

Distribution/abundance relations in a New Zealand grassland landscape

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Abstract: There are many examples in the literature of a positive correlation between the distribution of a species and its local abundance, i.e., widely occurring species tend to be more abundant locally when they do occur. Such relations have been documented over a wide range of taxa and spatial scales. There are five major hypotheses seeking to explain the relation: Random placement, Sampling error, Niche width, Demography, and Metapopulation dynamics. However, there is little evidence to distinguish between them, especially for plants. In this study, plant species presence in a short tussock grassland in inland Canterbury, New Zealand was sampled at three spatial scales (i.e. quadrat sizes; sizes of spatial grain): 0.2×0.3 m, 0.4×0.6 m, and 1.0×1.5 m, each divided into 0.1×0.15 m sub-quadrats for recording local frequency. The data were also analysed at different ranges of soil pH, water content, organic content and fertility (by bioassay). Significant positive correlations between species distribution and local abundance were found at the two larger spatial grain scales. There was no significant relation for native species, but the relation for exotic species was considerably stronger than that over all species. Reduction of environmental heterogeneity, by restricting the dataset to narrower ranges of soil factors, produced higher correlations at the two smaller grain scales. In contrast to reports in the literature, many species (most of them native) showed narrow regional distributions but high local abundance when they were at a site. It is concluded that the Sampling-error hypothesis cannot be an explanation of the results obtained here. Aspects of the results are inconsistent with the Random-placement, Demography and Niche-width hypotheses. The results are most compatible with the Metapopulation dynamics hypothesis. However, it is likely that several mechanisms are operating simultaneously. Whilst detailed analysis of empirical distributions at different spatial grains and over different ecological ranges can exclude some of the hypotheses, detailed studies of the autecology of species are the next necessary step.

Keywords: abundance; distribution; heterogeneity; macroecology; metapopulation; niche, sampling effect.

Introduction

In spite of the belief that “to do science is to search for repeated patterns” (MacArthur 1972), few general laws have been found in ecology. One emerging generalisation with much support is that there is a positive correlation between the distribution of a species and its local abundance. Species that are widespread on a geographic/regional/landscape level¹ tend to be more abundant in those sites in which they occur than species that are less widespread (Brown, 1984). Statistically significant correlations of this type are increasingly numerous, though they are generally weak, typically explaining 20–30% of the variance, with

many exceptions in individual species (Gaston *et al.*, 1997; Thompson *et al.*, 1998; Gaston and Blackburn, 2003).

A positive relation between distribution and abundance has been observed in a wide range of organisms: vascular plants, intertidal invertebrates, terrestrial arthropods, planktonic crustaceans and terrestrial vertebrates (Bock and Ricklefs, 1983; Brown, 1984). These relations may be found at a variety of spatial scales, from regional (e.g. 100 km² in Gaston *et al.*, 1998), down to 0.5 m² in the grassland study of Collins and Glenn (1990) and 0.1×0.1 m quadrats in the sand dune annual community studied by Rees (1995). Hanski *et al.*, (1993) stated that the relation is found “almost without exception”.

The widespread finding of such a correlation suggests that it is caused by a strong ecological sorting process, but the nature of that process remains obscure.

¹ Here, level refers to the region over which a study was done [the ‘extent’ of McGeoch and Gaston (2002)], and scale to its grain, i.e. the size of an individual sampling unit.

A number of hypotheses have been proposed, the five major ones being:

1. Random placement

With Random placement of the individuals of each species over sites, and variation in overall abundance between species, one would expect a positive relation between distribution and abundance, because species with higher abundance (i.e. more individuals to be scattered) would end up on more sites, and would also on average be more abundant within each site (Wright, 1991; Hartley, 1998). This can be seen as a null model.

2. Sampling error

Species that are locally sparse are more difficult to observe, and therefore more likely to be overlooked in a site, giving the appearance of lower regional site occupancy (Brown, 1984).

3. Niche width

In regions with a considerable species pool adapted to most of the environments present, species with broad resource niches (i.e., alpha niches) might find suitable resources in a wider range of sites (resulting in wide distribution), and also find several types of resource that they could use within each site (resulting in high abundance) (Brown, 1984).

4. Demography

Holt *et al.* (1997) suggested that species with higher intrinsic rates of increase (r) would thereby: (a) have a positive population growth rate, and hence form a viable population, at more sites, and (b) be able to form higher equilibrium population sizes at such sites. However, equilibrium populations are determined more by K than by r (MacArthur and Wilson, 1967).

