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Land management practices for combating desertification cause species replacement of desert lizards

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Summary

1. Patch structural complexity affects local species richness and population densities. Anthropogenic disturbance may alter complexity and heterogeneity, resulting in changes in community structure. Most studies in this area have dealt with human-induced habitat degradation. We investigated a converse situation, in which anthropogenic activity increases productivity and complexity of an arid habitat.

2. Recently, large areas in the northern Negev Desert have been altered: a series of contour catchments was constructed to accumulate run-off to support planted trees. We examined the effect of patch alteration by focusing on the lizard assemblage in the planted plots. Seven pairs of plots were established, one plot from each pair in a natural area and the other in an adjacent, altered slope. Lizards were captured using pitfall traps and environmental parameters were measured. To isolate the effects of trees as perches for avian predators, we 'planted' artificial trees in a loess plain and investigated the effect on an endemic lizard.

3. The structure of the lizard assemblage in the planted plots differed from that of the natural plots. Planted plots had a higher proportion of Mediterranean lizards and fewer desert species. Two local lizard species disappeared from the mosaic area of planted and natural plots. In addition, avian predators spent longer time in the artificial tree plots and reduced the lizard density compared to the natural plots.

4. The modification to the habitat generated only moderate changes in structure of the natural vegetation and this could not account for the observed changes in the lizard assemblage. Changes in the spatial use of the plots by avian predators was identified as the mechanism behind the observed distribution of lizard species.

5. *Synthesis and applications.* We argue that anthropogenic habitat modifications such as afforestation, urbanization, etc., can induce indirect biotic effects that may change the way and the scale at which different species respond to the habitat change. Such structural alteration may lead to species replacement and even to local extinction of specialist species. In order to protect biodiversity during large-scale management projects, alteration of biotic interactions should be considered in advance and large unaltered patches should be protected, otherwise indirect effects might cause greater impacts than the structural manipulation itself.

Key-words: *Acanthodactylus beershebensis*, avian predators, combating desertification, conservation, habitat complexity, spatial heterogeneity

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Introduction

Physical complexity (i.e. the number of structural elements per unit volume) is a major characteristic of patches, has significant ecological importance, and is relevant to conservation (Turner *et al*. 1999). Physical complexity may affect a species' vulnerability to adverse effects of predation and competition (Coull & Wells 1983), determine the effectiveness of physical and chemical stressors, and determine the availability of food and other resources needed for reproduction (Turner *et al*. 1999). Many studies have shown that habitats differing in their structural complexity may also favour different species and hence affect the relative abundance of species and community structure and dynamics (Pianka 1966; Taylor & Fox 2001; Fox, Taylor & Thompson 2003). In general, as the physical structure of a habitat becomes complex, the diversity of associated organisms increases too (Orth, Heck & Vanmontfrans 1984; Hansen 2000). However, several studies have not found this positive relationship between complexity and diversity, and some have even found negative relationships (Coull & Wells 1983; Kelaher 2003; Lassau & Hochuli 2004). Interactions between organisms may mask the predicted positive relationship, for example complex habitats may function as refugia from predators (Ellner *et al*. 2001; Ryer, Stoner & Titgen 2004; Warfe & Barmuta 2004), but may also enhance predator efficiency and density (Yosef & Grubb 1994; Langellotto & Denno 2004).

Anthropogenic habitat modifications may alter habitat structure and landscape physiognomy, which in turn affect community structure and dynamics (Diaz *et al*. 1998; Shachak, Sachs & Moshe 1998). The alteration of a community can occur within the altered patch or at the wider regional scale (Wiens 1989). Theoretical and experimental efforts have been invested recently to unravel these processes and to explore the consequent effects on biodiversity (Vitt & Caldwell 2001; Chalfoun, Thompson & Ratnaswamy 2002; Driscoll 2004; Jellinek, Driscoll & Kirkpatrick 2004). However, most of these studies considered a single direction of change: from a productive habitat into a poorer one. Moreover, most studies focused on extreme situations in which very productive and complex habitats (e.g. tropical rain forest and benthic habitats) are transformed into very simple ones (e.g. monoculture field and wasteland), causing severe reductions in biodiversity (for reviews on tropical forest and benthic habitat, respectively, see Bawa & Seidler 1998; Turner *et al*. 1999).

In this study we used a new approach by looking at the effects of a large-scale anthropogenic manipulation that turned a relatively simple habitat, with low productivity, into a more complex and productive one. Moreover, we describe a situation in which a relatively small portion of the natural habitat within each patch was directly altered by the land management practice. Similar large-scale land management projects to improve productivity of arid environments are becoming common (Shachak, Sachs & Moshe 1998; Gao, Zha & Ni 2001) and an understanding of their impact is essential for conserving biodiversity.

