Colonization by annual plants of an experimentally altered desert landscape: source–sink relationships

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Summary

1. We studied how annual plant species colonize a set of patches (natural and human-made) in a shrubland landscape in the Negev desert. We asked what patch properties and species’ attributes affect colonization during 4 years after experimental formation of eight sets of pits and mounds.

2. The ‘sink function’ of patches was measured as the numbers of colonizing species, the proportion of patches colonized during each year, and the abundance of the colonizers. The effects of species’ dispersal mode and propagule size were examined.

3. In the first growing season, pits and mounds were colonized by large numbers of species. The total number of colonizing species was similar for the two patch types, but incidence was higher in pits than in mounds.

4. The early colonizers were mainly wind-dispersed and showed both high abundance and incidence. Dispersal mode did not affect colonization in the second year and later, nor did propagule size throughout the experiment.

5. Most early colonizers became resident in the patches, but pits and mounds showed some further colonization during the second year. In the third and fourth year both the numbers of colonizing species and their incidence decreased.

6. Pits were mainly colonized from outside the experimental units to which they belonged, whereas mounds received species mostly from the adjacent pits within the same units.

7. From the second year on, patches of undisturbed crusted soil were also colonized, mainly from the adjacent pits and mounds. The number of colonizing species in undisturbed patches increased during the last, high-rainfall, year both per patch and for the whole set of patches.

8. We conclude that the sink function of patches for colonization increases with removal of vegetation, soil crust and seed bank, with patch capacity to capture resource and plant propagules, and with amount of rainfall. Sink function decreased with time due to decreasing availability of new species, but increased with the presence of stronger sink patches in the vicinity.

9. We suggest that the concept of sink function, in terms of the numbers, incidence and abundance of species colonizing sets of patches, can be a powerful tool for linking community and landscape processes.

Keywords: assemblage dynamics, desert shrubland, landscape mosaic, Negev, sink function


Introduction

A central question in plant community ecology is what determines the species richness and diversity of assemblages. It has long been appreciated that plant communities are the result of migration of species between landscape patches and their sorting by environmental conditions (Gleason 1926). MacArthur & Wilson (1967) were among the first to consider explicitly colonization by individual species, and this triggered experimental studies (Simberloff & Wilson 1969; Wilson & Simberloff 1969). It was not until

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more recently that emphasis has been put on spatio-temporal patterns in heterogeneous landscapes, focusing on species populations (Hanski 1982, 1987, 1994; Pulliam 1988; Kadmon & Shmida 1990; Gyllenberg & Hanski 1992; Wiens et al. 1993) and species assemblages (Collins 1987; Tilman 1993; Hanski et al. 1993). Large-scale processes can determine plant species richness, mediated by migration within and between species pools at various scales (Cornell & Lawton 1992; Tilman 1993; Pärtel et al. 1996; reviewed by Zobel 1997). Despite the importance of local abiotic factors and biotic interactions, spatial patterns of species richness in landscapes appear, to a large degree, to depend on the movement of individual species from patch to patch. We, however, are not aware of any experimental studies that consider colonization in a landscape context and include the arrival and establishment of new species in a patch within a landscape mosaic.

In this paper we study the dynamics of a species assemblage by focusing on the colonization by annual plant species of small-scale (1 m²) patches of three different types, distinguishing between the sink and source functions of patches. The sink function of a patch depends on the relation of the patch with its environment, and is reflected in the number of species that newly colonize the patch in each growing season, as a result of the successful establishment of seeds arriving from outside the patch. A patch is a sink for any species that colonizes it within a particular time interval, and a source when it is the likely origin of a colonizing species in another patch. The source function of a patch is determined by the number of species capable of colonization. Our sink patches differ from sink populations as defined by Pulliam (1988), which require continued immigration because population growth rate is very low (cf. Watkinson 1978; Kadmon & Shmida 1990). Analogous ‘sink communities’, maintained by repeated colonization because none of the immigrant populations has a positive growth rate, would be very rare and would shift the focus from spatial dynamics to local processes. Our definition of patches as sinks and sources is based on the flux of species across a patchy landscape, where sources donate species and sinks receive species. This is very similar to the usage of the terms in systems analysis (Bennet & Chorley 1978) and plant physiology (Salisbury & Ross 1978).

