

Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales

JUSTIN P. WRIGHT, CLIVE G. JONES*, BERTRAND BOEKEN† and MOSHE SHACHAK‡

Department of Biology, Box 90338, Duke University, Durham, NC 27708, USA, *Institute of Ecosystem Studies, PO Box AB, Millbrook, NY 12545, USA and †Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sede Boker Campus, Israel 84990

Summary

1 The effect of physical ecosystem engineering – structurally mediated modification of the abiotic environment by organisms – on species richness and composition probably depends on the area of observation and environmental context.

2 We develop specific hypotheses to evaluate how such effects will vary with spatial scale and environmental variability, and test these hypotheses by examining the effects of shrub mounds on the diversity of annual plant communities in the Negev Desert, Israel.

3 We find that previously reported increases in species richness at small spatial scales as a result of shrub mounds are maintained at large spatial scales because shrub mounds host a number of species never found in adjacent crust patches.

4 We find that the magnitude of this effect is dependent on annual precipitation, with shrub mounds having a smaller effect in years with higher precipitation.

5 The results generally support our hypotheses. Given the ubiquity of ecosystem engineering, these results have the potential to explain variation in patterns of ecosystem engineer-induced diversity across ecosystems and environmental gradients. In general, understanding the interactions between resources modified by an ecosystem engineer and the availability of these resources in unmodified habitats aids prediction of the magnitude of the effects of an ecosystem engineer on diversity.

Key-words: annual plants, diversity, gradients, Negev Desert, sampling, shrub mounds, soil crust, spatial extent.

Journal of Ecology (2006) **94**, 815–824

doi: 10.1111/j.1365-2745.2006.01132.x

Introduction

Physical ecosystem engineering, i.e. changes to the abiotic environment by organisms that result in the creation, modification, maintenance or destruction of habitats (Jones *et al.* 1994), is a consequence of numerous activities conducted by a great variety of organisms in most, if not all, ecosystems (Jones *et al.* 1994, 1997; Crooks 2002; Wright & Jones 2004). By altering the abiotic environment, ecosystem engineers have the potential to create patches with assemblages of organisms that differ from surrounding, unmodified habitats. If species differ in their response to abiotic conditions in modified and unmodified patches, the

presence of patches created by an ecosystem engineer should increase species richness at the landscape level, i.e. areas encompassing both patch types (Jones *et al.* 1997). Evidence for such a positive landscape-level effect of ecosystem engineering on species richness is growing (Wright *et al.* 2002; Lill & Marquis 2003; Castilla *et al.* 2004). However, to date, there has been little effort to ascertain what factors might control the magnitude of such a landscape-level effect. That is, if the ecosystem engineer were removed from the landscape, what factors would influence how many species are subsequently lost from the landscape? Such a question is important for understanding the general significance of ecosystem engineering as well as for conservation purposes where protection of a single engineering species may, or may not, impact on large numbers of additional species.

Correspondence: Justin P. Wright (fax +1 919 660 7293; e-mail jw67@duke.edu).

Two factors are likely to affect the magnitude of the effects of ecosystem engineering on species richness at a given level of organization (i.e. patch or landscape): spatial scale (Palmer & White 1994); and the degree to which engineered and unmodified patches differ in resources and other physical or chemical characteristics of relevance to species, e.g. salinity (Bertness & Hacker 1994), temperature (Cavieres *et al.* 2002), enemy-free space (Gutierrez *et al.* 2003) or accessibility to dispersing agents (Boeken & Shachak 1998b). For simplicity, we focus on engineer-induced changes in the availability of abiotic resources for species, while recognizing that the same basic principles should apply to the effects of engineers on other physical and chemical abiotic factors (e.g. increasing or decreasing stress, enemy-free space, living space).

Although we may not be able to predict the effects of ecosystem engineers at the patch level *a priori* (Jones *et al.* 1997), given the general principle that ecosystem engineers affect resources, we ought to be able to use basic ecological principles to predict how patch-level effects of ecosystem engineers will vary across environmental gradients (Wright & Jones 2004). Furthermore, at higher levels of organization (i.e. landscape level), a similar approach might be effective at predicting how the effects of ecosystem engineering on species richness will vary across environmental gradients. In the most basic sense, ecosystem engineers affect the distribution of species by creating patches with different levels of resources than surrounding, unmodified patches. Thus, if ecosystem engineering modifies a resource that drives community organization, one would predict that the greater the change in resource availability created by the engineer, the greater the difference in species richness and composition in the two patch types.

To predict how ecosystem engineering affects the change in species richness across spatial scales, one must understand how engineered and unmodified patches differ in terms of species abundance and identity (Tjorve 2002). In cases where engineered and unmodified patches are not so dissimilar in resource availability that one sees complete turnover in composition, the differences in resource availability in the two patch types could affect the rate at which species accumulate with area and the total number of species present in the regional species pool that can colonize and persist in each patch type. Each of these variables is likely to cause qualitative changes in how ecosystem engineering effects on species richness vary with spatial scale. Changes in resource availability can alter the rate at which species accumulate with area, such as changes in species density or changes in species richness *sensu stricto*, i.e. a higher species/individual ratio (Gotelli & Colwell 2001). By allowing greater degrees of coexistence, this is likely to lead to large ecosystem engineering effects at relatively small spatial scales. However, given a saturating species–area response, one would expect the number of species observed in

the more slowly accumulating patch type to approach the richness observed in the other patch type as more area is sampled. This would lead to decreasing engineering effects at larger spatial scales. We will refer to this type of influence as a ‘rate of accumulation’ effect.

