Causes of the species–area relationship by trophic level in a field-based microecosystem

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Using a natural microecosystem, I test the contribution of the metapopulation effect to the species–area relationship, relative to that of the combined effects of habitat heterogeneity and sampling. The relative contributions were approximately equal, but with further relaxation of the fragmented community, the metapopulation effect is expected to increase. Predators had a greater slope to their species–area relationship than non-predators, and the habitat-plus-sampling effect was greater in predators than non-predators. This is the first attempt, to my knowledge, to quantify the causes of the species–area relationship.

Keywords: species–area relationship; conservation; extinction; metapopulations; island biogeography; microcosm

1. INTRODUCTION

The relationship between species richness and area sampled is one of the most fundamental and most studied problems in all of ecology. Typically, the relationship $S = cA^z$ provides a good model for the increase in species richness with habitat area (Rosenzweig 1995), where S is the number of species and A is the area. The value z describes the strength of the increase in species richness with area. There are three types of species–area relationship (Rosenzweig 1995; Holt *et al.* 1999): assessing species richness and sample area in nested samples within a defined region (type 1), comparing species richness and area among regions differing in area, such as islands in an archipelago (type 2), and measuring species richness in samples of fixed size, among regions differing in area (type 3) (see figure 1).

There are three well-known possible explanations for the species–area relationship (Connor & McCoy 1979): the sampling, habitat-heterogeneity and metapopulation-dynamic effects. As the area of samples increases, so too will the probability of finding a given species purely by chance (the sampling effect) and the probability of encountering more habitat types. Some species may be restricted to certain habitats. Other species may require more than one habitat type, for example habitats used by different life stages. Hence, the number of species should increase with the number of habitats sampled (the habitat-heterogeneity effect). Local mainland areas are likely to have higher colonization and lower extinction rates than comparable areas on islands (MacArthur & Wilson 1967; Holt 1993). Hence, we would expect to find more species per unit area as patch size increases (the metapopulation effect). We expect the type 1 relationship to be affected by the habitat-heterogeneity and sampling effects, the type 2 relationship by the habitat-heterogeneity, sampling and metapopulation effects, and the type 3 relationship by just the metapopulation effect (Holt 1993; Holt *et al.* 1999).

The relative importance of sampling, habitat heterogeneity and metapopulation dynamics as explanations for the species–area relationship is the subject of much debate (Nilsson *et al.* 1988; Hart & Horwitz 1991) and is the main focus of this paper. Previously, the combined impact of sampling and metapopulation effects has been estimated for species inhabiting islands in Sweden (Nilsson *et al.* 1988) assuming no habitat heterogeneity. To my knowledge, just two studies have attempted to isolate the metapopulation component of the species–area relationship. For plants inhabiting islands in New Zealand (Kelly *et al.* 1989), fixed-sized quadrats eliminated the sampling effect and two habitat types were used to eliminate habitat heterogeneity. In the second study (Westman 1983), the metapopulation effect was estimated to be zero.

After fragmentation, habitats undergo a process of community disassembly, or ‘relaxation’ (Diamond 1972), and the number of species to be lost in the future is the ‘extinction debt’ (Tilman *et al.* 1994). The metapopulation component of the z value is expected to increase over time from the mainland value to the island value.

Theory predicts that predators may be more susceptible than non-predators to extinction after habitat fragmentation (Diamond 1984; Schoener 1989), and hence z is predicted to be greater for predators than for non-predators. The simplest explanation is that the greater movement of predators means that larger connected areas (and hence the metapopulation effect) are more important to them. Some experiments have agreed with this prediction (Patterson 1984; Wright & Coleman 1993; Kruess & Tschamntke 1994; Burkey 1997; Gilbert *et al.* 1998), but others have not (Mikkelsen 1993). There are several theories that predict higher z -values at higher trophic levels. First, this follows from the ‘stacked specialist’ model (Holt *et al.* 1999), whereby species at a higher trophic level are present only if their prey at lower levels are present. Generalism can either strengthen or weaken the impact of trophic rank on z . Obligate generalism may strengthen the relationship, but opportunistic generalism may weaken it. If generalism is present, interspecific interactions may reduce variation in z -values among trophic levels. In a second theory, if population sizes decline with increasing