Including the abundance of the colonizing species in the sink function allows us to differentiate between different species within a patch, and between different patches for the same species. Adding a third property, species incidence, defined as the proportion of patches each species has recently colonized, extends the use of this concept to a landscape mosaic. The position of a species in the incidence-abundance phase plane (Brown 1984; Gaston & Lawton 1990; Hanski et al. 1993; Gaston 1994, 1996; Boeken & Shachak 1998) reflects its colonization, population persistence and population growth in a metapopulation context. Abundance and incidence are here restricted to colonization events and reflect how many species colonize the set of patches, in how many patches, and with how many individuals on average. We can then compare between sets of patches whose sink functions differ as a result of different patch properties and climatic variation. Because this approach is as much species- as patch-centred, we can also compare sink strengths for different functional or structural groups of species.

In a previous study (Boeken & Shachak 1994) we found that species richness increased in small-scale (<1 m²) human-made patches in the Negev relative to undisturbed areas. We inferred that this was due to different patch properties such as microtopography and surface texture, which lead to variation in parameters such as capture of propagules, runoff water, soil and nutrients. The greatest effect on species richness was observed following disturbance of the soil crust, by creating sunken pits and raised mounds. This significantly increased trapping of seeds and establishment of species in the patch, even though mounds were drier than pits and undisturbed matrix.

In the present study we tested how species richness is affected by colonization processes, by comparing the sink functions of sets of different types of patches during a number of years. Since colonization also depends on species’ attributes, we compared sink function with respect to groups of species with different dispersal characteristics (Boeken & Shachak 1994; Boeken et al. 1995).

Specifically, we addressed two questions. (i) What patch properties and species’ attributes affect the sink function of landscape patches during 4 years of colonization by annual plant species? Matrix patches had a soil crust, vegetation and a seed bank, which were removed in the creation of the two disturbance types, sunken pits and raised mounds, which differed in soil moisture availability. The species’ attributes considered were dispersal mode and propagule size. (ii) What are the sources of colonization? A patch can be both a sink and a source for species colonization, if it receives new species and contributes (different) species to other patches, and adjacent patches may thus have an effect on each other’s sink functions. Answers to these questions will provide information about the spatial dynamics of species assemblages during colonization, as an essential step towards understanding the dynamics of species assemblages in landscape mosaics.

Methods

SITE DESCRIPTION

The research was done in the Sayeret Shaked Park near Beer-Sheva in the northern Negev desert of Israel (31°17’ N, 34°37’ E), a large hilly area of several km² from which livestock has been excluded since 1987.
Rainfall, which occurs between November and March, has a long-term annual average of 200 mm. Average daily minimum winter temperatures are 6-8°C, and average daily maximum summer temperatures are 32-34°C (Stern et al. 1986).

The research site was a gentle north-facing slope with an angle of c. 5%. The soil surface was covered with a microphytic crust, consisting of bacteria, cyanobacteria, algae, mosses and lichens (Zaady & Shachak 1994; Shachak et al. 1998), interrupted by patches of a loose soil mound with one or more shrubs and a herbaceous understorey. The most common shrubs were Thymelaea hirsuta (Thymelaeaceae), Noea muromata (Chenopodiaceae) and Atractylis serrulifolium (Asteraceae) (Feinbrun-Dothan & Danin 1991). The underlying soil was at least 1 m thick, and composed of loess with 14% clay, 27% silt and 59% sand. Salt content of the 0–25 cm soil layer was low, with electrical conductivity of 0.4 mMho (Teomim 1990).

### THE EXPERIMENTAL PATCHES

In the early spring of 1991, eight rectangular experimental units of 1 m x 3 m were randomly chosen from 48 such units that had been constructed with their short sides along a single contour line. The units were 1–4 m apart, over a length of 160 m. The eight units selected were 6.21 m ± 0.84 (mean ± SEM) apart and were located within larger areas of crusted matrix. Each unit consisted of three 1 m x 1 m patches in a down-slope row, with < 15 cm difference in overall elevation, and included an area of undisturbed crusted matrix, a pit sunk to a depth of 30 cm below the crust, and a soil mound raised 20 cm above the crust as the lowest patch.

