Implications of spatial pattern and local density on community-level interactions

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The importance of spatial aggregation and density dependence have been extensively explored in ecology. However, both factors might interact or modify one another to differentially influence net population or community-level dynamics. In a desert annual plant community, we experimentally tested for these effects at nested spatial scales by planting different number of patches within a plot but holding plot-level seed density constant, by manipulating the number of occupied patches adjacent to a target patch, and by varying local seed density within patches. In doing so, we addressed the following specific questions: (i) is there an effect of the number of patches of seeds planted on plot-level community measures, (ii) are there patch–patch interactions within plots, (iii) are there density-dependent responses to changing initial seed density within patches, and (iv) do patterns observed at finer spatial scales predict patterns at larger scales? Community parameters measured at the plot level-emergence, plant density, and mean plant size-were negatively affected by increasing seed aggregation into fewer patches within a plot. However, converse effects were detected at finer spatial scales. The presence of neighbouring patches increased emergence within a plot, while increased seed density within patches decreased emergence but strongly increased survival and mean plant size. Hence, the net negative effects detected at the arbitrary plot level do not necessarily correspond to the interactions occurring at finer spatial scales within the plot. These findings suggest that the use of single scales of inquiry can potentially misrepresent the importance of a particular interaction, such as competition, and that the experimental consideration of finer scales within a community reveal different patterns and do not predict final net effects within a community.

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Understanding the variability in time or space of a particular process is arguably one of the key goals of science. However, predicting changes in a biological or ecological process is often difficult – particularly since these processes are often nonlinear (Ruel and Ayres 1999). Predictions are typically based on means of the independent variables at arbitrary or convenient scales (Blackburn 1999, Dungan et al. 2002), but for nonlinear functions such as density-dependent interactions within a population, the mean of a function is not equal to the function of the mean (Jensen's inequality; Chesson 1997, Ruel and Ayres 1999). The two extremes of this averaging in plant ecology include the scale of the individual plant and the scale of the community. At the individual level, the 'plant's eye view' of communities prevails where individuals are assumed to experience

only their immediate neighbours (Turkington and Harper 1979), and at the community level, the mean-field assumption applies where communities are viewed as mixed, random assemblages of species interacting with equal probabilities in space (Murrell et al. 2001). However, multiple scales of interaction, between individuals within a patch or dynamics between patches within a community, could in theory influence the averaging to the community level (Hansson 2003). While the general importance of spatial effects and scale have been extensively explored in ecology through theoretical models and mensurative experiments (Tilman and Kareiva 1997), surprisingly few studies have explicitly manipulated spatial pattern and density concomitantly to determine whether different spatial scales within a community, i.e. the area sampled or manipulated (Dungan et al. 2002), corresponds to the net population or community-level dynamics (Schmid and Harper 1985, Brophy and Mundt 1991, Stoll and Prati 2001).

Spatial aggregation is common in natural plant communities as there is substantial evidence that neither seeds nor plants are uniformly distributed in space (Thompson 1986, Rees et al. 1996, Tilman and Kareiva 1997, Maranon 1998). Furthermore, seed banks in a wide range of habitats are generally clumped at least at the horizontal scale of a few meters (Schenkeveld and Verkaar 1984, Thompson 1986, Henderson et al. 1988, Crawford and Young 1998, Mitchell et al. 1998, Arroyo et al. 1999) and sometimes at much finer scales (Lortie and Turkington 2002c, Olano et al. 2002). Fine-scale spatial variation in the distribution of seeds has the potential to directly influence the plant community by providing gaps or unoccupied spaces which can affect the spread of a species or pathogen within a community (Brophy and Mundt 1991, Bergelson et al. 1993), influence local seed density within patches which at least partially determines the final plant density (Schmid and Harper 1985, Miller et al. 1994) or spatial pattern of plants (Houle 1998, Houle et al. 2001), or affect competitive interactions between species by placing competitors of varying superiority within a local neighbourhood (Stoll and Prati 2001). Experimental manipulations however (particularly density) are typically at a coarse scale such as an extent of 0.25 or 1 m^2 plot level (Goldberg et al. 2001, Lortie and Turkington 2002a) while natural aggregation of seed within seed banks may be up to $1/30 \times$ of this extent (Lortie and Turkington 2002c).