We chose to examine the effect of habitat manipulation on a lizard assemblage. Lizards are not only important contributors to arid ecosystems (Reynolds 1979; Pianka 1986) but have close relationships with habitat structure (Pianka 1966). Furthermore, lizard populations in arid environments do not fluctuate much in density. Population oscillations, such as those of birds and mammals following rain events, may mask anthropogenic effects (Read 2002).

Our results suggested that the lizard assemblage in a planted arid zone changed because of the alteration of an indirect biological interaction (i.e. predation pressure) rather than directly by the structural alteration (i.e. the addition of trees). To investigate this possibility, we 'planted' artificial trees that only increased predation without altering the structure of a loess habitat, 1 km from the main study area, and examined the effects on lizards.

Methods

STUDY SITE AND MANAGEMENT PRACTICE

The study was performed in Sayeret Shaked Park, near Beer Sheva, northern Negev Desert, Israel (31°17′N, 34°37′E). Annual rainfall averages 200 mm, with large fluctuation between years. Daily maximum temperatures in summer are 32–34 °C (Stern *et al*. 1986). The park is characterized by moderate chalky hills covered by a matrix of bare crusted loess soil, with microphytic communities and distinct macrophytic patches of perennials (Eldridge, Zaady & Shachak 2002). The macrophytic patches are mainly composed of the small woody shrubs *Noea mucronata* and *Atractylis comosa*, and they create an evenly distributed open scrubland. Dry riverbeds (wadis) that cross the relatively homogeneous arid landscape create a distinct habitat that supports relatively dense annual vegetation and a few large *Thymelaea hirsuta* shrubs. The *T. hirsuta* shrubs are almost the only natural perches suitable for the great grey shrike *Lanius excubitor* (Linnnaeus, 1758) and the kestrel *Falco tinnunculus* (Linnnaeus, 1758), which are the main lizard predators in this area. The lizard assemblage in the park is diverse and includes both desert species and species of Mediterranean origin. Representatives of the latter are more abundant in the wadis, while the desert species inhabit the arid slopes.

The conditions in this region are suitable for increasing plant biomass and species richness with the practices of water harvesting and reduction of resource leakage employed by the Forestry Department of the Jewish National Fund (JNF). This is done by constructing contour catchments, which are series of longitudinal pits and dykes along the contour line of the slopes (Eldridge, Zaady & Shachak 2002). These structures (2 m wide, 10–30 m long about 40 m apart from each other) simulate the effects of natural pits (e.g. porcupine digging; Boeken *et al*. 1995) but on a larger scale. The water-enriched pits accumulate run-off and nutrients and are used to support trees planted by the JNF as part of a large project of 'savannization' (Shachak,

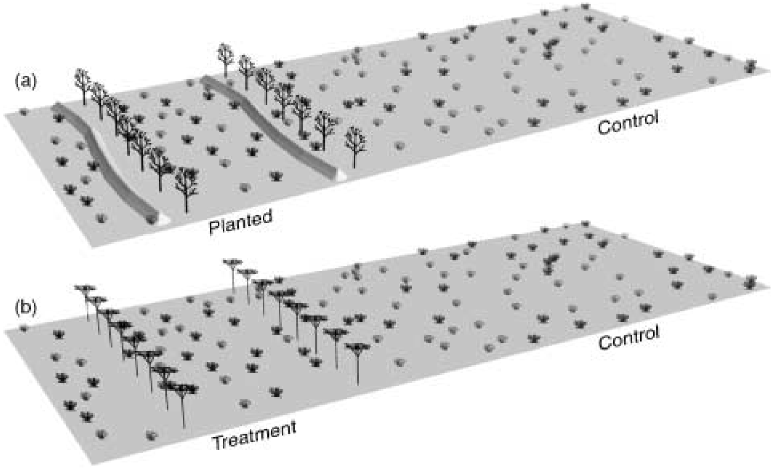

Fig. 1. Schematic descriptions of the management practice used in the 'savannization' project (a) and of the artificial 'trees' manipulation we used to mimic the role of trees as perches, while excluding other possible impacts on the natural habitat (b). (a) The surface of natural slopes is left unaltered between the pits and dykes, dividing the natural slopes into small fragments of 30–40 m. (b) The distance between the two rows of artificial trees is 40 m and the distance between the experimental plot and the control is 30 m.