We removed the top 10 cm of soil, and thus both above- and below-ground vegetation and the soil seed bank, which is usually confined to the top 2 cm of soil (Gutterman 1993), from each pit area before using the next 20 cm to form the adjacent mound. The soil in the mound was retained in a plastic frame and was mixed and flattened by hand. An area 1 m wide and 15 m long, up-slope from the pit, was enclosed by parallel plastic walls. Runoff water from that area (which included the undisturbed matrix patch) was therefore channelled into the pit. As well as differences in presence of a flat, dense soil crust, vegetation and seed banks (only in the matrix), matrix, pits and mounds differed in sink function for both resources and seeds. Pits collect runoff from the matrix, which supplies resources and seeds (Boeken & Shachak 1994), while the matrix both receives and loses runoff; mounds neither collect runoff nor, due to the 20-cm containing wall, do they lose it, but are good sinks for species with wind-dispersed or ballistic seeds (Boeken & Shachak 1994). The experimental set-up therefore allowed us to examine how patch properties affect the sink functions of different patch types.

### RAINFALL AND SOIL MOISTURE

Rainfall at the site was monitored throughout the study period. Soil moisture in each matrix, pit and mound of the eight experimental units was measured at four different times during the rainy seasons of 1991–92, 1992–93, 1993–94 and 1994–95 by Time Domain Reflectometry (Topp & Davis 1985) using a Tektronix 1502C Metallic Cable Tester. Two 15-cm long probes were used to estimate average volumetric soil water content in the 0–15 cm soil layer, which contains the rooting zone of the majority of annual plants (Evenari et al. 1982).

### SINK FUNCTION FOR SPECIES COLONIZATION

The colonization sink function of pits, mounds and matrix patches was assessed for each of the 4 years of the experiment (1992–95), both per patch type and for sets of patches of each type, based on plant counts per patch. Each year all individuals of vascular plant species in all of the 1-m² patches were identified and counted at the time of peak biomass in April. Nomenclature follows Feinbrun-Dothan & Danin (1991). Species not previously present in a patch were considered colonizers, while those already present were residents. For the pits and mounds all species found during the first growing season after construction were colonizers. Proportions of colonizers within the patch communities were also estimated.

Since species colonization is the result of the flux of seeds across the landscape followed by establishment in patches, the presence of dormant seeds could result in one or more seasons of absence as growing plants (Cohen 1966) although a species was already present in the patch. Numbers of colonizing and resident species per patch were therefore also calculated for 1 and 2 years of seed dormancy. Assuming one dormant season, species present in 1 year, absent in the next and present in the third year were classified as resident in the last year. Comparisons involving 2-year dormancy are rather coarse, as only one or two time intervals are available.

The overall sink function for species for each patch type was estimated each year as the mean number of newly colonizing species in all replicates of mound, pit and matrix patches. This resulted in the loss of species identity, so that individual patches may have variable numbers of colonizing species in common. In contrast, sink function per set of patches retained species identity. Every species that colonized during each year into at least one patch of each type was included, and was represented by a point in the incidence–abundance phase plane. Colonization incidence was calculated as the proportion of newly occupied patches for each species per year per patch type (Boeken & Shachak 1998). Abundance was calculated as the mean number of plants for each species in the colonized patches, per year and per patch type.
COLONIZATION SOURCES

Colonization source was differentiated into (i) colonizing species new to the patch but present in the previous year in one of the other patches of the same unit, and (ii) colonizing species not previously present in the same unit, with no distinction made between species present in other units or absent from the data set. Seed dormancy for one or two growing seasons was again incorporated, as above, to differentiate between newly colonized species and recolonizers after local extinction. Mean numbers of species and their total abundance were calculated for each colonization source per patch type per growing season. The proportion of colonization from each source was also calculated per individual species for each patch type. These species-specific data were further compared with species’ attributes.

SPECIES ATTRIBUTES

Dispersal mode and propagule size of the plant species were taken from Zohary (1966, 1972), Feinbrun-Dothan (1978, 1986) and Feinbrun-Dothan & Danin (1991). Dispersal mode was divided into three categories: (i) wind dispersal, i.e. seeds or achenes with pappus, wings or parachutes; (ii) ground dispersal, i.e. roundish seeds that roll across the soil surface (Boeken & Shachak 1994; Boeken et al. 1995); and (iii) other modes, including zoochory, direct rain dispersal (Gutterman 1993) and aleochoy (the deposition of seeds near the mother plant; Gutterman 1993). Propagule size was grouped into four categories: tiny, with maximum diameter <1 mm; small, from 1 to 3 mm; medium, from 3 to 5 mm; and large propagules >5 mm (Boeken & Shachak 1994; Boeken et al. 1995).

