once, during the summer months, and over a period of three months. However both *Isolepis* species appear to be tolerant of a greater separation from the water table (Fig 9). Esler (1969) found that some species can be correlated with the wetter parts of the wetlands, such as *Myriophyllum votschii* and *Eleocharis neozelandica.* However I found these plants to be tolerant of mid-range water table heights, and that in fact *Selliera rotundifolia* and *Ranunculus acaulis* appear to be the species with preferences for shallow water tables (i.e. close to the surface; Fig 9). This could be a product of the time of water table sampling (January - March 2014). However there is an overall absence of community patterning seen at these wetland sites and they all have differing compositional and community structures. This could be assessed further with future experimentation and more site visits.

Zones of turf species are correlated with the duration and periodicity of inundation events, such as rainfall periods (Johnson & Rogers, 2003). Water table height fluctuates throughout the year in these ephemeral wetlands (Singers, 1997), affecting the species inhabiting these areas. Timing and duration of these inundation events is important in determining community composition of a wetland.

Throughout this survey many possible sites (33) were found. These sites were going through later successional changes and had many rush and tall grass species present, and/or less than three turf species. This is thought to be due partly to the invasion of vigorous sand binding species, and due to the water level changes seen within these slacks as taller vegetation comes in, outcompeting the small turf species or moving the wetland into later successional stages.

Conclusions

Dune slacks are a unique ecosystem that ranks highly on the international conservation agenda, due to their high proportion of rare or threatened species (Grootjans, Ernst and Stuyfzand, 1998). The estimated area of duneland in New Zealand has declined significantly in the last 50 years, due to both stabilisation and planting of the dunes. The introduction of many vigorous exotic species, which have invaded into New Zealand's dunelands is one of the leading symptoms of this decline in both habitat area and native vegetation present (Sykes & Wilson, 1991). Of the 33 sites found, 18 were found to be inhabited by large rush species and *Ammophila arenaria*, an invasive exotic dune species. Due to the ephemeral nature of these wetlands their total area is difficult to determine, although this habitat is in decline (Johnson & Rogers, 2003).

New Zealand's ephemeral wetlands are widely distributed throughout the country but are a rare habitat type, in need of conservation. These habitats differ widely across the country and are influenced by a large suite of environmental variables; future work focusing on the distribution of these plants in relation to the water table and other environmental variables to assess community patterning in relation to any environmental factor or to the species themselves is needed.

Plant community descriptions provide a sound basis for the assessment of slack sites and therefore the conservation decisions of that site (Roxburgh et al., 1994). However it is clear that conservation of these sites is needed in order to protect the rare and/or threatened species that inhabit them. This is of high priority due to the lack of suitable sites found for this survey throughout New Zealand.

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Chapter 3

What structures the patterning of ephemeral wetland turf species within and between dune slacks?

Farewell Spit dune slack site

Abstract

Question: Are ephemeral wetland turf species structuring their own communities? What environmental variables structure their patterning within a dune slack wetland? Are these factors homogenous across New Zealand?

Location: New Zealand

Methods: 15 sites were investigated across New Zealand, and their community structure and environmental variables recorded to ascertain whether the species x environmental relationship is constant across the country. For each site species' presence and absence was assessed using quadrats placed along two perpendicular transects and environmental variables assessed. A species by quadrat ordination was performed to show the distance apart of these turf species in ordination space, followed by an association analysis to assess whether the species that occurred together within a site, occurred in the same microsite. Finally a general linear model was used to evaluate whether any of the environmental variables were related to the species patterning.

Results: *Isolepis basilaris* doesn't appear to co-occur with any of the other turf species. *Lilaeopsis orbicularis and Selliera rotundifolia* not only occur together within wetlands, but also share the same microsite 64% of the time. The pattern of turf species appears to be related to other species within their environment: i.e., the total species number, native: exotic ratio and native: ephemeral ratio were the most significant community descriptors across all wetland sites. *Eleocharis neozelandica* only occurs in sites with a low total species number, and *Myriophyllum votschii* is similar co-occurring with few species other than turves in a wetland site. *Selliera radicans* occurs in sites where the maximum vegetation height is less than 5cm tall. *Selliera rotundifolia* appears to be driving the Manawatu dune wetlands.

Conclusions: It appears that the environmental factors which influence these turf species distribution differ. However the driving factor of turf patterning appears to be the presence or absence of other wetland species. Thus these species are vulnerable to successional trends.

Keywords:

Ephemeral wetlands, turf species, community structure, patterning, environmental factors.

Introduction

Ephemeral wetlands occur throughout the world. In the Northern Hemisphere sites are typically closed depressions such as vernal pools or prairie pools. They are also known as furloughs in Ireland (Johnson, 2000). It is thought that New Zealand's species-rich turf communities are distinct and well developed, compared to other equivalent sites worldwide (Johnson, 2000). Ephemeral wetlands come in many different landform classifications; however our focus here is the coastal dune systems with wetlands in dune slacks. Thus better understanding of them is needed, in order to conserve these wetland sites and their species.

The dune plains throughout New Zealand contain many temporary and small wetlands. Elsewhere in the world, high species diversity has not been recorded for dune slacks; however the New Zealand sites differ in this respect (Sykes & Wilson, 1987). Within the New Zealand flora we can find a group of species specially adapted to living in these habitats, and once established, they spread quickly (Singers, 1997). These species are low lying and under 5cm tall, forming turves resistant to many harsh environmental factors associated with their coastal habitat. Turf species often form a ground-hugging dense carpet of intertwined plants, which can be difficult to tell apart from each other (Johnson, 2000). The main species are *Eleocharis neozelandica* (Ele neo), *Gunnera dentata* (Gun den), *Isolepis cernua* (Iso cer), *Isolepis basilaris* (Iso bas), *Myriophyllum votschii* (Myr vot), *Ranunculus acaulis* (Ran aca), *Limosella lineata* (Lim lin), *Lilaeopsis orbicularis* (Lil orb), *Selliera rotundifolia* (Sel rot) and *Selliera radicans* (Sel rad).

Within communities there are environmental factors which influence their structure (Weiher, Clarke, & Keddy, 1998). Patterns can be seen amongst species' assemblages and need to be investigated to determine if any rules are in play (Weiher, Clarke, & Keddy, 1998). Simple trends in influential factors should not be expected in such a complex habitat type (Sykes & Wilson, 1987) and many different factors can lead to patterns of species' association (Weiher, Clarke, & Keddy, 1998). Given the rarity of these systems an accurate set of predictive environmental variables would be a valuable tool in order to identify and conserve these sites.

Johnson & Rogers (2003) described the major environmental drivers of ephemeral wetlands as their physical geography, climate and hydrology. The wetlands infill with water in winter and dry out, at least partially in the summer (Singers, 1997). Heavy rains in the winter time can fully submerge the plants (Singers, 1997) although soil moisture is also increased in winter by lowered evapotranspiration rates. Micro-topography also has an influence on species' patterning as small topographic differences can cause a considerable difference in the environment (Sykes & Wilson, 1987). There is also a considerable amount of variation seen in the environmental variables within these sites, season to season (Johnson & Rogers, 2003). The majority of the previous work done has been based on species' patterning on water table preferences; here we test some other influential factors.

Here we will look into the focal species themselves, their community structure and their individual environmental preferences. The aim is to determine whether these sites all operate similarly or whether there are differences between and within them. These similarities or differences can be based on the location of the sites and their common environmental factors found throughout the duneland habitat.

Methods

Wetlands were sampled throughout New Zealand (Jan – March 2014), the North and South Islands, Stewart and Great Barrier Island. Wetlands were identified as being dish shaped depressions found within the dune fields, which have a minimum of three turf species present at the time of sampling. This was because I wanted to see species' interactions within a site. 15 wetland sites were found (Chapter 2). The selection of sites was aided by the help of local botanists and DOC personnel, who helped to identify possible sites.

Community structure and environmental variables were recorded at each site to ascertain whether the species and environmental relationship is constant across the country. Wetlands were sampled by running two transect lines at right angles to each other through a site. Additional perpendicular lines along the long axis of the wetland were used if the wetland was larger. Quadrats (25x25cm) were regularly spaced along the transect at 1-2m intervals, depending on the size of the wetland, using up to a maximum of 51 quadrats on one transect line. These quadrats were used to record species' presence and absence, as well as the percentages of vegetation (estimated cover of the shadow of live vegetation at solar zenith) and maximum vegetation standing height.

For each wetland site I recorded the slope of the site, distance to the sea, surrounding species' composition and surrounding dune height. The general percentage covers (which were estimated as shadow at solar zenith for each site) were live vegetation cover, bare sand, standing or flowing water, litter, rock cover, faecal matter and anthropogenic rubbish (data in Chapter 2). For each wetland site the distance to the water table was measured in the centre of the wetland along the transect line (Chapter 2) by digging a hole to below the zone of damp sand, and allowing it to infilll with water for 1 hour before the distance from the wetland surface to the standing water was measured. Recording was conducted in summer and therefore a lower water table result can be expected.

From these measurements the ratios of diversity of focal turf species to others, and of native to exotic species were calculated for each site, as was the total species' number within the quadrat (Table 4). Position of each quadrat was also recorded as a proportionate distance of the quadrat from the centre of the wetland.

Along all the transect lines the micro-topography of the site was measured, at regularly spaced intervals (of 1m) from end to end of the wetland (Chapter 2). The distance to the water table and the micro-topography data of the site was used to calculate each quadrat's distance to the water table. This was done by adding or subtracting the positive/negative topography values to the distance to the water table measurement (cm).

Statistical methods

The distance to the water table was plotted for each site, along with the average water table preferences for each species at each site sampled. CliFlo data (CliFlo: NIWA's National Climate Database on the web, 2015) was used to see how 2014's annual rainfall compared to previous years.

A species by quadrat NMDS ordination was performed using R [3.0.20] (R Core Team (2013), in the Vegan package (Oksanen et al, 2013), using the Bray-Curtis dissimilarity metric which is influenced by species abundance. The NMDS used the distance apart of the turf species in 4 dimensional ordination space after weighting for the contribution of each axis to the final ordination (Table 1). Rather than presenting the ordination these 4D distances were tabulated and examined. An association analysis (Jacard's, a dissimilarity measure) (Table 2) was also run in Systat 8.0 (Systat Software inc. San Jose, California) selecting the species' pairs with values below 0.8 as they are tightly associated (Table 1).

A general linear model (GLM) was then performed [Systat 8.0] (Systat Software inc. San Jose, California) for each species at each site and the environment data to see how environmental variables related to the species within a site and if these trends were similar throughout the country (Table 4). The environmental variables assessed were:

- Distance along the transect
- 'Posi' (which was % distance from the middle of the wetland – the wettest point)
- Maximum vegetation height
- % Live material
- % Bare sand
- % Dead plant material
- Distance to the water table.

Community composition indices were also used namely:

- the ephemeral: others ratio
- the native: exotic ratio
- the total number of species present per quadrat.

All variables were modelled and I then eliminated all the non-significant variables; the remaining variables were then analysed separately. Subsequently a GLM [Systat 8.0] (Systat Software inc. San Jose, California) was then run for each species (the dependent variable) regardless of the site (Table 3) to correlate environmental variables with the individual species.

Results

The range in distance to the water table varies from 13.5cm (closest to the surface) at Patea to the lowest 52cm (furthest from the surface) at Waipapa (Figure 1), the average being 32cm. There is a marked difference in water table heights when comparing the North to

South Island sites (Figure 1) probably as a result of seasonal differences. However the North Island water tables were measured in late February compared to early January in the South Island sites. All the North Island sites, excluding Great Barrier Island, had water tables less than 30cm from the surface. CliFlo data (CliFlo: NIWA's National Climate Database on the web, 2015) shows there was a drop in total rainfall from January 2014 (134mm) compared to February (29mm). This could be behind the difference in water tables across the North and South Islands. 2014's total rainfall (1428mm) was only slightly less when compared to 2013 (16402mm); however yearly fluctuations occur, plus or minus approximately 200mm (CliFlo: NIWA's National Climate Database on the web, 2015).

Limosella lineata in Stewart Island 3 was associated with the highest value for distance to the water table (water furthest away from the surface) out of all the turf species found (Figure 2a &b). On the other hand *Isolepis cernua* has a much narrower range fluctuating from 20-40cm. *Ranunculus acaulis* occurred in only 4 sites, 2 from each main Island with a water table height range from 15-55cm.

