Exercícios 07

Gustavo H. Carvalho

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Dados para o exercício

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library(semeco)
data(stiles)
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De acordo com os autores, eles transformaram as variáveis frag.area, isolation e mean.plant.density com log. Reproduza essas transformações antes de usar os dados.

- 1. Reproduza o modelo da figura 1 do artigo anexo.
- 2. Como o número de observações é muito baixo, reajuste o modelo calculando os erros por meio de bootstrapping com os argumentos se = "boot" e test = "boot".





A multi-scale analysis of fragmentation effects on remnant plant species richness in Phoenix, Arizona

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ABSTRACT

Aim Understanding complex ecological phenomena, such as the determinants of species richness, is best achieved by investigating their properties at different spatial scales. Factors significantly affecting the number of species occurring at one scale may not impact on richness at other scales. While this scale dependence has become increasingly recognized, there still remains a need to elucidate exactly how richness is structured across scales, and which mechanisms are influential for determining this important community property. This study explores how woody plant species richness varies in a fragmented system at multiple scales, and which factors are primarily responsible for these patterns.

Location The study area is located in the Sonoran Desert within the bounds of metropolitan Phoenix, Arizona, which is the locus of the Central Arizona–Phoenix Long-Term Ecological Research (CAP-LTER) site.

Methods Estimates of local and fragment plant species richness were generated from field data collected from 22 sites. Independent variables describing fragment sites were also calculated, including area, habitat heterogeneity, density of individuals, mean elevation, and extent of isolation. Structural equation modelling, multiple regression, and analysis of covariance were used to assess the contribution of independent variables to richness at the fragment and local scales.

Results Fragment species richness was significantly influenced by area, though not isolation, habitat heterogeneity, mean elevation, or density of individuals. Local richness was not significantly related to fragment area, but was positively related to fragment richness, plant density, and elevation.

Main conclusions The fragment species—area effect resulted from larger remnants supporting higher numbers of individuals at comparable densities, increasing richness through either passive sampling of progressively less common species and/or lower extinction rates among larger populations. Without using multi-temporal data it is not possible to disentangle these mechanisms. We found that patterns evident at one scale are not necessarily apparent at other scales, as elevation and density of individuals significantly affected richness at the local scale but not at the fragment scale. These results lend support to the concept that mechanisms influencing the species richness of natural communities may be operable only within certain domains and that relevant scales should be specified.

Keywords

Arizona, CAP-LTER, habitat fragmentation, plant community, Sonoran Desert, spatial scale, species richness, urban ecology, woody plants.

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INTRODUCTION

Ecological processes are complex phenomena that often operate over multiple scales to produce the patterns exhibited in nature. Scale-dependence has been demonstrated by research in multiple areas, including the determinants of species richness (Shmida & Wilson, 1985; Simmerling et al., 2006; Anderson et al., 2007; Pautasso, 2007); productivity—diversity relationships (Gross et al., 2000; Mittelbach et al., 2001; Chase & Leibold, 2002; Scheiner & Jones, 2002; Chalcraft et al., 2004); and species—area relationships (Palmer & White, 1994; Scheiner et al., 2000; Crawley & Harral, 2001; He et al., 2006). Additionally, processes at the local and regional scales often interact with each other to increase system complexity (Ricklefs, 1987; Caley & Schluter, 1997; Brown et al., 2000; Leibold et al., 2004).

Species richness is a community characteristic that generally exhibits nonlinear behaviour across scale transitions, and different mechanisms are often functional at different scales (Chalcraft *et al.*, 2004; Chesson *et al.*, 2005; Harrison *et al.*, 2006). While a number of scientists have studied the effects of fragmentation on plant communities (e.g. Levenson, 1981; Scanlan, 1981; Peterken & Game, 1984; Simberloff & Gotelli, 1984; Dzwonko & Loster, 1988; Soulé *et al.*, 1992; Drayton & Primack, 1996; Drinnan, 2005), we still do not have a good understanding of how fragmentation affects species richness at multiple scales. This study explores how woody plant species richness of remnant desert habitat fragments across the Phoenix metropolitan area, Arizona, is structured at different scales, and which mechanisms contribute to these properties.

