

Ecography

ECOG-04159

Kitzes, J. 2019. Evidence for power-law scaling in species aggregation. – Ecography doi: 10.1111/ecog.04159

Supplementary material

Appendix 1

Evidence for power-law scaling in species aggregation: Supplementary Information

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1. The sampled species-area relationship

The species-area relationship (SAR), a pattern describing the change in species richness with sampling area, is one of the oldest and most widely study quantitative patterns in ecology. The SAR is particularly notable for having enough consistency across taxa and ecosystems to suggest that it is one of the few “laws of ecology” (Rosenzweig 1995, Lawton 1999), as well as having enough variability to spur nearly a century of arguments over the nature, origins, and limits of this consistency.

Recent efforts to explain the shape of the SAR on theoretical grounds have frequently focused on one particular form of this pattern: the sampled species-area relationship. To construct a sampled SAR, a large landscape is first assumed to contain a fixed number of species S_0 whose abundances are described by a metacommunity abundance distribution, $\phi(n_0)$. The expected number of species found in a smaller plot of area A within this landscape, $\bar{S}(A)$, is then assumed to result from a spatial sampling process involving a conditional probability, $P(n > 0 \text{ in } A | n_0)$, which gives the probability that a species with n_0 individuals in the metacommunity will have at least one individual in a randomly chosen small plot of area A .

A complete sampled SAR is constructed by calculating $\bar{S}(A)$ for many possible values of A using the equation

$$\bar{S}(A) = S_0 \sum_{n_0=1}^{\infty} \phi(n_0) P(n > 0 \text{ in } A | n_0) \quad (\text{A1})$$

While the study of abundance distributions has a long history in ecology (Fisher et al. 1943, Preston 1962, McGill et al. 2007), far less attention has been paid to the spatial sampling term $P(n > 0 \text{ in } A | n_0)$. This term is most easily calculated as $1 - P(n = 0 \text{ in } A | n_0)$, where this probability of absence in a plot of area A is simply the quadrat count distribution evaluated at zero for a species with metacommunity abundance n_0 .

2. Stochastic birth-death-immigration model

Kendall (1949), and later Bailey (1964) and others, have described in detail a stochastic birth-death-immigration model that describes population growth in a single plot of fixed area. In this model, a single species' population is described by a stochastic, continuous-time, discrete-state Markov chain. This type of model has also been applied to the evaluation of the species-abundance distributions (Kendall 1948) and to mainland-island metapopulation systems (Nachman 2000, Alonso and Mckane 2002).

Consider a population inhabiting a plot of area A within a larger landscape. The goal is to derive an expression for the probability that this plot contains exactly n individuals at some time t , $P(n, t)$. Evaluated at any time t , $P(n, t)$ is equal to the quadrat count distribution at that t .

At a minimum, a mechanistic model of changes in population size in this plot should include the processes of birth, death, immigration, and emigration. Consider an interval of time dt that is small enough such that the only possible changes to the population are an increment of one individual, a decrement of one individual, or no change. For a plot containing n individuals of a species at t , presume that in dt

- The probability of a birth is $B n dt$
- The probability of a death is $D n dt$
- The probability of an immigration event is $I dt$

where B is the per-capita birth rate, D is the per-capita death rate, and I is a constant immigration rate that is independent of population size. An emigration term is not specifically included in Bailey's model, as a per-capita emigration rate can be included within the death rate term when applicable.

For a population with n individuals, the one-step transition probability for the population increasing by one individual is $e_n = B n + I$ and the probability for the population decreasing by one individual is $r_n = D n$. From these probabilities, a master equation describing the time evolution of this population can be written as

$$\frac{dP(n, t)}{dt} = e_{n-1}P(n-1, t) + r_{n+1}P(n+1, t) - [r_n + e_n]P(n, t) \quad (\text{A2})$$

Define $e_{-1} = I$ to account for the boundary $n = 0$, where the population can only grow via immigration. Finally, specify an initial condition for the population, $P(n = 0, t = 0) = 1$, such that the plot contains zero individuals at some initial time t_0 .

Under these conditions, for any time $t > 0$, $P(n, t)$ takes the form of a negative binomial distribution (Kendall 1949, Bailey 1964, Allen 2010), with the aggregation parameter k given by

$$k = \frac{I}{B} \quad (\text{A3})$$

The other parameter of the negative binomial distribution, the mean population size μ , can be expressed as a function of t :

$$\mu = \frac{I}{B - D} (e^{(B-D)t} - 1) \quad (\text{A4})$$

In the case that $B > D$, the mean population size grows exponentially without bound. For the special case in which $B = D$, the population can be shown to grow linearly at the rate It .

