



Spatial scaling of species richness–productivity relationships for local communities: analytical results from a neutral model

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Abstract

The relationship between species richness and productivity changes with spatial scale, but the way in which it changes and the underlying mechanisms remain unclear. We address this critical knowledge gap using a new mechanistic model of the spatial scaling of species richness–productivity (SP) relationships for a local community. Our model is neutral and hence assumes that species dynamics are driven by dispersal limitation and demographic stochasticity. We showed analytically that SP relationships predicted by our model are typically unimodal. Consistent with previous simulation-based studies, the positive phase of our unimodal SP relationship was driven by a sampling effect (“more-individuals effect”) whereas the negative phase was driven by relatively more propagules being of local as opposed to external origin (“dilution effect”). Our main novel finding related to the spatial scaling of the unimodal SP relationship: the peak shifted to the left with increasing spatial scale, such that the decreasing phase covered a greater range of productivity. This was driven by an increase in the strength of the dilution effect relative to the more-individuals effect, reflecting higher area/perimeter ratios at larger spatial scales. Our theoretical predictions are qualitatively consistent with the spatial scaling of SP relationships documented for trees in localized forest communities across the world.

Keywords Biodiversity · Neutral model · Productivity · Spatial grain · Species richness

Introduction

Ecological processes occur over a broad range of spatial scales. Plants obtain water and nutrients using root networks that typically stretch through meters of soil (Schenk and Jackson 2002); seeds typically disperse over tens to hundreds

of meters (Clark et al. 1999; Levin et al. 2003), and terrestrial animals may travel over kilometers of land (Tucker et al. 2018). Accordingly, the relative strengths of different processes change across spatial scales, resulting in non-trivial qualitative changes in community patterns. Classic examples include the different forms of species-abundance distributions from local to regional scales (Borda-de-Água et al. 2012; Rosindell and Cornell 2013) and the tri-phasic scaling of species richness with area (Preston 1960; O’Dwyer and Green 2010). Another well-studied pattern that exhibits spatial scaling is the species richness–productivity (SP) relationship, where productivity is plotted on the *x*-axis and species richness is plotted on the *y*-axis. Meta-analyses of observed SP relationships in different types of ecosystems have found that the relationships are typically unimodal or positive (Waide et al. 1999; Mittelbach et al. 2001; Gillman and Wright 2006). However, the corresponding debate as to which shape is more prevalent has been confounded partly by insufficient attention to the issue of scale (Whittaker 2010). To clarify matters, there is a clear need for empirical analyses that control for spatial scale (e.g., Adler et al. 2011; Fraser et al. 2015) and also for empirical analyses of the same system at different spatial scales (e.g., Chase and Leibold 2002; Chisholm et al.

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2013). In conjunction with these analyses, there is also a clear need for theoretical models that can be used to investigate how the spatial scaling of SP relationships is affected by the interaction of ecological mechanisms with different characteristic spatial scales (e.g., Weitz and Rothman 2003).

Most theoretical explanations for empirical SP relationships invoke niche mechanisms. For example, a local, unimodal SP relationship can theoretically arise from a trade-off between competitive ability and tolerance to stress or disturbance (Grime 1977, 1979; Connell 1978; Chapin 1980; Huston 1979, 1994; Abrams 1995; Kondoh 2001) or from a paucity of species adapted to extremely low or high productivities (the species pool hypothesis; Taylor et al. 1990; Schamp et al. 2003; Aarssen 2004). More recent theory has highlighted how SP relationships exhibit bivariate causality—not only does productivity affect species richness, but species richness also tends to have a positive effect on productivity via niche partitioning among species and facilitation between species (Gross and Cardinale 2007; Cardinale et al. 2009a; Grace et al. 2016; Hodapp et al. 2016). There is also increasing recognition that species richness and productivity are embedded in a causal network with other variables (Gross and Cardinale 2007; Cardinale et al. 2009a, 2009b; Grace et al. 2016; Lewandowska et al. 2016). This network approach emphasizes how species richness and productivity can be affected by other variables. For example, if species have trade-offs in how efficiently they use different resources, then species richness is expected to increase as the rates of supply of different resources become more balanced (Tilman 1982; Cardinale et al. 2009a).

However, instead of invoking niche mechanisms, a theoretical study by Kadmon and Benjamini (2006) surprisingly showed that local, unimodal SP relationships could arise from a neutral model, i.e., from just dispersal limitation and demographic stochasticity. In their model, a community with more individuals produces biomass at a higher rate and hence has greater productivity, defined as the rate of production of biomass per unit area. In addition, the greater number of individuals has a positive effect on species richness because of the tendency for more individuals to comprise more species, via a simple sampling effect. This indirectly induces a positive correlation between productivity and species richness, and is termed the “more-individuals effect” (this effect is related to the broader “more-individuals hypothesis,” which further posits that variation in the number of individuals is driven by variation in energy availability; Wright 1983; Srivastava and Lawton 1998; Yee and Juliano 2007; Storch et al. 2018). The more-individuals effect becomes weaker as the community becomes saturated with individuals. Based on these considerations alone, the SP relationship would exhibit an increasing, saturating shape. However, a different process acts in the opposing direction, serving to decrease species richness as productivity increases locally. This process is the increased production of propagules of local origin, which dilutes the proportion of immigrant propagules and thereby limits their

establishment, ultimately exerting a negative effect on species richness—the “dilution effect” (Kadmon and Benjamini 2006; Allouche and Kadmon 2009a, 2009b). Overall, as we move up the productivity gradient, the dilution effect increasingly dominates the more-individuals effect, resulting in unimodal SP relationships (Kadmon and Benjamini 2006; Fig. 1).

