

Are landscapes more than the sum of their patches?

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Abstract

Context The species–area relationship (SAR) is the most ubiquitous scaling relationship in ecology, yet we still do not know how different aspects of scale affect this relationship. Scale is defined by grain, extent, and focus. Focus here pertains to whether patches or landscapes are used to derive SARs.

Objective To explore whether altering the focal scale influences the resulting SAR. If the SAR is scale-invariant, patch-based and landscape-based SARs should be congruent.

Methods I fit a power-law function ($S = cA^z$) to arthropod data obtained from an experimental landscape system, in which habitat amount and configuration (clumped vs. fragmented) of red clover (*Trifolium pratense*) varied among plots (256 m²). The scaling coefficient (z) was compared among patch-based and landscape-based SARs for congruence.

Results Patches gained species at a faster rate than landscapes ($z = 0.37$ vs. 0.26 , respectively), producing domains of incongruity in the SAR. Landscape

richness (S_L) was greater than patch richness (S_P) below 30 % habitat, but $S_P > S_L$ above 60 % habitat. Landscape configuration contributed to this incongruity below 30 % habitat (fragmented $S_L >$ clumped S_L), but landscape context (whether the largest patch was embedded in a fragmented or clumped landscape) was important above 60 % habitat for understanding the SAR in this domain.

Conclusions Landscape configuration exerts both direct (<30 % habitat) and indirect (>60 % habitat) effects on the SAR. Because patch-based and landscape-based SARs may not be congruent, we should exercise care when extrapolating from patches to landscapes to make inferences about the effects of habitat loss and fragmentation on species richness.

Keywords Species–area relationship · Species richness · Scaling effects · Habitat amount · Habitat fragmentation · Arthropods

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Introduction

It has been nearly 100 years since Swedish ecologist Olof Arrhenius first published his landmark papers on species and area, in which he demonstrated that the number of plant species on islands in the Stockholm archipelago could be modeled as a power function of island size (Arrhenius 1920, 1921). The species–area relationship (SAR) has since become one of the

cornerstones of ecology, having influenced the development of both the theory of island biogeography and metapopulation theory (MacArthur and Wilson 1967; Hanski 1999), and having found applications in fields such as landscape ecology and conservation biology, where it is used to predict the consequences of habitat loss and fragmentation on species richness. Indeed, the SAR is so fundamental and ubiquitous that it has been called a general rule—and even a law—of ecology (Lawton 1999; Lomolino 2000).

In its power-law form ($S = cA^z$), the SAR implies scale invariance in the rate (z) at which species richness (S) increases with habitat area (A). Like most ecological phenomena, however, the SAR may be scale-dependent: different factors at different scales can influence the relationship between species and area, and thus the slope (z) of the SAR may vary across different domains of scale (Rosensweig 1995; Turner and Tjørve 2005; Drakare et al. 2006; Triantis et al. 2012). In assessing the effect of scale on the SAR, there are three components to consider: (1) *grain*, the smallest area over which species richness is measured, and thus, the smallest unit of analysis, (2) *extent*, the total area encompassing all survey or sampling sites (e.g., the size of the study area or region), and, (3) *focus*, the inference space represented by the data, such as whether each data point represents a single site or a mean value (Scheiner et al. 2000; Scheiner 2003). Focus can also pertain to what type of spatial units form the basis of the analysis; that is, whether individual islands (or habitat patches) or entire archipelagos (landscapes) are used to derive the SAR (Turner and Tjørve 2005). Although landscapes are made up of patches of varying sizes, it is not immediately obvious to what extent SARs derived from a patch-based approach is equivalent to one obtained from a landscape-based approach. Failure to recognize these sorts of scaling distinctions not only compromises our ability to make meaningful comparisons among studies, but can also affect our understanding of the factors or processes responsible for the relationship (Scheiner et al. 2000; Whittaker et al. 2001; Turner and Tjørve 2005), as well as the extent to which we can safely extrapolate across scales, such as from patches to landscapes (He and Legendre 1996).

Most studies that examine habitat-area effects on species richness adopt a patch-based approach, in which patches of different sizes are the focus. Patch-isolation effects might also be incorporated in the

study design to examine how habitat fragmentation additionally influences species richness. Given that a reduction in habitat area alone can increase distances between patches, however, it is unclear that patch isolation is really a fragmentation effect so much as a habitat-area effect (Fahrig 2003). Regardless, there are only so many patch size-by-distance configurations that can be studied, either in the field or in an experimental array, thereby limiting whatever inferences might be made as to how habitat area and fragmentation influence species richness at the broader landscape scale (Debinski and Holt 2000).

As an alternative to the patch-based approach, we might instead focus on the overall properties of the landscape, in terms of the total habitat area and degree of fragmentation, which in turn give rise to different patch attributes. Although experiments typically manipulate the size and isolation of patches to create fragmented landscape patterns (a “bottom-up” approach), one can also generate fragmented landscape patterns from the “top down” by varying the overall amount (p) and fragmentation (spatial contagion, H) of habitat using fractal neutral landscape models (With 1997). Because these parameters are adjusted independently of one another, we can tease apart the effects due to habitat area from those due to fragmentation per se. The resulting fractal distribution of habitat produces landscapes that differ in their patch properties as well (With and King 1999). Thus, fractal neutral landscapes offer a convenient means of generating complex landscape patterns in which it is possible to simultaneously evaluate habitat-area and fragmentation effects at both a patch and landscape scale.

The application of fractal neutral landscape models to the study of habitat-area and fragmentation effects on arthropod community patterns has been exploited previously through the development of an experimental landscape system in the field (With et al. 2002; With and Pavuk 2011, 2012). My objective here is thus to examine how the SAR for arthropod assemblages in this experimental system is influenced by scale (whether patch-based or landscape-based), and in turn, explore to what extent SARs based on patches can explain total species richness at a landscape scale. If a landscape is simply the sum total of its patches, in terms of habitat area, then we should see congruence between patch-based and landscape analyses. That is, the SAR derived

from a patch-based analysis should be congruent to that obtained at the landscape scale. If, however, landscape configuration is important and influences species richness, such as through differences in the spatial arrangement of patches (i.e., whether habitat is fragmented or clumped), then we should not expect to see a congruent relationship between these two scales of analysis.