Here, we tested the general importance of aggregation for a community in which we previously documented small-scale pattern but tested processes at larger scales (Goldberg et al. 2001, Lortie and Turkington 2002a, 2002b). To explore the importance of scale and its potential interaction with aggregation effects, three observational spatial scales were used, plot, patch–patch neighbourhoods, and within patches. By planting different numbers of patches of seed within a plot but holding total seed density constant and by independently manipulating both the number of patches adjacent to a target patch and local seed density within patches, we specifically addressed the following four questions: (i) is there an effect of the number of patches of seeds planted on plot-level community measures (null hypothesis), (ii) are there patch–patch interactions within plots, (iii) are there density-dependent responses to changing initial seed density within patches, and (iv) do patterns observed at finer spatial scales predict the patterns detected at larger scales?

Methods

Field site and seed collection

A semi-stabilized sand dune system in the central Negev desert, Israel (in the Holot Mashabim Nature Reserve; 31°00.212′N, 34°44.474E) was selected as the seed collection site for the following reasons. The seed bank is consistently clumped at a scale of 85 cm^2 (Lortie and Turkington 2002c), and there are typically about 20 species of annual plants in this community that is predominantly seed bank based (area of sand dune about 1 ha; Dyer et al. 2001, Goldberg et al. 2001). The growing season is short, and rainfall occurs primarily in the winter months (December to April) and has a 30 year average of 110 mm per year (Goldberg et al. 2001).

Seeds were collected November 5th, 1999 using a modified shovel which removed surface sand to a depth of 2 cm (Goldberg et al. 2001) and effectively samples at least 99% of the total seed bank (Venable 1989). The seed was separated from the sand using a 0.5 mm sieve which captures virtually all of the seed (Goldberg et al. 2001). To remove natural spatial structure for subsequent experimental manipulations, the seed was thoroughly mixed by hand. Natural seed bank density was approximately 600 g m^{-2} for this dune community.

Experimental design

Experiments were performed in a fenced outdoor garden at the Mitrani Department for Desert Ecology Research at the Sede Boker Campus (25 km SE of the field site). The experimental garden had 10 blocks each made of $1 \times 1 \times 1.2$ m deep corrugated plastic boxes filled with seedless sand. Seed for all three experiments was planted February 9th, 2000. To avoid edge effects within boxes, we planted seed into 0.5×0.5 m plots surrounded by an unplanted 25 cm wide buffer strip. Plots were then subdivided into 10×10 cm cells (patches). In general, a randomized block design was used to assign treatment levels to each plot. In addition to natural precipitation for that year (39.6 mm), plots were watered ten times

(approximately every two weeks) at 1.5 l per plot, which is equivalent to an additional 100 mm of precipitation.

I. Plot-level aggregation analysis

To address the first question, is there an effect of the number of patches planted within a 0.5×0.5 m plot, seed density at the plot level was held constant at ambient seed bank density (i.e. 150 g in each 0.5×0.5 m plot) while aggregation of seeds within the plot was varied. The plot was divided into 25 10×10 cm patches, and seed was planted into 25 patches of 6 g of seed per cell (uniform and ambient seed density), into 10 patches of 15 g per cell (aggregated), and into 5 patches of 30 g of seed per cell (highly aggregated). Community response parameters (described below) were measured at the whole plot level. This manipulation tested the null hypothesis that variation within plots with the same total amount of seed does not change plot-level measures of community structure. Varying aggregation within a plot however necessarily changes both the spatial arrangement of patches (adjacent patches empty or planted) and the local density within each patch (i.e. 6 g to 30 g within a 10×10 cm cell). As such, we performed two additional manipulations at the patch (or cell level) to test for effects of spatial arrangement and local within patch seed density.

II. Patch–patch interaction analysis

To test for potential interactions between patches within a plot, local seed density of a patch (10×10 cm cell) was held constant at either 1×6 g or 5×30 g ambient density while the number of planted cells adjacent to a given target cell (touching one of the four sides of the cell) were varied. The arrangement of cells included (a) no seed planted into any of the four adjacent cells around a planted target cell, (b) two adjacent cells planted with seed, or (c) four adjacent cells planted with seed. All response parameters were now measured at the patch level, and this manipulation allowed us to determine whether target patches with the same local seed density were influenced by the number of occupied surrounding patches.

