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Vegetation and ghost crabs in coastal dunes as indicators of putative stressors from tourism

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ABSTRACT

Coastal dunes provide important ecosystem services and are susceptible to human disturbance such as vehicle traffic and human trampling. Notwithstanding, on several Australian beaches dunes serves as camping areas, where camping sites are located on the primary dunes landwards of the foredunes. Because these activities have the potential to impact on the biota of the foredunes directly adjoining the camping zones, sustainable management of dunes for multiple uses requires that putative impacts are identified. Consequently, we quantified: (1) effects of dune camping on the vegetation in the foredunes abutting the camping zones, (2) ghost crab (*Ocypode cordimana*) abundance, distribution, body size, and body condition as biological indicators of human stressors, and (3) the degree to which habitat attributes are correlated with ghost crab abundance. Two percent of the foredune surface was disturbed by human activity (vehicle tracks, trampling, dog prints, litter). Camping in the primary dunes had some minor effects on the vegetation of the foredunes, but widespread changes in plant assemblages were not detected. Ghost crabs were attracted to camp sites, significantly changing their distribution across the dune field and increasing their body condition near camp sites—presumably a trophic subsidy from food scraps. Except for vegetation height which had a positive influence on crab density, there were no other strong and consistent predictors of ghost crab density either in terms of physical habitat attributes (e.g. dune width and height) or vegetation characteristics (e.g. plant cover, diversity). Because coastal managers must increasingly reconcile multiple uses of the environment with its protection, robust data on the type, extent and magnitude of impacts are critical to formulate efficient management strategies for dunes. Monitoring the efficacy of such strategies requires robust indicators, and we show that ghost crabs may be good candidate species for this.

1. Introduction

Coastal dunes provide essential habitat for plants and invertebrates, as well as feeding and nesting sites for birds and turtles (Baird and Dann, 2003; Groom et al., 2007; Lastra et al., 2010). They also deliver critical ecosystem services to humans, forming natural barriers that protect coastal communities against the effects of severe weather events, storing and filtering large amounts of water, and acting as sediment reservoirs for beach nourishment (Short, 1999).

A burgeoning human population in the coastal strip is placing escalating pressures on coastal dunes, and many dune systems around the world have been severely modified (Nordstrom, 2000; Coombes et al., 2008). Human pressures on dune systems are diverse, including the removal of dunes for infrastructure development, shore armouring, removal of vegetation, introduction of invasive species, vehicles and trampling, and camping (Nordstrom, 2000; Comor et al., 2008; Thompson and Schlacher, 2008; Defeo et al., 2009; Kutiel et al., 2000; Bonte and Maes, 2008). Frequent disturbance of dunes by human activity usually leads to reduced biodiversity, loss of habitat, destruction of native vegetation, and increased erosion during storms (Nordstrom and Mauriello, 2001; Feagin et al., 2005).

Beaches are prime sites for human recreation and rank amongst the most intensively used ecosystem types by humans (Houston, 2008). This is especially true in Australia, where 85% of the population lives within 50 km of the coast, and tourism centred around sandy beaches is an important component of the economy (Australian Bureau of Statistics, 2004; Houston, 2008). Tourist activities can, however, have negative ecological consequences for beaches and dunes. Ecological impacts linked to recreation include changes to sediment properties, dune morphology, stability and dynamics (Kutiel et al., 1999), destruction of dune vegetation, often resulting in increased erosion (Rickard et al., 1994), and injuries, disturbance and kills of wildlife such as turtles (Hosier et al., 1981), birds (Williams et al., 2004; Weston and Elgar, 2005, 2007), and

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invertebrates (Moss and McPhee, 2006; Schlacher et al., 2008a,c; Sheppard et al., 2009; Bonte, 2005; Comor et al., 2008).

Camping on coastal dunes is a popular form of recreation, and causes ecological changes mainly associated with the clearing of vegetation and the use of vehicles in the dunes (Rickard et al., 1994; Hockings and Twyford, 1997; Groom et al., 2007). Although generally less severe, intense human trampling can cause similar impacts (Yu et al., 2008; Grünewald, 2006). Campers also bring dogs which threaten birds (Burger et al., 2007), and disposal of food scraps by tourists (Strachan et al., 1999) may modify trophic dynamics in invertebrate consumers of dunes. Many of these ecological responses to human use of coastal dunes are likely to be species-specific and depend on local site conditions, making generalisations for particular locations problematic. Thus, our first objective is to determine whether human disturbance associated with camping results in measurable changes to plant assemblages in the foredunes seawards of the camping zones.

Ghost crabs (Genus Ocypode) are abundant, large, widespread, and they have predictable responses to human pressures; this makes them potentially good biological indicators of human stressors on beaches (Barros, 2001; Lucrezi et al., 2009a,b; Lucrezi and Schlacher, 2010). In crustaceans, the hepatopancreas is critical for nutrient storage and the metabolism of energy reserves (Kennish, 1997; Connell et al., 1999; Verri et al., 2001). The ratio of hepatopancreas mass to body mass (Body Condition Index—BCI) indicates body condition (Kennish, 1997; Young, 2008). In the present situation, we predicted that food discarded by campers changes the trophic status of crabs in the dunes; this was tested using changes in their BCI. Our second aim was to assess whether changes in the density and distribution of ghost crabs can detect putative camping impacts on the adjacent foredunes.

Despite the large amount information on the distribution and abundance of ghost crabs on sandy beaches (Barrass, 1963; Jones, 1972; Lucrezi et al., 2009b), little is known about which environmental factors influence ghost crab populations in coastal dunes. However, such information is important to identify measures of habitat management and restoration that maximize benefits for crab populations. More widely, coastal managers are increasingly required to minimize environmental impacts from leisure activities (Schlacher et al., 2008b). To this end, biological indicators are needed to monitor the efficacy of management interventions.

Here we addressed three main objectives: (1) assess the impact of dune camping on the vegetation in foredunes abutting camping zones, (2) evaluate the suitability of ghost crabs (*Ocypode cordimana*) as biological indicators of human stressors in coastal foredunes, and (3) determine which habitat attributes are correlated with ghost crab abundance.

2. Materials and methods

2.1. Study site

North Stradbroke Island is a sand barrier island, forming the eastern rim of Moreton Bay, in south-east Queensland, Australia. Being close to the major metropolitan centre of Brisbane, it is a popular holiday destination, attracting 400 000 visitors annually. A major attractions is ‘beach camping’, where visitors camp on the coastal dunes with close access to surf beaches. Camping is highly popular, with up to 600 campers occupying a single camp zone during peak periods (Carter, 2005). Visitors often combine camping with other recreational pursuits such as fishing, swimming, surfing, walking, bird watching, and four-wheel driving.

Flinders Beach is one of the most popular recreational beaches on the island. It forms the northern edge of the island, is 4.6 km long, and is protected from the predominant south-easterly swells and winds (Fig. 1). The beach is of the reflective to intermediate morphodynamic type, 50–80 m wide at low tide, with fine sands of 260–350 μm (Schlacher and Thompson, 2007; Schlacher and Morrison, 2008). Four camping areas are situated in the primary dunes just landward of the foredunes. All camping areas show signs of human impacts, such as vehicle ruts and tracks, footpaths, campfires, cleared vegetation, litter and ‘bush toilets’.

2.2. Field collections

The main design principle of the study centred on a spatial mapping of dune attributes and biological properties at a resolution that is fine enough to allow for use zoning by the local government authority. Consequently, available resources were allocated primarily to maximize spatial information. While it is recognised that there will be some variation in human pressures and possible biological response over time, the biological variables chosen integrate human pressures over time (e.g. ghost crab populations, plant assemblage structure), justifying a synoptic survey approach for this particular application.

We quantified vegetation community structure and ghost crab populations along the length of Flinders Beach (Fig. 1 and Electronic Appendix Table 1). Twenty-two sites were sampled where foredunes were present. Sites were positioned using a stratified random design where the entire length of the beach was divided into 200 m wide sections; sampling positions within each of these sections were determined also random, but constrained to fall within 50 m of the centre point of each section to achieve dispersion of sites amongst sections. To further avoid sampling bias, the entire site selection process was done in Google Earth before field work started. All foredunes at the southern end of the beach were completely eroded during the time of the survey (April–June 2009) and there were no foredunes at two other pre-determined locations (nominal sites 21 and 22).

