

SHRUB ENCROACHMENT EFFECTS ON HABITAT HETEROGENEITY AND BEETLE DIVERSITY IN A MEDITERRANEAN COASTAL DUNE SYSTEM

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ABSTRACT

Coastal dunes are fragile dynamic environments characterised by low productivity and high levels of bare and shifting sands. They are highly threatened by urbanisation and human development. The dunes in Nizzanim Dunes Nature Reserve, Israel, have additionally incurred shrub encroachment following exclusion of grazing and wood extraction from the area.

The temporal changes over the last few decades have been monitored in the Nizzanim Long-Term Ecological Research project and are reflected by spatial heterogeneity. Some dunes are fixed with high plant cover and associated characteristics, while other dunes are still in semi-fixed and mobile states.

Measures of beetle abundance, richness and diversity showed significant differences, among dune states. Cluster analysis and ordination of species composition revealed distinct assemblages for three different states, with more psammophilous species found in mobile dunes than in other dune states. Variation within a dune state was not significant for any dune state, while among states species composition was significantly different, demonstrating high β -diversity between dune states.

Landscape heterogeneity contributes to high β -diversity and γ -diversity in the coastal dunes and continued shrub encroachment, and the associated fixation of mobile dunes will lead to habitat homogenisation and a decline in γ -diversity. This finding highlights the importance of disturbance in dynamic Mediterranean coastal dunes. We recommend a restorative intervention that promotes disturbance and heterogeneity at the landscape level by conserving all three dune states. Copyright © 2017 John Wiley & Sons, Ltd.

KEY WORDS: beta-diversity; landscape heterogeneity; anthropogenic disturbance; dune stabilisation; LTER

INTRODUCTION

Coastal dune systems are some of the most important ecosystems in the Mediterranean, given their high habitat heterogeneity (HH) and variability in species composition (Pinna *et al.*, 2015; Malavasi *et al.*, 2016). They are also one of the most degraded and endangered ecosystem types due to intensive developments in infrastructure, industry, tourism and sand mining (Lithgow *et al.*, 2013; Carboni *et al.*, 2015), and 60% of the world's population is expected to live within 100 km of the shoreline by 2020 (UNCED, 1992). In addition, coastal dunes across the world have undergone rapid levels of dune fixation in the past 50 years (Kutiel *et al.*, 2004; Arens *et al.*, 2005; Provoost *et al.*, 2011; Álvarez-Molina *et al.*, 2012; Pye *et al.*, 2013). Note that dune fixation is often called 'stabilisation', but this is a term we reserve for temporal dynamics.

Dune fixation may be considered a natural process of succession and in fact is often promoted in restoration projects through dune nourishment, planting of vegetation and fencing (Isermann, 2011; Hanley *et al.*, 2014). However, coastal dunes are fragile, dynamic environments characterised by

low productivity and high levels of bare and mobile (shifting) sands (Maun, 2009; Fenu *et al.*, 2013). Some Mediterranean systems that have been exposed to human presence for thousands of years may have evolved with anthropogenic disturbance (Nocentini & Coll, 2013), and contemporary studies indicate that over-fixation of dunes may be reducing the availability of habitat for specialised, early successional, psammophilous and xeric species (Arens *et al.*, 2005; Provoost *et al.*, 2011; Bar (Kutiel), 2013; Pye *et al.*, 2013). Thus, while it may seem counter-intuitive, removal of anthropogenic disturbances may be causing a loss of biodiversity due to shrub encroachment and habitat homogeneity. We investigate the impact of shrub encroachment on coastal biodiversity in a system where anthropogenic disturbance has been removed.

The Nizzanim Dunes Nature Reserve (NDNR) is one of the last three remaining sand dune systems along the 188 km of Israeli Mediterranean coastline that still includes intact dune characteristics (Gabbay & Brachya, 2001). Inhibition of grazing and cutting as part of conservation policy, coupled with weak Aeolian dynamics have led to a reduction of mobile dune prevalence and an increase in fixed dunes (Tsoar & Blumberg, 2002; Kutiel *et al.*, 2004; Levin & Ben-Dor, 2004). Since 1948, conservation practices have restricted livestock movement and firewood collection in this protected area (Levin & Ben-Dor, 2004), and the

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perennial plant cover (PPC) of sand dunes in NDNR has increased from 4.3% in 1944 to 8.4% in 1974 and 17% in 1995 (Kutiel *et al.*, 2004; Tsoar *et al.*, 2005).

To understand the impact of shrub encroachment on biodiversity, it is important to understand the variation in composition among sites (β -diversity) and at spatial scales relevant to conservation goals (Socolar *et al.*, 2016). In this study, we monitor β -diversity of beetle species composition, which we consider as the variation in composition between dune states, at the scale of individual dunes within the landscape of the reserve.

