

Appendix B from A. L. Šizling et al., “Between Geometry and Biology: The Problem of Universality of the Species-Area Relationship” (Am. Nat., vol. 178, no. 5, p. 602)

Considerations of Consecutive Constraints

Constraints on the Jaccard Index

The Jaccard index between plots at a given scale constrains the Jaccard index at a coarser scale. Imagine four adjacent plots, A_1 , A_2 , B_1 , and B_2 (fig. 3). Assume equal Jaccard indices between all pairs of these four plots, denoted as J_n (we will relax this assumption below). We further denote the Jaccard index between the larger plots A and B ($A = A_1 \cup A_2$, $B = B_1 \cup B_2$) as J_{n+1} . By definition, $J_{n+1} = S_{A \cap B} / S_{A \cup B}$, where $S_{A \cap B} / S_{A \cup B}$ is the number of species shared by the plots A and B and $S_{A \cup B}$ is species richness of both plots combined. If we combine this definition with the mathematical identity $S_{A \cup B} \equiv S_A + S_B - S_{A \cap B}$, we get a formula for species richness of the combined plot, $S_{A \cup B} = (S_A + S_B) / (1 + J_{n+1})$. The same applies to the small subplots, that is, $S_{A_1 \cup B_1} = (S_{A_1} + S_{B_1}) / (1 + J_n)$, $S_{A_2 \cup B_2} = (S_{A_2} + S_{B_2}) / (1 + J_n)$, and so on. Similarly, the number of species shared by the two small subplots follows (by the definition of the Jaccard index) $S_{A_1 \cap B_1} = J_n S_{A_1 \cup B_1} = J_n (S_{A_1} + S_{B_1}) / (1 + J_n)$. The number of species shared by the two small plots is the lowest possible number of species that can be shared by the larger plots A and B , which happens if all pairs of the small subplots share the same species (fig. 3). On the other hand, if each pair of the small subplots shares a different set of species, then plots A and B share $4S_{A_1 \cap B_1}$ species (we assume $S_{A_1 \cap B_1} \equiv S_{A_1 \cap B_2} \equiv S_{A_2 \cap B_1} \equiv S_{A_2 \cap B_2}$; this condition will also be relaxed later; fig. 3). The actual number of species shared by plots A and B thus lies between one and four times $S_{A_1 \cap B_1}$. This reasoning obviously applies in the case of a transect where the plots are arranged in a row (e.g., A_1 , A_2 , B_1 , B_2) as well.

Let us introduce parameter K , whose value is between 1 and 4, so that

$$S_{A \cap B} = K S_{A_1 \cap B_1} = \frac{K J_n (S_{A_1} + S_{B_1})}{1 + J_n}. \quad (\text{B1})$$

Similarly, $S_{A \cup B} = [2(S_{A_1} + S_{B_1}) / (1 + J_{n+1})] / (1 + J_n)$. Combining the previous two equations with the definition of J_{n+1} (eqq. [7], [8]) follows.

The constraints introduced above can be derived under broader assumptions. We can relax both the assumptions that Jaccard indices at a finer scale, J_n , and a number of shared species between the smaller plots, $S_{A_i \cap B_j}$, do not vary with space. In this case we need to replace only $S_{A_1 \cap B_1}$ with the mean value $\bar{S}_{A_i \cap B_j} = (S_{A_1 \cap B_1} + S_{A_1 \cap B_2} + S_{A_2 \cap B_1} + S_{A_2 \cap B_2}) / 4$ and the Jaccard index with an effective value that is defined to have the same effect as the mean value of $J / (1 + J)$. Technically, the derivation remains the same. Unlike in the above derivation, the parameter K cannot reach the limit of 1 as long as spatial variability in species richness exists. The reason is that if we define K as

$$S_{A \cap B} = K \bar{S}_{A_i \cap B_j}, \quad (\text{B2})$$

where $\bar{S}_{A_i \cap B_j} = (S_{A_1 \cap B_1} + S_{A_1 \cap B_2} + S_{A_2 \cap B_1} + S_{A_2 \cap B_2}) / 4$, then $S_{A \cap B} \geq \max \{S_{A_1 \cap B_1}, S_{A_1 \cap B_2}, S_{A_2 \cap B_1}, S_{A_2 \cap B_2}\}$. Hence, $K \geq \max \{S_{A_1 \cap B_1}, S_{A_1 \cap B_2}, S_{A_2 \cap B_1}, S_{A_2 \cap B_2}\} / \bar{S}_{A_i \cap B_j} \geq 1$. As a result, K is higher than 1 ($K > 1$) if $S_{A_i \cap B_j}$ varies spatially. On the other hand, geometry does not prevent the K from reaching its upper limit. The reason is that $S_{A \cap B} \equiv S_{A_1 \cap B_1} + S_{A_1 \cap B_2} + S_{A_2 \cap B_1} + S_{A_2 \cap B_2}$ if all the smaller subplots share unique sets of species. In such a case $S_{A \cap B} \equiv 4 \bar{S}_{A_i \cap B_j}$ and $K = 4$. (Note, however, that the plots cannot share unique sets of species if z is low, and thus the upper limit of K is $1/J_n$ in this case.) This leads to the prevalence of high K values and consequently a decreasing z - D relationship in most cases.