We thus see that there are two broad classes of potential explanations for observed SP relationships: niche and neutral explanations. These explanations are by no means mutually exclusive, and both sets of mechanisms likely operate to some degree in any given ecosystem. But there is a need to tease out the relative importance of each in different contexts. To date, empirical SP patterns have mostly been uncritically attributed to niche mechanisms based on qualitative arguments. The lack of rigorous quantitative tests of the mechanisms driving SP patterns is largely due to lack of quantitative, mechanistic models that predict SP relationships at different spatial scales. Here, we address this key knowledge gap by developing such a model for communities at local scales. Our model is neutral in the sense that it does not incorporate differences in species’ demographic rates. The rationale for using a neutral model is that (i) it provides a useful baseline for comparison with more complex scenarios that have species differences and (ii) it is parsimonious with respect to model structure, which aids in development of quantitative predictions that can be tested empirically. Thus, the utility of the model is actually dependent on its neutral assumption—if instead species differences are included in the model, then the model cannot be used as a baseline that excludes the effects of species differences, and in addition, the model would likely be too complex to yield analytical formulae from which quantitative predictions can be made. Even if our neutral model predictions are found to deviate substantially from empirical observations for a particular system, then this is informative because it indicates the importance of non-neutral mechanisms (the model “fails” in an informative way; Wennekes et al. 2012). These considerations clearly distinguish the aim of our study from previous work that sought to synthesize the spectrum of mechanisms that underpin the SP relationship (e.g., Cardinale et al. 2009a; Grace et al. 2016).

Building on previous work that examined SP relationships from neutral models at a fixed spatial scale (Kadmon and Benjamini 2006; Allouche and Kadmon 2009a, 2009b), we hypothesize that with increasing spatial scale in a local community (where biotic interactions can have substantial effects on community patterns), the strength of the dilution effect relative to the more-individuals effect would increase because of a greater area/perimeter ratio, which increases the ratio of local to immigrant propagules. Consequently, we expect the peak of a unimodal SP relationship from our neutral model to move to the left with increasing spatial scale, such that the decreasing phase occupies an increasingly larger range of productivity (Fig. 1). In our analyses, we first derive a formula quantifying SP relationships from the model as a function of spatial scale. Secondly, we use this

