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Recruitment limitation of native species in invaded coastal dune communities

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Abstract

"Recruitment limitation may limit the ability of sites to regenerate after disturbances such as weed invasion and weed management. We investigated seed bank constraints and dispersal limitation in coastal dune communities on the east coast of Australia. The ability of sites to regenerate naturally following weed removal was assessed in coastal dune communities invaded by the invasive alien, bitou bush (Chrysanthemoides monilifera subsp. rotundata). To investigate recruitment limitation, seed banks and vegetation of invaded, native, intensively managed (selective application of herbicide and some re-vegetation) and extensively managed (large-scale, non-selective herbicide application) sites were compared. We investigated the dispersal mechanisms of species in the seed bank and vegetation to determine if communities might be dispersal-limited, i.e. contain significant numbers of species with only short-distance dispersal capabilities. Species richness and composition of soil seed banks differed from the vegetation in foredunes and hinddunes. Invasion depleted seed banks further. About half of the species had short-distance dispersal mechanisms indicating the potential for dispersal limitation. Secondary weed invasion following management was evident although alien species occurred in both seed banks and vegetation. Our results indicated that coastal dune communities suffer recruitment limitation. Native, managed and invaded dune communities appear to be both seed bank and dispersal-limited although management and invasion exacerbates recruitment. Regeneration of coastal dune communities will require active reintroduction of species, particularly those with short-distance dispersal mechanisms."

Keywords

Recruitment, limitation, native, species, invaded, coastal, dune, communities

Disciplines

Life Sciences | Physical Sciences and Mathematics | Social and Behavioral Sciences

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Recruitment limitation of native species in invaded coastal dune communities.

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Abstract . Recruitment limitation may limit the ability of sites to regenerate after disturbances such as weed invasion and weed management. We investigated seed bank constraints and dispersal limitation in coastal dune communities on the east coast of Australia. The ability of sites to regenerate naturally following weed removal was assessed in coastal dune communities invaded by the invasive alien, bitou bush (*Chrysanthemoides monilifera* subsp. *rotundata*). To investigate recruitment limitation, seed banks and vegetation of invaded, native, intensively managed (selective application of herbicide and some re-vegetation) and extensively managed (large-scale, non-selective herbicide application) sites were compared. We investigated the dispersal mechanisms of species in the seed bank and vegetation to determine if communities might be dispersal-limited i.e. contain significant numbers of species with only short-distance dispersal capabilities. Species richness and composition of soil seed banks differed from the vegetation in foredunes and hinddunes. Invasion depleted seed banks further. About half of the species had short-distance dispersal mechanisms indicating the potential for dispersal limitation. Secondary weed invasion following management was evident although alien species occurred in both seed banks and vegetation. Our results indicated that coastal dune communities suffer recruitment limitation. Native, managed and invaded dune communities appear to be both seed bank and dispersal limited although management and invasion exacerbates recruitment. Regeneration of coastal dune communities will require active reintroduction of species, particularly those with short-distance dispersal mechanisms.

Keywords bitou bush . foredune . hinddune . invasion . seed bank .seed dispersal

Introduction

Seed supply is a significant issue in natural and anthropogenically managed sites (Turnbull et al., 2000; Middleton, 2003; Standish et al., 2007). Natural regeneration of vegetation at disturbed sites is based on three recruitment processes: recruitment from remnant native plants remaining at sites (including cloning), establishment of plants from a soil-stored seed bank, and species arrival and establishment from propagule dispersal from outside the area. Recruitment limitation can result when inadequate seeds are available from any of these processes. Recruitment limitation as a result of a depauperate seed bank has been identified in a many natural habitats including fynbos (Holmes & Cowling, 1997), forested wetlands (Middleton, 2003; Li et al., 2008) and montane meadows (Lang & Halpern, 2007). Recruitment limitation has also been identified experimentally; seed addition experiments result in increases in numbers of existing species and establishment of new species at sites (Turnbull et al., 2000). Similarly, in communities affected by weed invasion, the assemblage of native species within soil seed banks is dissimilar to that of the standing vegetation (Holmes & Cowling, 1997).

Recruitment limitation as a result of a lack of propagules dispersing into sites (often defined as dispersal limitation) affects regeneration of riparian vegetation (Battaglia et al., 2008; Williams et al., 2008), tropical forests (Pejcar et al., 2008), abandoned mining sites (Kirmer et al., 2008), Mediterranean forests (Aparicio et al., 2008) and deciduous woodlands (Robinson & Handel, 2000). For dispersal limitation, distance to a seed source is critical in determining the probability of species arriving at sites (Robinson & Handel, 1993). Recruitment limitation as a result of both changes in seed bank and dispersal are not mutually exclusive (Honnay et al., 2002).

