

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

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Vandermeer and Perfecto (Reports, 17 February 2006, p. 1000) reported a general power law pattern in the distribution of a common agricultural pest. However, there is an exact analytical solution for the expected cluster distribution under the proposed null model of density-independent growth in a patchy landscape. Reanalysis of the data shows that the system is not in a critical state but confirms the importance of a mutualism.

Vandermeer and Perfecto (1) proposed that the distribution of the scale insect *Coccus viridis* in an organic coffee farm conforms to a lognormal distribution as the result of variability in the local growth parameter of the population in the different plants. They also proposed that local populations of the pest exhibit density-independent growth coupled with global dispersal between the patches. A power law is one of the simplest null models for density-independent growth in a fragmented population, but does the distribution of *C. viridis* necessarily represent a power function? We note that there is an analytical solution for the expected distribution, whose fit allows us to quantify the relative importance of regional processes (migration) versus local processes (density-independent growth) and to extract information on additional mechanisms such as density-dependent species interactions, in this case with a mutualistic ant. This analytical solution has natural connections with another important null model in ecology, Hubbell’s neutral theory for species diversity, providing an additional pattern to test this theory at the population level.

The simple population model can be written with a deterministic equation for the temporal evolution of insect abundance growing independently in each patch (coffee tree):

$$\frac{dN_i(t)}{dt} = (\beta - \delta)N_i + \lambda \quad (1)$$

where  $\beta$ ,  $\delta$ , and  $\lambda$  denote the birth, death, and migration rates, respectively (2). To allow for possible extinction in any given patch and for the dynamics of subpopulations with low numbers, we consider the stochastic dynamics of these processes at the level of individuals. Based on Kendall’s solution of his birth-death-immigration (BDI) model (3), we note that for very low rates of global migration, the Fisher-Kendall logseries is the expected distribution of

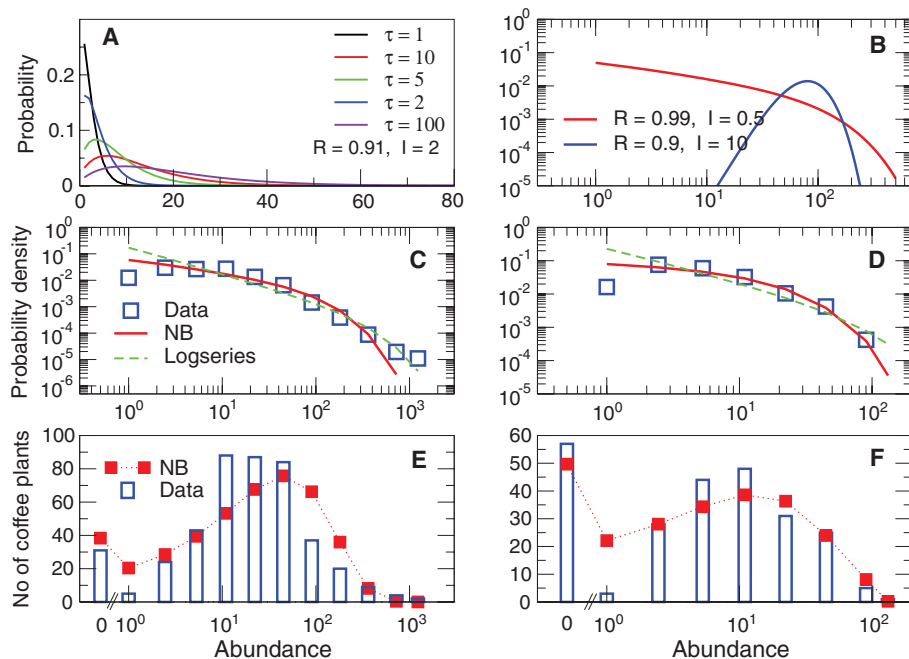
population sizes across coffee trees (3). Because a logseries is essentially a power law function with exponent  $-1$ , this exponent should be observed under this assumption. Why is this not the exponent reported by Vandermeer and Perfecto (1)? If migration is important, the expected distribution for the probability of a tree hosting  $n$  individuals is not given by the logseries but by the negative binomial obtained in (3):