At each site, five cross-shore transects were placed along the shore with individual transects separated by 30 m. Transects extended from the unvegetated beach 3 m seaward from the base of the foredune (level 1) to the edge of the vegetation line which marks the boundary between the foredune and the primary dune (level 9). This boundary was distinct, marked by a change from low grasses and herbs to trees, mostly *Casuarina equistifolia*. Distance between levels varied between 3 and 10 m depending on the width of the foredune. Dune profiles were measured at every transect using a theodolite, with the base of the foredune (level 2) as the reference point.

The typical dune profile was characterised by a small crest (mean elevation: 0.75 ± 0.04 m) inland from the driftline, followed by a concave depression (swale) from levels 5 to 7 (mean elevation: 0.59 ± 0.02 m). On average, slopes were steepest ($4.73 \pm 0.29^{\circ}$) at the seaward face of the incipient foredune, and gentlest (1.11 ± 0.09) in the centre of the swale (Fig. 2a). The width of the foredune ranged from 18 m (site 23) to 99 m (site 3), while the maximum rise – as measured from the base of the foredune – varied between 0.82 m (site 23) and 2.42 m (site 5).

As a diagnostic check for any possible confounding of habitat topography on contrasts for biological variables between camping and non-camping zones, key habitat metrics related to dune morphology were compared between camping and non-camping zones (i.e. mean, maximum and coefficient of variation of elevation, slope, and dune width). There was no significant separation of camping zones (ANOSIM; $R = -0.184$, $P = 0.93$), and hence the foredunes are fundamentally very similar in terms of their physical habitat properties in camping and non-camping zones. It is therefore improbable that any differences documented for biota between camping and non-camping zones resulted from physical habitat differences and not from human use.

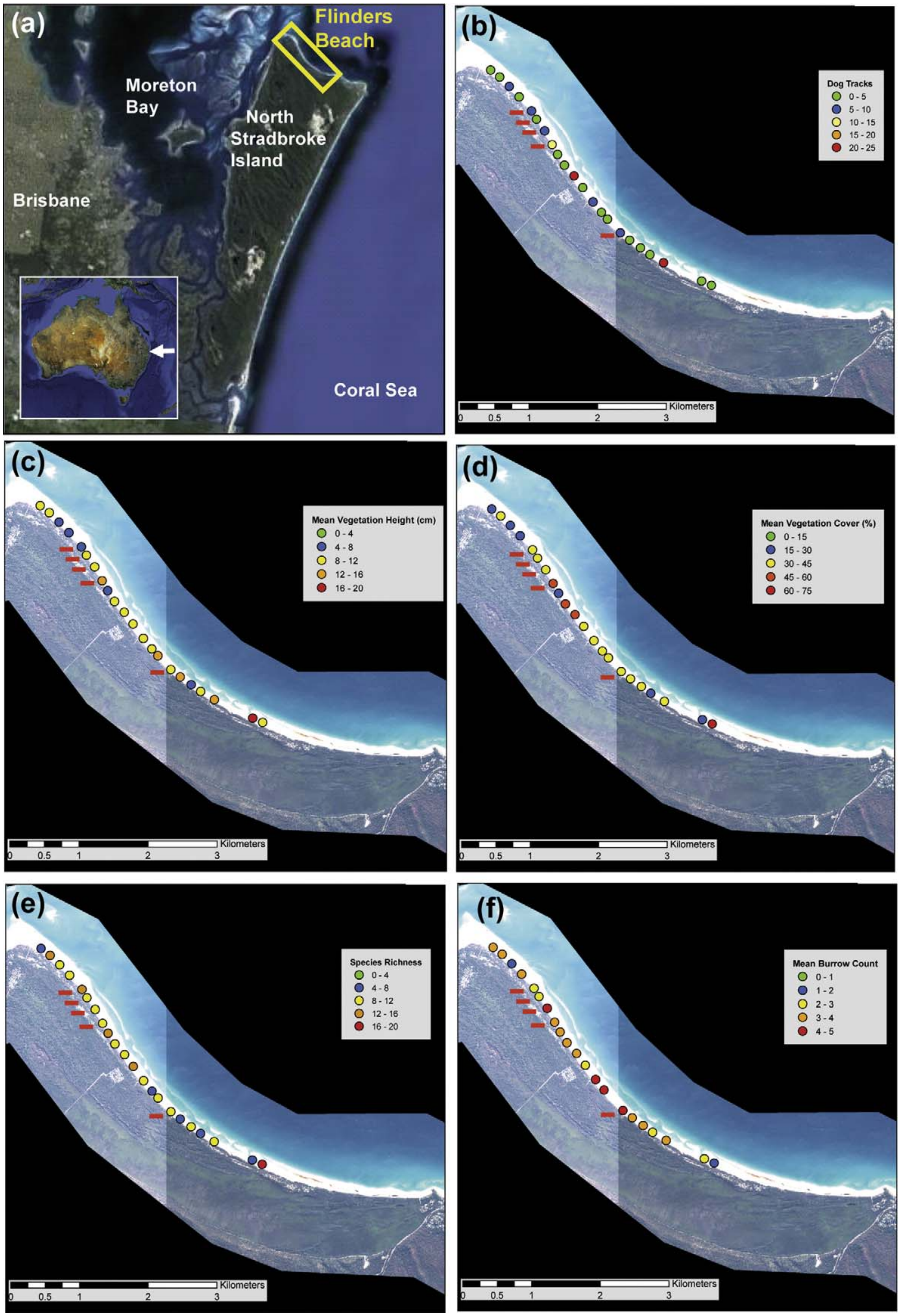

Fig. 1. Location of study area on North Stradbroke Island, Australia (a). Variation in (b) dog tracks, (c) mean vegetation height, (d) mean vegetation cover, (e) plant species richness, and (f) mean burrow densities of ghost crabs on Flinders Beach. Red hyphens indicated sites adjacent to camping zones. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of the article.)