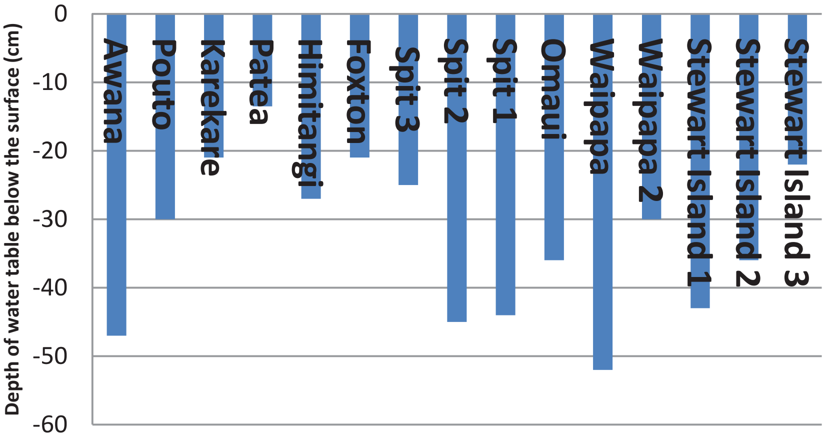

Figure 1: The distance to the water table (surveyed between January and March 2014) for each survey site. Sites are in latitudinal order.

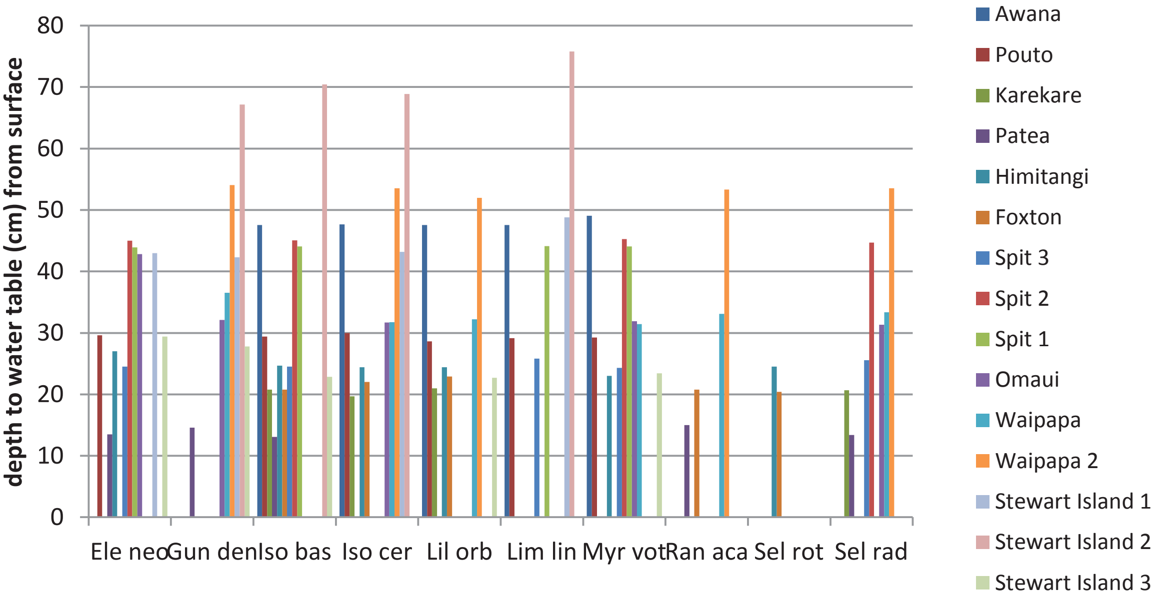

Figure 2a: The average distance to the water table from the surface of each focal species at each site. Species' abbreviations are presented in the introduction.

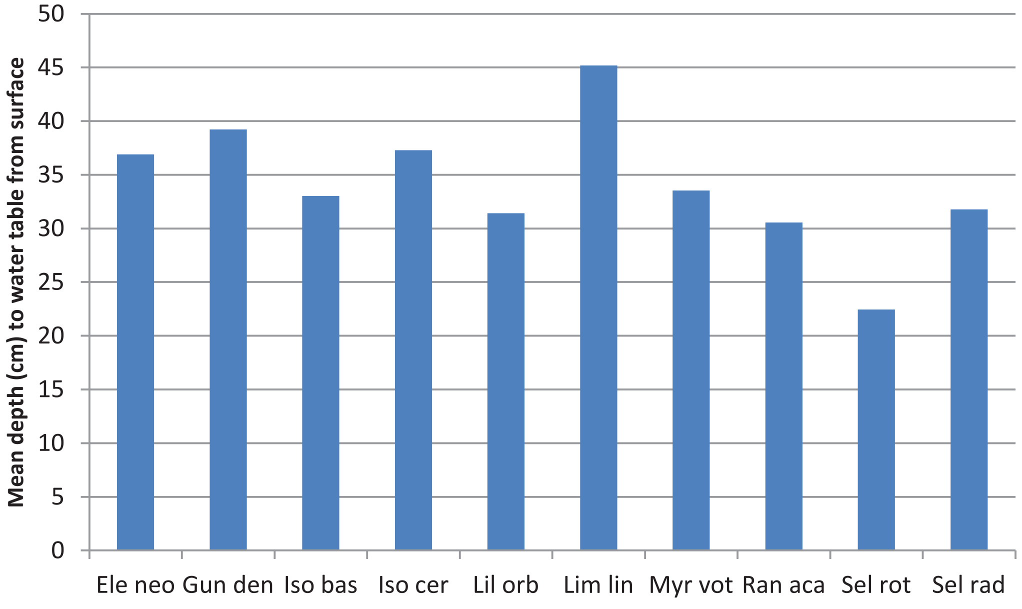

Figure 2b: The mean distance to water table for each species. Species' abbreviations are presented in the introduction.

Isolepis basilaris is isolated with no co-occurring species (Table 1), whereas *Ranunculus acaulis* is close in ordinational space to both the *Selliera* species (0.6, 0.8), and *Gunnera dentata* (0.7). *Lilaeopsis orbicularis* appears to occur in the same wetland sites as *Ranaunculus acaulis* and *Selliera rotundifolia* (0.7, 0.6) respectively. Lastly *Eleocharis* *neozelandica* occurs in the same habitats as *Myriophyllum votschii* (0.7). The values for the standard deviation in this table have a range of 0.8 to 1.3, a small range.

Lilaeopsis orbicularis and *Selliera rotundifolia* co-occur in the same quadrats 65% of the time (Table 2). *Selliera rotundifolia* and *Ranunculus acaulis* are rarely seen in the same quadrat, co-occurring only 6% of the time. However they are often close in ordinational space (Table 1), meaning they often occur in the same wetland site.

Table 1: The distances between pairs of species in four dimensional NMDS space after averaging across all species' pairs and weighting for the contribution of each axis to the final ordination. Shaded cells show values used for the association matrix below; they have values below 0.8 showing the pair of species tend to co-occur. Species abbreviations are as follows: Ele neo = *Eleocharis neozelandica,* Gun den = *Gunnera dentata,* Iso bas = *Isolepis basilaris,* Iso cer = *Isolepis cernua,* Lil orb = *Lilaeopsis orbicularis,* Lim lin = *Limosella lineata,* Myr vot = *Myriophyllum votschii,* Ran aca = *Ranunculus acaulis,* Sel rot = *Selliera rotundifolia,* Sel rad = *Selliera radicans.*

	Ele neo	Gun den	Iso bas	Iso cer	Lil orb	Lim lin	Myr vot	Ran aca	Sel rot	Sel rad
Ele neo	0									
Gun den	1.194	0								
Iso bas	1.357	2.212	0							
Iso cer	1.996	1.13	2.212	0						
Lil orb	1.331	1.089	1.801	1.093	0					
Lim lin	1.322	1.563	1.587	1.429	1.253	0				
Myr vot	0.754	1.374	1.535	1.615	1.039	1.462	0			
Ran aca	1.275	0.737	2.174	1.228	0.795	1.435	1.359	0		
Sel rot	1.067	0.9	1.674	1.28	0.682	1.364	1.206	0.699	0	
Sel rad	1.228	0.857	2.209	1.424	1.161	1.821	1.238	0.857	1.241	0

Table 2: Values of an association matrix using Jaccard based on the species with low (<0.8) distances apart in ordinational space (based on the greyed out numbers inTable 1), showing how common it is to see these pairs together in the same quadrat. - = no co- occurrence and 1= faithful species. Abbreviations in Table 1.

Dependant variable	**Sel rot**	**Lil orb**	**Ele neo**	**Gun den**
Ran aca	**0.064**	**0.440**	-	**0.315**
Sel rot	-	**0.649**	-	-
Myr vot	-	-	**0.488**	-

Eleocharis neozelandica was present in sites with a much lower total species' number, when compared to sites without it (Table 3). Additionally its native: exotic ratio preference was 0.83 compared to 0.99 for sites without this species, *s*howing a strong preference of *Eleocharis neozelandica* for sites without exotic species or that it has poor competitive ability. *Myriophyllum votschii* occurs in quadrats where there few 'other' species present (low ephemeral: others ratio), i.e. an environment rich in turf species ('other' is defined as any other species, both native and exotic, excluding those focal turf species). *Selliera radicans* is heavily influenced by the surrounding vegetation height and it seems that if the maximum vegetation height exceeds 5cm, then this species will not be present within a site.

Table 3: shows the significant environmental factors related to each species (as the dependent variable) regardless of site (obtained from the GLM), the actual values for the listed environmental variables, both for sites with those the species and for the sites without those species.

Species (dependant variable)	**Significant related environmental variable**	**P-value**	**Value of related variable in sites with the listed species**	**Value of related variable in sites without listed species**
Eleocharis neozelandica	Native: Exotic ratio Total species number	0.015 0.049	0.83 0.80	0.99 3.55
Myriophyllum votschii	Ephemeral: Others	0.002	0.03	1.00
Selliera radicans	Vegetation height	0.020	4.80cm	7.50cm

For the environmental factors related to the co-occurrences of each species across each site the greatest, i.e., the most frequently occurring, significant variable, across all species, was the total species number. 16% of the significant effects in Table 4 relate to the total species number. This is followed closely by the Ephemeral: others ratio and the Native: exotic ratio (both 10% of the tests). This suggests that these plants prefer more turf species present in a site compared to other or non-focal species. This in turn suggests that there may be some distribution patterns/community structure patterning in these sites.

The species all responded differently to the environmental variables. All environmental variables were modelled as significant for *Gunnera dentata.* For *Eleocharis neozelandica* the *Isolepis basilaris* was negatively related to vegetation height, whereas *Isolepis cernua* was found at species rich sites (being associated with an average of 4.2 species/site). *Lilaeopsis orbicularis* is related environmentally to both vegetation height and the proportion of ‘other’ species within a site. *Limosella lineata* is associated with the percentage of dead ground cover within a site (with a mean value of 3.42%). *Myriophyllum votschii* is also restricted by total species number (4.9); the most species found in a site was 19 (Spit 1).

The average value for the native: exotic ratio across all sites is 0.58, and the average ephemeral: others ratio is 1.05 (which includes all species from all sites). However *Myriophyllum votschii* had a much higher average for native:exotic ratio, regardless of site (2.31) as had *Selliera radicans* with a value of 2.7. Implying it is easily displaced by invading species.

Isolepis basilaris is associated with a lower water table requirement (1.16cm) than the mean (0.183cm), suggesting that this species in particular needs to be located in the wetter part of the slack, as does *Isolepis cernua* (Table 4), although this comes as no surprise as *Isolepis* species are generally associated with wet and swampy areas. Most of the surveyed sites were dish-shaped depressions (part of the selection criteria) and species with a low position % (the need to be closer to the centre of the wetland), would show a patterning relating to the water table height. These species are *Ranunculus acaulis, Gunnera dentata* and *Isolepis cernua.* Vegetation height preferences are on average 3.9cm; it appears that *Gunnera dentata* is associated with a higher stature of vegetation (7.75cm), as is *Isolepis basilaris* at the Stewart Island 3 site with a maximum vegetation height of 17.8.

The environmental parameters for *Eleocharis neozelandica* remain relatively constant across all the sites surveyed. *Gunnera dentata* was primarily found in South Island sites, except for one site in the North Island (Patea). *Isolepis basilaris* had different preferences for vegetation height and water table in the Stewart Island sites compared to all other sites it was found at, as did *Isolepis cernua* with a large change in water table preference.

Table 3: The environmental factors related to the occurrence of each species across each site and the average across all sites. Italicized factors are those which were significant at the 10% level and bold were significant at the 5%. Omaui has been removed from this table due to its lack of significant results. Shaded cells mark sites where species were not found. Non-significant factors are omitted. Site names abbreviations are in Figure 1. Environmental factors in a constant order are as follows, Dist on T (distance along the transect), Posi %(position along the transect as % of wetland bowl away from the centre of the site), Veg Ht. (maximum vegetation height), WT (distance to the water table below the surface), Eph: others (the ratio of ephemeral species to other species within a site), Native: exotic (the ratio of native species to exotic species within a site), total sp no (total species number found in a site), prop of sig effects (proportion of significant effects seen across each site). The averages are presented in the last row as a proportion of significant effects seen in each site, and means for each treatment are shown in the far right column. PTO.

