Humped Pattern of Diversity: Fact or Artifact?

Molino and Sabatier (*1*) claimed to have evidence for validation of the intermediate disturbance hypothesis (*2*) in a tropical rainforest. Here, we demonstrate that the humped pattern of species diversity in a gradient of disturbance [figure 2 in (*1*)] is a methodological artifact arising from the manner in which the relationship was constructed.

Molino and Sabatier estimated environmental disturbance as the proportion of pioneer or heliophilic species in the plots studied. They justified this approach by noting that "[b]ecause pioneer species establish only in gaps, their occurrence and density should record the recent history of canopy gap openings." The approach is well founded biologically but will always produce a statistically humped pattern.

For any pool of species classified into two groups, it is possible to calculate the expected richness of a sample of *n* individuals that contains a proportion *P* of individuals from either of the two groups. The total expected richness will be the sum of the expected richness in a sample of $P \times n$ individuals from one group, plus the expected richness of a sample of $(1-P) \times n$ individuals from the other group. Considering a parent distribution formed by $N(i)$ individuals, distributed among $S(i)$ species with $m(i)$ abundance, the expected richness can be calculated with a rarefaction procedure (*3*). With this procedure, we estimated the expected richness as a function of the proportion of species from one group. We assumed that individuals among species may be distributed normally (curve **a** in Fig. 1), uniformly (curve **b**), or lognormally (curve **c**). In all cases, the expected pattern has a markedly humped distribution.

The humped pattern is statistically generated without the need to invoke any biological process. The only requirement is variation among samples in the relative number of individuals from one species group. Variation of species proportions could result from disturbance; differences in recruitment, mortality, soil texture, or nutrient levels; or by chance. Regardless of the cause of variation, a plot that relates the proportion of individuals from one group to total species richness will always result in a humped pattern of diversity. Molino and Sabatier offered good arguments for using the proportion of heliophilic or pioneer species as a measure of disturbance; nevertheless, all variation in the abundance of these species, whether related to disturbance or not, will tend to validate the hypothesis. Their methodology forces the occurrence of a humped pattern in total richness and thus should not be used as a validation of the intermediate disturbance hypothesis.

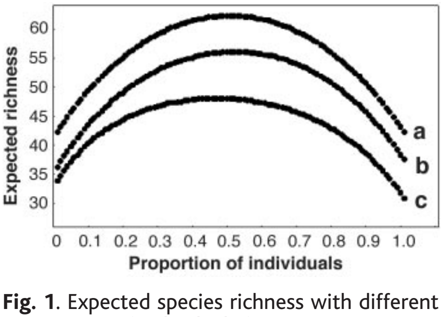

Fig. 1. Expected species richness with different proportions of individuals from any two species groups, with both groups of species assumed to follow a normal distribution of abundance (curve **a**), a uniform distribution (curve **b**), or a log-normal distribution (curve **c**). $S(i) = 50$; $N(i) = 10{,}000$; $n = 100$.

We hope that further studies on this topic will remind researchers that the null expectation for trends of diversity along a gradient defined by the proportional representation of species is humped rather than horizontal.

Matías Arim
Olga Barbosa
Center for Advanced Studies in Ecology and Biodiversity
Pontificia Universidad Católica de Chile
Casilla 114-D
Santiago, Chile
E-mail: marim@genes.bio.puc.cl

References

1. J.-F. Molino, D. Sabatier, *Science* **294**, 1702 (2001).
2. J. H. Connell, *Science* **199**, 1302 (1978).
3. N. J. Gotelli, G. R. Graves, *Null Models in Ecology* (Smithsonian Press, Washington, DC, 1996).

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Response: Although apparently trivial, the mixing effect described by Arim and Barbosa fits perfectly with the intermediate disturbance hypothesis. We can assume that the two groups of species are guilds, and that disturbance is the only force that can constrain them to mix (*2*). Since, as the comment demonstrates, mixing automatically increases diversity, a humped pattern must appear with any efficient disturbance indicator.

Interestingly, this mixing effect does not explain our disturbance-diversity relationship. We applied the procedure of Arim and Barbosa to the 3554 heliophilic stems (HS) (91 species) and 7972 nonheliophilic stems (NHS) (404 species) of figure 2 in (*1*). We used 40-stem samples and Hurlbert's rarefaction method (*3*) to calculate the expected species richness, $E(S_{40}) = E(S_{hs}) + E(S_{nhs})$, where $hs + nhs = 40$. In the corresponding model (curve **a** in Fig. 1A), variations in species richness result only from changes in group proportions along the gradient: When calculated separately within each group—that is, for pure heliophilic or nonheliophilic samples—$E(S_{40})$ does not vary with the percent of stems that are heliophilic (curves **a′** and **a″** in Fig. 1B). The observed values on quadrats (curve **c** in Fig. 1A) strongly depart from this model, which indicates that other processes are involved.