The dispersal mode of a species can provide a useful way to identify which species can arrive at sites. Those that possess mechanisms for long-distance dispersal (e.g. wind, water or vertebrate migration) are likely to be capable of getting to distant sites. For example, many species of tropical gallery forest (Barbosa & Pizo, 2006), subtropical rainforests (Neilan et al., 2006) and temperate deciduous forests (Robinson & Handel, 2000) use wind or vertebrate dispersal mechanisms.

Species which are locally extinct (in both vegetation and soil seed banks) and which are adapted for short-distance dispersal (e.g. ballistic, ant-adapted dispersal; Westoby et al., 1990) cannot passively gain representation at a site as seeds are only moved a few metres (Hughes et al., 1994). These species can be classified as dispersal-limited. Plant communities where short-distance dispersal is common, such as sandstone woodlands and heaths (Westoby et al., 1990) may experience poor recruitment if seed banks are depauperate.

Assessing the impact of different types of disturbances on seed supply is important in directing conservation efforts (Bannerjee et al., 2006). Disturbances, such as weed invasion and weed control, may influence the availability of seeds in the soil seed bank and may increase the number of species that are recruitment-limited. Weed invasion and management can increase the number of alien species present (Ogden & Rejmanek, 2005; Mason and French, 2007; Cox & Allen, 2008; Turner et al., 2008; Williams et al., 2008). Disturbances that result in fragmentation and isolation may influence the dispersal capacity of species to regenerate at sites (McIntyre & Hobbs, 1999).

We investigated recruitment limitation in coastal dune communities in eastern Australia disturbed as a result of invasion by bitou bush (*Chrysanthemoides monilifera* subsp. *Rotundata* (DC.) Norl.*)* (hereafter termed 'bitou') and weed control

activities. In the past, bitou was effectively used as a dune stabilizer and actively planted within foredune vegetation. It now threatens the integrity of foredune and hinddune communities, covering up to 80% of New South Wales coastal vegetation (Thomas and Leys 2002). Bitou invasion alters species diversity and composition (Mason & French, 2008), fauna (French & Eardley, 1997) and causes significant changes to micro-habitats (Lindsay & French, 2004) and ecosystem processes (Lindsay & French, 2005).

We asked the following questions:

1. How similar is the composition of the seed bank to that of the vegetation?
2. Does bitou invasion and/or management alter seed banks?
3. Does bitou invasion and/or management alter the dispersal spectra of vegetation or seed banks?
4. Is there evidence of recruitment limitation in coastal communities?

Materials and Methods

Study site

The study area extended along 1000 km of coastline of New South Wales from Batemans Bay (35° 41'S; 150° 11'E) in the south to Tweed Heads (28° 10'S; 153° 32'E) in the north. Study sites were selected and categorized according to their management (in terms of bitou control) and degree of invasion. The categories (hereafter termed 'invasion categories') were:

1. *Invaded*. High presence of bitou (averaging 40% cover) and no history of control activities.

2. *Extensively managed*. Bitou present and subject to large-scale herbicide (glyphosate) application (i.e. aerial or vehicle spraying).
3. *Intensively managed*. Bitou present and subject to selective application of herbicide (i.e. spraying from backpack, direct herbicide application to stems, hand removal) and some re-vegetation of native species.
4. *Native*. Low presence of bitou (isolated individuals, ≤ 5% total cover) and no history of control activities. Some sparsely-invaded sites are within this category as we were unable to find enough sites that were completely free of bitou.

Foredunes were closed shrubland on the front sand dune, exposed to winds but behind the incipient region. Hinddune sites were woodland communities partially protected from the winds by the front dune. Both communities are described in Walker & Hopkins (1990) and Mason and French (2007). As extensive management is not common in hinddunes due to the presence of a tree canopy limiting the effectiveness of spraying, managed sites in this habitat were only intensively managed.

Sampling of seed banks and standing vegetation

To monitor seedling emergence, we collected 100 soil samples (63 mm diameter, 0-5 cm depth) from each of 15 hinddune sites (n = 5 x 3 invasion categories) in February and March 2004. Samples were collected from a 20 m x 50 m (0.1 ha) quadrat and mixed to avoid within-site variation. All plant species present in the standing vegetation at each site were identified and recorded. Where necessary, species identities were confirmed at the Janet Cosh Herbarium. A pilot study had previously determined that 5 cm was an appropriate depth (Mason & French, 2007).