Species	Env factor	Aww	Po	Ka	Pa	Him	Fo	Sp3	Sp2	Sp1	Wa1	Wa2	St1	St2	St3	Mean
Ele neo	**Dist on T (m)**		**8.25**													8.25
	Veg Ht. (cm)								*3.07*							3.07
	% Dead							**2.04**								2.04
	Eph:others					**4.00**			**0.36**	**0.00**						1.45
	Native:exotic					**0.00**			**0.31**							0.16
	Total sp No		**3.50**							*3.60*						3.55
Gun den	**Dist on T (m)**				**21.40**						**9.60**	**11.50**		6.10		12.15
	Posi. %				**10.80**						**35.00**	**2.20**	5.00			13.25
	Veg Ht. (cm)										**6.00**	**13.50**				9.75
	% Live										**34.00**		*6.00*			20.00
	% Sand										**61.00**	*75.50*				68.25
	% Dead										**1.30**	**2.00**	**89.00**			30.77
	WT (cm)										**1.05**	**1.90**			**6.50**	3.15
	Eph:others										**1.90**	**0.30**				1.10
	Native:exotic										**2.70**	**0.30**	**0.00**			1.00
	Total sp No										**5.00**	**5.00**	**3.00**		**4.10**	4.28
Iso bas	**Dist on T (m)**					**52.00**							**3.00**			27.50
	Veg Ht. (cm)	**6.70**	**5.40**						**6.70**					**17.80**		9.15
	% Live									*19.40*						19.40
	% Dead							**2.04**								2.04
	WT (cm)					**0.60**							**-1.16**		**2.30**	0.58
	Eph:others								**0.34**					**1.90**		1.12
	Native:exotic								**0.31**					**1.20**		0.76
	Total sp No					**5.50**				**3.50**						4.50
Iso cer	**Dist on T (m)**	**25.00**											**3.50**			14.25
	Posi. %			**2.00**		**27.00**										14.50
	Veg Ht. (cm)		**2.00**			**5.30**										3.65
	% Dead		**4.00**													4.00
	WT (cm)												**-6.23**		**0.14**	-3.05
	Total sp No	**4.12**		**3.60**		**5.40**							**3.50**		**4.40**	4.20
Lil orb	**Dist on T (m)**		**2.00**													2.00
	Posi. %		**14.00**													14.00
	Veg Ht. (cm)	*2.30*				**5.30**										3.80
	% Dead					**1.10**										1.10
	Eph:others					**3.10**										3.10
	Total sp No	**4.12**									**5.00**					4.56
lim lin	**Dist on T (m)**	**6.17**													*19.00*	12.59
	Veg Ht. (cm)												**5.03**			5.03
	% Live									**18.70**						18.70
	% Dead												**0.84**	**6.00**		3.42
	WT (cm)		**-1.00**													-1.00
	Eph:others												*0.34*			0.34
	Native:exotic												**0.70**		*0.00*	0.35

Species	Env factor	Aww	Po	Ka	Pa	Him	Fo	Sp3	Sp2	Sp1	Wa1	Wa2	St1	St2	St3	Mean
	Total sp No									**3.80**						3.80
Myr vot	**Dist on T (m)**	**22.00**				**68.00**						*9.70*				33.23
	Veg Ht. (cm)											**1.50**				1.50
	% Live							**29.20**		*19.40*						24.30
	% Sand							**68.70**								68.70
	WT (cm)							**-0.60**				**2.20**				0.80
	Eph:others											**3.60**				3.60
	Native:exotic							**1.43**				*3.20*				2.32
	Total sp No					**6.20**		**4.56**		**3.50**		**5.70**				4.99
Ran aca	**Dist on T (m)**						**21.00**								**0.00**	10.50
	Posi. %												**0.00**			0.00
	% Live												*6.00*			6.00
	Eph:others						**0.90**									0.90
	Native:exotic						**0.70**						**0.00**		**0.00**	0.23
	Total sp No												**1.00**			1.00
Sel rad	**Dist on T (m)**			**11.00**												11.00
	Posi. %			**25.00**							**20.00**					22.50
	Veg Ht. (cm)										*7.40*					7.40
	% Live										**31.80**					31.80
	Eph:others			**1.30**	*1.00*			*1.40*			**1.80**					1.38
	Native:exotic										**2.70**					2.70
	Total sp No			**2.80**					**3.60**		**5.30**					3.90
Sel rot	**Posi. %**						**20.00**									20.00
	Veg Ht. (cm)					**5.20**										5.20
	% Dead					**1.10**										1.10
	WT (cm)															0.00
	Eph:others					**3.10**										3.10
	Native:exotic						**1.70**									1.70
	Total sp No						**4.50**									4.50
Averages	**Dist on T (m)**	17.72	5.13	**11.00**	21.40	60.00	21.00	0.00	0.00	0.00	9.60	10.60	3.25	6.10	9.50	12.52
	Posi. %	0.00	14.00	**13.50**	10.80	27.00	20.00	0.00	0.00	0.00	27.50	2.20	2.50	0.00	0.00	8.39
	Veg Ht. (cm)	4.50	3.70	**0.00**	0.00	5.27	0.00	0.00	4.89	0.00	6.70	7.50	5.03	17.80	0.00	3.96
	% Live	0.00	0.00	**0.00**	0.00	0.00	0.00	29.20	0.00	19.17	32.90	0.00	6.00	0.00	0.00	6.23
	% Sand	0.00	0.00	**0.00**	0.00	0.00	0.00	68.70	0.00	0.00	61.00	75.50	0.00	0.00	0.00	14.66
	% Dead	0.00	4.00	**0.00**	0.00	1.10	0.00	2.04	0.00	0.00	1.30	2.00	44.92	6.00	0.00	4.38
	WT (cm)	0.00	-1.00	**0.00**	0.00	0.60	0.00	-0.60	0.00	0.00	1.05	2.05	-3.70	0.00	2.98	0.10
	Eph:others	0.00	0.00	**1.30**	1.00	3.40	0.90	1.40	0.35	0.00	1.85	1.95	0.34	1.90	0.00	1.03
	Native:exotic	0.00	0.00	**0.00**	0.00	0.00	1.20	1.43	0.31	0.00	2.70	1.75	0.23	1.20	0.00	0.63
	Total sp No	4.12	3.50	**3.20**	0.00	5.70	4.50	4.56	3.60	3.60	5.10	5.35	2.50	0.00	4.25	3.57
	Prop of sig effects	24	24	23	20	29	23	24	23	24	30	28	31	22	25	

Discussion

Distinctive sand dune vegetation previously extended along a sizeable part of New Zealand's coastline (Sykes & Wilson, 1991). Sand plains (dune slacks) are a mosaic of habitats which support a range of species from typical dune species such as the exotic marram to the typically wet sand plain species which are native (Esler, 1970). The lower, flatter parts of these environments support wetland species (Esler, 1970); these are my focus.

There are fewer than 20 sand plain species in the New Zealand dune slacks, and these form complex communities due to a wide range of environmental tolerances (Esler, 1969). The most striking feature of these environments is the small scale community zonation, often assumed to be due to water table preferences (Esler, 1969), period of inundation, time of emergence, and salinity (Deil, 2005). I aim to look into these species and their community patterning as well as their individual habitat preferences.

Are the species driving the patterning themselves?

Gunnera dentata appears to be significantly related to more environmental variables than all turf species tested. On average more environmental variables were significant across all species in the South Island sites compared to the North (Table 4), which suggests that the North Island species patterns may be more opportunistic, and wetland sites may be due to chance introductions. However in the South Island sites, many environmental variables appear to be influencing the distribution seen in these species, suggesting tighter relationships. This could be due to the North Island dunes being more recently disturbed (human disturbance) than the South Island dunes.

Ephemeral wetland species intermingle and are surrounded by weedy species (Chapter 2, Fig6e). There is also little patterning with respect to water table height seen in any of these focal species; this can be seen by the location of *Selliera rotundifolia* on the outskirts of the ordination (Chapter 2, Fig6e). *Selliera* *rotundifolia* is widely distributed along the Manawatu coast, and also cosmopolitan within wetlands.

Which environmental variables are structuring the patterning of these turf species?

Interactions amongst species occur within a complex mix of abiotic and biotic processes (Callaway & Walker 1997). Community ecology measures environmental factors and uses these variables to predict which species will be present at a certain site (Keddy, 1992). Early attempts have been made to predict the species' composition seen in wetlands. It is difficult to correlate any environmental variable with species' distribution and patterning, due to the mosaic nature of the dunes (Sykes & Wilson, 1987). Not enough is known about the environmental conditions of the slack environment, to draw any conclusions regarding turf species' patterning (Sykes & Wilson, 1987). However environmental data were collected to assess whether the patterning of ephemeral wetland species was related to their environment, and whether these distribution patterns were constant across the country.

The patterning of ephemeral wetland species was suggested to be related to environmental dynamics seen in the dune slack systems (Singers, 1997). For the Manawatu coast Esler (1969) postulated that the summer water table was the main reason for the species' distribution currently seen. He compared the distributions of *Myriophyllum, Limosella, Eleocharis, Ranunculus,* and *Selliera.* For *Limosella lineata* and *Myriophyllum votschii* he reported that they exist in a very narrow habitat range, and often occur together (Esler, 1969). In my study *Myriophyllum votschii* and *Eleocharis neozelandica* were found to occur in the same wetland sites (Table 1) and to occur in the same microsites, which does suggest a narrow habitat range (Table 2). This was similar to *Selliera rotundifolia* and *Ranunculus acaulis* (Table 1&2). *Selliera rotundifolia* is a local endemic (de Lange et al., 2012), so patterning may be an artefact of the small range of environmental factors it is associated with. *Ranunculus acaulis* is widespread and may even occur in rocky environments. *Limosella lineata* however, was not found to co-occur with other turf species within a wetland site, let alone similar microsites. However variation in the results (table 1) for species associations shows at best weak patterning.

Despite Eslers' (1969) statement, water table was not found to be a significant controlling environmental factor for any of these species (Table 3). *Myriophyllum votschii* has a water table range from -0.6 -2.2cm and *Limosella lineata* with -1cm (Table 4). They were also rarely co-occurring. However here water table was only measured once per site, at different times of the summer and the information gained is at best indicative. Singers (1997) claimed that if annual fluctuations of water table remained constant then patterning of species' into zones would occur.

Studies have been conducted assessing the nature of species' patterning across the Manawatu coast by Esler (1969) and Singers (1997), as well as at Farewell Spit (Brown, 1978). For all the sites and species across New Zealand (Table 4), the total species number was the most significant factor, closely followed by the ephemeral: others ratio and the native: exotic ratio, suggesting that these turf species are particularly sensitive to the presence of other species within their habitats. However these three variables likely contain overlapping information and may be correlated. Larger numbers of exotic species results in fewer turf species being present within a site. This could be due to competition for water or light (a hypothesis examined further in Chapter 4). Competition is known to have a strong influence on species' patterning within dune slack sites (Wilson & Gitay, 1995), but there are many complicating factors which make this hard to asses in field studies (Wilson & Gitay, 1995). The average total species number across all wetland sites is 3.57 per quadrat, suggesting that these turf species tend to not occur in areas which are dominated by a large number of species. The average Ephemeral: Others ratio (1.03) suggests that these turf species tend to co-occur with each other, and they disappear when too many other species enter a site, probably due to poor competitive ability caused by their low stature (investigated in Chapter 4), though no allowance has been made for random co-occurrences. Alternatively they may occur in different habitats, and possibly in early successional stages only. Here turf species generally prefer sites with low total species' numbers and few exotic species present. Resource competition has been seen to have important effects on the organisation of a community (Callaway & Walker 1997).

The patterns of these turf species within wetlands are related to different environmental factors. *Eleocharis neozelandica* had the most significant results for the community composition indices with the ephemeral: others ratio having a mean of 1.45, showing a tendency to be associated with other ephemeral species. *Ranunculus acaulis,* regardless of site, is influenced by the native: exotic ratio and occurs on average when there is a greater number of exotic species present compared to natives (Table 4), perhaps reflecting its broad habitat range. However the sample size is small.

While *Ranunculus acaulis* and *Selliera rotundifolia* occur often in the same sites, they only occur together (i.e. within a quadrat) 6% of the time (Table 1 and 2). *Isolepis basilaris* and *Isolepis cernua* are rarely seen in the same site (Table 1). This could be due to niche limitation; they are congeneric and congeners compete strongly (Mayfield & Levine, 2010). *Isolepis basilaris* occurs in 14 of the 15 (Chapter 2) wetland sites, compared to *Isolepis cernua* which occurs in only 11 of the wetland sites. From this we would expect these species to co-occur in 60% of the sites, and data confirms this with both species occurring in 10 of the 15 sites (66%). This simple pattern supports their similar niches.

Chance dispersal, competition, or differing successional states appear to structure these communities. Environmental variables vary greatly from site to site, compared to the community composition indices which appear to structure species composition similarly across sites. Species may inhabit ephemeral wetlands on the basis of low competition or during early successional stages. Thus a window of opportunity is presented to plants which can tolerate the large variation in water tables resulting in wet and dry environments, as seen in these habitat types (Zedler, 2003).

Are all wetlands homogenous across New Zealand dune slacks?