To completely remove the mixing effect, we plotted separately $E(S_{40}) = E(S_{hs})$ and $E(S_{40}) = E(S_{nhs})$, to show the species richness for pure HS or NHS samples. We pooled quadrats in 10% HS intervals, in steps of 5% HS, to allow the calculation of $E(S_{40})$ for both groups all along the gradient. The humped patterns that appear in both cases (curves **b′** and **b″** in Fig. 1B) reveal a drift in the species abundance distributions within the individual groups along the disturbance gradient. The role of this drift

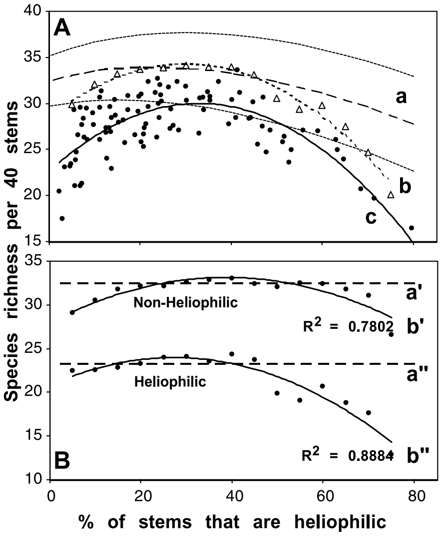

Fig. 1. Species richness in 40-stem samples [$E(S_{40})$] as a function of the percentage of heliophilic stems (%HS) [using data set of figure 2 in (*1*)]. (**A**) Expected and observed species richness, $E(S_{40}) = E(S_{hs}) + E(S_{nhs})$, for both heliophilic and nonheliophilic stems. Curve **a** shows the expectation of the Arim and Barbosa model, which assumes invariant species abundance distributions; the accompanying dotted curves show corresponding 95% confidence intervals (*4*). Regression curves for the data for pooled quadrats [open triangles and curve **b**; $R^2 = 0.9784$, $F(2,12) = 174.83$, $P << 0.001$] and for the observed values for all quadrats [solid dots and curve **c**; $F(2,96) = 55.86$, $P < 0.001$] are also shown. (**B**) Expected and observed species richness patterns for nonheliophilic [$E(S_{40}) = E(S_{nhs})$] and heliophilic [$E(S_{40}) = E(S_{hs})$] species, calculated separately. According to the Arim and Barbosa model, $E(S_{40})$ should not vary with %HS for nonheliophilic or heliophilic species (curves **a′** and **a″**). Actual data for pooled quadrats show a humped pattern for both nonheliophilic [curve **b′**; $F(2,12) = 21.29$, $P << 0.001$] and heliophilic [curve **b″**; $F(2,12) = 47.74$, $P << 0.001$] species. For calculating curves **b**, **b′**, and **b″**, quadrats were pooled in 10% intervals, in steps of 5%.

can be seen if we modify the procedure of Arim and Barbosa slightly by calculating $E(S_{40}) = E(S_{hs}) + E(S_{nhs})$ using distributions from pooled quadrats (as in curves **b′** and **b′** in Fig. 1B) rather than using the overall species' abundance distributions. The curvature of the resulting humped pattern (curve **b** in Fig. 1A) strongly differs from the expectation of Arim and Barbosa (curve **a** in Fig. 1A), but is similar in magnitude to the regression curve for the observed quadrat values (curve **c** in Fig. 1A).

These findings fit with the intermediate disturbance hypothesis and the niche partitioning theory: Low and high disturbance levels allow dominance of few species, whereas intermediate disturbances increase both the number of niches and species evenness.

Jean-François Molino
Daniel Sabatier
Institut de Recherche pour le
Développement
UMR AMAP
TA 40/PS2
34398 Montpellier Cedex 5, France
E-mail: molino@mpl.ird.fr

References and Notes

1. J.-F. Molino, D. Sabatier, *Science* **294**, 1702 (2001).
2. Note the impossibility of obtaining, among our quadrats, a 0% to 80% variation in group proportions without aggregating most of the heliophilic species [see supplemental figure 5 in (*1*)].
3. S. H. Hurlbert, *Ecology* **52**, 577 (1971).
4. R. Lande, *Oikos* **76**, 5 (1996).

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