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Vascular plant and epiphytic lichen communities in Canadian aspen parkland: scale-dependence of species-area relationships

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Abstract: Within-community species-area relationships were examined for vascular plants and epiphytic lichens on *Populus* spp within 100 treed patches in an area of less than 4 km^2 in the aspen parkland of south-central Alberta, Canada. Both plants and lichens were sampled on three scales (patch-scale and two within-patch scales). This study is one of the few to demonstrate scale-dependent species-area relationships at a small scale and highlights the importance of multi-scale sampling in ecology. At the larger patch scale, the relationship between plant species richness and area was positive for both the full plant dataset and the forest habitat specialist subset. For lichens, the species-area relationships were positive at all scales. However, for plants, at small scales, the species-area relationship was negative for all plants, but non-significant for forest habitat specialist species when considered separately. This difference reflects the different mechanisms behind the species-area relationships for the two taxa. For vascular plants, small-scale species richness decreased with patch size due to an edge effect within patches. The species-area relationships for the forest habitat specialist species were unaffected by this edge effect because these species were more common in larger patches. The distribution of lichens within patches was not significantly different from random. Therefore, the positive species-area relationships observed for this taxon reflect a passive sampling effect; where there are more individuals, there are more species.

Abbreviation: GLIM – Generalised Linear Models.

Nomenclature: Moss (1983) for vascular plants and Bird (1970), Tomson (1984), Johnson et al. (1995), and Vitt et al. (1998) for epiphytic lichens.

Introduction

One of the oldest and best-known relationships in community ecology is the change in species richness with area sampled (Arrhenius 1921, Gleason 1922, Hart and Horwitz 1991, Lomolino 2000). However, explanations for the species-area relationship are not always simple because there are a number of different factors and processes that influence species richness (Rosenzweig 1995, McGuiness 2000). In order to examine the possible causes of a species-area relationship for a given community, first the form or shape of the relationship must be determined. Larger areas contain more species than smaller areas in the same habitat and, often, published relationships show that species richness (S) increases with area (A) such that $S = CA^z$, where C and z are constants that determine the slope of the curve (e.g., MacArthur and Wilson 1967). Species-area relationships for different systems often differ in both their rate of increase in species richness (z) with area and whether or not richness reaches an asymptote at larger areas (e.g., Rosenzweig 1995). In addition, other functions such as linear and logistic may be fit to species-area curves (Lomolino 2000). Which of these functions can be best-fit to the curve may tell us something about the biology of the system in question.

The methods of sampling and relationship construction also affect the form of the species-area relationship. The slope of the power function relationship is affected by whether the samples come from island communities or from samples within a defined mainland area. Curves constructed from island data usually exhibit a greater rate of increase in species richness with area (higher z) than do those constructed from mainland samples (Rosenzweig 1995). However, the exact form of the species-area relationship depends on which factors determine the number of species in the community and how those factors vary with area.

The species-area relationship is thought to result from at least two different sets of processes: (1) the ‘passive sampling effect’ and (2) habitat heterogeneity. The passive sampling effect is the situation where the number of individuals within the sample area increases with area and therefore, so does species richness because as more individuals are encountered, the probability of encountering new species also increases (Coleman et al. 1982). Similarly, when the number of different habitats sampled increases, as often occurs with increasing area, the number of species encountered also tends to increase because individual species usually have different probabilities of occurring in different habitats (Rosenzweig 1995, Scheiner et al. 2000).

The effect of sampling scale on our perception of patterns in species richness is profound because the relative importance of different ecological processes in creating patterns in communities varies with spatial scale (Shmida and Wilson 1985, Auerbach and Shmida 1987, Huston 1999). The ‘appropriate’ sampling scale depends on the taxon under study because different taxa (e.g., birds and mammals), and even individual species within different families or genera, respond differently to processes at changing scales (Addicott et al. 1987, Levin 1992).