The Link between z and J (Eq. [9])

There are several ways to derive the relationship between J and z . The easiest one is to start with the definition of the Jaccard index, $J = S_{A \cap B} / S_{A \cup B}$, which is equivalent to $J = (S_A + S_B - S_{A \cup B}) / S_{A \cup B}$. It follows that $J + 1 = 2\bar{S}_{AB} / S_{A \cup B}$, where \bar{S}_{AB} is the mean across S_A and S_B . Therefore, $\ln(J + 1) = \ln 2 - (\ln S_{A \cup B} - \ln \bar{S}_{AB})$. Equation (9) follows directly from the equation above and the definition of z ($z = (\ln S_{A \cup B} - \ln \bar{S}_{AB}) / \ln 2$). The same relationship between J and z follows from a result of Koleff et al. (2003). They expressed the Jaccard index as $J = a / (a + b + c)$ and z as $z = 1 - \ln[(2a + b + c) / (a + b + c)] / \ln 2$. It follows that $J + 1 = (2a + b + c) / (a + b + c)$, hence equation (9).

Both of the above derivations ignore spatial variability in the Jaccard index. We thus offer a more general derivation that shows that the Jaccard index in equation (9) is the effective Jaccard index that drives species abundance distributions (SADs; Šizling et al. 2009a, 2009c). It starts from the equation

$$f_{A \cup B} = f_A + J f_A *_c f_B \quad (\text{B3})$$

(Kůrka et al. 2010; Šizling et al. 2009a, 2009c), where $f_{A \cup B}$ captures the SAD of two merged plots A and B and f_A captures the abundance distribution of subplot A (fig. 3). The function capturing the distribution of subplot B , f_B , is missing from equation (B3) since we assume for simplicity that the two subplots (A and B) have similar SADs, so that $f_B \equiv f_A$. The parameter J is the assumed effective Jaccard index between the two adjacent subplots, A and B , and $*_c$ is an operator of correlated convolution (for broader discussion of all assumptions see Kůrka et al. 2010).

Calculating the first moment for each side of equation (B3) (or, simply, say, estimating a mean value of the variables drawn from the distributions), it follows that $E(f_{A \cup B}) = E(f_A) + J 2E(f_A) = (1 + 2J)E(f_A)$, regardless of the particular model of the operator of the correlated convolution used (for various models of correlated convolution, $*_c$, see Šizling et al. 2009a; Kůrka et al. 2010; for the universality of the equation $E(f *_c f) = 2E(f)$, see the proposition below). Since $E(f) \equiv \bar{f} / \bar{S}$ and

$$D_A + \ln 2 = D_{A \cup B} + z_A \ln 2, \quad (\text{B4})$$

where $D_i = \ln \bar{f}_i / \bar{S}_i$ (see fig. 1a; note relabeling $\varepsilon = 2$ and $A \cup B = 2A$), it follows that $z_A \equiv [\ln E(f_{A \cup B}) - \ln E(f_A)] / \ln 2 + 1$, hence equation (9) (see bold line in fig. 4a). Note that the effective value of the Jaccard index can be estimated as the mean across all adjacent equal-sized plots of a given area, as shown in figure 4a.

Proposition. $E(f *_c f) = 2E(f)$ is independent of a particular model of correlated convolution.

Evidence. $E(f_x *_c f_y) = E(f_x) + E(f_y)$ regardless of the particular model of correlated convolution. It follows that $E(f *_c f) \equiv 2E(f)$, considering that $f_x \equiv f_y$. Standard convolution $f_x *_c f_y$ gives a distribution of numbers $x_1 + y_1, x_2 + y_2, \dots, x_n + y_n$, with each x_i and y_i being independently drawn from distribution f_x or f_y , respectively. Correlated convolution gives a distribution of numbers $x_1 + y_1, x_2 + y_2, \dots, x_n + y_n$, with each x_i and y_i being drawn from distribution f_x or f_y , respectively; however, y_i depends on x_i in this case. Nonetheless, when computing the mean of $x_1 + y_1, x_2 + y_2, \dots, x_n + y_n$, we can separate the corresponding x and y from each other ($\sum (x_i + y_i) / n = (\sum x_i + \sum y_i) / n = \sum x_i / n + \sum y_i / n = \bar{x} + \bar{y}$), which nullifies any effect of their mutual dependence. Finally, note that $\bar{x} \equiv E(f_x)$ and $\bar{y} \equiv E(f_y)$.

