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Impacts of a woody invader vary in different vegetation communities

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Abstract

The impact of an exotic species in natural systems may be dependent not only on invader attributes but also on characteristics of the invaded community. We examined impacts of the invader bitou bush, *Chrysanthemoides monilifera* ssp. *rotundata*, in fore and hind dune communities of coastal New South Wales, Australia. We compared invader impacts on vegetation structure, richness of both native and exotic growth forms and community variability in fore and hind dunes. We found that impacts of bitou invasion were context specific: in fore dune shrublands, functionally distinct graminoid, herb and climber rather than shrub growth forms had significantly reduced species richness following bitou invasion. However, in forested hind dunes, the functionally similar native shrub growth form had significantly reduced species richness following bitou invasion. Density of vegetation structure increased at the shrub level in both fore and hind dune invaded communities compared with non-invaded communities. Fore dune ground-level vegetation density declined at invaded sites compared with non-invaded sites, reflecting significant reductions in herb and graminoid species richness. Hind dune canopy-level vegetation density was reduced at invaded compared with non-invaded sites. Bitou bush invasion also affected fore dune community variability with significant increases in variability of species abundances observed in invaded compared with non-invaded sites. In contrast, variability among all hind dune sites was similar. The results suggest that effects of bitou bush invasion are mediated by the vegetation community. When bitou bush becomes abundant, community structure and functioning may be compromised.

Keywords

Impacts, woody, invader, vary, different, vegetation, communities

Disciplines

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

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Impacts of a woody invader vary in different vegetation communities

Running Title: Invader impacts in different communities

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(A) Abstract

The impact of an exotic species in natural systems may be dependent not only on invader attributes but also on characteristics of the invaded community. We examined impacts of the invader bitou bush, *Chrysanthemoides monilifera* ssp. *rotundata*, in fore and hind dune communities of coastal New South Wales, Australia. We compared invader impacts on vegetation structure, richness of both native and exotic growth forms and community variability in fore and hind dunes. We found impacts of bitou invasion were context specific: in fore dune shrublands, functionally distinct graminoid, herb and climber rather than shrub growth forms had significantly reduced species richness following bitou invasion. However, in forested hind dunes, the functionally similar native shrub growth form had significantly reduced species richness following bitou invasion. Density of vegetation structure increased at the shrub level in both fore and hind dune invaded communities compared with non-invaded communities. Fore dune ground-level vegetation density declined at invaded sites compared with non-invaded sites reflecting significant reductions in herb and graminoid species richness. Hind dune canopy-level vegetation density was reduced at invaded compared with non-invaded sites. Bitou bush invasion also affected fore dune community variability with significant increases in variability of species abundances observed in invaded compared with non-invaded sites. In contrast, variability among all hind dune sites was similar. The results suggest that effects of bitou bush invasion are mediated by the vegetation community. When bitou bush becomes abundant, community structure and functioning may be compromised.

(A) Keywords

Biological invasions, introduced species; growth form; structure; variability; coastal dune.

(A) Introduction

Plant invasion is a major cause of change in native communities around the world. Plant invaders have been documented as novel dominants (Ortega & Pearson, 2005), ecosystem transformers (Vitousek, 1990; Richardson *et al.*, 2000; Evans *et al.*, 2001) and agents of biodiversity decline (Enserink, 1999; McKinney & Lockwood, 1999). In light of profound ecological changes caused by the invasion process, considerable theoretical and experimental work has been conducted to understand invasion mechanisms, predict potential invaders and characterize invaded communities. Numerous plant traits which assist in competitive or colonizing superiority have been recognized in plant invaders (Baker, 1965; Bazzaz, 1986; Pywell *et al.*, 2003; Pyšek & Richardson, 2007). Invader success may also depend on environmental attributes. Disturbance and invasion success have been positively correlated in a number of studies (Hobbs & Huenneke, 1992; D'Antonio, 1993; Burke & Grime, 1996). External inputs of resources or their release by the resident community (through plant mortality or damage) following disturbance events may provide invasion opportunities (Davis *et al.*, 2000). Consequently the mechanisms by which a species invades and its effects may relate to attributes of the invader, environmental conditions of the invaded community (Bazzaz, 1986), or to a combination of invader and environmental attributes (Didham *et al.*, 2005).

While both invader attributes and community invasibility have been researched, the effects of a single invader on components of different resident communities have

rarely been reported (but see D'Antonio *et al.*, 2000; Alvarez & Cushman 2002; Jäger *et al.* 2007). Here we use comparative data to examine impacts of a single invader in two coastal vegetation communities. We focus on bitou bush *Chrysanthemoides monilifera* ssp. *rotundata* (D.C.) Norl. (hereafter termed bitou), a South African shrub, which has invaded both fore dune shrublands and hind dune woodland / forest communities on the east coast of Australia.