In foredunes, a pilot study determined collection depth and investigated whether sieving, to remove most of the sand, was an effective method for removing excess sand without losing small seeds. For the pilot study, 100 soil cores (63 mm diameter) from each of two soil depths: 0-5 cm and 5-10 cm were collected from a heavily-invaded beach on the Illawarra coast. Leaf litter was not included. Half of the samples from each depth were sieved using a 500 μm sieve. Sieved samples were divided into material retained within the sieve and waste material (soil that fell through the sieve). For half the samples, *Leptospermum laevigatum* seed was added prior to sieving to test whether small seeds were lost in the sieving process. Samples were spread over seedling trays (1:1 vermiculite:perlite base) and seeds allowed to germinate until no additional germination was observed for 4 weeks. As no unique species germinated in the deeper samples we concluded that the top 5 cm was an appropriate sampling depth for the seed bank. Sieving was an effective way to transport seeds without excess sand as no seedlings germinated in the waste material; all were retained in the sieve. .

For the main experiment, we collected 100 soil samples from each of 24 foredune sites (n = 6 x 4 invasion categories) during December 2006. Within a 20 m x 50 m quadrat, soil was collected from the top 5 cm of the substrate using 63 mm (diameter) soil corers and sieved. Material that remained within the sieve was retained and mixed with other cores collected within the same site. Standing vegetation was assessed in 20 x 50 m plots at each site.

Seedling emergence

In the glasshouse, samples were evenly spread (to a depth of approx. 5 mm) over pre-prepared seedling trays and covered by a layer of propagating sand. Sieving of

foredune samples meant that the amount of soil collected from foredune sites varied from 2 to 6 while hinddune samples covered 18 trays per site.

Seedling trays were placed within a glasshouse in a randomized block design and re-randomized each week. Trays were treated for 4 days with smoke-infused water. Smoke-water enhances germination in these communities and is made by bubbling smoke from burning local litter through water under vacuum (Dixon et al 1995; Mason et al., 2007). Tap water was then applied twice daily for 2 minutes. For foredune samples, seedling emergence was monitored until no emergence was observed for 4 weeks. Hinddune samples were monitored for one year. Emerging seedlings were removed from trays upon identification.

Dispersal spectra

The total species complement for foredunes and hinddunes along the NSW coast was compiled from surveyed sites in this study and extra sites from Mason and French (2007). The dispersal mechanisms for seeds of all species were determined from the literature (Harden, 1990; Westoby et al., 1990; Harden, 1992; Harden, 1993; Benson & McDougall, 1993-2005; Harden, 2002). Four dispersal categories were associated with long-distance dispersal: water, wind, endo- and exo-zoochoric. We defined long distance dispersal as being capable of moving seeds in the order of tens to hundreds of metres or more. Three were associated with short-distance dispersal: no dispersal mechanism, ant dispersal and ballistic. We defined short-distance dispersal as being capable of moving seeds up to 10m from the parent plant. Where multiple mechanisms were recorded we classified species with the longer distance mechanism. This may result in an over-estimation of the number of species using long-distance dispersal as a primary mechanism and may overestimate the importance of dispersal in recruitment. Most species for which this generalization was applied, possessed

awns and could be transported on animals (exozoochore). Exozoochory was a relatively rare dispersal mechanism and, therefore, the application of this generalisation was unlikely to change the main conclusions.

Statistical analyses

As management categories differed between foredunes and hinddunes, we compared species richness between vegetation and seed banks for each habitat separately. Two-factor ANOVAs determined differences in species richness between invasion categories (fixed factor) and the seed bank and vegetation (fixed factor). Data were transformed where necessary to stabilize variances and improve normality. The presence of bitou was removed from the data set prior to analysis as it was used for treatment selection. To investigate recruitment limitation in the seed bank we analysed native species only and to investigate the relationship between alien flora, and invasion category, we analysed alien species separately. To allow comparisons between foredunes and hinddunes, extensively managed foredune sites were excluded. The number of foredune sites per invasion category was also reduced (by random selection) from 6 to 5.

Differences in community assemblages between seed banks and vegetation, and management categories in each habitat were analysed using a permutational multivariate analysis of variance based on Bray Curtis indices of similarity for presence/absence data (999 permutations, PERMANOVA, PRIMER-E Ltd). NMDS ordination using 25 iterations was used to visualize differences. Native and alien species were analysed separately.

For each habitat, we derived the set of species that were missing in the seed bank but which occurred in the vegetation. For hinddunes we investigated whether the

dispersal spectra between native and impacted sites was different using a Pearson's chi-square test. We could not analyse differences in dispersal spectra of missing species in foredunes as there were too few species.

