

Appendix from A. H. Hurlbert and W. Jetz, ‘More than ‘More Individuals’: The Nonequivalence of Area and Energy in the Scaling of Species Richness’

(Am. Nat., vol. 176, no. 2, p. E50)

Supplementary Theory, Information, and Analyses

Testing for Equivalent Effects of Area and Energy: Functional Form versus Symmetry

Wright (1983) suggested that species richness (S) of a region was a function of the number of individuals (N) that could be supported in that region, $S = f(N)$. N was assumed to be proportional to the regional area (A) and mean energy availability ($\bar{E}$), and thus, $N = \kappa A \bar{E}$, where κ is the coefficient of the proportionality. Wright’s (1983) assumption is then equivalent to $S = f(\kappa A \bar{E})$, a function symmetric with respect to A and $\bar{E}$ where an x -fold increase in either A or $\bar{E}$ should result in an identical increase in S . Using arguments based on lognormal abundance distributions, Wright (1983) further suggested that f was a power function:

$$S = c(\kappa A \bar{E})^z. \quad (\text{A1})$$

Thus, there are two different ways in which Wright’s (1983) formulation might be inadequate. First, A and $\bar{E}$ might have asymmetric effects on S such that richness increases at a different rate along the two axes, where $S = f(A, \bar{E})$ as opposed to the single-variable model $S = f(\kappa A \bar{E})$. Second, S may not be a power function of N , such that the slope z depends on A or $\bar{E}$:

$$S = c(\kappa A \bar{E})^{z(A, \bar{E})}. \quad (\text{A2})$$

Models 3, 4 and 5 (see main text) allow us to distinguish among these possibilities. Model 3 is a power law model that is symmetric with respect to A and $\bar{E}$ (eq. [A1]), and thus, it is consistent with Wright’s (1983) formulation. Model 4 is a power law model that is asymmetric with respect to A and $\bar{E}$. In this model, a strict more-individual hypothesis, $S = f(N)$, is invalid, but there is support for f as a power function. The model follows the equation

$$S = c A^z \bar{E}^w, \quad (\text{A3})$$

where $z \neq w$. When doubling area, S increases by a multiplicative factor 2^z , while doubling E increases S by a factor 2^w . Hence, the model is asymmetric with respect to A and $\bar{E}$, and support for this model implies that the more-individuals hypothesis, $S = f(N)$, can be rejected.

Model 5 is equivalent to model 4 but with an interaction term. When log transformed, it can be written

$$\log S = c + z \log A + w \log \bar{E} + q \log A \log \bar{E}. \quad (\text{A4})$$

The addition of the interaction term implies that f is not a power law, but it does not necessarily imply symmetry, $S = f(N)$, or asymmetry, $S = f(A, \bar{E})$. Considering the effect of doubling either area or energy on species richness,

$$\log S(2A, \bar{E}) = c + z \log 2A + w \log \bar{E} + q \log 2A \log \bar{E}, \quad (\text{A5})$$

$$\log S(A, 2\bar{E}) = c + z \log A + w \log 2\bar{E} + q \log A \log 2\bar{E}. \quad (\text{A6})$$

Symmetry about A and $\bar{E}$ implies $\log S(2A, \bar{E}) = \log S(A, 2\bar{E})$, which is true only if $z + q \log \bar{E} = w + q \log A$, which cannot generally be met (i.e., for any A and $\bar{E}$). While support for model 5 disqualifies a power law-based model, it says nothing about the asymmetry of effects of area and energy, because we do not know whether the goodness of the fit is due to the effect of asymmetry or to the deviation from a power law.

In order to assess symmetry of the species-area-energy relationship in regions where there was majority support for model 5, we compared Akaike Information Criterion (AIC) values for model 3 with those of model 4. If the fitted equation from model 5 represented a symmetric surface, then the fit of a symmetric plane (model 3) should be greater than that of an asymmetric plane (model 4). In 20 of the 22 regions with majority support for model 5, the asymmetric model had lower AIC values (fig. A1), and hence, support for model 5, like support for model 4, can generally be taken as support for the idea that the more-individuals hypothesis is inadequate for explaining species-area-energy patterns.

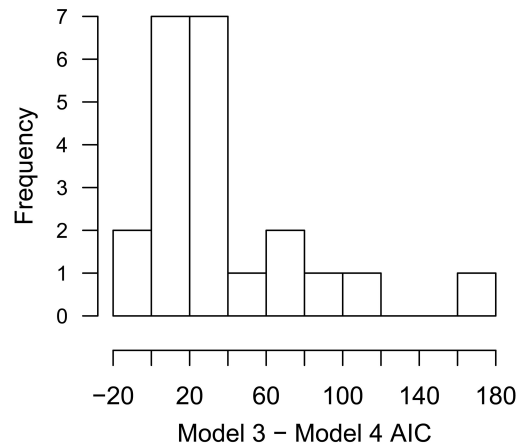


Figure A1: Difference in Akaike Information Criterion (AIC) values between model 3 and model 4 for the 22 regions with majority support for model 5. Positive difference values imply support for model 4, suggesting an asymmetric effect of area and energy on species richness in those regions.