Variation in species' dominance and diversity within slack sites, suggests that environmental patterning doesn't happen in the same way across sites or even within sites (Wilson & Gitay, 1995). For each survey site, species' composition was correlated with a different environmental variable or even with several. However the most common community composition indices were total species number and the native: exotic ratio as discussed above. On average, turf species occurred in a site if the maximum vegetation height was <3.9cm, suggesting that larger species are associated with the decline of turf species, or are later successional species occurring in different habitats (discussed in more detail in Chapter 4). Environmentally, sites differed across New Zealand, although species community composition indices such as the native: exotic ratio and ephemeral: others ratio as well as the total species number, were homogenous across all sites, with the turf species seen to occur in sites with few exotics, and more natives, particularly other turf species. A low total species number, was also seen across New Zealand for these wetland sites, with the highest seen across all wetlands being 18 species within a wetland site. However further investigating these species' responses to reduced light and water could explain the effects of competition on these turf species (Chapter 4).

Is there an indicator species that we can use to predict wetland decline?

There does not appear to be any single specific turf species which can be used to accurately predict wetland decline, although species are not very widespread. Possible combinations of indicator species that correlate negatively to a higher number of exotics within a site are *Eleocharis neozelandica, Isolepis basilaris, Limosella lineata* and *Ranunculus acaulis*. They could be useful in the simple environment of sand dunes. Those 5 of the 10 wetland turf species could be used as indicators of declining wetland health. When taller species invade a turf wetland that is the simplest predictor of wetland decline, as the turf species seem unlikely to associate with larger species.

Conclusion

Rare ecosystems often have a highly diverse and specialised flora characterised by a large proportion of endemic and/or nationally rare species (Williams et al., 2007). The framework for determining if an ecosystem is rare relies on soil age, parent material, topography, drainage, disturbance regime, and climate. Williams et al. (2007) considers dune slacks and damp sand plains to be a historically rare ecosystem. Some of these environmental variables were examined here, namely the topography of the site and the drainage. They were seen to be influential although varied across sites.

Conservation of remaining slack sites requires knowledge of the community types and dynamics present within them (Roxburgh et al., 1994). Many previous slacks have been destroyed by development. It appears that the environmental factors which influence these turf species' distribution differ across New Zealand; however the driving factor of turf patterning appears to be the rate of infill of the wetland by aeolian sand (Chapter 4) and the main indicator of wetland decline appears to be the presence or absence of certain sensitive species. Future work would include competition experiments in order to make solid conclusions about the effects of competition on these turf species and to further investigate the inundation and drying cycles of these plants and its links to explaining their compositional dynamics.

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Chapter 4

Environmental factors influencing the growth of ephemeral wetland turf species

Experimental setup in glasshouse

Abstract

Question: Which environmental factors influence the growth of ephemeral wetland turf species?

Location: Manawatu, New Zealand

Methods: Glasshouse experiments were conducted to non-destructively assess the influence of differing treatments on these turf species. Water logging tolerances were tested with three water table levels with an interaction with low or full light. A burial and nutrient interaction experiment was also conducted, to assess the influence of burial with or without the addition of nutrients. A small experiment was conducted to assess the impact of trampling on these turf species

Results: Plants under the low water/low light treatment decreased in size less than the low water/full light treatment, although low water resulted as a whole resulted in a size decrease. The medium and high levels of waterlogging, regardless of light treatment, resulted in an increase in plant growth. For the burial and nutrient interaction, the plant growth under the burial and nutrient treatment was more than double the unburied and no nutrient treatment. For the tamping experiment a general (though non-significant) trend of decrease in plant size was seen when plants were "trampled".

Conclusions: These dune slack turf species need a medium or high water table for optimum growth; they are not well adapted to low light situations, implying they may struggle amongst taller plants. These plants perform best with added nutrients. This may be adaptive as fresh sand from the foredunes, which bury these plants, brings with it additional nutrients.

Keywords: Dune slack, ephemeral wetland, environmental dynamics, growth, experimental, burial, waterlogging, nutrient addition, shade.

Introduction

Since the introduction of European settlers, the sand dune vegetation has slowly been destroyed. This destruction has been aided by introduced sand binding species, such as marram grass (Sykes & Wilson, 1991). Sand plains or dune slacks are low lying areas between dunes, the surfaces of which are close to the water table (Esler, 1969). Dune wetlands are generally colonised by ephemeral species which live in wet substrates and die out when the water levels dry up (Baird & Wilby, 1999). These species are “differentially attuned” to their environment, and this can be shown by their spatial or geographic distribution patterns (Esler, 1969). This study focuses on the ephemeral dune wetland plants *Gunnera dentata, Limosella lineata, Lilaeopsis orbicularis, Selliera radicans, Selliera rotundifolia, Ranunculus acaulis, Isolepis basilaris, Isolepis cernua,* and *Myriophyllum votschii.*

The ability to survive different levels of burial and waterlogging is of crucial importance to the survival of ephemeral wetland species (Sykes & Wilson, 1990) although they didn’t study turf species. Turf plants growing in dune slacks are subjected to burial and seasonal waterlogging (Singers, 1997). These plants endure extended periods of waterlogging or submergence in the winter months, and in the summer months they may experience either the same environment or times of drought (Sykes & Wilson, 1987). Dry weather can dry out the sand causing periods of burial in the summer months as well (Singers, 1997), as dry sand is more mobile during windy periods.

The zonation of dune slack vegetation has been seen to be closely related to the level of the water table, as the turf plants that occupy these habitats have varying tolerances to water logging (Singers, 1997). Talbot et al. (1986) found that high levels of continuous waterlogging were generally most damaging to plants which were used to growing in well drained substrate. Anoxic conditions in wetlands can cause many chemical and physical changes to the plants occupying these environments (Singers, 1997).

Dunes are highly mobile and due to the large supply of loose sand, are renowned for their movement (Singers, 1997). The wind transports sand from the fore dunes onto the smaller inland dunes or into the dune slacks themselves (Willis et al., 1959). Stabilization of sand is achieved by plants accumulating sand and then growing up through it (Sykes & Wilson, 1990). Dune specialist species need to cope with harsh environmental events such as blowouts in the fore dunes or strong wind events causing loose sand to bury the plants (Sykes & Wilson, 1990). The same applies to ephemeral wetland species, which are subject to constant sand movement.

Species' responses to sand accretion have seldom been studied in depth; however a few species can survive it (Martinez & Moreno-Cassasola, 1996). Sykes and Wilson (1990) conducted a study on the effects of burial on sand dune species (similar to the species tested here) and found that tolerance for burial in back-dune species is as important as it is for fore-dune species. They found that creeping herbs were generally tolerant of only partial burial, but they died when fully buried (Sykes & Wilson, 1990). Dune slacks frequently receive fresh sand deposits, which contain nutrients (Sykes & Wilson, 1990). Burial up to a certain threshold is beneficial to plants, due to the improved soil resources. Past this threshold however, the positive responses decline, even resulting in negative growth, which can reduce survival of adult plants (Maun, 1998). Here I tested the burial and nutrient interaction in a controlled experiment to investigate growth with both burial and nutrients.

Due to the location of dune slacks, trampling is a common introduced threat (Johnson & Rogers, 2003). Mammals and hooved animals can compact and fracture the turf vegetation as well as compacting the sand alone. The effects of trampling were tested on a few of the above species, as it is common for dune slack plants to be trampled, walked and driven over constantly due to human recreational activities and wandering stock.

Waterlogging tolerances were also tested at three levels (low, medium and high). This was tested in conjunction with responses to low light or full light, due to the assumption that as the water table rises due to the invasion of taller species, the smaller turf species will now also be competing for light.

Therefore aims of these experiments were to determine which environmental factors influence the growth of each of the ephemeral wetland species, and how these factors interact with each other. Do these factors structure the community patterning seen in these wetland habitats.

Methods

Experimental methods

Plants were collected from Basil Sexton's property near Himatangi beach. Species collected were *Gunnera dentata, Isolepis cernua, Isolepis basilaris, Ranunculus acaulis, Selliera rotundifolia, Lilaeopsis orbicularis,* and *Limosella lineata. Selliera radicans* was collected from Patea, Taranaki, as it is not found on the Manawatu coast.

The plants were planted into sand from the sites from which they were taken, and left to establish for two months. They were then planted into individual pots ($63cm^3$), and given an additional two weeks' establishment. Plants were then randomly assigned to different treatment groups, and tested for environmental tolerances in regards to a water table X low light experiment, a burial X nutrient experiment, and a tamping experiment. The species used for each experiment are listed below; due to availability not all focal species were used in all experiments. Replicates were set up in a random block design and plant pots were rearranged both within replicates and as replicates on a fortnightly basis. Plants were also weeded once a fortnight. All experiments were run for two months.

Waterlogging and low light experiment

This experiment used *Gunnera dentata, Myriophyllum votschii, Isolepis cernua, Isolepis basilaris, Selliera radicans, Selliera rotundifolia, Lilaeopsis orbicularis, Limosella lineata and Ranunculus acaulis.* Each species was allocated to all three levels of waterlogging (low, medium and high), along with either a low or a full light treatment. Waterlogging was managed using 125g yoghurt pottles, with two opposite holes punched into them at the base, mid-way up the side, or just under the lip of the pottle. Then the plant pots were individually placed into the appropriate yoghurt tub (Figure 1). To top up and refresh the water, each yoghurt tub (including the plant in its own pot within the yoghurt tub) was fully submerged in a bucket of water for 10 seconds twice a week and allowed to drain. The high light treatment was 100% ambient light on the individual plant and the shade treatment reduced the light intensity by 80% via 2 layers of shade cloth in the shape of a bag placed over them. There were 8 replicates.

Figure 1: Experimental set up for the waterlogging and low light experiment. Some pottles are experiencing low light and others can be seen with different water depths, as shown by the different levels of holes punched into the sides of the yoghurt pottles.

Burial and supplementary nutrients experiment

This experiment used *Gunnera dentata, Myriophyllum votschii, Isolepis cernua, Isolepis basilaris, Selliera radicans, Selliera rotundifolia, and Lilaeopsis orbicularis.* There were 4 treatments and 8 replicates.

The individual plant pots were placed into larger pots which were then filled with sand in, around and up to the level of the plant pot (Figure 2). This was to allow room for burial, as most plants were overtopping their pottles. Plants were then assigned to the different treatments (two levels of burial: full or none) and two nutrient levels of liquid nutrient solution (Peter's All-rounder, made up at a concentration of one gram/litre, containing 40ppm of Nitrogen, 17ppm Phosphorus and 34ppm Potassium in 20cm^3) or 20cm^3 of water (i.e., no nutrients). Nutrient treatments were applied once a week by pouring the 20cm^3 onto the plants. If nutrients were added, no plants were watered that day, and otherwise plants were watered daily.

Figure 2: The setup of the burial-nutrient interaction experimental, with smaller plant pots placed within larger ones.

Tamping

The tamping experiment was conducted in order to assess the impacts of trampling on dune-slack plants. Seven focal species were used in this experiment: *Gunnera dentata, Lilaeopsis orbicularis, Limosella lineata, Myriophyllum votschii, Ranunculus acaulis, Selliera rotundifolia* and *Selliera radicans*. There were two treatments: control and tamping. Tamping was conducted twice weekly, with a 1.3kg weight (with a footprint size of 3x3cm) placed gently on each plant for 1 minute (80 grams per unit of surface area). Plants were watered every day.

Figure 3: The tamping experimental setup and the tamping "foot" (circled in red) that was used. The weight is placed on one of the plants and the other replicates can be seen.

Analysis

Gunnera dentata was omitted from the results of the tamping experiment, as all individuals died, regardless of the treatment.

Due to the rare nature of many of the species used here, growth was measured non-destructively, so that surviving plants could be returned to their natural environments. Growth for all 3 experiments was measured photographically, using before and after photos (at 2x zoom) of each plant taken on a standard tripod, so that each image was the same size. The pixels were counted (by importing the photos into Adobe Photoshop and selecting the plant pixels) and the growth (change in foliage area over time) was assessed, before converting pixel number to plant surface area for analysis. For *Isolepis cernua* and *Isolepis basilaris,* photos were inappropriate due to their upright and linear growth forms. Instead, stem counts were done for each individual using the inside ring ($1cm^2$) of a paperclip placed at random on the plant, but with each sample 'full' of plant, and recording the number of stems within that ring both before and after the experimental treatment. An ANOVA was conducted for each experiment to assess the effect of each experiment on the species, the treatments individually and the species X treatment interaction for all appropriate variables.

Proportionate change (expressed as (final – initial)/final surface area), over time was also calculated to include all species in analyses.

Results

For the burial and nutrient experiment there were significant differences between the species for the leaf areal differences (excluding the *Isolepis* species), stem count change (for the *Isolepis* species), and for the proportionate change (which includes all species; Table 1). The burial and nutrient interaction was significant for all measures of growth (Table 1).

Table 1: Summary of the analyses of variance for the three different methods for measuring growth, showing the significant P values (in bold), the standard error and the degrees of freedom for each experiment. *Isolepis* species were not used in the tamping experiment.