Results

Evidence for seed bank limitation among invasion categories and vegetation communities

In foredunes, we recorded 84 species. For native species, 30 were present in the soil seed bank and 36 were in the vegetation. The standing vegetation had 22 native species (61%) that did not occur in the soil seed bank. Native species richness of foredunes was greater in standing vegetation compared with the soil seed bank ($F_{1,40}$ = 11.44 p = 0.002) and in native relative to invaded sites ($F_{3,40}$ = 3.00 p = 0.042; Figure 1a). Managed sites were intermediate.

In hinddunes, we recorded 304 species; 116 native species in the seed bank and 200 species within standing vegetation. In this habitat, the standing vegetation had 127 native species (63 %) that were not found in the soil seed bank. Hinddune standing vegetation was more speciose than the seed bank ($F_{1, 24}$ = 35.64, $p < 0.001$) but richness did not differ amongst invasion categories ($F_{2, 20}$ = 1.25, p = 0.30, Figure 1b).

Standing vegetation differed in composition from the seed bank in both foredunes and hinddunes (interaction term, *pseudo*-$F_{1,48}$ = 5.24, p = 0.001, Fig 2). Community composition also differed with invasion category, with the largest differences for invaded sites (*pseudo*-$F_{1,48}$ = 1.51, p = 0.025). Native and managed sites could not be distinguished.

Evidence for dispersal limitation among invasion categories and vegetation communities

Dune communities along the coast, supported 181 native species (53%) with propagules adapted for long-distance dispersal, particularly vertebrate-dispersal. Importantly, 160 species were likely to be dispersed short distances (47%). Alien species were represented by more species that had long-distance dispersal mechanisms (65%, 57 spp), mostly using wind (30% overall, 27spp). Interestingly, about a quarter of both alien and native species possessed no obvious dispersal mechanism.

There were significant differences in the dispersal spectra of alien and native species in each habitat (hinddunes: $\chi^2_6 = 15.87$, $p = 0.001$, foredunes: $\chi^2_6 = 21.85$, $p = 0.015$, Fig 3). In foredunes, the alien component was comprised of fewer species using short-distance dispersal (ant and ballistic dispersal) and more species dispersed using wind or water. Native species had more species using ant and vertebrate dispersal than expected, fewer with water and wind dispersal. In hinddunes, fewer alien species used short-distance dispersal (ant and ballistic dispersal) and more species used wind. More native species than expected used ant dispersal but fewer used wind dispersal. Dispersal spectra for hind and foredunes were not different for either native or alien species ($\chi^2_6 = 8.26$, $p = 0.220$, $\chi^2_6 = 4.33$, $p = 0.632$ respectively, Fig 3).

We tested whether the native species that were missing from the seed bank, but present in the vegetation, were likely to be dispersal-limited, ie use short-distance dispersal. We evaluated this for both native sites and impacted (managed and invaded) sites. For foredune sites, 22 species occurred only in standing vegetation and

many of these were rare. Only three species were unique to native sites. As a result there was insufficient data to test for differences in dispersal spectra in native and impacted sites. In hinddune sites, 71 species in native sites and 112 in impacted sites were found only in standing vegetation. There were no differences in the dispersal spectra of species missing from the seed bank relative to the standing vegetation between native and impacted sites (χ^2_5= 2.20, p = 0.821, Fig. 4).

The role of management in adding alien species

For alien species, 18 occurred in the foredune seed bank and 16 occurred in the vegetation. There were no differences in the richness of the seed bank compared with the vegetation ($F_{1, 40}$ = 0.09, p = 0.77), however there were differences with invasion category ($F_{3, 40}$ = 3.33, p = 0.03). Intensively managed sites had higher alien species richness than bitou invaded sites with both native and extensively managed sites showing intermediate richness. In hinddunes, 36 were in the seed bank and 27 were in the vegetation. The effect of invasion category on alien species richness varied above and below-ground ($F_{2,24}$ = 6.61, p = 0.005). While the seed bank had equivalent numbers of alien species in each invasion category, the richness of aliens in the standing vegetation in managed sites was greater than either native or bitou invaded sites (Fig 1b). Richness of aliens in the vegetation in managed sites was comparable to that in the seed bank.

The composition of aliens showed a similar pattern to native species. Within both foredunes and hinddunes, the alien species in the vegetation differed from the seed bank (interaction term, *pseudo* $F_{1,48}$ = 5.04, p = 0.001). Invasion category influenced community composition with managed sites different from native and invaded sites (*pseudo* $F_{1,48}$ = 1.82, p = 0.018).