Most interesting is the case in which $B < D$, such that the population would eventually decrease to extinction if it were not rescued by newly arriving immigrants. When $B < D$, the population reaches a dynamic equilibrium as $t \rightarrow \infty$, and the equilibrium quadrat count distribution is a stationary negative binomial distribution with k given in Eq. A3 and mean population size

$$\mu = \frac{I}{D - B} \quad (\text{A5})$$

At steady state, this stochastic process model thus predicts that the quadrat count distribution takes the form

$$P(n) = \frac{\Gamma(k + n)}{\Gamma(k)n!} \left(\frac{k}{k + \mu} \right)^k \left(\frac{\mu}{k + \mu} \right)^n \quad (\text{S.6})$$

which is a negative binomial distribution, expressed in its common ecological parameterization (Bolker 2008), with parameters k and μ given by Eq. A3 and A5.

3. Adding area dependence to the k parameter

The above equations can be used to derive a relationship between the aggregation parameter k and plot area. Consider a single species that now inhabits several plots of different areas, all contained within a larger landscape. We denote the potential area dependence of all parameters above with a subscript A .

To begin, we assume that the mean number of individuals in a plot scales linearly with plot area, so that

$$\mu_A = \lambda A \quad (\text{A7})$$

where λ represents the (constant) density of individuals per unit area. Note that in a gridded landscape in which plots of smaller areas are fully nested within plots of larger areas, this relationship must hold exactly. In a non-nested design, the expected mean number of individuals per plot will also scale linearly with area if plots are randomly sampled from the larger landscape.

Combining Eq. A5 and A7 and rearranging terms, the per capita birth rate B_A can be expressed as

$$B_A = \frac{\lambda A D_A - I_A}{\lambda A} \quad (\text{A8})$$

Additionally, Eq. A3 can be rearranged to give an alternative expression for B_A , which is

$$B_A = \frac{I_A}{k_A} \quad (\text{A9})$$

Equating Eq. A8 and A9 allows us to express the aggregation parameter k_A as

$$k_A = \frac{\lambda A I_A}{\lambda A D_A - I_A} \quad (\text{A10})$$

Next, consider the per capita death rate D_A . As the per capita rate at which individual organisms in the plot die should have no logical relationship to an arbitrarily drawn plot boundary, the parameter D can be taken to be a constant that is independent of plot area A . Note that this area independence contrasts with B_A and I_A , both of which exhibit potential area dependence due to their dependence on the rates at which offspring of parents within the plot disperse out of the plot and offspring of parents outside of the plot disperse into the plot, respectively.

Holding D constant leads to the final expression for the area scaling of k_A of

$$k_A = \frac{\lambda A I_A}{\lambda A D - I_A} \quad (\text{A11})$$

Eq. A11 demonstrates that, within the context of this stochastic process model, the scaling of k_A with plot area will depend on the form of I_A .

4. Deriving the area scaling of k_A under three immigration models

We now consider three proposed models of immigration into a plot of area A and how each of these affects the scaling of k_A with area.

First, consider a “target” immigration model, akin to a seed rain process. In this model, individuals enter the plot at a rate proportional to plot area, such that $I_A = cA$, where c is the rate of immigration per unit area. Substituting this expression into Eq. A11 and rearranging terms shows that

$$k_A = \frac{\lambda AcA}{\lambda AD - cA} = \left(\frac{\lambda c}{\lambda D - c} \right) A \quad (\text{A12})$$

As all terms in the parentheses above are constants, we can see that k_A scales linearly with area under this immigration model.

Second, consider an “area free” model of immigration, in which the immigration rate is constant and not affected by plot area, so that $I_A = c$. Now, Eq. A11 reduces to

$$k_A = \frac{\lambda Ac}{\lambda AD - c} \quad (\text{A13})$$

To gain intuition on the behavior of this function, note that the denominator must always be positive. Next, consider a relatively small plot with a mean number of individuals arbitrarily chosen to equal 0.1, a reasonable scale at which to begin analyzing the quadrat count distribution, so that $\lambda A = 0.1$. Since the denominator of Eq. A13 must be strictly positive, we thus require that $D > 10c$. Note that this inequality presumes that the stochastic birth-death-immigration model holds only down to this particular A , and assuming that the model holds to even smaller scales would further strengthen the implications described below.

