Shrubs, granivores and annual plant community stability in an arid ecosystem

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Compensatory population dynamics among species stabilise aggregate community variables. Inter-specific competition is thought to be stabilising as it promotes asynchrony among populations. However, we know little about other inter-specific interactions, such as facilitation and granivory. Such interactions are also likely to influence population synchrony and community stability, especially in harsh environments where they are thought to have relatively strong effects in plant communities. We use a manipulative experiment to test the effects of granivores (harvester ants) and nurse plants (dwarf shrubs) on annual plant community dynamics in the Negev desert, Israel. We present evidence for weak and inconsistent effects of harvester ants on plant abundance and on population and community stability. By contrast, we show that annual communities under shrubs were more species rich, had higher plant density and were temporally less variable than communities in the inter-shrub matrix. Species richness and plant abundance were also more resistant to drought in the shrub under-storey compared with the inter-shrub matrix, although population dynamics in both patch types were synchronised. Hence, we show that inter-specific interactions other than competition affect community stability, and that hypothesised mechanisms linking compensatory dynamics and community stability may not operate to the same extent in arid plant communities.

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The synchrony of species' population dynamics under varying abiotic conditions is considered to be an important determinant of community and ecosystem stability (McCann 2000, Cottingham et al. 2001). If species dynamics are asynchronous, aggregate community properties and ecosystem processes will be stabilised (Doak et al. 1998, Tilman et al. 1998, Ives et al. 1999, Yachi and Loreau 1999, Ives and Hughes 2002). Theory predicts that random dynamics of populations will provide enough asynchrony to stabilise community variables relative to population variables (Doak et al. 1998) and forces that act to increase negative covariance among populations will tend to stabilise aggregate community variables further. Competition, for example, tends to result in environmental niche separation and negative covariance among species abundance and this is thought to be one mechanism whereby species diversity promotes community stability in a variable environment (Tilman et al. 1997, Lehman and Tilman 2000).

There is some empirical support that increased species richness does indeed result in increased community stability (McNaughton 1977, Tilman 1996, McGrady-Steed et al. 1997, Naeem and Li 1997, Petchey et al. 1999). However, in ecosystems with high levels of abiotic stress synchronising forces may predominate, since species abundance may be controlled largely by abiotic

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factors, and facilitative interactions may increase in importance relative to competitive interactions (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997, Brooker and Callaghan 1998). Thus, it is unclear how population dynamics and community stability will be linked in such ecosystems. In addition, trophic interactions may influence the synchrony of population dynamics and community stability. Consumer organisms, for example, may constrain the effects of synchronising processes if consumption is frequency dependent. This may also be of particular importance in dry environments where herbivores tend to affect annual plant abundance through seed predation (Brown et al. 1979).

Although rainfall is considered to be the primary limiting factor to plant growth in arid systems (Noy-Meir 1973, Guo and Brown 1996), biological interactions, within and between trophic levels, also can have a substantial influence on plant population dynamics. Facilitative interactions between plant species are thought to be common in arid ecosystems, in particular the asymmetric positive interaction between large-stature perennials (often called 'nurse plants') and the plant community in their under-storey (FrancoPizana et al. 1996, Brittingham and Walker 2000, Facelli and Brock 2000, Tewksbury and Lloyd 2001). Considerable evidence suggests that such nurse plants moderate the local environment allowing higher rates of productivity, survival and establishment of under-storey plants. As well as increasing local productivity, nurse plants may affect the stability of populations by buffering climatic extremes. This would also stabilise aggregate community variables unless population synchrony was also increased. Community stabilisation would also occur if moderation of the environment increased the strength of inter-specific competition among under-storey annuals leading to greater asynchrony of population dynamics.

Consumer organisms can also have a major impact on plant community composition and on community and population stability (McNaughton 1977). In arid lands granivory is common (Brown et al. 1979), and can have a large impact on plant species composition both directly and via alteration of competitive hierarchies (Brown et al. 1979, Samson et al. 1992, Guo and Brown 1996), although in some areas, the effect of invertebrate granivores appears to be minimal (Davidson 1993, Brown and Human 1997, Anderson and MacMahon 2001). Previous research at our study site has shown that the most common harvester ant species at the site (*Messor arenarius*) has a strong preference for seeds of the numerically dominant annual species (*Stipa capensis*). The harvester ants were also shown to switch to other species when their preferred species was depleted. Such frequency dependent seed selection would be expected to stabilise population dynamics of individual plant species (Fryxell and Lundberg 1994), but may

destabilise aggregate community variables by constraining compensatory population dynamics. Destabilisation may also occur since ants will harvest a large proportion of production in years of low seed production intensifying the effects of drought. Conversely, in years of high seed production the ants will be satiated, and proportionately fewer seeds will be harvested.