Methods

Experimental model landscape system

This experimental landscape system was established at Bowling Green State University's Ecology Research Station, which is located about 2 km north-east of the campus in Bowling Green, Ohio, USA. Details of how the fractal landscape patterns were computer-generated and created in the field have been presented elsewhere (With et al. 2002; With and Pavuk 2011), and thus only a brief overview is given here. Red clover (*Trifolium pratense*) was seeded in a specified fractal distribution within each landscape plot (16 m × 16 m = 256 m²), which was then maintained over a 3-year period through a combination of hand-weeding (clover cells) and herbicide spraying (bareground matrix within plots). Landscape plots contained 10, 20, 40, 50, 60 or 80 % clover habitat (~25, 51, 102, 128, 154 or 205, 1 m² clover cells, respectively). Clover habitat possessed either a clumped ($H = 1.0$) or fragmented ($H = 0.0$) distribution (Fig. 1). There were three replicate plots for each landscape type (e.g., 20 % clumped), each with a different distribution of habitat (i.e., the habitat distributions among plots for a given landscape type were not identical).

A “patch” is defined here as one or more clover cells that are connected via an edge or vertex to other clover cells; in other words, an eight-cell neighborhood rule was used to define patches in this analysis. By this definition, patches are separated by at least one bareground cell (≥ 1 m) from other patches. The smallest patch possible is a single clover cell (1 m²) and the largest possible is theoretically 205 m² if all habitat is aggregated within a single patch in a plot with 80 % clover (256 cells × 0.8 = 205 cells). In practice, the size of the largest patch could be somewhat larger than this owing to statistical

“overages” created by the fractal algorithm used to generate the habitat distributions.

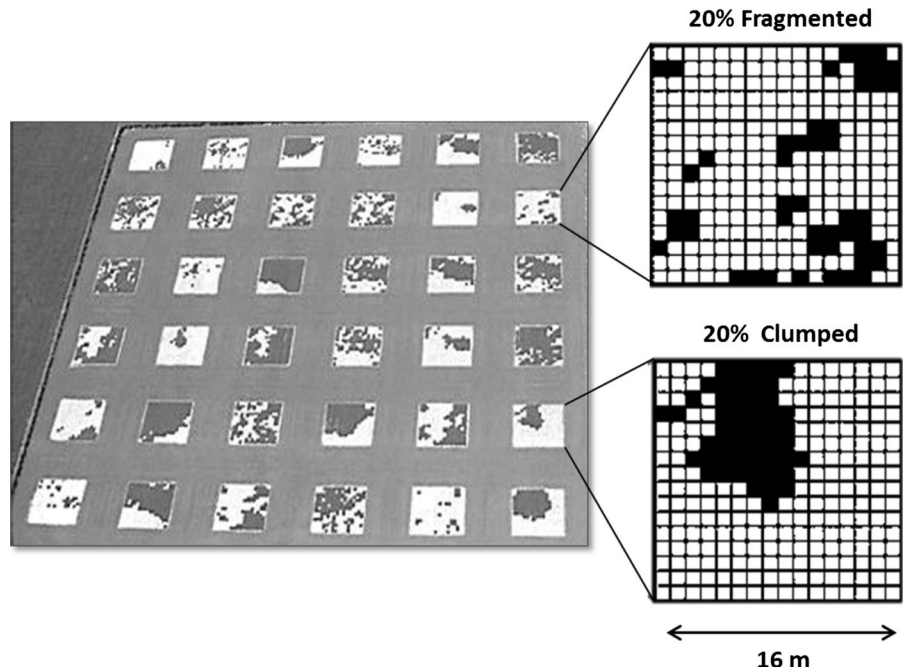
Patch properties were clearly influenced by the fractal distribution of habitat, and thus differed significantly between clumped and fragmented landscapes. Fragmented landscapes had up to 4× more patches than clumped landscapes, with the greatest difference occurring at 20 % habitat (Supplemental Fig. 1a). Overall, clumped landscapes averaged about 2 patches/plot (2.4 ± 1.33 SD, range = 1–5 patches, $n = 18$ plots) versus 7 patches/plot in fragmented landscapes (6.9 ± 3.79 SD, range = 1–15 patches, $n = 18$ plots). Patches were also smaller in fragmented than in clumped landscapes, with patch size increasing exponentially as a function of total habitat area (Supplemental Fig. 1b). The average patch size across all fragmented landscapes was 16 cells (16.3 ± 42.51 SD, range = 1–209 cells, $n = 124$ patches), whereas clumped landscapes had an average patch size that was nearly 3× larger at 48 cells (47.5 ± 65.81 SD, range = 1–224 cells, $n = 43$ patches).

Arthropod surveys

This analysis is based on an arthropod survey that was conducted 25 August–27 September 1997 as part of a 3-year study of arthropod community responses to fractal habitat distributions (August–Year 1 survey; With and Pavuk 2011). I restrict my analysis here to this particular survey because the experimental system was well-established by that point in the study, and thus had been colonized by a large number of arthropods (Table 1 in With and Pavuk 2011). Further, the SAR for this survey was shown to be essentially linear at the landscape scale, unlike many of the other surveys that exhibited a more complex relationship between species and area (Table 3; Supplemental Fig. 1 in With and Pavuk 2011).

Arthropod surveys were comprehensive, in that every clover cell was visited for ~1 min to record the number of arthropods present (including below the clover canopy), for a total of 4008 cells surveyed across all 36 landscape plots. Surveys were thus standardized in terms of the spatial grain (1 m²) of the landscape plots. Because arthropods were not collected, it was not possible to identify every individual to species, and thus the term “morphospecies” is used here to denote a morphologically distinct specimen or

Fig. 1 Experimental model landscape system. Aerial view of the 36 landscape plots ($16\text{ m} \times 16\text{ m}$) in which clover (*Trifolium pratense*) was seeded to produce different fractal habitat distributions with different habitat areas (10, 20, 40, 50, 60 or 80 % clover) and level of fragmentation (clumped, $H = 1.0$; fragmented, $H = 0.0$). The white area within plots is compacted soil, which contrasts with the clover habitat (dark areas within plots) and the recently plowed bare-ground matrix between plots



broader taxonomic unit (genus or family) that could be identified. Although visual surveys undoubtedly missed some arthropods, they have the advantage of permitting a complete survey of the entire system, which otherwise would be impossible using collection methods because of the enormous processing time required. For example, a single collection-based survey of this same experimental system, involving a random sampling of 10 % of the clover cells from a reduced number of plots ($n = 27$), resulted in >24,000 individuals, of which very few could be identified to species level without the expertise of a taxonomist specializing in that particular group (With and Pavuk 2012).