STATISTICAL ANALYSIS

The effects of patch-type differences and of annual variation on the variables of sink and source functions for species colonization per patch type were tested in a repeated-measures ANOVA (SuperAnova, SAS Inst. Inc., Cary, NC, USA), with intervals from 1 year to the next as the repeated measures variable and mean numbers of species per patch as the response variable. We included residency, which separated newly colonizing species from residents, as an independent group variable. Because patch-type differences are between patches within experimental units, units were included as an independent group variable in order to separate among-unit variation from the residual error term (Boeken & Shachak 1994). Proportions of colonizing species per patch (relative to residents and colonizers together) were analysed similarly, but excluding residency, after angular transformation (Sokal & Rohlf 1981).

The effect of time on the sink function of sets of patches was analysed for individual species using one-way ANOVAs for sets of mounds, pits or matrices separately, with colonization incidence (after angular transformation) and abundance of the species as response variables and time as independent variable. The proportion of occurrence of each species as resident or colonizer was analysed against patch type and against time as a repeated-measure variable, with incidence as a covariate. In a separate analysis, we used dispersal mode and propagule size as additional group variables to ascertain the effects of the morphology of dispersal units on species’ occurrence as colonizers or residents.

The effect of colonization source (within the same unit or from outside the unit) on the number of colonizing species per patch type was analysed in an ANOVA with time interval as the repeated-measures variable, and with units and colonization source, patch type and their interaction with time. In contrast to colonization sink function, the source functions were not analysed for sets of patches. Source identity was analysed for species, in ANOVAS with dispersal characteristics as covariates.

Results

RAINFALL AND SOIL MOISTURE

Rainfall was 163.5 and 157.0 mm (somewhat below average) in the first 2 years of the study, 97.5 mm in the third year and 283.0 mm in 1994-95 (above average). Pits were significantly wetter than undisturbed matrix ($P < 0.0003$ for all years separately), while raised mounds were significantly drier than the matrix ($P < 0.0008$ for all years separately) (Boeken & Shachak 1994, 1998). Only during the drought of 1993–94 were mounds and matrix similar ($P = 0.4250$). Pits were the wettest because in addition to direct rainfall they accumulated runoff; matrix patches both received and produced runoff, while mounds did neither and may have had worse soil moisture retention than the matrix due to the absence of a soil crust.

COLONIZATION OF THE PATCHES

During the first growing season after disturbance, both pits and mounds were colonized by large numbers of species (38.5 ± 2.4 per pit and 26.7 ± 3.0 per mound; Fig 1), with large numbers of individuals (236.5 ± 29.0 in pits and 108.8 ± 20.3 in mounds). Throughout the 4 years of the experiment, the pits remained richer in species than the mounds and matrix patches ($F_{2,15} = 51.116, P = 0.0001$ for patch-type effect on species number, and $F_{2,15} = 20.714$, $P = 0.0003$ on plant density, after removal of the unit differences). After the first year, species number and plant density ceased to reflect colonization alone, as many of the early colonizers became resident. In the second, third and fourth year after disturbance,
additional species continued to colonize all patch types. Total species richness and total plant density of the colonizers and residents combined both varied significantly in time ($F_{3,30} = 40.929$, $P = 0.0001$ and $F_{3,30} = 329.545$, $P = 0.0001$, respectively). There was a decrease in species number and plant density during the relatively dry year, followed by an increase in the last, wet year. Most of the variation of species richness through time was due to annual variation in the numbers of colonizing species, as 65.3% of its total variation was explained by differences between years ($F_{2,20} = 61.768$, $P = 0.0001$), compared with only 7.9% for residents ($F_{2,20} = 13.853$, $P = 0.0002$). Total plant density varied significantly with year differences for colonizers as well as residents (explaining 62.8% and 75.3% of total variance, respectively).

In contrast to the temporal variation in species number, the spatial variation between the patch types reflected the gradual accumulation of resident species, particularly in the pits (Fig. 1). In terms of species number, the differences in sink function between the patch types varied in time, because pits, mounds and matrix were colonized equally during the wet year (1994–95) but not in other years. In terms of total plant density, however, pits consistently remained stronger colonization sinks than mounds and matrix throughout the study, but these differences too were small after the first wave of colonization. This variation in the differences in sink function between patches in time after the first year resulted in an interaction between years and patch type that was marginally significant ($F_{1,20} = 2.836$, $P = 0.0517$) for species number, but not for plant density ($F_{1,20} = 2.327$, $P = 0.0915$). In spite of the greater access and site availability in pits than in mounds, colonizing species number of both disturbed patch types varied little after the first wave of colonization. In contrast, there was a significant increase in colonizing species in the matrix during the fourth, wet year, following a decrease in the previous relatively dry year. This suggests, somewhat unexpectedly, that even areas with an undisturbed soil surface are capable of receiving new colonizers after a period of high extinction rates or low coloniztion rates due to limited arrival of propagules. In terms of plant density, matrices and mounds showed a steeper increase in sink strength in 1995 than did pits, while density of the residents on mounds showed a simultaneous decrease.