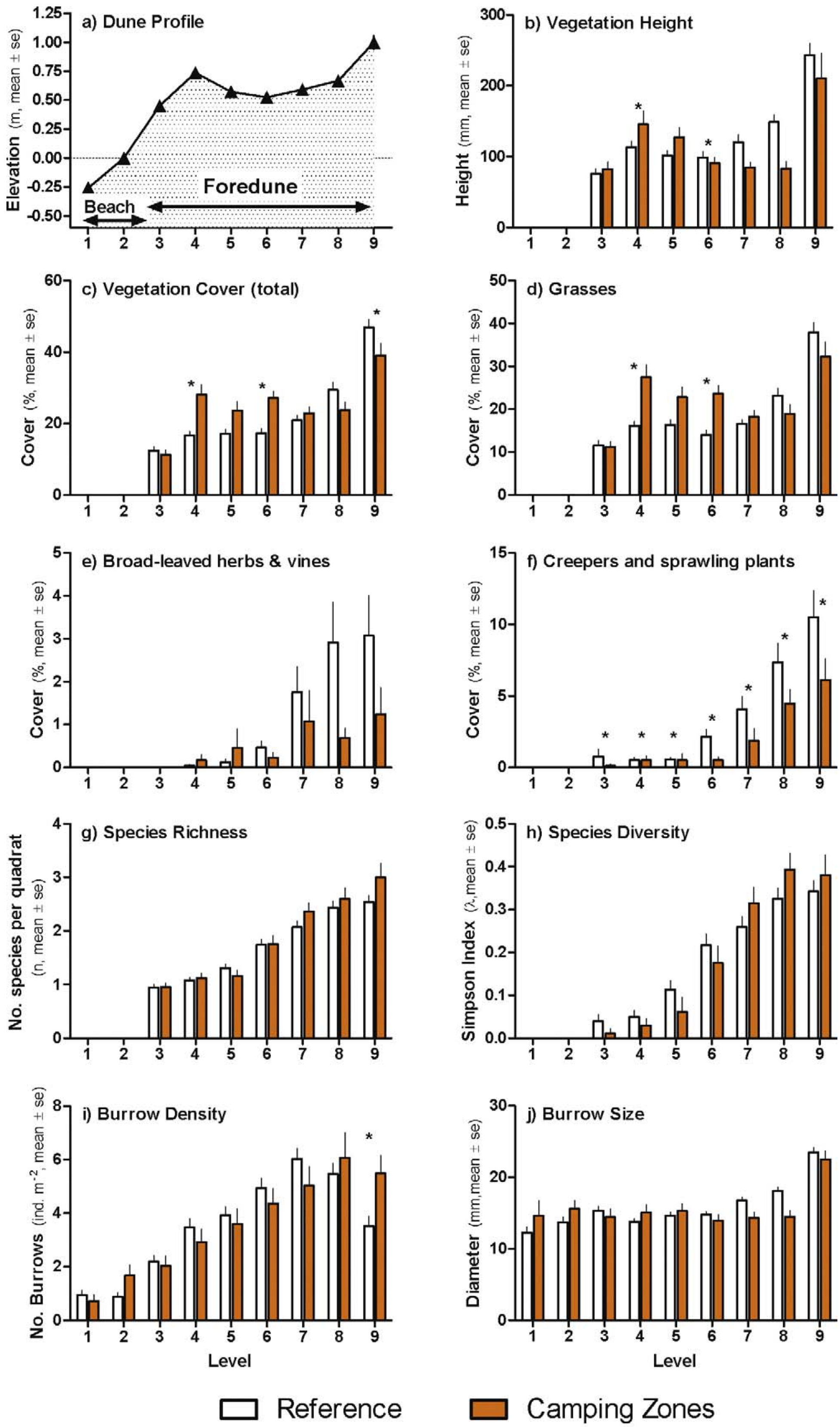

Fig. 2. Typical dune profile (a) and comparison between camping and non-camping zones for (b) vegetation height, (c) vegetation cover of all species, (d) cover of grasses, (e) cover of broad-leaved herbs and vines, (f) cover of creeping and sprawling plants, (g) plant species richness, (h) plant species diversity (Simpson diversity index), (i) burrow density of ghost crabs, and (j) burrow diameter of ghost crabs. * denotes significant ($P < 0.05$) difference identified by SNK tests.

Ghost crab burrow openings were counted and their diameter measured in 2 m × 1 m quadrat frames, with one frame per level. To quantify the vegetation community structure, the percentage cover, species composition and height of vegetation was measured using two complementary methods: (1) percent cover and species composition were determined from plan-view digital photographs taken of each frame; images were analysed in the laboratory using Corel Point Count (Kohler and Gill, 2006), (2) vegetation height was measured on site with a line-intercept method, recording the height of all plants which touched a 5 cm wide survey staff, placed diagonally across the frame, at 22 intersection points placed 10 cm apart. Thus, a total of 990 frames (9 frames per transect × 5 transects per site × 22 sites) were sampled, yielding 18 480 measurements of vegetation height and 3689 measurements of crab burrow diameter.

Crabs were collected using baited pitfall traps, placed in five camping (sites 5, 6, 7, 8, 16) and five non-camping sites (sites 3, 11, 15, 18, 23). The traps were upturned traffic cones (20 cm wide × 40 cm deep) placed flush with the substrate. At each site, three traps were placed on the foredune and three on the primary dune, with individual traps 50 m apart along the shore. Trapping was conducted over three consecutive nights on three separate occasions during May and June 2009, resulting in a sampling effort of 540 trap nights (6 traps per site × 10 sites × 9 nights of trapping = 540 trap nights). The traps were baited every night with pilchards and prawns. Captured crabs were collected early in the morning, euthanised in an ice slurry and kept on ice before freezing at −20 °C (within 1–2 h after collection).

2.3. Body condition index (BCI)

The crabs were defrosted and dissected to remove their hepatopancreas (digestive gland). The hepatopancreas and the rest of the body tissues were dried for 48 h at 60 °C and weighted separately. The body condition index, BCI was calculated as follows:

$$\mathrm{BCI}\,(\%) = \frac{H}{B} \times 100,$$

where H is the dry weight of the hepatopancreas, and B is the dry weight of the rest of the body. The BCI was calculated using the hepatopancreas weight as a proportion of the body weight minus the hepatopancreas weight (Kennish, 1997). This approach prevented any changes in the hepatopancreas from confounding the body weight and provides a more sensitive measure of changes in the crabs' condition than calculating the weight of the hepatopancreas as a proportion of the crabs' total body weight (Young, 2008).

2.4. Data analysis

To quantify vegetation community structure in terms of ground coverage, height, species richness and plant type (i.e. grass, shrub, succulent, etc.), images were analysed with Coral Point Count (Kohler and Gill, 2006); we also measured the percent surface area disturbed by human activity (trampling, vehicles), litter and rubbish, and dog tracks. For each individual image 72 points, spread randomly within a grid of three columns and two rows, overlaid over the image, were analysed.

Spatial variation in ghost crab burrow densities and opening diameters was partitioned with a two-way ANOVA that contained the design terms: (a) human use (i.e. camping vs. reference sites) and (b) level (i.e. levels 1–9 across the dune); the same model was used for vegetation height, cover, and plant species richness. The centre of abundance of ghost crabs across the dune field was calculated as the weighted mean position (WMP) of the population (Schlacher and Wooldridge, 1994) and compared between camping and non-camping areas using a t test. The distribution of catches across levels was compared between camping and non-camping sites with 9 × 2 contingency table. Multivariate patterns in plant assemblages were assessed based on similarities in species composition and species ground cover using Bray Curtis (B–C) resemblance coefficients as inputs for ANOSIM (Analysis of Similarities) and non-metric multidimensional scaling (Clarke, 1993).

3. Results

3.1. Environmental disturbance associated with camping

Human disturbances to the foredunes included human trampling, vehicle tracks, dog tracks and litter (Table 1). The area disturbed by human activity was significantly greater in camping sites than in reference sites (Table 1), with roughly four times the area ($\bar{x} = 5.40 \pm 1.01\%$) of dune surface disturbed in camping sites compared to reference sites ($\bar{x} = 1.15 \pm 0.22\%$; Table 1). This disturbance was mainly from human trampling ($\bar{x} = 1.43 \pm 0.21\%$) and vehicles ($\bar{x} = 0.12 \pm 0.03\%$). Dog tracks covered a much smaller surface area at 0.04 ± 0.01% of the dune surface (Table 1). Although dunes in front of camping zones showed greater signs of physical disturbance from mechanical impacts (e.g. human trampling, car tracks), and to a lesser extent from dogs, the average amount of litter did not differ. Litter was mostly plastic bottles, bags, and packaging material and covered on average 0.04% of the dune surface (Table 1).

3.2. Dune vegetation

Thirty plant species were recorded in the foredunes (Electronic Appendix Table 2). The family Poaceae (grasses) was the most speciose group with six species, followed by Fabaceae (legumes), with three species. The grass *Spinifex sericeus* dominated the vegetation, occurring at all sites and covering on average 17% of the dune surface. Other common species were Marine Couch (*Sporobolus virginicus*), Prickly Couch (*Zoysia macrantha*) and Variable Groundsel (*Senecio lautus*), all occurring at 15 sites or more. However, these species had comparatively low cover (max 1.7% for *S. virginicus*). Three species (*Actites mefalocarpa*, *Cassytha filiformis*, *Ipomoea indica*) were rare, with less than 0.01% cover.

Table 1
Comparison of human disturbance levels in the foredunes between camping and non-camping (reference) sites; all values are the percentage area disturbed by human activity.

	Reference (n = 595)		Camping (n = 175)		Contrast	Mann–Whitney test	All zones (n = 770)	
	$\bar{x}$	(se)	$\bar{x}$	(se)	(Camping/reference)	P	$\bar{x}$	(se)
Trampled	1.01	(0.22)	2.87	(0.52)	+2.84	<0.001	1.43	(0.21)
Vehicle tracks	0.00	(0.00)	2.26	(0.77)	+2.26	0.004	0.51	(0.18)
Dog tracks	0.10	(0.03)	0.21	(0.06)	+2.10	0.002	0.12	(0.03)
Litter	0.05	(0.01)	0.02	(0.01)	+0.40	0.233	0.04	(0.01)
Total	1.15	(0.22)	5.40	(1.01)	+4.70	<0.001	2.11	(0.29)

Vegetation cover varied considerably between sites, ranging from 13.27% (site 9) to 33.61% (site 24; Fig. 1). There was also considerable variation in species richness, with a maximum of 17 species recorded at site 24, compared to five species at sites 1, 5, and 19 (Fig. 1). Vegetation cover, height, and species richness all increased significantly toward the landward side of the foredune (Fig. 2). There was also a shift in species composition across the foredune, with the abundance of some species (e.g. *S. sericeus*, *Vigna sp.*, *Sesuvium portulacastrum*, *Carex bonariensis*), centred toward the marine edge of the foredune, while others (e.g. *Hydrocotyle bonariensis*, *S. virginicus*, *Z. macrantha*) were most abundant towards the landward edge of the foredunes.