Experiment	**Effects & Interactions**	**Area differences (Excluding *Isolepis* spp.)**	**Stem count change (Only for *Isolepis* spp.)**	**Proportionate change (All spp.)**
Burial and Nutrients	Species	**0.000**	**0.000**	**0.000**
	Burial treatment	**0.002**	0.909	0.325
	Nutrient treatment	**0.043**	0.427	0.163
	Species X burial	0.069	0.214	**0.032**
	Species X nutrients	**0.010**	0.982	**0.026**
	Burial X Nutrient interaction	**0.014**	**0.039**	**0.008**
	Spp. X burial x nutrient interaction	0.695	0.132	0.870
	Error Mean Square	$1.44703x10^{9}$	39.579	17.803
	Error DF	124	40	164
Waterlogging and Low light	Waterlogging	**0.005**	0.339	0.186
	Low light	0.962	0.357	0.508
	Species	0.540	0.492	0.202
	Species X Waterlogging	**0.000**	0.365	0.867
	Species X Low light	0.997	0.404	0.884
	Low light X Waterlogging	0.601	0.350	0.601
	Spp. x waterlogging X low light	0.996	0.471	0.934
	Standard error	$2.27157x10^{11}$	1061589.240	2823.797
	Error DF	222	84	306
Tamping	Species	**0.001**		0.070
	Tamping	0.356		0.308
	Species X Tamping	0.208		0.659
	Standard error	$1.36088x10^{10}$		26.857
	Error DF	22		22

For the burial and nutrient experiment on average, all species and plants had an increase in growth over the experimental period, excluding *Isolepis cernua* (Table 2). Both *Selliera* species and *Gunnera dentata* increased in size by 1.31, 1.44 and 1.25cm^2 compared to the other species used in this experiment who all had increases < 1cm^2.

The burial treatment resulted in an increase in plant growth (by areal difference) of 1.04cm^2 compared to the unburied treatment which resulted in a growth increase of only 0.14cm^2 comparatively (Table 3). However for the *Isolepis species* the opposite was found. A smaller value of (-0.73) resulted under the burial treatment compared to unburied equivalent to a stem density decrease of 0.37. When looking at the proportionate change (Table 3), burial resulted in a greater growth when compared to unburied (2.39 to 1.70cm^2). For the Nutrient treatment the proportionate change (including all species used in the experiment) showed that the addition of nutrients was beneficial to plant growth, resulting in a change of 2.6cm^2 (with nutrients) compared to no nutrients added which resulted in growth differences of 1.48cm^2. The buried plants with supplementary nutrients resulted in the greatest areal change seen throughout these experiments, 13 times more than the unburied plants with nutrient (UN). For *Isolepis* species all treatments for the burial x nutrient experiment had a decrease in stem count; however proportionate change shows that BN treatment resulted in a stem count change 4 times greater than buried alone (BO). The BN treatment's stem count was also nearly 2 times greater than the control (UO) which was unburied and no nutrients added.

Table 2: The mean growth differences for each species seen in each experiment, regardless of experimental treatment.

Experiment	Species	Area change (cm^2)	Stem count change	Proportionate change
Burial and nutrient	*Gunnera dentata*	1.25		-0.35
	Isolepis basilaris		6.00	1.10
	Isolepis cernua		-1.54	0.16
	Lilaeopsis orbicularis	0.39		1.95
	Myriophyllum votschii	0.63		2.17
	Selliera radicans	1.31		2.12
	Selliera rotundifolia	1.44		5.87
	Grand Mean	1.00	2.23	1.86
Water table and Low Light	*Gunnera dentata*	-0.46		0.03
	Isolepis basilaris		-0.35	-0.34
	Isolepis cernua		3.79	0.43
	Lilaeopsis orbicularis	-0.16		-0.42
	Limosella lineata	-0.33		-0.44
	Myriophyllum votschii	-0.04		-0.11
	Ranunculus acaulis	-0.04		-0.11
	Selliera radicans	-0.43		-0.21
	Selliera rotundifolia	0.08		1.37
	Grand mean	-0.19	1.72	0.02
Tamping	*Gunnera dentata*	-3.31		-1
	Lilaeopsis orbicularis	-0.23		-0.75
	Limosella lineata	0.12		0.02
	Myriophyllum votschii	-0.44		-0.55
	Ranunculus acaulis	-0.17		-0.48
	Selliera radicans	-0.37		1.39
	Selliera rotundifolia	-0.3		-0.64
	Grand mean	-0.67		-0.28

Table 3: Growth means for each treatment regardless of species, for the burial x nutrient experiment. B= burial, U = unburied, N = nutrients, O=no nutrients.

	Treatment	Area change	Stem count change	Proportionate change
Burial	B	1.04	-0.73	2.39
	U	0.14	-0.37	1.70
Nutrient	N	0.96	-0.53	2.60
	O	0.22	-0.58	1.48
B X N	BN	1.79	-0.70	3.82
	BO	0.29	-0.77	0.95
	UN	0.13	-0.35	1.38
	UO	0.15	-0.39	2.01
Grand mean		0.59	-0.5525	2.04

The effect of the nutrient x burial treatment was an increase in plant size from 2.2cm^2-3cm^2, all plants in the unburied treatments died. *Isolepis cernua* did poorly on average regardless of the treatment applied, as all treatments bar the control resulted in a stem count decrease. *Isolepis basilaris* tended to increase in stem count regardless of the treatment (Figure 4;Table 2), although its greatest stem increase was for the UN treatment after nutrient addition.

Lilaeopsis orbicularis had a general trend of size increase regardless of treatment from 0.6cm^2 when buried without nutrients, compared to the burial with nutrient treatment 0.6cm^2. The scale of increase was much smaller compared to all other species in this experiment; on average the surface area increase was below 1cm^2. *Myriophyllum votschii* had a general size increase excluding the UN treatment, but had the largest rate of change in the control i.e.: the UO treatment (Figure 4). There was, on average, a size increase across both *Selliera* species in all treatments; however *Selliera rotundifolia* did far better in all treatments when compared to *Selliera radicans. Selliera radicans* had the greatest average size increase when buried with supplementary nutrients, going from 1.2-4.9cm^2.

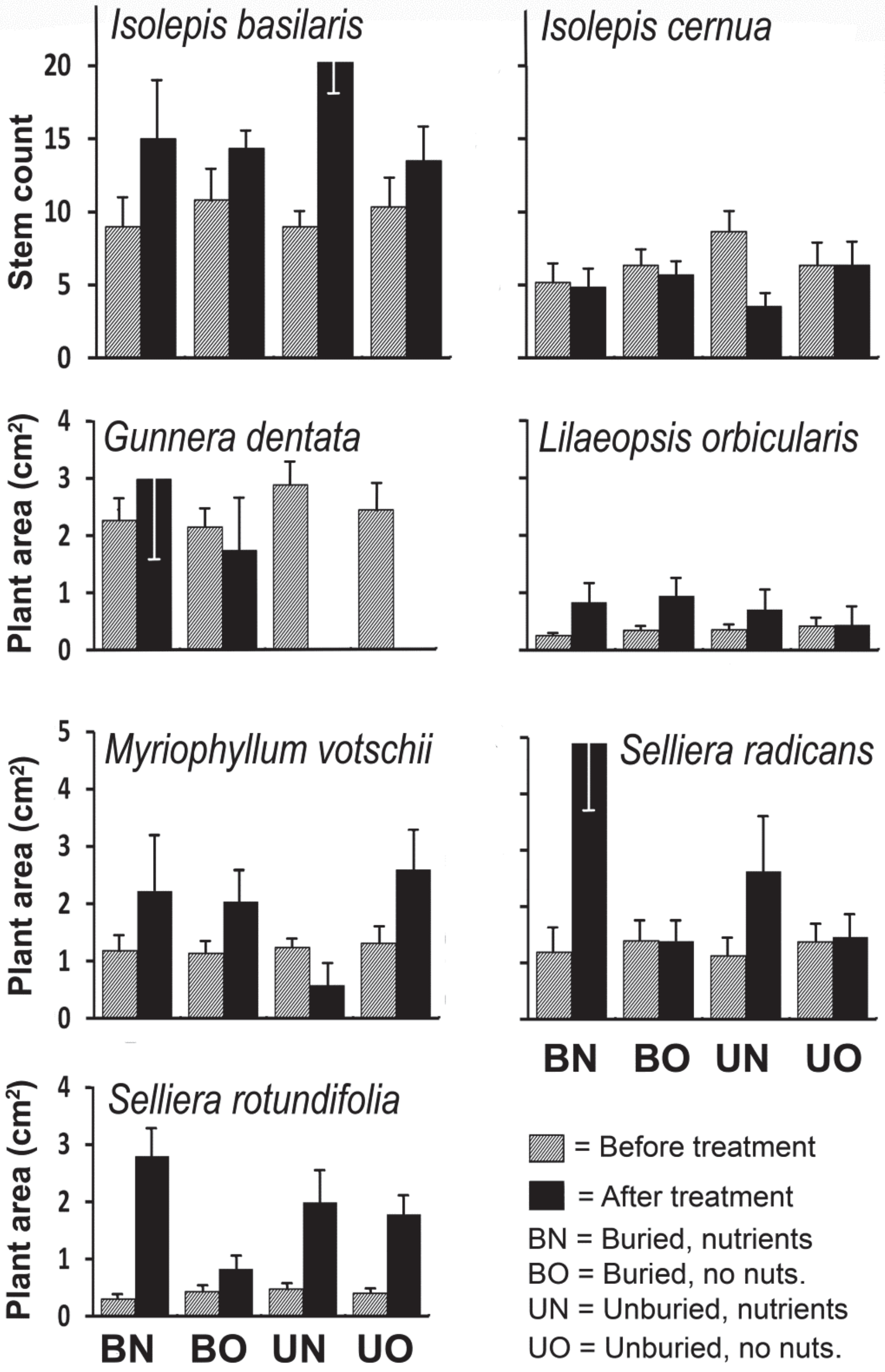

Figure 4: Average growth (either by area (cm^2) or by stem count) before and after treatments (T) for each species in each treatment used in the burial and nutrient experiment. B = buried, U = unburied, N = supplementary nutrients and O = no supplementary nutrients. *Gunnera dentata* was not included in the ANOVA

The water logging X light experiment only had significant effects in the ANOVA for the areal differences, which excludes *Isolepis* species (Table 1). The waterlogging treatments differed significantly on their effects on growth, and the species differed in their responses to waterlogging ($p < 0.000$).

The mean proportionate decline in leaf area for all species (Table 2), excluding *Gunnera dentata* which only had a very small mean increase of 0.03cm^2. *Isolepis cernua* had an increase of 0.43cm^2 growing more than *Isolepis basilaris*. Lastly *Selliera rotundifolia* had a large proportionate growth increase over all treatments (Table 2).

Under low and medium water table treatments there was a proportionate decrease in growth (0.25, 0.06; Table 4). Only the high water table treatment resulted in a proportionate growth increase of 50%. The low light treatment across all measurements of change resulted in a mean growth decrease. Of the interaction treatments both LS (low water with low light) and MS (medium water and low light) resulted in a growth decrease (0.44, 0.04) and HS (high water and low light) increased the mean growth by 0.71.

Table 4: Growth means for each treatment regardless of species, for the water and low light experiment. L = Low water, M = medium water, H = high water, S = low light, C = full ambient light.

	Treatment	**Area change (cm^2)**	**Stem count change**	**Proportionate change**
Water	L	-0.73	0.00	-0.25
	M	0.09	0.00	-0.06
	H	0.05	0.00	0.50
Light	S	-0.19	0.00	-0.09
	C	-0.20	0.00	0.20
Interactions	LS	-0.67	0.00	-0.44
	MS	0.12	0.00	-0.04
	HS	0.03	0.00	0.28
	LC	-0.80	0.00	-0.06
	MC	0.05	0.00	-0.08
	HC	0.06	0.00	0.71
Grand Mean		-0.20	0.00	0.06

Gunnera dentata tended to decrease in size or die when subjected to a low water table (Figure 5). The only treatments that caused an increase in plant size for *Gunnera dentata* involved the medium water table, for both full light and low light, with an average increase of approximately 0.6cm^2 and the high water table with low light. *Isolepis basilaris* decreased in size under the low water treatment, and had the most significant increases in size in both the other full light treatments from 11 to 15 stems (Figure 5). *Isolepis cernua* decreased in stem number for all treatments bar HF, where there was a slight stem count increase. *Lilaeopsis orbicularis* died under low water table conditions as did *Limosella lineata.* However for *Limosella lineata* the greatest average size increase was seen in the MF treatment. *Ranunculus acaulis* increased in surface area from under the high water and low light treatment (Figure 5) compared to a drop when under the HF (high water and full light) treatment however this was a small difference. The average surface area decreased for *Selliera radicans* under all treatments bar HF, where there was a slight increase in size. *Selliera rotundifolia* had a general upward trend of area increase across all treatments.