The above would not occur however, if the two patch types differ to such a degree that a significantly smaller proportion of the species in the regional species pool are capable of persisting in the resource conditions of one patch type relative to the other. In this case, the engineering effect could be small at small spatial scales because individual patches of the two patch types may not differ significantly in species richness. However, at large spatial scales the elimination of engineered patches from the landscape is likely to have a large negative (if the engineered patches contain more species) or positive (if the engineered patches contained fewer species) effect. We will refer to this increasing engineering effect with spatial scale as a ‘regional pool’ effect.

Shrub mounds in the Negev Desert (Israel) provide an ideal system for investigating the effects of resource availability and spatial scale on the magnitude of ecosystem engineering effects on species richness. In the Negev, as in many arid ecosystems (Belnap & Lange 2003), much of the soil is covered with a biotic crust that largely reduces run-off infiltration and seed germination (Boeken & Shachak 1994; Prasse & Bornkam 2000). By contrast, mounds of loose, uncrusted soil form around the base of shrubs, due to the capture of sediments carried by run-off, the direct deposition of atmospheric dust and the accumulation of detritus (Brown & Porembski 1997; Shachak & Lovett 1998). These mounds locally increase infiltration of run-off water. The end result is the ‘island of fertility’ effect with higher soil moisture under shrubs than in intershrub areas and greater annual plant productivity and diversity (Halverson & Patten 1975; Shmida & Whittaker 1981; Silvertown & Wilson 1994; Pugnaire *et al.* 1996; Guo 1998; Schlesinger & Pilmanis 1998; Hochstrasser & Peters 2004; Maestre & Cortina 2005). The effects of shrub mounds on species richness in the Negev have been well studied at the patch level, with significant increases in annual plant species richness, biomass and density occurring on mounds compared with equivalent areas of crust as a result of significantly higher soil moisture and nutrient availability in shrub mound soils than in crusted soils (Olsvig-Whittaker *et al.* 1983; Boeken & Shachak 1994, 1998a; Shachak *et al.* 1998). Although these local, patch-level effects are large and well studied, the implications for species richness at larger scales and across environmental gradients have not been evaluated.

This paper combines a mechanistic understanding of patch-level effects of ecosystem engineering by shrubs with observational data to address two key questions concerning the potential effect that removal of shrubs from the ecosystem could have on species richness. First, how does the significant interannual

variation in precipitation, the key limiting resource in this ecosystem, affect the landscape-level effect of engineering by shrubs on species richness? Second, how does the magnitude of the shrub engineering effect on species richness vary with spatial scale (i.e. from patch to landscapes of different total area sampled)? In addition to advancing our basic understanding of the effects of organisms as ecosystem engineers, these questions also have an applied relevance to the conservation of annual plant abundance and diversity. The Negev is an area of high annual plant diversity, there is substantial interannual variability in rainfall, annual plants are an important source of food for native grazing animals and livestock, and over-grazing can dramatically influence shrub cover and annual plants (Bruins 1990). Furthermore, as this is an arid region in which ecosystem engineering by shrubs has important patch-level effects on annual plant diversity, productivity and food for grazing animals, the potential impact of global climate change on these ecosystem engineering effects is of concern.

Our specific hypotheses were as follows. We expected that the magnitude of the shrub effect on species richness at the landscape level would decrease in years of higher precipitation. Although the patchiness of nutrients in shrub-dominated landscapes is likely to persist in wet years (Schlesinger & Pilmanis 1998), increasing precipitation should lead to higher soil moisture levels in crust patches, decreasing the difference in moisture availability in shrub mounds and crust patches. Previous studies at the research site have shown that mounds have higher average biomass and species richness than the crust matrix (Boeken & Shachak 1994), and general conceptual models of ecosystem engineering predict that in cases where engineers increase productivity at the patch level, the increases in ecosystem productivity that would be expected with higher precipitation should lead to decreased patch-level effects on richness (Wright & Jones 2004). In conditions where individual engineered and unmodified patches are more similar in resource availability, one would also predict that the landscape-level effect of removing engineered patches would be small. With respect to changes in the magnitude of the effect of shrub mounds on species richness with spatial scale, Boeken & Shachak (1994) showed that, on average, individual mounds had higher species richness and plant density than crust patches. Furthermore, they found that mounds had greater numbers of species that were at the edge of their range at the study site; in particular, mounds tended to host species typically found in more mesic areas. This suggests that in landscapes containing both shrub mounds and crust patches, species richness may increase at a more rapid rate as an increasing area is sampled and contain a greater number of species than if the entire area was occupied only by crust. If this is the case, we should observe an increase in the magnitude of the ecosystem engineering effect on species richness as the spatial scale increases due to the *regional pool* effect.

Methods

STUDY AREA

This study took place in Sayeret Shaked Park near Beer Sheva in the northern Negev Desert of Israel (31°17' N, 34°37' E), a hilly area of several km² from which livestock have been excluded since 1987. Rainfall, which only occurs between November and March, has a long-term annual average of 200 mm. Annual rainfall during the period of the study averaged 150 mm and included a 2-year drought with less than 50% of the long-term average precipitation in 1999 and 2000, an event that has only occurred once in the past 60 years (Arbel 2002). Average daily minimum winter temperatures are 6–8 °C, and average daily maximum summer temperatures are 32–34 °C (Stern *et al.* 1986). The 200-mm isohyet forms the transition zone between arid and semi-arid desert in Israel (Bruins 1990).