In addition to these effects on the density and stability of annual plant populations and communities, previous evidence suggests that there may be strong interactions between ant and shrub effects. Wilby and Shachak (2000) showed that harvester ant activity is not randomly distributed among shrub and inter-shrub patches and that their patch use varies between seasons. Observations of foraging ants revealed that during periods of high seed availability, they tend to forage more in the inter-shrub patches where total plant density and seed availability is lower. Later in the season, when preferred seeds in the inter-shrub patches are depleted, they forage preferentially in the shrub patches, but collect mainly shrub seeds. This suggests that strong interactions between the shrubs and ant granivores should influence plant community composition and that these effects should vary with season.

In this paper we report on an experimental study designed to test the main and interactive effects of shrubs and granivores on the annual plant community composition and stability over a period of several years in which rainfall varied considerably. We created experimental ant exclusions around paired plots containing shrubs (*Noaea mucronata*), which have previously been shown to have a strong nurse-plant effect on the under-storey annual community (Wilby and Shachak 2000), and the adjacent soil matrix. These experiments show that under shrubs and in the inter-shrub matrix population dynamics are strongly synchronised, but that local populations and communities are more stable under shrubs than in the inter-shrub matrix. By contrast harvester ant effects are minimal and appear to be variable in time and space.

Methods

The study was undertaken at Sayeret Shaked Park near Beer Sheva, Israel (31°17′N, 34°37′E) in an experimental area which has been fenced to exclude grazing animals since 1987 (Wilby and Shachak 2000). Precipitation falls only from November to March with a long-term average of around 190 mm per year. The average total annual rainfall at our study site from 1992–2001 was 150 mm per year (B. Boeken, pers. com.). Vegetation at the site is dominated by several dwarf shrub species (usually < 0.5 m in diameter): *Noaea mucronata*, *Atractylis serratuloides* and *Thymelaea hirsuta*, which occupy approximately 20% of the ground area in our experimental

areas. Most primary production occurs between November and March, and annual seeds mature and disperse in April and May. Several species of harvester ant (*Messor* spp.) inhabit the site, of which *M. arenarius* and *M. ebeninus* are the most common with colony density of approximately 19 ha^{-1} and 13 ha^{-1} respectively.

In March 1997, four experimental locations were chosen at the site representing a range of productivity due to their different aspects and position in the watershed. In each location, two experimental blocks were demarcated and in each block, four plots (1.0×0.5 m) were established to which one of four experimental treatments: full exclusion, winter exclusion, walled control and open control, was randomly assigned (the open control is not discussed further in this paper). The plots incorporated a down-slope shrub patch (under-storey of *N. mucronata*) and an up-slope inter-shrub matrix patch, each occupying approximately half of the plot. A 40×40-cm permanent quadrat was marked in each patch type, such that there was a 5-cm border between the quadrats and the edge of the plot. In the two exclusion treatments and the walled control, a 10-cm high PVC wall, buried to a depth of 3-cm and with a 5-cm external overhang, surrounded the plot. The under surface of the overhang was coated with an adhesive substance (Rimifoot, Yavnim Yafeh Ltd., Tel Aviv, Israel) to prevent scaling of the walls by ants. The down-slope edge of the wall was tapered to a point where a hole covered with fine mesh was constructed to prevent water accumulation following rainfall. In the walled control, and the winter exclusion treatments, two 30×1.5-cm gates were cut into each long side of the wall at ground level to allow access by ants. In the winter exclusion treatment these gates were closed from mid-September to mid-April. Observations confirmed that the exclusions were effective at excluding harvester ants.