III. Analysis of density dependence within patches

To determine whether density-dependent interactions were occurring between individual plants within patches, 10×10 cm cells were planted at three local seed densities with no adjacent cells planted. The three local seed densities included 1×6 g of seed per cell, 2.5×15 g per cell, and 5×30 g of seed per cell. All response parameters were measured at the patch level.

IV. Predicting responses at larger spatial scales from finer scales

To assess whether finer spatial scales predict the patterns detected at larger scales, the regression equations fit to the within-patch final response variables (survival and mean plant size) were used to predict responses at the patch and plot scales. The independent variable, final plant density, was extrapolated to encompass the full range of densities found at the larger scales by increasing the observed independent values to reflect the increased surface area tested (i.e. 100 cm^2 to 2500 cm^2). To assess the predictive ability of finer scales to larger scales, the observed responses at larger scales were plotted and if they fell within the 95% confidence interval for the fitted within-patch curves considered significantly predicted at the 0.05 level (Zar 1999). The mean residuals for larger scales were also compared to the finer scale mean residuals.

Dependent variables and statistical analyses

Plant density was recorded two weeks after initial planting (number of emergent seedlings) and at the end of the growing season (May 28th, 2000). All aboveground vegetation was harvested (per plot or per cell) at the end of the growing season, dried for 48 h at 60°C, and weighed. An emergence index (probability of emergence) was calculated by dividing the number of emergent seedlings by the number of seeds added (Goldberg et al. 2001, Lortie and Turkington 2002a). Survival (from initial density census to final census) and mean plant size (total biomass per plot or cell/final plant density) were also calculated. In addition, the following diversity indices were calculated for the final census: richness, reciprocal of Simpson's D, and E_{var} (Smith and Wilson 1996). For statistical analyses, all proportions were arcsine square root transformed to improve normality, mean plant size was log transformed, and final plant density was square root transformed to homogenize variances (Zar 1999). Data presented in figures are untransformed.

At the plot and patch–patch level, differences between treatment groups for emergence index, final plant density, survival, and mean plant size were tested using ANOVAs. The main effects for the plot-level analysis were number of patches per plot and block, and for the patch–patch analysis, seed density, number of adjacent cells planted, seed density $\times$ number of adjacent cells, and block. At the within patch density-dependence scale, the effects of initial seed density and block on emergence and final plant density per cell were tested with ANOVAs, and density dependence within patches was tested using regression analyses of final plant density by survival and mean plant size. Similar to previous criterion for density dependence, nonlinearity of survival indicates density dependence (concave = competition and convex = facilitation) and for the individual plant response measured here, mean plant size, a non-zero slope suggests density dependence (Goldberg et al. 2001,

Lortie and Turkington 2002a). Since the three diversity measures were not fully independent, mixed-model MANOVAs were used to test for treatment effects at all three observational scales (Scheiner and Gurevitch 2001).

Results

I. Plot-level aggregation effects

Emergence at the plot level was significantly affected by the number of patches planted within a plot with the most aggregated planting having the lowest emergence (Fig. 1a; $F_{2,18} = 5.2$, $p = 0.016$, Tukey multiple comparison tests, $p < 0.05$). Similarly, final plant density and mean plant size significantly decreased with aggregation within the plots relative to the uniform planting (Fig. 1b, 1d; $F_{2,18} = 39.5$, $p = 0.0001$, and $F_{2,18} = 4.4$, $p = 0.027$ respectively; Tukey multiple comparison tests, $p < 0.05$). However, survival (Fig. 1c) and diversity measures were not significantly affected by the number of patches within plots ($p > 0.10$).