5. Metapopulation dynamics

Species that are abundant within sites will produce more propagules, and hence have the opportunity to colonise more sites (Hanski, 1991). This hypothesis emphasises dispersal, as opposed to population growth rate in the Demography hypothesis.

Other models are either similar to one of those above, e.g. the Resource availability hypothesis to the Niche width hypothesis, or are not applicable to our landscape-level study, e.g. the Range position hypothesis (Gaston *et al.*, 2000) is not applicable because none of the species in the area is near the edge of its range.

Testing distribution/abundance relations has semantic as well as practical challenges. The term distribution has been used in the literature with at least

two different meanings: (1) a species' total geographic range, and (2) the fraction of a particular area that is used by the species ('occupancy'; Hanski *et al.*, 1993). These imply two different questions, both equally valid. Fractional occupancy has been less frequently examined, because the data are less readily available. It is examined here. Local abundance refers to the mean abundance in a local population or in a local sample, here a quadrat (Hanski *et al.*, 1993). To avoid circularity, the local abundance for a species should be calculated as the mean across only those quadrats in which it is present (Gaston *et al.*, 2000).

The distribution/abundance relation remains problematic because it is still not clear how widely it applies, and because the underlying mechanisms are not understood. We sampled in induced short tussock grassland on a landscape level in New Zealand with the intention of making two contributions to the debate. First, most of the reported correlations have been based on previously-published datasets that have distribution and abundance data, but were not originally collected for the purpose, and few of the datasets are for plants (Gaston, 1996); we collected a plant dataset especially for the purpose. Second, the causes of the distribution/abundance relation are poorly understood. Determining causality in ecology is difficult. We sampled: (a) at several spatial scales as recommended by McGeoch and Gaston (2002), and (b) several soil properties in the hope of obtaining insight into the causes of the relation by investigating over what scales (i.e. 'grain') and ecological ranges the relation holds.

Methods

Study site

We worked in the valleys north-east of Lake Coleridge, Canterbury, New Zealand (43° 13–20' S, 171° 27–37' E, annual rainfall *c.* 1100 mm yr⁻¹). We sampled only valley floors (at an altitude of *c.* 550 m): a band 0.5 km wide along 28.7 km of valley floors in four catchments. This scheme was intended as a compromise between minimising habitat variation (McGeoch and Gaston, 2002) and minimising problems of spatial autocorrelation by spreading the sites out (on average 275 m apart). The range of plant communities sampled included *Festuca novae-zelandiae* Armst. short tussock grassland, *Chionochloa rubra* Zotov tall tussock grassland (most of which had not received over-sowing or aerial fertilisation), *Carex* swards, *Discaria toumatou* Raoul shrubland and *Leptospermum scoparium* J.R. et G.Forst. shrubland. Most of the area had been grazed by sheep and cattle, as well as by feral lagomorphs, for more than 100 years.

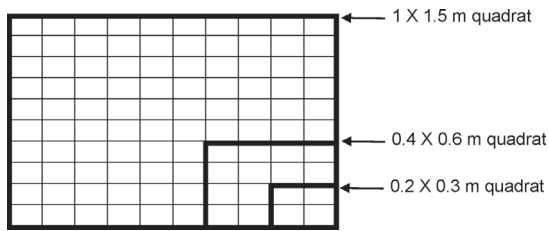


Figure 1. The sampling scheme used, with three nested quadrats, each divided into sub-quadrats.

Sampling

The sampling sites (105) were placed on a map by restricted randomisation (Greig-Smith, 1983) and located on the ground. A further randomisation was then made, of up to 10 m away from the located site, in a random direction, to ensure objectivity in selecting the exact site. To avoid highly-aberrant environments which would be likely to have a quite different species pool, sites were excluded which were more than 50% bare ground, more than 50% surface water, on a slope of more than 15°, or closer than 20 m to a road. At each sample site, three nested quadrats were placed (Fig. 1), giving local abundance at three scales: 0.2×0.3 m, divided into four 0.1×0.15 sub-quadrats; 0.4×0.6 m, divided into 16 0.1×0.15 sub-quadrats; 1.0×1.5 m, divided into 100 0.1×0.15 sub-quadrats. The maximum quadrat size was a compromise between being small enough to minimise within-quadrat habitat variation versus being appreciably larger than the size of individual plants ("Preston's rule of thumb": McGeoch and Gaston, 2002). Shoot presence/absence was recorded for all vascular plant species in each sub-quadrat, giving local frequency (the only practicable and objective measure of abundance in such a study) out of 4, 16, or 100 sub-quadrats respectively at the three scales. A soil sample c. 850 cm³ was taken from the centre of the 0.2×0.3 m quadrat at each site, for soil analysis.