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Figure 1. Species–area relationships for (a) type 1, (b) type 2 and (c) type 3. Dark shading represents moss sampled for microarthropods and grey shading represents moss not sampled. The type 1 relationship is influenced by the habitat-heterogeneity and sampling effects, the type 2 relationship by the habitat-heterogeneity, sampling and metapopulation effects, and the type 3 relationship by the metapopulation effect.

trophic rank (perhaps for energetic reasons), higher-ranked species should be more prone to extinction on small islands. Third, if higher-ranked taxa generally have lower abundances than do lower-ranked taxa, sample-size effects should be more pronounced over a wider range of island sizes for higher-ranked taxa. There are some examples consistent with this prediction (Itamies 1983; Nilsson *et al.* 1988; Kruess & Tscharntke 1994; Schoener *et al.* 1995).

Conversely, there may be processes that *reduce* the effect of trophic rank on z (Holt *et al.* 1999). If increasing area reduces overall rates of predator extinction, prey populations may then be more likely to become extinct in larger areas owing to the abundance of predators. Alternatively, high consumer mobility should weaken the effects of trophic rank on the species–area relationship.

Here, I use a moss–microarthropod microecosystem to estimate the contributions of the sampling, habitat-heterogeneity and metapopulation effects to the species–area relationship, and to test whether the pattern varies with trophic level. Experimental tests of population-dynamic processes have often used laboratory microcosms owing to their tractability and short time-scales of change (e.g. Burkey 1997). The moss–microarthropod microecosystem has the great advantage of being a completely natural system that occurs in the field in both continuous and fragmented states. Thus, experimental fragmentation merely reproduces patterns that occur naturally. The effects of habitat fragmentation on the microarthropod populations are measurable after just six months (Gilbert *et al.* 1998; Gonzalez *et al.* 1998; Gonzalez & Chaneton 2002). Relaxation of the microarthropod community has been observed over a year (Gonzalez 2000). There is some

evidence that z -values vary with fragmentation (Gonzalez 2000), and that predators suffer greater rates of extinction than do non-predators (Gilbert *et al.* 1998). In addition, connecting patches of moss habitat by moss ‘corridors’ slows the rate of species extinction (Gilbert *et al.* 1998; Gonzalez *et al.* 1998), possibly by the ‘rescue effect’, highlighting the relevance of the metapopulation effect in this study. To my knowledge, this is the first attempt to quantify the causes of the species–area relationship.

2. MATERIAL AND METHODS

Eight replicate moss (*Isothecium myosuroides* (Brid.) var. *myosuroides*) landscapes growing on eight large boulders were chosen in a randomized block design at a site in Snowdonia (UK, OS map reference SK 625507). Each replicate comprised four treatments: four circular islands each of area 39 cm² (one unit of area); two islands each of area 78 cm² (two units); one island of 117 cm² (three units); and one island of 156 cm² (four units) (figure 1). Treatments were placed in a random order on boulders each large enough to accommodate one experimental block.

Treatments were created in June 2001 by cutting around the edge of cardboard templates using a scalpel, keeping a minimum distance of 10 cm between the islands (Gilbert *et al.* 1998; Gonzalez *et al.* 1998). Fragments were isolated by removing the moss from around the templates, leaving them in a ‘sea’ of bare rock, considered relatively inhospitable to the microarthropods. Six months later (as in Gilbert *et al.* 1998), the moss was removed from the rocks in layers of one unit of area (figure 1), each patch was left in a separate Tullgren funnel for 48 h, and the emerging microarthropods were collected in an alcohol–glycerol–water (7 : 2 : 1) mixture. All moss patches were first cut into pieces of

similar size and shape, to ensure similar extraction efficiencies. The microarthropods were sorted into morphospecies (Krantz 1978) and identified with help from relevant experts (see Acknowledgements and electronic Appendix A). In the rest of this paper, I use the term ‘species’ to refer to these morphospecies.