Sachs & Moshe 1998). The surface of the natural slope is left unaltered between the pits and dykes, dividing the natural slopes into small fragments, about 30–40 m wide, bounded between rows of trees (Fig. 1a). Not all arid slopes in the park have been altered and thus, on a wider scale, a mosaic of natural and altered slopes has been created.

ENVIRONMENTAL VARIABLE MEASUREMENTS

Seven pairs of circular plots, 68 m in diameter, were established within the mosaic of habitats in Sayeret Shaked Park. One plot from each pair was established in an altered slope, and the other within an adjacent natural slope, about 50 m from the first. The distance between paired plots was chosen to attain high similarity (slopes, altitude, natural vegetation cover, etc.) in order to isolate the effect of the anthropogenic manipulation (i.e. planted trees in one of the plots). The distance between two paired plots may allow occasional flow of individuals between the plots (making any significant difference between the plots more robust) but the direct impact of perching predators was limited to less than 30 m from a perch (D. Hawlena, personal observation). The plots remained unfenced to avoid the effect of fencing on lizard populations (Weiss, Jennings & Moore 2002).

We measured cover by stones, perennials and annuals. Only stones that were larger than 5 cm in diameter were considered, because only these are likely to be important refuges for the lizards. We used continuous line transects in order to assess the absolute as well as the relative coverage. For each perennial species the relative cover was also recorded. In each plot we used a matrix of eight transects, with a total length of 380 m. Using the collector's curve technique, in preliminary transects we demonstrated that such a sampling effort is sufficient to represent properly the plant and stone cover in this habitat.

LIZARD TRAPPING AND MEASUREMENTS

In each plot, an array of seven pitfall traps in the shape of the letter Y was established. The traps were made from 18-L buckets, buried flush with the ground. During trapping periods, the bucket lids were raised on stands, 3 cm above the pitfall edge, to prevent the lizards from overheating and to prevent predation of the captured lizards. Between trapping periods, traps were tightly closed with lids. Drift fences, 16 m of dense plastic net, were erected along the legs of the array to increase the effectiveness of the traps.

All captured lizards were sexed and individually marked by the commonly used methods of toe clipping. We measured lizard snout–vent length (SVL) and tail length (to the nearest 1 mm) with a transparent ruler and mass (to the nearest 0·1 g) with an electronic field scale (ACCULAB, model PP250B Precision Weighing Balances, 10 Peabody St, Bradford, MA, USA).

We used the minimum number of individuals known to be alive as a density estimator, as trapping probability was too low to allow the use of open population mark–recapture models. Although very basic, this index allows an estimation of density without the need to make essential assumptions that are rarely met in wild populations of lizards.

ADDITION OF ARTIFICIAL TREES

To elucidate the effect of increased habitat complexity on desert lizards, we 'planted' artificial trees in a natural arid habitat situated 1 km away from the Sayeret Shaked Park. We established five pairs of plots, each pair located at least 300 m from the next, forming five independent replicates. All 10 plots consisted of homogeneous loess habitat lacking in natural bird perches. A 30-m corridor separated the 80 × 80-m plots in each pair. In each plot, 64 10-L buckets were inserted flush with the ground. In one plot of each pair (randomly selected) 2-m metal poles were erected to attract shrikes and kestrels (Fig. 1b). Barbed wire connected to a 50 × 50-cm metal frame was attached to the pole tops to mimic thorny branches, creating a suitable location for the shrikes to stand and impale their prey. These artificial trees were positioned in two rows, eight 'trees' in each row, in a pattern similar to the pattern of planted trees in the savannization project. The artificial trees had no impact on the natural habitat (i.e. they did not provide shade, produce organic matter or increase insect abundance) apart from serving as suitable perches for avian predators. We concentrated on the desert lizard *Acanthodactylus beershebensis* (Moravec *et al.* 1999) not only because it is the most common species in this habitat but also because it has shown the strongest reaction to the plantations; this species had disappeared from the mosaic landscape of the savannization project and was most likely to react fast enough to detect change even with a short-term manipulation. We captured the lizards for 3 consecutive days each month, during 4 winter months, using pitfall traps. All captured lizards were individually marked. Shrike activity was assessed by direct focal observation for 2 h per pair of plots. The shrike positions were recorded and the percentage of time the shrikes stayed in each plot was calculated as an average of three observations.