II. Patch-patch interactions

At both $1 \times$ and $5 \times$ seed densities, target patches with all four adjacent patches occupied had significantly greater emergence than targets with no adjacent patches occu-

pied (Fig. 2a, Table 1 with Tukey multiple comparison tests). Final plant density of target patches also significantly increased with the presence of occupied patches but only for the $5 \times$ density patches (Fig. 2b, Table 1). Survival per cell (Fig. 2c) and diversity measures of target patches were unaffected by the number of adjacent occupied patches at both densities (Table 1 and $p > 0.10$ respectively). The effect of adjacent occupied patches on the mean size of plants within target patches depended on initial planting density (Table 1). For $1 \times$ target patches, mean plant size significantly decreased when 2 adjacent patches were occupied (and weakly with 4). For $5 \times$ target patches however, mean plant size significantly increased with 4 adjacent patches occupied (Fig. 2d, Table 1 with Tukey multiple comparison tests).

III. Density dependence within patches

Within patches, seedling emergence was negatively affected by increasing local seed density (Fig. 3a; $F_{2,108} = 4.05$, $p = 0.02$). However, the final density of plants within patches was not significantly influenced by initial seed density (Fig. 3b; $F_{2,108} = 3.06$, $p = 0.35$). Both survival and mean plant size per patch exhibited positive density dependence (Fig. 3c, 3d; convex polynomial fit, $r^2 = 0.46$, $p = 0.0001$, and convex polynomial fit with positive slope, $r^2 = 0.21$, $p = 0.0082$ respectively). There were no significant differences in diversity measures with changes in density ($p > 0.10$).
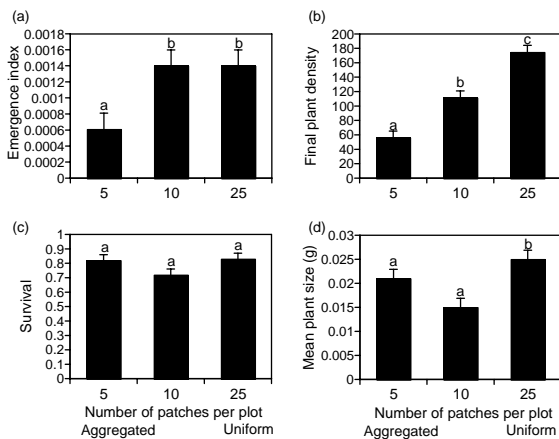

Fig. 1. The effect of varying the number of patches of seed planted within 0.5×0.5 m plots on plot-level community measures. The plot was divided into 25 10×10 cm patches, and in the uniform planting all 25 patches were planted with seed, while in the highly aggregated plots only 5 patches were planted with seed with the rest unoccupied. Total seed density per plot was held constant. Untransformed means (+1SE) are reported. Different letters denote significance in Tukey multiple comparison tests at $p < 0.05$. See text for description of response variables.
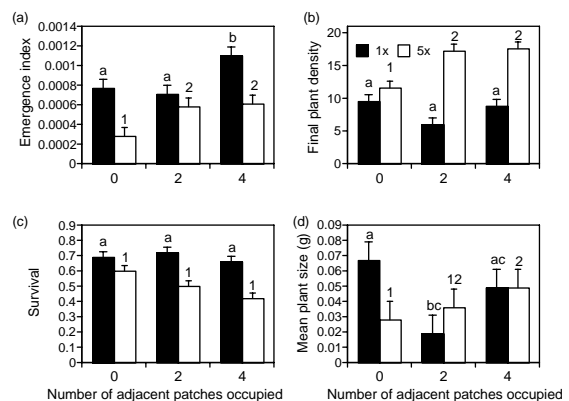

Fig. 2. The effect of number of occupied adjacent patches on target patch-level community measures for two initial seed densities. Patches were 10×10 cm, and the number of patches planted with seed surrounding a planted target patch was varied from 0 to 4 patches planted at the same seed density as targets (either $1 \times$ or $5 \times$ initial seed density). Untransformed means (+1SE) are reported. Different letters or numbers within a series denote significance in Tukey multiple comparison tests at $p < 0.05$. See text for description of response variables.

Table 1. Summary of the ANOVAs for the effect of number of occupied adjacent patches on target patch-level community measures for two initial seed densities. The two local seed densities tested were $1\times$ and $5\times$, and number of patches planted with seed surrounding a planted target patch included 0, 2, and 4 patches planted at the same initial seed density as targets (either $1\times$ or $5\times$). ANOVAs were done on transformed values (see text for transformations). Tukey multiple comparison tests were also performed within treatment groups with significant main effects (p <0.05) and differences are shown on figures. The DF denominator used for all three ANOVAs was the model error ($DF_{den} =234$).