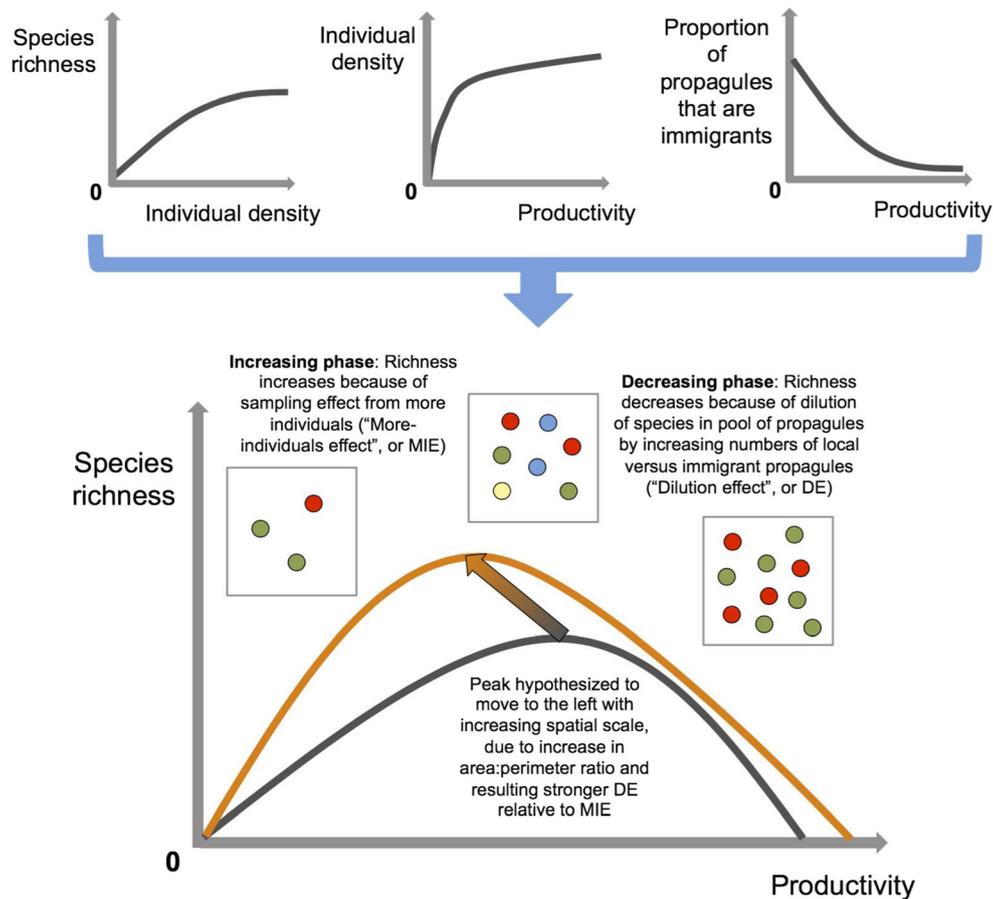


Fig. 1 Conceptual diagram showing how a unimodal relationship between species richness and productivity arises under a neutral model, and how the peak of this relationship is hypothesized to move to the left as spatial scale increases. The three bivariate relationships driving unimodal species richness–productivity relationships in the model. The number of species is conceptualized as increasing with the density of individuals in a saturating way, representing a sampling effect called the “more-individuals effect” (MIE) (first graph in top row). An increase in the density of individuals also gives rise to an increase in (realized) productivity, giving a positive relationship between these two variables (second graph in top row). As productivity increases,

the relative number of immigrant versus locally produced propagules decreases, representing the “dilution effect” (DE) (third graph in top row). The MIE and DE together produce the unimodal species richness–productivity relationship represented by the black line in the bottom panel. The three square insets illustrate in more detail how species richness increases due to the MIE and decreases due to the DE. In these insets, each circle corresponds to an individual and the different colors refer to different species. As spatial scale increases, the peak of the unimodal species richness–productivity relationship is hypothesized to move to the left, as represented by the arrow and orange line in the bottom panel

formula to examine how SP relationships are expected to change with spatial scale. Thirdly, we relate the observed trends to changes in the relative strengths of the underlying mechanisms, by deriving formulae quantifying the strengths of the more-individuals and dilution effects and using the formulae to examine how the relative strengths of the two effects are expected to change with spatial scale.

Methods

Overview of neutral model used

We started with a model specifying the neutral dynamics of a community of species competing for finite resources,

which is the “local” neutral model formulated by Hubbell (2001). In this model, individuals of all species have the same intrinsic per-capita birth and death rates (Hubbell 2001). The community receives immigrants from a surrounding metacommunity, which consists of a much larger number of individuals of different species, also undergoing neutral dynamics. Therefore, abundances vary across species within the local community only because of demographic stochasticity, which produces ecological drift, and different immigration rates arising from different abundances in the metacommunity (Hubbell 2001). In each time step, one individual dies and is replaced by a newborn individual in the community or an immigrant (Hubbell 2001). Thus, over time, the community remains at a constant size, which reflects a given amount of resources.

For this model, the expected number of species at dynamic equilibrium (for sufficiently large community sizes)

$$S \approx \theta \log \left(1 - \frac{Jm}{\theta(1-m)} \log(m) \right) \quad (1)$$

where J is the number of individuals in the local community, θ is the fundamental biodiversity number specifying the number of species in the surrounding metacommunity, and m is the probability that a new individual is an immigrant (Volkov et al. 2007). As originally formulated, this model does not explicitly refer to productivity or spatial scale. Therefore, we extended the model by explicitly including both factors, as described in the next subsection.

Extending the neutral model to include productivity and spatial scale

Formula (1) gives a relationship between species richness and the three parameters of the neutral model: J , m , and θ . To convert this into a spatial SP relationship, there is a need to express these three parameters in terms of productivity and the area of the local community. The metacommunity diversity θ can be assumed to be independent of both productivity and area of the local community, but for the other two parameters, J and m , the relationship with productivity and area is more complex. For simplicity, in our description below, we have assumed that the local community occupies a square area A of edge length L ; similar results obtain for rectangular and circular areas (see “Results”). Thus, we have interpreted L as a parameter defining the spatial scale. More precisely, if we consider the local community as a sample from a larger community, then L corresponds to the spatial grain of the sampled area (Whittaker and Heegaard 2003). Because L refers to a continuous area of suitable habitat, the local community does not consist of patches of suitable habitat surrounded by a matrix of unsuitable habitat, which instead refers to a fragmented landscape (as in the model of Gross and Cardinale (2007) and the empirical study by Chase and Leibold (2002), both of which examine the spatial scaling of SP relationships).

To derive a relationship of immigration parameter m to productivity P and area A , we first related m to propagule rain (cf. Chisholm and Lichstein 2009), which was then related to P . We conceptualized P as the rate of production of biomass per unit area, which measures the rate of carbon flux through individuals in a community. Thus, P represents the actual or realized productivity, which is different from the potential productivity that is determined by the rates of supply of all relevant resources (Loreau et al. 2001). Specifically, we defined m as the ratio of the number of immigrants arriving per unit time (I_{imm}) divided by the sum of I_{imm} and the number of

newborn individuals produced by individuals in the local community per unit time (I_{local}). We assumed that I_{imm} was proportional to the perimeter of the local community, such that $I_{\text{imm}} = 4\alpha L$, where $4L$ is the perimeter, and α is a constant. In addition, I_{local} was assumed to be proportional to total production AP , such that $I_{\text{local}} = \beta AP = \beta L^2 P$, where β is a constant. Putting all this together gave an expression for the immigration parameter in terms of the local community’s spatial geometry and productivity:

$$m = \frac{I_{\text{imm}}}{I_{\text{imm}} + I_{\text{local}}} = \frac{4\alpha L}{4\alpha L + \beta L^2 P} = \frac{1}{1 + \eta LP} \quad (2)$$

where $\eta = \beta/4\alpha$ is a “recruitment constant” measuring the rate at which local propagules are produced per unit production relative to the rate at which immigrant propagules arrive per unit perimeter of the modeled area.