(B) *Invasion impacts on native growth forms*

Bitou may achieve dominance in dune communities by competitively displacing subordinates by resource consumption: the invader population size increases until the limiting resource is at such a low level that subordinates are unable to survive (Tilman, 1988). Consequently, bitou may competitively exclude other shrub species which use similar resources (MacArthur, 1972; Johansson & Keddy, 1991). Bitou may also competitively exclude functionally dissimilar low architecture herb and graminoid species by reducing light penetration to lower strata. Such exclusion of herbaceous species following woody invasion has previously been documented (e.g. Hobbs & Mooney, 1986; Wearne & Morgan, 2004). Bitou may also become abundant at a site through tolerance of non-competitive processes such as novel disturbance and an ability to overcome recruitment limitation. These processes may limit the distribution of other species more than the invader (Seabloom *et al.*, 2003; MacDougall & Turkington, 2005).

Bitou has invaded two vegetation communities (fore dune shrubland and hind dune woodland / forest communities) which are distinct in terms of vegetation structure, composition and disturbance history. The fore dune environment is affected both by natural disturbance regimes such as wind and storm action (Viles & Spencer, 1995), and

anthropogenic disturbance such as sand mining or recreational activities (Chapman, 1989; Brown & McLachlan, 2002). The hind dune environment is buffered from much of the natural and human-induced disturbance experienced on fore dunes. The hind dune also has greater structural complexity than the fore dune: hind dune communities have tall shrub and canopy strata while fore dune communities have only a shrub layer with some isolated emergents. Vegetation composition and structure, coupled with disturbance history may moderate bitou impacts in different communities. We hypothesized that native species would be affected by invasion, but the direction of response of different growth forms in each community was unclear.

(B) Invasion impacts on vegetation structure

Invaders continue to interact with the resident community subsequent to the initial invasion. Over time, an invader shifts the proportion of biomass of each species in the assemblage (Johnston, 1986). Changes in representation of growth forms may then be expressed in the distribution of vegetation structure. We hypothesized that structural density in both fore and hind dune invaded communities would be re-distributed such that shrub-level vegetation density – corresponding with bitou biomass – would be higher than in non-invaded communities. Structural density at other vegetation heights may be unchanged or reduced following invasion: fore and hind dune ground level structure may be sparser, yet hind dune canopy level structure may be unchanged in invaded compared with non-invaded communities. Therefore at the community level, the invasion process creates a biotic filter, selectively reducing or eliminating particular morphologies and ultimately changing community structure.

(B) Invasion impacts on community variability

While we have described invasion mechanisms and impacts that may operate at the site level, species exclusion or reduced abundances following invasion may result in changes to community variability at larger spatial scales. Site-to-site variability may increase, decrease or remain the same following invasion. The invasion literature has viewed invaders as homogenizing regional and biome-level floras (McKinney & Lockwood, 1999), but there is little empirical evidence for changed species variability at the community level. If we consider invasion as a disturbance (Lockwood *et al.*, 2005), we find little consensus in the literature on the impacts of disturbance on community variability. For example in marine systems, increased (Warwick & Clarke, 1993), unchanged and reduced (Chapman *et al.*, 1995; Stark *et al.*, 2003) assemblage variability following disturbance have been reported.

Changes in community variability will depend on the composition of species affected by the invader. We hypothesized that site-to-site variability would increase following invasion if widespread or dominant species were lost from communities. This would leave each site with rarer or more restricted species and therefore increase the dissimilarity of invaded sites. In contrast, we hypothesized that site-to-site variability would decrease following invasion if rare or restricted species were lost from communities. Common species which were retained would increase homogeneity across invaded sites. Unchanged variability following invasion may indicate either a lack of invader impacts or a loss across sites of both widespread and restricted or rare species. According to our hypotheses, a change in variability of community assemblage following invasion would indicate that species representations have become discontinuous at regional scales. Reducing the size and increasing the isolation of populations may

increase their extinction risk due to inbreeding depression and stochastic events (van Groenendael *et al.*, 1998; Lennartsson, 2002). Local extinction of native species, expressed through changed community variability may then compound impacts of the original invasion.

In this study, our objective was to examine impacts of bitou invasion in two different coastal vegetation communities by comparing species richness of growth forms, vegetation structural density and site-to-site variability in species composition between invaded and non-invaded sites.