The major source of spatial variation in vegetation characteristics on the foredunes is across the sea-land gradient: for all metrics examined, there is a recurring pattern of highest values at the landward edge of the foredunes (Fig. 2). Camping behind the foredunes has, in comparison, a generally much smaller influence on vegetation height and plant cover, and was not detectable for species richness or diversity (Fig. 2 and Electronic Appendix Table 3). Differences in vegetation height between camping and reference sites were evident at the dune crest (level 4) where shorter plants were found in non-camping zones (reference: $\bar{x} = 113 \pm 8$ mm; camping: $\bar{x} = 146 \pm 18$ mm; Fig. 3).

Changes in vegetation cover on the foredunes in relation to camping zones depended on the growth form of plants: grasses were less affected by human disturbance whereas broad-leaved herbs and vines, as well as creepers and sprawling plants, were considerably less abundant in front of camping areas (Fig. 2). Total vegetation cover was significantly higher in camping zones on both the dune crest (level 4) and in the centre of the swale (level 6). At the landward edge of the foredunes where they abut the camping area, total vegetation cover was significantly reduced in camping zones (level 9—reference: $\bar{x} = 46.9 \pm 2.2$ mm; camping: $\bar{x} = 39.1 \pm 3.4\%$). This pattern of lower plant cover in front of camping zones was more pronounced for plants with broader leaves and herbs (level 9—reference: $\bar{x} = 4.7 \pm 1.0$ mm; camping: $\bar{x} = 2.9 \pm 1.2\%$). Significant declines in plant cover abutting camping zones occurred for creepers and for species that sprawl along the dune surface (reference: $\bar{x} = 5.7 \pm 0.4$ mm; camping: $\bar{x} = 4.2 \pm 0.5\%$).

The average number of plant species per quadrat frame was highly similar between camping ($\bar{x} = 1.85 \pm 0.08$ spp.) and reference areas ($\bar{x} = 1.73 \pm 0.04$ spp.), and mean values of Simpson diversity were the same ($\bar{x} = 0.20 \pm 0.01$ spp). Overall, there was no significant difference in assemblage structure of the foredune vegetation that could be related to the presence of camping zones, either for the entire complement of species or for specific growth forms (Fig. 3).

3.3. Ghost crabs: distribution, abundance, and size

Ghost crabs occupied the entire foredune, with burrows recorded in 95% of all samples. The mean density of crab burrows on the supratidal, unvegetated beach (0.97 ± 0.11 ind. 2 m^{-2}) is significantly (ANOVA, Effect Habitat: $F_{1,986} = 178$, $P < 0.001$) lower by a factor of 3.3 compared to counts in the foredunes (4.22 ± 0.12 ind. 2 m^{-2}); these higher densities of crab burrows in the dunes are independent of human use in the abutting primary dunes (ANOVA, Interaction Term Habitat × Human Use $F_{1,986} = 0.60$, $P = 0.44$).

Although camping zones appear to have no overall significant effect on burrow counts when measured over the entire

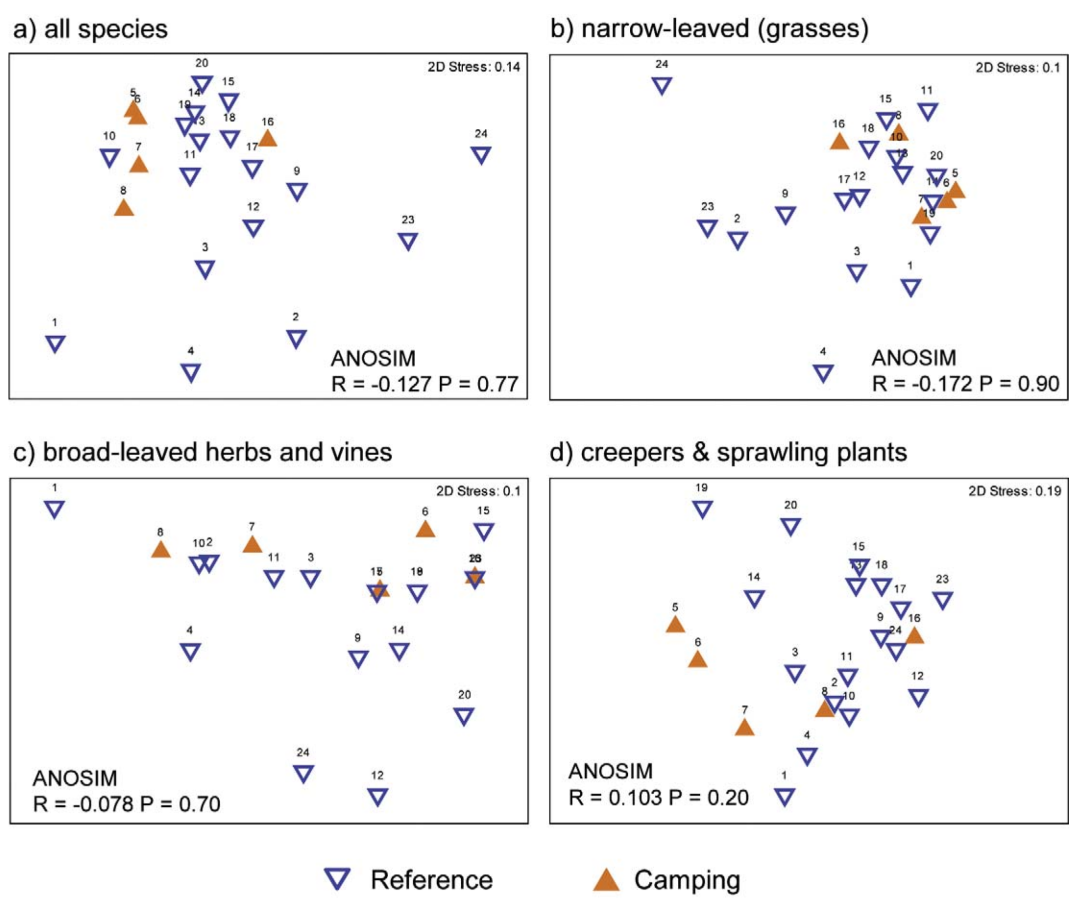

Fig. 3. Ordinations (non-metric multidimensional scaling) of sites based on their similarity (Bray Curtis) in (a) cover of all plant species, (b) grasses, (c) broad-leaved herbs and vines, and (d) creepers and sprawling plants, contrasting plant assemblages in the foredunes seawards of camping areas and with areas where no camping takes place.

Table 2
Comparison of crab condition index (BCI, %) between camping and non-camping areas, stratified by location and sex.

	Camping			Reference			Effect size
	n	$\bar{x}$	SE	n	$\bar{x}$	SE	(Camping/reference)
Males							
Foredunes	27	5.11	0.68	22	3.65	0.28	+1.40
Primary dunes	13	3.60	0.61	4	2.79	0.31	+1.29
Females							
Foredunes	8	2.44	0.44	1	5.56	–	+0.44
Primary dunes	2	4.22	0.25	2	2.45	0.45	+1.72

foredune field, there was a significant increase in density at the landward edge in front of camping zones compared to the same level in reference areas (reference: $\bar{x} = 3.52 \pm 0.38$ mm; camping: $\bar{x} = 5.48 \pm 0.69$ mm; Fig. 2). Crabs constructed burrows of very similar opening diameter irrespective of the presence of camping sites (reference: $\bar{x} = 16.56 \pm 0.20$ mm; camping: $\bar{x} = 16.03 \pm 0.38$ mm), with the largest individuals found at the landward edge of the foredune (Fig. 2).