Effect	DF	Emergence		Plant density		Survival		Plant size	
		F	P	F	P	F	P	F	P
Seed density (Sd)	1	5.3	0.02	74.8	0.0001	32.0	0.0001	0.7	0.4
Adjacent patches (Ap)	2	13.1	0.0001	6.2	0.002	2.1	0.1	5.1	0.008
Sd $\times$ Ap	2	9.8	0.0001	9.9	0.0001	2.1	0.1	4.3	0.01

IV. Predicting responses at larger spatial scales from finer scales

Neither survival nor mean plant size at the end of the growing season were significantly predicted at the patch or plot level by considering within patch interactions (all observed values fell outside the 95% CI of the within-patch regression model, Fig. 4). The mean residuals for the larger scales were also significantly greater than the mean residuals for the within-patch regression models (student t-tests, all p <0.05).

Discussion

Recently, the recognition of ecology as "a science of variability" has lead several ecologists to propose that single factors are unlikely to regulate global processes particularly when a diversity of spatial scales are considered (Ruel and Ayres 1999, Hansson 2003, Peek

et al. 2003). As such, we proposed that examining plant communities at single more or less arbitrary scales can lead to incomplete estimates of the importance of particular factors such as aggregation and negative

Fig. 4. An extrapolation of the regression models for within-patch density dependence to larger spatial scales. Actual response variables for patch and plot levels were plotted with the symbol 'x' (in bold =plot level). The 95% confidence intervals are delineated by dotted lines.
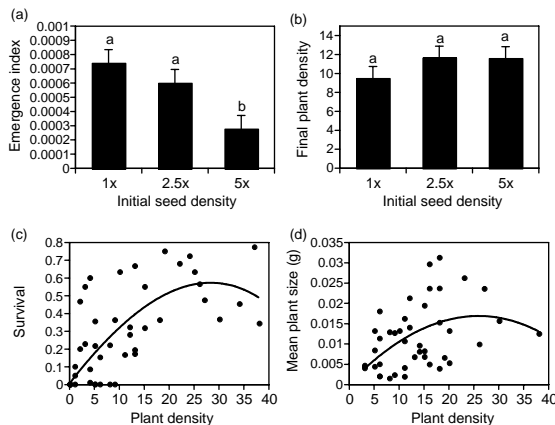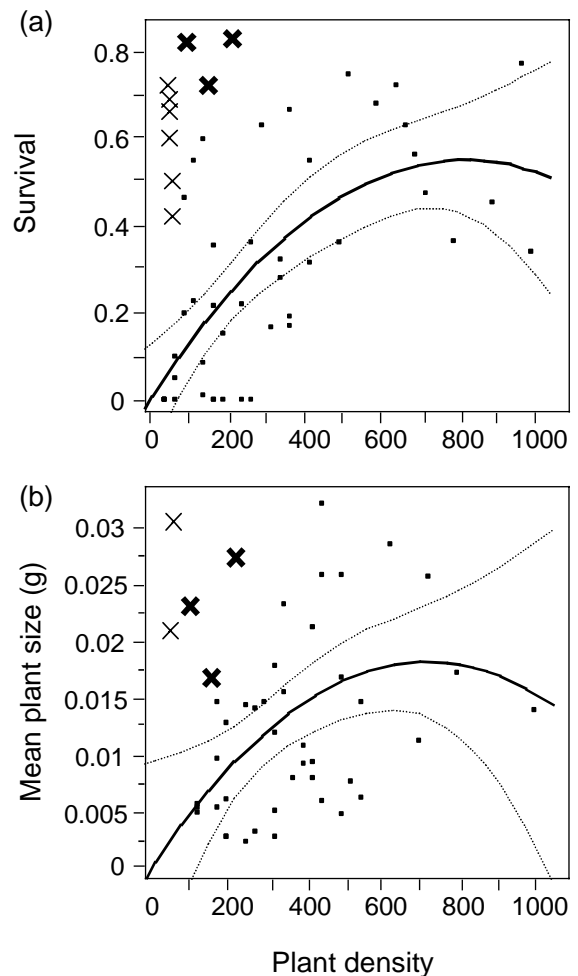
Fig. 3. The effect of initial local seed density planted and final plant density on patch-level community measures. There were no adjacent cells occupied near these 10×10 cm target patches in this experiment, and seed density within the patches was varied from $1\times$ to $5\times$ for this surface area. Untransformed means (+1SE) are reported in Fig. 3 a and b; different letters denote significance in Tukey multiple comparison tests at p < 0.05. In Fig. 3c and d, the community responses are regressed against final plant density and each point represents a replicate patch.