Species–area relationships were analysed by separately comparing the species richness of all microarthropods combined, the predatory and non-predatory mites among the four patch areas (figure 1*a–c*). In all cases, log-transformed response variables were analysed using a linear mixed-effects maximum-likelihood model of log(area) and block (a random factor of boulders selected from the population of suitable boulders), using the package R (Ihaka & Gentleman 1996; Crawley 2002). In separate analyses, patch area was included separately as a factor, and then as a covariate, to test for nonlinearity. The significance of predictor variables was assessed by deviance increase following deletion from the minimal adequate model, distributed as χ^2 . The constancy of the model variance was checked by inspection of the residual plots.

I tested for the presence of a particular interaction based on the following derivation. Using subscripts 1, 2 and 3 to denote the three types of species–area relationship (SA) as

$$SA_1 = f(H, S), SA_3 = f(M)$$

and

$$SA_2 = f(H, S, M),$$

then it seems reasonable to suppose that SA_2 might contain an interaction term, thus

$$SA_2 = f(H, S, M) = f(H, S) + f(M) + f(H, S) \cdot f(M),$$

where H is the effect of habitat heterogeneity, S is the sampling effect and M is the metapopulation effect, and therefore I tested for the presence of an interaction in the z -values

$$z_2 = z_1 + z_3 + (z_1 z_3).$$

The relative magnitudes of the metapopulation effect and the sum of the sampling, habitat-heterogeneity and metapopulation effects were estimated for all microarthropods combined, predatory mites and non-predatory mites, by 10 000 simulations of the quantity

$$\frac{\bar{z}_3}{\bar{z}_1 + \bar{z}_3},$$

where $\bar{z}_1$ and $\bar{z}_3$ are the estimated mean z values of the types 1 and 3 species–area relationships, respectively, and are asymptotically normally distributed, by the central limit theorem. The denominator was chosen as $\bar{z}_1 + \bar{z}_3$ and not as $\bar{z}_2$, because this might also contain an interaction term, as shown.

3. RESULTS

A total of 40 000 microarthropod individuals was recorded, mostly Acari (44%, only adults included) and Collembola (55%, all non-predatory). The Acari were Cryptostigmata (53%, non-predatory), Mesostigmata (2%, predatory) and Prostigmata (45%, predatory). There were 42 mite morphospecies (at least 22 of which probably consisted of a single species, unique to that morphospecies), nine Collembola morphospecies (at least four of which were probably monospecific) and 18 other

morphospecies (mostly beetles, spiders, centipedes, millipedes and pseudoscorpions). On average, over all treatments and blocks, per unit area of moss, there were 92 adult Cryptostigmata individuals of eight species, four adult Mesostigmata individuals of two species, 71 Prostigmata individuals of two species, 205 Collembola individuals of three species, and two other microarthropod individuals of two species.

For all microarthropods combined and for both trophic levels, the z -values for the metapopulation effect and the sampling and habitat-heterogeneity effects combined were significantly greater than 0 (table 1 and figure 2). The sum of the type 1 and type 3 slopes is not significantly different from the type 2 slope (table 2). The differences in slopes between the type 2 and type 1 and the type 2 and type 3 relationships are significant (standardized normal statistic = 2.69, $p < 0.005$ and 2.93, $p < 0.005$, respectively), but the difference in slope between the type 1 and type 3 relationships is not significant (standardized normal statistic = 1.26, $p > 0.05$).

For all three kinds of species–area relationship, the z -value for predators was greater than that for non-predators, significantly so for type 1 (figure 3; suggesting that the predatory mites are more affected by the combination of the habitat-heterogeneity and sampling effects than are the non-predatory mites), and close to significance for type 2.

The z -values for type 1 + type 3 are not significantly different from those for type 2 (table 2), and hence I conclude that the interaction term (see § 2) is absent. The ratios of the metapopulation effect to the total effect are not significantly different among total microarthropods, predators and non-predators (table 2).

4. DISCUSSION

The estimated values of z are in the region of 0.25, as found in many theoretical and field studies (Connor & McCoy 1979; Rosenzweig 1995), and for the equivalent type 2 species–area relationship the x -value is greater than, but not-significantly different from, the z -value found in a similar moss–microarthropod microcosm (Gonzalez 2000). Both the metapopulation effect and the combination of the habitat-heterogeneity and sampling effects were significantly greater than 0.