The landscape-level distribution of a species at each spatial scale was defined as the proportion of all the quadrats at that scale in which the species occurred (Hanski et al., 1993). This can be seen as their beta niche, controlled by both the soil variates we measured, and also other unmeasured or unknown variates, affecting their frequency across the landscape. The abundance of a species at each scale was defined as the sub-quadrat frequency averaged over the quadrats at that scale in which the species occurred. We compared the two with linear correlation, because there was no reason to suppose one to be the independent and one the dependent variate, because the *a priori* shape of the relation was not clear, and because linear correlation is

capable of finding a strong positive correlation even when it is not quite linear.

Soil analysis

Soil pH was measured on a 1:1 soil:water mixture, water content by loss of weight on drying (80°C, 24 h), and organic content by loss of weight on ignition (500°C, 12 h). To measure soil fertility in each quadrat, a bioassay was used. Each soil sample was sieved to remove large stones. An equal part of washed sand was mixed in to ensure that the assay measured soil fertility and was not affected by impeded drainage, and the mixture was placed in a 10×10×12 cm pot. An aliquot of 0.023 g of *Agrostis capillaris* L. seed was sown in each pot. Pots were watered daily as required, and illuminated for 9 h day⁻¹ at 300 μmol m⁻² s⁻¹ of photosynthetically active light. The shoots were harvested after 14 weeks, dried (80°C, 46 h) and weighed.

Environmentally-restricted datasets

Spatial heterogeneity in resources has been suggested as a cause for the distribution/abundance correlation (Gaston, 1991). We therefore examined whether reduction of heterogeneity would decrease the strength of the relation. For each soil variable (pH, water, organic and fertility) a frequency distribution of the values was constructed. Sites with extreme values for each variable were removed to form a second dataset with restricted (see below) variability in soil characteristics. The restricted data ranges were chosen according to the distributions of each factor to match discontinuities as much as possible, and thus excluded a different range of values for each factor, i.e. for pH 5–6 (the original range was 4.67–6.90, in a bimodal distribution with seven outliers; quadrats from one mode were used in order to restrict the data set to one environment, thus 44% of the quadrats were excluded), for water content 30–50% of dry soil weight (the original range was 16–473%; the distribution was unimodal with many outliers, thus 39% of the most extreme quadrats were excluded), for organic matter 10–20% of dry soil weight (the original range was 9–57%; the distribution was unimodal with some outliers, excluding these outliers removed the most extreme 16% of quadrats) and for soil fertility 0.15–0.5 g pot⁻¹ of dry biomass (the original range was 0.083–0.967; the distribution was right skewed and slightly playkurtic with three extreme outliers, by excluding the extreme right hand end of the tail and the outliers, 36% of the quadrats were removed).

Table 1. Correlation coefficients (Pearson product-moment; r) between regional distribution and local abundance, with associated P values (n.s. = not significant, i.e. $P > 0.05$). Bracketed P values are those between 0.1 and 0.05, which are not interpreted as significant but are given for information.

Species	Ecological restriction	0.2×0.3 m scale		0.4×0.6 m scale		1×1.5 m scale	
		r	P	r	P	r	P
All	None	+0.11	n.s.	+0.25	0.024	+0.42	<0.0001
Native	None	-0.07	n.s.	+0.08	n.s.	+0.18	n.s.
Exotic	None	+0.46	(0.053)	+0.59	0.0062	+0.82	<0.0001
All	By soil pH	+0.41	<0.0014	+0.43	0.0002	+0.49	<0.0001
All	By soil water	+0.23	(0.085)	+0.39	0.0007	+0.53	<0.0001
All	By soil organic matter	+0.19	n.s.	+0.35	0.0019	+0.49	<0.0001
All	By soil fertility (bioassay)	+0.15	n.s.	+0.27	0.018	+0.33	0.0012

Results

Distribution/abundance relations were tested at the three spatial scales. In the unrestricted dataset (i.e. including all environmental variation), with all species and at the smallest scale (0.2×0.3 m) the relation was positive (Table 1). It was non-significant in a linear correlation, presumably because the relation was triangular: species with wide regional abundance and low mean local abundance did not occur (Fig. 2a). (No significance test was made for the triangular relation, because it would have been an *a posteriori* test).