Data on the number of morphospecies (species richness, S) were collected at the scale (grain) of the individual clover cell (S_C), and were aggregated to give species richness within individual patches (S_P) as well as for the entire landscape (S_L). Note that the aggregate value here is the number of unique morphospecies encountered across all cells within the patch or landscape. For example, if a patch is made up of two cells, each with four species ($S_C = 4$) but only two in common, then the total richness at the patch scale (S_P) is six species, not eight.

Note that cell species richness equates to patch species richness ($S_C = S_P$) for single-celled patches

(patch size = 1 m^2), and patch species richness is equivalent to landscape richness ($S_P = S_L$) when the landscape is made up of a single patch.

Analysis of species–area relationships

Although the SAR was first presented as a power function (Arrhenius 1920, 1921), the convention has been to use linear regression to fit the relationship between species richness and area on a log–log plot. Linearizing this relationship may once have been easier computationally, but a linear relationship between species and area may not provide the best fit, either statistically or conceptually. In a comparison of some two dozen functions that have been used to describe SARs, Dengler (2009) found that the simple power-law function ($S = cA^z$) generally performed best (see also Triantis et al. 2012). Power functions are ubiquitous in nature, and may thus represent a general law governing the organization of complex systems (Brown et al. 2002), including the distribution of species in space (Storch et al. 2008). Subsequently, Dengler (2009) proposed that “the power law should be used to describe and compare any type of SAR while at the same time testing whether the exponent z changes with spatial scale.” Although a power-law function implies scale-invariance, the SAR may in fact

exhibit scale-dependence, such that the scaling coefficient (z) of the relationship changes as a function of spatial or focal scale (Rosenzweig 1995; Scheiner et al. 2000). For example, SARs obtained within a biogeographic province tend to have shallower slopes than SARs derived among different provinces (Fig. 9.11 in Rosenzweig 1995).

I therefore used nonlinear regression to fit a power function to the data, where S is the number of unique morphospecies (S_C , S_P or S_L) and A is the unit-area of interest; that is, the focus of the analysis (i.e., patch area, A_P , landscape area, A_L , or relative patch area, A_P/A_L). The resulting scaling coefficients (slopes) of the power function, z , were then compared between different scales (i.e., patch-based vs. landscape-based SARs) using Student's t , which is computed as the difference between two slopes ($z_1 - z_2$) divided by the standard error of the difference between the slopes ($s_{z_1-z_2} = \sqrt{s_{z_1}^2 - s_{z_2}^2}$). Similar z coefficients among SARs would indicate congruence in how species richness scales as a function of habitat area, regardless of whether we focus on individual patches or landscapes, or the average patch within landscapes. Thus, while the spatial grain (1 m² clover cell) and extent (the entire experimental model landscape system) were held constant for all analyses, the focus varied among analyses in terms of the inference space or spatial unit of analysis.

At the landscape scale, the focus was on the relationship between total species richness (S_L) and total habitat area ($A_L = 0.1$ – 0.8). Separate SARs were derived initially for clumped ($H = 1.0$) versus fragmented ($H = 0.0$) landscape plots to determine whether landscape configuration affected how species richness scaled as a function of habitat area. The overall effect of fragmentation on landscape richness (S_L) was tested with a two-way ANOVA (fragmentation \times habitat area), and because this proved not to be significant (see “Results” section), a landscape-based SAR was derived for all landscapes combined ($n = 36$ plots).

At the patch scale, the general focus was on the relationship between species richness within patches (S_P) and habitat area, but as there are a number of different ways of deriving this relationship, the inference space of the analysis also varied. A SAR was first derived between mean patch species richness within landscapes (\bar{S}_{PIL}) and total habitat area of

landscapes (A_L), based on the expectation that the average patch should be larger, and thus have more species, in landscapes with a greater amount of habitat. The overall effect of fragmentation on mean patch species richness (\bar{S}_{PIL}) was tested with a two-way ANOVA (fragmentation \times habitat area). As the fragmentation effect was significant (see “Results” section), separate SARs were derived for \bar{S}_{PIL} in clumped versus fragmented landscapes. Second, a patch-based SAR examined the relationship between patch richness (S_P) and individual patch size (A_P), on the premise that larger patches should have more species, regardless of the landscape in which they occur. A third patch-based SAR examined patch richness versus the relative size of the patch (A_P/A_L , the proportional contribution of the patch to the total habitat area on the landscape). This was done to standardize patch sizes and examine how landscape context might influence patch species richness (S_P). For example, patches that make up a larger proportion of the habitat area on the landscape should have more species than those that contribute less to total habitat area, regardless of the absolute amount or configuration of habitat on the landscape. Finally, a fourth patch-based SAR was derived to examine relative patch species richness (S_P/S_L) versus relative patch size (A_P/A_L), so as to more fully examine the proportional contribution of each patch to total species richness within landscapes.

At the finest scale (1 m² cell), I examined the relationships between the mean cell richness per landscape (\bar{S}_{CIL}) and per patch (\bar{S}_{CIP}) versus total habitat area (A_L), and the mean cell richness per patch (\bar{S}_{CIP}) against patch size (A_P). Although the individual clover cell represents the sampling grain and S_C is not expected to vary in an area of fixed size, it is still possible that patch or landscape context could influence local richness within a cell. For example, cells located in large patches or in landscapes with more habitat might themselves have more species than cells in smaller patches or landscapes with less habitat.

The goodness-of-fit for each of these SARs was assessed in terms of the proportion of variation in the dataset that was explained by the power function (i.e., the model R^2). Although it has been argued that a P value for the significance of this relationship may not be appropriate when curve-fitting SARs (the null hypothesis assumes no increase of species number

with area; Dengler 2009), I include P -values here to provide additional support for the model fit where warranted (He and Legendre 1996). In addition, the effect size (the strength of the relationship between species richness and area) was assessed using the correlation coefficient (R), which could be compared statistically between SARs using Fisher's Z test. The Z -transformed correlation coefficients were also used to calculate Cohen's q to compare the overall effect size of the difference between correlation coefficients for patch-based versus landscape-based SARs, in which $q > 0.5$ is considered a "large effect" (Cohen 1988).