The soil surface at the research site is covered with a microphytic crust consisting of bacteria, cyanobacteria, algae, mosses and lichens (Zaady *et al.* 1998), interspersed with patches of loose soil mounds with one or more shrubs and an herbaceous understory. The most common shrubs are *Thymelaea hirsuta* (Thymelaeaceae), *Noaea mucronata* (Chenopodiaceae) and *Atractylis serratuloides* (Asteraceae). The underlying soil is loessial with 14% clay, 27% silt and 59% sand, and is at least 1 m deep. Salt content of the 0–25 cm soil layer is low, with electrical conductivity of 0.4 mS.

VEGETATION SURVEY AND ENVIRONMENTAL VARIABILITY

In 1992 three control plots of 15 × 4 m were established across a slope of approximately 10% at Sayeret Shaked Park and were surrounded by a 25-cm-high earth wall. These plots were part of an experiment to determine the effect of crust removal on vegetation dynamics. Between 1992 and 1997, 13 pairs of 40 × 40 cm quadrats were selected in each plot. Pairs of quadrats were located on shrub mounds and nearby crust patches; these were surveyed annually with all species found in each quadrat being recorded. From 1998 to 2001, six pairs of 20 × 30 cm quadrats were selected in each plot and were surveyed annually for species richness. Quadrats were surveyed during the rainy season each year during the period of peak annual plant richness.

SURVEY OF VEGETATION ACROSS SPATIAL SCALES

To determine how the effect of ecosystem engineering on species richness varied with the spatial scale of observation, we sampled mound and crust vegetation on a north- and a south-facing slope in January 2001. On each slope, three 50-m transects orientated parallel to the contour of the slope were set up. To estimate shrub density along these transects, we noted whether

points located every 10 cm along the transect were located on shrub mounds or crust patches. We randomly selected 25 shrub mounds along each transect and set up pairs of 20 × 30 cm quadrats for each mound. One quadrat was placed on the mound, the other at a distance of 1 m (from the mound) in a random direction, on a crust patch. All the species in each quadrat were recorded and assigned species cover values based on a modified Braun–Blanquet scale (1 = a few individuals, 2 = 1–10% cover, 3 = 11–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%).

DATA ANALYSIS

The primary response variable of interest in these analyses is a measure of the magnitude of the effect of ecosystem engineering on species richness at the landscape level. In essence, this is an estimate of how much the species richness of an area that includes both engineered and unmodified patches would be expected to change if the engineered patches were eliminated from an ecosystem. One such estimate can be calculated using species accumulation curves from the two patch types and resampling techniques to generate the expected curve for a landscape containing both patch types. Species accumulation curves for shrub mounds and crust patches were generated using EstimateS (Colwell 2005). To account for differences in abundance of the two patch types in the landscape, landscape curves were generated by drawing quadrats at random from both patch types such that the probability of selecting a quadrat from either patch type was equal to the relative cover of that patch type in the landscape. The percentage cover of shrub mounds, as determined from the average shrub cover of the six transects, was 26.9%.

For any given sampling area, the effect of the ecosystem engineer can be estimated as the difference between the expected number of species in the landscape for that area and the number of species present in an equivalent area of crust patches. In order to standardize this number for comparisons across systems with varying species richness, this difference was expressed as a fraction of the expected number of species for crust patches only, a variable we term the Landscape Richness Enhancement (LRE). Expressed formally, for a given area A , $LRE = (L_A - U_A)/U_A$ where L_A is the number of species expected for the landscape curve and U_A is the number of species expected from the unmodified (crust) curve. This metric can be calculated for any given sampling area.

To compare the magnitude of the shrub mound effect on species richness as a function of environmental variability, the LRE was calculated using the number of species estimated by the Coleman rarefaction procedure at 1.08 m² (the largest area sampled in all years) for each year, to control for differences in sampling intensity between years (Colwell 2005). Coleman's estimates represent the mean value for 50 randomized runs. To determine the effect of rainfall on LRE, a

simple linear regression of LRE for each year against that year's precipitation was calculated. To examine what factors might be responsible for the observed relationship between LRE and precipitation, regressions of rarefied richness estimates from shrub mounds and crust patches against precipitation were also determined.

To compare the magnitude of the shrub mound effect on species richness across spatial scales, the LREs using rarefied estimates of species richness for areas ranging from 0.06 m² to 9 m², representing the expected number of species observed in 1–150 quadrats, were calculated. To estimate the LRE at larger spatial extents, we used the Chao 2 species richness estimator (Colwell & Coddington 1994).

To determine if *rate of accumulation* or *regional pool* effects were responsible for the observed patterns, estimates of the rate of species accumulation, the total number of species from the regional species pool capable of persisting in each habitat type, and the degree of compositional overlap between the two patch types were required. To estimate both the rate of species accumulation with area and the total number of species for each patch type, the species accumulation curves generated by EstimateS were fitted to a Michaelis–Menten function by using SigmaPlot. Although this function has most commonly been used in studies of enzyme kinetics, it has an established history in estimating species richness (Colwell & Coddington 1994). It is a particularly desirable function in this case because, in addition to estimating S_{max} (i.e. the total number of species found in a patch type), it contains the parameter k , which is an estimate of how rapidly species accumulate with area. The ecological interpretation of k is the area necessary to observe half the total species in a patch type. Thus, patch types with lower values of k accumulate species more rapidly than patch types with higher values of k . We assessed the degree of compositional similarity between shrub mound and crust patches using an NMS ordination calculated with presence/absence data from each plot (McCune & Mefford 1999).