STATISTICAL ANALYSES

Statistical analyses followed procedures in Zar (1998) and were performed with the program SPSS version 10·0 (SPSS Inc., 233 S. Wacker Drive, Chicago, IL, USA). All necessary assumptions were checked for each statistical test, following procedures described in Coakes & Steed (2001). In cases of deviation from the test assumptions, the data were transformed as required. In cases where all transformations failed to satisfy the assumptions, non-parametric tests were performed.

Lizard species diversity was calculated using the Fisher's α index of diversity (Fisher, Corbet & Williams 1943) and then compared with the two types of plots by paired *t*-test. The advantage of the Fisher's α index is that it does not depend on sample size. The composition of the lizard assemblage and the dynamics of changes between the natural and altered plots were represented on an incidence–abundance phase plane. In this technique, the log of the mean density of each species is plotted against the number of plots in which it occurs. Normally this technique is applied to dynamics in time by drawing arrows between two points for each species measured at different times (Boeken & Shachak 1998). We slightly modified the technique and, as a replacement to the situation before the plantation, used paired, unmanipulated plots (Fig. 3). The trajectories of the species on the phase plane reveal the dynamics of changes in the spatial distribution deriving from the anthropogenic alteration of the natural plots.

A paired *t*-test was used to compare the absolute and relative cover of the environmental variables between treatments. A stepwise multiple regression revealed the relationship between species abundance and environmental variables. We coded plot type as a dummy variable, to account for plot effect. We report only the results of the best model of each backward stepwise procedure.

In order to investigate the effect of patch alteration on lizards' body condition index, we compared lizards from the two plot types using either a univariate ANCOVA or a Mann–Whitney *U*-test, when the assumptions for a parametric test were not met. We calculated an index of body condition for each individual as the residuals from the regression equation of body mass (in g) on SVL (in mm); both variables were log-transformed (for a review see Green 2001).

To reveal the effect of artificial tree addition to the arid habitat, we compared lizard densities and shrike presence between the control and manipulated paired plots. As a relative measure of density we used the minimal number of different lizards found during the four winter trapping periods. As we only used five pairs of plots, we had to use the non-parametric Wilcoxon signed ranks test to compare lizard density and shrike presence between planted and control plots (Siegel & Castellan 1988).

Results

HABITAT CHARACTERISTICS AND THEIR EFFECT ON LIZARD SPECIES

Natural and planted plots did not differ in the percentage of either stone cover or perennial vegetation (stones, paired *t*-test, $t = -2{\cdot}018$, d.f. = 5, $P = 0{\cdot}1$; perennial, paired *t*-test, $t = -1{\cdot}83$, d.f. = 5, $P = 0{\cdot}127$; Fig. 2a). The power of the tests was 0·75 (stones) and 0·99 (perennials) for a difference of 1% and 5%, respectively. However, the percentage of annual cover was higher in the planted

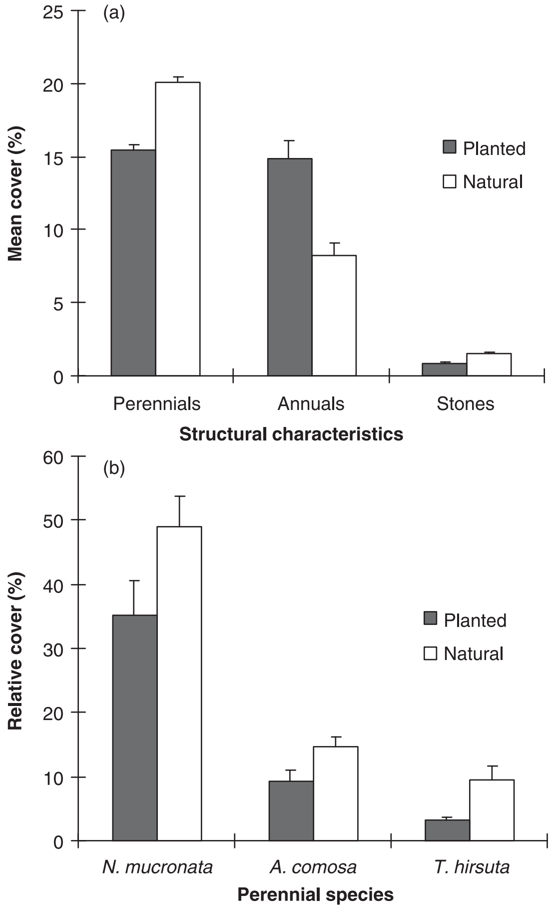

Fig. 2. Comparison of environmental variables between the two types of plots. (a) Comparison of the percentage cover of three habitat characteristics (perennial vegetation, annual vegetation and stones) between natural and planted plots. Only the cover of annuals was significantly different between the two types of plots ($P = 0{\cdot}045$). (b) Comparison of the relative cover of the three dominant shrub species in natural and altered plots [mean cover (%) (SE)]. Only the cover of *N. mucronata* was significantly different between the two types of plots ($P = 0{\cdot}016$).