(A) Methods

(B) Study area

Dune communities were sampled along approximately 1 330 km of the New South Wales (NSW) coast (28° 25' 45" S; 153° 33' 25" E to 36° 57' 37" S; 149° 56' 07" E). Fore dune sites were predominantly *Acacia longifolia* ssp. *sophorae* shrubland with occasional *Banksia integrifolia* emergents. Mid and lower strata species commonly included *Scaevola calendulacea*, *Lomandra longifolia* and *Spinifex sericeus*. Hind dune sites were woodland or forest communities. *Eucalyptus pilularis* and *Banksia integrifolia* were common canopy species. Mid stratum dominants included *Monotoca elliptica* and *Banksia serrata*, while lower stratum species included *Lomandra longifolia* and *Pteridium esculentum*. We defined non-invaded sites as those with little bitou cover (average of 5 %) and no history of weed control activities (fore dune: n = 17; hind dune: n = 10). These sites were the best representatives of relatively undisturbed coastal communities. We defined bitou-invaded sites as having high bitou cover (average of 60 %) and no history of control activities (fore dune: n = 16; hind dune: n = 12). Non-

invaded and invaded sites were interspersed along the coast. Site history was ascertained from (1) responses to a land manager survey, which was distributed to public agency and community group representatives, (2) site records and (3) personal observations (T.J. Mason).

(B) Sampling methods

Sampling was conducted between September 2002 and May 2003. At each site, a 20 x 50 m (0.1 ha) quadrat was used to measure species identity, vegetation structure and environmental variables. A nested 20 x 20 m quadrat was used to record cover of each species using an adapted Braun-Blanquet cover scale measure (Poore, 1955). The analysis used cover class midpoints. Species nomenclature followed Harden (1992; 1993; 2000; 2002). We measured environmental variables of standing dead vegetation, litter, bare ground and log (bole diameter > 0.1 m) percent cover, slope, aspect, distance to strandline and evidence of sand mining or recent fire (< 5 years). These physiogeographic and disturbance variables were measured to account for extrinsic factors that may co-vary with diversity of native and invading species in dune communities. Vegetation structure was estimated using an adapted point intercept method (Mueller-Dombois & Ellenberg, 1974; Chalmers & Parker, 1986). A 16 mm diameter, 3 m wooden pole was divided into seven height classes (0-0.2 m; 0.2-0.5 m and thereafter 0.5 m increments to 3 m). Fifty measurements were taken at 5 pace intervals around the perimeter and down the long axis centreline of the 20 x 50 m quadrat. At each position, the presence or absence of vegetation touching the pole at each height class was recorded. For the purposes of this study, vegetation >3 m tall was considered canopy cover and was estimated at the same

interval as understorey structure using a modified moosehorn crown closure estimator (Mueller-Dombois & Ellenberg, 1974).

(B) *Data analysis*

A general linear modelling (GLM) approach was used to assess the impact of bitou invasion on the species richness of native communities. Extrinsic physical, disturbance and biotic predictors were also included in models. Response variables were separated into native and exotic graminoid, herb, shrub, tree and climber species richness at each fore and hind dune site. We used growth forms to express gross differences in plant architecture and functionality (Johnston, 1986; Troumbis & Memtsas, 2000). Native or exotic status for each species was recorded. Species information was obtained from the NSW plant database (Plant Information Network System of the Botanic Gardens Trust Version 2.0: <http://plantnet.rbgsyd.nsw.gov.au/>). Exotics were defined as species introduced to the NSW coastal zone, and included species such as *Acacia saligna* which has been introduced from Western Australia.

Predictors were removed from each model using a backward elimination process when P values were > 0.05 . Non-significant variables are not presented. Data were transformed to reduce heteroscedasticity and improve normality when required. Multicollinearity was checked using Pearson and Spearman Correlation Coefficients. A number of variables were omitted due to high correlation: bitou cover was removed from fore and hind dune models, while longitudinal position and litter cover were omitted from hind dune models. One fore dune site was omitted from the analysis due to missing values for independent variables of the model. Complete interaction terms could not be included due to limited available degrees of freedom. For clarity, unadjusted mean

richness values of growth forms are graphically presented (trends are the same as adjusted mean value results).

One-way analysis of similarity (ANOSIM) was used to compare vegetation structure between non-invaded and invaded sites in fore or hind dune communities (Clarke & Warwick, 2001). Bitou bush was included in the analysis and the Bray-Curtis similarity index was used on untransformed data. T-tests were then used to determine whether vegetation structure classes were significantly different between non-invaded and invaded sites.