As area increases, the first term in the denominator grows while the second remains constant, ensuring that k_A will similarly be positive for all larger values of A . More importantly, note that the denominator $\lambda AD - c$ is increasingly well approximated by λAD as area increases.

Consider a particularly extreme case, in which the birth rate for individuals within a plot is nearly zero, and the population dynamics of the plot are dominated by only immigration and death (i.e., an extreme example of sink habitat), such that $D \approx c$. Numerical exploration of Eq. A13 suggests that when a plot reaches an area such that $\lambda A = 1$, representing a scale at which a plot contains on average 1 individuals of the species, Eq. A13 is well approximated by

$$k_A \approx \frac{\lambda A c}{\lambda A D} = \frac{c}{D} \quad (\text{A14})$$

As c becomes small relative to D , such that births within a plot play a larger role in population dynamics, this approximation becomes accurate for smaller areas. For example, when only 10% of new individuals in the plot are sourced from immigrants, such that $c = D/10$, the approximation in Eq. A14 holds closely down to the mean population size $\lambda A = 0.1$.

In the “area free” model where the immigration rate is constant with area, we thus expect k_A to be similarly constant and equal to the immigration rate divided by the per capita death rate. Note, however, that the assumption of a constant immigration rate is highly unusual, in that it presumes plots of all possible areas receive the same expected number of immigrants per unit time, an implication that is difficult to justify mechanistically. Within the context of this simple stochastic birth-death-immigration model, it appears that this relatively implausible immigration process is required to generate this prediction.

Finally, consider the “diffusion” model of immigration, in which immigrants arrive in a plot at a rate proportional to plot perimeter such that $I_A = c A^{0.5}$ (for square or circular plots). Now, Eq. A11 becomes to

$$k_A = \frac{\lambda A c A^{0.5}}{\lambda A D - c A^{0.5}} = \frac{\lambda A c}{\lambda A^{0.5} D - c} \quad (\text{A15})$$

Similar to the case of the “area free” model, note that the denominator of this equation must be positive for all areas A where the birth-death-immigration model applies. Numerical examination of Eq. A15 shows that, under the same assumptions as explored for the “area free” model above, the first term in the denominator begins to dominate the second for plot sizes around the smallest where the quadrat count distribution is assumed to apply, and this equation can then be approximated by

$$k_A \approx \frac{\lambda A c}{\lambda A^{0.5} D} = \frac{c}{D} A^{0.5} \quad (\text{A16})$$

In the “diffusion” model, we thus expect k_A to increase proportional to the square root of plot area A , with this approximation becoming increasingly exact for larger areas.

5. Taylor’s Law and the scaling of k_A

Consider once again a single species that inhabits one or more of many plots, each of area A , placed randomly across a large landscape. In this landscape, the spatial form of Taylor’s Law

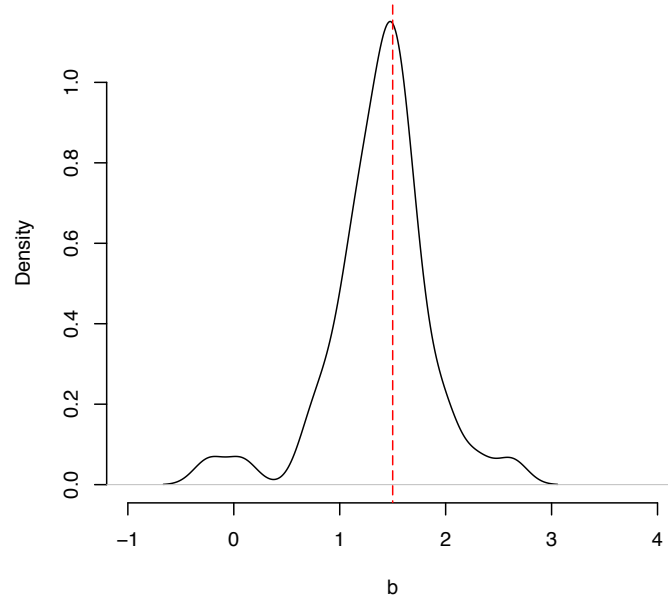


Figure A1: Density plot of best fit values of the constant b of Taylor's Law for 45 spatial relationships reviewed in Xiao et al. (2015). The plot peaks at $b \approx 1.5$, with the majority of values falling between $b = 1$ and $b = 2$.

relates the mean number of individuals per plot to the variance in the counts of individuals across all plots. Taylor's Law is often hypothesized to follow a power law, in which case it is written as

$$\sigma_A^2 = a\mu_A^b \quad (\text{A17})$$

where a and b are fitted constants for the particular species and landscape, and μ_A and σ_A^2 refer to the mean and variance in the counts of individuals per plot for some plot area A .