The standard form of the species–area relationship generally seems to fit the data well, with only limited evidence of nonlinearity (see table 1). The ratio of the metapopulation effect to the habitat-heterogeneity and sampling effects was greater for the non-predatory mites (65% : 35%) than for the predatory mites (43% : 57%), suggesting that the predatory mites are affected proportionally more by the combination of the habitat-heterogeneity and sampling effects, or, conversely, that the non-predatory mites are affected proportionally more by the metapopulation effect. However, these proportions do not differ significantly, either owing to a lack of sufficient statistical power, or because there is genuinely no difference, and neither do they differ significantly from 50% : 50%. Hence, it appears that the metapopulation effect is approximately equal to the combination of the habitat-heterogeneity and sampling effects. It is likely that the metapopulation effect observed in this study will

Table 1. Comparison of z -values and suitabilities of the relationship $S = cA^z$, as measured by the linearity of $\log(\text{species richness})$ versus $\log(\text{moss patch area})$ by species–area relationship type and by trophic rank. (H, habitat heterogeneity; S, sampling; M, metapopulation effects on the species–area relationship. All z -values were significant as assessed by deletion of the patch-size covariate from the minimal adequate model.)

species–area relationship	cause	total microarthropod species			predatory mite species			non-predatory mite species		
		mean z (s.e.)	linearity		mean z (s.e.)	linearity		mean z (s.e.)	linearity	probability ($z_{\text{predator}} = z_{\text{non-predator}}$)
type 1	H,S	0.224 (0.017)	linear		0.296 (0.068)	linear		0.096 (0.017)	linear	$p < 0.01$
type 2	H,S,M	0.381 (0.056)	linear		0.489 (0.110)	nonlinear, $\chi^2_1 = 6.42$, $p < 0.05$		0.328 (0.055)	linear	$0.05 < p < 0.10$
type 3	M	0.151 (0.055)	nonlinear, $\chi^2_1 = 6.23$, $p < 0.05$		0.224 (0.116)	linear		0.178 (0.054)	linear	$p > 0.05$

Figure 2. Plot of $\ln(\text{total microarthropod species})$ versus $\ln(\text{moss patch area})$ after the statistical block effect has been removed. Type 1 species–area relationship data points are shown by filled circles, type 2 points by open circles shifted slightly to the left for clarity, and type 3 points by triangles shifted slightly to the right. The type 1 relationship is affected by the habitat-heterogeneity and sampling (H,S) effects, the type 3 relationship by the metapopulation (M) effect, and the type 2 relationship by all three (H,S,M) effects. All three slopes are significantly greater than 0. Note that the sampling regime (figure 1) dictates that: the type 2 and type 3 regression lines should intersect at the smallest patch size; the type 1 and type 2 lines should intersect at the largest patch size; and the type 1 value at the smallest size should equal the type 3 value at the largest size.

increase after six months owing to community relaxation, and may eventually be significantly greater than the habitat-heterogeneity and sampling effects combined.

As predicted by theory (Holt *et al.* 1999), I found evidence that z is greater for predators than for non-predators for the types 1 and 2 relationships. This agrees with many (Itamies 1983; Nilsson *et al.* 1988; Kruess & Tschardt 1994; Schoener *et al.* 1995), but not all (Mikkelsen 1993) empirical studies. This implies that predatory mites were affected more by the combination of the habitat-heterogeneity and sampling effects, which in turn suggests that they may be more habitat specific or require a greater range of habitats. However, contrary to theory, predatory and non-predatory species were equally affected by the metapopulation effect.

I assumed that the minimum inter-patch distance of 10 cm created at the beginning of the experiment was sufficient to prevent high rates of dispersal between moss fragments, as a gap of 5 cm apparently represents a substantial dispersal barrier for these organisms (Gonzalez *et al.* 1998). However, dispersal is one of the least known aspects of the biology of microarthropods (Ojala & Huhta 2001). A high rate of microarthropod dispersal across the ‘sea’ of bare rock would reduce or abolish the metapopulation effect and hence the value of z for the type 3 species–area relationship. However, I found that the z -value for this relationship was significantly greater than 0, which

Table 2. Analysis of the interaction term and the relative value of the metapopulation effect compared with the habitat-heterogeneity and sampling effects combined, by microarthropod grouping.