Relative to the values for all species, species number and total density of colonizing species per patch type were, similarly to the absolute values, affected significantly by patch type ($F_{2,10} = 26.512$, $P = 0.0001$ for species number and $F_{2,10} = 4.857$, $P = 0.0336$ for plant density) and by between-year fluctuations in climate ($F_{2,20} = 44.397$, $P = 0.0001$ for species number and $F_{2,20} = 13.712$, $P = 0.0002$ for plant density). However, although absolute numbers of both residents and colonizers were higher in pits than mounds (Fig. 1), there was a small but significant increase in the proportion of colonizers in mounds compared with pits.

The inclusion of seed dormancy had a significant effect on the numbers and total density of colonizing and resident species, as more species were counted as residents (Fig. 1). Assumption of 1-year dormancy, representing species that recolonized after local extinction (irrespective of whether this is due to recruitment of dormant seeds or from outside the
patch) showed that they contributed to all patch types, particularly in the last, wet year. By 1995, mounds had three such recolonizers with c. 100 individual plants, pits eight species with c. 80 plants, and matrices 12 species with c. 80 plants. These values were only slightly increased by assuming 2-year dormancy, but because it could only be assessed during the last year this comparison is not very informative. The effects of patch type, residency, years and their interactions, on mean species number per patch, were not affected by assuming dormancy, but the proportions of colonizing species became similar for the patch types (from $F_{1,165} = 26.512, P = 0.0001$ for no dormancy to $F_{2,10} = 2.125, P = 0.1702$ for a 2-year dormant period), mainly because many of the 1995 matrix colonizers had previously been recorded there. Assuming dormancy also made the significant interaction between residency and patch type disappear (from $F_{2,25} = 6.103, P = 0.0069$ to $F_{2,25} = 1.065, P = 0.3598$), as patch-type differences in relative density of colonizers decreased (from $F_{2,10} = 4.857, P = 0.0336$ to $F_{2,10} = 0.983, P = 0.4075$).

INCIDENCE AND ABUNDANCE OF COLONIZATION

As numbers of colonizing species changed, so did the number of patches they invaded (incidence) and the mean abundance of their newly established populations, both in time and among the patch types (Fig. 2). Throughout the course of the experiment, incidence of new colonizers decreased significantly in all three patch types ($F_{3,165} = 15.052, P = 0.0001$ for the mounds, $F_{3,165} = 34.381, P = 0.0001$ for the pits and $F_{3,106} = 3.541, P = 0.0325$ for the matrices). There was a significant decrease in abundance over time in the pits, a marginal decrease in the mounds, and no effect in the matrices ($F_{3,165} = 3.050, P = 0.0299$; $F_{3,165} = 2.244, P = 0.0851$; and $F_{1,106} = 0.417, P = 0.6604$, respectively). Pits had more high-incidence colonizers than mounds during all years except the last.

Although species sink function per patch differed with patch type (Fig. 1), the total numbers of colonizing species found in the entire set of pits or mounds were very similar, especially at the beginning of the experiment (Fig. 2). This emphasizes that individual pits are colonized by more species than the individual mounds. The higher colonization incidence of pit species implies greater similarity than among the mounds. The mounds were colonized by smaller, less similar assemblages of species than the pits, but these came from a similar-sized species pool.

During the first year many species colonized both pits and mounds with high incidence, but then their numbers decreased drastically, especially in the mounds, as many became resident. These species were, by virtue of their high population growth rate, among the dominant species in the communities.

_Bupleurum semicompositum, Anagallis arvensis, Rosmaria cristata, Bromus fasciculatus and Centaurea hyalolepis_ colonized all mounds and pits during the first year, while _Plantago coronopus, Crepis aspera, Silene colorata, Torilis arvensis, Bromus rubens, Ammochloa palaeastina_ and _Paronychia arableica_, and five further low-abundance species, were found in all pits. In the second year, two more species colonized all pits (_Adonis dentata_ and _Reboudia pinnata_) and two colonized all mounds (_Adonis dentata_ and _Lotus peregrinus_), but none in the matrix. Colonization incidence was lowest in the relatively dry year of 1993–94, and coincided with the lowest numbers of species in all three patch types. Incidence–abundance plots for colonizing species were similar for all patch types after the first year.