A landscape with high HH provides a greater number of ways for individuals and species to exploit resources, increasing γ -diversity and influencing important ecological functions such as population structure, community composition and ecosystem processes (Simpson, 1949; MacArthur & Wilson, 1967; Rosenzweig *et al.*, 1984; Tilman, 2001; Tews *et al.*, 2004). Thus, high HH creates high β -diversity, which is the variation in composition among different local assemblages (Anderson *et al.*, 2011). Conversely, homogenisation of habitats will decrease β -diversity, resulting in a loss of γ -diversity in a given landscape.

In coastal environments, dune mobility can be modelled using vegetation cover (Yizhaq *et al.*, 2009), and both can be considered as drivers of HH at the dune and landscape scale (Tsoar *et al.*, 2005; Fenu *et al.*, 2013). We consider whether habitat homogenisation due to dune fixation in a coastal dune system would result in a change in species composition and loss of total richness (γ -diversity) in ground-dwelling beetles (order Coleoptera).

We focus on ground-dwelling beetles because of the relative ease in trapping and quantification and the stable taxonomic knowledge of this order (Pearce & Venier, 2006). Arthropods are one of the most diverse components of terrestrial ecosystems and are sensitive to changes in their environment across a wide array of spatial and temporal scales (Joern & Laws, 2013). Moreover, studies of HH in relation to species diversity are heavily biased to vertebrates and only rarely examine insect distributions (Tews *et al.*, 2004).

If the continuing temporal process of fixation is affecting biodiversity trends, we expect to see the resultant distribution differences in beetle diversity and composition to be represented spatially at the dune scale. We predict that as the landscape changes from mobile to fixed dunes, some key biodiversity changes will have also taken place and that there will be high variation (β -diversity) in species composition among dune states.

MATERIALS AND METHODS

Study Site

The study was conducted at the Nizzanim Long-Term Ecological Research (LTER) site in NDNR, Israel (31°42'–31°44'N, 34°35'–34°36'E) covering an area of 20 km² (Figure 1). The climate is Mediterranean with an annual average temperature of 20°C and annual rainfall of

400–500 mm falling mainly during winter (November–April). The common wind direction is south-west with a very low drift potential index (Tsoar & Blumberg, 2002). The LTER is an ongoing collaborative project that has been monitoring plant, arthropod, rodent and reptile diversity in NDNR since 2004.

The LTER site consists of mobile, semi-fixed and fixed dunes separated by densely vegetated interdune depressions (Levin *et al.*, 2008). The classification of the three fixation states was based on PPC, sand movement and visual indicators such as dune geomorphic structure, perennial plant distribution, dominant perennial species and soil colour (Kutiel *et al.*, 2004; Tsoar *et al.*, 2005; Ramot, 2007; Levin *et al.*, 2008; Perry, 2008). Dune state is a stronger explanatory variable than plant cover alone (Ramot, 2007), likely due to these local scale factors (Fenu *et al.*, 2013).

Mobile dunes (A-dunes) have 5–15% PPC that is mainly distributed on the dune crest and slip face. They make up approximately 20% of the dunes in the reserve (Kutiel *et al.*, 2004). Maritime grass (*Ammophila arenaria* L. Link) is characteristic only to the A-dunes and is the dominant perennial species here along with wormwood (*Artemisia monosperma* Delile).

Semi-fixed dunes (C-dunes) have 16–30% PPC, are dominated by wormwood and desert broom [*Retama raetam* (Forssk.) Webb] and cover approximately 70% of the area. Lastly, fixed dunes (D-dunes) vary between 30% and 50% PPC, which is distributed almost evenly across all slopes. They are dominated by desert broom and wormwood and have higher perennial plant species richness [Bar (Kutiel, 2013)]. They are the only dune state to have Mediterranean perennial species such as *Prasium majus*, L., and *Asparagus horridus* L. These dunes compose approximately 10% of the area of the reserve.

Data Collection

Ground-dwelling beetles were monitored in spring (March–May) between the years 2006 and 2016 (not all years sampled). Three dune replicates were selected from each dune state (not all dune states were sampled in all years). Beetles were collected using dry pitfall traps of 12-cm depth and 10-cm diameter, in a regularised pattern of 10 traps on each slope (windward, crest and slip face), alternating between open and shrub patches. Pitfall traps remained open for 36 h. The 30 traps per dune were then pooled to give one dune sample.

Beetles were trapped live, identified to morphospecies (*sensu* Krell, 2004) and released where possible or collected and later identified by experts. Some species remained as morphospecies or were identified to genus or family, that is, to the best recognisable taxonomic unit possible.