In contrast to the largely similar abundance and size structure of burrows between camping and non-camping zones, the distribution of crab burrows across the sampled levels of the foredune field differed markedly with respect to human use (Fig. 2). A significantly greater proportion of the total catch in camping zones comes from the most landward locations which abut the camping areas (9×2 contingency table: Chi-square = 39.6, $P < 0.0001$). This translates into a significant landward shift of the centre of the population in camping areas ($t = 2.122$, $P = 0.036$; df = 108).

Crabs captured in camping zones had higher body condition indices, but we did not find a significant (ANOVA, $F_{1,75} = 1.49$, $P = 0.23$) difference in mean values (Table 2). On the foredune, the mean value of the body condition index (BCI) was $4.50 \pm 0.56\%$ in sites adjacent to camping areas, compared with $3.72 \pm 0.28\%$ in reference sites. On the primary dunes where the camp sites are located, crabs captured inside camping zones had a mean BCI of $3.68 \pm 0.53\%$ compared with a BCI of $2.68 \pm 0.27\%$ for crabs from reference sites.

3.4. Ghost crab abundance in relation to habitat attributes

We did not find any strong and consistent environmental predictors of crab density (Fig. 4). If anything, there was a pattern of higher crab abundance at sites with higher vegetation (Fig. 4). Dune dimensions only related weakly to crab densities (R^2 0.164–0.219). Similarly, neither vegetation cover (either for all species or for specific growth forms), species richness and diversity, nor the amount of plant litter or woody debris were significantly related to the mean density of ghost crabs at a site (Fig. 4). Examined environmental factors related weakly to crab density, irrespective of whether habitat attributes were measured as mean values per site, or expressed as habitat heterogeneity in terms of the spatial variation of a potential predictor across the dune field for a particular site.

4. Discussion

4.1. Environmental consequences of dune camping

Camping on coastal dunes clearly can have ecological impacts. For example, human trampling and vehicle traffic reduce vegetation cover, height and diversity, and they affect the behaviour, reproductive success, survival, and population size of animals reliant on coastal dune habitats (Burger, 1994; Watson et al., 1996; Bonte, 2005; Van Dam and Van Dam, 2008). By contrast, we did not find strong and consistent effects of camping in the primary dunes on the vegetation, abundance and body condition of ghost crabs in the foredunes seawards of the camping zones. Instead, camping affected the distribution of dune biota across the dune field and slightly increased the body condition of crabs. Ghost crabs appeared to be attracted to camping sites, with a larger proportion of burrows found towards the landward side of the foredune where camping sites were present. We believe the difference between our study and others are in the main attributable to differences in the intensity, spatial ambit and location of physical disturbance caused by camping.

Vehicle traffic is considered an environmentally highly detrimental form of human dune use (Rickard et al., 1994; Priskin, 2003; Groom et al., 2007). On beaches where vehicle access to camp sites located behind the foredunes is not well managed, environmental damage may be severe. For example, on Fraser Island, vehicle tracks cut through the foredunes at an average density of eight tracks per km of shoreline. This causes substantial physical damage to the dune–beach interface and removes all vegetation inside the tracks (Thompson and Schlacher, 2008). By contrast, on Flinders Beach access to camping zones appears to be better managed, with much fewer vehicle tracks (<2 per km of shoreline). We found that only about 0.5% of the foredune surface was disturbed by vehicles in camping sites, and that this disturbance did not translate into significant reductions in plant cover, diversity or ghost crab density.

The most widespread physical disturbance to the foredunes associated with camping in our study was human trampling; intense trampling often reduces cover and species richness of dune plants (Kutiel et al., 1999, 2000). However, moderate or low levels of trampling may have a positive effect on vegetation cover and diversity (Kutiel et al., 2000; Farrel and Marion, 2002). On the foredunes near camping sites, trampling is likely to be more intense at the landward edge, while being lower on the seaward side of the foredune as walking tracks tend to fan out (Rudi de Jager, personal observation). This may explain why dune vegetation is generally lower and less abundant near camping sites (i.e. the landward side of the foredune). Conversely, the seaward edge of foredunes in front of camping zones had slightly more abundant and higher vegetation, possibly suggesting that the low-intensity trampling may be benign or neutral. This hypothesis remains untested and requires careful experimental evaluation where trampling intensity is controlled.

Ghost crabs may also be resilient – to some degree – to human trampling. Lucrezi et al. (2009a) showed that intense experimental trampling did not result in significant reductions in crab numbers over short periods. However, longer-term trampling on the same beach resulted in significantly lower numbers of crabs (Lucrezi et al., 2009b). This is consistent from other locations, usually reporting decreased burrow counts from sites where human beach use – and by inference trampling – is concentrated (Steiner and Leatherman, 1981; Christoffers, 1986; Neves and Bemvenuti, 2006; Noriega and Schlacher, in press). Thus, significant impacts on ghost crab populations from human trampling are only likely where human use is intense; this was, with the exception of a few tracks traversing the dunes, not the case on Flinders Beach. Camping in the primary

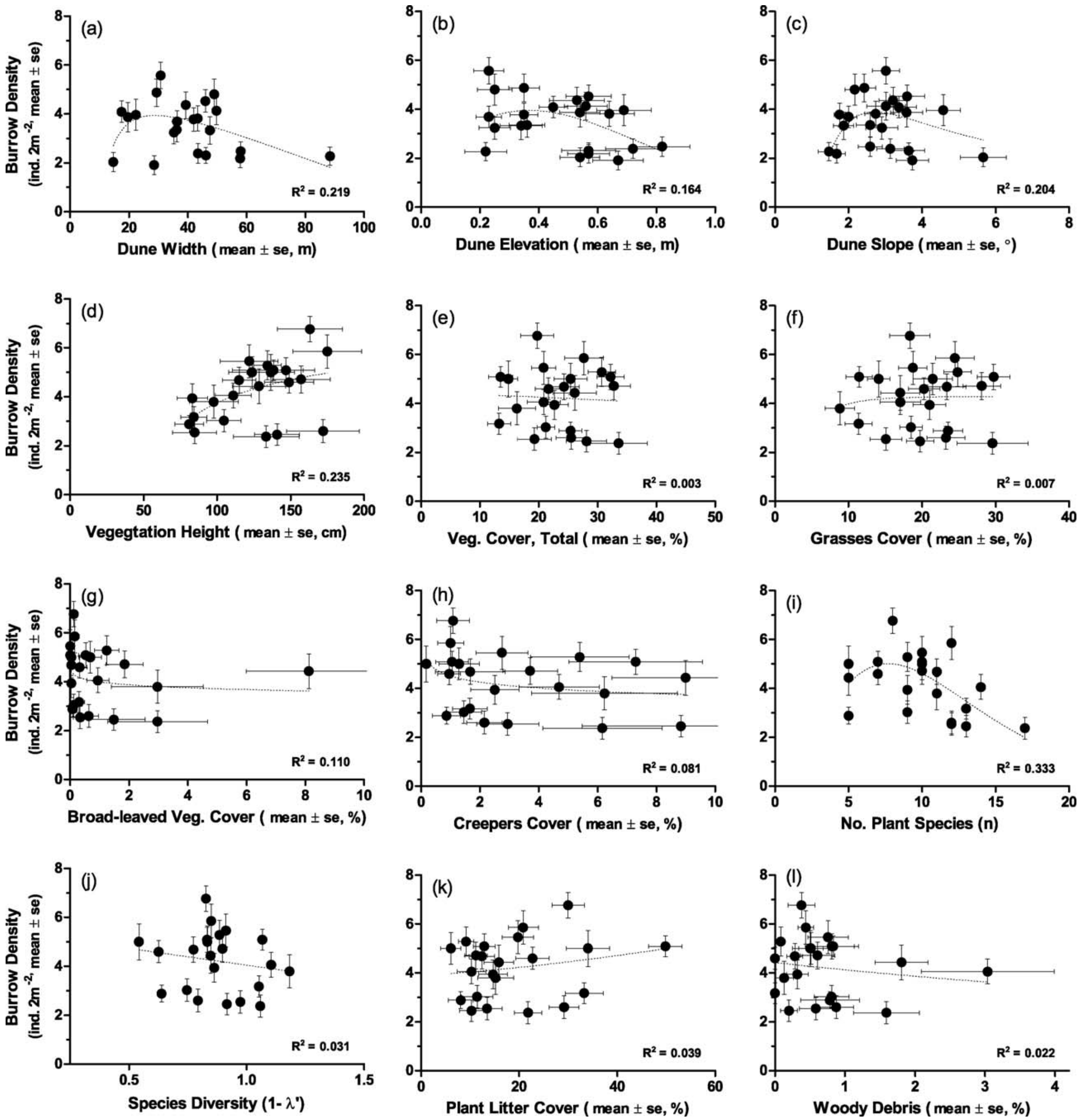

Fig. 4. Relationship between the density of ghost crabs and habitat attributes at the spatial scale of individual sites. Examined environmental variables include: dune width (a), dune height (b), dune slope (c) vegetation height (d), cover of all vegetation types (e), cover of grasses (f), cover of broad-leaved herbs (g), cover of creeping and sprawling species (h), species richness (i), species diversity (1-Simpson Index; j); cover of plant litter (k), and cover of woody debris (l).