$$P(n,t) = (1 - \hat{R}(t))^I \frac{[\hat{R}(t)]^n}{n!} (I)_n \quad (2)$$

where  $(I)_n = \Gamma(I + n)/\Gamma(I)$  and  $\hat{R}(t)$  is a time-dependent parameter given by:

$$\hat{R}(t) = \frac{1 - \exp[-(1 - \frac{1}{R})\tau]}{1 - \frac{1}{R} \exp[-(1 - \frac{1}{R})\tau]} \quad (3)$$

with dimensionless parameters  $R = \beta/\delta$ ,  $I = \lambda/\delta$ , and  $\tau = \beta t$ . At stationarity, the distribution of population sizes across coffee trees is also given by Eq. 2, replacing  $\hat{R}(t)$  by  $R$  (Fig. 1B). In the absence of temporal data, here we argue that the reported empirical distributions are consistent with this simple metapopulation stochastic model at stationary steady state. By using maximum likelihood, we can estimate two important parameters: the effective global coupling between local pest populations ( $I$ ) and the basic reproduction ratio of the insect ( $R$ ) (Fig. 1 and Table 1). Comparisons of the corresponding log likelihoods (for 2 and 3 in Table 1) indicate that global migration is significantly important and that, therefore, the negative binomial is a better model than the logseries for these data. This result is the same in sites with (Fig. 1, C and E) and without ants (Fig. 1, D and F). The effective  $R$  is close to and below a value of 1 (Table 1). In this regime, local populations are doomed to extinction but are constantly rescued by migration events. A



**Fig. 1.** Theoretical and empirical distributions of *C. viridis*. In the upper panels, time-dependent (A) and stationary (B) negative binomial probability distributions (Eq. 2) corresponding to Kendall’s BDI are shown at different times and parameter values. The distribution of population sizes across coffee trees is shown in sites far away from (D and F) and close to (C and E) ant nests. Middle panels [(C) and (D)] are log-log representations of the empirical data (13–15) and the theoretical logseries and negative binomial (NB) distributions, excluding zero observations (2 and 3 in Table 1). The bottom panels [(E) and (F)] present the data, including zero observations and the theoretical expectations for each abundance interval calculated from the negative binomial distribution (Eq. 2), but multiplying by the total number of coffee plants in each case. Parameter values are obtained by maximum likelihood estimation (Table 1).

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**Table 1.** Kendall model distributions (3). (1) Negative binomial probability distribution representing the probability of encountering  $n$  individuals in a coffee tree at the stationary state ( $R = \beta/\delta < 1$ ).  $P_0 = P(0|R, I)$  is the probability of local extinction (last column). (2) Probability of observing  $n$  individuals in a coffee tree conditioned to nonextinction. (3) Fisher-Kendall logseries representing the probability, which is defined also conditioned to nonextinction, of observing  $n$  individuals in a coffee plant when global spatial coupling through migration is vanishing small. Because independent local population growth is assumed, the corresponding parameter estimates of the three models can be obtained by building the likelihood  $L(R, I|n_1, \dots, n_p) = \prod_{k=1}^p P(n_k|R, I)$ , where  $p$  is the number of coffee plants. The negative log likelihoods are given for sites with ( $L_A^{(j)}$ ) and without ( $L_{NA}^{(j)}$ )