During the first year the majority of high-incidence colonizers in pits and mounds were wind dispersers (including _Bromus fasciculatus, Rosmaria cristata_ and _Centaurea hyalolepis_, although _Anagallis arvensis_ is a ground disperser and _Plantago coronopus_ is atelechorous). However, this may simply reflect the distribution of dispersal modes in the overall species assemblage, as dispersal mode had no statistically significant effect on the average position of species in the colonization incidence–abundance phase plane. Ratios of wind and ground dispersers and others were similar in all patch types and years (c. 10:8:2).

Dispersal mode affected the chance of a species becoming resident in the second year. Wind dispersers were significantly more likely than ground dispersers to be resident in 1993 ($F_{2,47} = 4.300, P = 0.0193$), a direct consequence of their high-incidence and high-abundance colonization in the previous year. Subsequently, dispersal mode was not correlated with colonization or patch type. Propagule size also played a role in colonization, but only during the dry year of 1993–94, when there was evidence of more resident species with tiny to small (≤3 mm) seeds than with medium and large seeds (>3 mm) ($F_{3,35} = 4.923, P = 0.0059$). This effect was smallest in pits ($F_{2,70} = 2.804, P = 0.0674$ for patch type, and $F_{5,70} = 2.144, P = 0.0589$ for the interaction between patch type and propagule size).

SOURCES OF COLONIZATION

Most species colonizing the pits came from outside the unit, whereas those colonizing the mounds and matrix patches could have come from the other patches in the same unit. Statistically, this resulted in a significant interaction effect between colonization source and patch type on species numbers ($F_{2,25} = 42.833, P = 0.0001$) for the years 1993, 1994 and 1995 together, and a significant main effect of patch type on proportion of same-unit colonizers ($F_{2,10} = 11.677, P = 0.0023$; Fig. 3). The effect of patch type on relative density of same-unit colonizers showed a similar pattern ($F_{2,10} = 9.643, P = 0.0052$). The proportion
Fig. 2 The position of colonizing species in the incidence–abundance phase plane for the eight mound, pit and matrix patches over 4 years, with their dispersal mode. (The numbers of species with the same values are marked near the data points.)

of same-unit colonizing species differed among years ($F_{2,20} = 3.678, P = 0.044$), as the number from outside the unit decreased with decreasing rainfall for pits and mounds, but did not vary for matrices (Fig. 3). There were no significant differences in relative density of same-unit colonizers between years ($F_{2,20} = 2.337, P = 0.122$).

The results indicate that pits remain sinks for outside species that have not yet colonized the units, while they become sources for the adjacent mounds and matrix. Total density showed a similar pattern to species number. The main trend in species source and sink functions with patch type was not affected by including recolonizers, assuming a 1- or 2-year period of seed dormancy, but the proportion of within-unit colonizers decreased in pits as many of these were then considered residents, and increased in mounds and matrices as many colonizing species were now counted as residents of pits.

Dispersal mode had a significant effect on the
colonization source of the species during the second year (1992–93) \( F_{2,164} = 3.870, P = 0.0228 \), as more wind dispersers colonized from patches in the same unit than from outside the unit. This effect was only marginally significant in 1994 and 1995. This reflects the fact that many wind-dispersed species had already colonized the majority of patches (particularly pits; Fig. 2) with high abundance during the first year. Propagule size had no effect on the origin of colonizers.

**Discussion**

Patch dynamics can be seen in most landscapes (Wiens 1997). The patchiness of the mosaic can change either as a result of formation of new patches resulting from disturbance by various biotic and abiotic agents (Connell 1978; Pickett & White 1985), or by gradual change in the properties of existing patches. Organisms respond to these temporal variations in spatial structure by changes in their abundance and incidence within the various patches. These responses are described by metapopulation dynamics (Hanski 1982, 1987; Gyllenberg & Hanski 1992; Wu & Levin 1994; Husband & Barrett 1996), where populations are connected by migration between patches. Species establish new populations by colonization, which may persist for short or long time periods. As Wiens (1997) and Husband & Barrett (1996) have recently pointed out, metapopulation dynamics are part of a continuum of spatial processes ranging from isolated populations with very restricted movement of individuals to single populations with very high dispersal rates leading to a homogeneous mosaic. In order to understand how species assemblages function in landscape mosaics, we have to link patch dynamics and metapopulation dynamics. In the terms used by Keddy (1992), this provides both species’ response and assembly rules, in the context of patch dynamics.