To derive a relationship of local community size (number of individuals) J to productivity and area, we first assumed that productivity P was a linear function $P = \kappa B$ of biomass density B , reflecting the generally positive relationship between these two ecosystem components in empirical data (e.g., Adler et al. 2011; Chisholm et al. 2013; Fraser et al. 2015). We then assumed for simplicity that individual density $\rho = J/A = J/L^2$ does not vary with spatial scale L , which implies that J varies proportionally with area A and also implies that B varies only with ρ and not L (Appendix A in Electronic Supplementary Material (ESM)). Therefore, we are conceptualizing ρ as the driver of B and hence P , i.e., the number of individuals in a given area drives productivity. This allowed us to write $P = \kappa B(\rho)$, which we subsequently inverted to give ρ as a function of P , $\rho(P)$. We note that the inverted function $\rho(P)$ is not to be interpreted as meaning that P drives ρ —our conceptualization is in fact the opposite. In our model, the variables driving changes in ρ are unspecified but one possibility is that ρ is driven by the potential productivity (Loreau et al. 2001).

Substituting expression (2) for m and the general function $\rho(P)$ into (1) resulted in the following scale-dependent SP relationship:

$$\begin{aligned} S(P, L) &\approx \theta \log \left[1 - \frac{J}{\eta \theta LP} \log \left(\frac{1}{1 + \eta LP} \right) \right] \\ &= \theta \log \left[1 + \frac{L \rho(P)}{\eta \theta P} \log (1 + \eta LP) \right] \end{aligned} \quad (3)$$

where community size J has been written as $A\rho(P) = L^2\rho(P)$.

We note here that because the model is neutral, there is no niche partitioning among species or facilitation between species, and thus there is no causal link from species richness to

productivity. The neutral assumption also means that in our model, it is not possible to represent changes in species richness arising from changes in the stoichiometric ratios of different limiting resources, because such changes in species richness depend on trade-offs in how efficiently different species use different resources (Tilman 1982).

Examining the spatial scaling of the species richness–productivity relationship

Using the formula relating species richness S , productivity P , and spatial scale L (Eq. (3)), we proceeded to examine how the SP relationship changes with L . We first determined how S changes with P given fixed L , by differentiating S with respect to P while holding L constant. By doing so, we found that S often exhibited a unimodal shape with increasing P regardless of spatial scale L (see “Results”). In this case, S reached a maximum at one value of P , which we refer to as the maximizing value of P . This value of P is ecologically important because it determines the range of P over which S is increasing or decreasing, and the maximum realized species richness of the system. Therefore, we next derived a formula specifying the maximizing value of P as a function of spatial scale L and determined how the maximizing value changes with L by differentiating the formula with respect to L .

To obtain a mechanistic insight into how the SP relationship changes with spatial scale L , we quantified the relative strengths of the more-individuals and dilution effects for given L , and then determined how these change with increasing L . Our expectation was that the relative strength of the dilution effect would increase with L because of an increase in the area/perimeter ratio, such that the maximizing P occurs at a smaller value for larger L . Specifically, we partitioned the rate of change of species richness S with P according to the more-individuals and dilution effects as follows:

$$\frac{dS}{dP} = \frac{\partial S}{\partial J} \frac{\partial J}{\partial P} + \frac{\partial S}{\partial m} \frac{\partial m}{\partial P} \quad (4)$$

The first term on the right is positive because $\partial S/\partial J > 0$, from Eq. (1), and $\partial J/\partial P > 0$, from the positive linear relationship between J and individual density ρ (see above) together with the positive relationship between ρ and P arising from model analysis (see condition (5b) in “Results”). Therefore, the first term measures the rate of increase in S due to any increase in J associated with greater P and was interpreted as the strength of the more-individuals effect. The second term on the right is negative because $\partial S/\partial m > 0$, from Eq. (1), and $\partial m/\partial P < 0$, from Eq. (2). Therefore, the second term measures the rate of decrease of S due to any decrease in the immigration probability m arising from greater P and was interpreted as the strength of the dilution effect. The ratio between the first and

second terms was used as a measure of the strength of the more-individuals effect relative to that of the dilution effect. We examined how this ratio changed across P as the spatial scale L increases.

Results

Examining how the species richness–productivity relationship changes with spatial scale

Using the formula that we derived for the SP relationship from our neutral model (Eq. (3)), we first calculated the rate of change of species richness S with productivity P given spatial scale L , that is, $\partial S(P, L)/\partial P$. By examining the resulting form of $\partial S(P, L)/\partial P$, we found that S exhibits a unimodal relationship with P if

$$1 + P \frac{d^2 \rho(P)/dP^2}{d\rho(P)/dP} \leq P \frac{d\rho(P)/dP}{\rho(P)} < 1 \quad (5a)$$

and

$$d\rho(P)/dP > 0 \quad (5b)$$

(Appendix B in ESM). Here, $\rho(P)$ is the individual density written as a function of P . Because the biomass density $B = P/\kappa$ (see “Methods”), where κ is a positive constant, we see that (5a) is equivalent to

$$1 + B \frac{d^2 \rho(B)/dB^2}{d\rho(B)/dB} \leq B \frac{d\rho(B)/dB}{\rho(B)} < 1 \quad (6a)$$