Results

A total of $S = 71$ morphospecies was recorded during this survey across the entire experimental landscape system ($n = 36$ landscape plots). On average, landscape plots contained about 23 morphospecies/plot ($22.7 + 5.52$ SD species/plot), although species richness (S_L) varied as a function of the total habitat area within landscapes (habitat-area effect: $F_{5,24} = 8.54$, $P < 0.0001$, two-way ANOVA; Fig. 2). The degree of habitat fragmentation (H) had no overall effect on species richness at the landscape scale (fragmentation effect: $F_{1,24} = 0.51$, $P = 0.48$). Although species richness was initially greater (on average) in fragmented landscapes (10–20 % habitat; Fig. 2a), clumped landscapes gained species at a faster rate than fragmented landscapes ($z = 0.32$ vs. 0.21, respectively), but this difference between slopes was not significant ($t_{32} = 1.32$, $P = 0.20$). Thus, a single landscape-based SAR was obtained by fitting a power function to the combined landscape data ($R^2 = 0.56$, $P < 0.0001$), in which species richness scaled as a power of 0.26 of the total habitat area within landscapes (A_L ; Fig. 2b). The effect size—the strength of the relationship between the amount of habitat and number of species at a landscape scale—was fairly large ($R = 0.75$), and thus the landscape-based SAR gave a good fit to the data in this experimental system.

At the patch scale, there was a pronounced difference in the scaling of mean patch richness (averaged over patches within each landscape, \bar{S}_{PIL}) between clumped and fragmented landscapes (fragmentation effect: $F_{1,24} = 17.45$, $P = 0.0003$, two-way

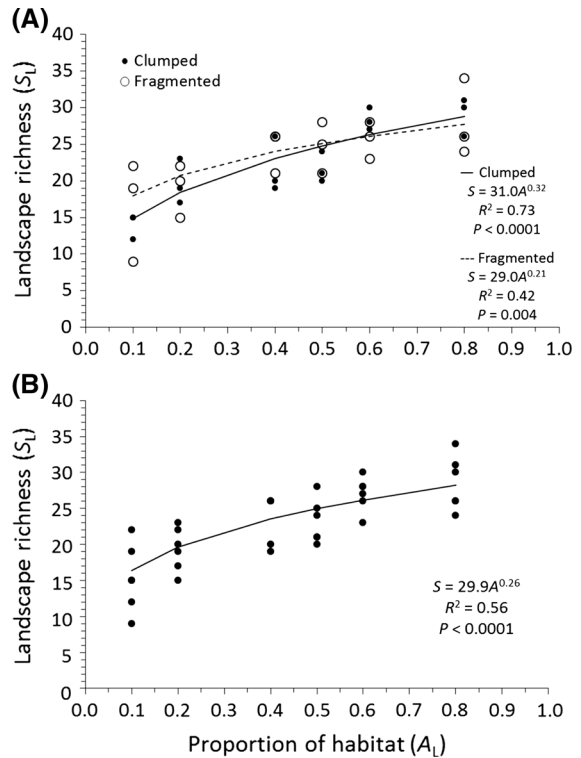


Fig. 2 Species–area relationship based on landscapes. **a** Comparison of clumped and fragmented landscapes ($n = 18$ plots each). **b** Combined species–area relationship over all landscapes ($n = 36$ plots)

ANOVA; Fig. 3a). The average patch on clumped landscapes had $1.7\times$ more species than the average patch on fragmented landscapes (clumped: $\bar{S}_{PIL} = 16.2 \pm 7.71$ SD, $n = 18$; fragmented: $\bar{S}_{PIL} = 9.5 \pm 5.27$ SD, $n = 18$), which might be expected given that the average patch size was greater in clumped than in fragmented landscapes (Supplemental Fig. 1b). Still, patches on fragmented landscapes gained species at a faster rate than those on clumped landscapes (fragmented: $z = 0.87$, clumped: $z = 0.47$), although the fit of this relationship was not particularly good for clumped landscapes (clumped: $R^2 = 0.34$, $P = 0.01$; fragmented: $R^2 = 0.59$, $P = 0.0002$), and the slopes were not in fact statistically different ($t_{32} = 1.44$, $P = 0.16$). A much better fit was obtained when individual patches were the unit of analysis and patch richness (S_P) was modeled as a function of patch area, A_P ($R^2 = 0.90$, $P < 0.0001$), where species richness scaled as a power of 0.37 of patch size (Fig. 3b). The effect size—the strength of the relationship between