A recent focus in the study of ecological patterns is how the species-area relationship changes with sampling scale and how this may affect our interpretation of relationships between diversity with a third variable, such as productivity (Waide et al. 1999, Scheiner et al. 2000). A number of studies predict that species-area relationships will take different forms at different scales (MacNally and Watson 1997, McGuinness 2000) and several other studies show this to be the case (Palmer and White 1994, Scheiner et al. 2000). However, the interpretation of these scale-dependent relationships is not easy due to the multitude of factors that may underlie species richness at different scales (McGuinness 2000).

This paper tests for scale-dependence of species-area relationships for vascular plants and epiphytic lichens that were both sampled within a set of 100 patches dominated by *Populus tremuloides* (aspen) trees at several spatial scales. Examining species-area relationships is rarely conducted on such a small scale and not often for different taxa within the same environment. Specifically, this study asks: (1) what are the forms of the species-area relationships for vascular plants and epiphytic lichens in aspen patches within a small area of the aspen parkland, (2) are these species-area relationships scale-dependent, (3) what are the possible underlying causes of these relationships, and (4) what are the similarities and differences between the species-area curves for the two taxa?

Methods

Study system

Data collection took place in the “groveland” (*sensu* Strong and Leggat 1992) at the southern limit of the aspen parkland ecoregion within the Rumsey Ecological Reserve (51.8^{o}N 122.6^{o}W), 225 km southeast of Edmonton, south-central Alberta, in western Canada. In this system, which is predominantly fescue prairie grassland (dominated by *Festuca hallii*), patches of aspen trees occur on the moister slopes that surround wet depressions. *Populus balsamifera* also occurs in these patches, but at a lower frequency. There are scattered patches of shrubs around the depression edges and throughout the prairie that are mainly composed of *Salix* spp, *Symphoricarpos occidentalis*, and *Rosa* spp. Sampling of vascular plants and epiphytic lichens took place within the aspen patches.

These two taxa differ in at least two sets of important ecological attributes. First, epiphytic lichens are more isolated in the patches because the habitat between patches is largely uninhabitable grassland, although, some species can occur on the shrub species scattered throughout the prairie. This is not the case for the vascular plants, many of which occur in the surrounding prairie, wet depressions, and shrub patches. Rather, many of these species found in the aspen patches are specialists in these other habitat types rather than in the aspen patches themselves. Therefore, a set of 30 species was identified as being forest habitat specialists, from the available literature (Johnson et al. 1995, Moss 1983), out of the 133 total vascular plants found in the aspen patches within this area. These species are considered separately as ‘forest specialists’ and are considered to be relatively well isolated within the patches.

Second, the reproductive and dispersal characteristics of the two taxa differ greatly. The epiphytic lichens reproduce and disperse primarily vegetatively via extremely light asexual propagules (soredia or isidia). Unfortunately, beyond this, little is known about the relative dispersal abilities of the different epiphytic lichen species in this area. More is known about the dispersal abilities of vascular plants, but much of the detailed knowledge is limited to plants of agricultural interest rather than the many native species of the aspen parkland that are considered here. The vascular plants have a wide range of dispersal modes and abilities. Many plants reproduce vegetatively by stolons or suckers, whereas others produce varying amounts and sizes of seed.

Table 1. A list of the environmental variables and spatial data recorded for all 100 patches within which species data were recorded.

Environmental variables recorded at the patch scale
Area (m^2) and perimeter (m)
Presence/absence of deadfall within patch
Presence/absence of adjacent willow patch
Presence/absence of adjacent depression
Relative animal use (scale: no use, little use, medium use, high use)
Mean percent canopy cover within the patch
Number of different substrate types per patch (forest floor, tree mound, animal mound, animal trail, willow mound)
X, Y position of patch centre relative to all other patch centres

Data collection

Species richness of vascular plants and epiphytic lichens was recorded in all the 100 aspen-dominated patches that occurred in an area of less than 4 km^2. This area was selected because of the large number of aspen patches with well-delimited edges that varied widely in area from 242 m^2 to 3,908 m^2 (Figure 1). The species richness of plants and lichens was measured at three different scales. For plants, richness was measured at the entire patch scale, at the 1.5 x 1.5 m plot scale within patches, and the 0.5 x 0.5 m quadrat scale within plots. For lichens, richness was measured at the patch scale, the tree stem scale within patches, and the 0.5 m section scale on tree stems. A range of environmental variables and the position of each patch relative to all other patches in space were recorded (Table 1).