Data Analysis

For all analyses, we removed species with a total abundance of less than two individuals across all years and all dunes. We also removed all species that had been found only in 1 year, irrespective of their total abundance. Full details of

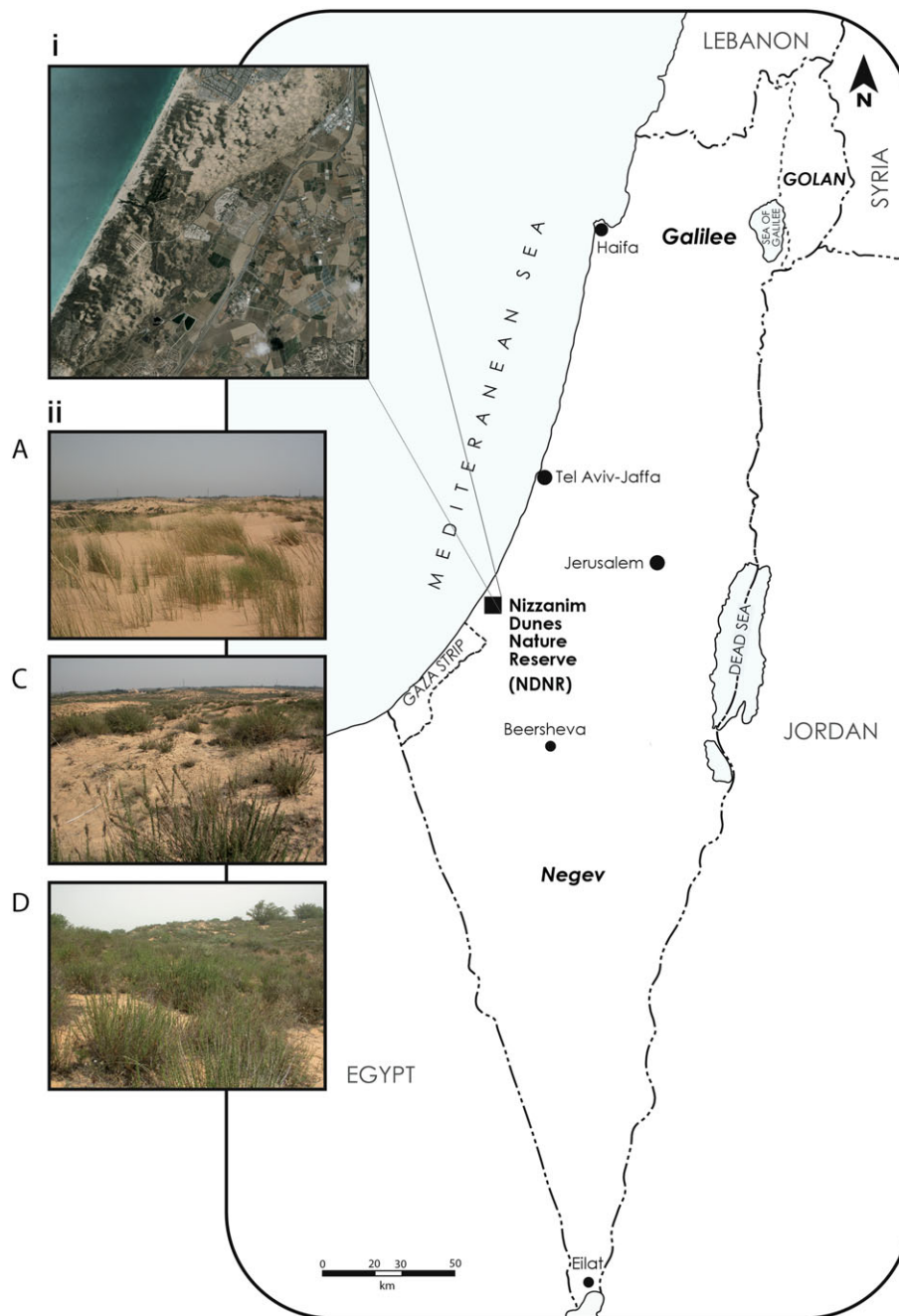


Figure 1. Map showing the location of Nizzanim Dune Nature Reserve (NDNR) in Israel. Inset (i) satellite image of NDNR showing the vegetation cover in 2012. Inset (ii) typical representation of A (mobile), C (semi-fixed) and D (fixed) dunes in NDNR, showing the increase in perennial vegetation from A through to D. [Colour figure can be viewed at wileyonlinelibrary.com]

software and formulae used in the analyses are given in Data S1.

Species abundance and α -diversity

Generalised linear mixed models (GLMMs) are useful for allowing the introduction of random effects when data are hierarchically dependent; in our case the random effect of sampling in different years (Zuur *et al.*, 2009). Differences in total abundance and species richness (per dune per year) of beetles were tested in a GLMM with penalised quasi-

likelihood, because both models were overdispersed (Data S1).

Differences in Shannon's (1948) H diversity between dune states were tested using a linear mixed effects model as described by Laird and Ware (1982) with some modifications to account for year as a random effect (described in Data S1).

Species composition and β -diversity

The Hellinger transformation is recommended for multivariate analysis of abundance data (Rao, 1995) and was applied

to the beetle count data. Hierarchical cluster analysis was used to see if clustering based on beetle species composition alone reflected the *a priori* classification of dune states. Species composition of dune states was further investigated with non-metric multidimensional scaling (NMDS), which is an unconstrained ordination considered most suitable for ecological data (Zuur *et al.*, 2009). Pairwise permutational multivariate analysis of variance (PERMANOVA) was used to test for significant differences between dune state, which is effectively a multivariate analysis of variance on the mean species composition (McArdle & Anderson, 2001). This can be seen as a test for significant β -diversity between dune states (see Data S1 for further details of these analyses).

