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**Do plant-plant interactions drive New Zealand's gravel beach plant
community structure?**

A thesis
submitted in partial fulfilment
of the requirements for the Degree of
Master of Science

at
Lincoln University
by
Elise Aimee Arnst

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Abstract of a thesis submitted in partial fulfilment of the requirements for the Degree of Master of Science.

Do plant-plant interactions drive New Zealand's gravel beach plant community structure?

by

Elise Aimee Arnst

Gravel beaches are a naturally rare ecosystem in New Zealand. Often poorly understood and managed, they also support a number of rare and threatened plant species. Extreme environmental conditions and high levels of disturbance combined with typically close proximity to highly modified landscapes make this a challenging environment for species survival. This study aims to understand some of the mechanisms structuring gravel beach plant communities. A survey of the plant community on the gravel beach at Birdlings Flat, Canterbury was carried out to identify plant co-occurrence patterns, the impact of invasion on these co-occurrence patterns and the spatial association between native and exotic species. This observational study demonstrated that species were segregated more than expected at random, indicating that spatial heterogeneity and competition are likely to be structuring the community. To investigate the factors influencing the recruitment of native woody shrub seedlings, in particular the role of facilitation, two experiments were established. The first experiment at Birdlings Flat, Canterbury involved planting native woody seedlings to assess the potential role of established native shrubs in facilitating seedling recruitment and whether either nutrient or water limitation had a significant impact on this interaction. The second planting experiment carried out at Tangoio, Napier was established to assess whether an exotic herb facilitates the recruitment of native plant seedlings. Environmental factors, specifically substrate composition, nutrient availability and distance from the sea, influence native seedling recruitment. Both experiments showed that facilitation is not actively promoting native woody seedling recruitment. The findings of this study contribute to the understanding of the importance of plant-plant interactions in highly stressed ecosystems and provide a basis for management decisions.

Keywords: Plant-plant interactions, invasion, competition, facilitation, community assembly, stress gradient hypothesis, gravel beaches, New Zealand.

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Chapter 1

Introduction

1.1 Theories of plant community structure: From Clements and Gleason to neutral theory and assembly rules

A plant community is a collection of various plant populations co-existing in a defined area that have the potential to interact (Townsend et al. 2003, Leibold et al. 2004). Describing the patterns within communities is important to allow the processes and mechanisms structuring the community to be understood. A number of biotic and abiotic factors determine community structure (Whittaker and Levin 1977, Micheli et al. 1999) including habitat, species interactions, environmental factors, e.g., disturbance (Noy-Meir and van der Maarel 1987) and chance events (or stochasticity) such as dispersal (Tilman 2004). These biotic and abiotic factors change over time and space, influencing factors such as species distributions, abundance and diversity (Menge and Sutherland 1987). Communities function in an interactive manner, and often it is difficult to determine which individual factor within a community has the greatest impact on its structure (Chave et al. 2002).

The theory of community structure has been well developed over the last century. Early theorists such as Clements (1916) saw the community as a complex organism and that the structure of communities is not random. Gleason (1917) and Watt (1964) saw habitat and environment as the key determining factors of community structure. It was thought that the structure of the community is directly influenced by the characteristics of the individuals within that community, and therefore any factors impacting on an individual would express themselves at the larger scale (Gleason 1917). A number of theories have been developed to explain variation in community structure. These include Grime's CSR theory, neutral, niche, metacommunity and patch theories, the resource-ratio hypothesis and assembly rules.

An important theory describing some of the processes which structure communities is Grime's (1979) CSR theory. Plants require resources and will interact with each other for access to those resources, using one of three key strategies. Competitive species (C) will grow rapidly and acquire resources, limiting the availability of those resources for other individuals. This strategy is often seen in low stress-low disturbance environments. Stress tolerant species (S) will grow slowly utilising limited resources. Ruderal species (R) are short-lived fast-growing species with high reproductive effort; they are often successful in highly disturbed environments.

The neutral and niche theories of community ecology are important models for describing community structure. Neutral theory assumes that all species are competitively equal (Chave 2004), and that space is the only limiting factor (Chase 2005). Niche theory takes into account that different species will react uniquely to a set of circumstances resulting in the composition of a population changing over time as a direct result of those circumstances (Chave et al. 2002). Niche theory states some species will hold a competitive advantage over others, resulting in competitive exclusion (Chave et al. 2002). Competition strongly encourages niche differentiation, which increases the number of possible coexisting species (Whittaker and Levin 1977, Tokeshi et al. 1993). Niche differentiation means that no single species is better off in all circumstances, leading to co-existence (Chave et al. 2002). As described by trade-off theory (Tilman 1985), niche differentiation is often a direct consequence of differing life history traits (Kneitel and Chase 2004). Organisms have a 'fundamental niche', which is the theoretical width of the niche it is possible for them to occupy without limitations, as determined by evolutionary processes (Tokeshi 1990, Townsend et al. 2003). In reality an organism does not occupy the entire fundamental niche; rather it exists within a 'realised niche' which is the actual part of the niche a species occupies in a given space at a point in time. The realised niche is maintained due to the effects of competition, facilitation and predation on the distribution of the species (Vandermeer 1972).

Community theory was further developed into metacommunity theory by combining both neutral and niche theories with metapopulation theory (Chase 2005). A metapopulation is a group of local populations which inhabit spatially distinct habitat patches and are linked by dispersal (Moilanen and Hanski 1998). A metacommunity is therefore a group of communities spatially connected by the dispersal of numerous interacting species (Leibold et al. 2004). Metacommunity theory helps to describe how space affects the structure of competitive communities (Pillai et al. 2010). There are four key processes in the metacommunity model, which are not always distinctly separated (Driscoll 2008). They are patch dynamics, species-sorting, mass effect, and neutral processes (Leibold et al. 2004). The patch dynamic approach is a continuation of Watt's (1947) patch theory involving the spatial division of a habitat into patches (Pickett 1985, Pillai et al. 2010). It assumes that dispersal is the limiting factor, and the species composition in identical patches is determined by a trade-off between dispersal ability and either competition or predation (Leibold et al. 2004, Driscoll 2008). The species-sorting approach is based on resource gradients and Tilman's (1985) resource ratio hypothesis. The species-sorting approach describes the effect abiotic factors have in influencing the spatial distribution of species. Local community composition will be influenced by resource gradients and patch differences, resulting in spatial niche separation (Leibold et al. 2004, Driscoll 2008). The mass-effect approach is based on migration; a species which is locally declining at a small scale can persist within a patch due to immigration of individuals from surrounding patches (Leibold et al.

2004, Driscoll 2008). Alternatively the competition-fecundity trade-off comes into play; an inferior competitor may survive due to a high reproductive rate (Orrock and Watling 2010). The neutral approach expands on neutral theory in that all species are considered to be competitively equal, and relative abundance occurs as a result of random interactions between species (Leibold et al. 2004).

Diamond's (1975) assembly rules describe non-random patterns of species associations based on competitive interactions (Weiher and Keddy 2001), determining whether species are likely to co-occur (Wallem et al. 2010). One of these rules is that some pairs of species, which are close competitors, will never co-exist, leading to checkerboard distributions (Gotelli and McCabe 2002, Ulrich and Gotelli 2012). A checkerboard distribution occurs when a given set of sites and species are combined in a matrix resulting in mutually exclusive species distributions (Stone and Roberts 1990). The initial assembly rules are encompassed in the general theory of community assembly which includes any filter on a regional species pool which defines local structure and composition (Holdaway and Sparrow 2006, HilleRisLambers et al. 2012). Two such concepts are limiting similarity, which assumes that plant-plant interactions tend to keep coexisting species from being too similar resulting in trait divergence and niche separation, and environmental filtering which assumes that species are present because they possess traits suited to the habitat (Pavoine et al. 2011, Maire et al. 2012).

Research in relation to assembly rules is often associated with the null model approach. Null models test how species are distributed within communities (Gotelli and Graves 1996) and are used to identify non-random patterns of species associations within a community by comparing observed data with randomised datasets (Götzenberger et al. 2012). Null models are named because they epitomize the null hypothesis; the initial premise is that there is no underlying structure or patterns in the community (Ulrich and Gotelli 2012). Initially null models were used to test the impact of interspecific competition on community assembly, based on assembly rules (Gotelli and Graves 1996, Gotelli and McCabe 2002), but they can also be used to test other ecological mechanisms such as facilitation (Gotelli 2001).

1.2 Non-random spatial patterns in plant communities

Spatial pattern in a plant community is defined as the predictability of the arrangement of plants in physical space (Dale 2000). Such patterns occur when the community is structured in a non-random manner (Law and Morton 1996). Different patterns occur at different spatial scales (Levin 1992, Leibold et al. 2004). Two common patterns in plant communities are species aggregation and the formation of gradients (Legendre and Fortin 1989).

Spatial pattern can be related to microhabitat and environmental factors, species traits or plant-plant interactions (Petit and Fried 2012); plant-plant interactions and environmental factors are particularly important at small spatial scales (HilleRisLambers et al. 2012). The ability of a given species to tolerate a particular physical environment means that a species can only occur when it is adapted to the specific environmental conditions (Sanders et al. 2007), resulting in certain species being more likely to be absent from some sites than others (Jabot et al. 2008). At a local scale some species exhibit a dormancy period during unfavourable conditions, and prolific growth and reproduction under good conditions (Kneitel and Chase 2004). Co-occurrence of species with similar habitat requirements or dispersal patterns can lead to clumped species distributions (Helmus et al. 2007). Spatial variation of resources means an individual species may be outcompeted in one patch, but be the superior competitor in another patch (Levin and Paine 1974). Species distribution is therefore related to environmental differences in a given patch (Watt 1947, Levin and Paine 1974, Whittaker and Levin 1977, Townsend et al. 2003). Although a species may be outcompeted at a small scale, it can still exist at a larger, regional scale (Kneitel and Chase 2004). A particular patch or microsite also may or may not be occupied at any given time (Whittaker and Levin 1977, Chave et al. 2002).

Observed patterns in species co-occurrences can be used to test if individuals or species within communities are being structured by an ecological process, or are simply randomly distributed (Connor and Simberloff 1979, Gotelli and Graves 1996). Competition and facilitation can influence patterns and spatial distributions of individuals within a community (Callaway 1995, Law and Morton 1996), thereby influencing community structure (Dale 2000, Gouhier et al. 2011). Species co-occurrence is often attributed to biotic interactions with species aggregation used to infer facilitation and segregation used to infer competition (Dullinger et al. 2007). Environmental heterogeneity and plant-plant interactions occur simultaneously and are confounding processes meaning that their effects cannot be distinguished by simple pattern analysis, and therefore experiments are necessary to infer mechanisms of plant coexistence (Callaway 1995, Helmus et al. 2007, Castanho et al. 2012).

1.3 The role of plant-plant interactions in structuring communities

Plant-plant interactions play an important role in structuring communities (Callaway and Walker 1997, Kikvidze et al. 2005, Brooker et al. 2008). Communities are structured by both negative and positive interactions, in particular competition, inhibition and facilitation (Callaway and Walker 1997). These interactions can impact on the survival, fecundity, growth and abundance of a species (Stachowicz 2001, Chave et al. 2002) through mechanisms such as crowding, shading, and zonation

(Hairston et al. 1960). The strength of the interactions can depend on the life-history stage of the individuals (Valiente-Banuet et al. 1991) or environmental factors (Bertness and Callaway 1994).

Competition is an interaction between individuals where both species are negatively affected. Inhibition occurs when one species has a negative impact on at least one other species, resulting in decreased fitness (Tilman 1987, Callaway and Walker 1997). Competition for limited resources is one of the key mechanisms influencing community structure (Whittaker 1965, Tilman 1985). A species' existence is determined by the number of individuals present in relation to the limiting resource (Watt 1947), resulting in the species with the least need for that limiting resource being the dominant competitor (Miller et al. 2005). The resources competed for and the intensity of competition will change over time and space (Tilman 1987). Resource competition for essential resources such as light, water or minerals is expressed in plant communities most often as spatial competition or density dependence (Hairston et al. 1960). Different species are sometimes limited by different factors, and therefore are only in direct competition with each other when they need the same limited resource (Hairston et al. 1960). The availability of limiting resources directly affects which species is dominant (Miller et al. 2005).

Differences in competitive advantage allow an equilibrium to be reached for more than one species, and therefore co-existence results (Whittaker and Levin 1977, Tilman 2004, Miller et al. 2005). The trade-off theory states that an individual has a high level of fitness under one set of environmental conditions, at the cost of being less fit for a different set of conditions (MacArthur and Levins 1964, Tilman 1990). Trade-offs allow species co-existence to occur at a range of spatial scales, and different traits are affected at different scales (Kneitel and Chase 2004). At a large scale, spatial heterogeneity also increases species richness by allowing a greater number of species to coexist than the number of limiting resources (Kneitel and Chase 2004). There is a trade-off between plant traits such as dispersal, growth or reproductive rate (including both survival and fecundity) and competitiveness; this trade-off determines the width of the realised niche a species occupies (Chave et al. 2002, Kneitel and Chase 2004). Each plant species is thought to be a superior competitor for a particular combination of limiting resources (Tilman 1985).

Facilitation is an interaction between individuals where at least one interacting species benefits in terms of increased fitness (Bruno et al. 2003, Cavieres and Badano 2009). Facilitation can involve protecting another individual from environmental conditions, herbivory, competition, or providing limiting resources e.g. nutrients (Callaway 1998, Bruno et al. 2003, Brooker et al. 2008). Facilitative relationships can benefit one species or multiple species, and can be mutualistic, commensalistic, mutually obligate or parasitic relationships (Pugnaire et al. 1996, Callaway 1998, Bruno and Bertness 2001).

Facilitation is particularly important in stressed environments and is likely to influence species diversity and abundances in these communities (Bertness and Callaway 1994). Facilitation often occurs in high stress conditions and in environments where consumer pressure is high, such as areas with high grazing pressure (Bertness and Callaway 1994), because neighbours buffer each other from the extremes (Pugnaire and Luque 2001). Stress intolerant species often benefit the most from facilitation (Michalet et al. 2006). Co-existence at small spatial scales often results from facilitation, where the presence of one species promotes the presence of another, which in some communities can lead to increased species richness at a larger spatial scale (Cavieres and Badano 2009). Facilitation can increase species diversity as a whole or increase the abundance of a poor competitor (Cavieres and Badano 2009).

Facilitation can occur through the phenomenon of nurse plants. Nurse plants are established individuals which facilitate the recruitment and growth of another species (Holmgren et al. 1997, Callaway 1998). Nurse plants can be facilitative generalists with non-specific mutualisms, or facilitative specialists providing biotic and/or abiotic benefits for only one species (Verdu and Valiente-Banuet 2008). In species-specific facilitation there are often positive associations between the adults of one species and the seedlings of another species (Callaway 1998). The adults provide facilitative effects through mechanisms such as increasing air humidity, preventing extreme temperature fluctuations, improving soil properties by accumulating nutrients and organic matter, and reducing the likelihood of herbivory and anthropogenic damage (Valiente-Banuet and Ezcurra 1991, Greenlee and Callaway 1996, Holmgren et al. 1997, Flores and Jurado 2003, King and Hobbs 2006, Butterfield et al. 2010). Facilitation by nurse plants can switch to inhibition once the seedling has established (Holmgren et al. 1997). For example, nurse plants can provide increased water and nutrient availability promoting seedling germination, but can limit the growth of those seedlings by shading (Holmgren et al. 1997, Rejmanek 2011).

Nurse plants promote species diversity in plant communities (Verdu and Valiente-Banuet 2008, Cavieres and Badano 2009). Although species diversity is not always higher under nurse plants than in the open, it is usually higher at the community scale because the different habitat types are suitable for species with different traits (Gigon and Leutert 1996, Cavieres and Badano 2009). In some communities, the vast majority of species require a facilitator for successful recruitment (Valiente-Banuet and Verdú 2007). The facilitator species provides a regeneration niche and is therefore an integral part of maintaining community diversity (Verdu and Valiente-Banuet 2008).

Indirect interactions occur when pair-wise interactions between species are altered by the interaction with an additional species, often changing either the strength or direction of the direct interaction (Levine 1999, Pages and Michalet 2003). Indirect interactions ultimately affect

community structure (Lortie et al. 2004), both negatively and positively (Wootton 1994). Understanding indirect impacts within a community is important because they can have wide-reaching implications for a number of species within the community, and therefore on the structure and diversity of the community (Strauss 1991, Wootton 1994, Callaway and Walker 1997).

Facilitation and competition are not mutually exclusive (Holmgren et al. 1997, Stachowicz 2001) and often occur at the same time, between the same species (Callaway 1995). An individual will benefit most when the positive effects of facilitation outweigh the negative effects of competition (Hay 1986, Cavieres and Badano 2009). Community richness and species fitness may be influenced by facilitation and competition (Michalet et al. 2006). Facilitation is thought to be more important in influencing community structure at levels of high stress or low levels of resources — although this may fail at extreme levels of stress, and competition is thought to be more important in areas with low stress and abundant resources (Bertness and Callaway 1994, Pugnaire and Luque 2001). This relationship is known as the Stress Gradient Hypothesis (Michalet et al. 2006, Brooker et al. 2008). Although the Stress Gradient Hypothesis suggests that there is a relationship between plant-plant interactions and environmental gradients (Bertness and Callaway 1994), this hypothesis needs to be more widely tested (Brooker et al. 2008) and it is still being refined (Michalet et al. 2013). Many tests of the Stress Gradient Hypothesis have been of single species or species pairs rather than at the community scale. This means that the shift in interaction patterns across species in relation to gradients has been relatively untested (Maestre et al. 2009).

1.4 The influence of exotic invaders on community structure

Invasion by exotic plants can influence plant community structure (Ehrenfeld 2010). Many species have been introduced to new localities as the result of an anthropogenic action, transporting them into a region where they would have otherwise been unable to colonise and establish (Richardson et al. 2000). If the introduced species can reproduce and maintain a population, it is referred to as 'naturalised' (Richardson et al. 2000, Rejmanek et al. 2005). Many species that naturalise do not have large negative effects on the native community (Levine et al. 2003). Propagule pressure, the physiological traits of the introduced species, and the invasibility of an environment determine a species ability to reproduce, spread and establish in a new location and therefore determine its invasiveness (Davis et al. 2000, Hellmann et al. 2011, Rejmanek 2011).

There are a number of contemporary ecological, environmental and economic problems that are the result of invading species (Pyšek and Pyšek 1995, Vitousek et al. 1997, Dukes and Mooney 2004). Exotic species invasion can affect biodiversity and is known to threaten native species globally

(D'Antonio and Vitousek 1992). These include impacts on populations of native species, for example by displacing them through competition, and by altering ecosystem level properties such as water availability, nutrient cycling and soil properties (D'Antonio and Vitousek 1992, Maron and Connors 1996).

Some exotic species can increase the diversity of the communities they invade by facilitating native species (Rodriguez 2006). Negative interactions between native and invading species are most likely to occur at a fine spatial scale, such as at the individual level, while positive interactions are more likely to occur at coarser spatial scales by interacting with environmental factors to favourably influence plant diversity and abundance (Meffin et al. 2010). In arid environments exotic species are more commonly found next to natives suggesting that the natives may be facilitating the exotics (Abella and Smith 2013). In contrast, early exotic arrivals can facilitate the establishment of additional exotic species, and in extreme cases this may result in an 'invasional meltdown' (Simberloff and Von Holle 1999).

1.5 Facilitation in conservation and restoration ecology

Plant conservation and habitat restoration provide the rationale for many contemporary ecological studies (Young et al. 2005). Facilitation theory can be applied advantageously as a management tool in restoration ecology (Gómez-Aparicio 2009, Markham et al. 2011) as a potential method in habitat restoration (Brooker et al. 2008), especially in highly degraded environments with high stress or extreme environmental conditions (Padilla and Pugnaire 2006). Nurse-plant interactions can be applied to habitat restoration schemes by using existing plants to alter unfavourable abiotic processes (King and Hobbs 2006), thereby facilitating the growth and survival of seedlings of desired species (Gomez-Aparicio et al. 2004). For example, Castro et al. (2002) planted *Pinus* seedlings under the shrub *Salvia lavandulifolia* to test whether *S. lavandulifolia* could serve as a nurse plant to restore the native *Pinus*-dominated community. After four years the seedlings planted under the shrubs showed significantly higher survival rates than those planted in the open, and did not exhibit any inhibition or competition from the shrubs (Castro et al. 2004). The facilitative mechanism was likely to be increased water availability as a result of the shade provided by the shrubs (Castro et al. 2002, Castro et al. 2004). The authors concluded that this is a viable restoration technique in arid ecosystems (Castro et al. 2004).

1.6 Gravel beaches

Gravel beaches are a naturally rare ecosystem in New Zealand; they also support a number of rare and threatened plant species (Wiser et al. 2010). The natural vegetation of gravel beaches is a mixture of coastal halophytes and woody and herbaceous mat plants (Cockayne 1928; Wiser et al. 2010). The vegetation appears to be aggregated suggesting that facilitative processes may be structuring the community (*pers. obs.*). The composition of substrate affects the growth and establishment of plants on gravel beaches (Fuller 1987, Randall et al. 1997). The spatially discrete nature of the ecosystem and high invasion levels makes this an ideal system to study the reasons for these spatial patterns and to determine the role of invasion and plant-plant interactions in the system (Wiser et al. 2010).

1.6.1 Native shrubs on gravel beaches

Native mat-forming shrubs are an iconic part of many New Zealand gravel beaches. Casual observations show that woody mat-forming plants may act in a facilitative role by providing shelter and ameliorating harsh conditions for herbaceous plants and other woody seedlings (*pers. obs.*). The importance of shrubs for maintaining either the diversity or function of the ecosystem is relatively unknown. Native lizards benefit from divaricating shrubs and vines present on gravel beaches. *Coprosma propinqua* A. Cunn, *Muehlenbeckia complexa* (A.Cunn.) Meisn. and *Melicytus alpinus* Kirk are all known to provide shelter and food in terms of fruit and by attracting invertebrates (Whitaker 1987, Lettink et al. 2008). Lizard species commonly disperse *Coprosma* and *Muehlenbeckia* seeds (Whitaker 1987, Wotton 2002), and these shrubs may have evolved to use lizards as dispersal mechanisms as the fruit are often difficult for birds to access (Whitaker 1987). There is also little known about the likelihood of the long-term survival of native shrubs and whether there are any factors that could be limiting their continued existence in this harsh environment.