For sampling vascular plants, a stratified-random sampling scheme was employed where one 1.5 x 1.5 m plot was placed randomly within every 15 x 15 m area of patch. Each plot was established at least 2 m away from the patch edge. Each of these plots was made up of a 3 x 3 grid of 0.5 x 0.5 m quadrats. A total of 256 plots were established within the 100 patches (2,304 quadrats); close to half the patches were small and contained only one plot, however, there were some that were very large and contained up to 14 plots. The area of each patch not sampled within plots was systematically searched and the presence of all species recorded to obtain a total patch species richness.

Species richness of epiphytic lichens on aspen stems within the 100 patches was recorded on the five aspen stems greater than 5 cm DBH that were closest to each vegetation plot. Each stem was divided into north-facing and south-facing sides and each side was divided up into four, 0.5 m height sections up to 2 m. A total of 1,272 stems were sampled in this manner, meaning that lichen species richness for 10,176 stem sections was obtained overall. Preliminary sampling indicated that sampling up to 2 m gave a good representation of total stem species richness. The remaining trees in each patch were searched for all lichen species to obtain a total patch species richness. One patch of the 100 had no stems greater than 5 cm DBH, thus only a total number of lichen species was obtained for this patch.

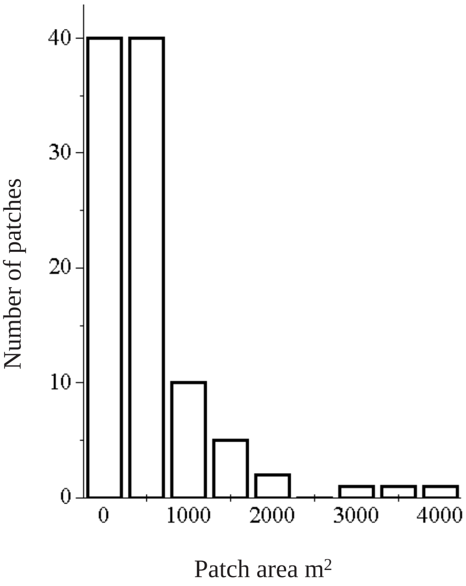

Figure 1. Histogram showing the frequency distribution of sampled patch areas (N = 100).

Data analysis

To examine the form of the species-area relationships for the three datasets (all vascular plants, forest specialists, and epiphytic lichens) first, scatterplots were created by graphing patch species richness against area. Non-linear regression was used to determine the function of best fit to each of the relationships. Second, to examine the scale-dependence of these species-area relationships for the three datasets, the mean small-scale species richness (i.e., the mean plot, quadrat, tree, or section richness) for patches was plotted against patch area. Simple linear regression of the log-transformed variables was used to determine the direction, strength, and significance of these relationships.

In order to determine whether or not a given species-area relationship differs from what would be expected if species were randomly distributed among sites, we need to test the passive sampling hypothesis. This means testing two different assumptions (1) that individuals occur at a site with a probability proportional to site area and (2) that individuals are distributed on islands randomly and independently (Gotelli and Graves 1996). In other words, under this hypothesis, larger sites will contain more species simply because there is a greater chance that individuals will colonise them (McGuinness 2000). A test of this hypothesis described by Simberloff and Gotelli (1984) was used for the vascular plant, forest specialist, and lichen species-area relationships in which each occurrence of each species is taken and randomly reassigned to a site with a probability based on site area (Gotelli and Graves 1996, Simberloff and Gotelli 1984). The expected number of species per site was then calculated. This was repeated 1000 times and a range of expected numbers of species per site was obtained. The observed richness for each site was compared to this and determined to be different (either more or less species rich than expected) if it fell outside the range. The passive sampling hypothesis was rejected if the observed richness of more than 33% of sites fell outside the range of expected values (Simberloff and Gotelli 1984).