At the 0.4×0.6 m scale, the triangular relation was less clear, and the linear positive relation was therefore stronger and significant (Table 1, Fig. 2b). At the 1×1.5 m scale the triangular effect was almost absent, and the linear correlation stronger again and highly significant (Table 1, Fig. 2c).

Among native species, although there tended to be a positive relationship between regional distribution and local abundance at the two larger scales, it was not significant (Table 1). In contrast, exotic species showed stronger positive distribution/abundance correlations than using all species; this was significant at the two largest scales used in spite of the considerably smaller number of exotic species (i.e., up to 24 exotic species depending on the scale; Table 1).

Restricting these analyses to habitats having less extreme resource conditions, and thus increasing environmental uniformity across sites, gave correlations between distribution and abundance that were almost without exception stronger than without restriction ('None' in Table 1). Restricting the analysis to soils which had moderate pH gave the most consistent effects, giving r values of 0.41 to 0.49, all of which were significant. Restricting by soil water content also had a large effect. In contrast, restricting to more uniform soil organic matter or soil fertility (by bioassay) gave correlations only marginally higher than in the 'None' restriction, and in one case lower. Over the four environmental factors, the increase in r was seen most

clearly at the smallest spatial scale (a mean increase of 0.14) and least at the largest (a mean increase of only 0.04).

Discussion

The distribution/abundance relation

In this study, the degree of correlation between species distribution and abundance (Table 1) and its shape (Fig. 2) depended on the spatial scale at which abundance was measured, with a weak and non-significant overall correlation (+0.11) at the smallest scale. This conflicts with the claims of Hanski *et al.* (1993) that a positive correlation will be found at all scales. There may be more sampling noise at a small scale: the frequency values 0–4 out of 4 sub-quadrats is a crude measure of abundance. There is also a rounding effect: at the largest scale a frequency of 100/100 = 100% in a particular quadrat is unlikely, but at the smallest scale a frequency of 4/4 = 100% could more readily be achieved. By the same argument, a score of 0/0 will more often be observed at the smallest scale, but by the calculations used in distribution/abundance studies such quadrats will not count towards the average abundance. This will give an upwards bias to frequencies at the smallest scale, which can be seen (Fig. 2). However, this cannot be a major effect, for with restriction by soil pH the relation was increased and strong enough to be detected above any noise (Table 1).

A major cause of low correlations was triangular relations, with a lack of wide-distribution/locally-sparse species. Many other workers have concluded that the proximal cause of the distribution/abundance relation is that the distribution is triangular, with no narrow-distribution/high-abundance species (Brown, 1984; Warren and Gaston, 1997; Gaston *et al.*, 1997), though the model of Hanski *et al.* (1993) encompassed species of this type. In this study, narrow-distribution/high-abundance species were common (Fig. 2), many

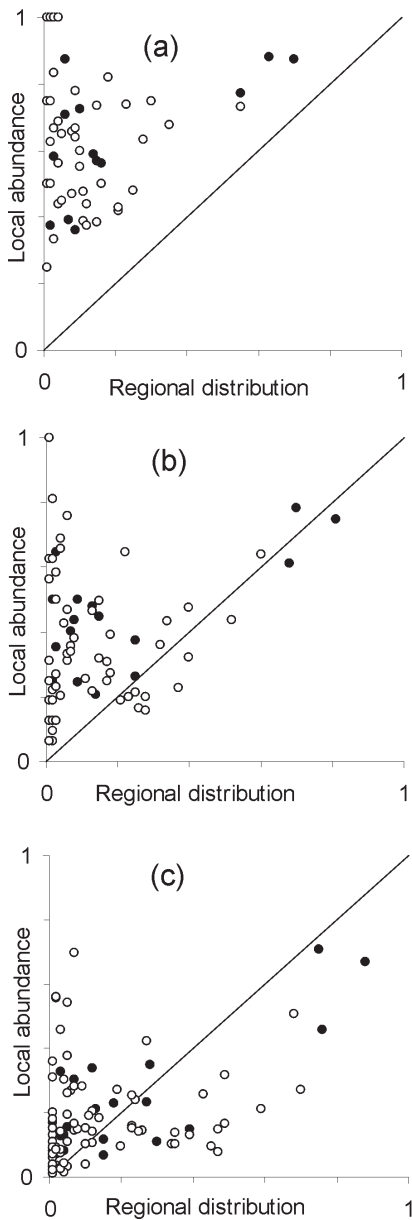


Figure 2. Relations between regional distribution (i.e. proportion of the sites occupied) and local abundance of a species at those sites in which it occurs (i.e. frequency in sub-quadrats). Sampling and analysis are at three sampling scales (i.e. sizes of spatial grain): (a) small quadrats 0.2×0.3 m; (b) intermediate-scale quadrats 0.4×0.6 m; and (c) large quadrats 1×1.5 m. The diagonal line connects minimum local-abundance/regional-distribution (0, 0) with maximum local-abundance/regional-distribution (1, 1). \circ = native species, \bullet = exotic species.