Species richness of a bounded community is highly influenced by total area. The tendency to observe a positive relationship between area and species richness has been recognized for about 150 years (de Candolle, 1855; Rosenzweig, 1995) and studied intensively for many years (e.g. Arrhenius, 1921; Gleason, 1922, 1925; Preston, 1962; Coleman, 1981; Coleman et al., 1982; Williams, 1995; Scheiner et al., 2000). This relationship may result because larger areas usually contain more individuals than smaller areas (Coleman, 1981; Coleman et al., 1982; Scheiner, 2003; Scheiner & Willig, 2005). The larger areas can support populations with more individuals, which may have a lower risk of local extinction from stochastic demographic events or inbreeding depression (Preston, 1962; MacArthur & Wilson, 1967). Alternatively, when more individuals are present, this increases the probability of observing progressively rarer species through the simple sampling of the regional species pool, a process often referred to as passive sampling. The species-area relationship may also occur when larger areas contain a greater diversity of habitat types than are found in smaller areas: a site may contain more species since a more varied assortment of taxa is capable of being supported by a wider range of environmental conditions (Lack, 1976; Scheiner, 2003; Scheiner & Willig, 2005).

Isolation can influence richness by affecting the probability of colonization by immigration, which decreases with distance (MacArthur & Wilson, 1967). Fragmentation decreases connectivity and increases isolation of patches on a landscape (Forman, 1995). A human-dominated area such as an agricultural or urban landscape can provide a strong barrier to species exchange, and the extent of isolation can be substantial (Matlack, 1994; Rebele, 1994). Consequently, even with all else being equal, isolated fragments may support fewer species at any given time than fragments that are more accessible to immigration and recolonization events since those taxa lost via local extinction take a longer time to be replaced, if at all.

In the Sonoran Desert, greater species richness and denser vegetation is usually observed at higher elevations (Yang & Lowe, 1956; Barbour, 1973; Halvorson & Patten, 1974; Phillips & MacMahon, 1978; Bowers & Lowe, 1986; Hope et al., 2003). In dry climates, the rockier, coarse-grained soils on mountains and hilltops promote greater water availability to plants because cobbles and gravels retard evaporation while sandier soils promote deeper percolation of rain water (Shreve & Wiggins, 1964; Lane et al., 1998). In contrast, finer-grained soils typically found on valley bottoms saturate quickly and promote greater surface runoff so that the deeper soil layers generally absorb relatively little moisture; evaporation soon renders the surface layers dry again. Given the extreme heat and aridity of the Sonoran Desert, even slight increases in the timing and quantity of soil moisture have drastic effects on the vegetation.

This study examines the factors that structure woody plant species richness in remnant fragments embedded within metropolitan Phoenix, Arizona. The woody community is a xeric scrub dominated by native trees, shrubs and cacti. Species richness is expressed at the fragment and the local scale, which correspond to levels at which different fundamental mechanisms are operating.

The fragment scale refers to the bounded, continuous area of remnant sites supporting stands of Sonoran Desert vegetation. At this scale, the insularity of each remnant means that new colonizers must arrive via long-distance dispersal. Community size (the number of individuals regardless of taxonomic identity) is determined by the combination of area and plant density. At this scale, we hypothesize that fragment richness would be positively correlated with habitat heterogeneity, the size of the fragment, density of individuals, and mean elevation, and would be negatively correlated with the extent of isolation.

The local scale is defined in terms of the field sampling units, a single 100-m² quadrat and a transect consisting of five quadrats. Analysing data at the quadrat and transect levels enables comparison between different grain sizes (the standardized unit of analysis; Scheiner *et al.*, 2000). At this scale, the species would have overwhelmingly arrived via short-distance dispersal from adjacent parts of the fragment. Community size would be a function of density alone, as sample area is fixed. A transect should include more species since it samples greater microhabitat heterogeneity and contains more individuals occupying a greater area.

Following Scheiner *et al.* (2000), we define focus as the scale to which grain sizes are aggregated for analysis. Thus, the focus of an analysis may be the values of individual sample units or the mean values of collections of sample units. In this study, two foci are considered: mean richness of samples averaged over the entire fragment and richness values of individual samples.

With the focus on the entire fragment, mean local richness should increase with fragment species richness and mean plant density, though the latter factor should have the stronger influence. Higher plant densities should allow the sample to capture a wider assortment of the more common species. On the other hand, an increase in fragment richness raises the maximum number of species that can be observed at the local scale, but those species are unlikely to be evenly distributed; observations of rarer species should accumulate more slowly at the local scale. We expect both factors to have a stronger influence on transect rather than quadrat richness since the former should sample more species, thus including a higher proportion of the fragment's flora.