Generalised linear models (GLIM) in the program S-PLUS Version 4.0 for Windows (Mathsoft 1997) were used to relate the species richness of plants and lichens at the patch scale to the recorded environmental and spatial variables (listed in Table 1). For comparison, both patch perimeter and patch shape, which was calculated as the perimeter to area ratio, were used as independent variables in the models in addition to area. Area was related to the other patch scale environmental and spatial variables using GLIM.

Results

In the 100 aspen patches, 133 vascular plant species and 27 epiphytic lichen species were recorded in total. Literature sources were used to identify 30 of the 133 vascular plant species as forest habitat specialists (Moss 1983, Johnson et al. 1995).

When the species-area relationships were constructed, patch species richness increased with patch area for all three datasets (Fig. 2a, d, g). For these three relationships, the power function ($S = CA^z$) fit the species-area relationships better than the Monod function (Table 2).

For all vascular plants, the mean number of species at the plot scale decreased significantly with increasing patch area (Table 3, Fig. 2b). This means that plots within larger patches contained fewer species on average than those in smaller patches did. At the quadrat scale, the relationship between richness and patch area was negative, but not significantly so (Table 3, Fig. 2c). However, fur-

Table 2. Parameter estimates and R^2 values for two different functions fitting the relationships between patch area and patch species richness for the three datasets. All *P*-values were less than 0.001 and N = 100 for all datasets. Monod function: $y=Cx/(1+Ax)$. Power function: $y=Cx^z$.

Dataset	Function	Parameters	Parameters	R^2
All vascular plants	Monod	C=0.592	A=0.011	0.388
	power	C=9.685	z=0.240	0.582
Forest habitat vascular plants	Monod	C=0.028	A=0.002	0.461
	power	C=0.862	z=0.344	0.564
Epiphytic lichens	Monod	C=0.564	A=0.028	0.414
	power	C=7.937	z=0.134	0.546

Table 3. Results from simple linear regression of the mean number of species (S) per plot and per quadrat of forest plants and all vascular plants and the mean number of epiphytic lichen species per tree and per section in patches against log-transformed patch area. All richness datasets were log-transformed. The sign indicates whether richness increased (+) or decreased (-) with patch area.

Dependent	R^2	Sign	*P*
Mean plot plant S	0.05	-	**<0.05**
Mean quadrat plant S	0.04	-	0.058
Mean plot forest S	0.01	+	0.317
Mean quadrat forest S	0.01	+	0.229
Mean tree lichen S	0.21	+	**<0.0001**
Mean section lichen S	0.28	+	**<0.0001**

ther analysis of these data presented elsewhere, shows that when variation in species richness due to habitat heterogeneity variables is removed, there is a significantly negative relationship between species richness and area at these smaller scales (Buckley 2001, Buckley 2002). For forest specialists there was no significant relationship between the mean number of species at the smaller scales (quadrat and plot) and patch area (Table 3, Fig. 2e, f). For epiphytic lichens, the mean number of species at the smaller scales (section and tree) increased significantly with increasing patch area (Table 3, Fig. 2h, i).

The passive sampling hypothesis tested using Simberloff and Gotelli's (1984) method was rejected for the vascular plant dataset. For this dataset, smaller patches had higher species richness than expected and larger patches had lower species richness than expected by chance. The passive sampling hypothesis was not rejected for the forest specialist dataset or the lichen dataset. For these datasets, the species richness of more than 66% of patches fell well within the expected richness values.