and $d\rho(P)/dP > 0$ is equivalent to

$$d\rho(B)/dB > 0 \quad (6b)$$

Given any functional form of individual density $\rho(B)$ satisfying (6a, 6b), we showed that the peak of the resulting unimodal SP relationship always moves to the left with increasing spatial scale L (Appendix C in ESM). As an illustrative example, if $\rho(B)$ is a concave power-law form with exponent less than one, then (6a, 6b) is satisfied (Appendix B in ESM). This power-law form corresponds to the biologically plausible situation where the number of individuals increases sublinearly with biomass due to the number of individuals in the community approaching a carrying capacity, which forces any further increase in biomass to be largely due to existing individuals growing bigger rather than the appearance of more individuals. Using this specific power-law form for $\rho(B)$, we illustrated the leftwards shift in the peak of the unimodal SP

relationship with increasing L for particular parameter values (Fig. 2).

Our result shows that for a large class of functions $\rho(B)$, the SP relationship is unimodal from our model and has a peak at lower values of productivity P when spatial scale L increases, corresponding to an ever broader decreasing phase. This is also the case when the focal area is rectangular or circular rather than square (Appendices B and C in ESM).

Partitioning effects of productivity on species richness according to underlying mechanisms

Using the expression for species richness S from our model (Eq. (1)) and the fact that community size $J = L^2 \rho(P)$, we derived the following expression for the more-individuals effect:

$$\text{MIE} = \frac{\partial S}{\partial J} \frac{\partial J}{\partial P} = L^2 \frac{d\rho(P)}{dP} \left(\frac{-\theta m \log(m)}{\theta(1-m) - Jm \log(m)} \right) \quad (7)$$

Because the immigration probability m lies in the range $0 < m < 1$, the more-individuals effect as specified by (7) is positive when $d\rho(P)/dP > 0$, which is the same as condition (5b) for the SP relationship to be unimodal. Similarly, using the

expression for S and the expression for m from our model (Eq. (2)), we derived the dilution effect as

$$\text{DE} = \frac{\partial S}{\partial m} \frac{\partial m}{\partial P} = -\frac{\eta L^3 \rho(P)}{(1 + \eta L P)^2} \times \left(\frac{\theta(-1 + m - \log(m))}{(1-m)(\theta(1-m) - Jm \log(m))} \right) \quad (8)$$

which is always negative because $0 < m < 1$ and $-1 + m - \log(m) > 0$. To determine how the strength of the more-individuals effect relative to the dilution effect changes with spatial scale L , we see from (7) and (8) that

$$\frac{\text{MIE}}{|\text{DE}|} = \left[\frac{d\rho(P)}{dP} \frac{1 + \eta L P}{\eta L \rho(P)} \right] \left[1 / \left(\frac{1}{\log(m)} + \frac{1}{1-m} \right) \right] \quad (9)$$

which is a decreasing function of L (using the form of m specified by Eq. (2)). Therefore, the relative strength of the more-individuals effect decreases with L at all values of P , such that the more-individuals effect is outweighed by the dilution effect at a lower value of P (Fig. 3). From Eq. (4), this means that S starts to decrease at a lower value of P as