With the focus on the individual quadrats or transects, local richness should increase with sample elevation and plant density. In this case, the relationship reflects how richness responds to site-specific factors rather than to general factors of area or environmental heterogeneity. We also expect transect richness to respond more strongly to these variables than quadrat richness, because transects allow for a wider range of species richness values and a potentially higher magnitude of response.

MATERIALS AND METHODS

Data sampling and calculation of variables

This study surveyed a variety of remnant fragments distributed throughout the urban matrix of the Central Arizona–Phoenix Long-Term Ecological Research (CAP-LTER) site, which is located in and around metropolitan Phoenix, Arizona, USA (see Appendix S1 in Supporting Information). The 22 fragments examined here included almost all potential sites present on the landscape, based on accessibility and the continuous coverage of undeveloped desert habitat within the boundary of the parcel. Most of these fragments are publicly owned nature preserves and recreation areas surrounded by urban land covers. Vacant lots displaying evidence of past land clearing or other heavy disturbance were excluded. The study sites varied broadly in terms of total area, habitat heterogeneity, degree of isolation, and elevation, and represented a diversity of conditions observable in many other landscapes.

In order to represent the vegetation adequately as it varies throughout each site and produce reliable measurements of species richness, sampling intensity was proportional to fragment area and was contingent on the complexity of geomorphic types, including flatlands, ephemeral washes, and slopes facing each cardinal direction. Thus, for two sites of equal area but differing topographic complexity (e.g. plains

versus mountainous terrain), the latter would require more samples to describe the plant communities adequately. See Appendix S2 for the sampling intensity of each site. Transects, consisting of five 100-m² circular quadrats separated by 20-m intervals, were randomly placed within each geomorphic type. Each woody plant species encountered per quadrat was counted and recorded in a single sampling event between 1998 and 2002.

Dependent variables describe species richness occurring at the three levels identified above: fragment, transect and quadrat. We estimated each fragment's total plant species richness using the first-order jackknife method, as recommended by Palmer (1990, 1991), by means of ESTIMATES software (Colwell, 1999). Since this method calculates an asymptotic richness value based on the empirical data, differences in the quantity of samples between sites, indispensable for adequately characterizing fragments of varied sizes, are compensated for; using the raw data consisting only of species observed would potentially lead to a confounding sampling effect on fragment species richness. For both quadrats and transects, mean local species richness in each fragment was determined as a weighted average calculated by summing the products of mean species richness per geomorphic type multiplied by the proportion of area comprising that type; surface area for each geomorphic type was derived from the GIS maps described below. For mean local species richness, the focus was on the fragment, and the grain size corresponded to either the transect or the quadrat (both with n = 22 values). Species richness of specific locations was calculated based on the total number of species observed per transect and on the mean number of species recorded per quadrat for each transect (both with n = 364 values). For specific sample species richness, the focus is on the transect, and the grain size corresponds to the sample units themselves: the transect and the quadrat. Calculating the values in this fashion allows us to investigate how varying the grain size, while keeping the focus constant, affects the results.

ARCVIEW 3.3 (ESRI, 2002a) and ARCGIS 8.3 (ESRI, 2002b) were employed to generate spatial data useful for calculating two of the independent variables examined in subsequent analyses. For each fragment, geomorphic type maps were created by tracing polygons over the corresponding areas based on digitized aerial photography (approximately 1/3 metre resolution) and 10-m-interval contour maps (developed using the Maricopa County Digital Elevation Model, DEM, downloadable from http://data.geocomm.com; accessed January 2003). Heavily disturbed areas and recreational facilities within each fragment, resolvable from the photos, were excluded from these maps. The geomorphic type maps were then combined with soil type maps (Soil Survey Geographic Database, 2002; there was a mean of 6.9 soil types per fragment with SD = 5.7) to create habitat diversity maps. In order to provide surface area measurements that would reflect conditions on the ground, the mapped two-dimensional area of each soil/ geomorphology class was divided by the cosine of the mean slope for that polygon, also generated from the Maricopa

County DEM, to yield three-dimensional areas. These values were used to calculate the relative proportion occupied by each soil/geomorphology class. These proportions were then used to compute the Shannon index (Magurran, 1988) in order to estimate habitat heterogeneity for each fragment. Fragment area resulted from summing the three-dimensional areas of all soil/geomorphology classes at a site.