Results

EFFECT OF ENVIRONMENTAL VARIABILITY

There was a negative relationship between LRE and annual precipitation, although this relationship was not statistically significant ($P = 0.499$, $R^2 = 0.059$) (Fig. 1a). However, when data from 2000, the second year of a severe drought and a substantial outlier, were removed, the relationship was marginally significant ($P = 0.053$, $R^2 = 0.434$). Increasing precipitation was associated with a linear increase in observed species richness on crust patches ($P = 0.010$, $R^2 = 0.582$) (Fig. 1b). Increasing precipitation was also associated with an increase in species richness on shrub mounds, but not in a linear fashion as the rate of increase in species richness levelled off at higher precipitation levels. A

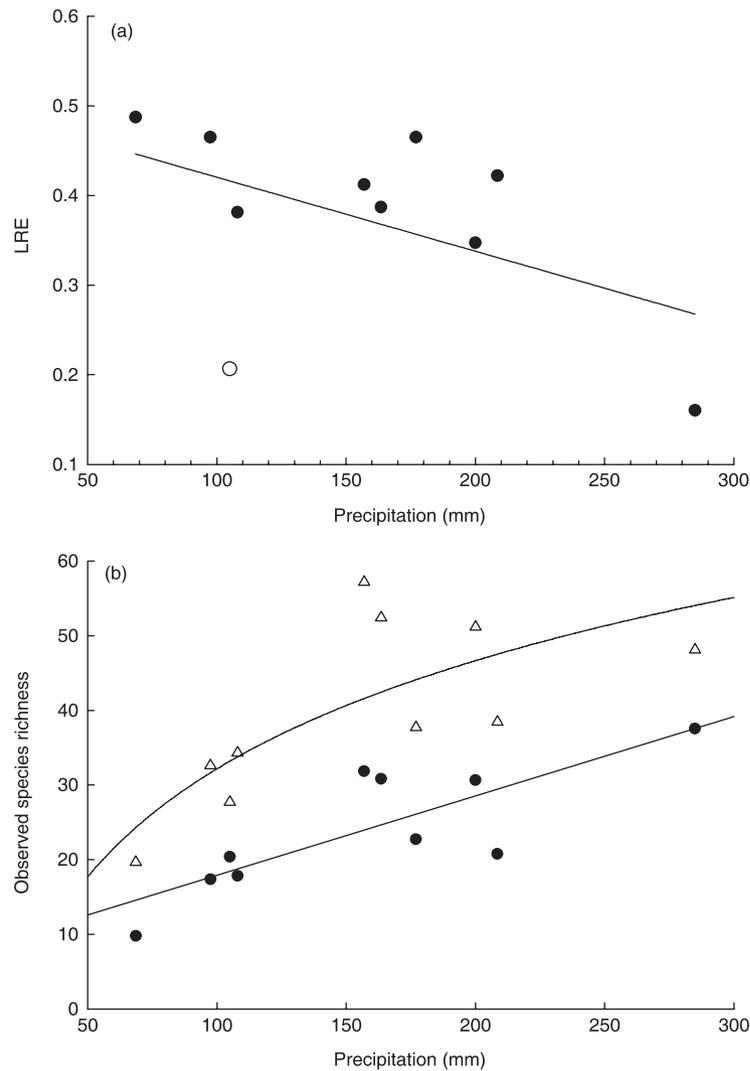


Fig. 1 Variation of Landscape Richness Enhancement (LRE) (a) and species richness on crust (filled circles) and shrub patches (open triangles) (b) across years as a function of annual precipitation (mm). The open point in (a) is 2000, an outlier that was removed from the regression analysis shown in the figure. Equations of the best-fit line for precipitation vs. LRE: $y = 0.59 - 0.0008x$; precipitation vs. crust richness: $y = 7.8 + 0.06x$; precipitation vs. shrub richness: $y = -9.3 + 0.45x - 0.001x^2$.

second-order polynomial regression of shrub mound species richness against precipitation provided the best fit to the data ($P = 0.001$, $R^2 = 0.822$).

EFFECT OF SPATIAL SCALE

The presence of shrub patches increased species richness by between 20% and 35% at all scales sampled (Fig. 2a). There was a peak in the LRE engineering effect at small spatial scales, equivalent to sampling five quadrats, followed by a decline in the effect magnitude at intermediate scales and an increase at larger scales (Fig. 2b). At the largest areas sampled, shrub mounds increased species richness by 32.9% compared with a landscape consisting entirely of crust patches.

The species accumulation curves for both shrub mounds and crust patches essentially reached an asymptote within the area sampled and the Chao 2 species richness estimates were within 5% of the total number of species

observed for each patch type (Fig. 2a), indicating that our sampling design effectively captured the diversity of both patch types. The Michaelis–Menten function provided a good fit for the species accumulations curves from both shrub mounds ($P < 0.0001$, $R^2 = 0.985$) and crust patches ($P < 0.001$, $R^2 = 0.994$). The parameter estimates from these regressions showed that a greater number of species are capable of persisting in shrub mounds, and that shrub mounds increase in species richness at a faster rate than crust patches as sample area increases (Table 1). Although there was some separation of mound and crust patches along both axes 1 and 3 of the NMS ordination, there was substantial overlap (Fig. 3). The number of species found only in shrub mounds relative to the number found only in crust patches, and the number of species more common in shrub patches than in crust patches, both indicated that the species found in crust patches largely represented a subset of those found on shrub mounds (Table 1).