dunes on this beach, in its current form and intensity, does therefore not measurably affect population sizes of ghost crabs in the foredunes abutting the camping zones.

Ghost crabs may, in some aspects, benefit from living in close proximity to camp sites. Ghost crabs exhibit complex behaviour and show great plasticity in their feeding habits (Jones, 1972; Brown, 1996). They are therefore likely to take advantage of any additional food sources in their environment, including those associated with camping. Steiner and Leatherman (1981) and Strachan et al. (1999) found higher densities of crabs in beach sections visited by humans and suggested that food scraps left by beachgoers subsidize crab diets, explaining the observed localized increases in abundance.

We show that on Flinders Beach crab populations shift towards the landward side of the foredune at camping sites. This suggests that ghost crabs are attracted to camping sites where food scraps are available. A trophic subsidy of ghost crabs by camping is also indicated by higher values of the body condition index in individuals captured in camping zones. While this appears to be a positive, or at least benign, effect of recreation, it does demonstrate that dune camping can modify the trophic dynamics in ghost crab populations on the dunes, which in itself represents an environmental impact. It is also not known whether there are detrimental physiological or other health effects caused by the consumption of human-introduced food for crabs. Food waste disposed carelessly by campers will also attract foxes, which are a serious environmental threat on the island, predating on dune birds, turtle eggs and hatchlings (D. Carter, personal communication). This stresses the need for continued visitor education on careful and appropriate waste handling.

From a beach management perspective, the level of environmental impact to the foredunes caused by camping in the primary dunes appears not to be a major concern at present, and the foredunes appear to be able to accommodate current visitor numbers. However, we suggest that visitor numbers should be capped within current usage levels. Most importantly, limiting the amount of vehicle access tracks across the foredune remains a critical issue and management should endeavour to provide alternative access to camp sites at the back of the dunes to limit damage to the beach and foredunes.

4.2. Ghost crabs as biological indicators on coastal dunes

Ghost crabs fulfil several criteria for an indicator taxon in that they: (a) respond in a largely predictable manner to human disturbances (Steiner and Leatherman, 1981; Wolcott and Wolcott, 1984; Barros, 2001; Moss and McPhee, 2006; Neves and Bemvenuti, 2006; Schlacher et al., 2007; Hobbs et al., 2008), (b) occur at relatively high densities (Lucrezi et al., 2009b), (c) are geographically widespread (Jones, 1972), and (d) can be rapidly counted using burrow openings (Lucrezi et al., 2009a) (Table 3).

Physiological condition is used in environmental monitoring (Stevenson and Woods, 2006), based on the assumption that the rates of physiological processes in an organism adjust in response to exposure to different environmental conditions (Dahlhoff, 2004). Thus, measurements of condition in biota can indicate changes in ecosystem state or functioning, particularly in species that have a substantial influence on ecosystem functioning (Chapin III et al., 1997). For example, changes in the physiological condition of brachyuran crabs inhabiting mangrove forests have been shown to act as an early warning signal of anthropogenic impacts in these ecosystems (Young, 2008; Amaral et al., 2009). Our results indicate that physiological condition in ghost crabs may be a useful indicator of impacts relating to food subsidies from human activity. We detected an increase in crab condition at camping sites, probably as a result of increased food availability.

4.3. Habitat heterogeneity and complexity vs. ghost crabs in dunes

Coastal dunes are structurally more complex than beaches, providing animals with a diversity of microclimates and habitats (Nordstrom, 2000). Plants structure habitats via provision of physical structures, shading, litter fall, root networks, and other processes (Alpert and Mooney, 1996). For example, Bertness and Miller (1984) showed that *Uca pugnax* burrow close to underground

Table 3
Compliance of ghost crabs against commonly used criteria for ecological indicators.

Selection criteria	1	2	3	4	5	Count	Comply	Comments
Easily and inexpensively measured	×	×	×	×	×	5	☑	Abundant and widespread in coastal dunes and backshore of beaches. Burrow counts provide an inexpensive method to rapidly assess density
Sensitivity to stressors	×	×	×	×		4	☑	This study suggests that low levels of stress can affect body condition and distribution
Be anticipatory: signify change before an impact occurs	×	×	×			3	☑	Changes in crab condition could indicate impact before dune systems become heavily degraded–needs further testing
Bear on fundamental processes in the ecosystem	×				×	2	☑	Likely to play key energetic role and function as ecosystem engineers (ghost crabs are the apex invertebrate predator on many beaches and dunes, provide a trophic link to higher-order consumers (e.g. birds), are prolific bioturbators. etc.)
Existing historical record of response to stressors		×		×		2	☑	Over 20 papers have documented their response to human stressors on beaches
Distinguish between natural and anthropogenic induced change		×			×	2	☑	Although ghost crab numbers fluctuate with changing environmental conditions, human impacts on their populations remain readily discernable
Widespread applicability				×	×	2	☑	Species of the genus *Ocypode* occur circumglobally in the tropics and subtropics and several species are found in coastal dunes
Predictability in response to stressors		×	×			2	☑	Documented monotonic response in density to a variety of stressors (e.g. beach armouring, vehicles, trampling)
Assess impact over a range of stress intensity	×				×	2	☑	A recurring pattern reported in the literature is significant reductions in ghost crab abundance with increasing levels of human disturbance
Public relevance			×			1	☑	Crabs are widely known to many users of beaches and dunes
Diagnostic: identify the source of an impact	×					1	☑	Changes in body condition are causally linked to food availability and changes in density have been shown to be directly traceable to crushing by vehicles
Detect impacts that can be averted by management		×				1	☑	Ghost crabs are mainly used to detect impacts from recreational activities. These impacts could be lowered by changing visitor behaviour and/or numbers

1. Carignan and Villard (2002).
2. Dale and Beyeler (2001).
3. Niemi and McDonald (2004).
4. Riley (2000).
5. Zacharias and Roff (2001).

parts of the cordgrass *Spartina altemiflora* to gain structural support for their burrows. Conversely, dense root systems may impede burrow construction where vegetation is very dense (Brook et al., 2009). Plants can provide crabs with refuge from predators (Nobbs, 2003), and leaf litter influences the abundance and distribution of invertebrates in coastal dunes (Sanderson et al., 1995; Bell, 1997; Brook et al., 2009).

We found no strong and consistent environmental predictors of crab density in the set of variables measured (Fig. 4), either in terms of physical habitat dimensions (e.g. dune height), the surface cover of vegetation, species diversity, or litter cover. Vegetation height was the only variable which showed moderate positive correlations with crab abundance. Vegetation height may be an important structural habitat component for ghost crabs for several reasons: taller plants provide more shade, which ameliorates the harsh physical conditions caused by high temperature and high evaporation rates, and taller vegetation may provide better camouflage from predators such as birds and foxes.