Biome Vertical Habitat Complexity

Table A1

Crude scores assigned on the basis of the height and complexity of the vegetation most characteristic for a biome

Biome	Typical height (m)	Score
Tropical and subtropical moist broadleaf forests	30	7
Tropical and subtropical dry broadleaf forests	25	6
Tropical and subtropical coniferous forests	25	6
Temperate broadleaf and mixed forests	25	6
Temperate conifer forests	25	6
Boreal forests/taiga	15	5
Tropical and subtropical grasslands, savannas, and shrublands	1	3
Temperate grasslands, savannas, and shrublands	.5	3
Flooded grasslands and savannas	.2	2
Montane grasslands and shrublands	.3	3
Tundra	.2	1
Mediterranean forests, woodlands, and scrub	20	6
Deserts and xeric shrublands	0	0
Mangroves	5	4

Note: Biome delineation follows Olson et al. (2001).

Slope Variation Model Results

Table A2

Top six models out of 63 for explaining variation in regional species-area slopes as ranked by the small sample-adjusted Akaike Information Criterion (AIC_c), including model weights (w_i) and relative importance weights of each of the six variables considered

Model	Model						Variable relative importance weight
	1	2	3	4	5	6	
R^2	.582	.560	.554	.530	.538	.537	
AIC_c	-400.8	-397.7	-396.2	-395.1	-394.7	-394.4	
ΔAIC_c	0	3.10	4.59	5.73	6.11	6.35	
w_i	.661	.140	.066	.038	.031	.028	
Mean NPP	1	1	1	0	1	0	.90
Elevational range	1	1	1	1	1	1	1.00
Habitat diversity	1	1	1	1	1	1	1.00
Habitat-area slope	1	1	1	1	1	1	1.00
Vertical complexity	1	1	0	0	0	1	.84
NPP range	1	0	1	0	0	0	.76

Note: Variable importance weights represent the sum of the model weights for all models in which a particular variable is entered (Burnham and Anderson 2002). NPP = net primary productivity.

Table A3

Top six models out of 63 for explaining variation in regional species net primary productivity (NPP) slopes as ranked by the small sample-adjusted Akaike Information Criterion (AIC_c), including model weights (w_i) and relative importance weights of each of the six variables considered

Model	Model						Variable relative importance weight
	1	2	3	4	5	6	
R^2	.169	.173	.171	.170	.169	.173	
AIC_c	156.3	158.1	158.3	158.4	158.5	160.2	
ΔAIC_c	0	1.78	2.01	2.08	2.16	3.92	
w_i	.288	.118	.105	.102	.098	.041	
Mean NPP	1	1	1	1	1	1	1
Elevational range	0	0	0	1	0	0	.26
Habitat diversity	0	0	0	0	1	0	.25
Habitat-area slope	1	1	1	1	1	1	.99
Vertical complexity	0	1	0	0	0	1	.29
NPP range	0	0	1	0	0	1	.26

Note: The variable importance weights represent the sum of the model weights for all models in which a particular variable is entered (Burnham and Anderson 2002).

Variable Correlation Matrix

Table A4

Spearman rank correlation coefficients (r_s) between species-area and species–mean net primary productivity (NPP) slopes (as estimated in model 4), occupancy, the range in species richness values, and six regional variables

	Area slope	NPP slope	Mean NPP	NPP range	Habitat-area slope	Habitat diversity	Elevation range	Vertical complexity
NPP slope	.28	1						
Mean NPP	−.37	.20	1					
NPP range	.55	−.08	−.82	1				
Habitat-area slope	.54	.11	−.76	.72	1			
Habitat diversity	−.33	−.02	.06	−.12	−.01	1		
Elevation range	.30	−.09	−.18	.36	.22	.44	1	
Vertical complexity	−.49	−.02	.63	−.58	−.55	.26	−.09	1
Richness range	.42	.46	.43	−.05	−.07	−.19	.18	.03
Occupancy	−.95	−.22	.42	−.61	−.57	.33	−.29	.49

Note: For $|r_s| \geq 0.25$, $P < .01$; for $|r_s| \geq 0.33$, $P < .001$; and for $|r_s| \geq 0.37$, $P < .0001$. Correlations were conducted across all 107 regions except for with NPP slope, where five outliers were removed (see text).