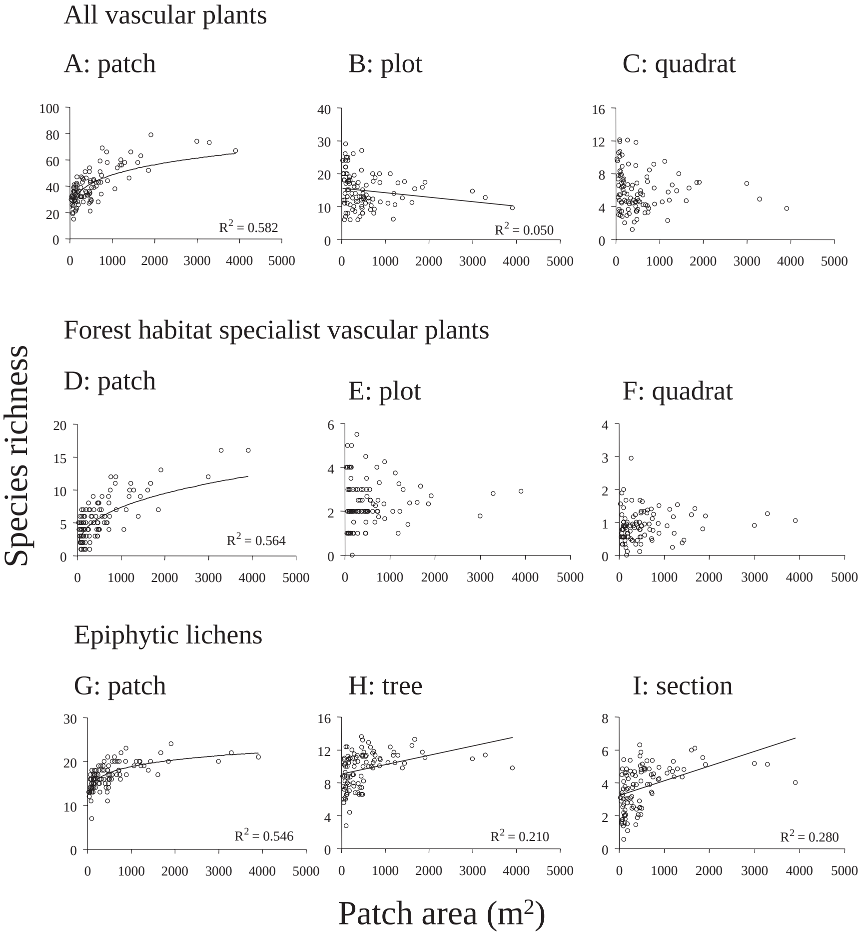

Figure 2. Scatterplots showing relationships between species richness and site area for (A) all vascular plants in patches, (B) the mean number of all vascular plants in plots (C) the mean number of all vascular plants in quadrats, (D) the number of forest habitat specialist vascular plants in patches, (E) the mean number of forest specialists in 1.5 x 1.5 m plots, (F) the mean number of forest specialists in 0.5 x 0.5 m quadrats, (G) the number of lichen species in patches, (H) the mean number of lichen species on aspen stems, and (I) the mean number of lichen species in 0.5m height sections on aspen stems. Statistically significant best-fit curves with their associated R^2 values are shown.

Table 4. Results from stepwise multiple linear regression using generalised linear models (assuming a Poisson error distribution) of the number of species (S) per site of all vascular plants, forest habitat specialist vascular plants, and epiphytic lichens against environmental predictors. Only those variables that were significant at $P<0.05$ were included in the models.

Dependent	N	Predictor	R^2	Sign	***P***
Plant S	100	Log-transformed patch perimeter	0.629	+	<0.00001
		Absence of deadfall	0.052	-	<0.00001
		Mean % canopy cover within patch	0.060	-	<0.00001
		Total =	**0.741**		
Forest S	100	Log-transformed patch perimeter	0.581	+	<0.00001
		Absence of adjacent depression	0.063	-	0.0027
		Total =	**0.644**		
Lichen S	100	Log-transformed patch perimeter	**0.531**	+	<0.00001

Table 5. Results from stepwise multiple linear regression using generalised linear models (assuming a Gaussian error distribution) of log-transformed patch area against patch-scale environmental predictors. Only those variables that were significant at $P<0.05$ were included in the models. Patch area was log-transformed. The sign of the coefficient is not given for factors with more than two levels.

Dependent	Predictor	R^2	Sign	*P*
Patch area	Absence of deadfall	0.350	-	<0.00001
	Relative animal use	0.063		0.021
	Total =	**0.413**		

For the three datasets, the best predictor of the number of species per patch was patch perimeter; patches with longer edge contained more species (Table 4). Obviously, patch perimeter is highly positively correlated with patch area. Patch shape significantly predicted species richness, but did not enter any of the models ahead of the other area variables. For the vascular plant and forest plant datasets, the amount of variance in species richness explained by the models was higher than that explained by the power functions alone. For lichen richness, patch perimeter was the only significant predictor. The other variables that significantly predicted increasing vascular plant richness were habitat heterogeneity variables: the presence of deadfall within a patch or an adjacent depression and lower mean percent canopy cover within the patch (higher light levels). Similarly, forest specialist richness, the number of species was also negatively related to the absence of an adjacent depression, meaning that more forest specialists were found in patches that were likely to have higher soil moisture levels because they were adjacent to a depression.