Recent developments in our understanding of the significance of incidence–abundance relationships (Gaston & Lawton 1990; Hanski et al. 1993; Gaston 1994; Boeken & Shachak 1998) make it possible to use assemblage dynamics. These describe the dynamics of metapopulations of all species in an assemblage in terms of abundance and incidence of their populations in all patches under consideration. Both incidence and abundance change in time as a function of within-patch population dynamics, colonization of unoccupied patches, and extinctions (Boeken & Shachak 1998). The colonization component is strongly related with patch dynamics, as newly formed patches are invaded by colonizing species and are further altered as a result.

Our approach consisted of changing patch dynamics by adding new experimental patches, in which the metapopulation dynamics of annual plants can be followed. The original landscape mosaic was composed of scattered shrub-dominated patches with a soil mound at their base and an understory of herbaceous plants, embedded in a matrix of flat soil covered with a biological ('microphytic') soil crust (Boeken & Shachak 1994; Shachak et al. 1998; Shachak & Pickett 1997).

**Patches as Sinks for Colonization**

We focused on how colonization of annual plant species within a set of patches depends on patch properties and species’ attributes. We quantified sink function of the patches for colonizing species by assessing numbers of colonizing species. Sink function reflects how many species colonize a set of patches, and with what incidence and abundance, i.e. how many new patches they colonize each year and with what density. Our results show that the sink function of patches for species colonization increases with (i) removal of vegetation, soil crust and seed bank (pits and mounds are stronger sinks than the intact matrix), (ii) the capacity of the patch to capture resources and plant propagules (sunken pits more than raised mounds or flat matrix), and (iii) the annual amount of rainfall (as between the average first and second year, the dry third and the wet fourth year). It also became clear that sink strength decreases in time, as predicted by MacArthur & Wilson’s (1967) Island Biogeography Theory. However, in our experiment this appears to be determined by
the decreasing availability of new species that had not yet colonized, rather than by an intrinsic upper bound of equilibrium species number that can be sustained by the environment, as proposed by MacArthur & Wilson (1967) and later demonstrated by Simberloff & Wilson (1969) for colonization of islands by terrestrial arthropods. In our results there is no evidence that the number of resident species in a patch restricts the number of colonizers, since the two are mostly positively correlated (with \( r = -0.540, 0.844 \) and 0.821 for mounds, \( r = 0.325, 0.960 \) and 0.828 for pits and \( r = 0.771, 0.976 \) and 0.635 for matrix in 1993, 1994 and 1995, respectively). The discrepancy between our findings and MacArthur & Wilson’s (1967) hypothesis is therefore because our patches are never species-saturated, and there remains room for new species without the need for extinctions.

Sink function is only affected by dispersal characteristics during the early stages when the majority of colonizers are wind dispersed. While it should be noted that seed morphology may be a poor predictor of actual dispersal ability or of actual numbers of seeds dispersing (Gaston 1994), there are similarities between our observations and those of Simberloff & Wilson (1969). At the smaller time scale of weeks, wind-dispersed invertebrates were the first to colonize empty islands but later colonization was not associated with dispersal characteristics. However, since the majority of species in our assemblage were wind dispersed, the lack of an effect of dispersal mode after the first wave indicates that other modes become more prevalent at that stage. Delayed colonization, particularly in the mounds, suggests that dispersal ability limits colonization of species with other modes of dispersal, at least immediately after disturbance, and is influenced by patch properties. In a previous paper on the same experimental set-up (Boeken & Shachak 1998), we proposed that distribution and population growth of most species were primarily site-limited, because incidence and abundance responded to availability of soil moisture during recruitment, rather than during seed production in the previous year. Although this implies that establishment ability rather than seed availability in the area at large limited incidence and abundance of the many rare, low-abundance species, it does not preclude seed limitation at the patch scale. Site and seed limitation are not necessarily mutually exclusive, as Eriksson & Ehrlen (1992) recently pointed out, especially for low-abundance species. Incidence and abundance of the most common species in our Negev assemblage, in contrast, were limited by the availability of seeds, as is the rule in density-independent population dynamics. This limitation was overcome first by migration of seeds into the patches during early colonization, and later by local production. In this situation colonization may be affected by dispersal ability only in so far as better dispersal may promote even faster colonization at higher abundances.