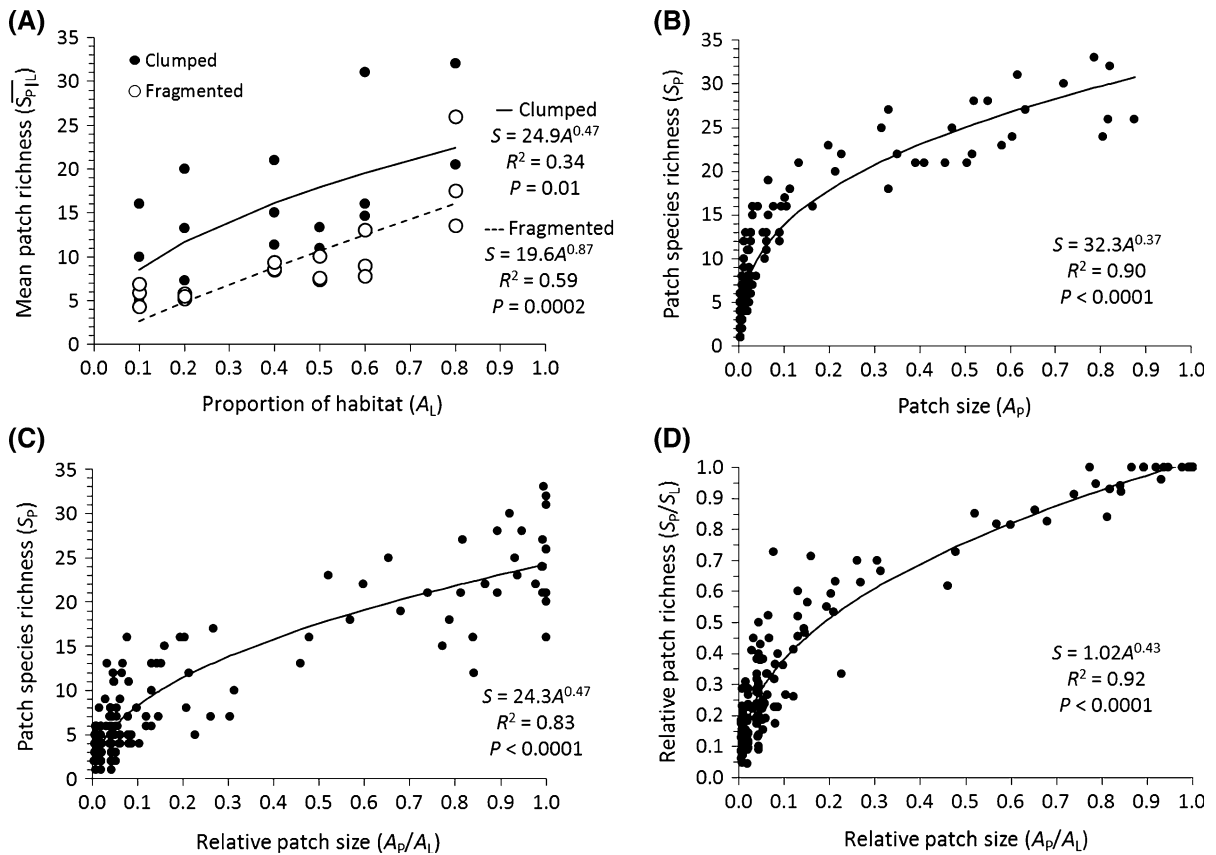


Fig. 3 Species–area relationships based on patches. **a** Comparison of mean patch species richness (\bar{S}_{PIL}) within clumped versus fragmented landscapes ($n = 18$ plots each). **b** Patch species richness (S_P) as a function of patch area ($n = 167$

patches). **c** Patch species richness (S_P) as a function of relative patch size (A_P/A_L ; $n = 167$ patches). **d** Relative patch species richness (S_{PIL}) and relative patch area (A_{PIL} ; $n = 167$ patches)

patch area and patch-species richness—was quite large ($R = 0.95$). If patch size is standardized as a function of available habitat on the landscape (relative patch size, A_P/A_L), species richness scaled as a power of 0.47 (Fig. 3c). The effect size for this relationship was also quite large ($R = 0.91$). Nevertheless, there was a good deal of variability among patches that made up $\geq 80\%$ of the available habitat on a given landscape, which may account for the slightly poorer fit ($R^2 = 0.83$, $P < 0.0001$) compared to the previous analysis. The patches in this domain (those making up $\geq 80\%$ of available habitat) came from a wide variety of landscapes: although all landscapes with $\geq 60\%$ habitat had most of that habitat concentrated in one large patch ($A_P/A_L \geq 0.8$), there were some fragmented landscapes with 40–50% habitat and even some clumped landscapes with only 10–20% habitat that

likewise had most of their habitat contained within a single patch. Thus, landscape context (whether this large patch is in a 10% clumped landscape or a 40% fragmented landscape) explains the wide range of variability in S_P observed within this domain (Supplemental Fig. 2). Finally, a power function fit to the relationship between relative patch richness (S_P/S_L) and relative patch area (A_P/A_L) gave the best fit with the strongest effect size of all the SARs considered here ($z = 0.43$, $R^2 = 0.92$, $R = 0.96$; Fig. 3d). Patches that made up 57% of the total habitat on the landscape were predicted to have 80% of the species found on that landscape.

In comparing the landscape-based SAR (Fig. 2b) with the most-relevant patch-based SAR (Fig. 3b), it appears that patches gained species at a faster rate ($z = 0.37$) than did landscapes ($z = 0.26$). Not only

was this difference between slopes statistically significant ($t_{199} = 2.38$, $P = 0.018$), but the correlation coefficients (R) between these two relationships also differed significantly ($Z = -4.5$; $P = 0.000$). This degree of difference between correlation coefficients thus gives a large effect size (Cohen's $q = 0.852$). Patch-based and landscape-based SARs are not congruent, therefore.

At the scale of the individual cell, neither patch nor landscape context (i.e., the size of the individual patch, A_P , the total amount of habitat within the plot, A_L , or relative patch area, A_P/A_L) had an overall effect on mean cell species richness (\bar{S}_{CIL} or \bar{S}_{CIP} ; all $z = 0$, $R^2 = 0$, $P = 1.000$). Cell species richness averaged about 3 morphospecies/cell, which represents the minimum effect of habitat area (1 m^2) on species richness in this system. However, there was a great deal of variability in the mean patch-cell richness (\bar{S}_{CIP}) for very small patches (≤ 7 cells or $A_P \leq 0.027$; Supplemental Fig. 3). This is reminiscent of a “small-island effect” (Lomolino and Weiser 2001), in which species richness cannot be predicted below some threshold patch (island) size, owing to the vagaries of colonization, degree of patch (island) isolation, or other stochastic environmental factors that are able to exert a greater influence on small patches than on larger ones (Triantis et al. 2006). Although mean cell richness within patches generally does not vary as a function of patch size (cells in large patches have as many species as cells in small patches, on average), very small patches—such as those made up of a single cell—have a more variable (and therefore less predictable) level of species richness. For example, $\bar{S}_{CIP} = 3.5$ (SD = 1.32, range = 1–6 morphospecies, $n = 70$ patches) for single-celled patches, but $\bar{S}_{CIP} = 3.0$ (SD = 0.83, range = 1.7–4.7 morphospecies, $n = 46$ patches) for larger patches ($A_P \geq 0.03$ or > 7 cells).

Discussion

From a spatial scaling standpoint, the SAR is as fundamental to landscape ecology as it is to the fields of biogeography, macroecology, and community ecology. Because the SAR reflects how species richness is structured spatially, it offers an opportunity to study how various factors influence the spatial

distribution of species at a community level, and at what scales (Scheiner et al. 2000). In this experimental model landscape system, in which the amount and distribution of habitat were controlled, the relationship between arthropod richness and habitat area was reasonably well-described by a power-law function at all scales ($R^2 = 0.56$ – 0.92). Furthermore, effect sizes—the strength of the relationship between species and area—were all considered to be “large” (all $R > 0.5$; Cohen 1988). Although a power law implies scale-invariance, scale is ultimately defined by three components: grain, extent, and focus (Scheiner et al. 2000; Scheiner 2003). In the context of this study, the focus was defined by the spatial unit of analysis (patches vs. landscapes), as well as by the inference space represented by the data (e.g., whether each data point represented an individual patch, S_P , or the average patch richness within landscapes, \bar{S}_{PIL}); both grain and extent were held constant. Thus, the SARs examined by this study differed in focal scale, producing very different scaling relationships (z) depending on whether patches or landscapes were assessed. This scaling distinction is important because most studies on habitat-area effects are conducted at a patch scale, which assumes that we can scale-up from patches to predict the consequences of habitat loss (a reduction in habitat area) on species richness at a landscape scale. The results of this study suggest we should approach such extrapolations with caution.