1.6.2 Exotic plants on gravel beaches

High levels of disturbance combined with close proximity to highly modified landscapes has resulted in high levels of exotic plant invasion on some beaches, with the vegetation being about 50% exotic on average (Wiser et al. 2010). However, little is known about the impacts of invading exotic species and their interactions with native plants. Coastal vegetation is threatened by invading exotic species which have the ability to change nutrient availability or substrate composition (Pickart et al. 1998). Established exotic plants may play a facilitative role by adding organic matter, although they often

reach high levels of biomass which may inhibit the growth of native vegetation (Wiser et al. 2010). The distribution of exotic species is often related to propagule pressure, and the invasion of exotics into coastal areas in New Zealand has been shown to be greater when the sites are closer to settlements (Sullivan et al. 2005).

Two exotic species of interest on gravel beaches are *Gazania* Gaertn (Asteraceae) and *Lupinus arboreus* Sims. The exotic herbaceous perennial *Gazania* spp. are common on many gravel beaches in New Zealand (*pers. obs.*). There are 16 species of *Gazania* from southern Africa, and they are popular in horticulture worldwide (Howis et al. 2009). There are two naturalised species in New Zealand, *G. linearis* and *G. rigens* which both became naturalised in the 1940s (Garnock-Jones 1987); these species hybridise and hereafter they are referred to as *Gazania*. *Gazania* has a high sand trapping ability, and much of the litter is trapped in the plant rather than being blown away (Hesp and McLachlan 2000). *Gazania* were planted in New Zealand for dune stabilisation and 'beautification' (Merrett 2007). *Lupinus arboreus* (lupin) is an exotic nitrogen-fixing shrub (Sprent 1973) which was planted for sand dune stabilisation in New Zealand from the early 1900s (Gadgil and Ede 1998). Planting became common practice throughout the 1970s and 1980s (Sprent and Silvester 1973). Consequently lupin is now common on sand dunes throughout New Zealand (Gadgil and Ede 1998). In California invading lupin has altered soil chemical properties and enabled the invasion of exotic annual species (Pickart et al. 1998).

1.7 Aims and Objectives

The overall aim of this thesis was to explore some of the mechanisms which influence plant community structure on gravel beaches. To achieve this three studies were carried out.

1.7.1 Spatial patterns in Birdlings Flat plant communities

The aim of this observational study was to describe the gravel beach plant community at Birdlings Flat, and to describe the plant-plant interactions at a whole-community scale allowing processes to be inferred from the observed patterns (Maestre et al. 2009, López et al. 2013).

The objectives were to:

- describe spatial pattern in the plant community composition,
- determine which environmental factors are related to the community structure,
- investigate the relative roles of competition and facilitation in determining spatial patterns in community structure by:

- inferring the potential role of facilitation and competition in structuring the plant community by analysing patterns in species co-occurrence,
- testing whether species co-occurrence decreases along the environmental stress gradient that exists from the high tide mark moving inland inferring a decline in the relative importance of facilitation compared with competition,
- assess the short term change in species diversity by comparing my observational survey data to that collected by Wisser et al. (2010) in 2006.

1.7.2 Native facilitation experiment

The main objective of the native facilitation experiment was to investigate the factors influencing the recruitment of native seedlings, and in particular the role of facilitation. The facilitative effect of woody native shrubs, specifically their role as nurse plants, was examined through a planting experiment. In addition, the importance of two factors potentially limiting recruitment, water and nutrients, were tested.

1.7.3 Exotic facilitation experiment

The main objective of the exotic facilitation experiment was to test whether an exotic plant can be used to facilitate the recruitment of native seedlings in a coastal habitat. I tested whether the exotic species *Gazania* has an impact (positive or negative) on the growth and survival of planted native seedlings.

1.8 Hypotheses

1.8.1 Plant community structure at Birdlings Flat

1. Spatial pattern in plant community composition at Birdlings Flat is related to environmental variables (Kent 2011) including proximity to the sea, substrate particle size, depth to fine material, and proximity to gardens, which are a potential weed source (Carboni et al. 2011).
2. In the vegetated areas of the highest stress that are close to the sea, facilitation will be the dominant process in determining community structure. As the levels of stress decrease with increasing distance from the sea, inhibition and competition will become more important (Pugnaire and Luque 2001, Schöb et al. 2013b). If the Stress Gradient Hypothesis holds true, I would expect that the co-occurrence analysis will show a decrease in the number of

checkerboard pairs observed compared to the number expected along the environmental gradient of distance from sea (Kikvidze et al. 2005, Dullinger et al. 2007).

3. There will be an increase in the number of exotic species present per quadrat at Birdlings Flat since the previous survey in 2006. This will be more pronounced close to gardens.

1.8.2 Native facilitation experiment

1. Planted seedlings will have a higher survival rate when they are sheltered by an established shrub. This is because the shrub will provide facilitative effects through mechanisms such as preventing extreme temperature fluctuations, improving soil properties by accumulating nutrients and organic matter, protection from wind borne sand and salt, and reducing the likelihood of anthropogenic damage (Valiente-Banuet and Ezcurra 1991, Greenlee and Callaway 1996, Holmgren et al. 1997, Flores and Jurado 2003, King and Hobbs 2006, Butterfield et al. 2010). Due to the harsh environmental conditions, it is expected that the positive facilitative effects of being planted near an established individual will outweigh the negative competitive effects (Bertness and Callaway 1994).
2. An increase in limiting factors such as soil nutrients and water availability will increase both initial survival and long term growth of planted seedlings. This is because in coastal environments plants often have both water and nutrient limitations (Bagousse-Pinguet et al. 2012). These factors are likely to interact. For example, where the seedlings are planted will affect the impact of the treatments (Tilman and Pacala 1993). Seedlings planted in bare gravel are likely to benefit more from receiving water or fertiliser than those planted near a shrub.
3. Native seedlings planted close to the sea will have a higher mortality rate than those further away. This is due to the higher levels of environmental stress close to the sea including higher salinity. Each species will reach the limit of its physiological stress tolerance range or fundamental niche at some point along the gradient across the beach profile to the sea's edge (Bruno et al. 2003, He et al. 2011).

1.8.3 Exotic facilitation experiment

1. Planted native seedlings will have a higher survival rate when they are planted close to an established exotic individual, as a result of increased shelter and organic material. This is thought to be the case because a previous study showed a positive relationship between cover of *Gazania* and the level of organic matter in the substrate (S. Wisser, unpublished data). Due to the harsh environmental conditions, it is expected that the positive facilitative effects of being

planted near an established individual will outweigh the negative competitive effects (Bertness and Callaway 1994).

2. Native seedlings planted close to the sea will have a higher mortality rate than those further away. This is due to the higher levels of environmental stress close to the sea including higher salinity, and an increased likelihood of waves reaching the plants. Each species will reach the limit of its physiological stress tolerance range or fundamental niche at some point along the gradient down the beach to the sea's edge (Bruno et al. 2003, He et al. 2011).
3. Planted native seedlings may be outcompeted when the nurse plant is present at high densities. This is because while facilitative effects are likely to be optimised at medium densities of the nurse plant, at high densities the facilitative effects of the nurse plant may be outweighed by competitive effects such as root or soil water competition (Holmgren et al. 1997, Riginos et al. 2005).

Chapter 2

Methods

2.1 Site Description

Data were collected from two gravel beach sites: Birdlings Flat, Canterbury and Tangoio, Hawkes Bay (Figure 2.1).

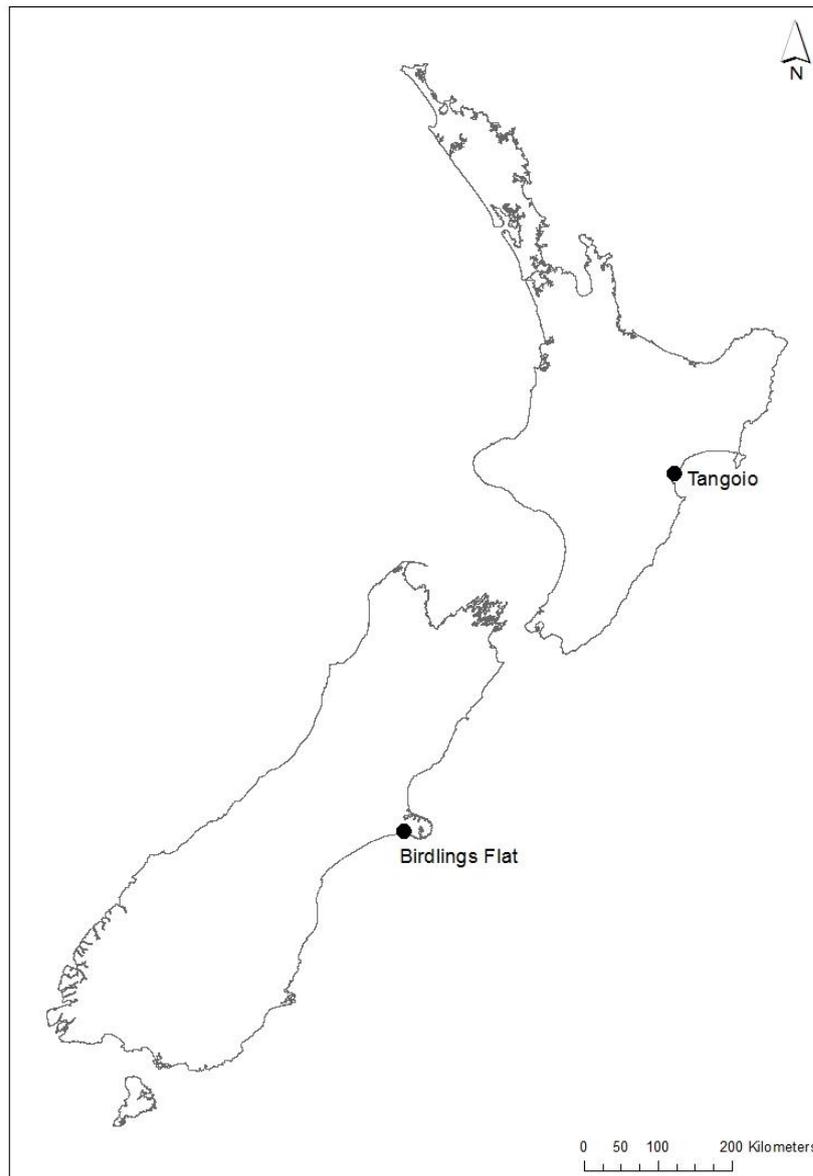


Figure 2.1 Locations of the study sites. Birdlings Flat is on the east coast of the South Island, and Tangoio is on the east coast of the North Island.

2.1.1 Birdlings Flat

Birdlings Flat is a gravel barrier beach located at the eastern end of Kaitorete Spit. Kaitorete Spit is on the South Canterbury Bight and separates Lake Ellesmere and Lake Forsyth from the Pacific Ocean (Soons et al. 1997). The southern side of Kaitorete Spit is a globally-rare mixed sand and gravel dune system approximately 1,000 years old (Burrows 1969, Soons et al. 1997), and one of the largest in New Zealand (Patrick 1994). Kaitorete Spit ranges from 2.4 km in width at the southern end to 4.9 km at the northern end (Widodo 1997), Birdlings Flat is located at the wider, north-eastern end of the spit. The gravel barrier is aggrading from river gravels deposited at the southern end by the Rakaia River (Armon 1974). Net deposition continues at the eastern end and net erosion at the western tip of the spit (Heatherington 2012).

Kaitorete Spit has a climate with many extremes. Summers are hot with maximum temperatures up to 40°C and winters are cold with minimum temperatures often below 0°C (Heatherington 2012). It is often windswept with dry or salt-laden winds (Burrows 1969, Patrick 1994, Widodo 1997). Kaitorete Spit is the driest place in Canterbury (Christchurch City Council 2006) with annual rainfall between 400–500 mm (Patrick 1994).

Birdlings Flat beach is bordered by a small township. The proximity of residential gardens and the dumping of green waste on the beach provides a seed source for many exotic garden plants now found on the beach (*pers. obs.*). At the western end of Birdlings Flat, a local resident removes *Gazania* plants by hand (Ken Sitars personal communication, 2011). The beach is also used for recreational purposes such as four-wheel driving, fishing and walking (Heatherington 2012) (Figure 2.2).

Native plants at Birdlings Flat are well adapted to the harsh environment (Peace 1975) and tend to have deep roots which can utilise water far below the surface. This includes species such as *Calystegia soldanella* (L.) R.Br. and *Carmichaelia appressa* G. Simpson (Burrows 1969). There are also many small-leaved plants, this leaf morphology is likely to be an adaptation to minimise water-loss; small-leaved plants includes species such as *Muehlenbeckia ephedroides* Hook. f. (Burrows 1969).



Figure 2.2 Birdlings Flat looking east along the commonly used four wheel drive track.

2.1.2 Tangoio

The study site, known as Tangoio South 27A, is part of a raised gravel terrace in the Hawkes Bay, on the eastern coast of the North Island of New Zealand (Figure 2.1). Tangoio is located 18 km north of Napier and 4 km north of Whirinaki. It is a 5.5 ha area protected under a Nga Whenua Rahui covenant or kawenata (Millsap et al. 2013). The Napier coastline was uplifted approximately 2 m in the 1931 Napier earthquake; Tangoio is located at the northern end (Komar 2010). The beach is now eroding due to upstream mining of gravel which has decreased supply to the beach (Komar 2010) and strong south-east coastal waves which redistribute gravel northwards along the coast, resulting in subsidence at the southern end (Marshall 1928, Komar 2010). On the terrace, the gravel is fairly uniformly sized with a very small proportion of organic matter and sand (S. Wiser, unpublished data). The presence of moss mats in some areas and the lack of driftwood indicates a stable site. Similar, although less extensive, sites exist in Hawkes Bay and the distribution of native plant species on these sites can be used as a guide of what species may have once been at Tangoio (Wiser, Unpublished). The dominant vegetation cover is the exotic herb *Gazania*. (Figure 2.3) and native plant richness is low with only 34 species present on the site (S. Wiser, unpublished data).

There are three Māori hapu based at the nearby Tangoio Marae: Marangatūhetaua (Ngati Tū), Ngai Tatara, Ngati Kurumokihi and Ngai Te Ruruku (ki Tangoio). These hapu all have a cultural connection to Tangoio, as it is of historical significance as a waka landing site. Additionally the hapu are concerned about its ecological state (Pollock 2012), which is shown by actions such as installing a covenant and placing boulders to prevent the public driving on the beach (R. McGowan, personal communication, 2012).



Figure 2.3 Tangoio looking south-east towards Napier across a field of *Gazania*.

2.2 Data Collection

2.2.1 Plant community structure at Birdlings Flat

Gravel beaches are defined by Wiser et al. (2010) as beaches in which at least 50% of the substrate in the top 10 cm is gravel; i.e. between 2 mm and 256 mm in diameter. In this study I chose to expand that definition and include sites that were less than 50% gravel to encompass all beach ecosystems at Birdlings Flat with a gravel component, rather than limiting the study to a pure gravel definition.

Randomly located transects were established along the length of the beach at a minimum distance of 10 m and a maximum distance of 100 m apart (Figure 2.5). These transects ran perpendicular to the sea from the individual plant closest to the sea to the fence line denoting the start of private property. Along each of these transects randomly-placed 1 m² quadrats (Figure 2.4) were established; a total of 333 quadrats were measured. Each transect had between nine and fifteen quadrats spaced at a minimum distance of 2 m and a maximum distance of 15 m apart. Within each quadrat all species present were recorded and given a cover score using the Braun-Blanquet cover classes (Mueller-Dombois and Ellenberg 1974) where <1% cover=1, 2-5% = 2, 5-25% = 3, 26-50% = 4, 51-75% = 5, >75% = 6. At each quadrat I also measured a number of covariates, including environmental variables. The mean and maximum plant heights were recorded. The type of ground cover was measured by estimating the percentage cover of vegetation, bare ground, vegetation litter, coarse woody debris (driftwood with a diameter >10 cm), bryophytes, lichens, bedrock and rubbish. Bryophyte and lichen cover can be used as a proxy to indicate substrate stability of gravel beaches (Oliver 1912; Lambley & Hodgetts 2001). Slope was measured using an abney level; aspect was measured by indicating if the plot was facing towards or away from the sea. Gravel particle size was measured using a Wentworth gravelometer to assess the size of 10 randomly selected particles. A sample of substrate from the top 10 cm of the substrate was taken from the centre of the quadrat and the volume determined of: vegetation litter, gravel, sand and humus using a graduated measuring cup after sieving the material through a 2 mm sieve. These methods are comparable to those of Wiser et al. (2010), and although the exact plots were not remeasured because their locations were not permanently marked, a site-level comparison between the data collected in 2006 and the data collected in 2012 can be made.



Figure 2.4 Quadrats set out ready to measure at Birdlings Flat in January 2012.

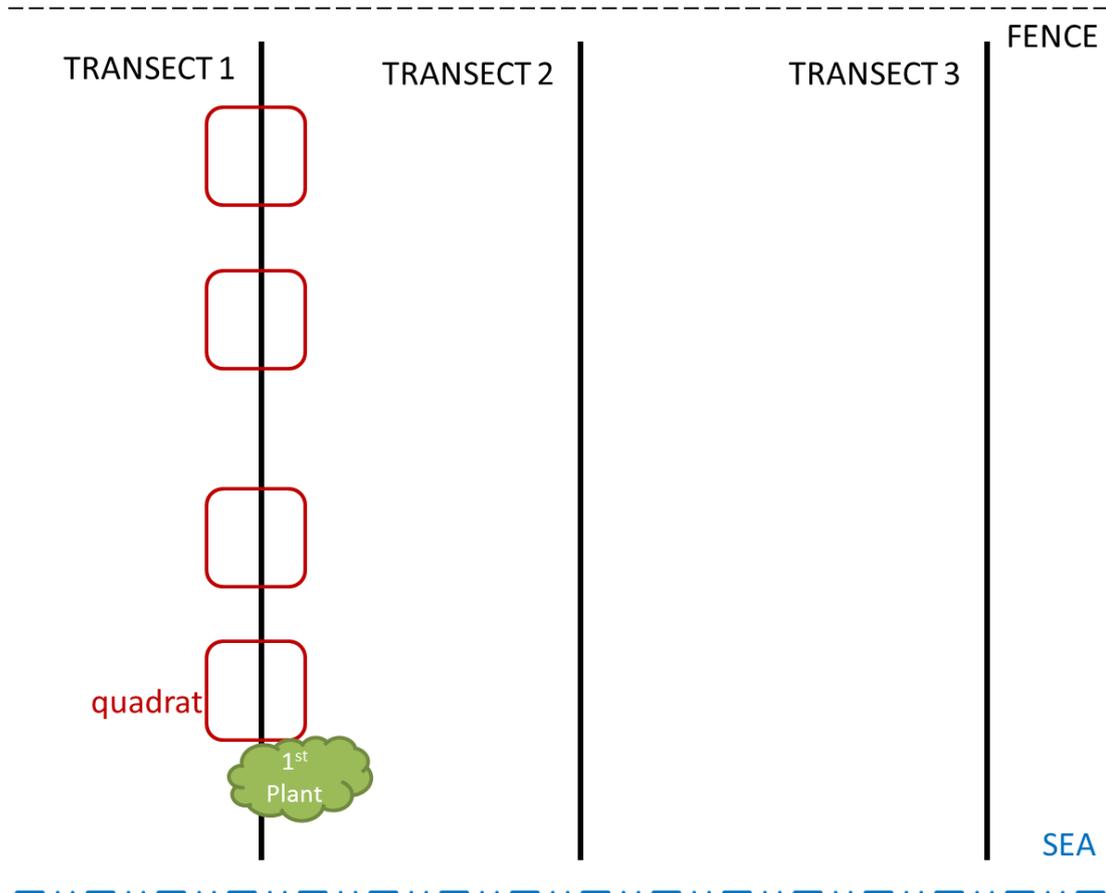


Figure 2.5 Design of observational study at Birdlings Flat. Quadrats were randomly located on transects starting from the plant closest to the sea.

2.2.2 Native facilitation experiment

The study was carried out at Birdlings Flat, Canterbury. Native woody seedlings of *Coprosma propinqua*, *Muehlenbeckia complexa* and *Muehlenbeckia ephedroides* grown from local seed were planted under the shelter of established *Coprosma propinqua* or *Muehlenbeckia ephedroides* shrubs, paired with planted seedlings in bare gravel (Figure 2.6 and Figure 2.7). Two sizes of *C. propinqua* were planted: small seedlings averaging 5 cm tall and large seedlings averaging 28 cm tall. The seedling species were selected after preliminary association analysis of the observational study (results not presented). The paired plots were randomly located along three transects at the rear of the beach running parallel to the sea at approximately 79 m, 98 m and 114 m from the high tide mark. Transects were randomly located within the area of the beach where native shrubs currently exist. The seedlings were planted in a randomised block design, with the addition of organic fish based liquid fertiliser (20 mL of Yates Nature's way fish emulsion) and/or water crystals (5 mL of pre-soaked Yates Waterwise Water Storage Crystals) to a subset of the planted seedlings to test whether either nutrient limitation or water limitation influences seedling growth and survival. Each seedling was marked with coloured wire and a numbered tag, and a GPS point recorded to aid relocation. Substrate characteristics (particle size and depth to fine material) were also measured to determine if these had any impact on survival (cf. Walmsley and Davy 1997). The site was re-visited monthly for a year and all seedlings relocated, allowing short-term survival between the treatments to be compared. Over the course of a year, approximately every eight weeks, with the specific timing adjusted to immediately follow a significant rainfall event, liquid fertiliser was added to the fertilised seedlings and the same volume of water added to the non-fertilised seedlings. Addition of fertiliser after rainfall events limits the possibility that adding a liquid fertiliser would break a drought. After twelve months the height of the seedlings was measured to determine growth of the surviving seedlings.



Figure 2.6 A *Muehlenbeckia complexa* seedling three months after planting. This seedling is planted in bare gravel as part of the native facilitation experiment at Birdlings Flat.