The environmental variables that were most strongly related to patch area were the habitat heterogeneity variables; absence of deadfall within the patch and relative animal use of the patch (Table 5). Larger patches were more likely to contain deadfall and have higher animal use.

Discussion

This study shows first, for all three datasets (vascular plants, forest habitat specialist plants, and epiphytic lichens), that species richness within aspen patches increased with patch area. Second, it shows that for all vascular plants this positive species-area relationship is scale-dependent. At the patch scale the relationship is positive, but it becomes negative at the within-patch scale. This was not the case for the forest habitat specialist or the epiphytic lichen datasets. These results are discussed in detail below.

Species-area relationships at the patch scale

Habitat heterogeneity appeared to be the most important variable underlying the positive species-area relationship for vascular plants. The fact that the passive sampling hypothesis was rejected for this dataset shows that species richness of patches is non-random. In addition, plant species richness was predicted by patch area and the presence of deadfall and the mean canopy cover within the patch. Many of the vascular plants encountered in this study have specific habitat preferences (Moss 1983, Johnson et al. 1995). Further, larger patches were more heterogeneous: they were more likely to contain deadfall and were more likely to have greater animal use, both of which provide a greater variety in light, temperature and moisture conditions (Table 5). As patches become larger, they contain both 'edge' habitat, which gets more light and therefore tends to be drier with more grasses and other typically prairie species, and 'interior' habitat, which is darker, moister, and supports fewer prairie species and more forest habitat specialist species. Small patches consist only of 'edge' habitat. This greater variety of habitat conditions in larger patches allowed more species to coexist. This is not surprising as it has been shown many times that where the species in a community have specific habitat preferences and the greater the habitat heterogeneity, the more species-rich the community (e.g., see review in Huston 1994).

For the forest habitat specialist vascular plants, the passive sampling hypothesis was not rejected for this dataset, so species richness within patches was probably not different from that of random expectation.However, after the variation in species richness due to area was removed, absence of an adjacent depression still entered the model. An adjacent depression provides greater soil moisture near to the downslope patch edge, increasing the habitat heterogeneity within the patch and therefore the number of forest species. Overall, these results suggest that the number of species, although largely determined by passive sampling, is also influenced by patch habitat heterogeneity. Although not possible in this study, the richness of similar-sized patches that differ in habitat heterogeneity (and *vice versa*) should be compared to determine the relative influences of area and habitat heterogeneity on species richness (McGuinness 2000).

For the lichen dataset, there was a positive relationship between species richness and area, richness and habitat heterogeneity, and habitat heterogeneity and patch area. In addition, the passive sampling hypothesis was not rejected for this dataset. This shows that lichen patch species richness can be attributed to a passive sampling effect. The relationship between habitat heterogeneity and patch richness can also be explained by a passive sampling effect for habitats within patches; the larger the patch, the greater the number of habitats it contains. Therefore, the larger the patch, the greater the number of individual lichen colonies and in turn the greater the number of lichen species (Coleman et al. 1982). Further, patch perimeter was the only variable to enter the model explaining lichen species richness, suggesting that there were no other important variables, at least out of the ones that were measured.

Scale-dependence of vascular plant species-area relationships and scale-independence of epiphytic lichen species-area relationships

Species-area relationships for vascular plants were scale-dependent. At the patch scale, species richness increased with patch area, whereas, at the plot and quadrat scales, mean species richness decreased with patch area. The reason for this is that small patches were comprised mostly of 'edge habitat' in which there was more light and, therefore, more shade-intolerant species (typically 'prairie' species). This resulted in a greater number of species recorded in total for smaller patches at the smaller scales (plot and quadrat) than in equivalent samples in the interior of larger patches. In larger, rounder patches, in which there was less 'edge habitat' relative to the total patch area and therefore lower light levels, many of these more shade-intolerant species were excluded. The consequence of this was that the mean number of species at the smaller scales was lower in larger patches, even though total patch species richness was higher. This also explains the rejection of the passive sampling hypothesis for the full plant dataset, where small patches contained more species than expected and larger patches contained fewer.