Discussion

Recruitment limitation in the seed bank

Seed banks had low species richness and poor similarity with the vegetation. Only 40% of species were common. Like many other habitats (Turnbull et al., 2000), coastal dune communities are likely to suffer from recruitment limitation. Recruitment is likely to be further decreased in disturbed and fragmented landscapes where seed bank dynamics (Polley et al., 2005) and dispersal activities are disrupted (Battaglia et al., 2008; Moran et al., 2009). We found that native seed banks were more depauperate in invaded than native sites in foredune communities but not in hinddune communities. Foredune communities are species poor, relative to hinddunes, and impacts of disturbances may dramatically increase the proportion of species that suffer recruitment limitation. Furthermore, these habitats are limited in their capacity to develop long lasting seed reserves as sand movement and storm action are likely to move seeds to ineffective positions within the soil profile. Under these conditions additional disturbances, such as weed invasion, are likely to have important additional effects on seed supply. The more recent invasion by bitou bush into hinddune vegetation may indicate a lag effect where seed banks are not yet affected by the invasion process. If this is true, then we consider that future impacts are possible as seed banks have a limited life span and may decline with long term weed invasions.

Alien species were present in the seed bank in relatively undisturbed foredunes and hinddunes areas. In hinddunes, there was a low richness in the vegetation in both native and bitou-invaded sites suggesting that, following a disturbance, there will be a potential increase in alien establishment. Management

activities to remove bitou bush resulted in an increase in alien species establishing. A similar pattern was found in foredunes for sites that were intensively managed rather than extensively managed, suggesting the soil disturbance involved in more intensive weed control is providing better recruitment opportunities for alien species (Mason et al., 2007). Thus while management tends to improve the native richness, it increases the risk of secondary invasion. Recruitment is not only from the soil seed bank; differences found between invaded and managed sites indicate that management adds species, perhaps by contamination from equipment and personnel at the sites.

Evidence for dispersal limitation

Nearly half of the native species in foredunes and hinddunes had mechanisms for long-distance dispersal. These species have the capacity to recruit into sites dependent on the proximity of sources. These nutrient-poor habitats contrast with sclerophyll woodlands nearby which have similar nutrient levels but which are more dominated by species with short distance dispersal (Westoby et al., 1990; Westoby et al., 1991). The importance of vertebrate dispersal in these coastal dune communities suggests that seed-dispersing birds and mammals are an important attribute.

A greater proportion of alien species used wind; these species often produce large numbers of light seeds. In contrast, vertebrate seeds are frequently larger and are therefore not produced in such large numbers (Westoby et al 1991). This has implications for competition with long-distance dispersed native species as the probability of alien species establishing is likely to be greater as more seeds are likely to be dispersed for wind dispersed species than vertebrate-dispersed species.

Nearly half of the native species had morphology suggestive of short-distance dispersal. While species with long-distance dispersal mechanisms may recruit from

outside the site, we identified over 30 species with short-distance dispersal mechanisms that are not present in any seed banks in hinddune vegetation. These species are of conservation concern as, at present, there is no capacity for natural regeneration. Many of these species were small species such as ferns, graminoids, herbs and small shrubs suggesting that this structural layer in coastal dunes is likely to become locally extinct if seed banks become depleted. Such species need to be targeted for restoration activities.

A relatively large proportion of alien species (and native species) also possessed no mechanism for dispersal. The arrival of these species to sites may be particularly assisted by human activities transporting soil. However, this also highlights an important biological process that is not encompassed when assigning dispersal modes to plant species. Clearly there is a small probability that some seeds will travel further than they are 'designed' to do, as a result of unusual activities of animals or abiotic processes. For example, seeds with no dispersal mechanism may float downstream or become entangled in mud on an animal. The consequences for regeneration are positive however the likelihood of such events occurring is very small and thus becomes less significant in managing disturbed landscapes. Assuming species with no dispersal mechanisms (or short-distance dispersal) will not arrive at sites is the more likely scenario.

Interestingly, for species missing from the seed bank but present in the vegetation, there was no change in the percentage of species with different dispersal mechanisms in native versus disturbed areas. Losses are occurring for both short- and long-distance dispersed species, indicating a range of constraints are influencing seed supply. This is occurring whether sites have been weed invaded or not and a range of management options need to be considered to address this recruitment limitation as a

result of both restrictions in dispersal and soil seed bank supply. These management options may need to include planting of species with short-distance dispersal mechanisms and reducing the probability of alien dispersal and contamination. A landscape perspective will also be required to assess the viability of passive recruitment of long-distance dispersed native species. If managed sites are very isolated by either invaded or anthropogenically modified habitat, it may be appropriate to actively reintroduce these species to managed sites.