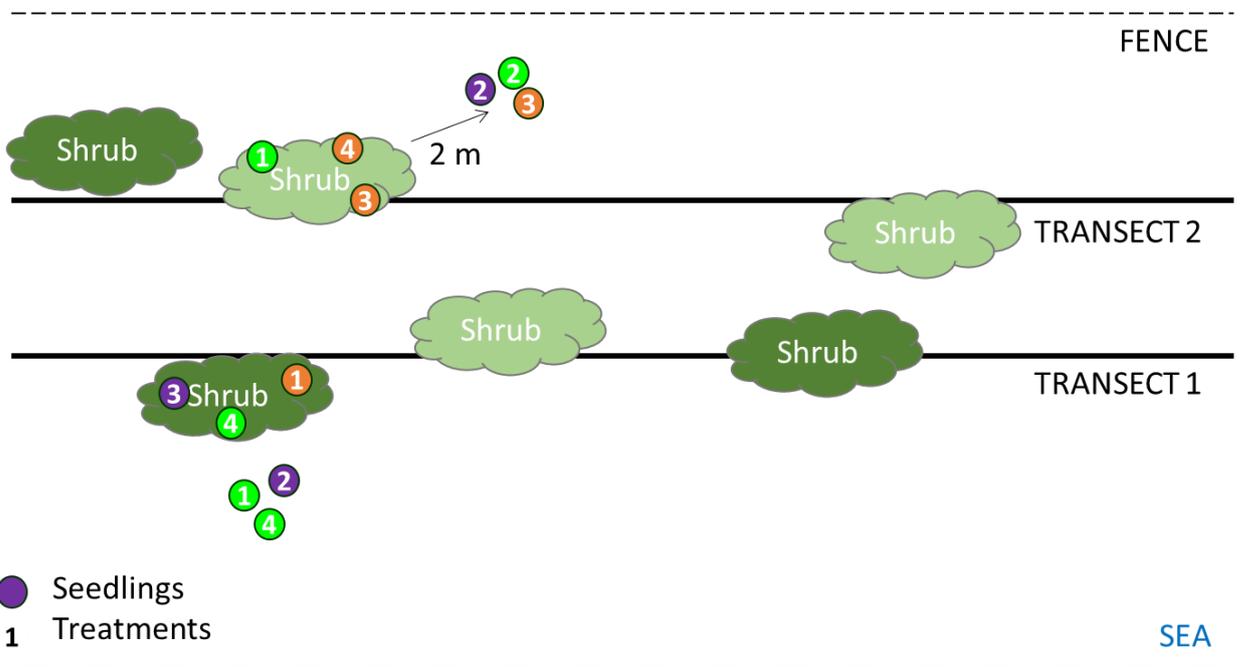


Figure 2.7 Design of native facilitation experiment at Birdlings Flat. Seedlings (circles) of different species were planted next to shrubs and 2m away in bare gravel. Treatments of water, fertiliser, both water and fertiliser, or no treatment were randomly applied to the seedlings.

2.2.3 Exotic facilitation experiment

This experiment was set up at Tangoio by Susan Wiser (Landcare Research) and Nga Whenua Rahui in 2010 (Figure 2.8). Seedlings of three native species, *Ficinia nodosa* Rottb, *Muehlenbeckia ephedroides* and *Coprosma acerosa* A. Cunn were planted in 1 m² quadrats with one of three planting treatments applied. In the first treatment seedlings were planted in a patch of bare gravel within 20 cm proximity of an established *Gazania* plant. A minimum of three *Gazania* individuals per 1 m² quadrat were required for this treatment. In the second treatment seedlings were planted in sites where all *Gazania* plants within the quadrat were removed by hand-pulling, including the roots. In the third treatment seedlings were planted in bare gravel. Approximately 20 replicates of each treatment were applied for each species (Table 2.1). Within each quadrat three seedlings of the same species were planted. The exception to this was for *M. ephedroides* where in 39 quadrats only two individuals were planted due to the limited number of seedlings available.

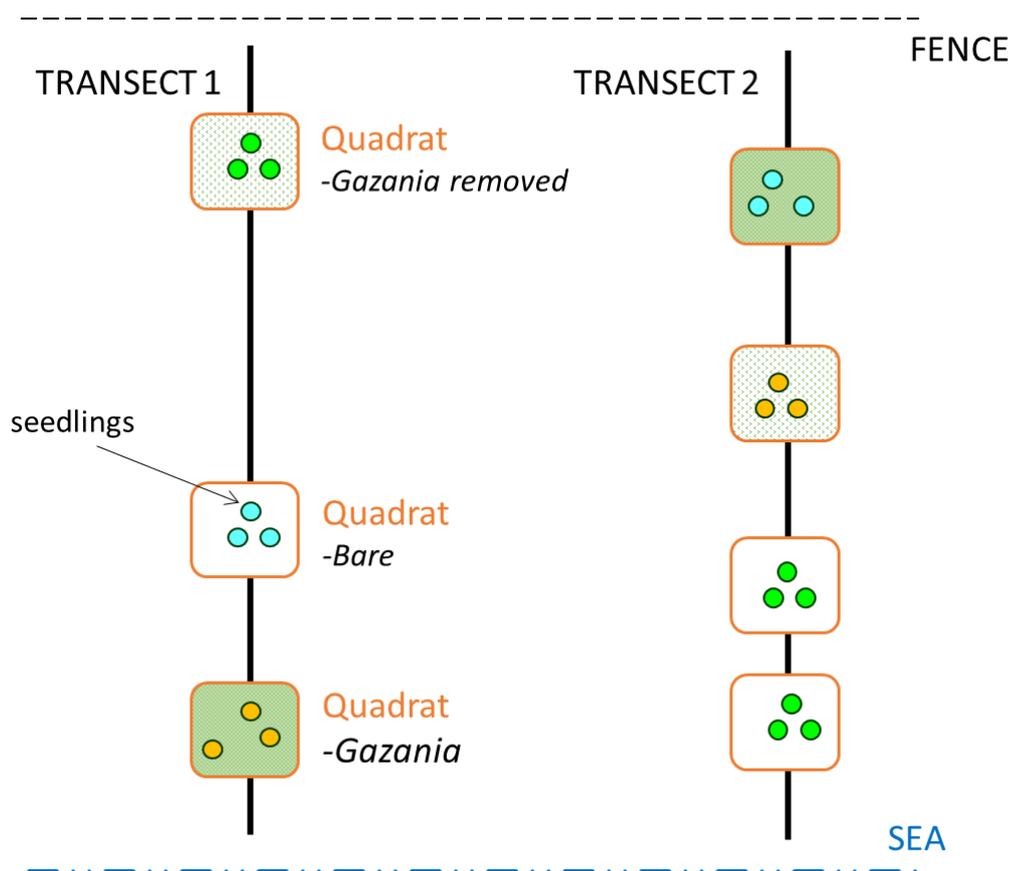


Figure 2.8 Design of exotic facilitation experiment at Tangoio. Three seedlings (circles) of the same species were planted in a quadrat of either bare gravel, with *Gazania* present, or *Gazania* removed.

Table 2.1 Number of replicates of each treatment applied per species in the Tangoio exotic facilitation experiment. The number of *M. ephedroides* quadrats with only two individuals planted is given in parentheses.

	Treatment			Number of quadrats	Number of plants
	Bare Gravel	Gazania	Gazania Removed		
<i>Coprosma acerosa</i>	20	20	20	60	180
<i>Ficinia nodosa</i>	20	22	19	61	183
<i>Muehlenbeckia ephedroides</i>	20 (13)	21 (14)	18 (12)	59 (39)	138
Total number	60	60	60	180	501

The quadrats were established along 24 transects. These transects ran perpendicular to the sea in random locations along the beach, at a minimum of 10 m apart. Transects ranged in length from 10 m to 29.8 m, with between three and 11 quadrats per transect. The transect origin was located at the first point inland from the sea where rooted vegetation occurred. This is because it was assumed plants could not survive closer to the sea than the current vegetation limit. Along each transect 1 m² quadrats were established at random locations at least 1 m apart. Treatments and species were randomly assigned to each quadrat.

The three native species were chosen because they are known to occur naturally on gravel beaches in the Hawkes Bay area. *Muehlenbeckia ephedroides* is known to be present at other nearby gravel beaches including Bay View and Te Awanga, and *C. acerosa* is known to be present on the gravel terrace near the Napier Airport (Wiser, Unpublished). With the exception of a small number of *F. nodosa* individuals being present, these species were absent from Tangoio at the start of the experiment, although it is likely they would have occurred there in the past. Seedlings were purchased from a local nursery and grown from local seed sources.

Gazania density was measured at the time of planting as well as when the seedlings were remeasured in 2012 to show whether the *Gazania* removal treatments endured over time. This was calculated as the mean change in *Gazania* cover per quadrat.

This site was revisited in January and September 2012 to measure the survival and growth of the seedlings (Figure 2.9) and therefore to determine the impact of the treatments and facilitative effects. Growth was measured as the pulled height of the longest branch for *C. acerosa* and *M. ephedroides*. For *F. nodosa* growth was measured as the basal width of the individual.

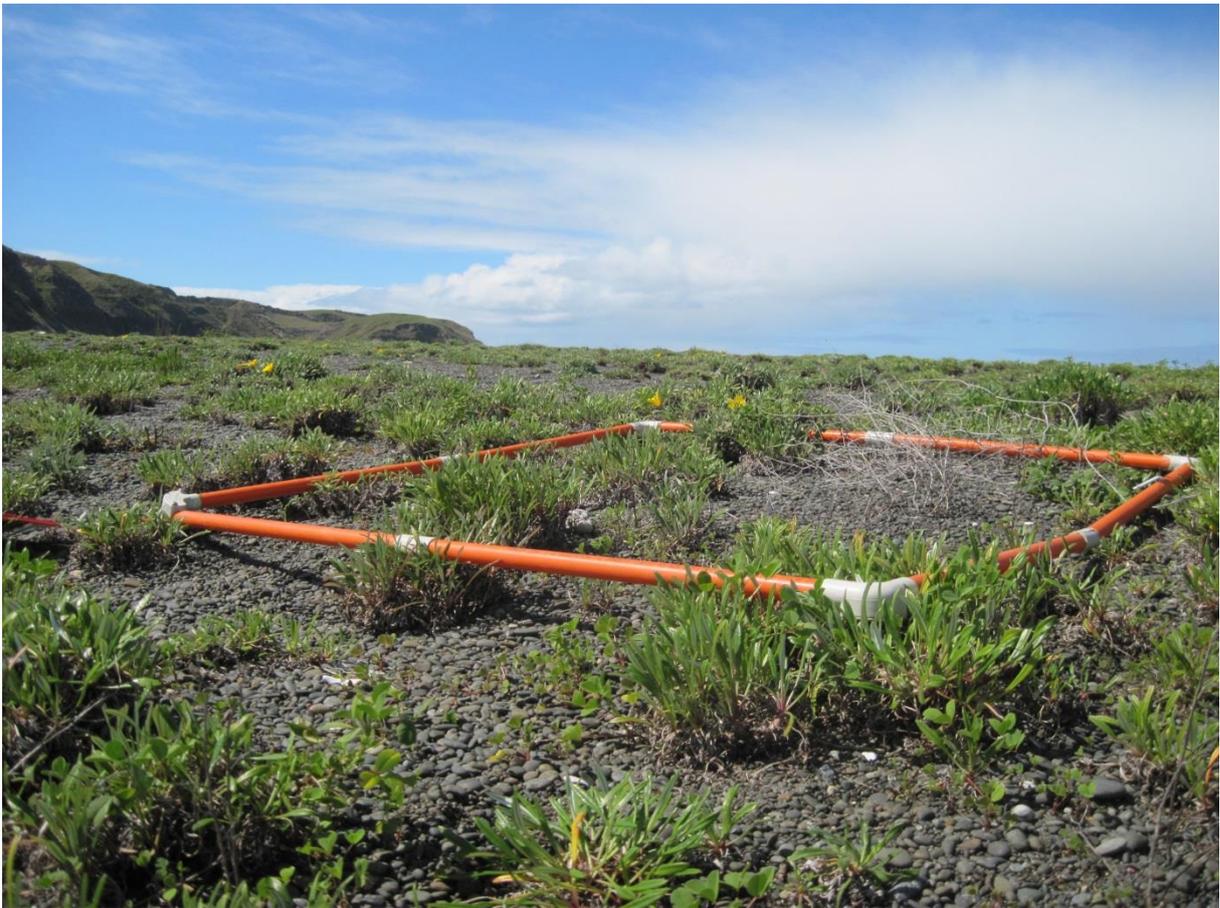


Figure 2.9 A relocated quadrat with dead *Coprosma acerosa* being remeasured in 2012 at Tangoio.

2.3 Data Analysis

2.3.1 Plant community structure at Birdlings Flat

Temporal and spatial patterns

To describe the changes in species composition over time I compared the results of the 2006 and 2012 surveys. To describe the spatial pattern within the community I carried out indirect gradient analysis using nonmetric multi-dimensional scaling (NMDS). Ordination arranges sites in sample space so that they are placed relative to their similarity in species composition (Kent 2011). NMDS is considered to be the best ordination method for detecting vegetation gradients (Minchin 1987, McCune et al. 2002). NMDS is an unconstrained ordination method based on pairwise site dissimilarities (Väre et al. 1995) and is ideal for non-normal data (McCune et al. 2002). Scores are assigned to new sample units on the basis of species composition using ranked dissimilarity distances between samples (Faith et al. 1987, McCune et al. 2002), therefore distances in ordination space represent the similarity between sample plots. Species cover scores were converted to the mid-point of the percentage range represented by the scores to gain relative abundances. I calculated species

scores as weighted averages of site scores; values were weighted by the proportional species abundance (ter Braak 1995). Weighted averaging was used because it adds more weight to sites where a given species is more abundant (Oksanen et al. 2013). Species bio-status and life form was recorded based on the New Zealand Plant Names Database (Allan Herbarium 2000). The exception to this was for two trees which are native to New Zealand, *Pittosporum crassifolium* and *Coprosma repens*, but are not native to Canterbury and have therefore been listed as exotic.

NMDS is iterative, converging on an ideal solution, although convergence does not always occur (Väre et al. 1995). To select a good dissimilarity measure I compared ranked order correlations of several dissimilarity indices to determine which measure best detected gradients in the dataset (Faith et al. 1987, Oksanen et al. 2013). Based on the ranked order correlations I selected Bray-Curtis distance as the dissimilarity measure to determine the difference in composition between sites. Data were transformed using a Wisconsin double standardization, which is consistent with using Bray-Curtis dissimilarity metric (Faith et al. 1987). Double standardisation was carried out to improve the gradient detection ability of the dissimilarity index, which therefore gives a better ordination result (Oksanen et al. 2013).

The stress value is a measure of goodness of fit; specifically it measures how well the ordination distances correspond to the observed dissimilarity values (ter Braak 1995). I assessed the dimensionality of the data using a scree plot of the final stress versus the number of dimensions. The number of axes beyond which reductions in stress were small was chosen (McCune & Grace 2002); in this case three. The ordination was run with 100 iterations using the observed data. I started with random configurations to increase the likelihood of convergence (McCune et al. 2002), and to increase the likelihood of finding the solution with the lowest stress (Oksanen et al. 2013).

The relationships and relative importance of environmental variables were assessed by fitting environmental vectors. Environmental vectors are estimates of the correlation between the ordination and the environmental variables, and show the strength and direction of the correlation between the ordination output and a given environmental variable (Oksanen et al. 2013). I used this technique to indicate if one or more environmental variables are associated with differences between sites/samples as represented in the NMDS ordination (ter Braak 1995).

To describe the changes in species richness between the 2006 and 2012 surveys and to test which variables are affecting the proportion of exotic/native species richness at the quadrat level I used Generalised Linear Modelling. I used an information theoretic framework to fit candidate models to the data. Explanatory variables were selected from *a priori* hypotheses (Burnham and Anderson 2002, Mazerolle 2006) developed when designing the observational study (Table 2.2). These models were for two subsets of the data: quadrats with woody species present and quadrats with

herbaceous species present. Herbaceous and woody plant richness and abundance are expected to change at different rates because they have different life history strategies (Silvertown et al. 1993). The subsetting was carried out to ensure that only plots with the target life-form were included in the models because some plots have only herbaceous or only woody plants. Each model included the proportion of exotic species per quadrat as a binomial response variable. Explanatory variables added to the models were year, substrate type, distance from the sea and distance along the beach. I also included a null model in the candidate model sets to allow me to determine whether or not the best model(s) were explaining the data better than what could be expected at random (Burnham and Anderson 2002). The response and explanatory variables were linked using a logit link function and fitted using maximum likelihood estimation (McCullagh and Nelder 1989). When comparing models, second-order Akaike Information Criterion (AICc) was used to correct for the small sample sizes (Burnham and Anderson 2002, Millsap et al. 2013). Models were selected using quasi AICc values to account for the over-dispersion in the data. Over-dispersion occurs when there is more variability in the data than what is expected from a fitted model; this is indicated by a variance-inflation factor (\hat{c}) greater than 1, which is calculated during the model fitting process (Burnham and Anderson 2001, Symonds and Moussalli 2011).

To determine which models are most likely given the data I used the candidate model approach, specifically Akaike's Information Criterion, to compare and rank multiple competing models. The data was subsetted into two categories: herbaceous and woody. Six models were fitted to each subset of the data (Table 2.2). I chose to run the simplest set of models to ensure parsimony and avoid over-fitting-models (Burnham and Anderson 2002). AICc compares models relative to each other (Symonds and Moussalli 2011), to test which of the models in the candidate set best represent the data. This approach tests multiple working hypotheses (Anderson 2010). I also calculated an evidence ratio between the two best models in each candidate set to how much better the most likely model was than the next candidate model (Symonds and Moussalli 2011). To test whether there was spatial autocorrelation in the residuals I used a Mantel correlogram (Mantel 1967, Oden and Sokal 1986). Spatial autocorrelation occurs when the outcomes of two points (or quadrats) is related to their distance apart, and violates the assumption of independence (Legendre 1993). The Mantel test assesses the relationship between distance and site similarity (Koenig 1999). The test showed no spatial autocorrelation, and therefore I did not need to account for it in the model structure.

I carried out multimodel inference by using model averaging to generate parameter estimates and derived unconditional standard errors based on the most plausible candidate models (Burnham and Anderson 2002), this determines the magnitude and direction of the effect shown as important in the most likely candidate model (Mazerolle 2006). Model averaging predicts the proportion of exotic

species present with increasing distance from the sea based on the experimental data and all of the models in the candidate set, therefore testing my hypotheses.

I used an informal approach (McCullagh and Nelder 1989) for model checking by comparing the model results against basic summaries of the raw data to check for consistency and ensuring the model output seemed sensible. All analyses were run using the statistical program “R” (R Development Core Team 2013) and in particular the package “AICcmodavg” (Mazerolle 2013).

Table 2.2 Models fitted to test influences on proportion of exotic to native species per quadrat and corresponding hypotheses justifying inclusion in the candidate set.

Model	<i>A priori</i> hypothesis
Year	There will be an increase in the proportion of exotic species between 2006 and 2012.
Substrate	Substrate type will affect which species grow in an area.
Bio-status	Native species richness will be similar but exotic species richness will increase.
Distance from sea	Herbaceous plants are able to grow closer to the sea than woody plants. Empty niche for exotics to fill close to the sea.
Distance along beach	Increase in exotics close to township as plants escape from gardens.
A null model (i.e. intercept only)	To provide a baseline against which to compare the relative support for the other models.

Co-occurrence Patterns

To describe the species co-occurrence patterns I used null models to test whether species co-occur more or less frequently than expected at random. Null models provide more in-depth analysis of the co-occurrence patterns than association analysis because they assess how similar species are in the sites they occupy rather than the similarity of the sites (Gotelli and Graves 1996). This allowed me to determine whether the observed patterns of species co-occurrence are consistent with the patterns predicted by the Stress Gradient Hypothesis. The null model randomises species occurrences across sample space, and is designed to construct a pattern that would be expected in the absence of a particular ecological mechanism (Gotelli and Graves 1996). When the observed data are different from the null we can conclude that biological interactions within the community are significant (Connor and Simberloff 1986; Gotelli and Graves 1996) and make inferences about the ecological mechanism which has created the observed patterns (Gotelli and Graves 1996).

Checkerboard distributions were introduced by Diamond (1975). A checkerboard unit is a combination of sites and species in a matrix which results in all species occurrences being mutually exclusive (Table 2.3). The C-score is a co-occurrence index based on the number of checkerboard units in the site by species matrix (Stone and Roberts 1992). It is the average number of checkerboard units across all possible species pairs (Stone and Roberts 1990). The C-score quantifies the degree of species co-occurrence by measuring the extent to which species pairs are segregated across sites (Gotelli and Rohde 2002). When species pairs have a higher C-score than expected by chance the pair occurs together less often than would be expected at random, suggesting segregation as the result of either a competitive interaction or differing habitat requirements. When species pairs have a lower C-score than expected by chance the pair occurs together more often than expected, suggesting aggregation as the result of either a positive interaction or similar habitat requirements (Stone and Roberts 1992, Dullinger et al. 2007). The C-score is considered a good index to determine species co-occurrence patterns as it has low Type I error and good power (Gotelli 2000).

Table 2.3 An example of a perfect checkerboard, in which species are segregated and never co-occur in any site. A one denotes an occurrence of a species at a site and a zero is an absence.

	<i>Species A</i>	<i>Species B</i>
Site A	1	0
Site B	0	1

To account for environmental variation, and increase the likelihood that co-occurrence patterns were based on species interactions rather than habitat suitability, I subsetted the data based on a priori hypotheses (Table 2.4). The null models were run for each subset of quadrats. I used a site by species matrix to test for non-random structure in species occurrences across the community (Gotelli and Graves 1996, Gotelli 2000) by generating standardised C-scores (Stone and Roberts 1990). I calculated the observed C-score for each subset of quadrats and compared these against expected C-scores (Gotelli and Entsminger 2001). The expected values were calculated by using a sequential swap algorithm which randomizes species occurrences among samples. I fixed the row and column totals, known as a ‘fixed-fixed’ algorithm (Gotelli and Ellison 2002) so that the differences in the frequency of occurrence of each species (column sums) and differences in the number of species per site (row sums) are preserved (Connor and Simberloff 1979). This accounts for the differences in the quality of sites, as not all sites provide suitable habitat for all species (Gotelli and Rohde 2002). Empty sites, sites with fewer than four species and species that occurred fewer than four times were excluded from the analysis as they cannot be sufficiently randomised (Dullinger et al. 2007). I ran this

randomisation in R (R Development Core Team 2013) 1000 times which generates 1000 new matrices and therefore 1000 expected C-Scores were calculated and compared to the observed C-score.

C-score values vary depending on species number, abundance and co-occurrences observed at each locality. To account for this I calculated a standardized effect size (SES) for each matrix which enables the results between the subsets to be compared (Gotelli and McCabe 2002, Dullinger et al. 2007).