If the quadrat count distribution is assumed to follow a negative binomial distribution at all scales, Taylor's Law can be used to relate the aggregation parameter k_A of the negative binomial distribution to the mean of that distribution, μ_A . Recognizing that the variance of the negative binomial can be written generally as $\sigma^2 = \mu + \mu^2/k$, the power law form of Taylor's Law can be rearranged to yield

$$k_A = \frac{1}{a\mu_A^{b-2} - \frac{1}{\mu_A}} \quad (\text{A18})$$

For species and plot areas where the expected number of individuals per plot is large, so that $\mu_A \gg 1$, Eq. A18 can be approximated by

$$k_A \approx a\mu_A^{2-b} \quad (\text{A19})$$

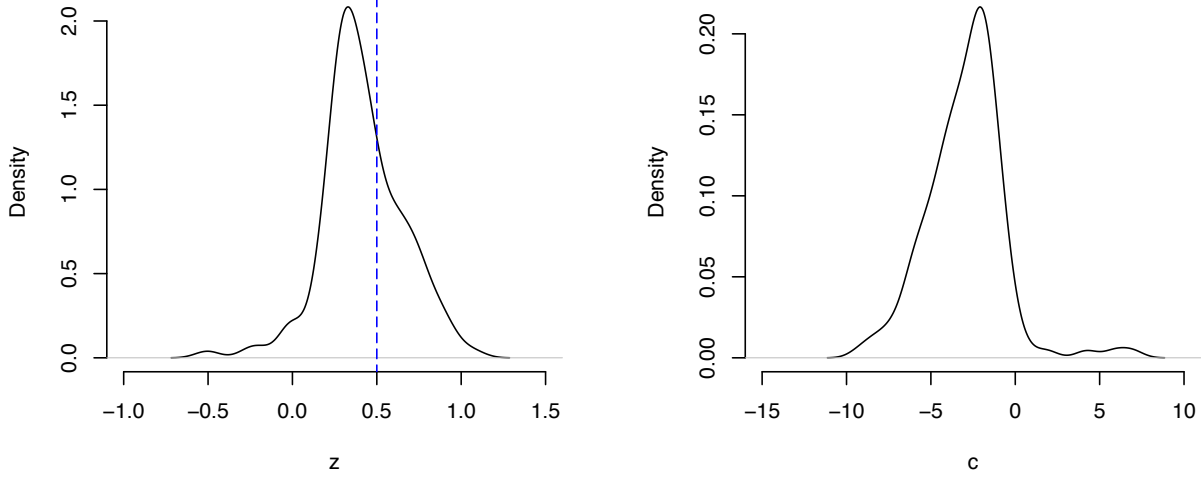


Figure A2: Density plot of best fit values of slope z of power law relationship between plot area and k_A for 146 species of tropical trees (all species with > 100 individuals) at Barro Colorado Island. The diffusion model predicts $z \approx 0.5$. These data have a mean of 0.42 (median 0.38). The intercept of the log-log regression, c , falls between -10 and 0 for most species.

Next, note that for any set of randomly placed plots, μ_A can be written equivalently as λA , where A is plot area and λ is the species' density, which gives the expected number of individuals per unit area across the larger landscape. Making this substitution and dropping constants, Eq. A19 can then be written in the proportionality relationship

$$k_A \propto A^{2-b} \quad (\text{A20})$$

Equation A20 demonstrates that if the power law form of Taylor's Law and a negative binomial quadrat count distribution are both assumed, the aggregation parameter k_A of the quadrat count distribution scales as a power law with area.

The question then becomes what values of b are most often observed in empirical landscapes. Figure A1 presents a density plot of the fitted b constants from the 45 spatial Taylor's Law relationships included in a recent review (Xiao et al. 2015). Fitted values of b peak very close to 1.5, which suggests that k_A often scales as approximately $A^{0.5}$ in real ecosystems.