All herbaceous plants in each 40×40-cm quadrat were recorded around the time of peak biomass (late March) each year from 1997 (pre-treatment sample) to 2001. A severe drought hit Israel in the winters of 1998–1999 and 1999–2000 resulting in large reductions in plant abundance at our study site. Stability measures in response to the drought were calculated for each quadrat:

1) Resistance reflects the extent to which density was perturbed by the drought and was calculated as the proportion of pre-drought abundance (1998) maintained at the peak of the drought (2000).
2) Resilience reflects the extent to which density recovered from the peak of the drought in 2000 to the following year 2001. This was calculated as the change in abundance between 2000 and 2001 expressed as a proportion of the pre-drought density recorded in 1998. It should be noted that

resilience and resistance as defined here are not strictly independent as resilience is constrained by the extent that density was perturbed by the drought.
3) Coefficients of variation (expressed as a ratio: temporal standard deviation/temporal mean) for abundance (CV_{ab}) and species richness (CV_{sr}) across all post-treatment years of the study were used to indicate temporal variability. In addition, CV_{ab} was also calculated for all the common species (defined as those species which occurred in $> 50\%$ of samples from at least one patch type, across all years of the study).

To test for synchrony among the annual species, we used the 'variance ratio' proposed by Klug et al. (2000) and promoted by Ernest and Brown (2001):

$$\mathrm{Var}\left(\sum_{i=1}^{n} S_i\right) \Big/ \left[\sum_{i=1}^{n}(\mathrm{Var}\ S_i)\right]$$

This ratio compares the variance of total abundance with the summed variances of species' abundances. If species' abundances are independent then their summed covariances are zero and the variance ratio equals 1. If species abundances are synchronised on average, then the summed covariance is positive, the variance of total abundance exceeds the summed variances of species' abundances and the variance ratio is therefore greater than one. Alternatively, if species abundances are asynchronous, the variance ratio is less than one.

All statistical analyses were performed in R version 1.2.0 (the R Development Core Team, 2000) using generalised linear models with least squares parameter estimation. Variance attributed to explanatory variables was obtained by deletion from a maximal model including all terms of interest. Due to the split-plot nature of the experimental design several error terms were employed. The significance of location effects was tested against the blocks within location term. Ant exclusion treatment and its interaction with location were tested against the ant exclusion within blocks within location terms. The remaining terms involving patch type (shrub vs inter-shrub) were tested against residual error. In all abundance and species richness analyses the pre-treatment data recorded in 1997 were introduced to the model as covariates. Thus, change in these variables with respect to initial conditions was tested. All models were checked for mis-specification against residual plots.

The effect of species richness on the community stability measures was also tested using two methods, which produced concordant results in all cases. First, pre-treatment species richness was deleted from a full model including all fixed and random terms of interest, and the resulting change in deviance tested against the residual error. Secondly, automated stepwise deletion

procedures were performed on a model including only the fixed factors ant exclusion, shrub, the ant exclusion × shrub interaction, and the species richness term.

Results

During this study, the first two years were of above average rainfall, but in the third year there was a drought in which annual rainfall totalled 45% of the 10-yr average. The fourth year was also one of relative drought with 69% of the average yearly rainfall (Fig. 1). The annual variation in rainfall during the experimental years 1997–2001 is reflected in the plant community data. Species richness in both the shrub patches and the inter-shrub patches closely followed the rainfall pattern, decreasing to 1999 and increasing in 2000 and 2001 (Fig. 1b). Minimum plant abundance was recorded in 2000 reflecting very low levels of seed production in 1999 (Fig. 1a). There was also evidence of spatial differences in plant abundance across our study area. In two years the different locations within the study site differed significantly in total plant abundance, though there was no evidence of a significant location effect on species richness (Table 1) or any of the stability measures calculated (Table 2). Pre-treatment data were consistently highly significant covariates in the analyses of plant abundance and local species richness indicating that there was consistency across years in the relative abundance and species richness of quadrats. There was no significant effect of pre-treatment species richness on the resistance and resilience of total annual plant abundance to the drought of 1999 nor on the CV_{ab} or CV_{sr} of the annual community.