density dependence. This general assertion was supported. In the three experimental manipulations, the null hypothesis of no effect of aggregation at constant plot-level density was rejected, patch–patch interactions were detected and differed in sign from the plot-level community responses to aggregation, and within patch density dependence was expressed and did not predict larger-scale responses to varying density. At least for this plant community, single scales considered independently do not wholly capture the relative importance in nonlinear processes.

A relatively common assumption in plant ecology is that fine-scale interactions can influence community structure (Harper 1977) and that aggregation, primarily in the form of increased density, generally has negative effects on the average performance of individuals (Goldberg and Barton 1992). Some would likely correctly argue that we have perhaps overextended our interpretation of these negative interactions and that is now time to more thoroughly investigate positive interactions (Bruno et al. 2003). However, current theory also predicts that there might be an interplay between positive and negative interactions depending on external factors such as abiotic stress (Bertness and Callaway 1994, Callaway and Walker 1997, Olofsson et al. 1999). In the second and third experiments in this study, observational spatial scale and aggregation were varied to determine if there is a similar interplay between positive and negative interactions. A shift in the sign of interactions was detected as different spatial scales were observed with interactions between patches frequently positive while interactions within patches varied from positive to negative depending on the community response measured. Hence, the net negative effects of experimental aggregation commonly detected at the more coarse plot level were not directly related to interactions occurring at finer scales within a plot. By restricting focus to single scales of inquiry, such as at the plot level or to interactions between individual plants, we may be biasing the types of interactions detected while missing the interesting interplay between competition and facilitation. While few studies have either considered the implications of intermediate scales such as neighbourhood-level interactions (Kikvidze 1996, Rees et al. 1996) or experimentally manipulated aggregation within plant communities (Schmid and Harper 1985, Brophy and Mundt 1991, Stoll and Prati 2001), it is now clear that competition between individuals or negative density dependence is not a complete explanation for plant community structure.

To more effectively explore these interactions within communities, it was crucial to assess whether net effects at the plot level result from variation in patch–patch interactions or density-dependent interactions within the patches, or both. The latter option is intriguing as it suggests that competition or interference between individuals may be mitigated by facilitation at other spatial scales. Consistent with this possibility, seedling emergence was negatively affected by aggregation at the plot level, positively influenced by presence of neighbouring patches, and negatively influenced by increasing seed density within patches. While mean plant size was also negatively affected by aggregation at the plot level, it was both positively and negatively influenced by neighbouring patches and positively density dependent within patches. In both instances the net average effect of aggregation measured at the plot level was negative. However, the net decrease in plant size with aggregation was not generated by interactions between individual plants but by patch–patch interactions at ambient seed density. An additional implication of these switches in interaction sign with spatial scale is that the vast majority of competition studies, which focus on individual species interactions, detect negative effects of increasing density (Goldberg and Barton 1992) could also include positive interactions which may only be manifested by testing alternative spatial or temporal scales (the converse could also be true for facilitation studies). Arguably, one could assert that only the final net effects matter whether positive or negative. However, there is no reason to expect that positive and negative interactions will change in the same way with perturbations (Olofsson et al. 1999), thereby potentially generating different trajectories for communities.