of them native. Thus, the relation is triangular the other way around from that described in previous work, with a severe lack of species with a wide distribution and low local abundance, especially at the smaller scales (Fig. 2a, b). Among the microcosms of Holt *et al.* (2002), the closest match in shape is between our small scale results (Fig. 2a) and their no-dispersal, non-interacting microcosms after eight weeks. This is surprising since the plant communities we were sampling are probably characterised by reasonable dispersal, considerable competition and a near-equilibrium state in that endogenous changes of species composition had essentially ceased.

Environmental and guild restriction

Restriction to an environmentally more homogenous subset increased distribution/abundance correlations at the two smaller scales (Table 1). This matches the results of Thompson *et al.* (1998), who found that at the landscape-level local abundance was not related to regional distribution, whereas within separate habitats correlations were common, and it also matches the prediction of Gaston *et al.* (1997) that the relation would be strongest in assemblages of species similar in their ecology. However, environmental restriction had little effect at the largest spatial scale (1×1.5 m), or even a negative effect in one case: restricted by soil fertility. This is certainly not a large scale in comparison with those used in some studies.

The lack of a correlation when using only the native guild, even though it comprised the majority of species, could be because the native vegetation component comprises remnants of formerly abundant species, persisting at low abundance over much of their distributions and on the way to local extinction. Other native species might have persisted at high abundance locally, in undisturbed sites, as Wilson (1989) suggested was the case in drier parts of New Zealand. In either case, the distribution/abundance relation would be weak or absent. In contrast, the exotic species are generally good colonisers. They have been favoured by the grazing of stock and lagomorphs, and in a small part of the area by aerial fertilization. If Boeken & Shackak (1998) are right that the distribution/abundance relation arises through community development, the present result would confirm that the exotic species have reached their equilibrium abundances.

Holt and Gaston (2003), working with bird data, questioned whether it was profitable in examining distribution/abundance relations to take into account the characteristics of the species. This seems to be an over-generalisation. We have found considerable differences between the native and exotic guilds. We have also found that the distribution/abundance relation changes when the chorology of the species is taken

into account by restricting the soil environmental range (Table 1).

Hypotheses

1. *Random placement*

Randomness is always impossible finally to prove or disprove. The increases in the strength of the distribution/abundance relation with environmental restriction are not incompatible with the Random-placement hypothesis. If a dataset comprises a number of subsets of quadrats with different species frequencies, the same effect would be seen under Random placement: higher correlations in each subset than overall. However, under such a model the overall correlation is weaker with larger samples (a larger number of individuals scattered at random), and in our data the correlations increase with quadrat size (i.e. including a larger number of individuals). Moreover, a random-placement model will give a correlation with a deficit of high-distribution/low-abundance species, as in our data, but also a lack of low-distribution/high-abundance species, which is not true of our data. Our conclusion is that the Random placement process is, at most, only part of the answer.

2. *Sampling error*

Animal ecologists have suggested that distribution/abundance correlations might be a sampling artefact (Bock and Ricklefs, 1983; Brown, 1984). This hardly applies to quadrat sampling with plants, where it is possible for diligent workers to observe all species in a 1×1.5 m quadrat (especially because there are relatively few seasonally-green species in the New Zealand flora). At the 0.2×0.3 m scale, where significant correlations were found with environmental restriction, species would be even harder to overlook. Moreover, increases in correlation when environmental restriction was applied are inexplicable in terms of a sampling artefact. Thus, we do not believe sampling artefacts are the explanation here. Krüger and McGavin (2000), working with insects, reached a similar conclusion.