In this experimental landscape system, patches gained species at a faster rate than did landscapes ($z = 0.37$ vs. 0.26 , respectively). This difference in slopes, which was significant, contributed to domains of incongruity between patch-based and landscape-based SARs (Fig. 4). Below about 30 % habitat, landscape richness (S_L) exceeded patch richness (S_P) for a given area (i.e., where $A_L = A_P$). Information on species richness obtained at a patch scale (S_P) would thus tend to underestimate species richness at the landscape scale (S_L) for these lower habitat amounts. In this domain, the details of how patches are arrayed (landscape configuration) clearly matter, for species richness is greater for collections of patches (landscapes) than for individual patches of the same area. In particular, 10–20 % fragmented landscapes had more species (on average) than 10–20 % clumped landscapes (Fig. 2a). This may at first seem surprising, as fragmentation is generally viewed as having a

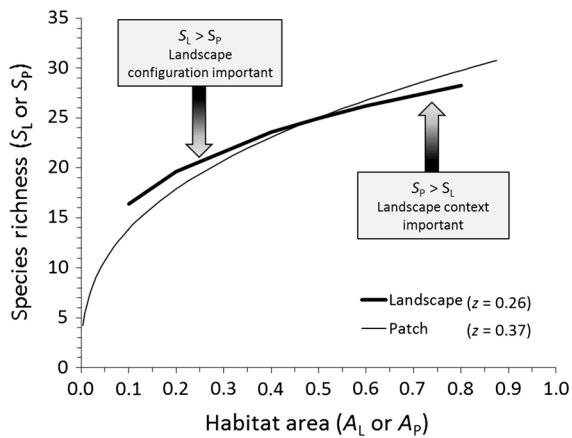


Fig. 4 Comparison of species–area curves derived for patches versus landscapes, illustrating the domains where landscape richness exceeds patch richness ($S_L > S_P$ when $A \leq 0.3$) and where patch richness exceeds landscape richness ($S_P > S_L$ when $A \geq 0.6$)

negative effect on species richness, especially at low levels of habitat (Andrén 1994; Fahrig 2003). Given that these clover landscapes are colonized through a process of random assembly, however, small patches have few species (low α diversity) but high species turnover (β diversity; With and Pavuk 2012). The result is that 10–20 % fragmented landscapes, which have many patches of small size compared to 10–20 % clumped landscapes (Supplemental Fig. 1), tend to have more species at the landscape scale (S_L) in this domain. Thus, landscapes could be said to be more than the sum of their patch areas, at least when habitat is limiting. In this domain, landscape configuration (i.e., the degree of habitat fragmentation, H) influences species richness, such that the number of species cannot be predicted based on habitat area alone.

Above 60 % habitat, however, patch richness (S_P) exceeded landscape richness (S_L) for a given habitat area (Fig. 4). Most landscapes in this domain (9/12 = 75 %) were dominated by a very large patch ($A_P/A_L \geq 0.9$), and thus the distinction between patch and landscape should begin to blur. That it does not entirely do so is apparently a consequence of the broader landscape context in which large patches ($A_P \geq 0.6$) occurred; that is, whether the large patch was in a fragmented or clumped landscape. Although the size of the largest patch did not differ between clumped and fragmented landscapes that had ≥ 60 % habitat (clumped: 179.8 ± 32.19 cells, $n = 6$ patches;

fragmented: 175.5 ± 33.56 cells, $n = 6$ patches), the mean patch size was still lower in fragmented landscapes owing to a greater number of small patches (1–8 cells), especially at 60 % habitat (Supplemental Fig. 1). The presence of small patches in landscapes with otherwise abundant habitat had the effect of reducing the average patch-species richness (\bar{S}_{PIL}), especially for fragmented landscapes (Fig. 3a). In addition, large patches ($A_P \geq 0.6$) in fragmented landscapes had twice as much edge as similarly large patches in clumped landscapes (fragmented: 164.5 ± 18.63 edges/large patch, $n = 4$ patches; clumped = $77.4 + 14.06$ edges/large patch, $n = 5$ patches), as well as a more complex geometry (P/A ; fragmented: 0.87 ± 0.217 , clumped: 0.42 ± 0.092). Negative edge effects may thus have contributed to the lower richness of species found on these large patches in fragmented landscapes (clumped: 29.2 ± 2.59 species/large patch, fragmented: 26.8 ± 4.27 species/large patch). Together, these findings help to explain why species richness at the landscape scale (S_L) is lower than species richness at the patch scale (S_P) when habitat is abundant. In this system, landscapes with abundant habitat (≥ 60 %) are not simply large patches, even though these landscapes are dominated by a large patch that contains most of the species found in that landscape (Fig. 3d; Supplemental Fig. 2). Instead, landscape context—whether the large patch is located within a clumped or fragmented landscape—is important for understanding SARs in this domain.

Recently, there has been some debate in the literature as to the relative importance of the amount versus the configuration of habitat on species richness (i.e., the “habitat-amount hypothesis,” Fahrig 2013, 2015; Hanski 2015). Although the current study was not intended as a formal test of that hypothesis, it does demonstrate that habitat-area effects are ubiquitous, whether one is focused on patches or landscapes (collections of patches) as the spatial unit of interest. Still, there are domains of habitat area where landscape configuration (the arrangement of patches in space) clearly matters. At 10–20 % habitat, species richness was higher within landscapes (collections of patches) than in individual patches of the same total area (Fig. 4), and is higher within fragmented landscapes than in clumped landscapes in that same domain (Fig. 2a). Landscape configuration (H) is thus

clearly having an effect beyond habitat area alone. Conversely, where habitat is abundant and landscape configuration should not matter, large patches ($A_p \geq 0.6$) have more species than landscapes of a similar total habitat area. Even in this domain, fragmented landscapes have more small patches and more edge habitat, which reduces species richness at the scale of the entire landscape relative to patches having the same habitat area. This is more an indirect consequence of landscape configuration, however, because the focus here is on the patch and its broader landscape context (the type of landscape in which the large patch is embedded), rather than on the landscape per se. In short, even if habitat area by itself is the best predictor of species richness, we should not ignore the potential for landscape configuration to directly (or indirectly) influence the scaling of this relationship, causing domains of incongruity between patch-based and landscape-based approaches.

As a caveat, it is worth noting that species richness is only being under- or over-estimated by about two species within these domains of incongruity ($0.3 \geq A \geq 0.6$). In an agriculturally dominated system such as this, which is made up of many widespread and generalist species (With and Pavuk 2011, 2012), most of the species in the regional species pool are able to colonize most of the available habitat. Colonization appears to be a highly stochastic process, such that local species assembly is influenced more by constraints on the broader-scale biogeographic, climatic or land-use factors that influence the regional species pool than by habitat availability per se (Drakare et al. 2006). That may not be the case in systems that are made up of a greater number of more highly specialized, dispersal- and/or area-limited species, however. In that case, such differences between patch-based and landscape-based SARs might well be magnified beyond the differences observed in this experimental system.