plots than in the natural plots (paired t-test, $t = 2{\cdot}66$, d.f. = 5, $P = 0{\cdot}045$; Fig. 2a). The relative cover of the main shrub species differed between the two plot types for *N. mucronata* (paired t-test, $t = -3{\cdot}569$, d.f. = 5, $P = 0{\cdot}016$; Fig. 2b). No differences were found in the comparisons of the two other main shrub species (paired t-test, *T. hirsuta*, $t = -1{\cdot}22$, d.f. = 5, $P = 0{\cdot}277$; *A. comosa*, $t = -0{\cdot}882$, d.f. = 5, $P = 0{\cdot}418$). The power of these tests for a difference of 5% was 0·81 for *T. hirsuta* and 0·73 for *A. comosa*.

The abundance of *Stenodactylus sthenodactylus* (Lichtenstein, 1823) (transformed by square root) was positively correlated with the cover of perennial vegetation ($R^2 = 0{\cdot}627$, $P = 0{\cdot}002$). The abundance of *Chalcides ocellatus* (Forsskal, 1775) was inversely related to the percentage of stone cover, although the overall stone cover was relatively low (less than 3%; $R^2 = 0{\cdot}499$, $P = 0{\cdot}01$). The abundance of *Mesalina guttulata* (Lichtenstein, 1823) was only related to the plot effect ($R^2 = 0{\cdot}868$, $P = 0{\cdot}007$) and no effect of the measured environmental variables was detected. There was no significant correlation between abundances of other species and the cover of perennial vegetation, annual vegetation or stones. There was a negative correlation between the abundance of *M. guttulata* and the relative cover of *T. hirsuta*, with a significant plot effect [$R^2 = 0{\cdot}694$, P(*T. hirsuta*) = 0·026, P(plot) = 0·002]. There was a positive correlation between the abundance of *C. ocellatus* and the relative cover of *N. mucronata*, with a significant plot effect [$R^2 = 0{\cdot}566$, P(*N. mucronata*) = 0·018, P(plot) = 0·034]. We found a similar pattern in the relationship between *S. sthenodactylus* and the relative cover of *N. mucronata*, but with no plot effect ($R^2 = 0{\cdot}875$, $P < 0{\cdot}001$).

EFFECTS OF PLANTED TREES ON LIZARD ASSEMBLAGE

Of the 10 species of lizard that we recorded within Sayeret Shaked Park, seven were captured by pitfall traps and only these species were included in the analysis. Lizard species diversity did not differ between the two plot types (paired t-test, $t = 0{\cdot}212$; d.f. = 5, $P = 0{\cdot}841$). Nevertheless, the standard deviation of the Fisher's α index of diversity was higher for the natural plots (0·902) than for the planted plots (0·385).

The incidence–abundance phase plane (Fig. 3) revealed that the diurnal lizard *Ophisops elegans* (Menetries, 1832) was found in similar incidence and abundance in the two types of plots. However, *M. guttulata* had different affinities to plot types: it was abundant and occurred in most natural plots but was less abundant and occurred in fewer planted plots. *Chalcides ocellatus* demonstrated the opposite pattern. Two additional species, *S. sthenodactylus* and *Mabuya vittata* (Olivier, 1804), maintained approximately the same densities in both types of plots but replaced each other in terms of incidence. While *S. sthenodactylus* was found in few planted plots but in many natural plots, *M. vittata* showed the opposite pattern. The endemic and critically endangered species *A. beershebensis* was captured only in natural plots situated on the park border, adjacent to the natural habitat surrounding the park. The only specimen of the gecko *Hemidactylus turcicus* (Linnaeus, 1758) was captured in a natural plot. *Trapelus pallida* (Reuss, 1834) was not captured or observed in the park, although it is relatively abundant in all the natural areas surrounding the park.