The standardized effect size is calculated as:

$$\text{SES} = (\text{observed C-score} - \text{mean of simulated C-scores}) / \text{standard deviation of simulated C-scores}.$$

I calculated the proportion of randomised C-score values above or below the observed value, testing if the observed C-score is lower or higher than expected, consistent with species aggregation or species segregation respectively (Boschilia et al. 2008). Random distributions can be interpreted as either no pattern or that a number of contrasting processes are acting simultaneously and confounding the result (Boschilia et al. 2008).

Table 2.4 Data were categorised into subsets according to *a priori* hypotheses prior to C-score analyses.

Subset name	<i>A priori</i> hypothesis	Categories
Distance from town	More exotic species closer to the town.	Quadrats were subsetted into two categories: An arbitrary line was drawn where the township ends as a proxy for distance from town. Data corresponding to plots located in front of the town were labelled Birdlings Flat. Data corresponding to plots located away from the town were labelled Kaitorete Spit.
Distance from sea	Species co-occur together more often than random close to the sea and less often than random further away from the sea.	Quadrats were subsetted into three categories: near, mid and far distance from sea. An equal number of quadrats in are in each category.
Vegetation type	Native shrubs are facilitative, <i>Lupinus arboreus</i> is competitive.	Quadrats were subsetted into three categories: <i>Lupinus arboreus</i> present covering more than 5% of quadrat, native shrubs present covering more than 5% of quadrat, no shrubs in the quadrat.
Substrate	Microhabitat affects which species can grow in an area.	Quadrats were subsetted into two categories: Proportionally more sand or more stones.

2.3.2 Native facilitation experiment

To test which variables are affecting seedling survival, including testing whether there was any difference between planting treatments, I used Generalised Linear Modelling. Survival and treatment effects are likely to vary significantly between species; therefore all analyses were run separately for each species. Due to the high seedling mortality the sample size was too small to analyse the growth rates. To account for transplant shock seedlings that died in the first month after planting were excluded from further analyses (Gomez-Aparicio et al. 2004). The methodology and rationale for selecting and fitting models is described in section 2.3.1 above. Ten models were fitted (Table 2.5). These models were only run for *M. complexa* and *M. ephedroides* as the mortality rate of *C. propinqua* was too high to conduct meaningful analyses. Each model included seedling survival or mortality as a binary response variable. Explanatory variables were treatment, distance from the sea, seedling height when planted, shrub cover and height, depth to fine material and mean gravel size. The species of facilitator was not included in the model as it was confounded with shrub height; all *C. propinqua* shrubs were taller than *M. ephedroides* shrubs. These explanatory variables were selected from *a priori* hypotheses developed when designing the experiment (Table 2.5).

Table 2.5 Models fitted to test which factors impact on seedling survival at Birdlings Flat and corresponding hypotheses justifying inclusion in the candidate set. The dependent variable is survival/mortality of the planted seedlings.

Model	<i>A priori</i> hypothesis
Treatment	Seedlings with either water or fertiliser will do better than those with none, seedlings with both treatments will have the highest survival rates.
Cover	Seedlings planted next to shrubs will have a higher survival rate than those planted in the bare gravel.
Treatment + Cover	Treatment and cover would both be important factors in seedling survival, with the combination having a stronger effect than only one of the factors.
Treatment * Cover	Treatment and cover are likely to interact with the treatment being more important in bare gravel.
Distance from sea	Seedling survival will be lowest closest to the sea.
Gravel size	Seedling survival will change with gravel size, dependant on species.
Depth to fine material	Seedling survival will be highest when fine material is closer to the surface.
Shrub Height	Seedling survival will be highest at a medium shrub height, as protection will be provided but the seedling will not have to compete for light.
Seedling height when planted	Seedlings which are larger when planted will have a higher survival rate.
A null model (i.e. intercept only)	To provide a baseline against which to compare the relative support for the other models.

2.3.3 Exotic facilitation experiment

To test which variables are affecting seedling survival, including testing if there is any difference between planting treatments, I used Generalised Linear Modelling. Survival and treatment effects are likely to vary significantly between species, and therefore analyses were run separately for each species. I carried out analyses at a quadrat level as individual seedlings were not marked and therefore the success or failure of individuals could not be followed. *Gazania* densities over time were compared at the quadrat level, by calculating the mean of the per quadrat change, to determine if the treatments endured over the course of the study. Due to the high mortality rates all analyses were carried out using the January 2012 survival results, and growth rates were not analysed. The methodology and rationale for selecting and fitting models is described in section

2.3.1 above. Five candidate models were fitted (Table 2.6). Each model included seedling survival or mortality as a binomial response variable. Explanatory variables considered include treatment, distance from the sea and *Gazania* cover; these were selected from *a priori* hypotheses developed when designing the experiment (Table 2.6).

Table 2.6 Models fitted to test which factors impact on seedling survival at Tangoio and corresponding hypotheses justifying inclusion in the candidate set. The dependent variable is survival/mortality of the planted seedlings.

Model	<i>A priori</i> hypothesis
<i>Gazania</i> treatment	Seedling survival would be highest with <i>Gazania</i> removal, as the seedlings benefit from the facilitative effects of additional organic matter but do not experience root competition. Survival would be lowest in bare gravel.
Distance from sea	Seedling survival would be lowest closest to the sea.
<i>Gazania</i> treatment + Distance from sea	Treatment and distance to the sea would both be important factors in seedling survival, with the combination having a stronger effect than only one of the factors.
Distance from sea + <i>Gazania</i> cover at start and end of experiment	<i>Gazania</i> treatments should explain more than the other variables, meaning this model would have little support.
A null model (i.e. intercept only)	To provide a baseline against which to compare the relative support for the other models.

Chapter 3

Results

3.1 Plant community structure at Birdlings Flat

Temporal and spatial patterns

The findings from my observational study at Birdlings Flat support my hypothesis that temporal and spatial patterns in plant community composition are related to environmental variables. In 2012 I recorded 43 species, 70% of which were exotic (Table 3.2). The dominant category was exotic forbs with 19 species recorded, and overall forbs constitute 55% of the species recorded. There were no native tree species recorded. The species most commonly encountered were *Lagurus ovatus* L. (recorded in 144 quadrats), *Raoulia australis* Hook.f. (recorded in 99 quadrats), and *Gazania* (recorded in 85 quadrats). Four species (*Acaena* spp., *Cotyledon orbiculata* L., *Crepis capillaris* (L.) Wallr. and *Jacobaea maritima* (L.) Pels & Meijden) were only recorded once.

A comparison of species data with a previous survey by Wiser et al. in 2006 shows a decrease in the species richness of quadrats measured but not in the overall observed species richness (Table 3.1; Table A.1). The 2006 survey was carried out in December and the 2012 survey was carried out in January which may account for some of these differences. The emergence of winter annual species, which flower in spring and then die, could mean that by January these plants were no longer present. There were more exotic forbs and grasses in 2006, but the diversity of native forbs and grasses stayed the same. The additional exotic shrub recorded in 2012 was *Echium candicans* L.f., which is only found in a small area and so random sampling could have missed this in 2006. The native shrub *Carmichaelia appressa* was found on an area of the beach which was less than 50% gravel and so would not have been included in the 2006 survey. The change in species richness over time indicated that exotic woody species diversity per quadrat is increasing but exotic herbaceous species and native species diversity is stable.

Table 3.1 Change in species richness between the 2006 and 2012 surveys of vegetation at Birdlings Flat observed using randomly located quadrats.

Growth Form	December 2006		January 2012	
	Number of exotic species	Number of native species	Number of exotic species	Number of native species
Grass	10	2	5	2
Forb	31	4	19	4
Shrub	3	3	4	5
Tree	2	0	2	0
Total	46	10	30	12

The gradient analysis of the plant community based on my 2012 observational study showed spatial patterns do relate to environmental gradients. A three-dimensional solution was chosen because the NMDS stress level stabilised, falling below 15 with three dimensions (Figure 3.1). The strongest gradients in the NMDS related to compositional variation were 1) A complex gradient reflecting distance from the township and substrate size, with substrate size increasing closer to the township; 2) Plots which have a high proportion of bare ground compared to those which have vegetation; and 3) Distance from the high tide mark (Figure 3.2 - Figure 3.4). The difference in vegetation height can also clearly be seen on the beach (Figure 3.5 & Figure 3.6). Species which tend to be found in sandy substrate, away from the Birdlings Flat township include: *Ficinia spiralis* (A.Rich.) Muasya & de Lange, *Raoulia australis* and *Hypochaeris radicata* L. Species which tend to be found in stony substrate, adjacent to the Birdlings Flat township include: *Lupinus arboreus*, *Senecio elegans* L. and *Carpobrotus edulis* (L.) N.E.Br. Some species show strong preferences for certain environmental conditions, for example *Glaucium flavum* Crantz is most often found close to the sea, and prefers to colonise bare ground (Scott 1963).

The gradient analysis showed that native and exotic species co-occur along all axes, although there was some clustering of species which is consistent regardless of the axes (Figure 3.7 – Figure 3.9). There is some similarity in habitat preferences of some exotic grasses and forbs, with seven species, including *L. ovatus*, closely associating along axis 2 (Figure 3.7). The two tree species *Pittosporum crassifolium* Banks & Sol. ex A.Cunn. and *Coprosma repens* A. Rich. are found away from the sea, but close to the township in areas where the substrate is stable, indicated by the presence of bryophytes. A full species list and species codes are given in Appendix A. The full ordination plots with all variables shown are given in Appendix B.

Spatial patterns also influence the proportion of exotic and native species richness. The candidate models evaluated using AICc showed that in woody plots the model which best approximates the

data is the 'Distance from sea' (Table 3.2). The evidence ratio between the two best models showed that 'Distance from sea' was 1,987 times more likely to be the best approximating model than the Null model (which was the next best model). Model comparisons for the herbaceous plots showed strongest support for the null model, indicating none of the candidate models were supported (Table 3.2). Model averaging was only carried out for the woody plots; this prediction showed that there is a higher proportion of exotic woody species closer to the sea, with an increasing proportion of native species as the distance from the sea increases (Figure 3.10).

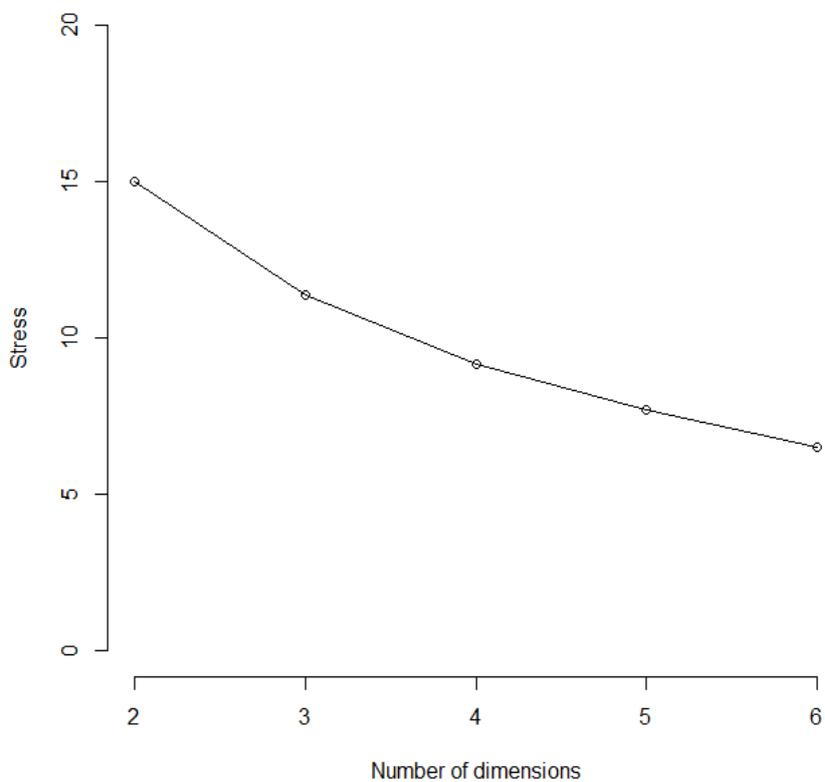


Figure 3.1 Scree plot showing NMDS stress levels. The number of dimensions selected for ordination analyses was three, since this provides an adequately low stress value.

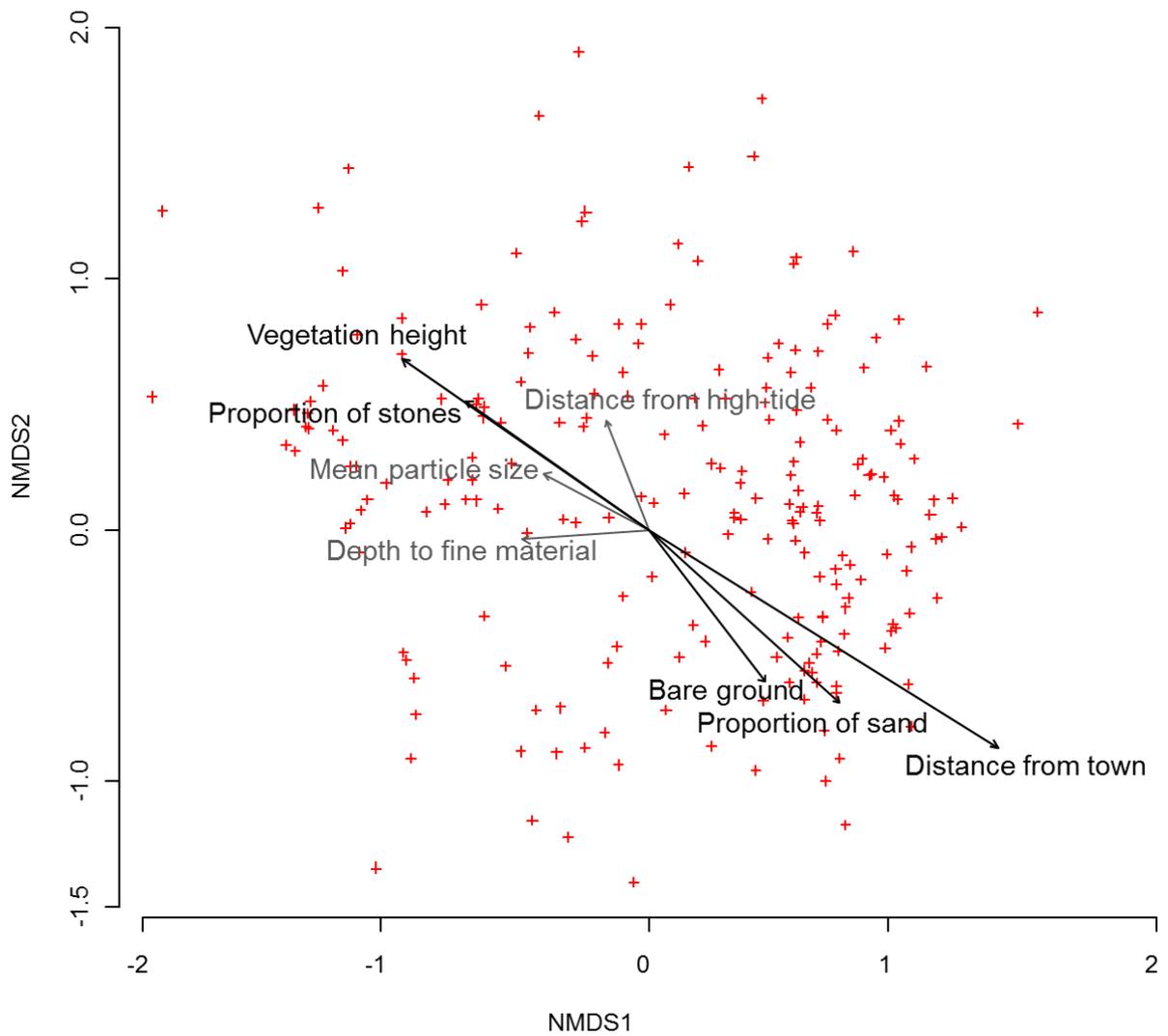


Figure 3.2 NMDS showing the relationship of sites (red crosses) in ordination space, representing axes 1 and 2 of a three-dimensional solution. The environmental variables are overlaid as vectors, with the length of the vector being proportional to the strength of the relationship. Black vectors indicate a highly significant relationship ($p \leq 0.01$) and grey vectors indicate less significant relationships ($p > 0.01$). The stress level is 12.

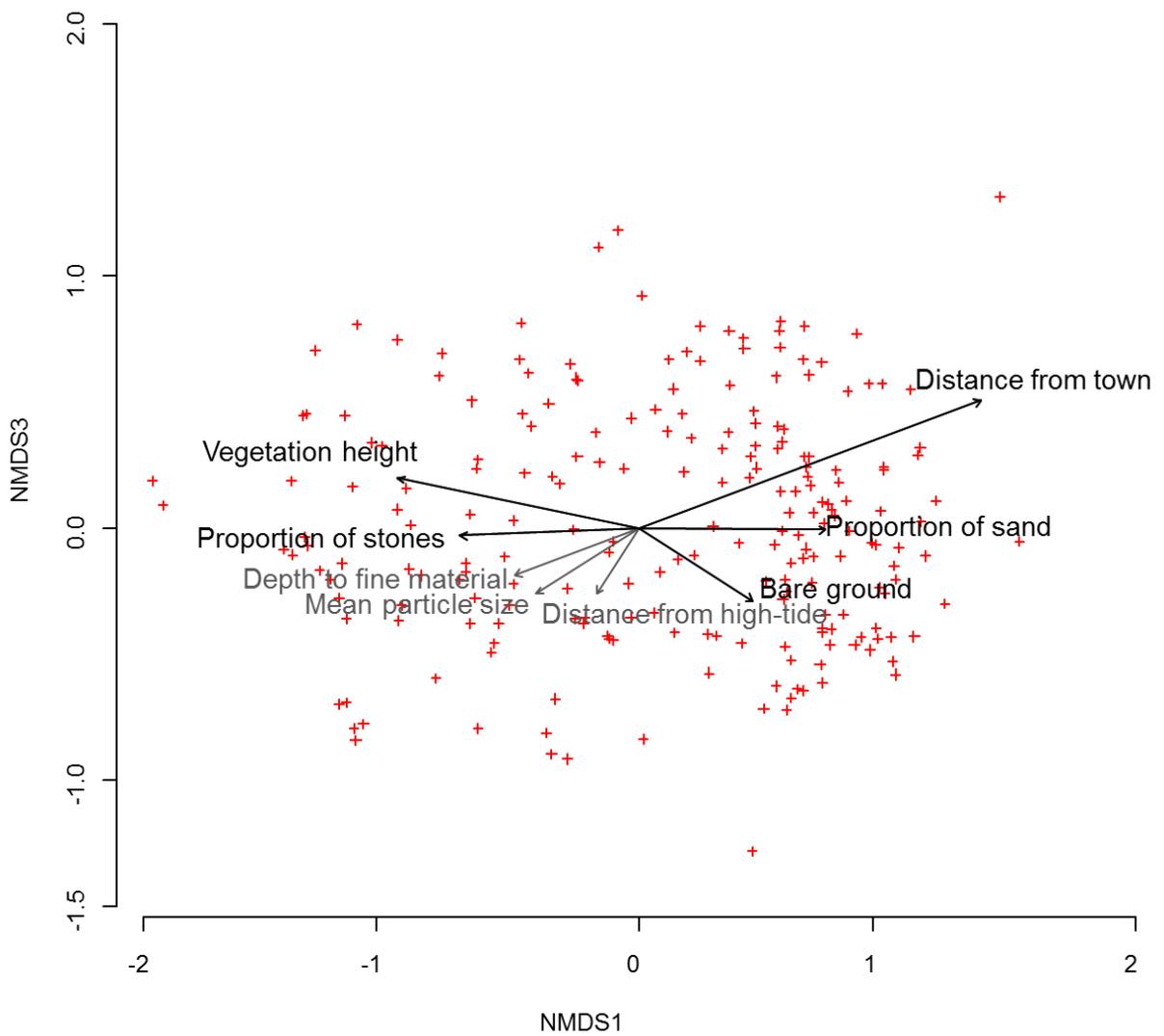


Figure 3.3 NMDS showing the relationship of sites (red crosses) in ordination space, representing axes 1 and 3 of a three-dimensional solution. The environmental variables are overlaid as vectors, with the length of the vector being proportional to the strength of the relationship. Black vectors indicate a highly significant relationship ($p \leq 0.01$) and grey vectors indicate less significant relationships ($p > 0.01$). The stress level is 12.