The PERMANOVA method can find significant differences between dune states if there are large differences of within-state variation (dispersion) rather than truly different mean values (McArdle & Anderson, 2001). So to check for differences in dispersion among dune states, we tested the homogeneity of variance with a Tukey test (see Data S1 for details).

Indicator species

An indicator value (IV) (De Cáceres & Legendre, 2009) was calculated for each species to understand which species contributed most to β -diversity. An IV is a measure of association in the 0–1 range, where $IV = 1$ if all individuals of a species are observed in all dunes of only one dune state (i.e. the indicated dune state) and $IV = 0$ when the individuals are spread equally between the dune states. Species with significant IVs are then considered to be strong indicator species.

To assess the species affinity to dune mobility, we used the sandiness index (SI) developed for coastal systems (Ramat, 2007; Rubinstein *et al.*, 2013), adapted from weighted average methods of Lepš and Šmilauer (2003). SI is a value in the 0–1 range, where $SI = 0$ occurs when a species distribution is limited to fixed dunes and $SI = 1$ when they are restricted to mobile dunes. Hence, when IV is high, SI can be close to 1 or close to 0, but when $IV = 0$, the SI will be around 0.5. We expected that indicator species for mobile dunes would have a higher SI than fixed dune species.

Canonical correspondence analysis was used on raw count data with dune state specified as the explanatory variable and year as a covariate, to present affiliation of each indicator species (and other species that are not shown) to each dune state.

RESULTS

Species Abundance and α -Diversity

Altogether, 4,912 individuals were included in the analysis across 55 samples; $n = 24$, 14 and 17 for A (mobile), C (semi-fixed) and D (fixed) dunes, respectively. γ -Diversity in Nizzanim LTER was 39 morphospecies across 10 families of Coleoptera, including 17 species of darkling beetles (Tenebrionidae) and seven species of ground beetles family (Carabidae) (Table S2).

Total abundance per sample was significantly higher for D-dunes in the mixed effects model ($t = 2.31$, $p < 0.05$) (Figure 2a). Meanwhile, both C-dunes and D-dunes were significantly lower than A-dunes in both species richness ($t = -2.10$, $p < 0.05$ and $t = -4.0$, $p < 0.001$, respectively) and Shannon's H diversity ($t = -4.31$, $p < 0.001$ and $t = -7.20$, $p < 0.001$, respectively) (Figure 2b and c). Details of the mixed effects model outputs are given in Table S3.

Species Composition and β -Diversity

Hierarchical cluster analysis of species composition in individual dunes was averaged across all sampling years and clearly showed a high degree of clustering by dune state (Figure 3). C-dunes and D-dunes appeared more similar in composition than A-dunes. In hierarchical cluster analysis, clustering was based entirely on the similarity of species composition between different dunes, with labels of dune state only added *post hoc*. Consistent clustering was also obtained when considering yearly samples rather than averages (Figure S4).

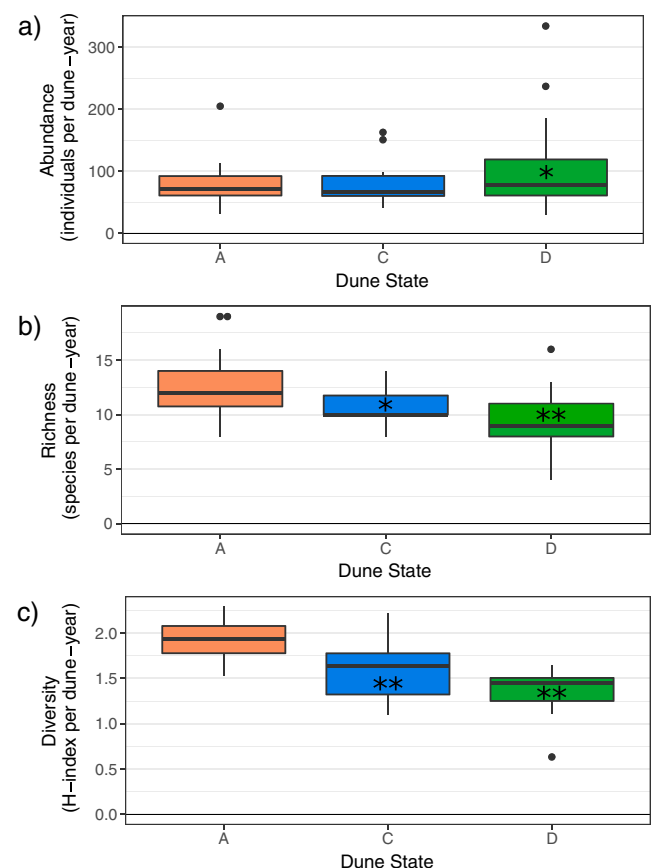


Figure 2. Distribution of (a) total abundance, (b) total species richness and (c) Shannon H diversity, across dune/year samples for A (mobile), C (semi-fixed) and D (fixed) dunes. The upper and lower 'hinges' correspond to the first (25%) and third (75%) quartiles. Significant differences from A-dunes are derived from the mixed effects models described in the Data Analysis section: * $p < 0.05$, ** $p < 0.001$. [Colour figure can be viewed at wileyonlinelibrary.com]