Other independent variables were calculated by various methods. Mean elevation per fragment was computed by averaging all DEM measurements located therein; the horizontal distance between values was 30 m. Mean plant density resulted from averaging the number of individuals (ignoring species identity) counted in each sample unit. Extent of fragment isolation from other potential propagule sources was calculated from the formula $I = \Sigma \left[\ln(\text{Area}) / (\text{Distance}^2) \right]$, which incorporates the minimum distance from the focal fragment to other fragments and the outlying desert (Gustafson & Parker, 1992). To enable computation, the outlying desert was assigned the area value of 9000 ha, which is approximately equivalent to South Mountain Park, the largest fragment in this study. Fragment area, extent of isolation and mean plant density were natural-logarithmically transformed in order to normalize the distribution of values, reduce the leverage and influence of a few outlying data points, and homogenize the variance of residuals.

Data analysis

Hypothesized relationships between fragment species richness and independent variables describing site properties are depicted in Fig. 1. The statistical significance of these relationships was analysed with structural equation modelling using AMOS v. 5.0 (Arbuckle, 2003). Structural equation models are useful because they can account for complex causal relationships (Grace, 2006). For example, in this system, area may directly affect species richness through its positive relationship with the number of individuals capable of being supported on a fragment. Area can also indirectly affect fragment richness through its positive correlation with habitat heterogeneity and mean elevation.

SYSTAT 6.1 (SPSS, 1994) was used to examine relationships at the local scale. We used multiple regression to analyse the relationship between mean local richness and the independent variables mean plant density and fragment richness. The relationship between specific local-scale richness values and the independent variables was analysed using analysis of covariance. This method enables one to explore how the continuous variables elevation and plant density, and a categorical variable, fragment identity, affect how many species are observed within the sample units. Fragment identity accounts for variation not influenced by the other factors. Three small fragments, together containing five transects, were excluded from this analysis since they contained no variation in elevation and prevented the convergence to a solution.

RESULTS

Fragment-scale species richness

Fragments varied in size, habitat heterogeneity, density of individuals, elevation, isolation and species richness (Appendix S2 and S3). A structural equation model relating fragment

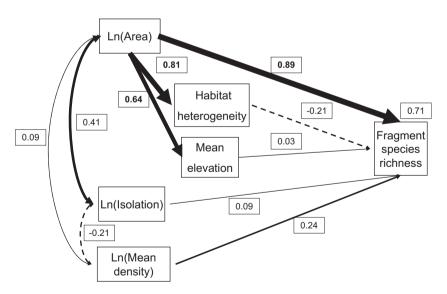


Figure 1 Structural equation model of the hypothesized factors determining fragment species richness of woody plants in the Sonoran Desert, Arizona. Values adjacent to each arrow are standardized effects: correlations (double-headed, curved arrows) or standardized partial regressions (single-headed, straight arrows). Arrow widths are proportional to those standardized effects; negative relationships are shown by dashed arrows. Values that are significant by standard statistical criteria (P < 0.05) are shown in bold. Area is the only variable significantly affecting fragment species richness (R = 0.89, P = 0.014). The model accounts for 71% of the variation in fragment richness. In addition, fragment area is related to mean elevation and habitat heterogeneity, but neither variable is significantly related to species richness.

area, habitat heterogeneity, mean elevation, fragment isolation and mean plant density to fragment species richness provided a successful fit to the data (Fig. 1; $\chi^2 = 9.24$, d.f. = 5, P = 0.10; root mean square error of approximation (RMSEA) = 0.20, P = 0.12). In the structural equation model, non-significant χ^2 and RMSEA values indicate that the model fits the data. There was a significant direct effect of fragment area on species richness (P = 0.014), but no other variables were significantly related to fragment species richness. Area was significantly correlated with habitat heterogeneity (P = 0.003) and mean elevation (P = 0.004), as expected. Area was uncorrelated with mean plant density (r = 0.09).