Variability among species assemblages of non-invaded and invaded sites was compared using a Permutational Test of Multivariate Dispersion (PERMDISP) (Anderson, 2004). The program investigates variability in sets of sites in multidimensional space by calculating (using a similarity index) how distant each site is from an average site (centroid). In our case, dimensions were associated with species identity and cover abundance. PERMDISP then tests whether variability in two sets of sites (non-invaded and invaded) differs through a randomization permutation procedure. The test requires a balanced design so one non-invaded fore dune and two invaded hind dune sites were omitted from each one way analysis (fore dune: $n = 16$; hind dune: $n = 10$). Tests used Bray-Curtis dissimilarities with 9999 permutations on unstandardised data. We used untransformed, square root transformed, fourth root transformed and presence / absence data to progressively down-weight the effects of abundant species and increase the importance of rare species. We omitted bitou cover abundance values to analyze invader effects on the remainder of the dune community. We used the SIMPER

procedure (Clarke & Warwick, 2001) to select species with high contributions to invasion category dissimilarities.

(A) Results

(B) Growth form responses

In fore dune communities, non-invaded sites had significantly more native graminoid, herb and climber species than invaded sites (Table 1; Fig. 1(a-c)). In contrast, invasion category explained little variation in native shrub and tree richness and was not retained in the final models (Table 1). Exotic herb richness was higher in non-invaded compared with invaded sites (Table 1; Fig. 1(d)) but invasion category was not a significant predictor for exotic graminoid and climber species richness (Table 1). As there were only two records of exotic trees in fore dune communities (*Acacia saligna* and *Coprosma repens*), this growth form was not analyzed. When bitou was excluded from the analysis, exotic shrubs did not respond significantly to invasion category. It should be noted that the final exotic shrub model was non normal and heterogeneous indicating the significance of factors remaining in the model may be equivocal. However, as invasion category was not significant in the final model, the central finding that native and exotic shrub species responded similarly to bitou invasion was unaffected.

A number of disturbance and environmental predictors remained significant in final fore dune models (Table 1). Shrub species richness was reduced in sand mined sites. Aspect, latitudinal position and distance to strandline were significant environmental predictors but trends were not consistent across growth forms. Litter cover was positively correlated with native shrub richness, while log cover was negatively correlated with

exotic graminoid richness. Native herb and exotic graminoid richness values were higher in western than eastern sites in the study area.

[Insert Table 1]

[Insert Fig. 1]

In hind dune communities, non-invaded sites had significantly more native shrub species than invaded sites (Table 2; Fig. 1(e)). Native shrub species richness was negatively correlated with distance to strandline and cover of standing dead vegetation, but positively correlated with cover of bare ground. Native shrub species richness was also reduced at sand mined sites. The native graminoid, herb, tree and climber species richness models were non significant (Table 2), indicating that recognized factors and covariates were unable to explain hind dune richness for these growth forms. Similarly, invasion category was not a significant factor predicting exotic graminoid, herb, shrub and climber richness in hind dune communities (Table 2). As the study did not record any exotic tree species in the hind dune, tree growth form responses were not analyzed. Exotic shrub richness was higher in areas that were sand mined and in northern sections of the study area, but richness was not related to invasion category (Table 2).

[Insert Table 2]

(B) *Vegetation structure*

Vegetation structure was significantly different in invaded and non-invaded sites in both fore and hind dune communities (Table 3). In fore dune communities, invaded sites were characterized by a denser shrub layer (0.2-1 m) and sparser ground cover layer (0-0.2m) than reference non-invaded sites (Table 3). In hind dune communities, structural

differences consisted of greater understorey density (0.2-1.5 m) but reduced canopy density (>3 m) in invaded sites compared with non-invaded sites (Table 3).

[Insert Table 3]

(B) *Community variability*

In fore dune communities, invaded sites were significantly more variable than non-invaded sites when species cover abundances were considered (Table 4). Native species with strong contributions to dissimilarities between site categories had lower cover in invaded sites than in non-invaded sites (Table 5). These species also occurred less frequently in invaded than non-invaded sites, but *Acacia longifolia* ssp. *sophorae*, *Banksia integrifolia* and *Hibbertia scandens* had similar frequencies in non-invaded and invaded sites (Table 5). However, when presence / absence data were considered, there was similar variability between fore dune non-invaded and invaded sites (Table 4), suggesting that a change in species cover, rather than identity, was the primary driver of increased fore dune variability following bitou invasion.

In hind dune communities, non-invaded and invaded sites had similar community variability regardless of species cover weightings (i.e. untransformed, square root and fourth root transformed or presence / absence data) (Table 4). This result indicated that either bitou invasion did not affect overall cover of species and their identity, or that both widespread and restricted / rare species were affected by invasion. We previously found that overall native species richness and composition were similar among hind dune non-invaded and invaded sites (Mason & French, 2007), so we discounted the second possibility and concluded that bitou invasion had not affected hind dune community variability.