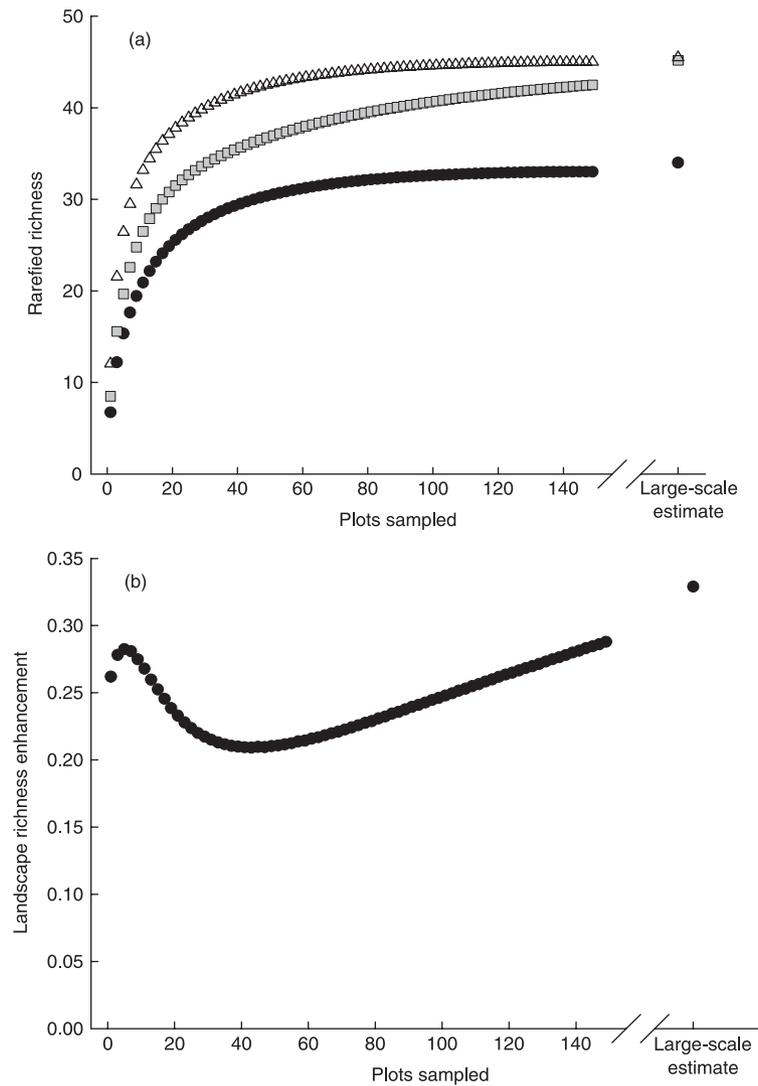


Fig. 2 Variation in number of species observed (a) and Landscape Richness Enhancement (LRE) (b) as a function of area sampled. In (a), open triangles represent the species accumulation curve from sampling only shrub patches, filled circles represent the species accumulation curve from sampling only crust patches, and shaded squares represent the species accumulation curve from randomly sampling plots of both patch types in proportion to their occurrence in the landscape. In both (a) and (b), the large-scale estimate is derived from the Chao 2 species richness estimator.

Table 1 Summary of differences between patch types. S_{max} and k are parameter estimates from fitting a Michaelis–Menten model to species accumulation curves from each patch type. Species density is the average number of species observed per quadrat. Unique species are those found only in one patch type, while more common species are those observed in at least twice as many quadrats of one patch type. Where applicable, standard errors are shown in parentheses

	S_{max}	k	Species density	Unique species	More common species
Crust	35.0 (0.08)	10.0 (0.13)	5.89 (0.18)	0	2
Shrub	46.4 (0.11)	6.49 (0.12)	9.48 (0.21)	12	19

equivalent areas of crust patches, as has previously been noted in this (Boeken & Shachak 1994) and other arid ecosystems (e.g. Went 1942; Whittaker *et al.* 1979). We also found that this effect, which is known to result from the modification of the abiotic environment by shrub mounds (Shachak *et al.* 1998), is important at larger spatial scales, but varied in response to annual precipitation levels. Both these findings generally matched our hypotheses, lending support to the utility of the concept of organisms as ecosystem engineers in generating general and testable hypotheses regarding species richness and composition that can be linked to ecosystem structure and function.

The effect of shrub mounds on species richness in this desert ecosystem is largely due the retention of run-off water generated by rainfall on upslope crusted soil (Shachak *et al.* 1998) in addition to seed-trapping (Boeken & Shachak 1994). The mechanism of the ecosystem engineering effect on species richness in this

Discussion

We found that, on average, individual shrub mounds contain significantly more annual plant species than