In addition to structural habitat elements, it is plausible that the amount, quality and distribution of food resources are pivotal in determining the size and distribution of ghost crab populations on beaches and dunes. Ghost crabs from other parts of the world appear to be omnivorous scavengers with a catholic diet, including a pronounced carnivorous component in larger species and individuals (Cott, 1929; Hendrickson, 1958; Wolcott, 1978). Our data on changes in body condition indices probably linked to trophic subsidies by humans suggest an important, but as yet unquantified, role of resource availability for ghost crabs in dunes; this emphasises the need to integrate trophic ecology in future assessments of biological responses to environmental changes linked to human uses of beaches and dunes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolind.2010.05.006.

References

Alpert, P., Mooney, H.A., 1996. Resource heterogeneity generated by shrubs and topography on coastal sand dunes. Vegetation 122, 83–93.

Amaral, V., Penha-Lopes, G., Paula, J., 2009. Effects of vegetation and sewage load on mangrove crab condition using experimental mesocosms. Est. Coast. Shelf Sci. 84, 300–304.

Australian Bureau of Statistics, 2004. How many people live in Australia’s coastal areas? Year Book Australia, 2004. Australian Bureau of Statistics, Canberra.

Baird, B., Dann, P., 2003. The breeding biology of hooded plovers, *Thinornis rubricollis*, on Phillip Island, Victoria. Emu 103, 323–328.

Barrass, R., 1963. The burrows of *Ocypode ceratophthalmus* (Pallas) (Crustacea, Ocypodidae) on a tidal wave beach at Inhaca Island, Mocambique. J. Anim. Ecol. 32, 73–85.

Barros, F., 2001. Ghost crabs as a tool for rapid assessment of human impacts on exposed sandy beaches. Biol. Cons. 97, 399–404.

Bell, G.P., 1997. Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in southern California. In: Brock, J.H., Wade, M., Pysek, P., Green, D. (Eds.), Plant Invasions: Studies from North America and Europe. Backhuys Publishers, Leiden (Netherlands), pp. 103–113.

Bertness, M.D., Miller, T., 1984. The distribution and dynamics of *Uca pugnax* burrows in a New England salt marsh. J. Exp. Mar. Biol. Ecol. 83, 211–237.

Bonte, D., 2005. Anthropogenic induced changes in nesting densities of the dune-specialised digger wasp Bembix rostrata (Hymenoptera: Sphecidae). Eur. J. Entom. 102, 809–812.

Bonte, D., Maes, D., 2008. Trampling affects the distribution of specialised coastal dune arthropods. Basic Appl. Ecol. 9, 726–734.

Brook, S., Grant, A., Bell, D., 2009. Can land crabs be used as a rapid ecosystem evaluation tool? A test using distribution and abundance of several genera from the Seychelles. Acta Oecol. 35, 711–719.

Brown, A.C., 1996. Behavioural plasticity as a key factor in the survival and evolution of the macrofauna on exposed sandy beaches. Rev. Chil. Hist. Nat. 69, 469–474.

Burger, J., 1994. The effect of human disturbance on foraging behaviour and habitat use in Piping Plover (*Charadrius melodus*). Estuar 17, 695–701.

Burger, J., Carlucci, S.A., Jeitner, C.W., Niles, L., 2007. Habitat choice, disturbance, and management of foraging shorebirds and gulls at a migratory stopover. J. Coast. Res. 23, 1159–1166.

Carignan, V., Villard, M.-A., 2002. Selecting indicator species to monitor ecological integrity: a review. Environ. Monit. Assess. 78, 45–61.

Carter, D., 2005. Flinders Beach, draft land management plan. Redland Shire Council, Cleveland, Australia.

Chapin III, F.S., Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., Tilman, D., 1997. Biotic control over the functioning of ecosystems. Science 277, 500–504.

Christoffers, E.W., 1986. Ecology of the ghost crab *Ocypode quadrata* (Fabricius) on Assateague Island, Maryland and the impacts of various human uses of the beach on their distribution and abundance. Ph.D. Thesis, Michigan State University, Ann Harbor, Michigan, USA.

Clarke, K.R., 1993. Nonparametric multivariate analyses of changes in community structure. Aus. J. Ecol. 18, 117–143.

Comor, V., Orgeas, J., Ponel, P., Rolando, C., Delettre, Y.R., 2008. Impact of anthropogenic disturbances on beetle communities of French Mediterranean coastal dunes. Biodiv. Cons. 17, 1837–1852.

Connell, D., Lam, P., Richardson, B., Wu, R., 1999. Introduction to Ecotoxicology. Wiley–Blackwell, Oxford, UK.

Coombes, E.G., Jones, A.P., Sutherland, W.J., 2008. The biodiversity implications of changes in coastal tourism due to climate change. Env. Cons. 35, 319–330.

Cott, H., 1929. Observations on the natural history of the racing-crab Ocypode ceratophthalma from Beira. Proc. Zool. Soc. Lond. 1929, 755–765.

Dahlhoff, E.P., 2004. Biochemical indicators of stress and metabolism: applications for marine ecological studies. Ann. Rev. Phys. 66, 183–207.

Dale, V.H., Beyeler, S.C., 2001. Challenges in the development and use of ecological indicators. Ecol. Ind. 1, 3–10.

Defeo, O., McLachlan, A., Schoeman, D.S., Schlacher, T.A., Dugan, J., Jones, A., Lastra, M., Scapini, F., 2009. Threats to sandy beach ecosystems: a review. Est. Coast. Shelf Sci. 81, 1–12.

Farrel, T., Marion, J., 2002. Trail impacts and trail impact management related to visitation at Torres del Paine National Park, Chile. Leisure: J. Can. Assoc. Leis. Stud. 26, 31–59.

Feagin, R.A., Sherman, D.J., Grant, W.E., 2005. Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. Front. Ecol. Environ. 3, 359–364.

Groom, J.D., McKinney, L.B., Ball, L.C., Winchell, C.S., 2007. Quantifying off-highway vehicle impacts on density and survival of a threatened dune-endemic plant. Biol. Cons. 135, 119–134.

Grünewald, R., 2006. Assessment of damages from recreational activities on coastal dunes of the southern Baltic Sea. J. Coast. Res. 22, 1145–1157.

Hendrickson, J.R., 1958. The Green Sea Turtle, Chelonia mydas (Linn.) in Malaya and Sarawak. Proc. Zool. Soc. Lond. 130, 455–535.

Hobbs, C.H., Landry, C.B., Perry, J.E., 2008. Assessing anthropogenic and natural impacts on Ghost Crabs (*Ocypode quadrata*) at Cape Hatteras National Seashore, North Carolina. J. Coast. Res. 24, 1450–1458.

Hockings, M., Twyford, K., 1997. Assessment and management of beach camping within Fraser Island World Heritage Area, South East Queensland. Aust. J. Environ. Manage. 4, 25–39.

Hosier, P.E., Kochhar, M., Thayer, V., 1981. Off-road vehicle and pedestrian track effects on the sea-approach of hatchling loggerhead turtles. Environ. Cons. 8, 158–161.

Houston, J.R., 2008. The economic value of beaches—a 2008 update. Shore Beach 76, 22–26.

Jones, D.A., 1972. Aspects of the ecology and behaviour of *Ocypode ceratophthalmus* (Pallas) and *O. kublii* de Haan (Crustacea: Ocypodidae). J. Exp. Mar. Biol. Ecol. 8, 31–43.

Kennish, R., 1997. Seasonal patterns of food availability: influences on the reproductive output and body condition of the herbivorous crab *Grapsus albolineatus*. Oecology 109, 209–218.

Kohler, K.E., Gill, S.M., 2006. Coral point count with excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. Comp. Geosci. 32, 1259–1269.

Kutiel, P., Zhevelev, H., Harrison, R., 1999. The effect of recreational impacts on soil and vegetation of stabilised coastal dunes in the Sharon Park, Israel. Ocean. Coast. Manage. 42, 1041–1060.

Kutiel, P., Eden, E., Zhevelev, Y., 2000. Effect of experimental trampling and off-road motorcycle traffic on soil and vegetation of stabilized coastal dunes, Israel. Environ. Cons. 27, 14–23.

Lastra, M., Schlacher, T.A., Olabarria, C., 2010. Niche segregation in sandy beach animals: an analysis with surface-active peracarid crustaceans on the Atlantic coast of Spain. Mar. Biol. 157, 613–625.