Probability distribution and negative loglikelihood	Maximum likelihood estimates			Probability of local extinction $P_0 = (1 - R)^I$		
		A	NA		A	NA
1. $P(n R, I) = (1-R)^I \frac{R^n}{n!} (I)_n$ $L_A^{(1)} = 2101.12, L_{NA}^{(1)} = 853.9$	$I$	0.538	0.46	Observed	0.07	0.23
	$R$	0.989	0.968	Expected	0.088	0.205
	$m$	0.025	0.03			
2. $P(n R, I) = \frac{(1-R)^I}{1 - (1-R)^I} \frac{R^n}{n!} (I)_n$ $L_A^{(2)} = 1988.1, L_{NA}^{(2)} = 716.8$	$I$	0.479	0.78	Observed	0.07	0.23
	$R$	0.99	0.95	Expected	0.11	0.096
	$m$	0.01	0.047			
3. $P(n R) = \frac{1}{\log(\frac{1}{1-R})} \frac{R^n}{n}$ $L_A^{(3)} = 2052.12, L_{NA}^{(3)} = 751.94$	$R$	0.997	0.987			

constant fraction of coffee trees is expected to be uninfected.

Vandermeer and Perfecto ( $I$ ) further considered the deviations of the data from the expected distribution to identify important processes not accounted for by this simple model. We show here that the simple model perfectly explains the deviation in the distribution of population sizes from a symmetric lognormal shape, both in sites close to (Fig. 1E) and in sites far away from (Fig. 1F) ant nests, particularly at low population sizes. This lognormal distribution would result from spatial or temporal environmental variability in  $R$ . The asymmetrical shape of the distribution for the fitted parameters, with a higher probability of low population sizes, is a signature of the importance of demographic stochasticity relative to spatiotemporal environmental variability. For high population sizes, however, our reanalysis confirms the deviation from the simple model. For those sites close to ant colonies, some coffee trees are more populated than predicted by the model (see Fig. 1C). Vandermeer and Perfecto propose that this deviation at the high end of the spectrum results from the mutualistic interaction with the ants that protect scales from natural enemies. Model fits confirm the expectation that the basic reproduction ratio  $R$  in sites close to ant nests is indeed higher than the value for ant-free sites (Table 1). Although a higher  $R$  shifts the distribution to higher values, it cannot account for the deviations from the general

shape of the negative binomial. Because such deviations are only observed in sites close to ant colonies (see high abundances in Fig. 1C), density-dependent factors related to the ant-scale interaction are a likely explanation for these deviations.

The correspondence between patterns and underlying biological processes is not unique, as a number of studies in community ecology have shown (4, 5). However, few examples in ecology furnish such a straightforward testable application of a simple null model (Kendall's BDI model). This model should apply to other agricultural pests and to other fragmented populations in ecology. It has already found applications to population genetics (6) and has natural connections to Hubbell's neutral theory in community ecology (7, 8, 9). If density-independent growth applies, with negligible species interactions, the BDI model should apply to the observed distribution of population sizes of individual species in metacommunities assembled by global dispersal. This type of data provides an additional pattern, within populations that are fragmented, that ecologists can consider when evaluating neutral theory.

Although the reported pattern does not support the original idea of a self-organized critical state [see (10–12) for ecological examples], it indicates a value of local growth close to the boundary separating local extinction from persistence in the absence of global dispersal. Whether life-history strategies for pest populations evolve to this boundary is an open

question. Fisher-Kendall logseries can be seen as the limiting distribution of model 2 when dispersal,  $I$ , tends to zero. Therefore, the models are nested and the difference in negative loglikelihoods ( $L^{(3)} - L^{(2)}$ ) allows us to assess the unambiguous statistical significance of the dispersal parameter  $I$  both in sites with ant nests and in those without ant nests (16). The parameter  $I$  is the analog of the fundamental dispersal number in neutral community ecology (7). It is related to the size-dependent parameter,  $m = I/(I + N)$  (7), which measures the probability of immigration given a total abundance,  $N$ , in the coffee tree. Comparisons of this quantity indicate that, in relative terms, the importance of global migration versus local growth is more pronounced in sites without ants, where average abundances per coffee tree at the stationary state are lower, than in sites with ants.

question. So is the importance of extending Kendall's BDI model to incorporate environmental variability in local growth rates.

**References and Notes**

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