3. *Niche width*

This family of explanations of the distribution/abundance relation operates in terms of the availability of resources (Brown, 1984; Gregory and Gaston 2000). Species that use a wide range of resource types will have a larger resource supply in one locality, and hence be locally abundant. They will also find suitable resources in many different sites. Gaston *et al.* (1997) suggested that this mechanism would not operate for a group of species that share a common resource base, but whilst most plants share requirements for

macronutrients, water and CO₂, species do differ in niche (Grime *et al.*, 1988). In the environmentally restricted analyses, there will be less variation in resource use, and so less opportunity for the Niche width mechanism to operate, but in fact our correlations tended to be stronger with environmental restriction at the two small scales. Krüger & McGavin (2000) found a similar situation to us — closer distribution/abundance relations when the resource base was restricted — and similarly concluded that the Niche width hypothesis was not the explanation for their data. Gregory and Gaston (2000) arrived at the same conclusion by a different route examining birds and mammal data: niche width was not correlated with distribution or abundance as the Niche width hypothesis implies it should be. Moreover, exotic species tend to be generalists (Morgan 1998), so the Niche width mechanism should not operate effectively with them, yet here the overall distribution/abundance relation is seen only with the exotics.

Care is needed here, because the Niche width hypothesis implies width in alpha niche — the range of resources that are used in one local community (Wilson 1999). It is not clear how it extends to the land-use and environmental variates used by Gregory and Gaston (2000) or to the soil characteristics that we used, which are really beta-niche differences.

4. *Demography*

Holt *et al.* (1997) indicated that their Demographic hypothesis for distribution/abundance relations would not operate if: (a) population regulation was density-dependent, or (b) the species differed in their environmental responses, or (c) there were differences in the frequency of habitats of different types. All three reservations are likely to apply to plant communities. Density-dependent population regulation must be almost ubiquitous, for a population without it will move to either extinction or infinite density. Conditions (b) and (c) would become less true with environmental restriction, which could explain the increased correlation with restriction seen at the smaller two scales, though not at the third scale (Table 1). Holt *et al.* (1997) suggested that under the Demographic hypothesis the relation would be weak or absent if species differed considerably in the 'sharpness' of their response to an environmental gradient (i.e. their beta niche width) or in their degree of density dependence. This would suggest a weaker relation for all species than for natives and exotics separately (especially since the exotics tend to be generalists), which is not the case (Table 1). The Demographic hypothesis does not seem to fit well.

5. Metapopulation dynamics

This hypothesis is based on greater colonisation chances for a species that has high local abundance and hence produces many propagules (Hanski, 1991; Hanski *et al.*, 1993). It will operate only when dispersal is effective. That is probably true for most of the native species because they have had centuries to disperse, though changes induced by land management may have altered their range, resulting in the weak relationship observed in this study. It could be true for the exotics if they had greater dispersal ability, as Richardson and Cowling (1992) found in South Africa and Gruberová *et al.* (2001) in central Europe. The species with wide distribution and high abundance should, under this theory, be species with effective dispersal (Gaston *et al.*, 1997), and that is true of at least the exotics in that category in our dataset. The Metapopulation model operates essentially within one environment, and if there are environmental differences within a metapopulation there are likely to be source and sink populations. This might explain the generally better correlations with environmental restrictions. The restriction that gave the greatest increase in the correlation, that of pH, produced at least a slight improvement at all three spatial scales, and this may have been because it excluded environmentally marginal sink populations for many of the species.

Gaston *et al.* (2000) dismissed metapopulation explanations for British birds. The concept of a metapopulation might be less realistic for plant species. Few studies have documented plant metapopulations, though this may be partly due to methodological problems and questions of definitions (Ehrlén and Eriksson, 2003). However, the Metapopulation dynamics hypothesis does fit the data in the present study better than the other hypotheses do. However, there is no reason to expect an effect, either way, of scale under the Metapopulation dynamics hypothesis, and the effect seen in the all-species analyses represents a conflict with this theory.

Conclusion

A significant positive relation between species distribution and local abundance was found at several spatial scales within the grassland landscape that we sampled. At smaller scales (0.2×0.3 and 0.4×0.6 m) the relation was enhanced with greater environmental homogeneity. The results show inconsistencies with the Random-placement, Sampling error, Niche-width and Demography hypotheses. The least conflict with the available evidence from this landscape is with the Metapopulation dynamics hypothesis. A clear verdict in favour of one hypothesis would be elegant, but the facts suggest that no single hypothesis is responsible for the distribution/abundance relation in this system,

as Eriksson and Jakobsson (1998) concluded for theirs. Moreover, field correlations are weak evidence for causes. Experimental determination of autecological tolerance and of within-community niche (e.g. Lloyd *et al.* 2002, 2003) would lead to a greater understanding of distribution/abundance relations.

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