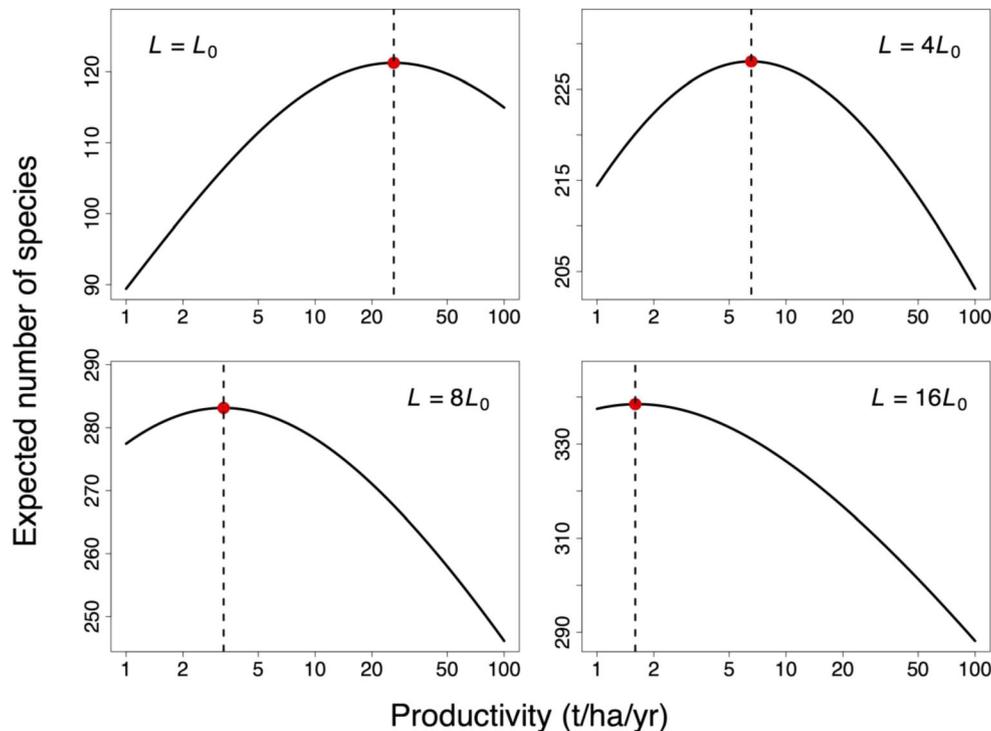
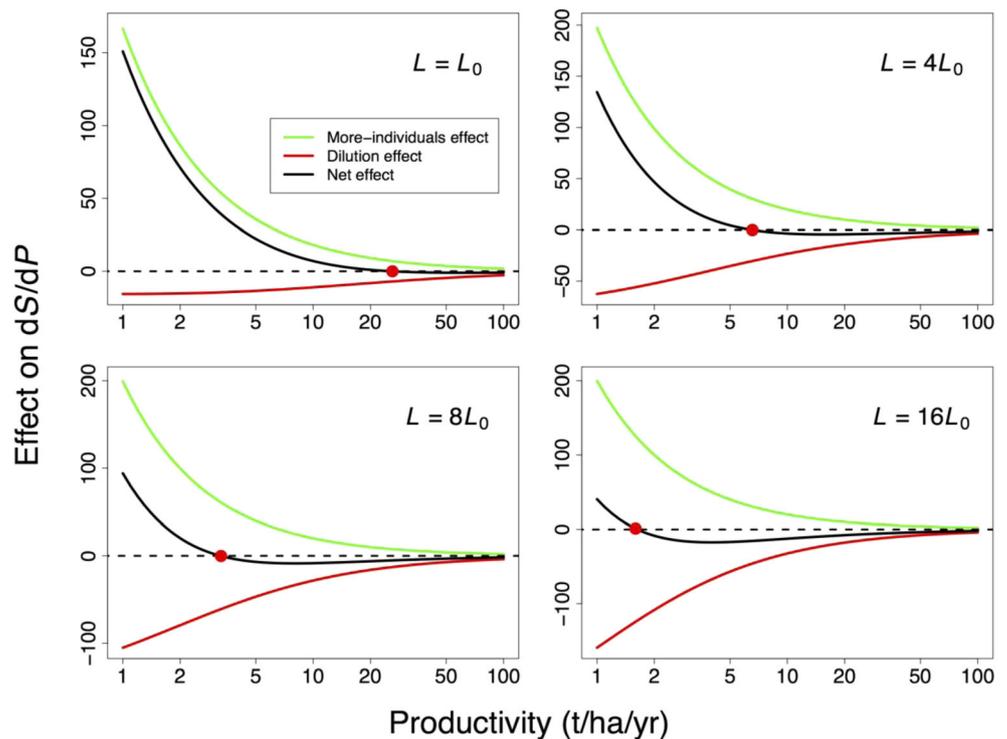


Fig. 2 Relationships between (expected) species richness and productivity from a neutral model, as the spatial scale (edge length of a square) increases from $L = L_0$ to $16L_0$, where $L_0 = \sqrt{1000}$ m = 31.6 m. The dashed vertical lines mark the peaks of the unimodal relationships. The solid black lines refer to species richness values obtained from Eq. (3) with fundamental biodiversity number $\theta = 50$, recruitment constant $\eta =$

0.8, and individual density $\rho(P)$ following the concave power-law $26P^{0.4}$. The fundamental biodiversity number θ determines the number of species in the metacommunity, whereas the recruitment constant η measures the rate at which local propagules are produced per unit production (productivity \times area) relative to the rate at which immigrant propagules arrive per unit perimeter of the modeled area

Fig. 3 For the relationships between species richness and productivity presented in Fig. 2 (derived using our neutral model), partitioning of the rate of change of species richness with respect to productivity (dS/dP) according to the “more-individuals effect” and “dilution effect.” The sum of these two effects is also shown (“net effect”). The red dots mark the productivity values at which the net effects are zero, which correspond to the peaks of the (unimodal) relationships between species richness and productivity



spatial scale L increases, i.e., the peak of the unimodal SP relationship shifts to a lower value of P as L increases (Fig. 2).

The results also hold if we consider different plot geometries for our local community. For example, we can interpret L as the length of the longer edge of a rectangular area or the radius of a circular area, in which case we again obtain Eq. (9), with the only difference being that the constant η takes a different value. Therefore, the peak of the unimodal SP relationship again shifts to a lower value of P as spatial scale L increases.

Furthermore, it is clear from Eq. (7) that, regardless of the shape of the area occupied by the local community, the more-individuals effect only operates to increase species richness S when J increases with P for given spatial scale L , i.e., if the density of individuals ρ is associated with greater P for given L . If ρ is held constant across P , then only the dilution effect remains and S always decreases with P (Appendix B in ESM; Fig. 4).