[Insert Table 4]

[Insert Table 5]

(A) Discussion

(B) Changes to species richness within growth forms and vegetation structure following bitou invasion

Bitou invasion affected different complements of native growth forms in fore and hind dune communities. Functionally distinct native graminoid, native and exotic herb and native climber species were negatively affected by bitou invasion in fore dune communities. Bitou invasion also shifted the distribution of vegetation structure in fore dune communities. Structural density was higher at the shrub level for invaded compared with non-invaded sites, reflecting increased bitou biomass following invasion. In contrast, structural density at the ground-cover level was lower for invaded compared with non-invaded sites. It may be that bitou shading effects (Lindsay & French, 2004) competitively reduce richness and reduce regeneration potential of low architecture herbaceous growth forms (see Rhazi *et al.* (2004) for a related discussion).

Climber richness was also reduced in invaded compared with non-invaded fore dune communities. As climbers scramble over the shrub canopy, they will be less constrained by bitou shading effects than graminoids and herbs and adult survival may not be closely linked with bitou invasion. However, relatively short generation times of native climbers (e.g. *Stephania japonica* longevity is < 5 years (Clarke, 1989)) and long establishment of bitou in fore dunes (> 10 years) suggest that climbers may senesce at invaded sites without replacement.

In addition, novel disturbance regimes in the fore dune environment may limit recruitment opportunities for herbaceous species. A review by Turnbull *et al.* (2000) reported that herbaceous species were more seed limited than woody species. We recorded mining and fire disturbance at each site but did not record other disturbance regimes such as recreation activities, pollution and altered sand budgets which operate in the fore dune (Morley, 1981; Viles & Spencer, 1995; Brown & McLachlan, 2002). Herbaceous species may therefore be affected by both invasion and disturbance and suffer reduced representation in fore dune environments. While native and exotic shrub species appeared unaffected by the invasion process in fore dune communities, shrub species richness was reduced in sites subject to sand mining. Woody species may therefore be intolerant of mining disturbance but may effectively compete with the functionally similar bitou bush in fore dune communities.

In contrast to fore dune patterns, hind dune invaded sites had reduced native shrub species richness when compared with non-invaded sites. Native shrub richness was also reduced at sites where sand mining had occurred. Native and exotic graminoid, herb and climber species richness values were unaffected by both invasion and mining processes. This finding indicates that outcomes in hind dune communities cannot be inferred from fore dune responses to bitou invasion. The presence of multiple overstorey layers (tree and shrub canopies) in hind dune communities may pre-adapt low architecture herbaceous species to bitou shading effects. Further, hind dune shrub assemblages may be less competitive against bitou invasion than fore dune shrub assemblages.

Similarly to fore dune vegetation, structural density was higher at the shrub level for hind dune invaded compared with non-invaded sites, reflecting increased bitou

biomass following invasion. However, bitou invasion was also implicated in canopy-level changes to hind dune vegetation structure with canopy closure higher at non-invaded sites compared with invaded sites. This result may indicate that native canopy species are senescing in hind dune invaded communities and are not being replaced as bitou invasion suppresses or inhibits germination and seedling growth. Alternatively, canopy health may be reduced by bitou invasion. Long established bitou individuals use tree boles and branches as a physical support (T. Mason pers. obs.) and bitou biomass may cause breakages in the tree canopy. Our observational dataset was unable to discount the possibility that hind dune sites were invaded *because* they had a sparser canopy rather than bitou invasion *causing* sparse canopy cover. Demographic studies and manipulation of bitou biomass may address this limitation.

Our results indicated that a range of other exotic species were unable to exploit niches vacated by native species following bitou invasion. Exotic herbs had reduced richness while exotic graminoid, climber and shrub species had unchanged richness in fore dune invaded compared with non-invaded sites. In hind dune communities, bitou invasion was not a significant predictor of richness within exotic growth forms. Our results concur with findings by McIntyre and Martin (2002) that many exotic and native species had similar responses to disturbance in sub-tropical eucalypt woodlands. In our case, bitou may be a superior competitor, stress tolerator or propagule disperser compared with other exotic species.

(B) Impacts of invasion on community variability are different in the fore and hind dune

Fore dune community variability results were consistent with our hypothesis that site-to-site variability increases if widespread or dominant species are most affected by

plant invasion. We found that a reduction in cover of common native species following invasion accounted for much of the dissimilarity between non-invaded and invaded sites. The lack of significance when using presence / absence data indicated that changed species cover rather than identity drove variability responses. While the compensatory role of the invader requires investigation, reduced abundance of dominant native species may reduce community resistance and stability (Smith & Knapp, 2003). Increased variability of species cover abundances following invasion may disrupt dispersal and recruitment dynamics and ultimately feed back with further fluctuations in abundance patterns. We are unable to exclude the possibility that other factors such as latitude contributed to fore dune variability results. Low replication precluded consideration of latitudinal position as a factor in the analysis. However, if latitudinal effects were driving variability results, we would have expected consistent results across all transformations. Similar variability between invaded and non-invaded sites when species identity alone was considered indicated that variability results were most likely explained by invader effects.