Consecutive Constraints

The value of z_n at the finer scale determines an envelope of possible z_{n+1} values at the consecutive scale. A particular z_{n+1} drawn from the envelope for a given D_n then determines D_{n+1} (fig. 1a), and this process can be applied repeatedly to construct possible shapes of the z - D relationship. These constraints are calculated as $D_{n+1} = D_n + (1 - z_n) \ln 2$ and $z_{n+1} \equiv \ln[2 - K(2^{1-z_n} - 1)] / \ln 2$ (K obeys eq. [8]). The latter is given by equations (7) and (9), and the former follows from figure 1a, particularly from the equation $D_A + \ln 2 = D_{A \cup B} + z_A \ln 2$, where $D_i = \ln \bar{f}_i / \bar{S}_i$ (note relabeling $\varepsilon = 2$ and $A \cup B = 2A$ in fig. 1a).

Is z Increasing or Decreasing with D ?

Equations (7) and (8) suggest that z can be either increasing or decreasing when doubling area (i.e., when increasing D). However, there is actually a much higher chance that the z - D relationship is decreasing and downward decelerating, as predicted by Harte et al. (2009). The critical value of K (K_c) that separates K with increasing and decreasing z values is found by setting $J_{n+1} = J_n$, and it obeys $K_c = 2 / (1 + J_n)$. If $1 \leq K < K_c$,

then the Jaccard index is decreasing and z is increasing when doubling the area; if $K_c < K \leq \min(4, 1/J_n)$, then the Jaccard index is increasing and z is decreasing with increasing D (fig. 4c). The apparent disproportion between extents of K values below and above the critical K (fig. 4c) is prominent for high z , while this proportion approaches 0.5 for low z . Hence, if taking a null assumption that K values are distributed regularly (or symmetrically) within these constraints, we should expect either (i) a steep, decreasing z - D relationship if z is high or (ii) little decrease in the z - D relationship if z is low. Overall, we should expect a decreasing, downward-decelerating (i.e., hollow) z - D relationship, as predicted by Harte et al. (2009). Nonetheless, we could also expect some deviations from this overwhelming trend toward z increasing with D , particularly for low z , that is, especially at large scales.

The Slope z Approaches 1 Where D Approaches 0

The reason for the increase of the SAR slope at fine spatial scales is that if we follow the SAR (fig. 1a) toward smaller areas, we necessarily approach the individual-area relationship (IAR) with a slope of 1 ($\ln \bar{I} = \ln \rho + \ln A$ for $\bar{I} = \rho A$; see “Thesis I” in app. A). Thus, the distance between the SAR and the IAR, D , approaches 0, and the slope of the logarithmically transformed SAR, z , approaches 1 unless (scenario 1) we have to stop at some privileged small area (the very beginning of the SAR) or (scenario 2) the SAR and IAR touch each other at some scale and the SAR abruptly branches off from the IAR. However, neither scenario is likely to happen. (Scenario 1) There is no privileged area at which to stop, as species richness and number of individuals are mean values applicable to any area. It has long been known that the species richness of an assemblage can be captured in terms of probabilities of occurrences of individual species; particularly, it is a summation of the probabilities across all the species that may occur in the focal assemblage (Coleman 1981; He and Legendre 2002; Šizling and Storch 2004). As these probabilities can be substantially lower than 1, neither the SAR nor the IAR has a lower limit. (Scenario 2) The IAR rises more steeply than the SAR, but the two curves approach each other for low D without crossing (as there cannot be more species than individuals in a given area). The SAR must thus either touch the IAR or approach it asymptotically with z approaching 1. If the SAR touches the IAR, it inevitably scales down with z precisely equal to 1, as it cannot stop at a particular logarithmically transformed area (see scenario 1). In both of the cases, however, the consecutive slope of the logarithmically transformed SAR is either exactly or nearly 1. The reason is that if $J_n = 0$, then $J_{n+1} \cong 0$ (i.e., if $z_n = 1$, then $z_{n+1} \cong 1$), which follows from equation (7). Intuitively, low Jaccard indices between small patches A_1 , A_2 , B_1 , and B_2 are unlikely to produce a high Jaccard index between the larger patches A and B .

The Meaning of K

The higher the value of K is within the envelope given by the particular z_n , the lower the following value of z_{n+1} will be. Let us now focus on figure 4c, particularly on a line parallel to the Y -axis, because only those values of K with equal z are mutually comparable. Let us have two different K values for one particular z , so that $K_A < K_B$. This inequality implies an inequality between corresponding subsequent z values (and Jaccard indices), and thus K and these two measures should be interpreted in the same terms. The inequality $K_A < K_B$ implies that $2K_A + J_n K_A K_B < 2K_B + J_n K_A K_B$, where J_n is uniquely attributed to the focal z . It follows that $K_A / (2 + J_n K_A) < K_B / (2 + J_n K_B)$, which is in accord with equation (7), $J_{n+1}^A < J_{n+1}^B$. Hence $z_{n+1}^A > z_{n+1}^B$.