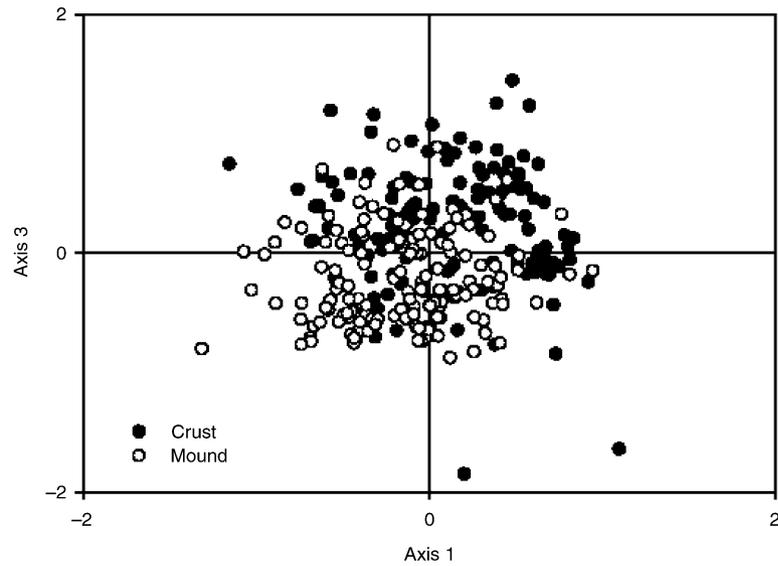


Fig. 3 NMS ordination of 150 quadrats from the survey conducted in 2001 using species presence–absence.

case is largely via the modification of water availability. Consequently, we predicted that as overall water availability (i.e. precipitation) increased, the engineering effect at the landscape level should decrease. We found that in dry years, the estimated effect of removing shrubs from the landscape was marginally significantly greater than the effect in wet years. This was particularly the case when data from the second year of an extended drought were excluded; this was a period during which patches were potentially both seed-limited and water-limited. Although increasing precipitation resulted in an increase in species richness on both patch types, the number of species found on shrub mounds appeared to saturate at levels of precipitation above approximately 200 mm, the long-term average annual precipitation at this site. By contrast, the crust patch type showed a linear increase in species richness across the range of precipitation observed in this study. Thus, in years with higher precipitation, we observed species in crust patches that were only found in shrub mound patches in dryer years, leading to a decreased landscape-level effect of engineering. This effect could be due to the fact that in wet years, shrub mounds are harbouring essentially all of the species in the regional species pool capable of persisting in the area. Alternatively, as growing conditions improve in shrub patches, with higher precipitation, the species assembly may begin to undergo the process of competitive exclusion, leading to lower species richness. Guo & Berry (1998) observed this pattern, accompanied by a positive relationship between biomass and species richness in the more resource-poor intershrub areas. However, our data did not indicate a decline in species richness at the highest levels of precipitation observed during the time course of this study.

In some respects these predictions conform to those developed to predict the importance of facilitation across environmental gradients (Bertness & Callaway 1994; Callaway *et al.* 2002). However, it is important to

note that although some facilitative interactions are due to ecosystem engineering, not all facilitation is caused by ecosystem engineering (e.g. pollination), and ecosystem engineering can have negative effects (Collins & Uno 1983; Rogers *et al.* 2001) as well as positive effects (Guo 1996; Boeken *et al.* 1998) on resource availability and species richness (Wright & Jones 2004). Furthermore, facilitation hypotheses largely refer to effects at the patch level and do not generally address effects at higher, landscape levels of organization. Our results also seem to contradict the conceptual model developed by Tielborger & Kadmon (2000) who proposed that the positive effects of shrubs on the reproductive success of plants should increase with increasing precipitation. However, this conceptual model was developed based on a field site where intershrub areas were loose sand rather than microphytic crust. Therefore, little run-off was probably generated by the intershrub areas that might counteract the negative effects of precipitation interception by the shrub canopies, unlike the situation observed at our field site (Shachak & Lovett 1998).

We found that in a single year, crust patches largely contain a subset of the species found in shrub mound patches, similar to the findings of Boeken & Shachak (1994) for artificial water-trapping patches in the same ecosystem, and to the findings of patterns of perennial plant distribution in the Chihuahuan Desert (Guo 1998). Fitting the species-accumulation curves from both patch types to a Michaelis–Menten function provided further evidence that the total number of species found in shrub mounds was higher than in crust patches. These facts suggest that there is a significant *regional pool effect* in this system, leading to the prediction that the magnitude of the engineering effect at the landscape level should increase as the spatial scale increases. However, we also found that species accumulate at a faster rate within areas in shrub mound patches than in crust patches, suggesting that we might

also see a decline in the engineering effect as the spatial scale increases, as would be expected under a *rate of accumulation* effect. The pattern observed in LRE, our estimate of the magnitude of the effect of shrub mounds on species richness at the landscape level, indicated that at small cumulative sampled areas, the differences in the rate of accumulation of species between the two habitats is the most important factor, resulting in a decline in LRE as area sampled increases. However, as the spatial scale increases further, the higher total number of species found in shrub mound patches relative to crust patches becomes more important and LRE increases. Although our estimates are based on sampling a total area of 9 m², the sampling curves from both shrub mounds and crust patches had largely saturated, and thus we are confident that we have sampled adequately to capture most of the diversity in the system. At the scale of the entire region, we estimate that the presence of shrub mounds increases species richness by just over one-third.