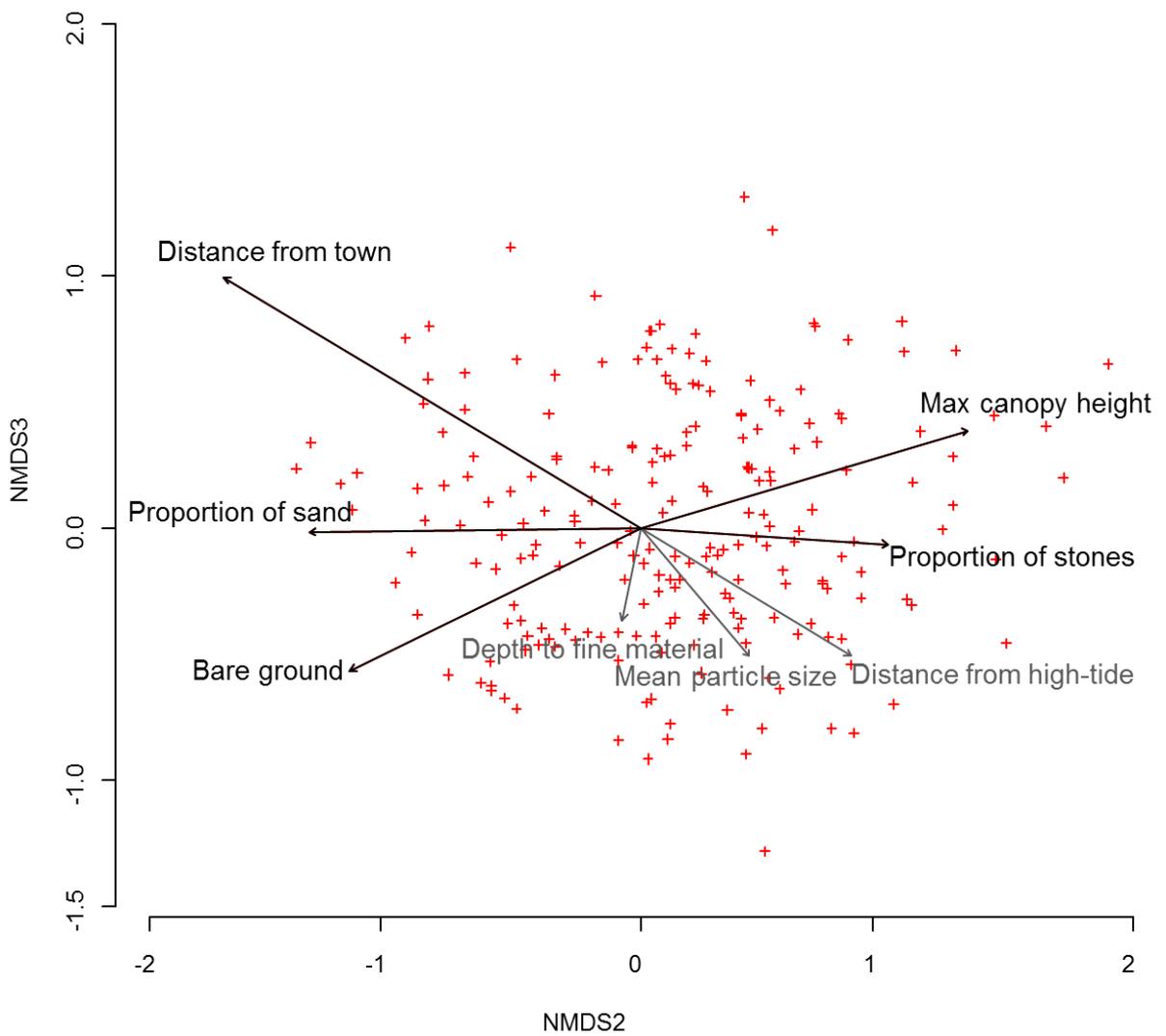


Figure 3.4 NMDS showing the relationship of sites (red crosses) in ordination space, representing axes 2 and 3 of a three-dimensional solution. The environmental variables are overlaid as vectors, with the length of the vector being proportional to the strength of the relationship. Black vectors indicate a highly significant relationship ($p \leq 0.01$) and grey vectors indicate less significant relationships ($p > 0.01$). The stress level is 12.



Figure 3.5 The vegetation has a low stature away from Birdlings Flat township.



Figure 3.6 The mean vegetation height is taller in front of the Birdlings Flat township.

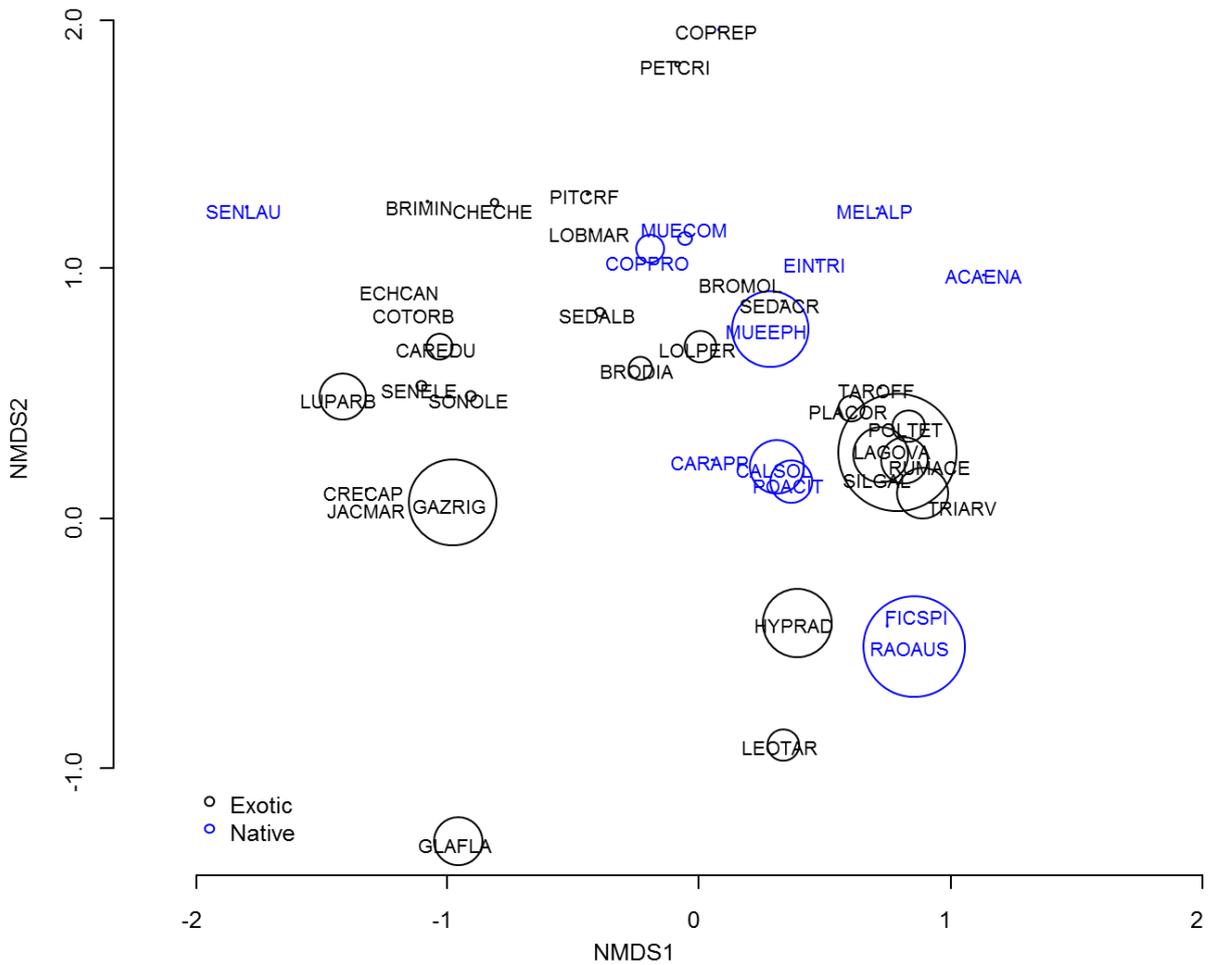


Figure 3.7 NMDS ordination plot of quadrat-scale composition patterns showing weighted average species scores in ordination space. The ordination is based on Bray-Curtis dissimilarities, showing the first two axes of the three-dimensional solution. Circles are proportional to the number of quadrats each species occurs in. Exotic species are shown in black, native species in blue. Stress level is 12. Species codes are provided in Appendix A.

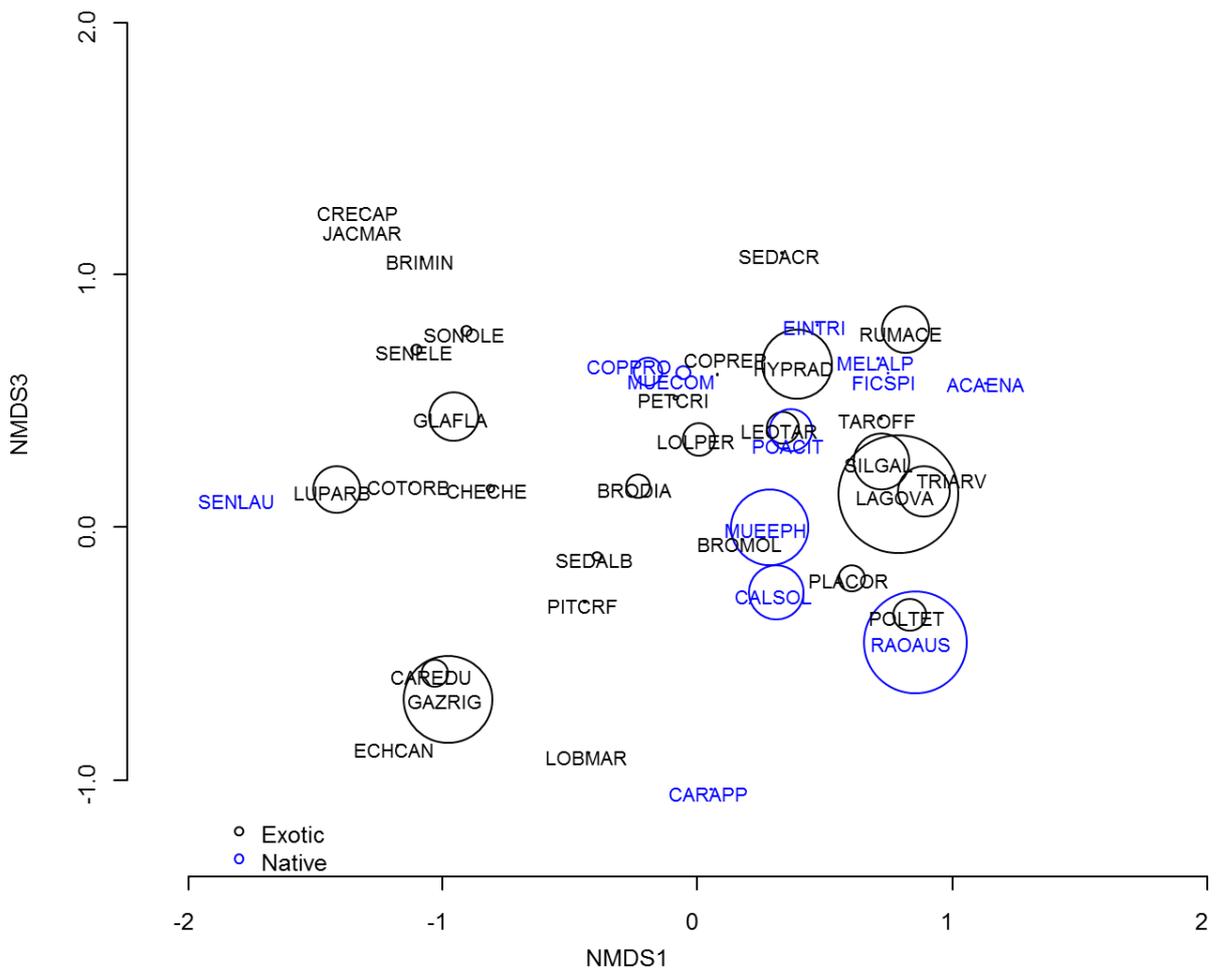


Figure 3.8 NMDS ordination plot of quadrat-scale composition patterns showing weighted average species scores in ordination space. The ordination is based on Bray-Curtis dissimilarities, showing the axes 1 and 3 of the three-dimensional solution. Circles are proportional to the number of quadrats each species occurs in. Exotic species are shown in black, native species in blue. Stress level is 12. Species codes are provided in Appendix A.

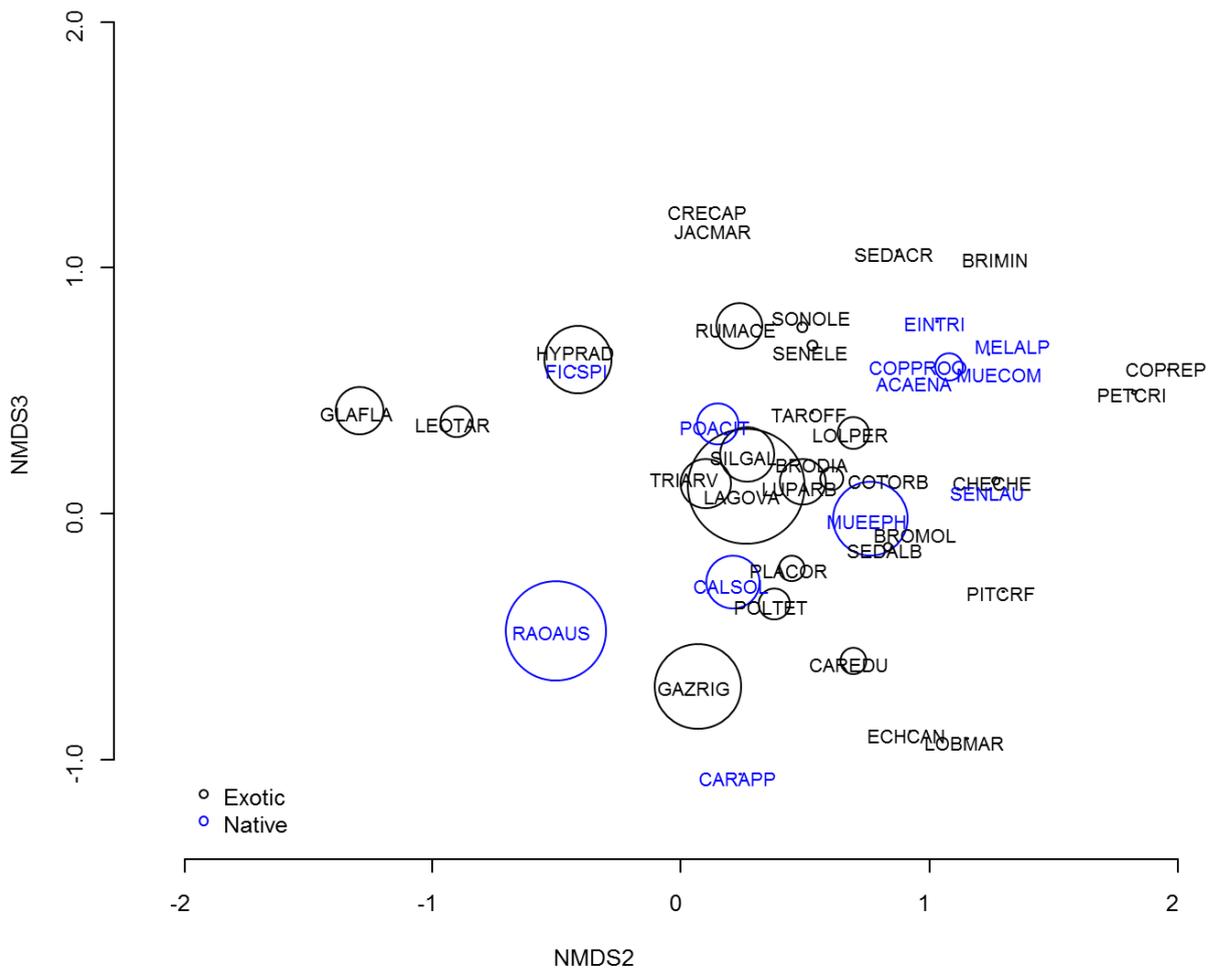


Figure 3.9 NMDS ordination plot of quadrat-scale composition patterns showing weighted average species scores in ordination space. The ordination is based on Bray-Curtis dissimilarities, showing the axes 2 and 3 of the three-dimensional solution. Circles are proportional to the number of quadrats each species occurs in. Exotic species are shown in black, native species in blue. Stress level is 12. Species codes are provided in Appendix A.

Table 3.2 Comparison of candidate models predicting which variables impact on the proportion of exotic and native species per quadrat, based on woody and herbaceous quadrats. Models with QAICc $\Delta_i \leq 2$ have equally strong support (*sensu* Burnham and Anderson 2002) and these models are shown in bold. K = number of estimated parameters in the model; QAICc = Quasi Akaike's Information Criteria (corrected for K); QAICc Δ_i = difference in QAICc between best model (i.e. with smallest value of AICc) and remaining candidate models; QAICc W_i = Akaike weights; Quasi likelihood = the maximum likelihood estimate.

<i>Subset</i>	<i>Model</i>	<i>K</i>	<i>QAICc</i>	Δ_i <i>QAICc</i>	<i>QAICc Weight</i>	<i>Quasi Likelihood</i>
<i>Woody</i>	Distance from sea	2	109.64	0.0	1	-52.74
	Null	1	124.83	15.19	0	-61.39
	Year	2	125.78	16.15	0	-60.81
	Substrate	2	126.22	16.58	0	-61.03
	Distance from town	2	126.81	17.17	0	-61.32
<i>Herbaceous</i>	Null	1	111.48	0	0.31	-54.72
	Substrate	2	112.16	0.67	0.22	-54.02
	Distance from sea	2	112.43	0.94	0.19	-54.15
	Distance from town	2	112.7	1.22	0.17	-54.29
	Year	2	113.51	2.02	0.11	-54.69

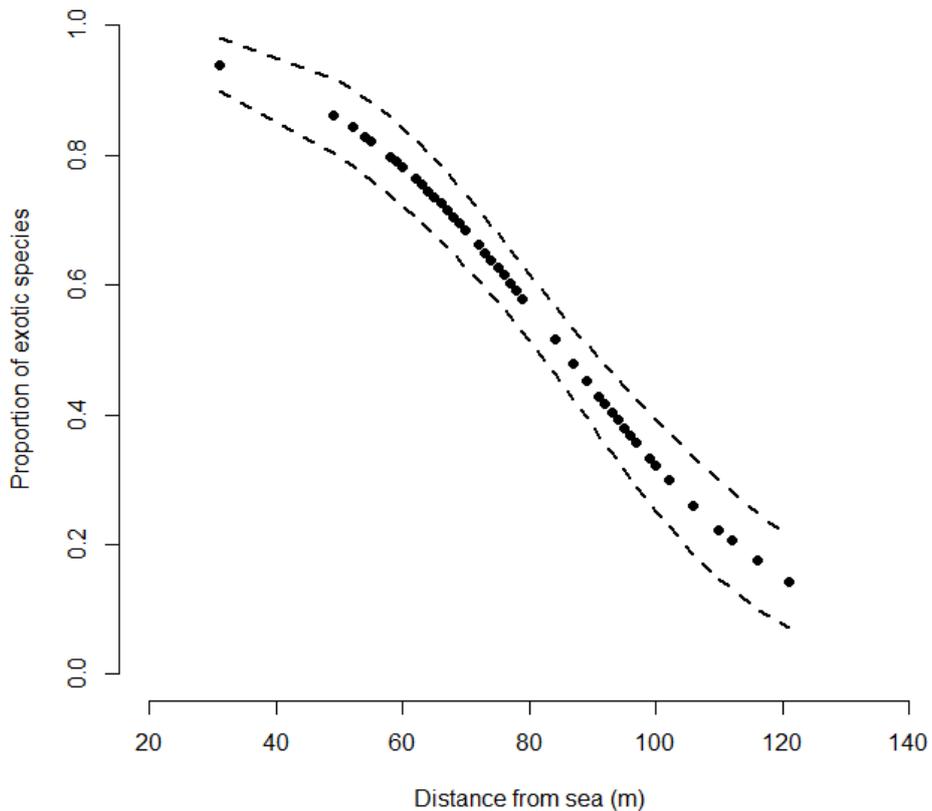


Figure 3.10 Predicted proportion of exotic woody species to native woody species presence in any given quadrat based on 2006 and 2012 survey data. The points indicate the mean probability of an exotic woody species being present based on the distance from high tide. Dotted lines indicate the unconditional standard errors (± 1.96) for these estimates.

Co-occurrence Patterns

The null model analyses do not support my hypothesis that facilitation is the dominant process determining community structure in gravel beach communities. The null models compare the observed number of species pairs co-occurring to the number of species pairs expected to co-occur. The data were split into 54 subsets based on environmental variables. In 50 of the data subsets the randomised C-score was less than the observed value, and for 23 of those data subsets this result was statistically significant (Table 3.1). For example, in the subset of sites which included those at Kaitorete Spit, being the area not adjacent to the Birdlings Flat town, with all vegetation and substrate types, the observed C-score was higher than the null model C-scores in all 1000 randomisations (Figure 3.11). The occurrence of the observed number of C-scores being greater than

the randomised subset is consistent with competition, or differing habitat requirements. There were four data subsets for which the randomised C-score was greater than the observed value, suggesting species aggregation, although none of the values were statistically significant (Table 3.3). The occurrence of the observed number of C-scores being less than the randomised subset is consistent with facilitation, or similar habitat requirements. The data subsets which showed significant species segregation or non-significant species aggregations did not contain similar environmental variables.

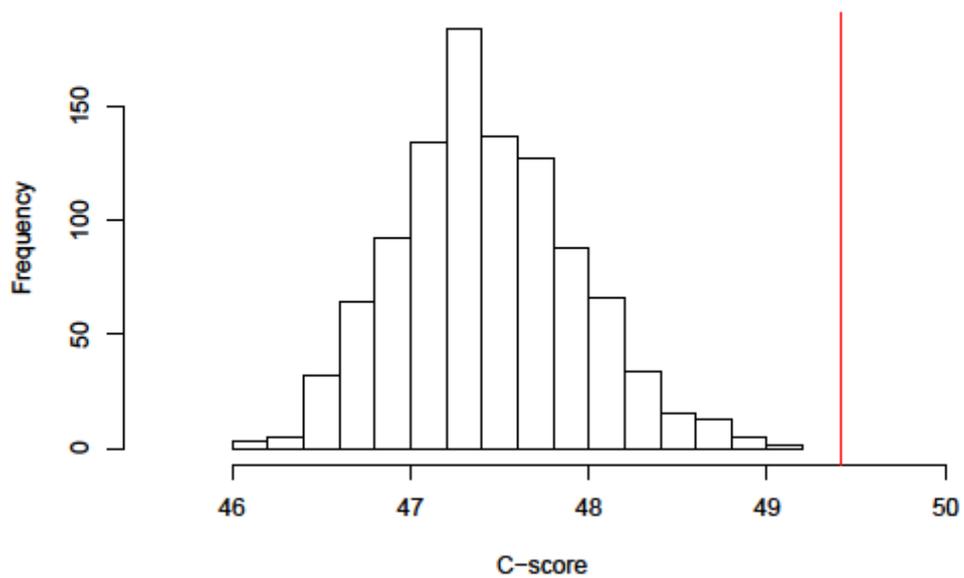


Figure 3.11 Observed C-score (red line) compared to the distribution of randomised C-scores (histogram) for the data subset Kaitorete Spit, being the area not adjacent to the Birdlings Flat town, but otherwise including all vegetation and all substrate sizes.

Table 3.3 Null model analysis showing observed and expected C-scores and the proportion lower/higher than expected for each subset of the data. The C-scores where the value of observed is significantly lower/higher than expected are highlighted in bold.