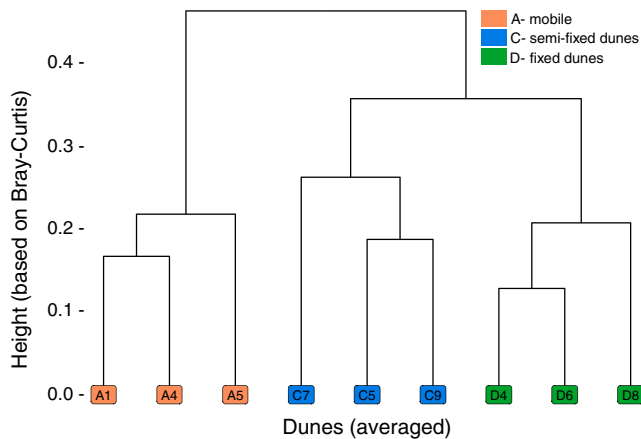


Figure 3. Hierarchical cluster analysis of average species composition per dune across all years (2006–2016) for A (mobile), C (semi-fixed) and D (fixed) dunes. The dune names are the Nizzanim Long-Term Ecological Research site references; the first letter of each site reference code (e.g. A1) refers to the dune state classification; the second digit is the replicate number within the dune state. [Colour figure can be viewed at wileyonlinelibrary.com]

The NMDS showed community compositions could be clustered into three distinct dune states, with C as an intermediary state along the first axis, and almost no overlap between the three states (Figure 4). The non-linear regression of observed dissimilarity against NMDS distance was very strong ($R^2 = 0.975$). The NMDS stress factor was 0.16 after 20 iterations, which is the goodness of fit of the two-dimensional representation of the ordination to the observed variation in all dimensions and tends to 0 in a perfect fit. Both values suggest good fit of the NMDS to the observed data. The first axis always displays the greatest degree of

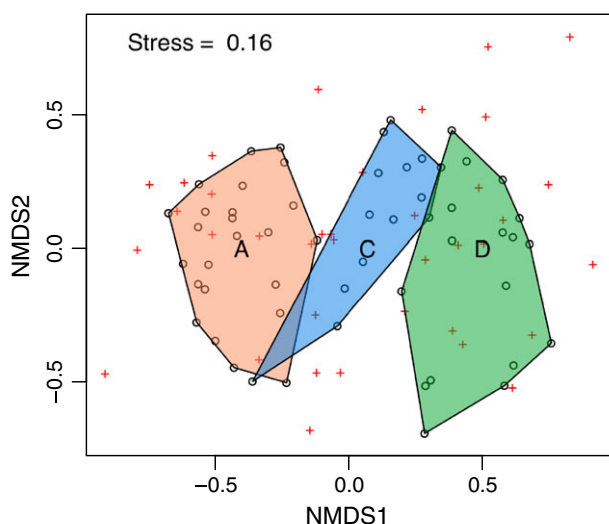


Figure 4. Non-metric multidimensional scaling (NMDS) of beetle composition showing the differences in composition between A (mobile), C (semi-fixed) and D (fixed) dunes. Points are sample scores (dune/year) and species scores are given by '+' symbols. The non-linear regression of observed dissimilarity against NMDS distance was very strong; $R^2 = 0.975$. [Colour figure can be viewed at wileyonlinelibrary.com]

explained variation in the NMDS ordination (Oksanen *et al.*, 2016), so from the horizontal gradient from A-dunes to D-dunes, we can infer that dune fixation is a strong predictor of differences in species composition.

Homogeneity of variance was not significantly different between dune states (Table S5). Therefore, we could conclude that differences in the PERMANOVA were due to differences in mean composition between dune states rather than differences in variation. The pairwise PERMANOVA showed that all dune states were significantly different ($p < 0.01$) from each other in terms of species composition across all pairwise models (Table S6). Thus, β -diversity between dune states was high at the landscape scale.

Indicator Species

Eleven morphospecies were identified as being significantly associated with a specific dune state or dune state combinations ($p < 0.05$; Table I). A-dunes had the highest number of indicator species ($n = 4$), and the SI was higher for A-associated species than for other species. Only *Graphipterus serrator* Forskal indicated D-dunes. We present these indicator species in the canonical correspondence analysis ordination (Figure 5), where the pie segments represent the proportions of total presence. Boxplots of relative abundance in each dune state are given for further detail in Figure S7. The number of indicator species was greatest in mobile dunes, and these species had the highest SI values compared with other species as expected (Rubinstein *et al.*, 2013).