In the case of shrub mounds in the Negev Desert, the data largely supported our hypotheses with respect to how the effects of ecosystem engineering on species richness should vary depending on environmental context and the area sampled. It is important to consider to what degree these results may be generalized. One major consideration is the degree to which the two patch types in this system are interdependent. Shrub mounds trap water that is generated in upslope crust patches, so shrub mounds depend on crust patches for water – a hydrological source–sink relationship (Boeken & Shachak 1994; Shachak & Lovett 1998; Shachak *et al.* 1998). However, shrub mounds can also serve as sources of seeds that colonize surrounding areas of crusted soil (Boeken & Shachak 1998b). Thus, the number of species found in both patch types can potentially be dependent on the existence of the other patch type (but see Kadmon & Tielborger 1999). This suggests that our estimate of the effect of removing shrub mounds from the landscape may actually underestimate the true magnitude of this effect as it does not take into account the possibility that some species are only found in crust patches when there is propagule input from shrub mounds. It also suggests that in conditions where crust structure is degraded, such as areas of heavy trampling, there may be significantly less run-off water for shrub mounds to trap, resulting in lower overall diversity. The degree to which engineered and unmodified patch types are interdependent may have important implications for understanding how the effects of the ecosystem engineer may vary across environmental gradients. However, we feel that the general approach of studying how the effects of ecosystem engineering varies across environmental gradients holds great potential for understanding the degree to which assemblages are structured by local environmental conditions, be they naturally occurring or modified by organisms.

Jones *et al.* (1997) highlighted the importance of spatial scale in predicting the effects of ecosystem

engineers on species richness. They pointed out that at the patch level, i.e. comparing individual engineered patches with individual unmodified patches, predicting the effects of engineers *a priori* is not possible because it requires understanding how the engineer changes resources and how species respond to these altered resources. By contrast, at the landscape level, i.e. at scales that encompass both engineered and unmodified patches, they argued that the effect on species richness will generally be positive due to increased habitat diversity. These early uses of the concept of organisms as ecosystem engineers in order to understand patterns of biodiversity have subsequently been refined at both the patch (Crooks 2002; Wright & Jones 2004) and the landscape level (Wright *et al.* 2002). However, as is apparent from this study, it is also important to recognize that the effects of an ecosystem engineer at the landscape level can vary depending on the spatial scale. Here, we introduced a general approach using the metric LRE, using species-accumulation curves from different patch types and resampling techniques to estimate the effect of removing engineered patches. Our conceptual model proved useful in interpreting the pattern of change in the effect of shrub mounds on species richness with spatial scale, and this approach should be broadly applicable to systems in which engineers create discrete, distinctive patches that do not have complete turnover in species composition. Although we focused here on the effects on species richness arising from ecosystem engineer control on resource availability, our conceptual model and approach should also be applicable to species richness effects of engineer-induced changes in physical and chemical non-resource abiotic factors (e.g. increasing/decreasing stress, living space, enemy-free space).

Our results also have important implications for the conservation of semi-arid shrublands. In many areas, these ecosystems are overgrazed, leading to a decrease in shrub cover (Bruins 1990; Brown & Porembski 1997). The loss of shrubs, and the subsequent loss of mounds, has the potential to decrease biodiversity at large spatial scales significantly. Our results suggest that one cannot simply protect larger areas of crusted soil and hope to capture the full range of diversity supported when shrub mounds are present in the ecosystem. The effects of losing shrubs from this ecosystem could be exacerbated if future global change scenarios lead to decreased precipitation, as the magnitude of the engineering effect of shrub mounds was greatest at lower precipitation levels. In general, recognizing the key role that many species play in structuring the physical environment in this and other ecosystems (Ellison *et al.* 2005) should become an increasingly important goal of conservation-orientated ecology.

Acknowledgements

L. Linde provided valuable field assistance. We thank the Jacob Blaustein Institute for Desert Research for

logistical support, Sigma Xi and the Laurel Foundation (J.P.W.) and the Institute of Ecosystem Studies (C.G.J., M.S.) for financial support. This paper is a contribution to the programme of the Institute of Ecosystem Studies.