<i>Location</i>	<i>Distance from high tide</i>	<i>Vegetation type</i>	<i>Substrate</i>	<i>Number of rows (sites)</i>	<i>Number of columns (species)</i>	<i>Observed checkerboard pairs</i>	<i>Observed C-score</i>	<i>Standardised effect size of C-score</i>	<i>Proportion of random C-scores lower than observed</i>	<i>Proportion of random C-scores higher than observed</i>	
Birdlings Flat	far	all	more sand	13	20	649	3.42	5.22	1	0	
			more stones	13	19	635	3.71	3.03	0.99	0.01	
		lupin	all	26	26	3011	9.26	3.31	0.99	0.01	
			more sand	4	13	38	0.49	2.57	0.96	0.04	
			more stones	4	14	65	0.71	-0.77	0.26	0.74	
			all	8	19	308	1.80	2.62	0.99	0.01	
		native shrub	more sand	5	15	98	0.93	2.54	0.98	0.02	
			more stones	6	15	146	1.39	1.89	0.96	0.04	
		mid	all	all	11	21	678	3.23	1.58	0.93	0.07
				more sand	13	15	281	2.68	1.81	0.93	0.07
	more stones			13	17	294	2.16	-0.25	0.47	0.53	
	all			26	21	1200	5.71	0.63	0.75	0.25	
	more sand			7	12	80	1.21	4.30	0.99	0.01	
	lupin		more stones	6	14	71	0.78	0.45	0.68	0.32	
			all	13	19	339	1.98	2.39	0.97	0.03	
			more sand	2	8	NA	NA	NA	NA	NA	
	native shrub		more stones	2	8	NA	NA	NA	NA	NA	
			all	4	12	54	0.82	0.24	0.66	0.34	

<i>Location</i>	<i>Distance from high tide</i>	<i>Vegetation type</i>	<i>Substrate</i>	<i>Number of rows (sites)</i>	<i>Number of columns (species)</i>	<i>Observed checkerboard pairs</i>	<i>Observed C-score</i>	<i>Standardised effect size of C-score</i>	<i>Proportion of random C-scores lower than observed</i>	<i>Proportion of random C-scores higher than observed</i>
Kaitorete Spit	near	all	more sand	12	9	57	1.58	0.63	0.79	0.21
			more stones	12	12	154	2.33	2.79	0.98	0.02
			all	24	17	518	3.81	3.60	0.99	0.01
		lupin	more sand	3	5	NA	NA	NA	NA	NA
			more stones	3	5	NA	NA	NA	NA	NA
			all	6	7	13	0.62	-0.82	0.27	0.73
		native shrub	more sand	1	6	NA	NA	NA	NA	NA
			more stones	2	8	NA	NA	NA	NA	NA
			all	3	11	NA	NA	NA	NA	NA
	far	all	more sand	29	20	2446	12.87	1.92	0.96	0.04
			more stones	30	22	4356	18.86	3.43	0.99	0.01
			all	59	24	13639	49.42	4.18	0.99	0.01
		lupin	more sand	9	18	355	2.32	0.94	0.84	0.16
			more stones	9	19	460	2.69	1.99	0.96	0.04
			all	18	19	1604	9.38	3.31	0.99	0.01
		native shrub	more sand	21	17	1073	7.89	2.39	0.99	0.01
			more stones	20	18	1340	8.76	1.01	0.85	0.15
			all	41	21	4911	23.39	2.85	0.99	0.01
mid	all	more sand	30	18	2340	15.29	3.50	0.99	0.01	
		more stones	30	22	3553	15.38	2.04	0.97	0.03	

<i>Location</i>	<i>Distance from high tide</i>	<i>Vegetation type</i>	<i>Substrate</i>	<i>Number of rows (sites)</i>	<i>Number of columns (species)</i>	<i>Observed checkerboard pairs</i>	<i>Observed C-score</i>	<i>Standardised effect size of C-score</i>	<i>Proportion of random C-scores lower than observed</i>	<i>Proportion of random C-scores higher than observed</i>
			all	60	23	11691	46.21	4.16	1	0
		lupin	more sand	7	17	189	1.39	-0.65	0.28	0.72
			more stones	6	16	209	1.74	3.25	0.99	0.01
			all	13	20	806	4.24	0.90	0.85	0.15
		native shrub	more sand	23	17	1160	8.53	4.05	0.99	0.01
			more stones	24	17	1524	11.21	2.39	0.99	0.01
			all	47	19	5354	31.31	4.89	1	0
	near	all	more sand	29	22	3131	13.56	3.22	0.99	0.01
			more stones	29	24	3805	13.79	2.03	0.97	0.03
			all	58	28	14228	37.64	3.15	0.99	0.01
		lupin	more sand	9	18	408	2.67	1.53	0.93	0.07
			more stones	10	24	746	2.70	0.69	0.78	0.22
			all	19	26	2357	7.25	0.71	0.78	0.22
		native shrub	more sand	19	12	509	7.71	-0.72	0.25	0.75
			more stones	20	17	1348	9.91	3.03	0.99	0.01
			all	39	17	3753	27.56	3.30	0.99	0.01

3.2 Native facilitation experiment

Seedling mortality was high for all species, ranging from 39% to 100% (Figure 3.12). Only 0.01% of *Coprosma propinqua* seedlings survived the 12 month experiment. Eighty-seven percent of small *C. propinqua* seedlings died within the first month (September 2012) and none were alive by February 2013. Larger *C. propinqua* seedlings survived longer than the smaller seedlings, but they had the highest mortality between January and February 2013. *Muehlenbeckia complexa* and *M. ephedroides* had the highest survival rates. *Muehlenbeckia ephedroides* showed a steady decline over the year, with 61% survival. *Muehlenbeckia complexa* individuals died at a steady rate, with a sharper increase in mortality from mid-summer into early autumn.

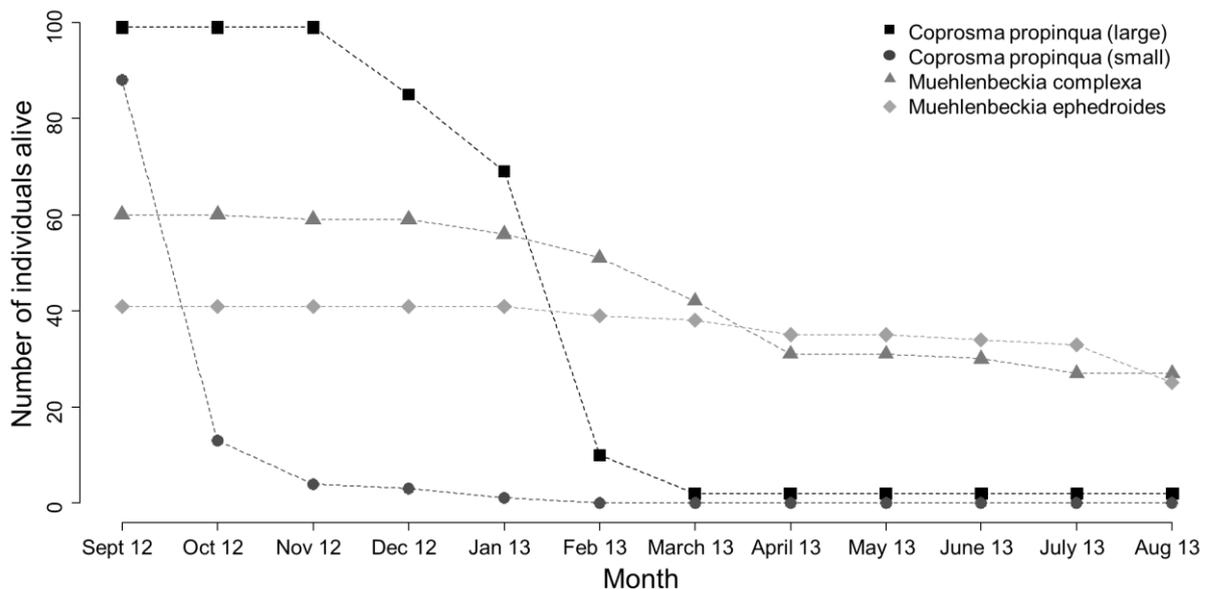


Figure 3.12 Seedling mortality by species over time. Planting occurred in September 2012 and mortality was measured monthly for 12 months.

Candidate models evaluated using QAICc show that different models best approximate the data for each species (Table 3.4). For *M. complexa* the best model was 'Depth to fine material'; the evidence ratio between the two best models showed that 'Depth to fine material' was 8.05 times more likely to be the best approximating model than 'Distance from sea'. For *M. ephedroides* the best model is 'Cover + Treatment', which is a combination of whether the seedling was planted in bare gravel or next to a shrub along with whether it received fertiliser or water treatments. The evidence ratio between the two best models show that 'Cover + Treatment' is 4.55 times more likely to be the best approximating model than 'Treatment'.

The models average predictions show that the survival of each species is affected by different factors. *Muehlenbeckia complexa* has a higher chance of survival when planted in areas where fine material (< 2 mm) is close to the surface (Figure 3.13), or when planted closer to the sea (Figure 3.14). The water and fertiliser treatments and nurse shrubs appear to have little impact on its survival.

In contrast, *Muehlenbeckia ephedroides* has the best chance of survival when planted with only fertiliser, and a lower chance of survival when planted with both fertiliser and water treatments (Figure 3.15). *Muehlenbeckia ephedroides* seedlings also appear to have a higher probability of survival when planted in bare gravel rather than with a nurse shrub. The distance from the sea appears to have little impact.

These findings do not support my hypothesis that native seedling survival will increase when individuals are sheltered by an established shrub, or that survival will be higher at greater distances from the sea. The survival rates do support my hypotheses that nutrient availability is a limiting factor, but there is not strong support to indicate that water availability is a limiting factor.

Table 3.4 Comparison of candidate models predicting which variables impact on seedling survival. Models with QAICc $\Delta_i \leq 2$ have equally strong support (sensu Burnham and Anderson 2002) and these models are shown in bold. K = number of estimated parameters in the model; QAICc = Quasi Akaike's Information Criteria (corrected for K); QAICc Δ_i = difference in QAICc between best model (i.e. with smallest value of AICc) and remaining candidate models; QAICc W_i = Akaike weights; Quasi likelihood = the maximum likelihood estimate.

<i>Species</i>	<i>Model</i>	<i>K</i>	<i>QAICc</i>	Δ_i <i>QAICc</i>	<i>QAICc Weight</i>	<i>Quasi Likelihood</i>
<i>Muehlenbeckia complexa</i>	Depth to fine material	2	79.1	0.0	0.72	-37.4
	Distance from sea	2	83.2	4.2	0.09	-39.5
	Gravel Size	2	84.1	5.0	0.06	-39.9
	Null model	1	84.1	5.6	0.04	-41.3
	Cover	2	85.1	6.0	0.04	-40.4
	Shrub Height	2	86.0	6.9	0.02	-40.9
	Seedling Height	2	86.7	7.7	0.02	-41.3
	Treatment	4	89.0	10.0	0.00	-40.2
	Cover + Treatment	5	89.6	10.5	0.00	-39.2
	Cover * Treatment	8	96.6	17.5	0.00	-38.9
<i>Muehlenbeckia ephedroides</i>	Cover + Treatment	5	48.9	0.0	0.61	-18.6
	Treatment	4	52.0	3.0	0.13	-21.4
	Depth to fine material	2	52.6	3.6	0.10	-24.1
	Cover	2	53.0	4.1	0.08	-24.4
	Cover * Treatment	8	54.3	5.3	0.04	-16.9
	Null model	1	57.0	8.0	0.01	-27.4
	Seedling height	2	57.4	8.5	0.01	-26.5
	Gravel size	2	58.1	9.1	0.01	-26.9
	Distance from sea	2	58.6	9.6	0.01	-27.1
	Shrub Height	2	59.1	10.2	0.00	-27.4

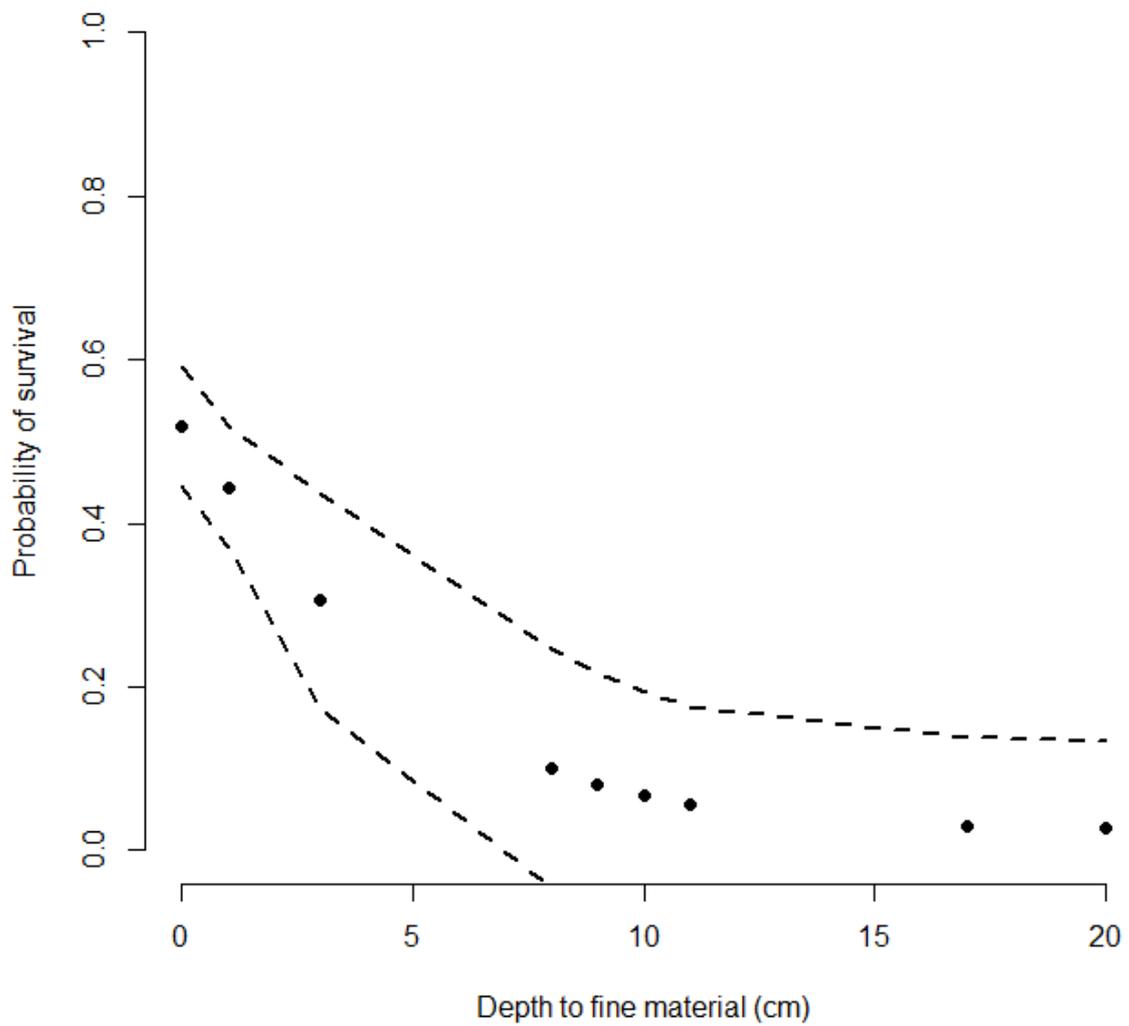


Figure 3.13 Predicted probability of survival of *Muehlenbeckia complexa* seedlings based on model averaging. The points indicate mean likelihood of survival in relation to the depth to fine material. Dotted lines indicate the unconditional standard errors (± 1.96) for these estimates.

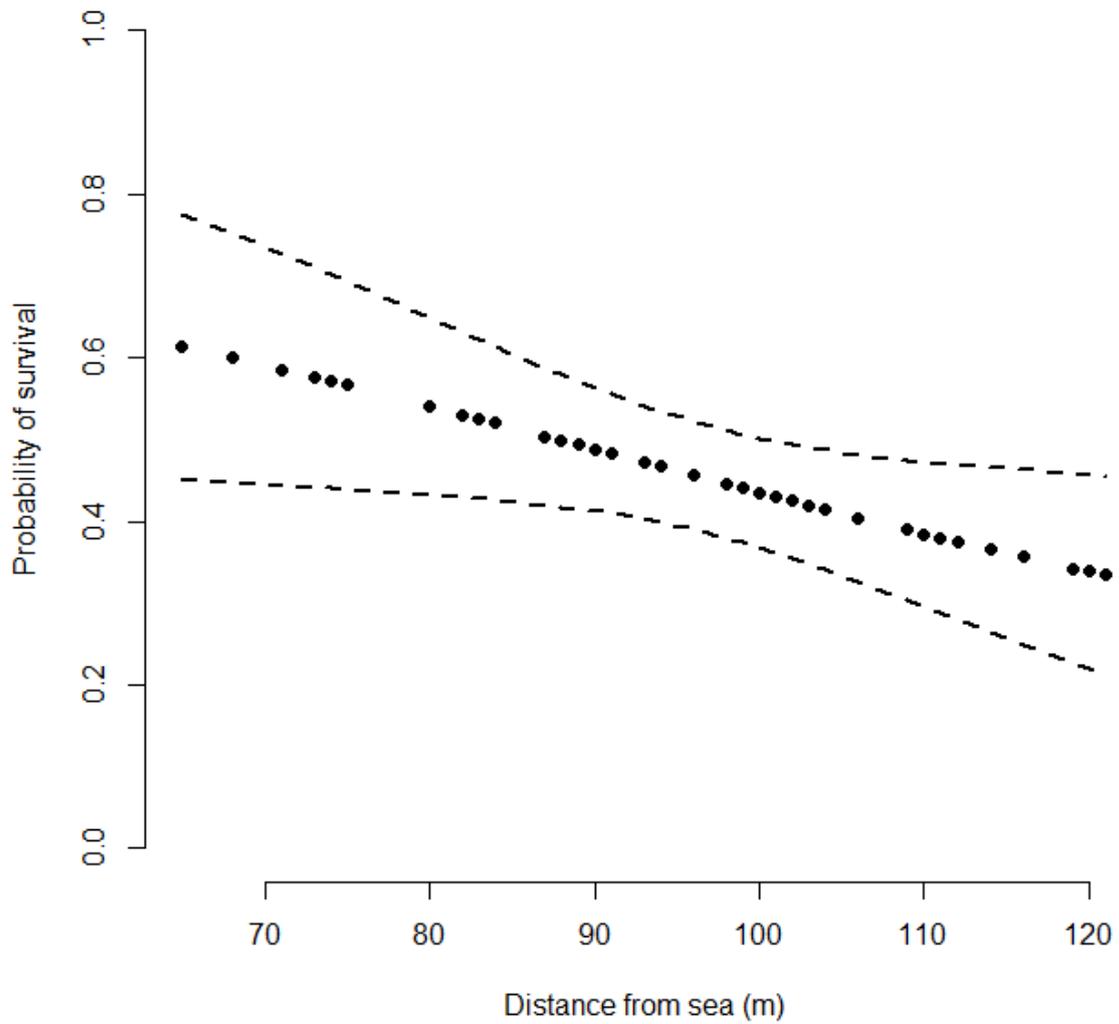


Figure 3.14 Predicted probability of survival of *Muehlenbeckia complexa* seedlings based on model averaging. The points indicate mean likelihood of survival based on the distance from the sea. Dotted lines indicate the unconditional standard errors (± 1.96) for these estimates.

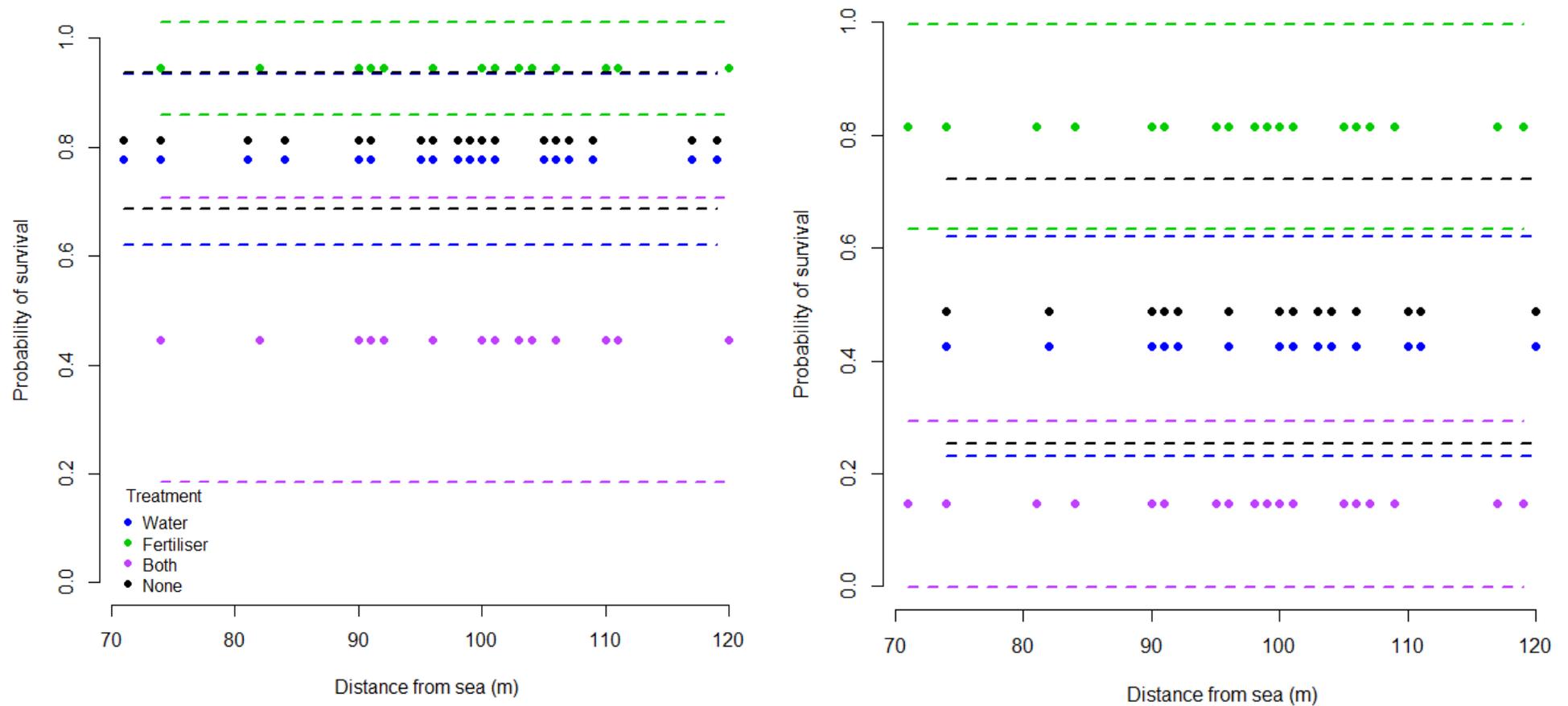


Figure 3.15 Predicted probability of survival of *Muehlenbeckia ephedroides* seedlings, planted in bare gravel (left) or planted next to a shrub (right), based on model averaging. The points indicate mean likelihood of survival of seedlings based on treatment and the distance from the sea. Dotted lines indicate the unconditional standard errors (± 1.96) for these estimates.