General synchrony of population abundance among annual species was suggested by positive variance ratios in all plots in both patch types. For shrub patches this ratio was 3.56 (± 0.23 se, range 1.35–5.78) and for inter-shrub patches, 2.50 (± 0.28 se, range 1.01–7.30). The majority of annual species responded in a similar way to the variation in rainfall during the study. Between 1998 and the drought year of 1999, most species with the exception of *Stipa capensis* decreased or maintained approximately constant abundance in the shrub and inter-shrub patches. Slightly higher rainfall in 2000 resulted in a recovery of incidence (proportion of quadrats occupied) in most species, but recovery of abundance was slight, particularly in the inter-shrub patches. The exception was the mean abundance of *S. capensis*, which declined from 61.2 individuals per quadrat in shrub patches and 69.0 in inter-shrub patches to 16.1 and 15.0, respectively between 1999 and 2000. For most species incidence and abundance in both patch types further increased from 2000 to 2001. Thus, through the experimental years of the study, shrub and inter-shrub patches behaved ostensibly in a similar way and there is little evidence for substantial dynamic asynchrony among the species, with the possible exception of *S. capensis*.
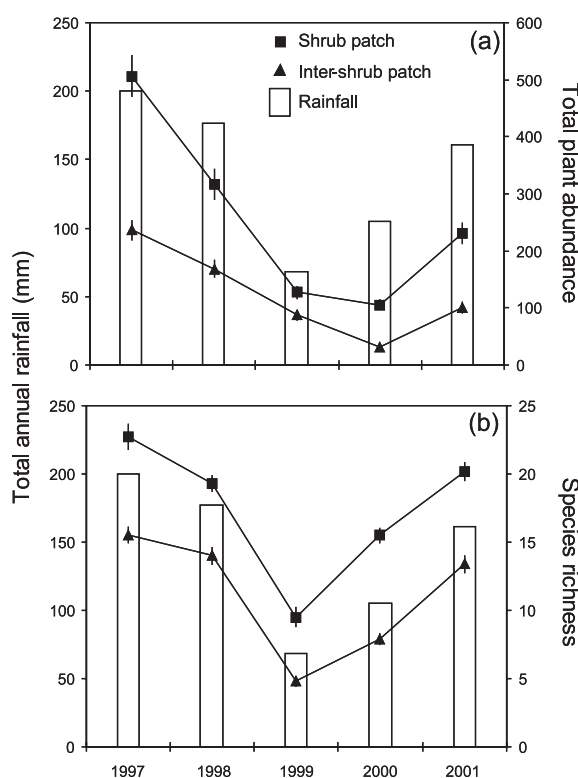

Fig. 1. Changes in the aggregate community variables total plant abundance (a) and species richness (b), in relation to total annual rainfall. Data shown are mean and standard errors for shrub and inter-shrub quadrats.

The influence of shrubs on annual plant density, species richness and stability

Species richness was significantly higher in the understorey of the shrubs than in the inter-shrub matrix in all years apart from the severe drought year of 1999 (Fig. 1b, Table 1). Similarly, total plant abundance was significantly higher in the shrub patches in 1998, 2000 and marginally so in 2001 (Fig. 1a, Table 1). Species composition of the plant communities in the two patch types was very similar. A total of 36 species were recorded in the inter-shrub patches during the course of the experiment compared with 54 species recorded in the shrub patches. The inter-shrub community was a sub-set of the shrub community – only two species occurred in the inter-shrub patches and not in the shrub patches and these were both extremely rare, occurring in only one plot.

Table 1. Analysis results of plant abundance and species richness during the post-treatment years of the study. Pre-treatment data were used as covariates in each of the analyses. Statistical significance is denoted: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Source	df (factor, error)	F values							
		Abundance				Species richness			
		1998	1999	2000	2001	1998	1999	2000	2001
Pre-treatment (1997)	1	112.20***	54.15***	76.05***	60.63***	37.06***	24.00***	164.70***	195.60***
Location	3, 4	11.77**	6.02	2.31	12.88*	0.46	4.08	2.32	0.62
Ant exclusion	2, 8	0.65	1.32	1.66	1.36	0.58	0.34	2.78	2.43
Shrub	1, 11	17.46**	0.41	6.89*	4.25	8.28*	3.81	27.21***	87.08***
Location × ant exclusion	6, 8	1.62	2.40	2.33	1.05	0.45	0.54	0.54	1.53
Shrub × ant exclusion	2, 11	0.53	0.24	0.64	0.89	0.80	0.12	1.71	0.89
Shrub × ant exclusion × location	9, 11	3.79*	2.32	0.99	0.94	0.31	1.08	2.81	3.87*

In addition to greater plant abundance and species richness, the annual community in the shrub under-storey was also more stable than that of the inter-shrub patches (Fig. 2, Table 2). Plant abundance was more resistant to drought in the shrub patches than the inter-shrub patches. In 2000, plant abundance in the shrub patches was on average 38% of the pre-drought abundance, whereas in inter-shrub patches abundance was reduced to only 21% of the pre-drought abundance. The shrub patch annual community was also dynamically more stable than the inter-shrub patches in terms of CV_{sr} and marginally so for CV_{ab}. Resilience, however, was very similar in the two patch types both recovering approximately 40% of pre-drought abundance between 2000 and 2001.