The assessment of the potential of disturbed sites to naturally regenerate needs to be accompanied by an understanding of the dispersal strategies of all species that should be present in the community. The conservation of species that are affected strongly by disturbances will depend on our ability to identify which species suffer recruitment limitation.

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		Foredune		Hinddune	
		Native	**Alien**	**Native**	**Alien**
Short distance	Ant	20	1	49	1
	Ballistic	9	1	14	1
	No dispersal	40	18	75	18
Long distance	Exozoochore	11	2	10	2
	Vertebrate	54	15	103	18
	Water	3	5	1	1
	Wind	28	23	37	14
	Total	165	65	289	55

Table 1. Number of species within each dispersal category for native and alien species found in foredune and hinddune habitats along the NSW coast.

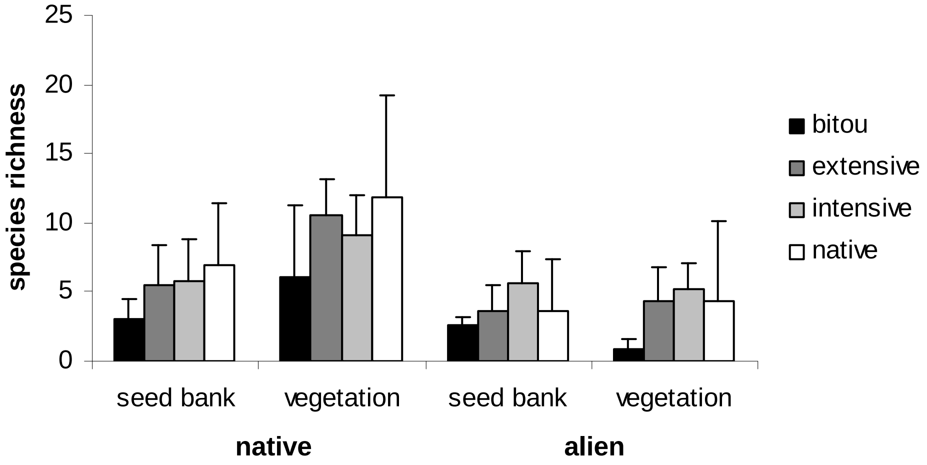
Figure legends

Figure 1. Species richness of a) hinddune and b) foredune vegetation for the seedbank and standing vegetation (vegetation) at sites that have experienced different management. Native species richness of foredunes was greater in standing vegetation compared with the soil seed bank ($F_{1,40} = 11.44$ $p = 0.002$) and in native relative to invaded sites ($F_{3,40} = 3.00$ $p = 0.042$). Managed sites were intermediate. Hinddune standing vegetation was more speciose than the seed bank ($F_{1,24} = 35.64$, $p < 0.001$) but richness did not differ amongst invasion categories ($F_{2,20} = 1.25$, $p = 0.30$)

Figure 2. NMDS Ordination of differences in species composition of the native seed bank and standing vegetation (vegetation) in foredune and hinddune vegetation. Habitat types grouped by oval shapes are ▲ foredune seed bank, ♦foredune vegetation, ●hinddune seed bank, ■hinddune vegetation. Management categories are native (black filled), managed (grey filled), invaded (unfilled). Ordination is based on Bray Curtis similarities for presence/absence data with 25 interations.

Figure 3. Percentage of native and exotic species in each dispersal category for a) foredune and b) hinddune sites. Ant, ballistic and no dispersal categories are considered to be short dispersal strategies while exozoochore, vertebrate (i.e. endozooochore), water and wind dispersal are considered long-distance dispersal strategies.

Figure 4. Dispersal spectra of native species from native and impacted (weed invaded and managed) sites that are present in the standing vegetation but missing from the seed bank.


25
20
15
10
5
0
species richness
bitou
extensive
intensive
native
seed bank
vegetation
seed bank
vegetation
native
alien