Local-scale species richness: quadrat and transect

Fragment area had no significant effect on mean local species richness at either the quadrat (P = 0.12) or the transect level (P = 0.40). Mean local richness was significantly correlated with mean plant density at both grain sizes (Table 1). Mean local richness at the quadrat level was also significantly related to fragment species richness, though the relationship was marginally short of significance (P = 0.056) at the transect level. Thus, while fragment species richness and mean plant density both influence mean local richness, the relationship between plant density and mean local richness was stronger. Plant density had a significant effect on the number of species observed at the local scale, but it did not significantly influence richness at the fragment scale. The prediction that transect richness, with the focus on the entire fragment, would be influenced more strongly than quadrat richness by the independent variables was rejected (Table 1).

With the focus on individual sample units, local-scale species richness at both grain sizes was significantly affected by the density of individuals, elevation and fragment identity (Table 2). Even though some of the fragments were sufficiently idiosyncratic to influence the richness of sample units, this was not enough to override effects of elevation and plant density. Thus, as predicted, species richness of specific localities increases through the effects of passive sampling of denser

Table 1 Multiple regression analysis of factors affecting local-scale species richness of woody plants in the Sonoran Desert, Arizona, aggregated and averaged across each fragment (n = 22).

Variable	Standardized coefficient	P
I. Quadrat level		
Fragment species richness	0.374	0.019
Ln (mean plant density)	0.602	0.001
II. Transect level		
Fragment species richness	0.324	0.056
Ln (mean plant density)	0.588	0.002

 $R^2 = 0.585$ and 0.507, respectively. Species richness was analysed at two grain sizes, quadrats (100-m² plots) and transects (five quadrats arrayed along a line with each separated by 20 m). Grain size refers to the standardized unit of analysis.

Table 2 Analysis of covariance (ANCOVA) assessing hypothesized contributors to local-scale woody plant species richness of specific locations in the Sonoran Desert, Arizona, using two grain sizes (n = 364).

Variables	d.f.	F	P
I. Quadrat level			
Elevation	1	64.961	0.0001
Ln (plant density)	1	79.769	0.0001
Fragment ID	18	3.843	0.0001
II. Transect level			
Elevation	1	71.329	0.0001
Ln (plant density)	1	15.700	0.0001
Fragment ID	18	5.660	0.0001

 $R^2 = 0.527$ and 0.455, respectively. Quadrat-level richness was calculated as the mean of the five component quadrats in each transect; transect richness was the total species observed per transect. Grain size refers to the standardized unit of analysis.

stands and with increasing elevation. The relative strengths of the relationships differed between grain sizes. For quadrats, plant density had a slightly stronger relationship with richness, while transect richness was much more highly correlated with elevation. Contrary to expectations, transect richness was not consistently more sensitive than quadrat richness to changes in elevation and plant density.

DISCUSSION

Fragment-scale species richness

Fragment species richness was positively correlated with area. As plant density does not depend on fragment area, the species-area effect is particularly strong at this scale: larger fragments support communities with greater numbers of individuals. With more individuals in a continuous area, fragment richness increases either through the passive sampling of progressively less-common species, or the buffering of populations from collapse with a lowering of the extinction rate. We cannot separate the effects of passive sampling from extinction of smaller populations at this scale because our data represent a single point in time; such separation requires tracking population sizes and species richness over time. Despite the high correlations between area and mean elevation and habitat heterogeneity, the structural equation model demonstrated that the strong, direct relationship between area and fragment richness dominated the pattern. In contrast, the significant influence that elevation has on local species richness exhibits how these relationships can be scale-dependent.

Habitat heterogeneity, defined in terms of geomorphology and soil type, did not significantly influence species richness. This is not entirely surprising because, in the Sonoran Desert, woody plant species are able to grow wherever moisture and climatic conditions are favourable for their survival, provided salinity is not excessive (Shreve & Wiggins, 1964; Turner & Brown, 1982). Apart from moisture gradients associated with

elevation and washes, strict species segregation to geomorphic type was generally not strong, though highly xeric species were more common on south-facing than north-facing slopes.

Isolation was not significantly correlated with fragment richness. This outcome probably resulted from the long time lag necessary to alter the woody community. Without catastrophic and widespread disturbance that clears out adult plants, individuals can live for many decades (McAuliffe, 1994, 1999; Pierson & Turner, 1998; Bowers, 2005). This is not to imply that fluctuations in the woody vegetation are absent over long intervals. Goldberg & Turner (1986) reported that over a 72-year period on permanent Sonoran Desert plots, there were shifts in abundance and vegetative cover. However, there was no evidence of consistent, directional change, and the relative cover of dominants was relatively constant over that period. Fire can bring about extensive disturbance and great change in Sonoran Desert woody communities (Cave & Patten, 1984; Schmid & Rogers, 1988; McAuliffe, 1995), but unburned areas are currently far more extensive than burned areas. While seedling survivorship in this system is typically low (Pierson & Turner, 1998; Bowers & Turner, 2002; Bowers et al., 2004), propagule flow from unburned areas within a fragment should greatly exceed immigration from more distant fragments.