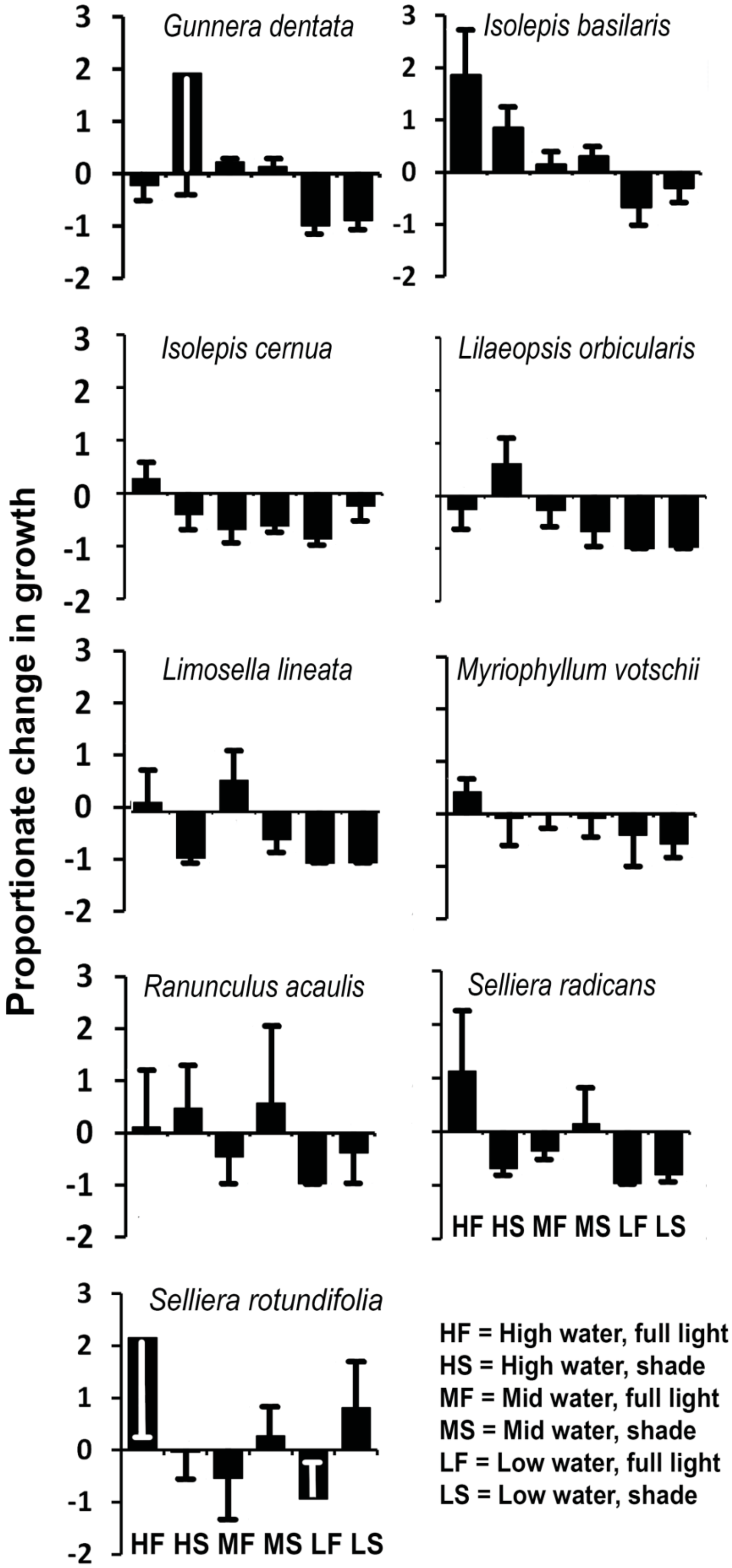

Figure 5: Proportionate change in surface area for each species. LS = low water with low light, LF = low water with full light, MS = medium water with low light, MF = medium water with full light, HS = high water with low light, HF = high water with full light.

Table 5: Growth means for each treatment regardless of species for the tamping experiment

	Treatment	**Area change (cm^2)**	**Proportionate change**
Tamping	T	-0.99	-0.28
	O	-0.42	-0.57

Lastly the Tamping experiment was seen to have significant results for area differences for species only (no *Isolepis* species were used in this experiment). No significant treatment effects were seen (Table 1).

The tamping experiment resulted in a proportionate decrease across all species regardless of treatment, excluding *Limosella lineata,* of 0.02 (Table 2). All *Gunnera dentata* died regardless of treatment by the end of the experimental period. The tamping treatment resulted in a greater area decrease than the no tamping treatment (0.99 to 0.42); however the difference was non-significant.

Selliera radicans, Ranunculus acaulis and *Limosella lineata* had a mean increase in growth when under the tamping treatment, with *Selliera* increasing the most by approximately 0.7cm^2. *Selliera rotundifolia, Myriophyllum votschii* and *Lilaeopsis orbicularis* all decreased in growth throughout the experimental process, regardless of treatment (Figure 6).

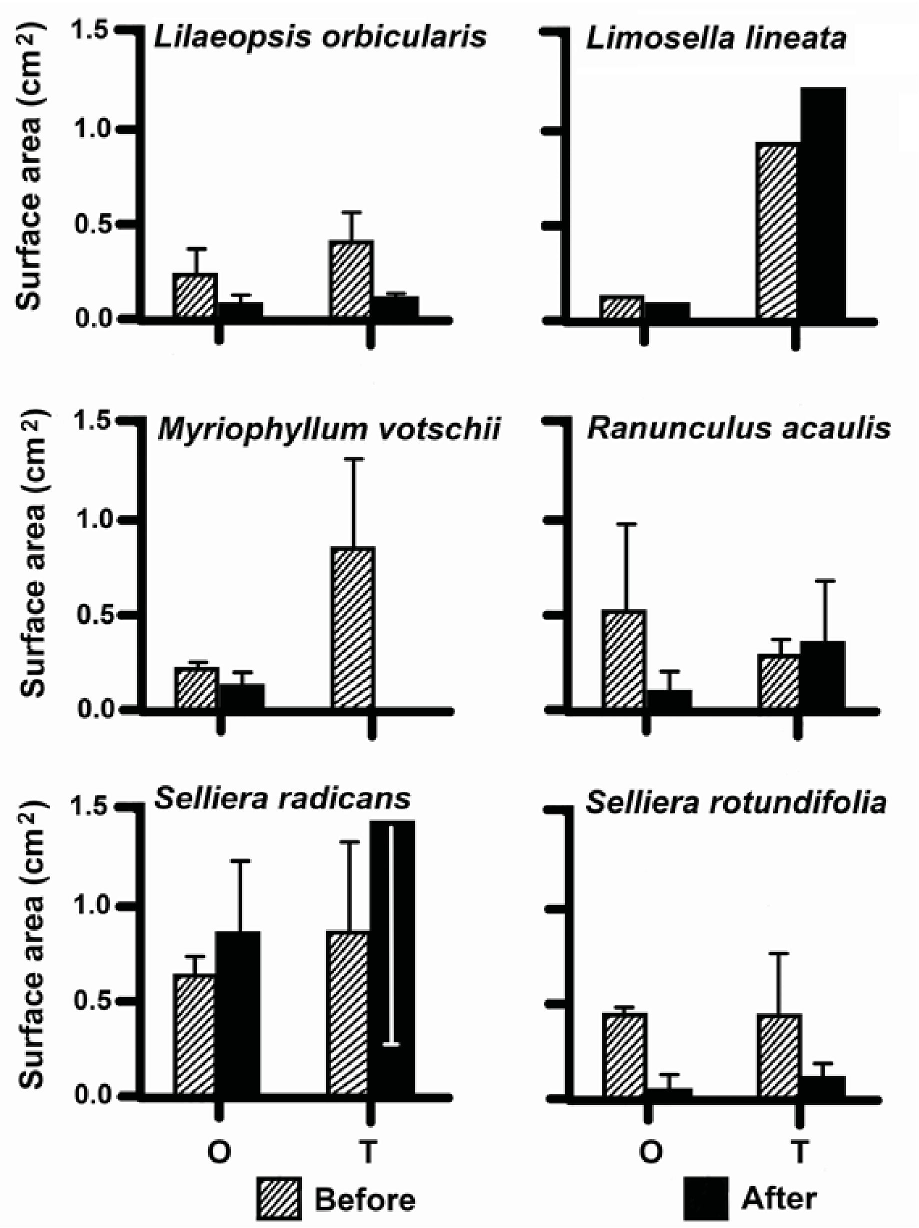

Figure 6: The surface area of each species used in the tamping experiment. All *Gunnera dentata* died regardless of treatment, so results are not graphed. T = Tamping, O = no tamping.

Discussion

These experiments aimed to test which environmental factors influence the growth of ephemeral wetland species: *Gunnera dentata, Limosella lineata, Lilaeopsis orbicularis, Selliera radicans, Selliera rotundifolia, Ranunculus acaulis, Isolepis basilaris, Isolepis cernua,* and *Myriophyllum votschii.* Turf species are known to withstand differing levels of burial and waterlogging in their environments (Sykes & Wilson, 1990) although no authors have tested these species. Here I expanded my experiments to assess the influence of light environment on differing water table heights. The assumption was that when potentially larger plants move into these dune slacks, they are associated with a drop in water table, and the turf species would then be competing for light, in an increasingly dry environment. Later-successional species move in as the wetlands infill with sand. I also looked at burial, tamping and nutrients.

What are the effects of a changing water table?

Water regime can be defined as a changing depth to water over time, the term encompassing the duration, frequency and timing of water events such as inundation (Web et al., 2006). Webb et al. (2006) found that long periods of inundation produce species' assemblages which are low in species' abundance and richness. The inundation period can determine which species will remain as it stimulates germination of some species while supressing others (Webb et al., 2006). In my experiment tolerance of high levels of water logging was seen in *Isolepis species,* Selliera *species, Gunnera dentata, Myriophyllum votschii* and *Ranunculus acaulis* (Figure 5). They had an increase in growth when under high water levels, with full light. This situation is typical of young wetlands so these species may be adapted to early successional wetlands. However *Ranunculus acaulis* had a higher mean increase in growth when under the low light, high water treatment, suggesting that this species is adapted to some levels of light competition, but still needs a high water table*,* i.e. is transitional. *Myriophyllum votschii,* the most aquatic of all these turf species, increased in size when under the high water table treatment regardless of light levels, suggesting that it is tolerant of waterlogging conditions. However the experimental treatments may have been too harsh and plants may have had bigger growth changes simply due to etiolation.

Waterlogging induces anoxia and interrelated chemical and biological changes to the plant substrate, e.g. respiration at low oxygen levels may result in X-OH accumulation in plant tissues, and a low energy yield and a high cost to detoxify tissues (Schat, 1984). Anoxia is one of the consequences of waterlogging or submergence in plants; however some wetland plants have certain levels of tolerance to this condition (Gibbs & Greenway, 2003), with either morphological or metabolic adaptations (Etherington, 1982). The medium and high levels of water logging resulted in an average decrease in plant size regardless of light levels (Table 2) suggesting that they must have suffered some effects of anoxia. Wetland communities can tolerate moderate levels of disturbance; however periods of submergence are quite damaging (Harwell & Havens, 2003), as the above results show.

How do these species respond to successional changes?

When the ephemeral wetlands start to dry and gradually infill with sand *Carex pumila* becomes dominant and is seen to form a band around the depressions and to collect sand forming a low dune surrounding the slack (Johnson & Rogers, 2003). This allows marram or rush species to eventually establish within these areas (Esler, 1970). After long periods of openness the turf vegetation can give way to rushland dominated by *Apodasmis similis* (Johnson & Rogers, 2003). Nearly all pioneer plants disappear from the dune slacks as the areas become shaded, and dry (Esler, 1969). Thus suggests the ephemeral wetland species are not well adapted to competing for light, as happens when taller species invade. The invasion of larger species and the lowering of the surface water table is an interaction that is not well suited to the ephemeral wetland turf species.

How do turf species respond to sand accretion and nutrient addition?

The formation of dunes involves both sand accretion and erosion. As sand mobility is rarely measured, little is known about how much sand can move in one event (Maun, 1998). The rate at which sand is blown into plants’ environments depends on many different factors: wind speed and direction, humidity, and sand moisture along with the location and aspect of the dunes (Maun, 1998). Large sand movement events are often caused by extreme seasonal or storm events (Maun, 1998).

The deposition of windblown sand causes changes in physical factors for the plants such as moisture, nutrients, access to the water table, temperature, soil aeration and pH levels as well as changing the micro-environment of the plant itself (Maun, 1998). For my experiment the plants were buried with sand from the sites from which they were found, and either had nutrients added or not. The addition of nutrients to the experimental plants, tended to increase the growth regardless of burial depth. However the nutrient levels added were equivalent to normal pasture situations and were probably much richer than for wind blown sand.

The addition of windblown sand will bring with it some amounts of nutrients to the experimental plants, however nutrient-poor sand will result in a decrease in plant growth.