DISCUSSION

Coastal dunes naturally express high HH (Fenu *et al.*, 2013), which is a major driver of β -diversity (Simpson, 1949; MacArthur & Wilson, 1967; Rosenzweig *et al.*, 1984) and maintains high γ -diversity for many taxa (Tews *et al.*, 2004; Haddad *et al.*, 2009; Joern & Laws, 2013). Understanding patterns of β -diversity is therefore crucial to conservation at the landscape level (Socolar *et al.*, 2016). We found high β -diversity between dune states in NDNR and suggest that homogenisation of habitats (dunes) will lead to a concurrent loss of species diversity within NDNR. In particular, species found only on mobile (A) dunes may be lost due to fixation.

Arthropod distributions in coastal systems are dependent on a range of environmental variables, such as vegetation cover (Comor *et al.*, 2008), soil humidity and moss encroachment (Schirmel & Buchholz, 2011), distance from the beach (Bonte *et al.*, 2012), experimental stabilisation (Webb *et al.*, 2000), as well as anthropogenic disturbances such as burning and trampling (Comor *et al.*, 2008; Brunbjerg *et al.*, 2015). We found beetle total abundance was greatest in the fixed dunes (Figure 1a), likely due to the greater vegetation biomass productivity and associated availability of resources (Siemann, 1998; Groner & Novoplansky, 2003).

Table I. Indicator species identified for each dune state

Morphospecies	Family	Species code for Figure 5	Dune states indicated	IV	<i>p</i> -value	Affinity to sand	Biogeographic distribution	SI	Feeding guild	Global distribution
<i>Mecynotarsus bison</i> Olivier, 1811	Anthicidae	Mec-bis	A	0.97	<0.001	Xerophyl	Psammophil	0.94	Zoophag	Africa, Canary Islands, Arabian Peninsula, Jordan, Southeast Mediterranean
<i>Scarites striatus</i> Dejean, 1825	Carabidae	Sea-str	A	0.95	<0.001	Xerophyl	Eurizonal	0.92	Zoophag	N. Africa, Arabian Peninsula, Egypt (Sinai), Israel
<i>Eurycaulus henoni</i> Fairmaire, 1897	Tenebrionidae	Eur-hen	A + C	0.995	0.004	Xerophyl	Psammophil	0.78	Detritophag	Egypt (Sinai), Israel
<i>Cardiophorus reitteri</i> Schwarz, 1891	Elateridae	Car-rei	A	0.63	0.002	Mezophyl	Psammophil	0.91	Phytophag	Cyprus, Syria, Israel
<i>Scaurus puncticollis</i> Solier, 1838	Tenebrionidae	Sea-pun	A	0.48	0.029	Xerophyl	Psammophil	0.77	Detritophag	N. Africa, Syria, Cyprus, Arabian Peninsula, Iraq, Egypt (Sinai), Jordan, Israel
<i>Dendarus piceus</i> Olivier, 1811	Tenebrionidae	Den-pic	C	0.59	0.014	Xerophyl	Psammophil	0.73	Detritophag	Egypt (Sinai), Syria, Lebanon, Jordan, Israel
<i>Achradius ochraceus</i> Tournier, 1874 ^a	Curculionidae	Ach-och	C	0.46	0.011	Mesophyl	Eurizonal	0.49	Phytophag ^a	Egypt (Sinai), Israel, Syria ^a
<i>Mesostena angustata</i> Fabricius, 1775	Tenebrionidae	Mes-ang	C + D	0.818	0.012	Xerophyl	Psammophil	0.48	Detritophag	Africa, Arabian Peninsula, Iran, Iraq, Egypt (Sinai), Jordan, Israel
<i>Brenskiella flavomicans</i> Brenske, 1897 ^a	Scarabidae	Bre-fla	C + D	0.497	0.004	Mesophyl	Psammophil	0.48	Phytophag ^b	Israel (endemic to the coastal plain) ^b
<i>Carabus impressus hybridus</i> Ganglbauer, 1887	Carabidae	Car-imp	C + D	0.499	0.037	Mezophyl	Psammophil	0.39	Zoophag	Lebanon, Egypt (Sinai), Israel
<i>Graphipterus serrator</i> Forskal, 1775	Carabidae	Gra-ser	D	0.93	<0.001	Xerophyl	Psammophil	0.30	Zoophag	N. Africa, Egypt (Sinai), Israel

Indicator value (IV) is an association index by Dufréne and Legendre (2009). Sandiness index (SI) is an affiliation to sandy conditions (Ramot, 2007). Species attributes sources detailed by Ramot (2007) unless otherwise stated.

^aL. Friedmann, unpublished data.

^bO. Rittner, pers. comm.