All of the common species showed higher variability in abundance in the inter-shrub patches compared with the shrub patches and these differences were statistically significant in 7 out of 10 of the species studied (Table 3). Only *S. capensis, Rostraria cristata* and *Reboudia pinnata* (marginally significant at $p < 0.1$) showed no significant difference in temporal variability (CV_{ab}) between the two patch types.

Harvester ant exclusion and annual plant density, species richness and stability

Significant ant-exclusion effects were rarely observed in the study. There were no significant differences in any of the community stability measures among the three exclusion treatments (Table 2), nor were there significant differences among treatments in species richness, total abundance (Table 1), or CV_{ab} of the individual species analysed (Table 3). There was a significant three-way interactive effect of shrub, exclusion and location on total abundance in 1998 and on species richness in 2001 (Table 1). There were also few significant treatment effects on the abundance of individual species. In 2001, there was a significant three-way interaction of shrub,
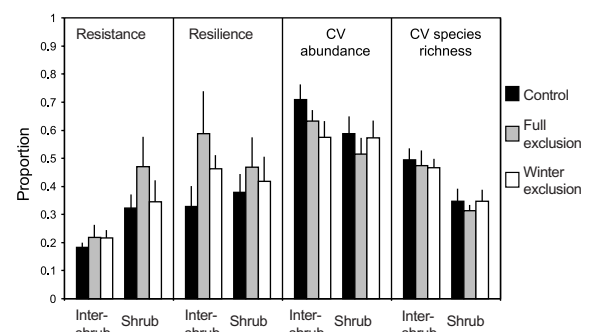

Fig. 2. Comparison of annual-plant community stability in shrub and inter-shrub patches and in the three ant-exclusion treatments. Bars denote standard errors. See text for definition of the four stability measures used.

Table 2. Analysis results of four different measures of community stability.

Source	df (factor, error)	F value			
		CV abundance	CV species richness	Resilience	Resistance
Location	3, 4	4.72	4.76	4.29	1.95
Ant exclusion	2, 8	0.93	0.30	2.21	0.96
Shrub	1, 12	6.31*	21.3***	0.00	36.98***
Location × ant exclusion	6, 8	0.37	1.25	1.48	1.99
Shrub × ant exclusion	2, 12	1.46	0.16	0.78	1.04
Shrub × ant exclusion × location	9, 12	1.56	1.40	0.47	0.67

exclusion and location on the abundance of *Silene colorata* ($F_{9,11} = 2.93$, $p = 0.049$) and *Rostratria cristata* ($F_{9,11} = 3.219$, $p = 0.036$), and a significant interaction between exclusion and location with *S. colorata* ($F_{2,11} = 4.419$, $p = 0.039$).

Discussion

Our results suggest that the total annual rainfall is a major determinant of annual plant abundance and local species richness at our study site. Local species richness mirrored quite closely total annual rainfall, suggesting that germination and establishment of some species are limited by water availability. Annual plant abundance, on the other hand, showed evidence of a one-year time lag in response to rainfall, as minimal abundance occurred the year after the severe drought in 1999. This suggests that seed limitation may occur following drought years with plant abundance reflecting seed production in the previous year.

In recent years, the synchrony of species' population dynamics in fluctuating environments has been an area of intense research in community ecology (Klug et al. 2000, Ernest and Brown 2001) due in part to its relevance to community stability. Our study provides evidence that compensatory dynamics can be extremely constrained in annual plant assemblages in arid ecosystems. In fact, our data show that rather than negative covariance, suggestive of negative inter-specific interactions or neutral covariance suggestive of random dynamics, positive covariance is the overwhelming general pattern among the annual plant species at our study site in both shrub patches, where environmental extremes are buffered to some extent, and in inter-shrub patches. The overall synchrony of population dynamics also seems to reduce the effectiveness of some of the proposed mechanisms whereby species diversity stabilises community attributes due to the asynchrony of population dynamics (Doak et al. 1998, Tilman et al. 1998, Yachi and Loreau 1999). We found no evidence to suggest that the more species-rich quadrats were more stable in any of the stability measures taken, suggesting the synchronising forces act against those promoting complementary dynamics and community stability. It could be argued that species diversity effects form part of the shrub effect in our analysis, since the shrub patches were more diverse than the inter-shrub patches. This is unlikely as there was no relationship between stability and species richness within patch types over quite large gradients of species richness, and the shrub term was retained in favour of species richness in the stepwise deletion procedures during model simplification.