In the United Kingdom, wetlands experience burial events annually (Walker, 1970). This can also be seen in New Zealand, as our dunes are more active than those in the UK. Walker (1970) showed that dune basins (or dune slacks) fill gradually with around 3-6mm of sand per year, and the species that inhabit these areas are capable of withstanding accumulations to this level. Due to land use change and human impacts these levels have risen and plants are not capable of surviving larger sand accumulation events (Maun, 1998). This is thought to be the same for ephemeral dune slack species in New Zealand. Few suitable sites were seen throughout New Zealand (a national survey was conducted to determine these species distribution throughout New Zealand). Ideally shaped sites were often found colonised by these specialist turf species, and remained as bare sand or were colonised by larger sand-accumulating species.

The burial and nutrient experiment showed a greater overall increase in proportionate growth when plants were buried compared to unburied. This suggests dune slack species have adapted to burial, but the addition of nutrients produced 3X greater growth rates compared to buried alone. This was also found by Singers (1997). The species that grew the most when buried was *Selliera rotundifolia,* suggesting that this turf species has a higher tolerance for burial, especially when liquid fertilizer is added, another odd response of this species which also is widespread within the Manawatu dunes.

Fertilization experiments have shown that nitrogen is a limiting factor in dry dune soils (Lammerts & Grootjans, 1997), little is known about nutrient limitation in wet dune slacks. 20ml of Peters all-rounder nutrient solution showed a significant positive effect, on the growth of these turf species, especially when combined with the burial treatment.

In natural dune slacks the nutrient status is controlled by the water table (Lammerts & Grootjans, 1997). The sparse growth of turf vegetation in dune slacks is due to limiting nutrient levels, especially nitrogen and phosphorus (Willis, 1963). My results suggest that fertilizing the dune slacks would increase the growth, especially the addition of nutrients when plants are under burial stress. However, there is little to no data on the nutrient levels of New Zealand's dune slacks and no clear trends in vegetation growth to macronutrient addition were seen in the Braunton Burrows' greenhouse experiment, which assessed the effects of nutrient addition on European dune slacks (Willis, 1963). Nutrient leakage from nearby pastoral land may positively affect the growth of these turf species. This was seen in the focal turf species in a cow paddock in Great Barrier Island, where the vegetation height increased from approximately 2-3cm tall to 5-7cm when growing in a cow pasture (Chapter 2). Further experiments are needed to assess the nutrient levels of sand from the foredunes, and of sand within the slacks themselves to assess the levels of nutrients being bought into a site with windblown sand.

Influence of disturbance effects?

Tamping was assessed to gauge the effects of human disturbance, such as vehicle damage, foot traffic and grazing on these turf species. All 6 turf species used in this experiment grew larger when there was no tamping. Though non-significant *Selliera radicans* and *Gunnera dentata* in particular performed very poorly when the tamping treatment was used and all *Gunnera dentata* plants died.

Conclusions

Ephemeral dune slack turf species were subjected to differing water table levels, light levels as well as constant burial and environmental stress (Sykes & Wilson, 1991). During succession larger species invade the dune slacks as the surface gets further from the water table, and the light levels available to turf species decrease.

Wetlands are in general poorly understood in New Zealand (Johnson & Rogers, 2003). Since dune slacks are temporary wetlands, most dune slack species are adapted to both wet and dry conditions. These turf species are scattered and variable in the nature of their habitats (Johnson & Rogers, 2003). Large losses of both dune slack wetlands and their turf ecosystems have occurred due to the agricultural conversion of New Zealand's lowlands (Johnson & Rogers, 2003). Ephemeral wetlands are important principal habitats for these turf species and contain a high proportion of threatened plants (Johnson & Rogers, 2003). Future work needs to focus on the environmental variates structuring these turf species' communities and where else these species occur. Are they just opportunists or due to chance introductions? How do these turf species disperse?

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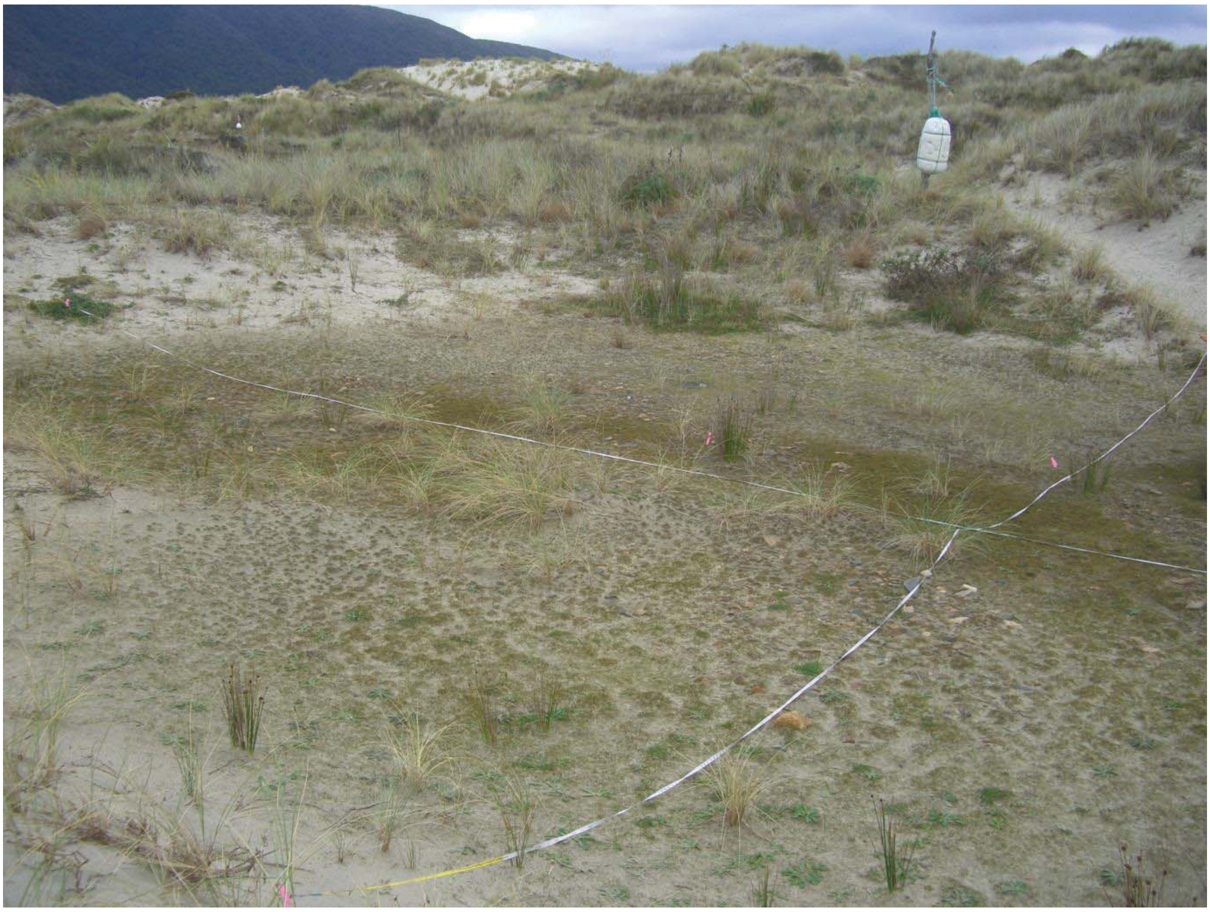
Chapter 5

General Discussion



Mason’s Bay ephemeral wetland in Stewart Island

Ephemeral wetlands and their turf species

New Zealand's dune areas are limited and slacks are a rare habitat type, holding many threatened species in need of conservation. Management of New Zealand's dune systems requires a full and recent inventory of the remaining areas, with a focus on the location of these ephemeral dune slacks.

Ephemeral dune slack wetlands are located within New Zealand's duneland; they are damp or wet depressions within the dunes themselves. Dune slack wetlands are transient in nature, and hold water in the wetter periods of the year (Singers, 1997), or they occur where the water table is close to the surface (Roxburg et al., 1994). The vegetation of the slack environment has been of interest to ecologist's worldwide (Roxburg et al., 1994). Despite the occurrence of dunefields throughout New Zealand, the distribution of New Zealand's dune slacks appears to be restricted to three main latitudinal zones, the northern North Island, the northern South Island and the southern South Island.

The flora of young deflation hollows is dependent on the on-going formation of new habitats (Singers, 1997). The endangered species within the dune slacks are principally rare as a result of habitat modification and loss (Singers, 1997). Within the New Zealand flora we can find a group of species which have adapted to inhabiting these dune slacks, and once they have established will spread rapidly (Singers, 1997). These species are turf species, meaning they are short in stature (under 5cm), low lying, form a dense carpet and are resistant to the many harsh environmental influences within these sites (Johnson, 2000).

Understanding ephemeral dune slack wetlands and their dynamics is a complicated topic, involving many different facets. Due to the ephemeral nature of these systems and the complexities of the dune movements themselves, these systems do not remain in the same locations for extended periods of time. Dunes themselves act as major obstacles to airflow, thus by disturbing the airflow they create these deflation hollows or dune slacks, which are then colonised by the turf species (Esler 1969).

In my research I surveyed a range of potential ephemeral wetland sites throughout New Zealand. Of the 33 sites found only 15 were surveyed, due to the others going through successional changes and/or having less than three turf species present. Sites were chosen with a minimum of 3 focal species in order to assess interactions between the species themselves, and sites with less than three species were excluded (although sometimes sampled as POI sites). This selection criterion does not bias the results as the aims of this work were to assess species' interactions with each other and their environment. These turf species which were previously thought to only occur in dune slacks, were also found in a cow paddock and on rocky cliff faces, in a golf course drain (G Rapson, personal communication) as well as growing up the sides of the dunes themselves. This suggests that these species have a wider habitat range than was previously thought.

Glasshouse experiments tested the tolerances of these species. The overall results of these experiments indicate that these turf species perform better growth wise under low water full light treatment, when compared to a low water low light treatment. This suggests that turf species are not adapted to competing for light, and need access to the water table. This agrees with Singers (1997) who stated that it was likely that these small statured turf species are being eliminated from sites due to the presence of larger rush and sedge species. However the addition of nutrients has a positive effect on the majority of the turf species growth, even when under burial stress. There is a lack of any references in the literature on the effects of nutrient addition on burial experiments.

On average across all sites, the majority of these turf species were located where the water table was only 30cm from the surface. The turf species all responded to different environmental variables. With the addition of nutrients to the majority of these species resulted in an increase in growth, this was seen experimentally and in the field. The addition of nutrients appears to allow these species to adapt to partial levels of burial, as was seen in the majority of these turf species.

The previous range of *Gunnera dentata* was thought to be throughout most of the West Coast of New Zealand (de Lange et al., 2012). Interestingly the results of my national distribution survey suggest that it has a much wider distribution as it was found all through sites in the south of the South Island as well as in Patea, Taranaki. *Gunnera dentata* had a growth increase when buried with the addition of nutrients, compared to the unburied treatments where it died suggesting an adaptation to burial, which is odd for such a prostrate species. *Gunnera dentata* was one of the few species to increase in growth when under the low light treatment. This species appears adapted to a medium water table, as was seen in field surveys with this species found growing in the edges of the wetland sites, which are the slightly drier habitats. This shows that this species has adapted to some level of light competition. This could be due to its position within the wetland itself, as being near the edge of the wetland may increase its chances of interacting with larger macrophytic species; this can be seen by its position values with a range of 10-35% away from the centre of the wetland (Chapter 3).

Isolepis basilaris is a nationally vulnerable species, classified as sparse and range restricted (de Lange et al., 2012). It was found in 18 of the 21 sites throughout New Zealand, suggesting it is not as rare as previously thought. Both *Isolepis cernua* and *Isolepis basilaris* were found to have greater leaf lengths (nearly double the average) when in Awana, which was located in a cow paddock. This implies that nutrient addition results in greater growth. This was confirmed in the burial and nutrient experiment for *Isolepis basilaris,* as nutrient addition resulted in more growth. *Isolepis basilaris* seems to have its own habitat and is not close in ordinational space to any other turf species; this could be one reason for its rarity. However *Isolepis cernua,* a common turf species, responded negatively to the addition of nutrients under experimental conditions. Both *Isolepis* species responded positively to a high water table and full light, suggesting they have not adapted to co-exist with larger species or to survive moisture deficits. These two close relatives responded negatively to vegetation height, preferring a habitat with a low maximum vegetation height and a low total species number.

Limosella lineata is distributed throughout New Zealand and its offshore islands. It appears to respond well to nutrient addition as an increase in leaf length is seen when comparing those of Awana to the average across all the surveyed sites. *Limosella lineata* died under the low water table treatments and increased in size in only the medium water table with full light (i.e. appears a pioneer species of open ground). This was also one of the few species found to respond positively to tamping. *Limosella lineata* also appears to have its own habitat range, as it was not found to co-occur with any other turf species. Esler (1969) believed both *Limosella lineata* and *Myriophyllum votschii* to be early colonizers of the wet dune slacks, and subsequent to their invasion of new habitats other turf species ‘move in’ which my results support.