As an analogue to the present study, biogeographers have typically assumed that archipelagos follow the same species–area curve as their constituent islands (e.g., Fig. 2.11 in Rosensweig 1995). Regional factors acting on the entire archipelago, such as its geological age and distance from the mainland, are thought to have a homogenizing effect on the types and distribution of species among islands (Santos et al. 2010). That is not to say that species do not differ among

islands within an archipelago, only that these broader-scale factors act as a sort of “filter,” such that the species found on individual islands are a reflection of the species pool of the archipelago as a whole. Indeed, an analysis of SARs for various taxa within 38 island groups (97 taxon/archipelago combinations in total) found congruence between 88 % of archipelagic and island-based SARs (Santos et al. 2010). Thus, archipelagos are generally the sum of their islands, largely because regional-scale processes (degree of isolation, geological characteristics, evolutionary processes) are similar among islands within an archipelago.

Interestingly, a lack of congruence between archipelagic and island-based SARs occurred in systems that exhibited either a high degree of species nestedness, or conversely, a complete lack of nestedness (Santos et al. 2010). Nestedness refers to the degree to which species found within small areas are a nested subset of species found within larger areas (Patterson and Atmar 1986; Ulrich and Almeida-Neto 2012). In highly nested systems, for example, the largest island would contain virtually all of the species found within the archipelago. This is similar to the present study, in which large patches (≥ 57 % total habitat area) contained ≥ 80 % of the species found in the landscape (Fig. 3d). At the other extreme, highly non-nested systems are ones in which each island has its own unique complement of species. Again, this is perhaps akin to the high degree of species turnover that occurs among small habitat patches (e.g., single-celled patches; With and Pavuk 2012), which are particularly common within the 10–20 % fragmented landscapes (60 % of habitat patches within 10 % fragmented landscapes vs. 43 % of patches in 10 % clumped landscapes were single cells). Among single-celled patches, mean patch-cell richness (\bar{S}_{CIP}) was higher within 10 % fragmented landscapes than in 10 % clumped landscapes (fragmented: $3.7 + 1.29$ SD species/cell, $n = 15$ single-celled patches; clumped: $2.7 + 0.58$ SD, $n = 3$ single-celled patches), which again may account for the higher landscape richness observed in fragmented than in clumped landscapes in this domain. Habitat patches may not be true islands, but there appear to be certain similarities here in terms of how incongruities might develop between SARs derived from landscapes or archipelagos, and SARs based on their constituent patches or islands.

Conclusions and implications

In sum, patch-based and landscape-based SARs derived from an experimental model landscape system were not congruent. Fragmented landscapes had more species (on average) than clumped landscapes at low habitat amounts (10–20 %), but patches gained species at a faster rate than did landscapes, resulting in domains of incongruity where the patch-based SAR either under-estimated (at low habitat levels) or over-estimated (at high habitat levels) species richness at the landscape scale. Given that most habitat fragmentation studies are patch-based (Debinski and Holt 2000), such scaling differences between patch- and landscape-based SARs imply that we may not be able to infer the effects of habitat loss and fragmentation (a landscape-wide property) on species richness from the study of patch-area effects.

A lack of congruence between patch-based and landscape-based SARs also has implications for how we should go about studying species–area effects in the first place. For example, the results of this study suggest that although we might be able to capture most of the species present at a landscape scale (S_L) by targeting the largest patch in landscapes having abundant habitat, surveying the largest patch within a landscape with only 10–20 % habitat will likely underestimate the total species present within that landscape. In that case, we need to survey the entire landscape (i.e., all habitat patches) in order to obtain a more precise estimate of species richness at the landscape scale (S_L). That is, we might be able to make a patch-for-landscape substitution in landscapes where habitat is abundant, but not in landscapes where habitat is limiting. It is these latter landscape scenarios that are typically viewed as “fragmented” and in which species diversity is most likely to be threatened, and thus where accurate estimates of SARs are most important (Hanski 2015). Whether we can make these sorts of substitutions or inferences, however, will ultimately depend on how nested species assemblages are within the system, in terms of whether small patches harbor a subset of those species found in larger patches (e.g., Crist and Veech 2006). Further study is therefore needed to determine the generality of these findings, as well as the implications for the study and prediction of species–area effects when using patches versus landscapes as the spatial unit or focus of analysis.