Despite the positive variance ratio in both patch types, community attributes in the shrub under-storey were generally more stable than those in the inter-shrub matrix. At first this seems to conflict with our data on population synchrony. However, variability of community abundance reflects both variability of individual species abundances and their covariances. Since covariances remained positive on average in the shrub patches, we suggest that the decrease in variability at the

Table 3. Comparison of temporal variability of abundance (CV = temporal sd/temporal mean) in shrub and inter-shrub patches for the common species encountered during the study.

Species	CV abundance 1998–2001		Error df	F	p-value
	Shrub	Inter-shrub			
Anagallis arvensis	1.08	1.54	6	77.59	< 0.001
Anthemis pseudocotula	1.28	1.70	10	14.02	0.003
Avena barbata	0.84	1.06	10	9.11	0.013
Bromus fasciculatus	1.15	1.38	9	7.19	0.025
Ononis reclinata	1.22	1.26	9	6.15	0.035
Reboudia pinnata	1.42	1.60	12	3.98	0.069
Rostraria cristata	1.41	1.54	9	2.87	0.125
Senecio glaucus	0.92	1.22	11	16.30	0.002
Silene colorata	1.31	1.68	7	27.29	0.001
Stipa capensis	0.70	0.72	12	0.11	0.744

community level may be a result of decreased population variability, probably as a result of environmental buffering. This is also consistent with the greater resistance to drought in the shrub under-storey. It has been suggested that positive interactions increase in importance relative to negative interactions as environments increase in severity (Bertness and Callaway 1994). Hence, we may expect to find more evidence of compensatory dynamics in the shrub under-storey communities than in the inter-shrub matrix. Generally however, responses of the annual plant community to yearly variation in rainfall were similar in the shrub and inter-shrub patches, and the variance ratio consistently suggested synchronous dynamics. Hence, our data provide little evidence that competitive interactions were relatively more important in the shrub patches. Further experimentation is required to determine the relative importance of environmental forcing, facilitation and competition in determining community dynamics in the two patch types.

While our data show marked effects of shrub patches on local species richness, abundance, and stability of the annual plant community, the effect of granivory by harvester ants was much less clear. Though harvester ants are known to harvest considerable numbers of annual plant seeds at the site, particularly from the inter-shrub patches (Wilby and Shachak 2000), their effect on community composition and dynamics was slight. There were occasional significant interactions between exclusion treatment, location and patch, but these did not represent consistent effects through time or space. Thus, it appears that the presence of foraging ants does have some effect on the abundance of some plant species, the abundance of the plant community and even the local species richness of the plant community, but these effects were generally weak and inconsistent in space and time. Our prediction that there would be strong interactive effects between patch type and treatment was generally not supported. Similarly, there was only weak evidence that the major effect of ant granivory occurred during the summer, the main period in which annual seeds are collected.

The lack of effect of harvester ant exclusion is surprising given previous evidence that *M. arenarius* has a strong preference for *S. capensis* seed, the numerically dominant species at the site (Wilby and Shachak 2000). There are several possible explanations for the weak effects of ant granivory. It may be that recruitment in the system is generally not seed limited, or that a persistent long-lived seed bank exists such that seed predation effects are not expressed over the relatively short period of our study. Both these explanations are unlikely since we saw large reductions in abundance following low seed production in 1999, particularly among the annual grass species which are favoured by harvester ants at this site (Wilby and Shachak 2000). A possible explanation is that seed dispersal occurs at scales larger than our study plots so that local effects of granivores are negated by incoming seeds. These mechanisms may explain difference between our results and those in the deserts of the southern United States, where large-scale ant exclusions resulted in changes in community composition since ants foraged preferentially on dominant species (Brown et al. 1979, Inouye et al. 1980, Samson et al. 1992).

To conclude, our data show that compensatory dynamics in response to environmental variation may not be the norm in arid environments, where the harsh environment tends to synchronise species' abundances. This synchrony means that many of the commonly proposed mechanisms whereby species diversity increases stability are negated (negative covariance effect) or reduced in effectiveness (portfolio effect). However, our study showed that facilitative interactions, particularly between shrubs and annual plants, can have a marked impact on annual plant community composition and stability, but that granivory by harvester ants, despite being a major ecological process in this system, had only weak and spatially variable effects. We call for wider testing of community stability theory in range of ecosystem types.

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