	$\bar{z}_1 + \bar{z}_3$ ($\pm$ s.e.)	difference from $\bar{z}_2 = \bar{z}_1 + \bar{z}_3 + (\bar{z}_1 \bar{z}_3)$ (see table 1)	$\frac{\bar{z}_3}{\bar{z}_1 + \bar{z}_3}$	95% confidence limits
all microarthropods	0.375 ± 0.058	standardized normal statistic = -0.07 , $p > 0.05$	0.40	(0.16–0.54)
predatory mites	0.520 ± 0.134	standardized normal statistic = 0.18 , $p > 0.05$	0.43	(-0.01 – 0.66)
non-predatory mites	0.274 ± 0.057	standardized normal statistic = -0.68 , $p > 0.05$	0.65	(0.42 – 0.78)

Figure 3. Plot of $\ln(\text{type 1 species richness})$ versus $\ln(\text{area})$ for predatory and non-predatory mites, after the statistical block effect has been removed. The type 1 species–area relationship is affected by the habitat-heterogeneity and sampling effects. The predatory-mite slope is significantly greater than the non-predatory-mite slope ($p < 0.01$).

suggests that dispersal across the rock was at least restricted.

Despite their small size, microarthropods actually have quite long generation times relative to the six-month duration of this experiment. For example, *Cryptostigmata* mites probably live several months in the field (Norton 1994). This suggests that the effect of demographic stochasticity in this study is probably limited. However, mortality resulting from extreme weather conditions may depend on factors such as aspect and exposure of the moss-covered boulders. Populations particularly adversely affected may be rescued from extinction by neighbouring communities. Hence, environmental stochasticity and the metapopulation effect may still be anticipated.

There are difficulties in quantifying the way the environment varies and relating this to the number of species (Williamson 1988), and it is also difficult to gauge the degree of microarthropod habitat heterogeneity in the moss. Despite using just one species of moss, on the micro-scale there may be differences in microclimate among the patches owing to differences in the contours and aspects of the boulders (Alpert 1991). The

habitat-heterogeneity effect depends on the degree of habitat specialization of the microarthropods, and may depend on the ratio of the area of the region sampled to the size of the organism. Species may require a range of different habitats (e.g. habitats used by different life stages, or for oviposition by gravid females), and hence will be found only in moss patches that encompass this range of habitats, which is perhaps the cause of the generally highly significant block effect. It is very difficult to separate the habitat-heterogeneity and sampling effects, but there is no evidence that moss wetness varies within my moss patches (M. Hoyle, unpublished data), and hence I discount variation in moisture as a factor contributing to habitat heterogeneity in this study. If there is no heterogeneity of habitats among the moss patches in my experiment, the type 1 relationship would then be entirely caused by sampling effects.

The species–area relationship is known to obey different scaling rules over different spatial scales (Palmer & White 1994; Crawley & Harral 2001), and may be triphasic.

At very local spatial scales, the species–area relationship is sensitive to the local commonness and rarity of species. However, on regional to sub-continental spatial scales, the rate of encounter of new species depends much less on relative species abundance, and more on rates of speciation, dispersal and extinction. At very large intercontinental scales, species accumulate faster as major barriers to dispersal are crossed—barriers between different biogeographical realms with long-separate evolutionary histories (Rosenzweig 1995).

Despite its small scale (cf. Lawton 1999), this experiment can be viewed as a model of population processes operating at the larger scale of the nature reserve.

The author thanks R. Norton, P. Martinez, H. Klompen, M. Skorupski and W. Welbourn for mite identification, B. Cave for Collembola identification, and A. Smith for moss identification. The author also thanks A. Sylvester and M. Roberts for help with microarthropod counting, and F. Gilbert and two anonymous referees for comments on an earlier version of the paper. The author was supported by a NERC studentship.

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