**p* < 0.05.

****p* < 0.001.

Mobile dunes had the highest α -diversity in terms of both average species richness and Shannon's *H* diversity, highlighting the importance of sand mobility to coastal

biodiversity (Arens *et al.*, 2005; Lithgow *et al.*, 2013). Similar patterns of higher α -diversity in more disturbed and more sandy dunes are reported for both annual plants and

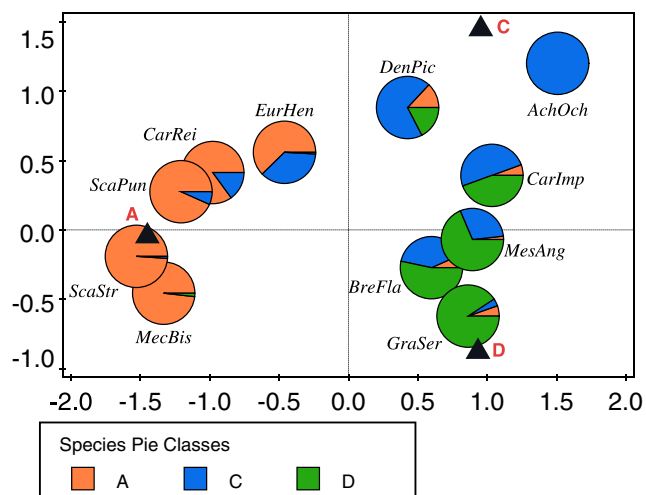


Figure 5. Canonical cluster analysis of species composition for A (mobile), C (semi-fixed) and D (fixed dunes), with year as a covariate (2006–2016), presented using type II scaling. Affiliation pies depict the relative abundance of each indicator species in each dune state (centroids as triangles). Partial variation was 2.16, explanatory variables account for 19.0% (adjusted explained variation = 16.3%). (Full species names are given in Table I). [Colour figure can be viewed at wileyonlinelibrary.com]

arthropods in Mediterranean and ocean coastal systems (Webb *et al.*, 2000; Howe *et al.*, 2010; Brunbjerg *et al.*, 2015). Indeed, dune fixation had a negative impact on species diversity in all coastal studies reviewed by Bonte & Hoffman (2005). Several theories could explain these patterns, including multiple adaptive strategies in more sandy dune states (Ciccarelli, 2015), higher colonisation rates in the less productive mobile dunes or competitive interactions in fixed dunes (Huston, 1979, 2014).

In contrast, Diptera and annual plants are often found to be more diverse on fixed dunes (Web, 2000), while intermediate disturbance explained the highest species diversity of rodents and plants in other coastal dune systems (e.g. Ferreira & Van Aarde, 2000; Isermann, 2011). It is possible that our disturbance range was too narrow to detect low diversity, such as might be found in more disturbed embryonic foredunes (e.g. Fenu *et al.*, 2013). Multitaxon approaches are important for evaluating restoration and conservation efforts (Lithgow *et al.*, 2013), and it will be interesting to compare the distribution patterns of other taxa that have been monitored in the Nizzanim LTER project in future research.

There is also the consideration of scale; at the patch scale, mobile dunes may be more heterogeneous and patchy due to the stark differences between bare sand and shrubs patches (Perry, 2008), while the fixed dunes may be more structurally homogenous despite higher perennial diversity (Kutiel *et al.*, 2004). HH at the patch scale could explain the higher α -diversity found in the mobile dunes. Further investigation into the structural complexity of perennial vegetation may help to tease out the mechanisms driving α -diversity patterns found in NDNR.

At the landscape scale, dune fixation state was as a major predictive factor for beetle composition in NDNR, as shown by both the multivariate analyses (Figures 4 and 5). β -Diversity between dune states was high, and mobile dunes

contributed most to the overall γ -diversity with the highest number of indicator species. We do not differentiate cause and effect of vegetation cover and geomorphological aspects of dune fixation, because sand stabilisation allows shrubs to grow, and shrub growth stabilises the sand, but there is a high correlation between both [Bar (Kutiel), 2013; Rubinstein *et al.*, 2013].

It is the heterogeneity and high β -diversity found in NDNR that allows a high γ -diversity to exist in this coastal system. Management of NDNR in previous decades has reduced the presence of anthropogenic disturbances by diligently protecting the reserve from grazing and firewood extraction resulting in a reduction in the prevalence of mobile dunes (Kutiel *et al.*, 2004; Levin & Ben-Dor, 2004). If no conservation action is taken, the current trend of dune fixation will continue across all dunes, and we expect the species composition of mobile to become more similar to semi-fixed, and eventually to fixed dunes. In other words, as predicted by theories of HH (Simpson, 1949; MacArthur & Wilson, 1967; Rosenzweig *et al.*, 1984), homogenisation of the dunes will reduce the β -diversity between dunes and γ -diversity will be reduced.

In this scenario, the psammophilous, xeric species that are mostly associated with mobile dunes will disappear or decline significantly, such as *Mecynotarsus bison* Olivier, 1811, and *Scarites striatus* Dejean, 1825. In addition, species with low SI, such as *Mesostena angustata* Fabricius, 1775, and *Carabus impressus hybridus* Ganglbauer, 1887, will increase in population size. The latter are generalist species with a wide global distribution.