6. Case Study at Barro Colorado Island

In support of the general conclusions of the Taylor's Law analysis, we can also specifically examine the scaling of k_A for species in the widely studied Barro Colorado Island 50 ha forest plot (see <http://ctfs.si.edu/webatlas/datasets/bci/>).

Figure A2 is constructed by first dividing the full 50 ha plot into different cell sizes, ranging from 8 square cells to 392 square cells. For each species with more than 100 individuals in the entire plot, the k_A parameter is then fit using maximum likelihood estimation at each cell size. Finally, for each species, a log-log linear regression of $\log(A)$ versus $\log(k_A)$ is used to estimate the slope, z , of the power law scaling relationship of k_A with A .

As noted above, the diffusion immigration model and the empirical review of Taylor's Law data both predict the power law exponent $z = 0.5$. The z values for the 143 species analyzed at Barro Colorado Island have the kernel density shown in Fig. A2, with a mean z across all species of 0.42.

The second panel shows a kernel density plot for c , the intercept of the log-log linear regression. As noted in the main manuscript, knowledge of this intercept across species is needed for quantitative integration of the k_A scaling described here into species-area models.

7. Comments on Chisholm and Lichstein (2009) and Conlisk et al. (2002)

Here, I comment briefly on the relationship between the work presented in this manuscript and two prior analyses.

First, Chisholm and Lichstein (2009) present an analysis that relates plot geometry to the m parameter of Hubbell's neutral theory. In the process, they derive the general approximation

$$m \approx \frac{Pd}{\pi A} \quad (\text{A21})$$

where m is the probability that a death in the plot is replaced by an immigrant from outside the plot, d is mean dispersal distance, P is plot perimeter, and A is plot area.

Consider the context of a single species in a neutral community. The product $I' = mDf$ can be defined as the number of immigrants of that species into the plot per discrete time step, where m is defined as above, D is the total number of deaths within the plot in a time step, and f is the fraction of immigrants into the plot belonging to the species of interest (in the original neutral theory formulation, this is equal to the species' fractional abundance in the larger metacommunity). The parameter I' is thus a discrete time analogue to the immigration rate parameter I in the previously described stochastic process model.

We can thus extend Eq. A21 to

$$I' = \frac{PdDf}{\pi A} \quad (\text{A22})$$

Importantly, note that only P , D , and A in this equation are functions of area. Furthermore, D , the total number of deaths in a plot, can be assumed to scale linearly with plot area. As a result, I' scales as plot perimeter, or proportionally to $A^{0.5}$ for square or circular plots. This approximation thus also supports the logic of a diffusion immigration model.

Second, Conlisk et al. (2012) present one of the few prior empirical analyses of changes in the shape of the quadrat count distribution across scales. They analyze patterns in the “relative mode,” RM , of the quadrat count distribution for several empirical systems, finding that this relative mode generally increases with plot area. They argue heuristically for the presence of this pattern on the basis of central limit considerations.

Assume, as before, that the quadrat count distribution for a species of interest can be described with a negative binomial distribution, parameterized as in Eq. A6, across all scales of interest. Conlisk et al.’s relative mode metric is calculated by dividing the mode of this distribution by its mean. In Eq. A6, the mean of the distribution is given simply by μ . The mode is given by (Johnson et al. 2005, p. 217)

$$Mo = \left\lfloor \frac{\mu(k-1)}{k} \right\rfloor \quad (A23)$$

where $\lfloor \cdot \rfloor$ is the floor operator (note that Johnson et al.’s P equals μ/k in the notation used here). This equation applies so long as the quantity within the floor operator is greater than 1, otherwise the mode is found at 0.

Consider only cases in which the mode, and hence relative mode, for a species is greater than zero, which implies $k > 1$. Given the definition of the floor operator, we can write

$$Mo = \left\lfloor \frac{\mu(k-1)}{k} \right\rfloor \leq \frac{\mu(k-1)}{k} \quad (A24)$$

Dividing both sides by μ , which must be positive, we find.

$$RM \leq \frac{k-1}{k} \quad (A25)$$

Eq. A25 demonstrates that an increase in the relative mode implies necessarily that the quantity $(k-1)/k$ increases, which requires that k increases. To the extent that the results of Conlisk et al. show relative modes increasing for individual species as area increases, this implies that the k parameter of a negative binomial quadrat count distribution must necessarily also be increasing with area.

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