

Comment on “A Keystone Mutualism Drives Pattern in a Power Function”

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Vandermeer and Perfecto (Reports, 17 February 2006, p. 1000) maintain that a mutualist ant disrupts the power law distribution of scale insect abundances. However, reanalysis of the data reveals that ants cause an increase in the range of the power law and modify its exponent. We present a tentative, but more realistic, model that is suitable for quantitative predictions.

Scaling laws and their underlying mechanisms pervade biological research (1, 2). In particular, several authors (3–5) have suggested that animal group sizes display a power law statistical distribution

$$f(x) = ax^{-\beta} \quad (1)$$

where x is abundance, f is probability density, and a and β are constants, which corresponds to a straight line in a plot of $\log(x)$ versus $\log[f(x)]$ (e.g., Fig. 1B).

Vandermeer and Perfecto (6) compared the abundances of the scale *Coccus viridis* in coffee plants with and without the mutualist ant *Azteca instabilis*, which is thought to protect scale insects from parasitoids and predators. They identified a power law in the frequency distribution of scale insect numbers, but with deviations at high and low scale densities. However, only in the presence of ants did they find an upward deviation from the power function at high population densities (i.e., a curvature in the log-log plot, such that large values of x are more frequent than expected from a power law). This effect was attributed to the positive enemy-release effect of ants. The authors also offered a biological explanation for the power law and presented it as an instance of criticality.

A more refined analysis of the data suggests that the upward deviation from the power law noted in (6) is an artifact (Fig. 2). Instead of disrupting the power law, ants cause an increase in its range (longer straight line marked with circles in Fig. 2) and a change in β (Eq. 1). The artifact is due to the use of common histograms, which are not reliable for power laws. Instead, multiplicative bins should be used (7) (Fig. 1).

Furthermore, the authors incorrectly explained the power law with a model that leads to a lognormal. Figure 2B in (6) gives the lognormal probability function for an ever-decreasing fraction of the range of abundances (which is an ever-increasing function of time in their model). This mimics the emergence of a power law (7), because a small part of any curve

approaches a straight line. It is true that the empirically observed power laws are limited to the upper range of the distribution [x between ~ 30 and 1500 (Fig. 2)], but the spots in this range are too well aligned to be part of a lognormal. Indeed, we were able to reject the lognormal hypothesis (8), both with ants ($P < 10^{-4}$) and without ants ($P < 10^{-2}$) (9).

As an alternative to their model, we assume that the relative growth rate $\frac{1}{x} \frac{dx}{dt}$ is an uncorrelated random variable with a nearly constant mean [$(r - m) < 0$] and variance (σ^2) in the upper range, but not in the lower range [t , time; r , reproduction; m , mortality; the rate of migration is comparatively low (10)]. From equation 11 in (11), it follows that the steady-state distribution of x in the upper range is a power law (Eq. 1) with an exponent

$$\beta = 2 \left(1 + \frac{m - r}{\sigma^2} \right) \quad (2)$$

This model must be tested by time-series analysis, but it is more robust than the model proposed by Vandermeer and Perfecto (6). Their model assumes a similar x in all of the plants at $t = 0$ and gives a lognormal only transiently, in the exponential growth phase. In contrast, our model is insensitive to initial conditions and produces a power law that lasts indefinitely.

Our model makes clear that ecological systems could develop scale invariance without the need of complex mechanisms. Contrary to the authors' claims, neither their model nor ours represent instances of criticality. “Criticality” is the condition of a system when it undergoes a second-order phase transition (12), and neither of the models discussed here implies such a transition. Power laws are found at criticality, but also in other situations (13). Moreover, our approach allows us to tentatively estimate eco-

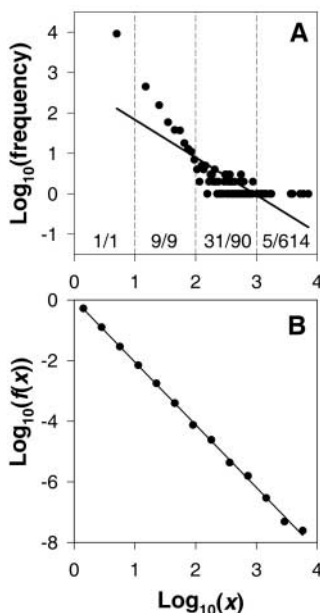


Fig. 1. Comparison of log-log plots using (A) linear bins (i.e., [1,10], [10,20], [20,30]...) (6) and (B) multiplicative bins (i.e., [1,2], [2,4], [4,8]...) (7) for a set of 10,000 power law distributed pseudorandom deviates with $\beta = 2.08$, which is the exponent found for scale insects in the presence of ants (x denotes Abundance, and f is its probability density). Simple linear regression gives a strongly biased slope of -0.93 ($r^2 = 0.71$) in (A), and a largely correct slope of -2.07 ($r^2 = 0.9997$) in (B). The plot in (A) displays the same spurious deviation from a power law as figures 1 and 4 in (6). We also give the number of used bins versus total bins in each section of the histogram in (A). The high proportion of empty bins is one of the reasons that common histograms are inappropriate for long-tailed distributions (7); these bins are not plotted, because $\log(0) \rightarrow -\infty$.

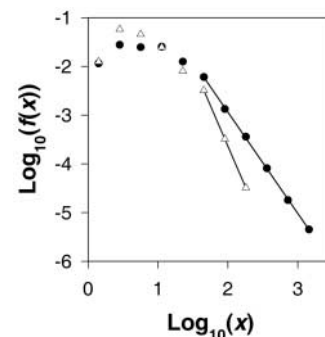


Fig. 2. Empirical probability densities (7) of the number of scale insects per coffee plant, in a log-log scale. Circles, with ants; triangles, without ants. The difference in the power law slopes ($\beta = 2.08$ with ants, $\beta = 3.32$ without ants) at high abundances could have a simple quantitative relationship with the enemy-release effect of mutualist ants, as suggested by our population model.

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logical interaction parameters from snapshot data. The slopes in Fig. 2 are $\beta = 2.08$ with ants and $\beta = 3.32$ without ants, as compared with $\beta = 2$ for $m = r$ in Eq. 2. According to the model, this implies an $m - r$ value 16.5 times as large without ants (assuming equal σ), which is consistent with the smaller population sizes in this case ($P < 10^{-4}$, Mann-Whitney U test).

In summary, our findings are in agreement with the enemy-release hypothesis supported by Vandermeer and Perfecto (6) but not with the patterns and processes that they reported. Although our results invalidate the management recommendations noted in (6), they might open the door to new management tools based on quantitative predictions.

References and Notes

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8. We calculated the Pearson correlation r^2 between $\log(x)$ and $\log[f(x)]$ in the upper range of the abundance distribution. We compared it with r^2 in the same range for 10^5 sets of lognormal pseudorandom deviates (14), with the same mean and variance of $\log(x)$ as the empirical data. We performed this operation with and without ants.
9. The authors pointed out a different mismatch to the lognormal, at the first bin in their figure 3. However, this was caused by the undue inclusion of plants with $x = 0$ in this bin, which covers from $\ln(x) = -0.35$ to $\ln(x) = 0.35$ [note that $\ln(0) \rightarrow -\infty$].
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