References

- Arbell, S. (2002) *Report on Drought Damage in Forests of the Southern Region*. Jewish National Fund/Keren Kayemet LeYisreal, Gilat, Israel.
- Belnap, J. & Lange, O.L. (2003) *Biology of Soil Crusts: Structure, Function, and Management*. Springer, New York.
- Bertness, M.D. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.
- Bertness, M.D. & Hacker, S.D. (1994) Physical stress and positive associations among marsh plants. *American Naturalist*, **144**, 363–372.
- Boeken, B., Lipchin, C., Guterman, Y. & van Rooyen, N. (1998) Annual plant community responses to density of small-scale soil disturbances in the Negev Desert of Israel. *Oecologia*, **114**, 106–117.
- Boeken, B. & Shachak, M. (1994) Desert plant communities in human-made patches – implications for management. *Ecological Applications*, **4**, 702–716.
- Boeken, B. & Shachak, M. (1998a) Colonization by annual plants of an experimentally altered desert landscape: source–sink relationships. *Journal of Ecology*, **86**, 804–814.
- Boeken, B. & Shachak, M. (1998b) The dynamics of abundance and incidence of annual plant species during colonization in a desert. *Ecography*, **21**, 63–73.
- Brown, G. & Porembski, S. (1997) The maintenance of species diversity by miniature dunes in a sand-depleted *Haloxylon salicornicum* community in Kuwait. *Journal of Arid Environments*, **37**, 461–473.
- Bruins, H.J. (1990) The impact of man and climate on the central Negev and northeastern Sinai Deserts during the late Holocene. *Man's Role in the Shaping of the Eastern Mediterranean Landscape* (eds S.S. Bottenma, G. Entjes-Nielborg & W. van Zeist), pp. 87–99. Balkema, Rotterdam, the Netherlands.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.L., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D. & Cook, B.J. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.
- Castilla, J.C., Lagos, N.A. & Cerda, M. (2004) Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore. *Marine Ecology-Progress Series*, **268**, 119–130.
- Cavieres, L., Arroyo, M.T.K., Penaloza, A., Molina-Montenegro, M. & Torres, C. (2002) Nurse effect of *Bolax gummifera* cushion plants in the alpine vegetation of the Chilean Patagonian Andes. *Journal of Vegetation Science*, **13**, 547–554.
- Collins, S.L. & Uno, G.E. (1983) The effect of early spring burning on vegetation in buffalo wallows. *Bulletin of the Torrey Botanical Club*, **110**, 474–481.
- Colwell, R.K. (2005) EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. User's guide and application published at <http://purl.oclc.org/estimates>
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London*, **345**, 101–118.
- Crooks, J.A. (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, **97**, 153–166.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliot, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knowepp, J.D., Lovett, G., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Van Holle, B. & Webster, J.R. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology*, **9**, 479–486.
- Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- Guo, Q. (1996) Effects of bannertail kangaroo rat mounds on small-scale plant community structure. *Oecologia*, **106**, 247–256.
- Guo, Q.F. (1998) Microhabitat differentiation in Chihuahuan Desert plant communities. *Plant Ecology*, **139**, 71–80.
- Guo, Q. & Berry, W.L. (1998) Species richness and biomass: dissection of the hump-shaped relationship. *Ecology*, **79**, 2555–2559.
- Gutierrez, J.L., Jones, C.G., Strayer, D.L. & Iribarne, O.O. (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos*, **101**, 79–90.
- Halverson, W.L. & Patten, D.T. (1975) Productivity and flowering of winter ephemerals in relation to Sonoran desert Shrubs. *American Midland Naturalist*, **93**, 311–319.
- Hochstrasser, T. & Peters, D.P.C. (2004) Subdominant species distribution in microsites around two life forms at a desert grassland-shrubland transition zone. *Journal of Vegetation Science*, **15**, 615–622.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**, 1946–1957.
- Kadmon, R. & Tielborger, K. (1999) Testing for source–sink population dynamics: an experimental approach exemplified with desert annuals. *Oikos*, **86**, 417–429.
- Lill, J.T. & Marquis, R.J. (2003) Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. *Ecology*, **84**, 682–690.
- Maestre, F.T. & Cortina, J. (2005) Remnant shrubs in Mediterranean semi-arid steppes: effects of shrub size, abiotic factors and species identity on understorey richness and occurrence. *Acta Oecologica-International Journal of Ecologica*, **27**, 161–169.
- McCune, B. & Mefford, M.J. (1999) *PC-ORD Multivariate analysis of ecological data*. MjM Software Design, Gleneden Beach, OR.
- Olsvig-Whittaker, L., Shachak, M. & Yair, A. (1983) Vegetation patterns related to environmental factors in a Negev Desert watershed. *Vegetatio*, **54**, 153–165.
- Palmer, M.W. & White, P.S. (1994) Scale dependence and the species–area relationship. *American Naturalist*, **144**, 717–740.
- Prasse, R. & Bornkam, R. (2000) Effect of microbiotic soil surface crusts on emergence of vascular plants. *Plant Ecology*, **150**, 65–75.
- Pugnaire, F.I., Haase, P., Puigdefabregas, J., Cueto, M., Clark, S.C. & Incoll, L.D. (1996) Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos*, **76**, 455–464.
- Rogers, W.E., Hartnett, D.C. & Elder, B. (2001) Effects of plains pocket gopher (*Geomys bursarius*) disturbances on tallgrass-prairie plant community structure. *American Midland Naturalist*, **145**, 344–357.
- Schlesinger, W.H. & Pilmanis, A.M. (1998) Plant–soil interactions in deserts. *Biogeochemistry*, **42**, 169–187.
- Shachak, M. & Lovett, G.M. (1998) Atmospheric deposition to a desert ecosystem and its implications for management. *Ecological Applications*, **8**, 455–463.

- Shachak, M., Sachs, M. & Moshe, I. (1998) Ecosystem management of desertified shrublands in Israel. *Ecosystems*, **1**, 475–483.
- Shmida, A. & Whittaker, R.H. (1981) Patterns and biological microsite effects in two shrub communities, Southern California. *Ecology*, **62**, 234–251.
- Silvertown, J. & Wilson, J.B. (1994) Community structure in a desert perennial community. *Ecology*, **75**, 409–417.
- Stern, A., Gradus, Y., Meir, A., Krakover, S. & Tsoar, H. (1986) *Atlas of the Negev*. Ben-Gurion University of the Negev, Beersheva, Israel.
- Tielborger, K. & Kadmon, R. (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, **81**, 1544–1553.
- Tjorve, E. (2002) Habitat size and number in multi-habitat landscapes: a model approach based on species–area curves. *Ecography*, **25**, 17–24.
- Went, F.W. (1942) The dependence of certain annual plants on shrubs in southern California deserts. *Bulletin of the Torrey Botanical Club*, **69**, 100–114.
- Whittaker, R.H., Gilbert, L.E. & Connell, J.H. (1979) Analysis of 2-Phase Pattern in a Mesquite Grassland, Texas. *Journal of Ecology*, **67**, 935–952.
- Wright, J.P. & Jones, C.G. (2004) Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology*, **85**, 2071–2081.
- Wright, J.P., Jones, C.G. & Flecker, A.S. (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, **132**, 96–101.
- Zaady, E., Groffman, P. & Shachak, M. (1998) Nitrogen fixation in macro- and microphytic patches in the Negev desert. *Soil Biology and Biochemistry*, **30**, 449–454.

Received 18 October 2005

revision accepted 23 February 2006

Handling Editor: Robert Brooker