Conversely, anthropogenic disturbance and grazing are often cited as major contributors to desertification, land degradation and global biodiversity loss (Rutherford *et al.*, 2014, but see Rowntree *et al.*, 2004), and the introduction of excessive disturbance such as intensive grazing and trampling have reduced species richness of plants and arthropods in other coastal systems (Bonte & Hoffmann, 2005; De Luca *et al.*, 2011; Santoro *et al.*, 2012; Pedley *et al.*, 2013; Ciccarelli, 2014). A shift to an entirely mobile dune landscape in NDNR would likely result in the loss of the unique species found on fixed dunes such as *G. serrator* Forskal. Indeed, *Brenskiella flavomicans* Brenske is highly endemic to the Israeli coastal plain (O. Rittner, pers. comm.) but is found only on the semi-fixed and fixed dunes.

Nevertheless, grazing and other disturbances such as trampling can increase abundance and species richness of annual plants, carabids and other insects (e.g. Attorre *et al.*, 2013; Damgaard *et al.*, 2013; Pedley *et al.*, 2013; Brunbjerg *et al.*, 2015). Furthermore, in this study, we support evidence that Mediterranean species and habitats have co-evolved with anthropogenic disturbance (see Nocentini & Coll, 2013, and references therein). While many coastal projects continue to promote dune fixation through planting of Maritime grass and other species, we suggest these activities may be deleterious to some taxa and in particular to arthropods in these dynamic ecosystems (see Arens *et al.*, 2005, 2013; Lithgow *et al.*, 2013; Pye *et al.*, 2013).

A heterogeneous landscape that includes all dune states will contribute to the greatest γ -diversity at the landscape and regional scale (Tews *et al.*, 2004; Pacheco & Vasconcelos, 2012). As discussed, different taxa respond differently to dune fixation and disturbances (Gossner *et al.*, 2013), so measures that would maintain the continued presence of all three dune states would be recommended (Lithgow *et al.*, 2013).

Although we encourage a cautionary approach, we suggest that action to preserve heterogeneity at the dune scale is needed in NDNR. While our findings may seem counter-intuitive, for the psammophilous and xeric species that have evolved to cope with the dynamic arid conditions found in coastal environments, this conclusion is not unexpected (Howe *et al.*, 2010; Brunbjerg *et al.*, 2015). Reintroduction of non-intensive livestock grazing and/or an intervention to remove perennial cover and restore dune mobility in some dunes is likely to promote landscape heterogeneity, maintain high β -diversity and conserve the highest γ -diversity in coastal dune ecosystems.

Contribution of authors

P. B., E. G. and A. B.: LTER project design and concept. A. R.: data collection. T. B. and M. D.: statistical analyses. T. B.: data collation, data collection and lead writer, with significant contribution from E. G., P. B. and A. B.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Data S1: Data analysis methods in detail

Table S2: Number of distinct Coleoptera species, by family, encountered in each dune state. The total number of samples (dune and year replicates) for each dune state is specified in parentheses.

Table S3: Results of the mixed effect models for (a) abundance and (b) species richness tested with generalised linear mixed models with penalised quasi-linearization (GLMM-PQL) and (c) Shannon's H' diversity tested with a linear mixed effect model (LME). See Data Analysis Section S1 for details. * $p < 0.05$, ** $p < 0.001$.

Table S5: Results of the Tukey test on homogeneity of variance (HV). HV is calculated using the Bray–Curtis distance calculated with the *betadisper* function in *vegan* (Oksanen *et al.*,). The Tukey test compares the difference between pairs in terms of the distance of each dune/year sample from the centroid of each dune state in ordination space (Bray–Curtis dissimilarity). The lower and upper limits refer to the maximum and minimum differences in distances between pairs. A Bonferroni correction was applied to p -values for taking into account multiple comparisons.

Table S6: Results of the pairwise permutational multivariate analysis of variance (PERMANOVA), showing significant differences between the mean compositions of each dune state. F is the multivariate equivalent of the F statistic in simple analysis of variance, generated by permutation of the pairwise data. R^2 is the amount of variance explained by the classification of observations in two dune states. A Bonferroni correction was applied to p -values for taking into account multiple comparisons.

Figure S4: Hierarchical cluster analysis of dune/year species composition observations. Dune/year observations belonging to different dune treatments are marked by different colours.

Figure S7: Boxplots showing abundance of indicator species identified using the *Multiplatt* R package. The dune state each species was 'indicating' is specified in the upper-right corner of each box. Note that a species may indicate a combination of two dune states (e.g. A and C for *Eur.hen*). The upper and lower 'hinges' correspond to the first (25%) and third (75%) quartiles. The upper whiskers extend from the hinge to the highest value that is within 1.5 of the interquartile range (25–75%). Data beyond the end of the whiskers are outliers and plotted as points.