Sink-source shifts

Continued colonization in the mounds and matrix shows that the sink function of a patch increases if there are other strong sink patches, i.e. pits, in the vicinity. The matrix is undoubtedly part of the source for initial colonization in disturbed patches, although it is probably small relative to shrub patches and natural disturbances (Boeken & Shachak 1994, 1998). Matrix patches also functioned as a sink for colonization by species that had become established in the new patches. Species richness in undisturbed matrix is constrained by the availability of sites on the flat soil crust surface where seeds are protected from removal by wind, runoff water and ants (Boeken & Shachak 1994, 1998). Colonization from the pits augments plant density and species richness in the matrix, providing another example where no one single factor alone limits plant communities (cf. Eriksson & Ehrlen 1992). This also provides an interesting illustration, at a small spatial scale, of Shmida & Wilson’s (1985) mass effect. Mounds too were affected by nearby pits: they are weaker sinks, both because they are simply harder for propagules to reach than pits, and because of site limitation due to lower soil moisture, resulting in frequent failure of establishment (Boeken & Shachak 1998). The sink function of mounds depended, after the first year, upon species colonization from the pits and there was therefore a delay in colonization of mounds by many species. From the second year, the pit functioned as a source of species for both mounds and matrix, in addition to its role as a sink for species from the environment. Thus, pits act as ‘stepping stones’ for colonization in mounds and matrix (Forman 1995), although the individual species colonizing these weaker sink patches would probably have reached them eventually without pits. These sink–source relationships illustrate a central issue of vegetation dynamics (Pickett & McDonnell 1989) and community dynamics in general (Wiens 1997), that species diversity in a community depends to a large degree on its spatial position within the landscape relative to other components.

We propose that, in a set of patches, the sink function of one patch is affected by the sink function of its neighbouring patches. The sink function of a patch depends on (i) the environmental species pool (Zobel 1997) surrounding the set of patches and (ii) the sink function of the other patches in the set. In other words, if A and B are two neighbouring patches within a set of patches, and A is a stronger sink than B for species colonization from the environmental species pool, then B’s sink function increases due to A’s presence. This also implies that A’s source function is proportional to its sink strength relative to B. Note that if the population-level definition of sinks (Pulliam 1988) is applied, this significant spatial relationship would escape notice, since sink function is then determined by extinction or the inability to
become resident. The population-level definition therefore implies that the sink function of one patch could only be influenced by that of another if the inability to produce surplus propagules in one patch somehow causes the same effect in another patch. Since sink populations are defined by local dynamics within the patch, this would be an illogical proposition.

Particularly strong sinks for species colonization, such as pits that capture many seeds and provide ample opportunities for recruitment, rapidly become sources for weaker sinks (mounds and matrix). Thus, creating new patches by disturbance sets in motion a flow of species into these new sinks using the species pool in the surroundings as a source, followed by a flow from the stronger sinks to the weaker ones, and a return flow of species to augment diversity of adjacent undisturbed areas.

Conclusions

The explicit study of source–sink relationships in terms of species flow across patches can be a powerful tool for understanding ecological system dynamics within the context of a landscape mosaic. Source–sink relationships enable integration of three distinct dynamics that occur simultaneously, since flows of both organisms (here seeds) and resources (nutrients, water and sediment) (Shachak & Jones 1995) are, among others, a function of patch dynamics. Such relationships form the background for resource dynamics (Vitousek & Denslow 1986; Gardner & Turner 1991; Shaver et al. 1991; Likens & Bormann 1995), metapopulation dynamics (Hanski 1983, 1987, 1994; Pulliam 1988; Kadmon & Shmida 1990; Gyllenberg & Hanski 1992; Wiens et al. 1993) and species assemblage dynamics (Collins 1987; Tilman 1993; Hanski et al. 1993; Boeken & Shachak 1998).

Source–sink relationships of species assemblages can be successfully applied to many processes in landscape ecology implying connectivity (O’Neill et al. 1988) such as corridors, edge effects and fragmentation, and in cellular automata or other percolation models (Gardner & Turner 1991). Assemblage dynamics employing incidence and abundance (Boeken & Shachak 1998) form a set of constraints on the populations modelled, while source–sink relationships specify rules for species flow between patches.

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