Local-scale species richness: quadrat and transect

Mean local species richness at the quadrat level was significantly influenced by fragment richness, and the influence at the transect level was marginally short of significance (P=0.056; Table 1). While area was significantly correlated with fragment richness, and fragment richness was correlated with local richness, fragment area did not significantly influence local richness. This may result from an accumulation of stochastic variation across the two relationships. In other words, the residual values of the former and latter relationships sum together to increase the random variation in the relationship between fragment area and local richness to prevent statistical significance.

Density effects had a stronger influence on mean local richness than fragment species richness (Table 1). Increases in density translate into more individuals observed per sample unit, so that a wider assortment of the more common species is recorded. On the other hand, a sizeable proportion of the larger-fragment species pool would consist of infrequent taxa less likely to be captured within a given plot. As species-poor fragments tended to be occupied by more common taxa, this system had a nested structure in which species found in depauperate fragments were subsets of those observed in progressively richer fragments (Stiles & Scheiner, 2008).

For specific local richness, the relative magnitude of response to plant density differed between the two grain sizes, transect and quadrat. While significant, density effects were weaker for the transect data because transects extend across subtle microsite variations and beyond local clumping of species. Lower densities depress transect richness, but the

strength of this effect is offset by the aforementioned influences, which do not affect quadrat richness in a more limited, continuous area.

A similar reason also accounts for the tighter association between fragment area and mean quadrat richness than that with mean transect richness (Appendix S4). On the quadrat-level graph, three fragments yielded outlier data points that increased the variation around the regression line and prevented a statistically significant species—area relationship; other sites clustered more closely around this line. On the other hand, the transect-level graph displays no clear association. Aside from the species—poor outlier, larger fragments on this plot contain more species. However, smaller fragments are also capable of relatively high mean transect richness. As transects sample across microsites and clumps, these influences compensate for smaller fragment extents and augment the richness of these samples in species—poor fragments.

CONCLUSIONS

This study provides an important baseline for understanding changes in species richness, density and composition in remnants of different size and isolation over time. At the fragment scale, a positive species—area effect was the primary influence on species richness. The hypothesized dependence of richness on habitat heterogeneity, mean elevation and isolation was rejected in this study. Fragmentation in this system influenced woody plant species richness through effects on remnant site character, rather than how sites were distributed throughout the urban matrix. It remains to be seen whether isolation will be a more significant factor as the remnants age. Systems with low recruitment rates should make colonization by new species a very slow process. At the local scale, more species were observed with increases in the fragment species pool, plant density and elevation.

It is important to remember that the species—area effect arising from the number of individuals in a bounded area does not result from extinction processes alone. One must also consider passive sampling in this context. Multi-temporal data are needed in order to adequately separate these influences. Particularly with the emphasis on conservation issues in relation to fragmentation, it is important to know accurately whether remnants are losing or retaining species, and tracking communities through time is a crucial means by which to make that determination.

This study demonstrated the value of explicitly defining the grain size and focus of analyses when determining how mechanisms structure the species richness of communities. In this study, we varied both grain size and focus while holding extent constant (the whole archipelago of remnant fragments). Our results support the conjecture that one cannot assume phenomena at one scale may be directly applied to observations at other scales (Schneider, 2001). For example, plant density and elevation significantly affected local richness, but not fragment richness. This research reinforces the utility of focus as a tool for studying scale-dependence (Scheiner *et al.*,

2000; Anderson *et al.*, 2007). By changing focus, we could examine relationships of different factors. The contribution of site idiosyncrasy to a relationship cannot be assessed using a single data point per site, and the influence of the site species pool on local richness cannot be analysed when the focus is on the sample unit.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Map of remnant sites examined in this study.

Appendix S2 Data for the dependent variables.

Appendix S3 Data for the independent variables.

Appendix S4 Plots showing the relationship between local-scale species richness and fragment area.

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