Appendix A 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)

Theses and Derivations

Derivation I: derivation of equation (4). From equations (1) and (2), $\overline{S}_{\varepsilon A}/\overline{S}_A = \varepsilon^{z_S}$ and $\bar{\sigma}_{\varepsilon A}/\bar{\sigma}_A = \varepsilon^{\sigma_S}$, respectively, and thus (from eq. [3]) $z_{S\cup\sigma} = \ln[\pi_A \varepsilon^{z_S} + (1 - \pi_A)\varepsilon^{\sigma_S}]/\ln \varepsilon$, where $\pi_A := \overline{S}_A/(\bar{\sigma}_A + \overline{S}_A)$. Then equation (4) follows.

    Derivation II: derivation of the relationship between D_S, D_σ, *and* $D_{S\cup\sigma}$. While D_S and D_σ are assumed mathematically independent from each other, $D_{S\cup\sigma}$ is strictly determined by the former two (fig. 1c). Denote $\bar{a}_S$, $\bar{a}_\sigma$, and $\bar{a}_{S\cup\sigma}$ to corresponding mean abundances per species ($D_S = \ln \bar{a}_S$, $D_\sigma = \ln \bar{a}_\sigma$, and $D_{S\cup\sigma} = \ln \bar{a}_{S\cup\sigma}$). Similarly to equations (1)–(3), $\bar{a}_S = \overline{I}_S/\overline{S}$, $\bar{a}_\sigma = \bar{\eta}/\bar{\sigma}$, and $\bar{a}_{S\cup\sigma} = (\overline{I} + \bar{\eta})/(\overline{S} + \bar{\sigma})$, where $\overline{I}$ and $\bar{\eta}$ are the mean numbers of individuals of the assemblage S and σ, respectively. The mean is given across all samples of the area A. It follows that $\bar{a}_{S\cup\sigma} = \pi_A \bar{a}_S + (1 - \pi_A)\bar{a}_\sigma$, where $\pi_A := \overline{S}_A/(\bar{\sigma}_A + \overline{S}_A)$. Hence, $\exp(D_{S\cup\sigma}) = \pi_A \exp(D_S) + (1 - \pi_A)\exp(D_\sigma)$.

    Thesis I. The average number of individuals scales linearly with area. Theoretically, it is easy to show a linear scaling between sampling area and mean number of individuals per sample on an infinite plane (i.e., to show that $\overline{I} = \rho A$; where $\overline{I}$ is the mean number of individuals, ρ is the density of individuals, and A is area). Imagine a sampling area composed of two adjacent subareas, each of area A. The sampling area is thus $2A$. The mean number of individuals across all samples is computed as $\overline{I}(2A) = [(I_{\alpha 1} + I_{\beta 1}) + (I_{\alpha 2} + I_{\beta 2}) + \ldots + (I_{\alpha n} + I_{\beta n})]/n$, where indices α and β label the first and second subplots, respectively, and indices $1 \ldots n$ label the first, second, and so on sampling, up to the nth sampling. This formula can be split into $\overline{I}(2A) = \sum I_{\alpha i}/n + \sum I_{\beta i}/n$. Since on an infinite plane $\sum I_{\alpha i}/n = \sum I_{\beta i}/n = \overline{I}(A)$, it follows that $\overline{I}(2A) = 2\overline{I}(A)$. Hence, $\overline{I}$ scales linearly with A.

    However, this can be violated on a finite plane. The reason is that the two adjacent plots are mutually dependent; they cannot overlap each other, and they must touch each other at the same time. This causes more intensive sampling in the center of the sampled finite area, especially when the sampling area is large. Therefore, if there is a cluster of a high density of individuals in the center of the whole sampled area, then large sampling areas capture the higher density of individuals, ρ, than do smaller sampling areas. Hence, a deviation from the linear scaling ($\overline{I} = \rho A$) may occur. For this reason we tested this assumption by using data on real assemblages. Visually, all 125 individual-area relationships (i.e., 123 bird relationships + one fish relationship, each consisting of five points, and one tree relationship with 11 points) were perfectly linear, with correlation coefficients above 0.999 and slopes of the relationships in the log-log scale between 0.939 and 1.041 in all cases.