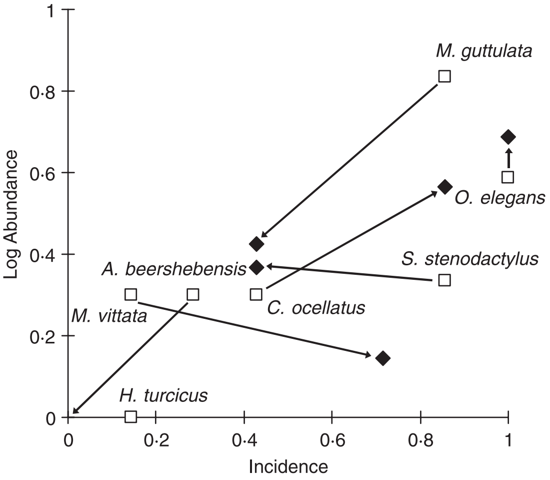

Fig. 3. Comparison between the two types of plots using an incidence–abundance phase plane. The incidence is represented by the proportion of plots in which a species occurs. The abundance is represented by the log of the average number of specimens captured in one type of plot. The arrows represent the trajectories of changes between the species situation in the natural plots (squares) and the situation within the modified plots (diamonds).

Body condition index of *M. guttulata* differed between plot types ($F = 7{\cdot}00$, d.f. = 1, $P = 0{\cdot}012$). Individuals inhabiting the natural plots had a higher body condition index (mean –0·260, SE 0·092) than individuals in the planted plots (mean 0·0612, SE 0·050). No effect was found in the comparison of body condition between plot types of *O. elegans*, *S. sthenodactylus* and *C. ocellatus*.

EFFECTS OF ARTIFICIAL TREES ON PREDATOR AND PREY SPECIES

The shrikes spent a longer time in the manipulated plots than they did in the control plots (Wilcoxon signed ranks test, $Z = -2{\cdot}023$, $P = 0{\cdot}043$; Fig. 4). The few shrikes that we observed in the control plots were standing on the ground or on small shrubs, and from our observations they do not attack lizards from these positions. A comparison of *A. beershebensis* densities in control and manipulated plots (with perches) revealed lower abundance in the manipulated plots (Wilcoxon signed ranks test, $Z = -2{\cdot}032$, $P = 0{\cdot}042$; Fig. 5).

Discussion

THE OBSERVED PATTERN

The savannization project is a large-scale alteration of a relatively homogeneous arid landscape into a

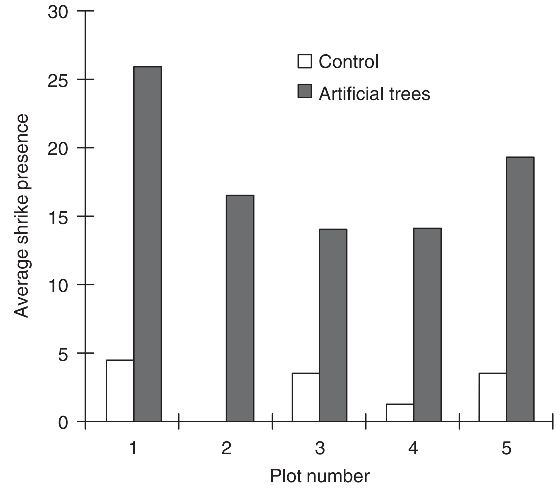

Fig. 4. Comparison of the mean shrike presence in the experimental (manipulated) and control plots. The shrikes spent much more time in the manipulated plots.

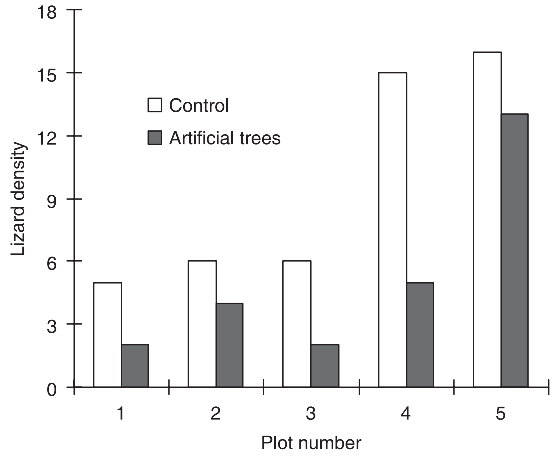

Fig. 5. Comparison of *A. beershebensis* density in the experimental (manipulated) and control plots. The lizards were less abundant in the manipulated plots.

heterogeneous and more productive landscape. The increased complexity occurs both at a local scale (i.e. within a patch), at a broader scale (i.e. within the park) and at a regional scale (i.e. between the park and the natural area that surrounds it). The complexity is increased mostly as a result of the anthropogenic manipulation itself (i.e. the pits and dykes and the planted trees) and, to a lesser extent, as a result of subsequent biological processes.