3.3 Exotic facilitation experiment

Gazania cover per quadrat increased on average over the course of the experiment (Table 3.5), returning to all of the quadrats where it had been removed as well as colonising all except for one of the previously bare sites. The maximum cover of *Gazania* per quadrat was lower on average for all treatment types in 2012 than it was prior to the experiment in 2011. Mortality was high for all planted seedlings, with less than 20% survival by September 2012 (Figure 3.16 - Figure 3.18).

Table 3.5 Mean *Gazania* cover measured in quadrats at the start and end of the experiment; 1 standard error is given in parentheses.

	<i>Gazania</i> Cover 2010 (%)	<i>Gazania</i> Cover 2012 (%)	Mean change in <i>Gazania</i> cover
Gazania	27.3 (1.97)	18.6 (1.09)	-8.7 (1.75)
Gazania Removed	0 (0)	10.4 (0.79)	+10.4 (0.79)
Bare Gravel	0 (0)	6.9 (0.70)	+6.9 (0.70)

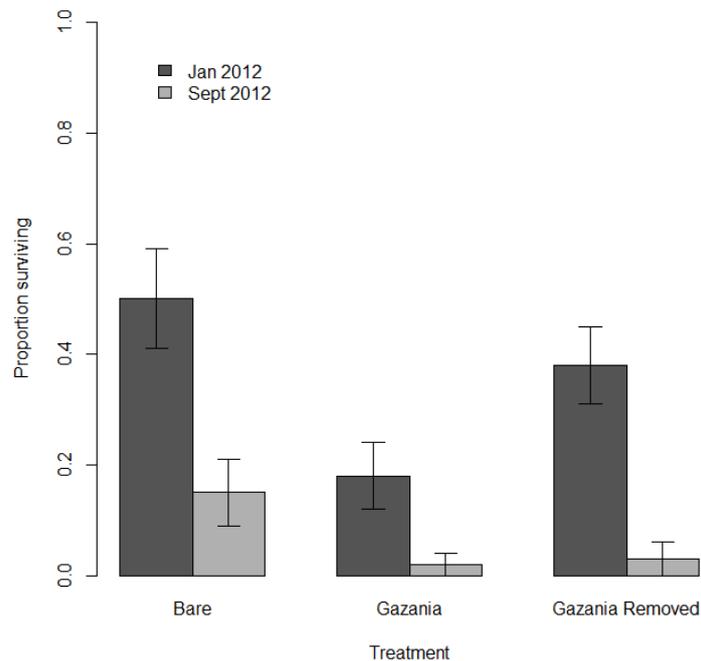


Figure 3.16 Survival of *Coprosma acerosa* seedlings planted with three different *Gazania* treatments. Survival was calculated as the mean proportion of individuals surviving per quadrat. Error bars are 1 standard error of the mean.

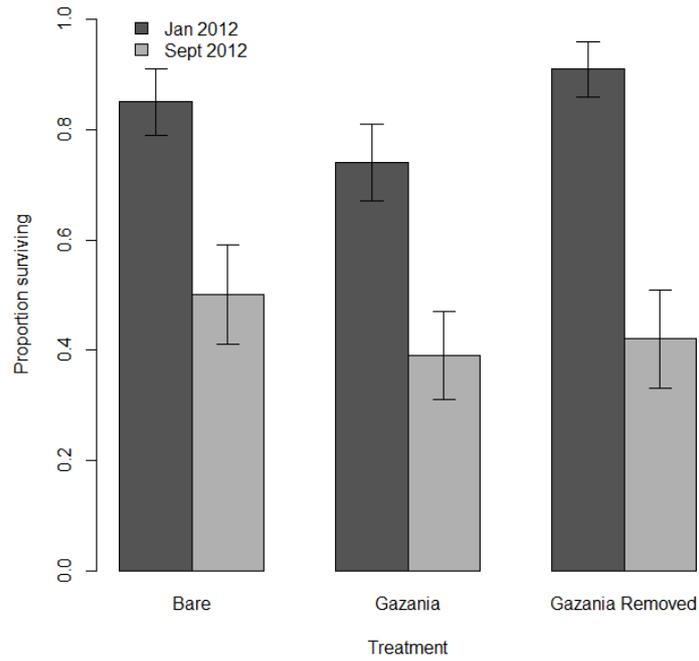


Figure 3.17 Survival of *Ficinia nodosa* seedlings planted with three different *Gazania* treatments. Survival was calculated as the mean proportion of individuals surviving per quadrat. Error bars are 1 standard error of the mean.

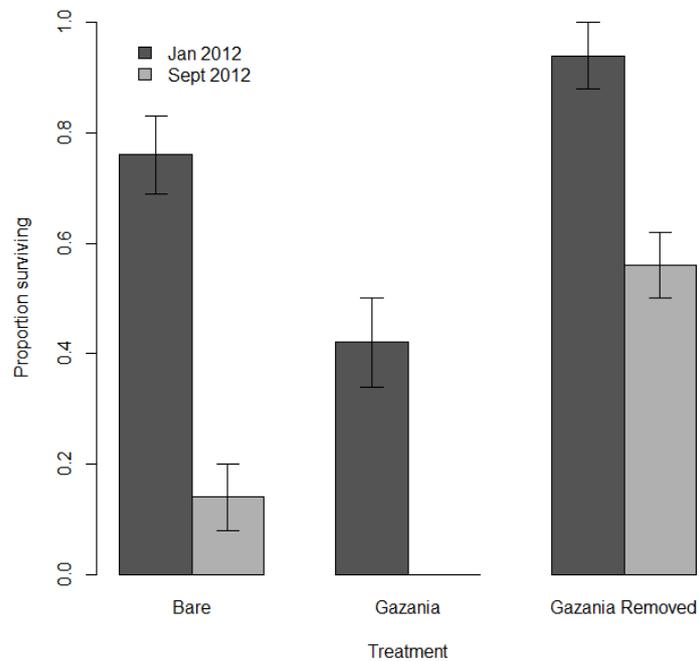


Figure 3.18 Survival of *Muehlenbeckia ephedroides* seedlings planted with three different *Gazania* treatments. Survival was calculated as the mean proportion of individuals surviving per quadrat. Error bars are 1 standard error of the mean.

The candidate models evaluated using QAICc showed that different models best approximate the data for each species (Table 3.6). For *Coprosma acerosa* the best model was 'Treatment'. The evidence ratio between the two best models shows that 'Treatment' was 2.98 times more likely to be the best approximating model than 'Distance from sea + Treatment'. For *Ficinia nodosa* the best model was 'Distance from sea + Treatment', but the evidence ratio between the two best models shows that it was only 1.05 times more likely to be the best approximating model than 'Distance from sea'. For *Muehlenbeckia ephedroides* the best model was 'Treatment' and the evidence ratio between the two best models shows that it was 1.27 times more likely to be the best approximating model than 'Distance from sea + Treatment'.

The model average predictions showed that for each species survival is affected by different factors. *Coprosma acerosa* had a lower chance of survival when planted with *Gazania*, and the best chance of survival when planted in bare gravel. The distance from the sea appeared to have little impact (Figure 3.19). *Ficinia nodosa* only showed a small change in likelihood of survival based on planting treatments, but had a much higher chance of survival with increasing distance from the sea (Figure 3.20). *Muehlenbeckia ephedroides* had a lower chance of survival when planted with *Gazania*, and the best chance of survival in plots where *Gazania* was removed. The distance from the sea appeared to have a small impact (Figure 3.21).

These findings support my hypothesis that native seedling survival is related to the presence of *Gazania*, but contrary to my hypothesis *Gazania* has an inhibitory rather than facilitative effect. There is some support for my hypothesis that native seedling survival will be higher at greater distances from the sea, with this being evident for *F. nodosa* and *M. ephedroides*, but not for *C. acerosa*.

Table 3.6 Comparison of candidate models predicting which variables impact on seedling survival. Models with QAICc $\Delta_i \leq 2$ have equally strong support (sensu Burnham and Anderson 2002) and these models are shown in bold. K = number of estimated parameters in the model; QAICc = Quasi Akaike's Information Criteria (corrected for K); QAICc Δ_i = difference in QAICc between best model (i.e. with smallest value of AICc) and remaining candidate models; QAICc W_i = Akaike weights; Quasi likelihood = the maximum likelihood estimate.

<i>Species</i>	<i>Model</i>	<i>K</i>	<i>QAICc</i>	<i>QAICc Δ_i</i>	<i>QAICc W_i</i>	<i>Quasi Likelihood</i>
<i>Coprosma acerosa</i>	Treatment	4	111.8	0.0	0.64	-51.5
	Distance from sea + Treatment	5	114.13	2.3	0.20	-51.5
	All factors except treatment	5	116.19	4.4	0.07	-52.5
	Null model	2	116.57	4.8	0.06	-56.2
	Distance from sea	3	118.55	6.7	0.02	-56.1
<i>Ficinia nodosa</i>	Distance from sea	3	69.72	0.0	0.65	-31.7
	Distance from sea + Treatment	5	71.76	2.0	0.23	-30.3
	All factors except treatment	5	74.26	4.5	0.07	-31.6
	Null model	2	76.02	6.3	0.03	-35.9
	Treatment	4	76.73	7.0	0.02	-34.0
<i>Muehlenbeckia ephedroides</i>	Treatment	4	72.20	0.0	0.66	-31.7
	Distance from sea + Treatment	5	73.51	1.3	0.34	-31.2
	Null model	2	89.6	17.4	0.00	-42.7
	Distance from sea	3	90.77	18.6	0.00	-42.2
	All factors except treatment	5	92.87	20.7	0.00	-40.9

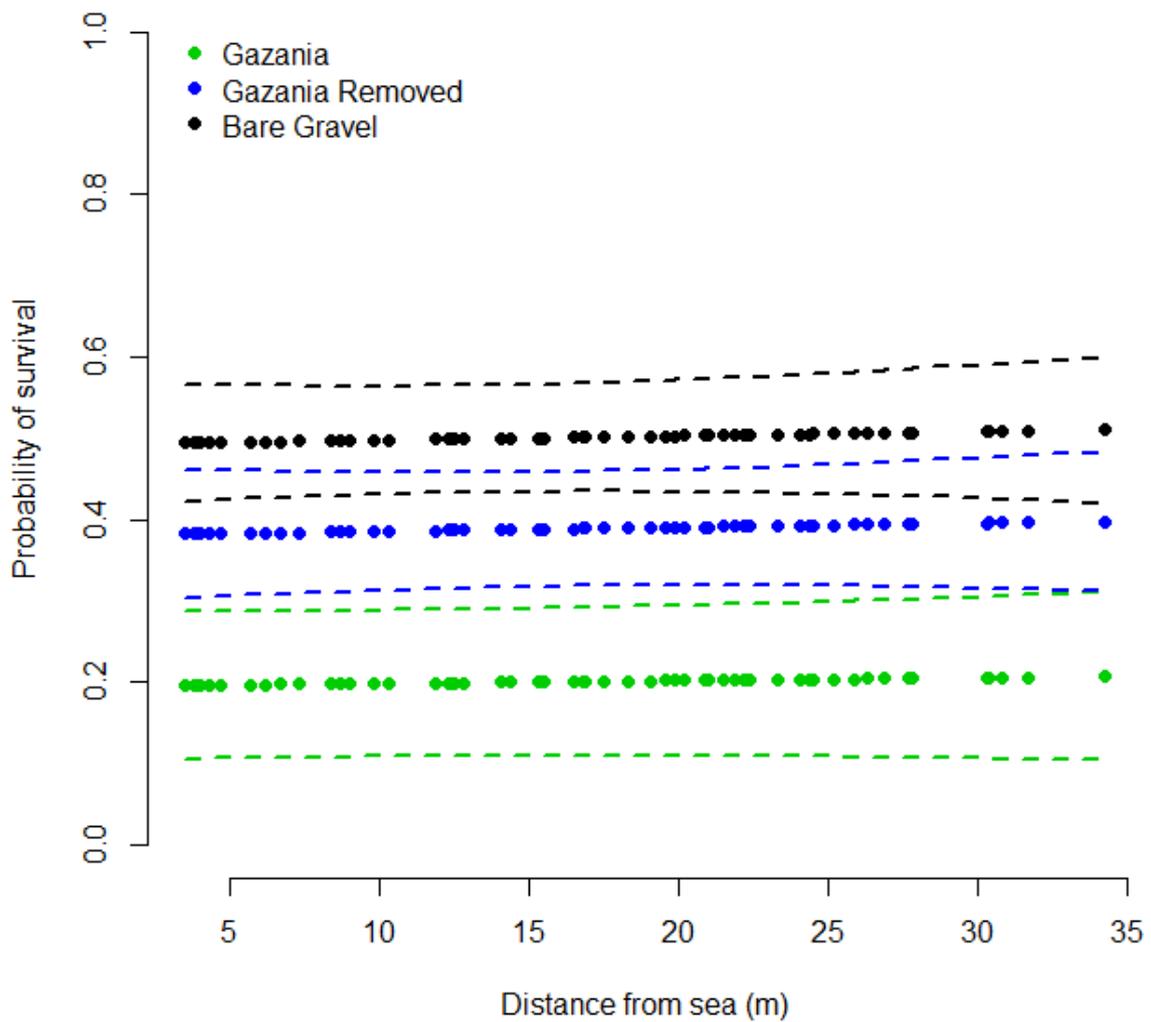


Figure 3.19 Predicted probability of survival of *Coprosma acerosa* seedlings based on January 2012 survival based on model averaging. The points indicate mean likelihood of survival based on distance from the sea and the *Gazania* treatment method. Dotted lines indicate the unconditional standard errors (± 1.96) for these estimates.

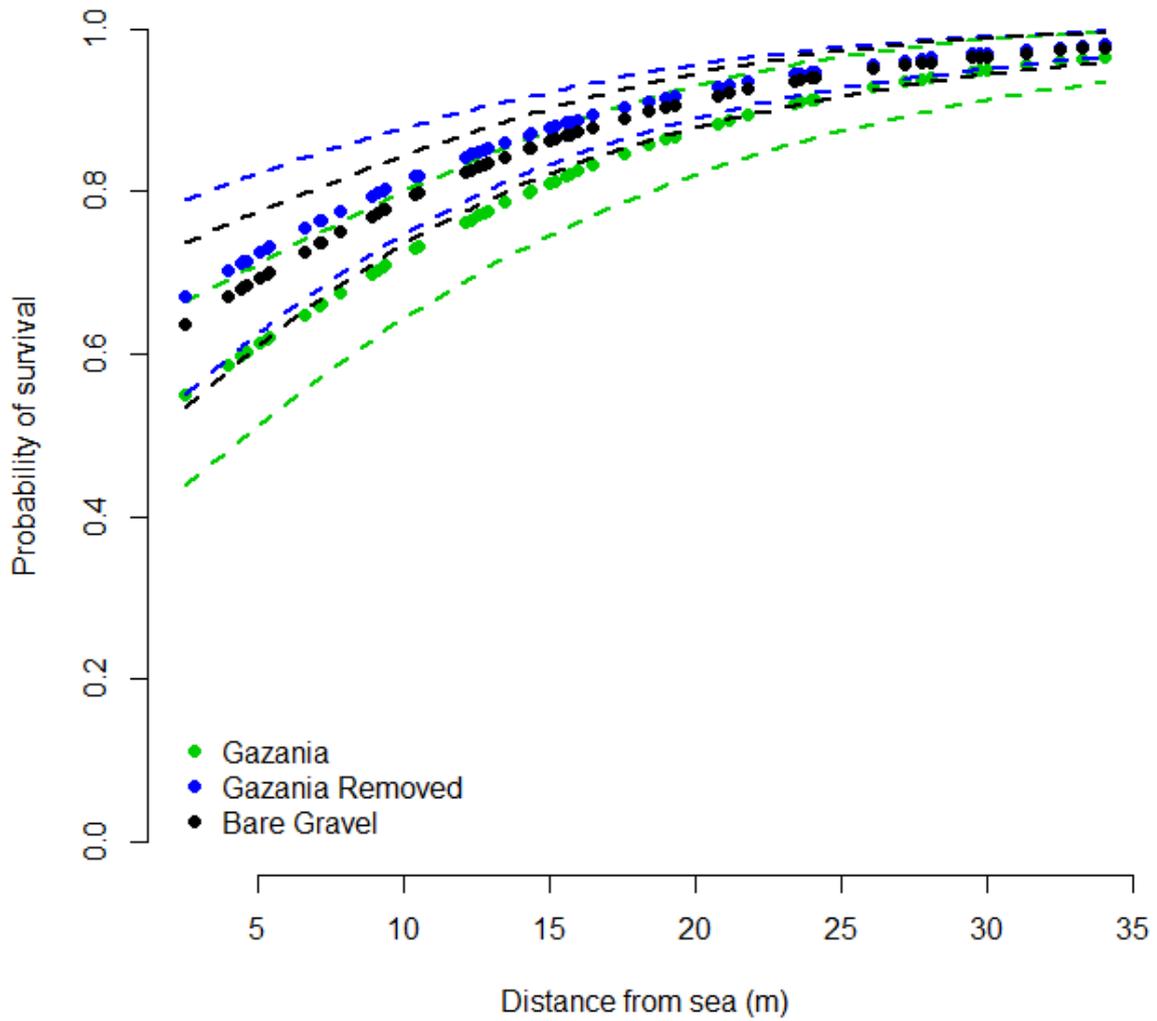


Figure 3.20 Predicted probability of survival of *Ficinia nodosa* seedlings based on January 2012 survival based on model averaging. The points indicate mean likelihood of survival based on distance from the sea and the *Gazania* treatment method. Dotted lines indicate the unconditional standard errors (± 1.96) for these estimates.

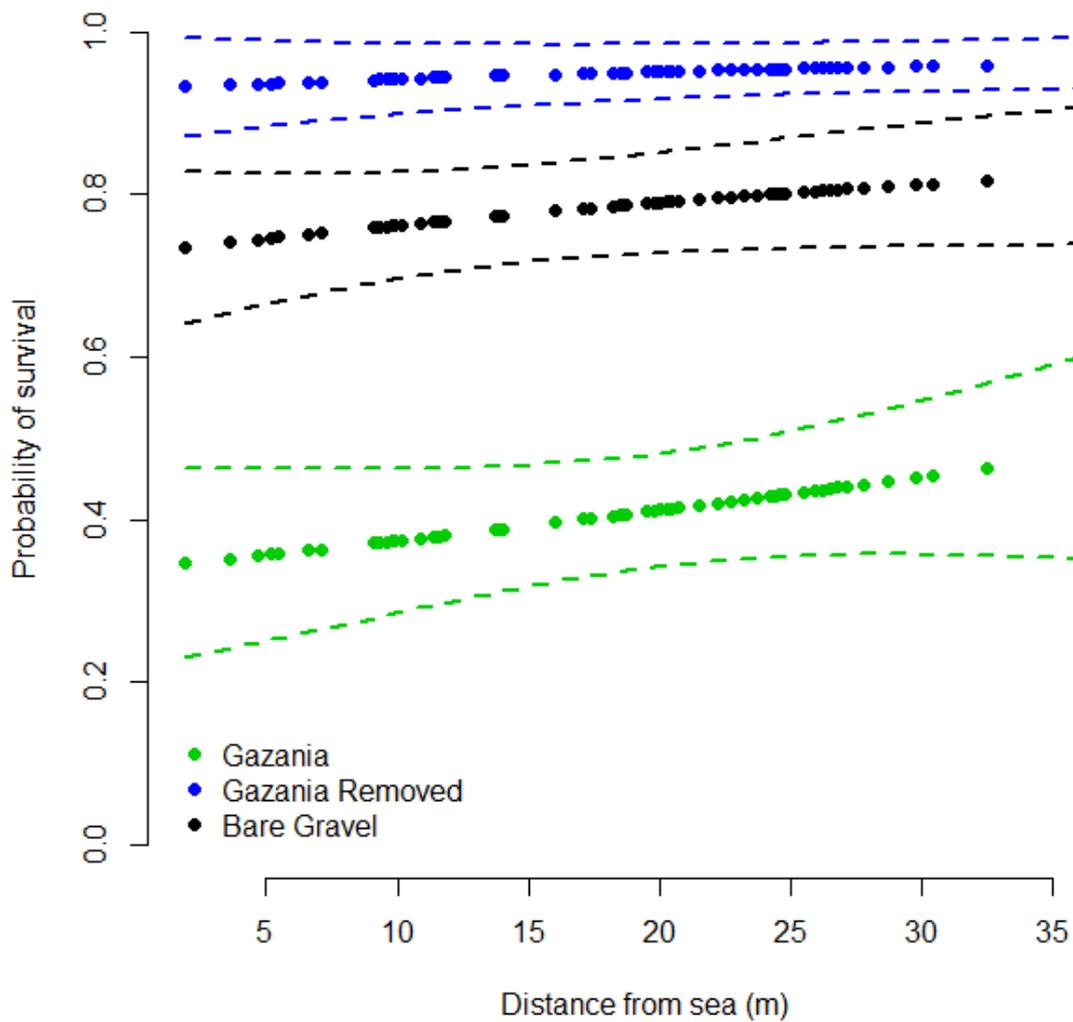


Figure 3.21 Predicted probability of *Muehlenbeckia ephedroides* seedlings surviving based on January 2012 survival based on model averaging. The points indicate mean likelihood of survival based on distance from the sea and the *Gazania* treatment method. Dotted lines indicate the unconditional standard errors (± 1.96) for these estimates.

Chapter 4

Discussion

The overall aim of this thesis was to explore some of the mechanisms structuring gravel beach plant communities. The occurrence of species was strongly segregated, indicating that some combination of differing habitat preferences and competition are structuring the community. Evidence for facilitation was surprisingly weak, and there was stronger support for environmental variability driving community structure. The mechanisms tested in this thesis that may be structuring the community included competition, facilitation, substrate, distance from sea, and the presence of limiting resources.