    The linear scaling between sampling area and mean number of individuals per sample has been derived for nested sampling design within a contiguous area. We thus should not expect the relationship $\overline{I} = \rho A$ for archipelagos of any kind.

    Thesis II. The unique solution of equation (5) follows equation (6). To solve equation (5), we assume that $D_S(A) \neq D_\sigma(A)$, and then we substitute $x := \exp(D_S)$, $y := \exp(D_\sigma)$, and $F(\lambda) := \varepsilon^{z(\ln(\lambda))}$, where λ substitutes for x, y, or $\pi x + (1 - \pi)y$. This transforms equation (5) into

$$F[\pi x - (1 - \pi)y] = \pi F(x) + (1 - \pi)F(y), \tag{A1}$$

whose only solution follows $F(x) = \alpha x + \beta$ (see the proposition below). Transforming back, we get equation (6) and conditions (i) $\alpha + \beta > 0$ and (ii) $0 \leq D < \ln(-\beta/\alpha)$.

    Proposition I. $F(x) = \alpha x + \beta$, where α and β are real coefficients, is the only solution of equation (A1) ($0 < \pi < 1$) if F is defined at each $x \in \langle 0, x_{\max}\rangle$ and is continuous at $x \to 0^+$.

    Proof. (i) Putting $y := 0$, we get $F(x) = [F(\pi x) - (1 - \pi)F(0)]/\pi$. Putting $x := 0$, we get $F(y) = \{F[(1 -$

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$\pi)y] - \pi F(0)\}/(1 - \pi)$. (ii) Putting $y: = x$ and $F(x) = F(y)$, we get $F(\pi x)/\pi - (1 - \pi)/\pi F(0) = F[(1 - \pi)x]/(1 - \pi) - \pi/(1 - \pi)F(0)$. (iii) Since $(1 - \pi)/\pi - \pi/(1 - \pi) \equiv 1/\pi - 1/(1 - \pi)$, it follows that $[F(\pi x) - F(0)]/\pi = \{F[(1 - \pi)x] - F(0)\}/(1 - \pi)$. (iv) Substituting $G: = F + F(0)$, we get $G(\pi x)/\pi = G[(1 - \pi)x]/(1 - \pi)$. (v) Putting $z: = \pi x$ and $\xi: = (1 - \pi)/\pi$, we get $\xi G(z) = G(\xi z)$. (vi) Putting $z: = 1$, $x: = \xi$ (because $\xi > 0$, we use the continuity of F at $x \rightarrow 0^+$), and $\alpha: = G(1)$, we get $G(x) = \alpha x$. (vii) Substituting back and setting $\beta: = F(0)$, we get $F(x) = \alpha x + \beta$.

Note I. (i) If $\pi = 0.5$, then equation (A1) becomes the Jensen functional equation. (ii) The condition that $0 < \pi < 1$ is biologically realistic, since $\pi = 0$ or $\pi = 1$, would mean the lack of the first or the second assemblage to compose.

Thesis III. Equation (6) captures a strictly decreasing function iff $\alpha < 0$ and $\beta > 0$.

Proof. Equation (6) is strictly decreasing iff $(dz/dD) = (1/\ln \varepsilon)[(1/(\alpha e^D + \beta)]\alpha e^D < 0$. It happens only if $\alpha < 0$ because the existence of a logarithm in equation (6) requires that $\alpha e^D + \beta > 0$. As a consequence, $\beta > 0$.

Thesis IV. Equation (6) captures downward accelerating function iff $\alpha < 0$ and $\beta > 0$.

Proof. Equation (6) is downward accelerating iff $(d^2z/dD^2) = (1/\ln \varepsilon)[\beta/(\alpha e^D + \beta)^2]\alpha e^D < 0$. It holds iff $\alpha\beta < 0$.

Thesis V. Any function following equation (6) intersects the X-axis at $D > 0$ iff $\alpha < 0$ and $\beta > 0$.

Proof. If equation (6) is defined and $\alpha < 0$, then there is always a $D1$ so that $0 < \alpha e^{D1} + \beta < 1$, which makes $\ln(\alpha e^{D1} + \beta) < 0$. If there is at least one $D2$ to make $z(D2) > 0$ (a biologically relevant condition), then $z(D)$ intersects the X-axis, as equation (6) captures a continuous function.