Unlike the moderate effect that the manipulation imposed on the natural vegetation structure, a considerable effect was observed on the lizard assemblage. Although no differences were apparent in the total species diversity, marked changes were found in the species composition and relative population abundances. A clear pattern was observed: replacement of xeric specialist species (e.g. *M. guttulata*) by species with a Mediterranean distribution (e.g. *M. vittata*) or even wider distributions (e.g. *C. ocellatus*) (for regional distributions see Disi *et al*. 2001). The replacement pattern was especially clear where species were almost substitutes to each other in the incidence–abundance phase plane (Fig. 3). Two species were not found within the planted landscape of the park, although they occur just outside its borders. All the Mediterranean species that invaded the planted slopes are indigenous to the northern Negev desert, usually inhabiting dry riverbeds and other densely vegetated patches within the natural arid landscape mosaic. No invasion by alien species was recorded. Therefore, the pattern of replacement indicates an alteration in the spatial distribution within the regional pool of species. This redistribution of the local species in space increases the relative portion of the landscape inhabited by Mediterranean and generalist species at the expense of the typical desert species. In the next sections we explore the mechanisms that may have generated such a replacement pattern.

HABITAT ALTERATION AND SPECIES REPLACEMENT

Successional changes in habitat complexity induced changes in species composition (Monamy & Fox 2000). The general trend is that an increase in habitat quality and complexity facilitates invasion of superior competitors to the patch, leading to a reduction or extinction of the local species (i.e. competitive exclusion; Abramsky, Dyer & Harrison 1979; Shochat, Abramsky & Pinshow 2001; Fox, Taylor & Thompson 2003). The transformation of the physical structure, either through natural processes or as a result of anthropogenic manipulation, may make the modified habitat more hospitable to species that evolved elsewhere. Such a situation may happen if the modified habitat resembles the selective environment of the non-indigenous species more than it resembles the habitat that shaped the native species (Byers 2002). The savannization project did not alter the arid environment to such an extent that it resembles other habitats that exist in the northern Negev desert, nor did it modify the habitat to resemble a Mediterranean habitat. All environmental characteristics that affected lizard abundance, except for the relationship between *N. mucronata* cover and *S. sthenodactylus* abundance, were similar in both plot types and thus cannot offer an adequate explanation. In addition, the direct environmental effects of planted trees (shade, soil moisture, etc.) are restricted to the elongated pits and do not affect most of the unaltered parts of the patch. Thus, the major question is how the addition of only a few dominant structural elements alters the local community structure in a way that benefits species from dense and well-developed vegetation.

THE INCREASED PREDATION HYPOTHESIS

Langellotto & Denno (2004), in their extensive review, show that by incorporating the effect of alteration of habitat complexity on natural enemies we may understand better the habitat modification effect on prey species. Changes in habitat structural complexity may support higher predator densities by supplying essential structures needed for foraging and reproduction (perches, refugia, nesting places, etc.; Wolff *et al*. 1999; Kenward *et al*. 2001). However, a more complex habitat may also supply refugia for the prey (Ellner *et al*. 2001; Sheffield *et al*. 2001; Tchabovsky *et al*. 2001). Adding perches (trees, fences, etc.) to open scrubland considerably increases the ability of avian predators to exploit the habitat (Hall, Howard & Marsh 1981; Wolff *et al*. 1999), generating negative effects on prey populations (Van Gulck *et al*. 1998). In our system, the modification of habitat structure led to greater use of the habitat by avian predators, and thus an increase in predation pressure (R. Boochnik & A. Bouskila, unpublished data). The great grey shrike, the main lizard predator in the study site (D. Hawlena, unpublished data), hunts exclusively from perches (Yosef 1993). Thus addition of trees to arid slopes enabled shrikes to invade the previously unexploited habitat. The radius of impact of a shrike is much broader than the actual radius of the perch it uses and, in our case, reaches up to 30 m (D. Hawlena, personal observation). As a result, the spatial effect of a single tree may reach 2827 m^2, which, from a lizard's perspective, alters the entire patch within the planted plots to be uniformly risky (the open habitat between the tree lines is about 40 m wide). Thus, we hypothesize that, although physically subtle, the structural alteration may affect lizard populations in the entire altered plots. Lizards may have been captured in the planted plots and/or may have abandoned them because of the increased risk.