In hind dune communities, variability was unchanged between non-invaded and invaded sites. Discrepancies in fore and hind dune results may relate to the presence of canopy cover in the hind dune which may limit invader effects (Hutchinson & Vankat, 1997; Meiners *et al.*, 2002; Setterfield *et al.*, 2005). In addition, anecdotally, invasion is more recent in hind dunes than fore dunes, thus bitou impacts on hind dune species diversity may manifest as species senescence without replacement.

Invader effects such as low redundancy within growth forms and increased site-to-site variability may affect ecosystem productivity. Graminoids, herbs and climbers in

fore dune communities and shrubs in hind dune communities contribute to maximizing CO₂ uptake by filling gaps and creating three dimensional canopies which efficiently intercept light and increase productivity (Lawton, 1994). In addition, root systems of herb, climber and shrub growth forms exploit different soil layers which collectively promote efficient uptake of water and nutrients (Troumbis & Memtsas, 2000).

Complementarity among species of diverse communities maximizes resource utilization (Tilman *et al.*, 1996) and may inhibit invasion (Knops *et al.*, 1999; Stachowicz *et al.*, 1999). Indeed Fargione and Tilman (2005) found that diverse grassland plots better inhibited invasion than a monoculture of the most competitive species. Following invader control, replanting or reseeded efforts should focus on native graminoid, herb and climber species in fore dune communities and shrub species in hind dune communities to maintain ecosystem productivity and functioning. Previous research has indicated that bitou is a strong competitor (Weiss 1984) and an ecosystem transformer, altering litter quality, decomposition rates (Lindsay and French 2004) and nutrient cycling (Lindsay and French 2005). As a consequence, bitou invasion may continue to have legacy effects (e.g. Lett and Knapp 2005) following its control. Managers should consider whether activities such as soil conditioning or spray-burn regimes (Lindsay and French 2005) are necessary prior to replanting to effect successful establishment of under-represented native growth forms.

We found that growth form analyses provided greater resolution in understanding the impacts of bitou invasion than simple species richness. A previous study found similar native species richness values between non-invaded and invaded hind dune sites (Mason & French, 2007). However, the present study signalled that native shrub species

richness was reduced at invaded sites. Other studies have also found that species richness within functional groups is useful in detecting invader impacts: Holmes and Cowling (1997) found that guild structure of fynbos vegetation changed with the duration of *Acacia saligna* invasion. Further, Holmes and Richardson (1999) advocated monitoring strategies which measure richness within functional groups to assess restoration success.

In summary, the impacts of bitou invasion differed in fore and hind dune communities. The invader had different impacts on native plant growth forms, vegetation structure and community variability in fore and hind dune sites. While the concept of context-specific invasion outcomes has been reported elsewhere (Orians, 1986; Crawley, 1987; D'Antonio, 1993), the modulating effects of different resident communities on impacts of a single invader require further investigation (D'Antonio *et al.*, 2000). Our results indicate that restoration efforts in fore and hind dune communities require different foci: replanting of herbaceous ground cover in fore dunes and the woody shrub layer in hind dunes may provide better outcomes than non-targeted replanting alone. In addition, restoration must redress reduced abundance of common fore dune species following bitou invasion.