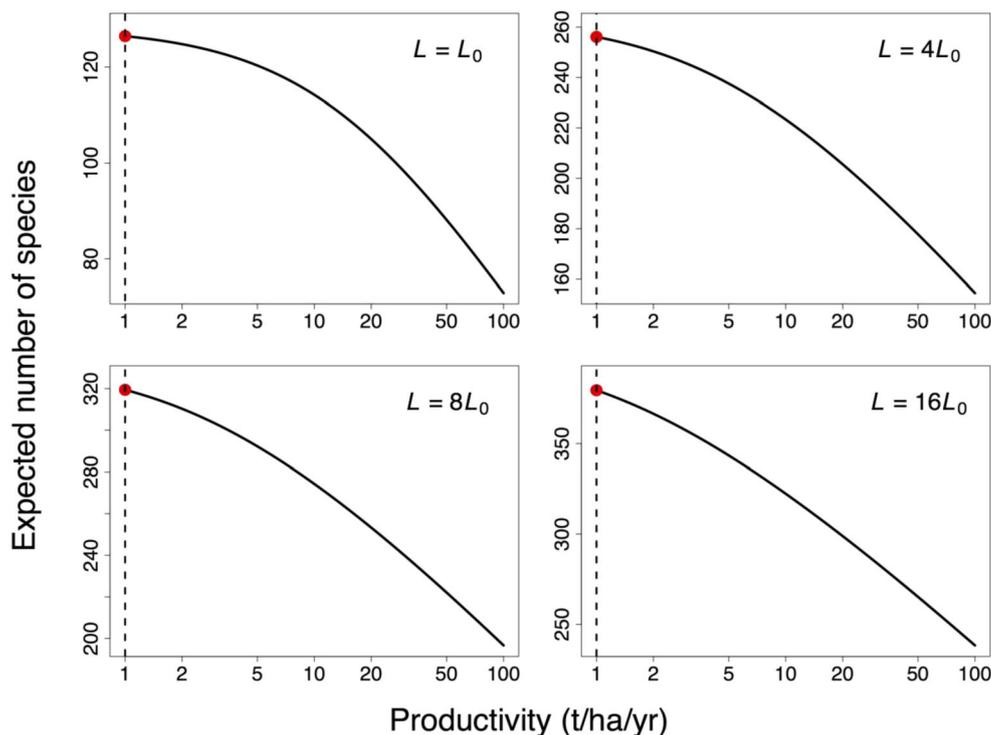
Discussion

The species richness–productivity (SP) relationship has been studied extensively over the last half-century (Grime 1973, 1979; Tilman 1982; Abrams 1988; Tilman and Pacala 1993; Huston and DeAngelis 1994; Mittelbach et al. 2001; Gillman and Wright 2006; Adler et al. 2011; Chisholm et al. 2013; Fraser et al. 2015), but it remains unclear how the shape of the relationship and the mechanisms driving it changes across

spatial scales (Whittaker and Heegaard 2003; Whittaker 2010). A major reason is lack of mechanistic models that can be used to generate quantitative predictions, against which empirical data can be tested. In this context, our main contribution is development of a quantitative, mechanistic model of the spatial scaling of SP relationships at local, within-community scales. This model is neutral, such that species have the same demographic rates and their abundances differ only because of dispersal limitation and demographic stochasticity (Hubbell 2001). Thus, our theory provides baseline predictions against which the effects of species differences can be compared.

The central and most novel result from our analyses is that under neutrality and liberal constraints on how productivity is related to the number of individuals, the peak of the unimodal SP relationship shifts to the left with increasing spatial scale. In our neutral setting, a unimodal SP relationship arises from a balance between two effects. Firstly, the increasing species richness phase of this relationship is driven by a sampling effect from the greater number of individuals associated with higher productivity—the more-individuals effect (Wright 1983; Srivastava and Lawton 1998; Yee and Juliano 2007; Storch et al. 2018). This mechanism has the strongest effect on richness when a local community is far from being saturated by individuals. Secondly, the decreasing species richness phase is driven by lowered immigration of new species as productivity increases, which arises from more locally produced propagules competing with immigrant propagules for space—the dilution effect (Kadmon and Benjamini 2006). In

Fig. 4 The relationships between species richness and productivity for the same parameter values as in Fig. 2 (derived using our neutral model), except with the individual density held constant at 600 individuals/ha. The dashed vertical lines mark the highest richness value for each relationship, which always occurs at the smallest productivity value for this parameterisation



contrast to the more-individuals effect, this mechanism has the strongest effect on richness when a local community is close to saturation and productivity is the highest, because this is when the relative number of local to immigrant propagules approaches its maximum. Our mathematical analyses showed that as the spatial scale increases, the strength of the dilution effect relative to the more-individuals effect increases, with the underlying driver being an increase in the area/perimeter ratio (Eq. (9)). As the area/perimeter ratio increases, propagules of local origin, which scale with area, increasingly dominate immigrant propagules of external origin, which scale with the perimeter. This causes an increase in the strength of the dilution effect and hence greater suppression of the rate of introduction of new species due to immigration. As a result, the unimodal SP relationship starts to decrease at a lower productivity value—i.e., the peak of the relationship shifts to the left. The biological significance of this shift is that species richness decreases over a larger proportion of the full range of productivity. Thus, if a part of the full range is sampled, then there is a lower probability of the sample exhibiting a positive SP relationship and a higher probability of it exhibiting a negative or idiosyncratic SP relationship. This trend is consistent with a cross-site analysis of SP relationships in 12 forest tree communities worldwide (Chisholm et al. 2013), which found dominance of positive relationships at a spatial scale (sample unit size) of 0.04 ha and increasing dominance of negative and idiosyncratic relationships at larger spatial scales of 0.25 ha and 1 ha. Similarly, Poorter et al. (2015) did a meta-analysis of 2050 forest plots in the Neotropics

and found that there was a consistent positive relationship between tree species richness and aboveground biomass, which is positively correlated with productivity (Chisholm et al. 2013), at a spatial scale of 0.1 ha but not at a larger spatial scale of 1 ha. However, we caution that future work is required to quantify the relative contributions of neutral and niche mechanisms in producing these observed relationships.