Support for the central role of predation in shaping the lizard assemblage is provided by the results of the manipulative experiments. First, the addition of artificial trees to an open scrubland increased the time spent by avian predators in the manipulated patches compared with the adjacent control plots. Secondly, the local density of *A. beershebensis* in the increased predation plots decreased markedly. The significant population reduction was already observed 3 months after the artificial trees were planted. Moreover, the manipulated plots affected a relatively small portion of the habitat, unlike the savannization project that created a large-scale mosaic landscape. Thus we strongly believe that, given a longer time and a larger scale, such a manipulation could provide a valid explanation for the local extinction of *A. beershebensis* from the mosaic landscape of the savannization project.

The spatial distribution of *M. guttulata* and its body condition serve as supplementary indications that support the increased predation hypothesis. The abundance of *T. hirsuta*, a relatively tall indigenous shrub used by shrikes as a perch, was negatively correlated with the abundance of *M. guttulata*. The high density of this bush in riverbeds can explain the natural scarcity of desert lizard species in this habitat. Specimens of *M. guttulata* captured in altered plots (in which trees were planted on top of the few natural shrubs) had a lower index of body condition compared with those in natural plots. Body condition indicates the sum of environmental factors affecting the individual. Therefore, a patch in which the average body condition of the population is lower then elsewhere is considered to be less suitable for that species. In high-risk situations lizards should allocate more time and energy to anti-predator behaviours at the expense of other essential activities, such as feeding, reproduction, etc. (Ydenberg & Dill 1986; Lima & Bednekoff 1999). In other lizards such behavioural alterations have reduced the condition of the animals, their growth rate and adult size (reviewed by Lima & Dill 1990; for lizards see Downes 2001).

If an increase in predation following habitat alteration is so influential, why do certain species replace others under these apparently adverse conditions? Mediterranean species are better adapted to cope with avian predators, because they inhabit open Mediterranean scrubland scattered with a large number of perches for avian predators. As Mediterranean species co-evolved with a high risk of predation, the behavioural and morphological mechanisms that allow them to evade predation may provide an advantage over the desert-adapted lizards. For example, *O. elegans* uses a more cautious foraging mode than *M. guttulata* (R. Boochnik & A. Bouskila, unpublished data). The ability to forage safely, in spite of the presence of predators, can provide a competitive advantage, and this may be a case where predation and competition operate together (Bouskila 1995) to create the pattern of change in the lizard assemblage.

GLOBAL PERSPECTIVE

Large-scale land-management projects are becoming common practice in many parts of the world (Smith *et al*. 1996; Shachak, Sachs & Moshe 1998; Gao, Zha & Ni 2001). For this reason, it is important to view our results in a broad global perspective. Anthropogenic alteration of habitat structure can impose profound effects on local fauna, including local species extirpations (Shochat, Abramsky & Pinshow 2001; Kiffney, Richardson & Bull 2003). As demonstrated in this study, the effects need not result directly from the structural manipulation, but can often result from indirect biotic interactions (Perry & Dmi'el 1995) such as predator–prey interactions (Schneider 2001). The importance of the predator–prey relationship for applied issues was recognized and reviewed by Ormerod (2002). Our study provides additional support to this notion and demonstrates that changes in habitat structure and landscape physiognomy can be an important management tool to either support predator populations or control them (Schneider 2001; Thirgood *et al*. 2002). As many habitat manipulations, such as fragmentation (Oehler & Litvaitis 1996; Rushton *et al*. 2000), deforestation (Vitt *et al*. 1998) and urbanization (Engels & Sexton 1994), alter predator–prey relationships, we should always considered this possibility when assessing the environmental impacts of a development project.

The complex nature of predator–prey interactions makes it very difficult to predict the magnitude and scale of a manipulation effect on the local community. Management practices that physically affect a relatively small portion of the natural landscape may exert much larger impacts on specific species even in areas that are not affected by the structural alteration itself. Moreover, not all species are equally likely to be adversely affected by the manipulation consequences. Specialist species inhabiting structurally homogeneous habitats may fail to evolve the ability to identify rare structural elements (i.e. trees and big bushes) as cues for biotic interactions and may lack the behavioural plasticity to respond to such structural cues. As a result, supplementation of structural elements that are naturally rare can have profound effects on these species, while having minor effects on generalist species that evolved in more heterogeneous habitats. Such dissimilar effects on species from different origins may alter relative abundance of species and can induce species replacement.

To protect biodiversity, large-scale management practices should be carefully planned to include conservation patches that will be large enough to support the indigenous species and supply favourable conditions. However, it is not sufficient to rely on observations of physical complexity alone in order to decide on the size of these patches: we also need to understand the biotic interactions that are associated with the alteration.

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