(A) Acknowledgements

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Tables and figures

Table 1

Growth form species richness	Model P value	R ²	Predictor variable	df	Mean square	F	P	Direction of response
Native graminoids	0.0001	0.366	Intercept	1	699.427	158.012	0.0001	see Fig. 1(a)
			Invasion category	1	76.677	17.323	0.0001	
			Error	30	4.426			
Native herbs	0.0001	0.742	Intercept	1	74.973	16.719	0.0001	see Fig. 1(b) NE-SE > NW-SW, SE-SW negative correlation
			Invasion category	1	137.848	30.741	0.0001	
			Aspect	3	28.930	6.452	0.002	
			Longitudinal position	1	20.805	4.640	0.041	
			Error	26	4.484			
Native shrubs	0.001	0.527	Intercept	1	0.502	0.180	0.674	SE-SW > NW-SW absent > present positive correlation
			Aspect	3	12.933	4.647	0.010	
			Sand mining	1	54.727	19.662	0.0001	
			Litter	1	18.352	6.594	0.016	
			Error	26	2.783			
Native trees	0.461		Model non significant					
Native climbers	0.001	0.382	Intercept	1	42.040	13.007	0.001	see Fig. 1(c) positive correlation
			Invasion category	1	29.886	9.247	0.005	
			Latitudinal position	1	49.769	15.399	0.0001	
			Error	29	3.232			
Exotic graminoids	0.003	0.330	Intercept	1	4.631	77.509	0.0001	negative correlation negative correlation
			Longitudinal position	1	0.823	13.779	0.001	
			Log	1	0.286	4.793	0.037	
			Error	29	0.060			
Exotic herbs	0.0001	0.742	Intercept	1	0.383	15.057	0.001	see Fig. 1(d) negative correlation positive correlation
			Invasion category	1	0.701	27.543	0.0001	
			Latitudinal position	1	0.301	11.842	0.002	
			Distance to strandline	1	0.142	5.567	0.026	
			Error	28	0.025			
Exotic shrubs	0.022	0.232	Intercept	1	0.306	8.709	0.006	absent > present negative correlation
			Sand mining	1	0.199	5.677	0.024	
			Distance to strandline	1	0.194	5.522	0.026	
			Error	29	0.035			
Exotic climbers	0.056		Model non significant					

Table 2

Growth form species richness	Model P value	R²	Predictor variable	df	Mean square	F	P	Direction of response
Native shrubs	0.001	0.811	Intercept	1	487.639	35.184	0.0001	
			Invasion category	1	79.726	5.752	0.032	see Fig. 1(e)
			Aspect	3	126.656	9.138	0.002	NE-NW > NE-SE, NW-SW and SE- SW > NW-SW
			Sand mining	1	65.894	4.754	0.048	absent > present
			Distance to strandline	1	95.146	6.865	0.021	negative correlation
			% Bare ground	1	83.079	5.994	0.029	positive correlation
			% Standing dead vegetation	1	93.489	6.745	0.022	negative correlation
			Error	13	13.860			
Exotic shrubs	0.002	0.489	Intercept	1	0.123	1.894	0.185	
			Sand mining	1	0.367	5.662	0.028	absent < present
			Latitudinal position	1	0.326	5.039	0.037	positive correlation
			Error	19	0.065			
Native graminoids	0.085		Model non significant					
Native herbs	0.184		Model non significant					
Native trees	0.119		Model non significant					
Native climbers	0.095		Model non significant					
Exotic graminoids	0.181		Model non significant					
Exotic herbs	0.155		Model non significant					
Exotic climbers	0.281		Model non significant					

Table 3

Community	ANOSIM results		t-test results		
	R Statistic	P value	Height categories (m)	P value	Invaded vs. Non-invaded*
Fore dune	0.143	0.012	0-0.2	0.043	I < N
			0.2-0.5	0.001	I > N
			0.5-1.0	0.006	I > N
			1.0-1.5	0.128	I = N
			1.5-2.0	0.626	I = N
			2.0-2.5	0.887	I = N
			2.5-3.0	0.578	I = N
			> 3.0	0.545	I = N
Hind dune	0.246	0.003	0-0.2	0.375	I = N
			0.2-0.5	0.027	I > N
			0.5-1.0	0.004	I > N
			1.0-1.5	0.003	I > N
			1.5-2.0	0.869	I = N
			2.0-2.5	0.205	I = N
			2.5-3.0	0.131	I = N
			> 3.0	0.007	I < N