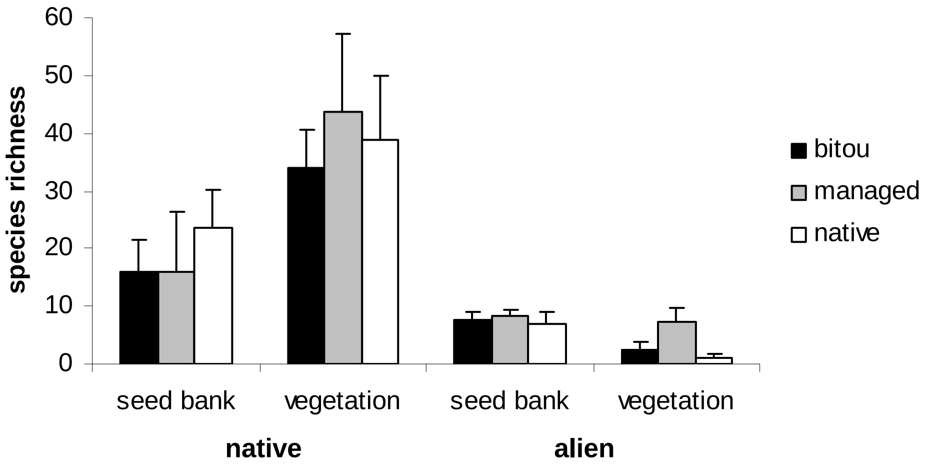

60
50
40
30
20
10
0
species richness
bitou
managed
native
seed bank
vegetation
seed bank
vegetation
native
alien