Another species confirmed to be well distributed throughout New Zealand is *Lilaeopsis orbicularis.* On average it has leaf lengths of 3cm and when found in a high nutrient site (Awana) the leaf length increased to an average of 5cm. *Lilaeopsis orbicularis* was found to increase in plant size regardless of treatment in the burial and nutrient experiment but these were only small changes, and this species did poorly under the water table experiment, with all treatments resulting in a size decrease. Both treatments in the tamping experiment resulted in a plant size decrease, implying the glasshouse conditions were not correct for this species. The temperature was possibly too high and little air movement (evaporative cooling) was occurring in the glasshouse compared to within the dunes. *Lilaeopsis orbicularis* and *Selliera rotundifolia* not only occur together spatially but also commonly share the same microsite.

Myriophyllum votschii is commonly found throughout New Zealand’s wetter areas. It responded with a growth increase under the burial treatment, though was not responsive to nutrients. This species prefers a high water table with full light and died under the tamping treatment, confirming its status as a pioneer species, and indeed the genus is aquatic.

Eleocharis neozelandica is a nationally declining species (de Lange et al., 2012). It is endemic to the North Island and Farewell Spit, and its distribution was found to be as such, having died out in the Manawatu (Murphy; pers. obs.). *Eleocharis neozelandica* was not used in experimentation due to its rarity. This species was found to only occur in sites with a low total species number, as was *Myriophyllum votschii* so these species were found to co-occur with each other. Their occurrence is also correlated with a high native: exotic ratio, preferring sites with fewer exotic species present in a site.

Selliera radicans is distributed throughout New Zealand and offshore islands, unlike its close relative *Selliera rotundifolia* which has a distribution limited to the Manawatu coast of the North Island. However, these two species do not co-occur together. Both species responded well to nutrient addition. Both species are affected by their maximum vegetation height, less than 5cm tall, suggesting poor competitive ability. However they differed in their responses to the water table experiment, with the greatest growth seen for *Selliera rotundifolia* in the low water treatments, although this was a very small increase, compared to *Selliera radicans* with a growth increase seen in the high water table with full light treatment. It occupies a greater range of habitats at Manawatu (Murphy, pers. obs.) and appears highly adaptable in my experiments. It may be excluding *Selliera radicans,* by competitive interactions though intermediate forms are known.

Ranunculus acaulis is indigenous to New Zealand. It is found to commonly occur in wetland sites with *Selliera rotundifolia, Lilaeopsis orbicularis* and *Gunnera dentata* suggesting it shares similar environmental preferences with these species. This species responded with the greatest growth increase under the high water table and full light treatment, with plants doing poorly under low water table treatments. However it appears to have a broad range of tolerances.

Conservation implications

In 1908 Cockayne (1911) estimated the total area of active duneland to be approximately 128 740ha and 118 900ha was located in the North Island with the remaining 9840ha in the South Island and Stewart Island. The basis of these estimates were never explained; however he mentioned that this estimate did include the inter-dune wetlands (dune slacks). His estimates were again repeated in 1985, the total being 127 000ha with 117 300ha in the North and only 9700ha in the South and Stewart island (Hilton et al., 2000). The total areas of active dune land at this period of time were estimated at 52000ha and 40 000ha of back dune, which was dominated by a mixture of lupins, shrub and marram grass (Hilton et al., 2000). Which implies there were lots of sites (in the past) for ephemeral wetlands to occur, and a specialist flora would be expected.

Causes of duneland decline are agricultural development, uncontrolled grazing and waste disposal (Hilton et al., 2000). Due to water tables being lowered by extraction for irrigation for farming, the slack water table has been declining leading to a drying out of habitats, thus changing the vegetation type present and removing habitats for the small turf species (Grootjans et al., 2004). The exploitation of dune water has led to a large-scale lowering of the slacks' water tables (Grootjans et al., 2004). Dune slacks with a lower water table tend to go through successional changes and end up as rush lands or scrub lands thus losing the threatened turf species. My study shows that these turf species are poor competitors; they are also relatively intolerant of low light levels and lowered water tables. Ephemeral dune slack wetlands are in decline, though networks of small wetlands are critical for safe-guarding rare species (Richardson et al., 2015).

Restoration options

Restoration projects are based on the historical features of the landscape and aim to restore wetland habitat by reversing negative impacts on the system (de Lange et al., 2012). This can be done by re-wetting the slacks, therefore re-establishing the hydrological regime (Martinez et al., 2013). Many restoration projects have started in the last few years to restore European dune slack biodiversity (Grootjans et al., 2004). Mowing and/or grazing of the dune slack areas restores overgrown and invaded dune slacks and allows the pioneer species to re-establish and once again dominate the slack (Grootjans et al., 2004). This technique removes the competition for light which has been seen to have a negative effect on turves' growth. Regular maintenance is often required such as continual mowing or grazing when other species invade (Martinez et al., 2013). However if dune slacks are going through successional changes, and the problem is infilling of the slacks then mowing is not enough to restore the wetland as a turf habitat. Excavation possibilities need to be assessed if the wetland holds threatened turf species.

A full classification of dune types and systems is needed, as well as an inventory of different habitats within the dune lands and their associated species, to assess each sites representativeness and value as an area of conservation (Hilton et al., 2000). This was attempted here, although more work needs to be done on finding the other non-dune habitats of these turf species. Future work is needed on the ability of these turves to survive complete burial, and testing should be with actual nutrient addition that comes from the fresh foredune sand which buries these species. The impact of salt spray and differing salinity levels on these turf species should also be assessed. Work is needed on how these species disperse to new wetland sites: do they persist in the seed bank or are they wind dispersed? Or are these turf species simply occurring together due to chance introductions, expressed as lack of strong patterning between this group of species, such as I observed. This is important in order to conserve the threatened turf species. Finally how old are these ephemeral wetland sites and how long do they remain a habitat for turf species, before infilling and drying out? These are all questions which need to be answered in order to gain an understanding of these species themselves and the wetland system they inhabit.

Are these ephemeral dune slack wetlands worth conserving or are they just products of an anthropogenic system? They contain rare and threatened turf species, and appear to be one of the few habitats in which these species can survive. Further work is needed on what other habitats these turf species inhabit. Ephemeral wetlands are a very broad ranging habitat type and these turf species could occur in other ephemeral wetland types. The turf species themselves are dispersing to new habitats, large distances away from each other, suggesting they have a range of dispersal abilities. Future work should focus on how these turf species can disperse such large distances, i.e. wind, animals, insect. Ephemeral dune slack wetlands are a distinct environment, containing a suite of unique species, this habitat and its inhabitants should be conserved for future generations and to further discover the role of the turf species within these sites

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Appendix 1: Full Species list for each site surveyed

Location	Pouto	Awana	Whatipu POI	Kare	Patea	Sextons	Foxton	Spit 1	Spit 2	Spit 3	Om	Wa 1	Wa 2	Wai POI	Ste 1	Ste 2	Ste 3	Ste 1 POI	Ste 2 POI	Ste 3 POI	Ste 4 POI
#Q	27	20	4	48	35	88	57	39	38	40	22	19	41	2	26	29	35	2	2	2	2
Eleocharis neozelandica (Ele neo)	18	0	0	0	10	1	0	28	33	35	0	0	0	2	0	0	0	2	2	2	2
Gunnera dentata (Gun den)	0	0	4	0	6	0	0	0	0	0	11	16	27	0	1	17	2	2	2	2	2
Isolepis basilaris (Iso bas)	25	19	0	46	22	62	50	30	33	38	0	0	0	2	6	8	1	2	0	2	0
Isolepis cernua (Iso cer)	1	8	4	4	0	81	11	0	0	0	17	10	27	0	13	18	33	0	2	0	2
Lilaeopsis orbicularis (Lil orb)	10	11	0	7	0	86	2	0	0	0	0	8	8	0	0	0	0	0	0	0	0
Limosella lineata (lim lin)	11	19	0	0	0	0	0	15	0	7	0	0	0	0	20	1	28	0	0	0	0
Myriophyllum votschii (Myr vot)	11	0	0	0	0	30	0	32	18	27	13	0	13	2	0	0	0	2	0	0	2
Ranunculus acaulis (Ran aca)	0	0	0	0	1	0	17	0	0	0	0	15	15	0	1	0	11	0	0	2	0
Selliera rotundifolia (sel rot)	0	0	0	0	0	86	47	0	0	0	0	0	0	2	0	0	0	0	2	0	0
Selliera radicans (sel rad)	0	0	0	15	34	0	0	0	9	13	13	15	28	2	0	0	0	2	0	0	0
Ammophila arenaria (amm are)	11	0	4	6	2	60	15	7	6	7	0	4	4	0	8	10	5	0	0	0	0
Apodasmia similis (Apo sim)	0	0	0	1	0	0	0	0	1	2	1	0	1	0	1	5	1	0	0	0	0
Apium prostratum (Api pro)	0	0	0	0	0	0	0	0	0	0	4	0	4	0	0	0	0	0	0	0	2
Cenchrus clathratus (Cen cla)	0	11	0	0	0	5	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Craspedia robusta var.	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	4	9	0	0	0	0

pedicellata (Cra rob var. ped)																					
Chionochloa rigida (Chi rig)	0	0	0	0	0	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	2
Coprosma acerosa (Cop ace)	0	0	0	0	0	0	0	0	1	2	3	0	3	0	3	11	9	0	0	0	0
Euphrasia revolute (Eup rev)	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	0	0	0	2	0	0
Euphrasia aff. Reoluta (Eup aff. rev)	0	0	0	0	0	0	0	0	0	0	1	0	1	2	0	0	0	2	0	0	0
Ficinia nodosa (Fic nod)	0	2	0	0	5	13	10	0	3	1	1	5	6	0	2	9	3	0	0	0	0
Pseudognaphalium luteoalbum (Gna lut)	0	0	0	0	0	5	19	0	0	0	2	0	2	2	0	2	8	2	0	0	0
Hypochaeris radicata (Hyp rad)	0	0	0	4	12	8	20	0	2	1	13	1	14	0	0	0	0	0	0	0	0
Holcus lanatus (Hol lan)	0	0	0	0	5	1	4	0	0	2	2	0	2	0	0	0	4	0	0	0	0
Juncus australis (Jun aus)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juncus aff. caespiticius (Jun aff. cae)	0	0	0	0	0	0	0	0	0	0	11	0	11	0	0	1	1	0	0	0	0
Juncus bufonius (Jun buf)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
Juncus novaezelandae (Jun nov)	0	0	0	0	0	0	23	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Leodonton taraxacoides (Leo tar)	0	0	0	0	0	0	0	0	0	0	3	15	18	0	0	2	4	0	0	0	0
Lobelia anceps (Lob anc)	0	0	4	0	0	0	17	0	0	0	0	0	0	2	0	22	0	2	0	0	0
Lupinus arboreis (Lup arb)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
nostoc	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plantago major (Pla maj)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plantago triandra (Pla tri)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	19	0	0	0	0

Pilosella officinarum (Pil off)	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Pimelea lyalii (Pim lya)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Rannunculus aff. glabrifolius (Ran aff. gla)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex acetosa (Rum ace)	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	0	0	0
Rytidiosperma setifolium (Ryt set)	0	0	0	0	0	4	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Samolus repens (Sam rep)	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sarcocornia quinqueflora (Sar qui)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trifolium pratense (Tri pra)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	7	0	0	0	14
Trifolium repens (Tri rep)	0	0	0	0	4	1	1	0	0	0	1	1	2	0	0	0	0	0	0	12	0
Wahlenbergia albomarginata (Wah alb)	0	0	0	0	0	0	0	0	3	3	0	0	0	0	0	0	0	0	12	0	0
Zoysia minima (Zoy min)	0	0	20	0	21	0	0	0	0	0	0	0	0	16	0	0	0	16	0	0	0

Appendix 2: Glossary

Dune slack: The hollow between two dunes.

Dune slack wetland: The hollow between two dunes that holds water at some stage of the year.

Ephemeral: Internationally ephemeral is defined as seasonal, meaning vernal, however in the context of this thesis it means transitory (Murphy, et al., in press).

Jaccard co-efficient: The number of shared species/total species.

Microtopography: Small scale variations in ground surface.

NMDS: Non metric multidimensional scaling.

Ordisurf: A vegan procedure in R which fits smooth surfaces to the variables modelled.

POI: Point of interest sites, were sites that were NOT defined as typical ephemeral dune wetlands, as in not conforming to the standards of being dish shaped, with standing water at some stage of the year.

Rare flora: Flora that is scarce, infrequently encountered or uncommon for instance the rare flora of these dune wetlands.

Tamping: to pack down into something, in this instance to add weight to the surface of a plant.

Turf species: Commonly under 5cm tall, consisting mainly of herbaceous, vascular plants, which are prostrate and tightly interlaced, and form a dense group (Johnson & Rogers, 2003).

Water table: The height of the water with respect to the ground surface.