The scale-dependence of this species-area relationship was not observed for the forest plant and lichen datasets. For the forest plants, there was no significant relationship between small scale species richness and patch area. One possible reason for this is because forest plant richness was related to soil moisture, which was not measured directly, but is reflected in the relationship between forest plant richness and presence of an adjacent depression. Presence of a depression, and probably soil moisture in general, were not associated with patch area. This means that small scale species richness also did not vary with area.

The lack of scale-dependence for the lichen dataset is not surprising because small-scale lichen richness was dependent on habitat heterogeneity in the same way as patch-scale lichen richness and there was no ‘edge effect’ apparent for this taxon. The fact that this pattern differs for these two taxa is a reflection of their differences in life histories. Plant species richness appears to be dependent on light and soil moisture availability, which are determined by the canopy composition and cover. Lichen species richness appears to be more dependent on moisture availability on tree bark, which is determined by tree characteristics such as tree size and the aspect of the sample (north- or south-facing).

This scale-dependence of the plant species-area relationship, although simple to explain, is an illustration of how a multi-scale approach is essential in understanding the way communities are structured. It allows us to better answer questions such as, how does diversity interact with environmental variables like habitat heterogeneity and what role does spatial scale play in our perception and interpretation of pattern? This study clearly demonstrates the importance of taking a multi-scale approach to sampling.

Comparison of the taxa

The three datasets can be ordered by their rate of increase in species richness with area sampled (z-values from the power function). This result can be used to generate a hypothesis of the relative immigration rates of these taxa in this system, or in other words, how relatively isolated within patches the taxa are. The prediction is that more vagile taxa will have lower z-values (Rosenzweig 1995). It appears that forest plants are the least vagile of the taxa, followed by all vascular plants, and finally lichens (Table 2). The observed z-values are within the range of values that have been previously reported for similar systems (Rosenzweig 1995). These results are interesting because there is not much life history information, especially dispersal characteristics, available for most of the species within these taxa. Many of the lichen species in this study produce soredia or isidia. These tiny vegetative propagules are so light that they would be available at every site in the study area. However, the requirements for the establishment of lichens via these propagules have not been determined beyond the general requirements for lichen growth (Lindsay 1977, Vitt et al. 1988). The dispersal mechanisms of the vascular plants encountered in this study were relatively varied. Some species were wind dispersed, others were animal dispersed, and many species had no morphological adaptations at all for dispersal. Two thirds of the forest species were either wind or animal dispersed, whereas for all vascular plants, most species were unspecialised in their dispersal mechanism. Therefore, we would expect that forest species, as a group, would be better-dispersed within the study area than all vascular plants generally. However, this is not the case, probably because the majority of forest species occurred in very few patches, and therefore, forest species as a group would appear more insular.

Scale and species-area relationships

The species-area relationship has applied uses as well as having its own intrinsic interest. It can be used as a scaling function to predict the changes of other ecological relationships with scale (e.g., Scheiner et al. 2000). Richness is the simplest way to measure species diversity and, in order to understand changes in species diversity for any community, we must understand the relationship between area and diversity. One current major focus in the study of species-area relationships is the relationship between diversity and productivity (e.g., Waide et al. 1999). Understanding the interaction and relationships between these three factors, diversity, area, and productivity is of great importance if we want to be able to predict changes in both natural and highly human-influenced systems. For instance, if we can predict how productivity of native grasslands will change with increasing proportions of introduced species, maybe then we can better manage both these systems and those utilised for grazing and other agricultural purposes. Area effects must be removed before any relationship of diversity with another variable, such as productivity or habitat heterogeneity, can be considered. But in order to do this we must fully understand the influence of area on diversity.

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