Our finding that the increasing phase of a unimodal SP relationship could be driven by a neutral sampling effect (more-individuals effect) demonstrates that the positive phase need not be driven by niche complementarity or facilitation, which requires functional differences among species. The underlying driver of the neutral sampling effect that we identified is an increase in the number of individuals at a given spatial scale, which increases species richness and also productivity (more precisely, realized productivity), such that we see a concurrent increase in species richness and productivity in the increasing phase of the SP relationship. A corollary is that our neutral model predicts that if the number of individuals is held constant at a given spatial scale, then the more-individuals effect disappears and only a negative SP relationship remains (Fig. 4). This is consistent with the empirical findings of Chisholm et al. (2013), who found that when stem density of trees was controlled in 12 localized forest communities, positive SP relationships became much weaker. Strong effects of stem density on species richness have generally been found in plant communities (Vilà et al. 2007; Cavanaugh et al. 2014; Poorter et al. 2015). Therefore, the more-individuals effect appears to be a prominent mechanism underlying

positive regions of SP relationships, at least for plant communities at local scales.

It may come as a surprise that scale-dependent SP relationships observed in nature can be explained by a theory that invokes only dispersal limitation, competition for space, and demographic stochasticity. We do not claim that our explanation is definitive, but our findings do motivate a more critical examination of the mechanisms underlying SP relationships in general, and specifically the traditional niche-based explanations. More generally, we conjecture that the scale-dependent unimodal SP relationships observed in our model will typically arise in models where productivity is positively related to individual density, and in which some mechanism drives down local diversity at high individual densities. In our model, this mechanism is the dilution effect, but in other situations, it could be a niche-based mechanism such as competitive exclusion arising from density-dependent competition among species with different traits. Thus, the mechanistic model that we developed could be extended to form a bridge between neutral and niche theories, which would provide a more nuanced and holistic explanation of scale-dependent SP relationships observed in natural communities.

Our finding of a unimodal SP relationship from our neutral model also corroborates earlier results by Kadmon and Benjamini (2006) and Allouche and Kadmon (2009a, 2009b). The previous studies on this topic (Kadmon and Benjamini 2006; Allouche and Kadmon 2009a, 2009b) relied on numerical simulations, and thus were unable to establish general conditions under which the unimodal shape occurs. Our study builds on these previous studies by deriving analytical conditions under which a unimodal shape is found. The conditions (inequalities (5)) show that unimodality arises when the number of individuals increases monotonically with productivity, so that multiple modes do not appear, and when the number of individuals does not increase too quickly with productivity, so that the more-individuals effect is eventually outweighed by the dilution effect. Our results together with those from earlier studies (Kadmon and Benjamini 2006; Allouche and Kadmon 2009a, 2009b) demonstrate that empirical documentation of a unimodal SP relationship in terrestrial (e.g., Grime 1973, 1979; Axmanová et al. 2013; Fraser et al. 2015) or aquatic (e.g., Thackeray 2007; Simões et al. 2013) communities is insufficient on its own to differentiate between the dominance of neutral or niche-based mechanisms, such as a trade-off between competitive ability and tolerance to stress or disturbance (Grime 1977; Connell 1978; Chapin 1980; Huston 1979, 1994; Abrams 1995). Differentiating these two types of mechanisms would require either experimental manipulation or confronting the data with additional model predictions, such as the spatial scaling of SP relationships that we have derived here. We also emphasize that the previous studies (Kadmon and Benjamini 2006; Allouche and Kadmon 2009a, 2009b) did not examine how

the SP relationship changes with the spatial grain (sample area) of the neutral model communities considered.

In conclusion, we have presented a quantitative, mechanistic model of the spatial scaling of SP relationships at local scales. Our model is based on a community of individuals competing for finite resources, and is hence limited to competitive systems consisting of species in one guild. In addition, our model is neutral and neglects species differences that may be important in the spatial scaling of SP relationships (Grime 1977; Connell 1978; Chapin 1980; Huston 1979, 1994; Taylor et al. 1990; Abrams 1995; Schamp et al. 2003; Aarssen 2004). Thus, there is scope to extend our theory to communities with other types of interactions (e.g., predation, mutualism) and species differences. Furthermore, our model is spatially implicit and hence there is also scope to extend our analyses by using a spatially explicit neutral model, for which analytical results on community patterns are accumulating (O'Dwyer and Green 2010; Chisholm et al. 2018; O'Dwyer and Cornell 2018). Moreover, our model pertains only to local, within-community scales. At regional or continental scales encompassing different habitat types, productivity may be governed less by local biotic factors such as dispersal limitation and competition, and more by larger-scale abiotic factors such as soil fertility and the availability of water or solar energy (Aarssen 2004). To examine the spatial scaling of SP relationships at regional to continental scales, our model would need to be extended to include the relevant larger-scale abiotic factors. Despite the limitations of our model, we emphasize that the value of our present work is to provide a solid, quantitative foundation upon which to explore the effects of extra complexity on the spatial scaling of SP relationships.

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