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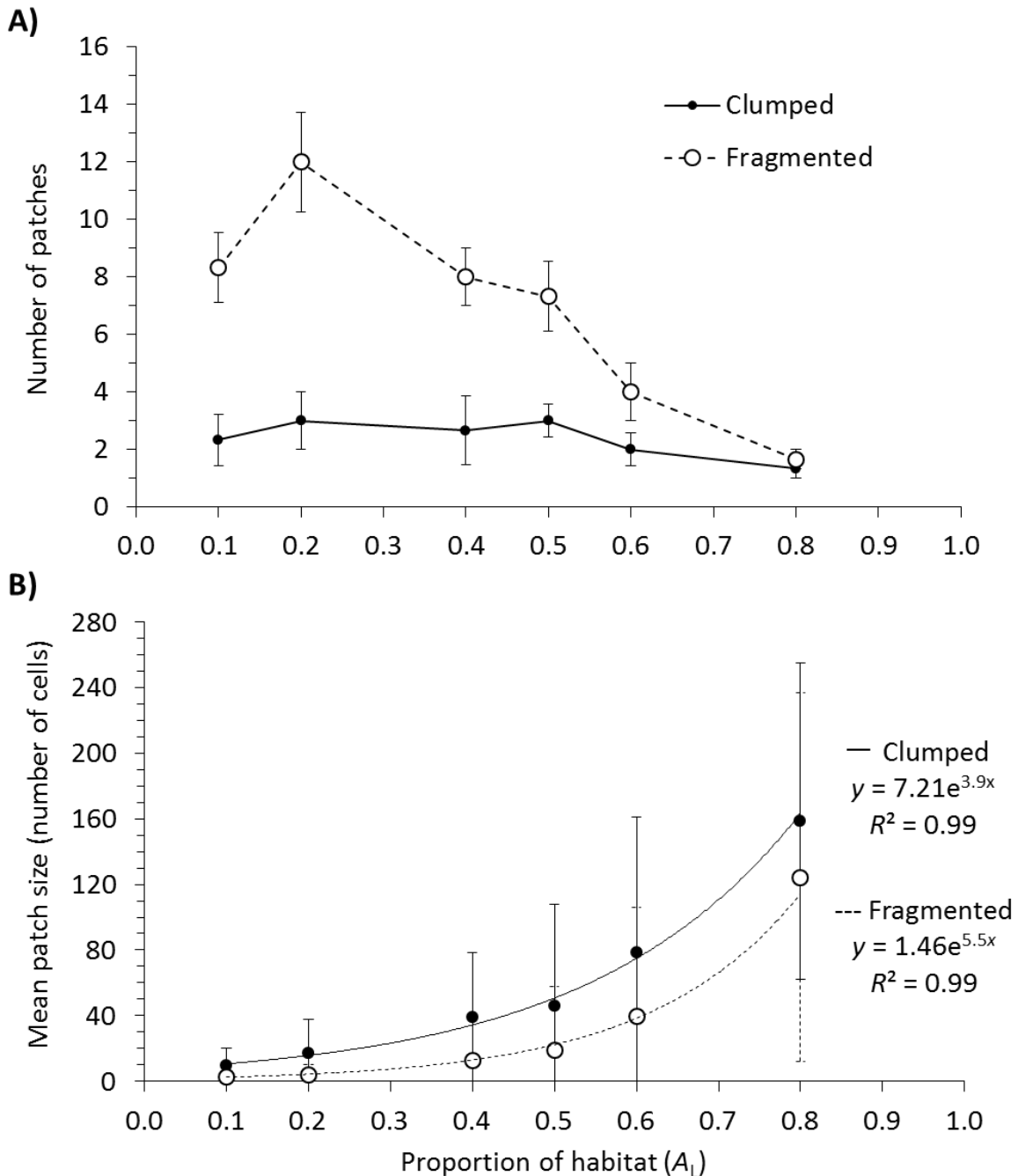
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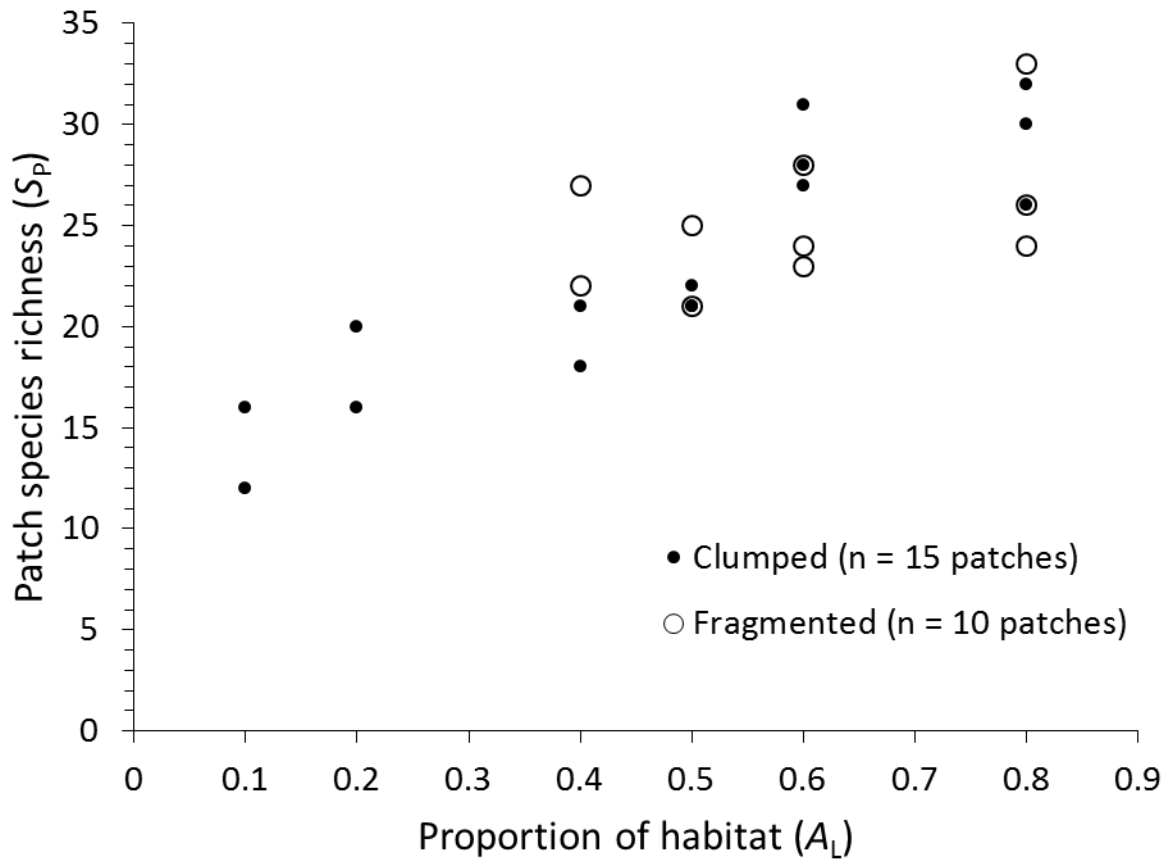
Are landscapes more than the sum of their patches? *Kimberly A. With*

Supplementary Materials

Supplemental Fig. 1 Patch properties of fractal landscapes featured in this experimental model landscape system (cf. Fig. 1). **A)** Difference in the number of patches between clumped and fragmented landscapes ($n = 18$ plots each) as a function of total habitat area. **B)** Difference in patch size between clumped and fragmented landscapes as a function of total habitat area.



Supplemental Fig. 2. Patch-species richness (S_p) within patches that comprised 80% or more of the available habitat on the landscape (i.e., $A_p/A_L \geq 0.8$; $n = 25$ patches), as a function of landscape context, defined in terms of the amount (A_L) and configuration of habitat (clumped vs. fragmented) on the landscape. Note that whereas all landscapes with 60% or more habitat ($A_L \geq 0.6$) are dominated by a large patch ($A_p/A_L \geq 0.8$), even some 10-20% clumped landscapes have most habitat concentrated within one patch. Landscape context thus accounts for the variability in patch-species richness (S_p) observed as a function of relative patch size in this domain (i.e., $A_p/A_L \geq 0.8$; Fig. 3C).



Supplemental Fig. 3 Although mean patch-cell richness ($\bar{S}_{C|P}$) does not vary as a function of patch size overall, there is a great deal of variability evident for very small patches ($A_p \leq 0.027$ or patch size ≤ 7 cells). This is reminiscent of a “small-island effect,” in which stochastic influences on colonization outweigh the minimum-area effects on species richness.