* I = Invaded sites; N = Non-invaded sites

Table 4

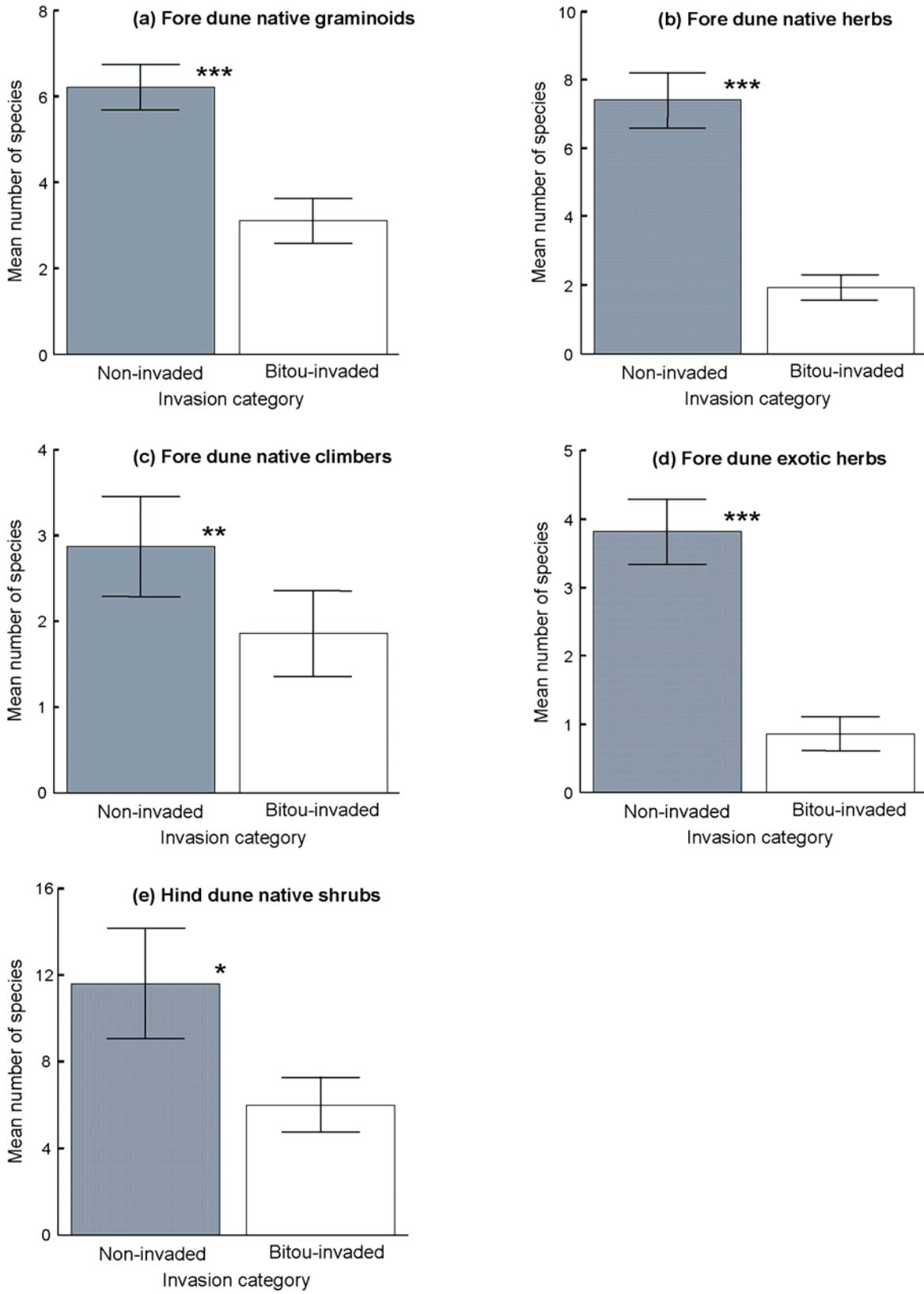
Transformation sequence:	Untransformed (raw abundances)	Square root ($\sqrt{}$)	Fourth root ($\sqrt[4]{}$)	Presence /Absence
Transformation explanation:	Weighted for abundant species	—————▶		Equal weighting for all species
Fore dune	N<I *	N<I *	N<I *	ns
Hind dune	ns	ns	ns	ns

*P < 0.05; ns = non significant N = Non-invaded sites; I = Invaded sites.

Table 5

Species	Average abundance (% cover)		Frequency (%)	
	Non-invaded	Invaded	Non-invaded	Invaded
<i>Acacia longifolia</i> ssp. <i>sophorae</i>	27.00	13.25	100	94
<i>Banksia integrifolia</i>	7.53	7.00	76	81
<i>Spinifex sericeus</i>	6.00	1.00	100	50
<i>Lomandra longifolia</i>	5.29	1.38	71	31
<i>Leucopogon parviflorus</i>	5.06	2.69	94	56
<i>Hibbertia scandens</i>	2.71	0.81	53	50
<i>Carpobrotus glaucescens</i>	1.94	1.00	94	44
<i>Ficinia nodosa</i>	1.82	1.06	82	44

Fig. 1



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Table captions

Table 1: General linear models for fore dune (n = 32) communities predicting species richness of growth form groups using environmental and disturbance factors and covariates.

Table 2: General linear models for hind dune (n =22) communities predicting species richness of growth form groups using environmental and disturbance factors and covariates.

Table 3: One-way analysis of similarities (ANOSIM) test and post hoc t-test results for vegetation structure of non-invaded and invaded sites in fore dune and hind dune communities (untransformed data)

Table 4: Permutational analysis of multivariate dispersions (PERMDISP) for fore and hind dune communities under various transformations (analyses excluded bitou abundances).

Table 5: SIMPER results and associated abundance and frequency information for native species with the highest contribution to dissimilarities between non-invaded and invaded fore dune sites.

Figure captions

Figure 1: Mean species richness of different growth forms for non-invaded and invaded fore dune and hind dune sites (\pm one standard error) * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.