Similar to several previous studies, there were significant spatial interactions between neighbouring patches relative to gaps (Bergelson 1990, Bergelson et al. 1993, Stoll and Prati 2001). While emergence was positively influenced by neighbouring patches, other measures were positive, negative, or independent of nearby patches often depending on initial seed density. This suggests that patches can influence one another through different potential mechanistic pathways. For instance, larger aggregations of seeds might have a higher tolerance for salinity (Waite and Hutchings 1978), aggregation might allow roots of seedlings to en masse penetrate the soil more effectively (Linhart 1976), and nearby patches could reduce evapotranspiration by buffering wind (Kikvidze 1996) or possibly even increase available soil moisture through hydraulic lift or dew capture (Dawson 1993, 1998). Nonetheless, only two other studies have detected a positive effect of the neighbourhood itself, i.e., a patch effect of a group of similar plants versus a single larger plant such as a shrub (Kikvidze 1996, Callaway et al. 2002). It is therefore reasonable to propose that the proximity of groups of individuals, or presence of a neighbourhood in general, can significantly influence community structure but that these spatial interactions do not necessarily function independently of plant density or abiotic stress. Hence, spatial associations between plants may simultaneously

"ameliorate and deteriorate the abiotic environment" (Olofsson et al. 1999) depending on scale and density.

At the larger spatial scales previously tested in this same community, density dependence (both positive and negative) was commonly detected through manipulations of total initial seed density for both 0.5×0.5 m and 1×1 m plots (Goldberg et al. 2001, Lortie and Turkington 2002a). In general, there was good agreement between the local density manipulations within the 10×10 cm patches in this study with the overall effects detected in the more coarse 0.25 or 1 m^2 plot-level manipulations. Emergence in all three studies was negatively affected by initial seed density which suggests that there are consistent negative interactions between seedlings at the emergent plant stage likely through direct interference (Palmblad 1968) or possibly leachates (Murray 1998). Survival in the two plot-level studies was either density independent (Lortie and Turkington 2002a) or facilitative (Goldberg et al. 2001) and here at the within patch level also facilitative. Hence, negative interactions may not commonly occur once annual plants become established in systems such as deserts where abiotic stress is high or the growing season short (Fowler 1986). Furthermore, it is possible that facilitation is the dominant interaction in these systems through mechanisms such as reduced water stress or temperature with increasing plant densities which could in turn increase survival once individual plants become established (Callaway 1995, Holmgren et al. 1997).

Interestingly, the three different diversity measures tested were unaffected by any of the experimental manipulations of seed planting, either through changes in spatial arrangement or local within patch seed density. This trend is similar to our previous manipulations of initial seed density at the plot level where diversity measures were unaffected by density or did not differ from expected null values for a given density (Lortie and Turkington 2002a). This suggests that (i) the failure of previous plot-level manipulations to detect differences in diversity with seed density were not due to scale effects, (ii) interactions between different plant species within this system were predominantly expressed through differences in mean plant size and not establishment or survival, (iii) the representation of emergent plants of most species within this community is well buffered by a persistent soil seed bank, and (iv) mixing the seed bank thoroughly prior to planting removed any natural variation in the presence of seeds of different species with location on the dune. This does not however imply that spatial effects or local density cannot affect the maintenance of biodiversity. Under naturally occurring field conditions, it is likely that the seed bank is neither mixed nor spread evenly over the dune-particularly at smaller spatial scales such as 85 cm^2 (Lortie and Turkington 2002c). Fine scale spatial heterogeneity of the seeds of different species could emerge due to

dispersal, and variation in movement between specific species may even further exacerbate the effects of patchiness within the natural plant community that we detected here (Murrell et al. 2001, Stoll and Prati 2001). It would thus be informative to quantify differences in species diversity with spatial aggregation in the field and test whether spatial structure of seed influences species composition.

Conclusions

The bias demonstrated in this study was that using only arbitrary plots dramatically underestimates the importance of the interplay between positive and negative interactions. Hence, we recommend that for relatively simple plant communities, use of appropriately sized plots to assess net responses to coarse changes in the biotic environment is adequate while use of patches is preferable for assessing positive and negative interactions and relative importance of aggregation. This is particularly relevant if a strong spatial structure is present in the natural vegetation or seedbank. Furthermore, the explicit manipulation of density and spatial pattern concomitantly will likely lead to a more complete understanding of the relationship between patterns at multiple scales and processes within plant communities.

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