Competition and inhibition are likely to play an important role in structuring the community. This was demonstrated by the patterns of species segregation revealed by the null model analyses. Inhibition influenced *M. ephedroides* seedling survival at Birdlings Flat, which had higher survival rates in the open than when next to a shrub. Seedlings at Tangoio experienced inhibition, shown by the low survival rates when *Gazania* was present. At Tangoio inhibition by *Gazania* was the dominant factor influencing the survival of *Coprosma acerosa*.

I initially hypothesised that facilitation was one of the main factors driving gravel beach plant community structure. This was based on casual observations that some species appeared to be associated and vegetation appeared to occur in discrete patches. The strong patterns of species segregation and the results of the experiments show that it is unlikely that facilitation is having a strong influence on the community. In contrast, facilitation through sand accumulation may be important at Tangoio where *M. ephedroides* seedlings had the highest survival where *Gazania* had been removed.

Substrate variability and habitat heterogeneity influence spatial patterns on gravel beaches. There was variation in species composition caused by variation in substrate characteristics, which includes the size of the gravel and the proportion of fine materials (sand and humus). This was demonstrated in both the observational study and the native facilitation experiment. At Birdlings Flat the vegetation height was taller on average at the stony end of the beach, with grasses being more dominant at the sandier end of the beach. These patterns were also found in earlier surveys by Wraight (1957) and Wiser et al. (2010). Survival of *M. complexa* seedlings at Birdlings Flat was strongly related to the depth to fine material, with survival rates increasing when fine material was closer to the surface.

The distance from the sea also strongly influences community structure. The proximity to the sea affects levels of disturbance and salt exposure which are better tolerated by some species than others. The model averaging based on the observational studies showed an increase in woody exotic species closer to the sea, which may be because these species are filling an empty niche that native woody shrubs cannot fill as the native species are less tolerant of the increasing stress levels closer to the sea. Interestingly *M. complexa* seedling survival was greater closer to the sea, although no seedlings were planted closer than 65 m from the high tide mark. Distance from the sea was also a major influence on the survival of *F. nodosa* at Tangoio, with survival higher at increasing distances from the sea.

The availability of a limiting resource impacts on the ability of species to survive (Keddy 2007). In particular the availability of nutrients is important. This was shown in for *M. ephedroides* at Birdlings Flat where the addition of fertiliser improved survival rates. Interestingly the addition of water crystals had little effect on the survival of any species. The summer of 2012/2013 was dry and hot (Ministry for Primary Industries 2013) and it is likely that the seedlings were not watered often enough to compensate for this so the treatment may have been ineffective, meaning that any potentially positive effect on survival was not detected. Larger *C. propinqua* seedlings survived longer than the smaller seedlings, but high mortality between January and February 2013 suggests that harsh summer conditions such as drought were an important factor.

The addition of both fertiliser and water crystals together caused an increase in mortality, indicating some interaction between these treatments occurred. The combined effect of water and fertiliser increasing mortality was possibly due to an adverse interaction between the water crystals and the fertiliser, potentially concentrating the nutrients and damaging the plant roots. There have been no studies on this and further investigation is required. Alternatively, the experiment could be repeated by watering the plants at regular intervals rather than using water crystals.

4.1.1 Interacting factors structure plant communities

The results of all three studies show that interactions between the factors which structure plant communities can be incredibly complex. It is often difficult to separate out the effects of the different factors in determining what influence each factor is having (Helmus et al. 2007). Plants that prefer a similar environment are likely to be aggregated, but because they have similar requirements they are also likely to compete for resources. Likewise it is difficult without experimentation to assess whether species co-occur simply because they both prefer the same type of environment or if

facilitation is influencing the co-occurrence patterns. These confounding processes can lead to similar co-occurrence patterns and can act simultaneously (McCreadie and Bedwell 2013).

One aim of this study was to infer plant-plant interactions from observed patterns and experiments. The segregation of species may be confounded with habitat requirements which could be overshadowing the interspecific interactions as different mechanisms can lead to the same community pattern (Gotelli 2004). The C-score analysis indicates that species were segregated more than would be expected if they were randomly distributed. Although subsetting the data accounted for some of the environmental variability, it is likely that species' habitat preferences and microhabitat variation among quadrats still play a part in the observed patterns. Some of the species aggregation patterns are caused by competitive interactions between species. The competition for limited resources may be having a stronger effect than any possible facilitation that could be occurring. Species segregation can be explained by the species-sorting component of the metacommunity model (Leibold et al. 2004). Species-sorting describes the environmental heterogeneity and the distribution of resources; in particular, the resource-ratio hypothesis explains how competition for scarce resources results in niche separation and determines species' distributions. Each species responded differently to the experimental treatments, this potentially shows some trade-offs between life history traits, such as would be predicted by Grime's (1979) CSR theory.

4.1.2 Impacts of plant-plant interactions on community structure

Facilitation can play an important role in maintaining community structure in stressed environments (Bertness and Callaway 1994). Facilitation often occurs when one of the species has both a low tolerance to an abiotic stress and has a strong competitive ability (Liancourt et al. 2005). Species that are intolerant to abiotic stress often benefit the most from facilitation (Michalet et al. 2006). Any change in the nature of the interactions between individuals at high levels of stress is usually either an increase in facilitation or a decrease in competition; increases in competition are rarely observed (He et al. 2013). My results are not consistent with widespread facilitation within the study system being in a highly stressed environment.

My native facilitation experiment tested whether facilitation by amelioration of harsh conditions by a nurse shrub or the provision of a limiting resource (water or nutrients) could increase the survival rates of native shrub seedlings. The exotic facilitation experiment tested whether facilitation by the accumulation of sand/substrate or nutrients by a forb could increase the survival rates of native shrub seedlings. There was no evidence of facilitation from either of these experiments. The apparent lack of facilitation could be related to the way facilitation was measured (He et al. 2013)

because both of my experimental studies measured seedling survival. In previous studies facilitation success has been measured as either establishment, survival or growth, and the measure chosen has been shown to affect the outcome (Maestre et al. 2009). Facilitation can occur at any, but not necessarily all, of these stages, and through differing mechanisms (Stachowicz 2001, Chave et al. 2002). For example the facilitation by ameliorating harsh conditions can improve an individual's fecundity (Tielborger and Kadmon 1995).

The competitive response of a species is often a trade-off with its ability to tolerate abiotic stress (Liancourt et al. 2005). Not all species experience abiotic stress in the same way and therefore will react differently to different types of stress. Some species may be at their distributional limit while others are not stressed (Soliveres et al. 2011, López et al. 2013). Close to the sea there are very few species which can cope with the harsh conditions, which is likely to account for some of the segregation in my data. In high levels of stress plants may be able to survive but be unable to reproduce. For example *Glaucium flavum* is found close to the sea, can tolerate low levels of nutrients and water but has noticeably higher fitness in terms of both growth and reproduction in more favourable conditions (Scott 1963). The way in which a species reacts to stress may influence interspecific interactions (Liancourt et al. 2005). Plant traits and vigour can affect the facilitative success of a nurse plant (Schöb et al. 2013a), so if the nurse plants themselves are stressed then they may have a reduced capacity to facilitate other individuals.

There is no support for either facilitation or the Stress Gradient Hypothesis from my results. Stress can be either resource or non-resource based (Maestre et al. 2009). Coastal systems exhibit both resource (water and nutrient) and non-resource (temperature and salinity) stress (Bagousse-Pinguet et al. 2012). The Stress Gradient Hypothesis may not be as applicable to resource based stress such as nutrient or water limitation (Maestre et al. 2005, Michalet 2007, Maestre et al. 2009). This may account for the apparent lack of facilitation in the native facilitation experiment, which showed that shrub seedlings are nutrient-limited. The high mortality rates of *C. propinqua* also indicate that it may be severely water-limited. Resource competition is often exhibited spatially (Hairston et al. 1960), resulting in spatial segregation between species competing for limited resources (Porensky et al. 2013). When resource limitation is severe, competition may dominate plant-plant relationships (Maestre et al. 2009), meaning that facilitation may be over-ruled by resource competition in highly stressed environments (Holmgren and Scheffer 2010). This scenario contradicts the Stress Gradient Hypothesis. Strong resource competition and a highly stressed environment may have a stronger effect on the community, thus accounting for the observed segregation patterns and lack of facilitation in the planting experiments.

The lack of support for the Stress Gradient Hypothesis may be related to the stress gradient-length or the fact that the gradient does not vary linearly in space, i.e. stress levels may change rapidly over very short distances. This may be the case at Birdlings Flat where the density and diversity of plants increases rapidly over a relatively short distance from the sea. Alternatively, the scale of the observational study may not have been appropriate for detecting individual interactions. Interactions potentially occur at a smaller scale than measured and the 1 m² quadrat size may have been too coarse to detect these effects. Many tests of the Stress Gradient Hypothesis have been of single species or species pairs rather than at the community scale (Maestre et al. 2009). My study at a community scale and the corresponding species specific experiments is a unique test of the Stress Gradient Hypothesis, and it shows that facilitation can be unimportant in stressful conditions.

4.1.3 Impacts of exotic invasion on native plant communities

The observational study showed a high proportion (71%) of the species present at Birdlings Flat to be exotic. An earlier survey of Tangoio also showed high exotic abundance, dominated by *Gazania* (S. Wisser, unpublished data). Exotic herbaceous species diversity per quadrat at Birdlings Flat between 2006 and 2012 was relatively static, possibly because saturation level has been reached. An increase in exotic woody species diversity was observed, with these taxa being closer to the sea, on average, than existing native-dominated woody vegetation. The increase in exotic woody species diversity is likely to be a result of propagule pressure, with the local gardens and green waste dumping providing a seed source (Sullivan et al. 2005). An increase in exotic diversity over such a short time period shows that species continue to invade the community. There appears to be little impact on the native species richness. The exotics may be establishing in locations that are as yet uncolonised by native species and as such have little effect on the native plant communities, resulting in an overall increase in species richness.

The potential for exotic species to impact on natives was demonstrated in the exotic facilitation experiment. *Gazania* had an inhibitory effect on the survival of native shrub seedlings. *Gazania* also creates microhabitats by trapping sand. When the *Gazania* (and therefore inhibition) is removed then certain native seedlings species, such as *M. ephedroides*, can benefit. The advantage from the creation of habitat appears to be minor and the inhibitive effects have a greater negative impact on native species.

4.2 Recommendations

4.2.1 Management

The facilitative planting experiments have given some insight into appropriate conservation management practises on gravel beaches. Restoration planting, weed removal and the limitation of coastal development and gravel extraction can all help protect this naturally rare ecosystem.

In some areas, restoration planting may be desirable. This includes more degraded sites where there is human interest. Tangoio is a good example of a suitable restoration site. The planting experiments have given some key ideas for actions which increase seedling survival. The mortality rate of planted seedlings was high, meaning that a large number of seedlings need to be planted to ensure some level of restoration success. Timing is also likely to influence survival rates and planting in winter rather than spring is recommended. The size of the seedlings may also be important. For example at Birdlings Flat the high mortality of small *C. propinqua* seedlings within the first month suggests transplant shock; it is likely that they were too small to survive the sudden transition to harsh conditions. Also, large seedlings two to three years old may also be unable to survive the sudden transition to harsh coastal conditions (S. Wiser, unpublished data). While facilitation was thought to have a positive effect on survival, this has shown not to be the case and planting next to established individuals is not recommended. The addition of fertiliser both increased the survival of *M. ephedroides* at Birdlings Flat, and the depth to fine material was important for *M. complexa*; neither treatment was detrimental to the survival of other species. Therefore, the addition of fine material (sand or organic material) and fertiliser is likely to increase seedling survival rates. Also, the distance from the sea is important for *M. complexa* and *F. nodosa* which suggests that planting should be concentrated on certain zones on the beach. Occurrence patterns of the target species from the observational study could be used to influence where individuals are planted. Future propagule pressure from well-established native populations may potentially allow colonisation of more exposed areas and re-invasion of areas closer to the sea after population declines due to storm events. Restoration to improve the proportion of native individuals in adjacent vegetation could also benefit the beach community by removing the seed source of potentially invasive exotics, and increasing the seed source of desirable native species.

Monitoring and removing weeds is also a useful way to manage the gravel beach plant communities. *Gazania* is inhibiting native shrub recruitment and removal may be essential for the long-term viability of native woody vegetation on gravel beaches. Removal may also be beneficial due to increased sand and nutrient availability without the competition/inhibition of the *Gazania* plants. Overall, *Gazania* has a detrimental effect on native shrub survival and should be eliminated. Removal of strongly competitive exotics may be the best management option to maintain native diversity on

gravel beaches. Involving local people in the removal of weeds on the beach and in neighbouring gardens can be an effective way to manage weed invasion and spread.

4.2.2 Further research

To gain further insight into plant-plant interactions the establishment of permanent remeasurable plots at a range of spatial scales would be useful. Smaller quadrats than those used in this study with tagged individuals would allow the observation of changes in individual interactions over time. This methodology could be useful to test if an established individual acts as a nurse until the juvenile plant gets to a certain size and is then able to out-compete the nurse plant. Trait-based research could also provide further insight because the plant-plant interactions and spatial distributions may be dependant on plant traits rather than individual species (Callaway 1998).

It would be useful to further explore the stages at which native shrub recruitment may be failing. This could include testing if recruitment is limited by seed production and viability, dispersal or germination. The abiotic limitations on plant growth and reproduction, including water and nutrient availability, could be tested further. For example, *Coprosma propinqua* seedling survival rates were very low. The hypothesis that the low survival rates may be because *C. propinqua* only establishes in infrequent, unusually wet years is worth exploring further.

There are few tests of the Stress Gradient Hypothesis at a community scale (Maestre et al. 2009), so it would be interesting to carry out further testing at the community scale in other communities. Specifically, in New Zealand, this could include other naturally rare ecosystems identified by Williams et al. (2007), which have gradients from extreme to low stress, including geothermal areas, volcanic dunes or frost hollows. In addition, it would be helpful to include direct physiological measures of plant stress in the different species along these gradients.

Further research is needed to test if the increase in exotic diversity is facilitating the invasion of more exotics while competitively removing natives, or if exotics are mostly filling empty niches with little effect on natives. Invasional meltdown scenarios are difficult to test in field experiments as it is ethically questionable to plant potentially invasive exotic species into a naturally rare ecosystem. Also, it is difficult to justify removal experiments where established native shrubs are

removed. Nevertheless, tracking the changes in native populations over time across a range of sites of varying levels of invasion would be informative.

4.3 Conclusions

The aim of this thesis was to explore the mechanisms structuring gravel beach plant communities. I have shown that communities are structured by both biotic and abiotic interactions. These interactions occur simultaneously and it is thus often difficult to determine the driving factor(s). Competition by both native and exotic species does have an influence on the community structure of gravel beaches. In a stressed environment resource availability is important and may result in patterns determined by both spatial heterogeneity and resource competition. These interactions impact on species diversity, the ability of exotics to invade and the recruitment of native woody shrubs. Overall, my results show that a combination of plant-plant interactions and environmental factors are important in defining spatial, co-occurrence and temporal patterns on gravel beaches.

Appendix A

Full species list

Table A.1 Full list of species found in quadrats at Birdlings Flat by (Wiser et al. 2010) in 2006 and this study in 2012. “Quadrats” indicates species were found in a measured quadrat, observed indicates the species was not found in a quadrat but was observed on the beach.

<i>Species code</i>	<i>Species Name</i>	<i>Bio Status</i>	<i>Growth Form</i>	<i>2006 quadrats</i>	<i>2006 observed</i>	<i>2012 quadrats</i>	<i>2012 observed</i>
ACAENA	<i>Acaena</i> spp.	Indigenous Non-Endemic	Forb	-	-	√	√
AGAAVM	<i>Agave americana</i> var. <i>marginata</i>	Exotic	Forb	-	√	-	√
AMMARE	<i>Ammophila arenaria</i>	Exotic	Graminoid	√	-	-	-
ANAARV	<i>Anagallis arvensis</i>	Exotic	Forb	-	√	-	√
ARESER	<i>Arenaria serpyllifolia</i>	Exotic	Forb	√	√	-	-
ASTER	<i>Asteraceae</i>	Exotic	Forb	√	√	-	-
BRIMIN	<i>Briza minor</i>	Exotic	Graminoid	-	√	√	√
BRODIA	<i>Bromus diandrus</i>	Exotic	Graminoid	√	√	√	√
BROMOL	<i>Bromus mollis</i>	Exotic	Graminoid	√	√	√	√
BROUNI	<i>Bromus unioloides</i>	Exotic	Graminoid	√	√	-	-
CALSOL	<i>Calystegia soldanella</i>	Indigenous Non-Endemic	Forb	√	√	√	√
CARAPP	<i>Carmichaelia appressa</i>	Indigenous Endemic	Shrub	-	-	√	√
CAREDU	<i>Carpobrotus edulis</i>	Exotic	Forb	√	√	√	√
CHECHE	<i>Cheiranthus cheiri</i>	Exotic	Forb	√	√	√	√
CHRMON	<i>Chrysanthemoides monilifera</i>	Exotic	Shrub	√	√	-	√
CIRARV	<i>Cirsium arvense</i>	Exotic	Forb	√	√	-	√
CIRVUL	<i>Cirsium vulgare</i>	Exotic	Forb	√	√	-	√
COPPRO	<i>Coprosma propinqua</i>	Indigenous Endemic	Shrub	√	√	√	√
COPREP	<i>Coprosma repens</i>	Exotic	Tree	√	√	√	√
COPRUB	<i>Coprosma rubra</i>	Indigenous Endemic	Shrub	√	√	-	-
COTCOR	<i>Cotula coronopifolia</i>	Indigenous Non-Endemic	Forb	√	√	-	-
COTORB	<i>Cotyledon orbiculata</i>	Exotic	Shrub	√	√	√	√

CRECAP	<i>Crepis capillaris</i>	Exotic	Forb	√	√	√	√
DAUCAR	<i>Daucus carota</i>	Exotic	Forb	√	√	-	√
DICHCRI	<i>Dichelachne crinita</i>	Indigenous Non-Endemic	Graminoid	-	√	-	-
EHCAN	<i>Echium candicans</i>	Exotic	Shrub	-	-	√	√
ECHVUL	<i>Echium vulgare</i>	Exotic	Forb	√	√	-	√
EINTRI	<i>Einadia triandra</i>	Indigenous Endemic	Shrub	-	-	√	√
ESCCAL	<i>Eschscholzia californica</i>	Exotic	Forb	-	-	-	√
FICSPI	<i>Ficinia spiralis</i>	Indigenous Endemic	Graminoid	√	√	√	√
GAZRIG	<i>Gazania rigens</i>	Exotic	Forb	√	√	√	√
GLAFLA	<i>Glaucium flavum</i>	Exotic	Forb	√	√	√	√
HIRINC	<i>Hirschfeldia incana</i>	Exotic	Forb	√	√	-	-
HOLLAN	<i>Holcus lanatus</i>	Exotic	Graminoid	√	√	-	√
HYPRAD	<i>Hypochaeris radicata</i>	Exotic	Forb	√	√	√	√
JACMAR	<i>Jacobaea maritima</i>	Exotic	Shrub	-	-	√	√
LAGOVA	<i>Lagurus ovatus</i>	Exotic	Graminoid	√	√	√	√
LEOTAR	<i>Leontodon taraxacoides</i>	Exotic	Forb	√	√	√	√
LOBMAR	<i>Lobularia maritima</i>	Exotic	Forb	√	√	√	√
LOLPER	<i>Lolium perenne</i>	Exotic	Graminoid	√	√	√	√
LUPARB	<i>Lupinus arboreus</i>	Exotic	Shrub	√	√	√	√
MALPAR	<i>Malva parviflora</i>	Exotic	Forb	-	√	-	√
MELALP	<i>Melicytus alpinus</i>	Indigenous Endemic	Shrub	-	√	√	√
MELIND	<i>Melilotus indicus</i>	Exotic	Forb	√	√	-	-
MUECOM	<i>Muehlenbeckia complexa</i>	Indigenous Non-Endemic	Shrub	√	√	√	√
MUEEPH	<i>Muehlenbeckia ephedroides</i>	Indigenous Endemic	Shrub	√	√	√	√
PETCRI	<i>Petroselinum crispum</i>	Exotic	Forb	√	√	√	√
PITCRF	<i>Pittosporum crassifolium</i>	Exotic	Tree	√	√	√	√
PLACOR	<i>Plantago coronopus</i>	Exotic	Forb	√	√	√	√
PLALAN	<i>Plantago lanceolata</i>	Exotic	Forb	√	√	-	-
POAANN	<i>Poa annua</i>	Exotic	Graminoid	√	√	-	-
POACIT	<i>Poa cita</i>	Indigenous Endemic	Graminoid	√	√	√	√
POLTET	<i>Polycarpon tetraphyllum</i>	Exotic	Forb	√	√	√	√
RAO AUS	<i>Raoulia australis</i>	Indigenous Endemic	Forb	√	√	√	√
RUMACE	<i>Rumex acetosella</i>	Exotic	Forb	√	√	√	√

SAGPRO	<i>Sagina procumbens</i>	Exotic	Forb	√	√	-	-
SCHPHO	<i>Schedonorus phoenix</i>	Exotic	Graminoid	√	√	-	-
SEDACR	<i>Sedum acre</i>	Exotic	Forb	√	√	√	√
SEDALB	<i>Sedum album</i>	Exotic	Forb	-	-	√	√
SENELE	<i>Senecio elegans</i>	Exotic	Forb	√	√	√	√
SENLAU	<i>Senecio lautus</i>	Indigenous Non-Endemic	Forb	√	√	√	√
SILGAL	<i>Silene gallica</i>	Exotic	Forb	√	√	√	√
SISOFF	<i>Sisymbrium officinale</i>	Exotic	Forb	√	√	-	-
SONASP	<i>Sonchus asper</i>	Exotic	Forb	√	√	-	-
SONOLE	<i>Sonchus oleraceus</i>	Exotic	Forb	√	√	√	√
TAROFF	<i>Taraxacum officinale</i>	Exotic	Forb	-	-	√	√
TRIARV	<i>Trifolium arvense</i>	Exotic	Forb	-	√	√	√
TRIDUB	<i>Trifolium dubium</i>	Exotic	Forb	√	-	-	-
VERANA	<i>Veronica anagallis-aquatica</i>	Exotic	Forb	√	-	-	-
VERVIR	<i>Verbascum virgatum</i>	Exotic	Forb	√	-	-	-
VULBRO	<i>Vulpia bromoides</i>	Exotic	Graminoid	√	-	-	-

Note: *Pittosporum crassifolium* and *Coprosma repens* have been listed as exotic. They are both native to New Zealand but are not native to Canterbury.

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