Lucrezi, S., Schlacher, T.A., Robinson, W., 2009a. Human disturbance as a cause of bias in ecological indicators for sandy beaches: experimental evidence for the effects of human trampling on ghost crabs (Ocypode spp.). Ecol. Ind. 9, 913–921.
Lucrezi, S., Schlacher, T.A., Walker, S.J., 2009b. Monitoring human impacts on sandy shore ecosystems: a test of ghost crabs (*Ocypode* spp.) as biological indicators on an urban beach. Env. Monit. Assess. 152, 413–424.
Lucrezi, S., Schlacher, T.A., 2010. Impacts of off-road vehicles (ORVs) on burrow architecture of Ghost Crabs (Genus Ocypode) on sandy beaches. Env. Manag. online first:, doi:101007/s00267-010-9491-5.
Moss, D., McPhee, D.P., 2006. The impacts of recreational four-wheel driving on the abundance of the ghost crab (*Ocypode cordimanus*) on a subtropical sandy beach in SE Queensland. Coast. Manage. 34, 133–140.
Neves, F.M., Bemvenuti, C.E., 2006. The ghost crab *Ocypode quadrata* (Fabricius, 1787) as a potential indicator of anthropic impact along the Rio Grande do Sul coast, Brazil. Biol. Cons. 133, 431–435.
Niemi, G.J., McDonald, M.E., 2004. Application of ecological indicators. Ann. Rev. Ecol. Evol. Syst. 35, 89–111.
Nobbs, M., 2003. Effects of vegetation differ among three species of fiddler crabs (Uca spp.). J. Exp. Mar. Biol. Ecol. 284, 41–50.
Nordstrom, K.F., 2000. Beaches and Dunes on Developed Coasts. Cambridge University Press, Cambridge, UK.
Nordstrom, K.F., Mauriello, M.N., 2001. Restoring and maintaining naturally-functioning landforms and biota on intensively developed barrier islands under a no-retreat alternative. Shore Beach 69, 19–28.
Noriega, R., Schlacher, T.A., in press. Reductions in ghost crab populations reflect urbanization of beaches and dunes. J. Coast. Res.
Priskin, J., 2003. Physical impacts of four-wheel drive related tourism and recreation in a semi-arid, natural environment. Ocean. Coast. Manage. 46, 127–155.
Rickard, C.A., McLachlan, A., Kerley, G.I.H., 1994. The effects of vehicular and pedestrian traffic on dune vegetation in South Africa. Ocean. Coast. Manage. 23, 225–247.
Riley, J., 2000. Summary of the discussion session contributions to topic 1: what should a set of guidelines with regard to indicators contain? In: Riley, J., Harwood, K. (Eds.), UNIQUAIMS Newsletter no. 10. Harpenden,. IACR-Rothamsted, UK, pp. 5–6.
Sanderson, R.A., Rushton, S.P., Cherrill, A.J., Byrne, J.P., 1995. Soil, vegetation and space: an analysis of their effects on the invertebrate communities of a moorland in north-east England. J. Appl. Ecol. 32, 506–518.
Schlacher, T.A., Wooldridge, T., 1994. Tidal influence on distribution and behaviour of the estuarine opossum shrimp Gastrosaccus brevifissura. In: Dyer, K.R., Orth, R.J. (Eds.), Changes in Fluxes in Estuaries. Olsen and Olsen, Fredensborg, pp. 307–312.
Schlacher, T.A., Thompson, L.M.C., 2007. Exposure of fauna to off-road vehicle (ORV) traffic on sandy beaches. Coast. Manage. 35, 567–583.
Schlacher, T.A., Thompson, L.M.C., Price, S., 2007. Vehicles versus conservation of invertebrates on sandy beaches: quantifying direct mortalities inflicted by off-road vehicles (ORVs) on ghost crabs. Mar. Ecol.—Evol. Persp. 28, 354–367.
Schlacher, T.A., Morrison, J.M., 2008. Beach Disturbance caused by off-road Vehicles (ORVs) on Sandy Shores: Relationship with Traffic Volumes and a New Method to Quantify Impacts using Image-based Data Acquisition and Analysis, vol. 56, pp. 1646–1649.
Schlacher, T.A., Richardson, D., McLean, I., 2008a. Impacts of off-road vehicles (ORVs) on macrobenthic assemblages on sandy beaches. Environ. Manage. 41, 878–892.
Schlacher, T.A., Schoeman, D.S., Dugan, J.E., Lastra, M., Jones, A., Scapini, F., McLachlan, A., 2008b. Sandy beach ecosystems: key features, sampling issues, management challenges and climate change impacts. PSZN I: Mar. Ecol. 29 (S1), 70–90.
Schlacher, T.A., Thompson, L.M.C., Walker, S.J., 2008c. Mortalities caused by off-road vehicles (ORVs) to a key member of sandy beach assemblages, the surf clam *Donax deltoides*. Hydrobiology 610, 345–350.
Sheppard, N., Pitt, K.A., Schlacher, T.A., 2009. Sub-lethal effects of off-road vehicles (ORVs) on surf clams on sandy beaches. J. Exp. Mar. Biol. Ecol. 380, 113–118.
Short, A.D. (Ed.), 1999. Handbook of Beach and Shoreface Morphodynamics. John Wiley & Sons, New York.
Steiner, A.J., Leatherman, S.P., 1981. Recreational impacts on the distribution of Ghost Crabs (*Ocypode quadrata*). Biol. Cons. 20, 111–122.
Stevenson, R.D., Woods, W.A., 2006. Condition indices for conservation: new uses for evolving tools. Integr. Comp. Biol. 46, 1169–1190.
Strachan, P.H., Smith, R.C., Hamilton, D.A.B., Taylor, A.C., Atkinson, R.J.A., 1999. Studies on the ecology and behaviour of the ghost crab, Ocypode cursor (L.) in northern Cyprus. Sci. Mar. 63, 51–60.
Thompson, L.M.C., Schlacher, T.A., 2008. Physical damage to coastal foredunes and ecological impacts caused by vehicle tracks associated with beach camping on sandy shores: a case study from Fraser Island, Australia. J. Coast. Cons. 12, 67–82.
Van Dam, A.R., Van Dam, M.H., 2008. Impact of off-road vehicle use on dune endemic Coleoptera. Annal. Entomol. Soc. Amer. 101, 411–417.
Verri, T., Mandal, A., et al., 2001. D-Glucose transport in decapod crustacean hepatopancreas. Comp. Bioch. Physiol. A—Mol. Integr. Physiol. 130, 585–606.
Watson, J.J., Kerley, G.I.H., McLachlan, A., 1996. Human activity and potential impacts on dune breeding birds in the Alexandria Coastal Dunefield. Landsc. Urban Plan. 34, 315–322.
Weston, M.A., Elgar, M.A., 2005. Disturbance to brood-rearing Hooded Plover *Thinornis rubricollis*: responses and consequences. Bird Cons. Int. 15, 193–209.
Weston, M.A., Elgar, M.A., 2007. Responses of incubating Hooded Plovers (*Thinornis rubricollis*) to disturbance. J. Coast. Res. 23, 569–576.
Williams, J.A., Ward, V.L., Underhill, L.G., 2004. Waders respond quickly and positively to the banning of off-road vehicles from beaches in South Africa. Wader Study Group Bull. 104, 79–81.
Wolcott, T.G., 1978. Ecological role of ghost crabs, *Ocypode quadrata* (Fab.) on an ocean beach: scavengers or predators? J. Exp. Mar. Biol. Ecol. 31, 67–82.
Wolcott, T.G., Wolcott, D.L., 1984. Impact of off-road vehicles on macroinvertebrates of a Mid-Atlantic beach. Biol. Cons. 29, 217–240.
Young, R.A. (2008) Biotic responses to urbanisation in mangrove dominated estuaries. Ph.D. Thesis, Griffith University, Brisbane, Australia.
Yu, S., Bell, D., Sternberg, M., Kutiel, P., 2008. The effect of microhabitats on vegetation and its relationships with seedlings and soil seed bank in a Mediterranean coastal sand dune community. J. Arid Environ. 72, 2040–2053.
Zacharias, M.A., Roff, J.C., 2001. Use of focal species in marine conservation and management: a review and critique. Aquat. Cons. Mar. Freshwater Ecosyst. 11, 59–76.