Fig 1

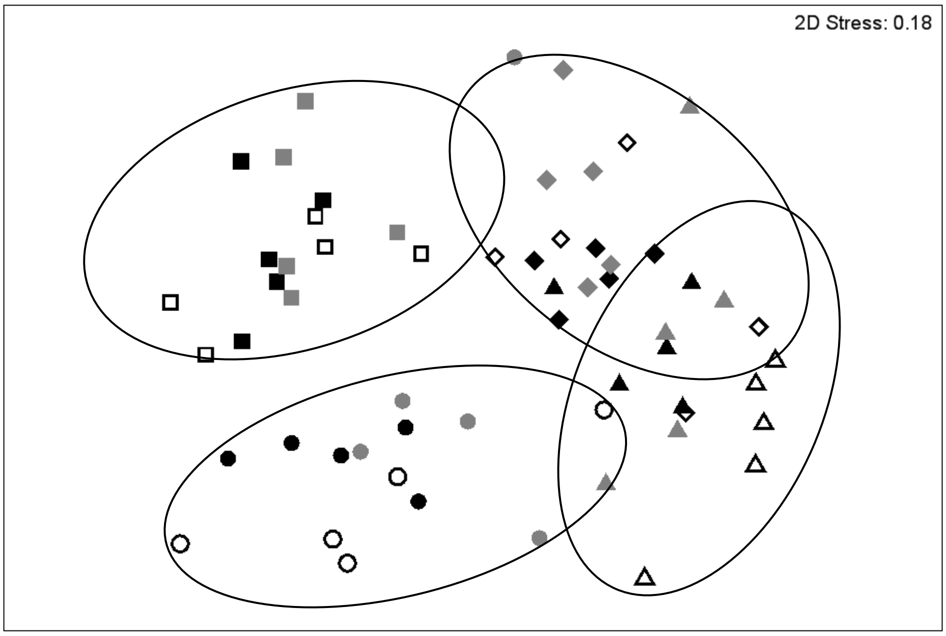


Fig 2

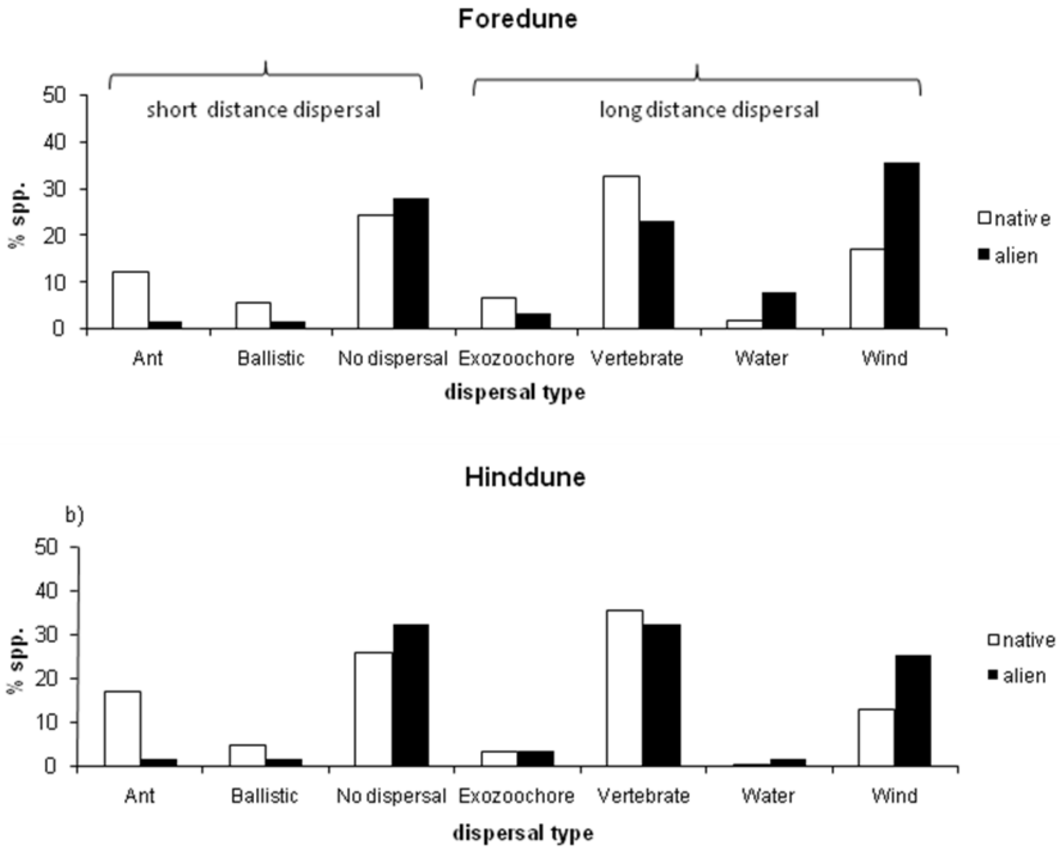
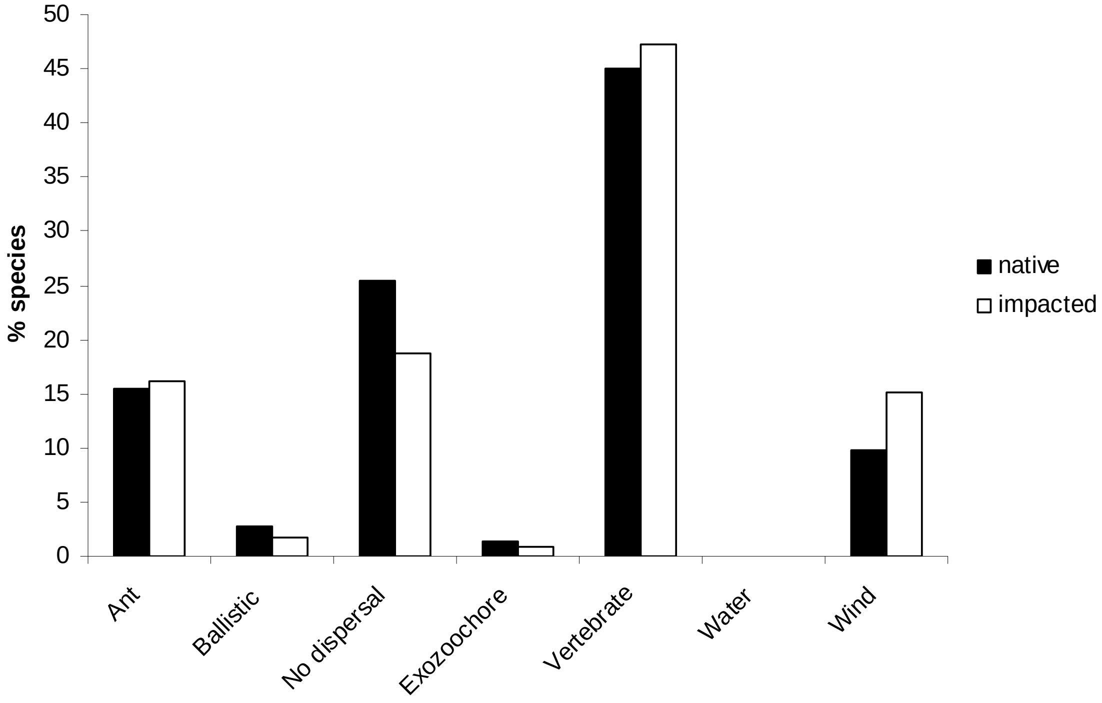

Foredune
short distance dispersal
long distance dispersal
% spp.
50
40
30
20
10
0
native
alien
Ant
Ballistic
No dispersal
Exozoochore
Vertebrate
Water
Wind
dispersal type
Hinddune
b)
% spp.
50
40
30
20
10
0
native
alien
Ant
Ballistic
No dispersal
Exozoochore
Vertebrate
Water
Wind
dispersal type

Fig 3



50
45
40
35
30
25
20
15
10
5
0
% species
Ant
Ballistic
No dispersal
Exozoochore
Vertebrate
Water
Wind
native
impacted

Fig 4.