Thesis VI. The theses III–V hold true regardless of the method of z calculation (z can be computed as the slope between A/ε and εA or, alternatively, as the slope between A and εA; see fig. 1a).

Harte et al. (2009) computed the slope of the logarithmically transformed species-area relationship (SAR), z, as the mean value of two subsequent values of z when doubling area; that is, they computed the mean value from z between A/ε and A and from z between A and εA. The slope of a logarithmically transformed SAR between A and εA is z at D_A. It is given by equation (6), which can be modified to

$$\varepsilon^{z_A(D_A)} = \alpha_A e^{D_A} + \beta_A, \tag{A2}$$

where index A indicates that the exact values of parameters were set for area A (fig. 1a). The same holds true for the preceding sequence of two areas (i.e., A/ε and A). Hence, we can write

$$\varepsilon^{z_{A/\varepsilon}(D_{A/\varepsilon})} = \alpha_{A/\varepsilon} e^{D_{A/\varepsilon}} + \beta_{A/\varepsilon}. \tag{A3}$$

The parameters α and β may vary between the two focal areas. (The possible variation in the parameters is not caused by variation in π, for π does not affect the exact value of either α or β; see "Thesis II"). Nonetheless, we prove that the z-D relationship constructed by Harte et al. (2009) would be downward accelerating had it been universal (taxon invariant). Again, we allow variation in all parameters with scale to avoid constraining our results by the assumption of their scale invariance.

According to figure 1a, $D_A = D_{A/\varepsilon} + \ln \varepsilon - z_{A/\varepsilon} \ln \varepsilon$. Hence, $\varepsilon^{z_{A/\varepsilon}(D_A)} = \varepsilon \beta_{A/\varepsilon}/(\varepsilon - \alpha_{A/\varepsilon} e^{D_A})$. It follows that

$$\bar{z}_A(D_A): = \frac{z_{A/\varepsilon}(D_A) + z_A(D_A)}{2} = \frac{\ln\left(\varepsilon \frac{\alpha_A \beta_{A/\varepsilon} e^{D_A} + \beta_{A/\varepsilon}\beta_A}{\varepsilon - \alpha_{A/\varepsilon} e^{D_A}}\right)}{\ln \varepsilon}, \tag{A4}$$

where $\bar{z}_A$ is the estimate of the SAR slope in logarithmic space used by Harte et al. (2009) if $\varepsilon = 2$. Clearly, $\bar{z}_A$ is strictly decreasing, attaining 0, and downward accelerating with D. The reason is that

$$\frac{d^2\bar{z}}{dD^2} = \frac{1}{\ln \varepsilon}\left(\frac{\alpha_A \beta_A e^{D_A}}{(\alpha_A e^{D_A} + \beta_A)^2} + \frac{\alpha_{A/2} \varepsilon e^{D_A}}{(\varepsilon - \alpha_{A/2} e^{D_A})^2}\right) < 0 \tag{A5}$$

for $\alpha_A < 0$, $\alpha_{A/2} < 0$, $\beta_A > 0$, and $\varepsilon > 1$. (Note that the first additive term in eq. [A5] is the derivative of eq. [6].) In sum, the taxon-invariant z-D relationship computed following Harte et al. (2009) has the same properties as its bottom limit (given that the SAR in logarithmic space is concave; eq. [6]).

Our theory provides a tool to compute the exact value of the derivative of the SAR in the case of a universal z-D relationship. If ε approaches 1 ($\varepsilon \rightarrow 1^+$ still being greater than 1), the two subsequent areas, A and εA, approach each other, and $z(A)$ approaches the derivative. Apparently, the z-D relationship drops very steeply

(from $z[0] = 1$), being still downward accelerating, in this case. The reason is that $(dz/dD) = (1/\ln \varepsilon)[1/(\alpha e^D + \beta)]\alpha e^D \to -\infty$ if $\varepsilon \to 1^+$, which follows from equation (6). This means that all species would be absolutely widespread at all scales had the relationship between D and the exact derivative of the SAR along area been universal.