

# Response to Comments on “A Keystone Mutualism Drives Pattern in a Power Function”

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The comments by Alonso and Pascual and by Pueyo and Jovani clarify the power law distribution of subpopulations of the scale insect *Coccus viridis*. The low density deviations are now seen as part of a negative binomial distribution and the high density deviations as resulting from a change in the parameters of the power law. Our biological conclusion that an ant mutualism modifies the form of the power law is thus strengthened.

Alonso and Pascual (1) provide a perceptive analysis of our data on subpopulations of *Coccus viridis* in an organic coffee plantation in Mexico (2). Our initial interpretation of the distribution as a modified lognormal approaching a power function is clearly inferior to their interpretation of the same data as representing a negative binomial. We emphasize, however, that while one class of “deviation” from the power function is better explained by the negative binomial, Alonso and Pascual verify our interpretation of the other deviation as due to the keystone mutualistic association with the ant *Azteca instabilis*. Indeed, their quantitative analysis reinforces our qualitative observation. Furthermore, their projection of these results into the general field of neutral community theory is a perceptive addition to our study.

We had been unaware of the 1948 Kendall (3) paper, which is basic to their analysis, and agree that our situation is an example of precisely the birth-death-immigration (BDI) situation that Kendall analyzed. However, we remain convinced that there is something of a lognormal distribution hidden in the processes that are intrinsic to our, their, and Kendall’s analyses and suggest that a broader study of these sorts of distributions may be in order. For example, taking their equation 1,  $(dN_i/dt) = r_i N_i + I$ , where we have substituted  $r_i$  for their  $(\beta - \delta)$ , MacArthur (4) noted that this basic structure, if  $I = 0$  and the  $r_i$  are distributed normally, would lead eventually to the  $N_i$  being distributed lognormally, which is the point we made. If  $I = 0$ , the integrated form of their equation is  $N_i = N_0 \exp(r_i t)$ , or  $\ln(N_i) = r_i t$ . Thus, if the  $r_i$  are normally distributed, it is obvious that  $N_i$  will be lognormal. In our simulations (in which the  $r_i$  were drawn from a normal distribution

but were then held constant over time, and the immigration rates were cast as a series of immigrations drawn from a Poisson distribution), there was an approach to what appeared to be a lognormal distribution, but during the approach (the transient state) the deviation from the lognormal was evident. That deviation slowly disappeared as the simulation proceeded in time, as would be expected because the constant  $I$  must become small relative to  $r_i N_i$ . In subsequent simulations (not originally reported), we allow  $r_i$  to vary, according to a normal distribution, at each time step with the same qualitative results.

According to Kendall, if each subpopulation is initiated by a single propagule and subsequent immigration is trivial, the distribution of populations will be the geometric series. On the other hand, if populations are continually growing, but also continually being invaded by new individuals, the distribution of populations will be a negative binomial. Yet, simple simulations, with normally distributed  $r_i$ , in fact do result in data that seem to fit a lognormal distribution of  $N_i$ , as equation 1 of Alonso and Pascual (1) indicates should happen. Furthermore, there is now an extensive literature in the context of community theory noting the empirical relation between the logseries and lognormal (5–7). Yet, as Kendall notes, the continuous analog of the logseries is not the lognormal. We tentatively suggest that, in practice, if populations are allowed to grow to large sizes and immigration is relatively small compared with the sizes of those populations, the eventual distribution of population sizes will be indistinguishable from the lognormal, but during the approach to that lognormal status the distribution will be logseries. On the other hand, if immigration remains relatively large compared with the attained population densities of the subpopulations, the eventual distribution of population sizes will follow the gamma distribution, the limiting form of the negative binomial. We now realize that the data we presented in (2) was from a set of populations that were far

from their final state, and thus the question that should have been asked was whether the distribution was negative binomial or logseries, as correctly pointed out by Alonso and Pascual.

Pueyo and Jovani (8) take issue with our interpretation of the upward deviation from the power law at high densities as due to mutualistic ants disturbing an underlying power law. Their approach is effectively to ask whether the underlying parameters in the power law are themselves modified by the ants, and they conclude that indeed such is the case. We are in complete agreement with their approach and insist that what they argue agrees with our underlying notion. By demonstrating that the within-ant patch parameters are distinct from the outside ant patches, Pueyo and Jovani provide stronger evidence for the conclusion that this key mutualism is the driving force for what we claimed to be a deviation from the underlying power law. Their approach is clearly superior to ours, but the biological interpretation is the same. The authors also note that our data do not correspond to a lognormal distribution, which is consistent with the suggestion that we should have been asking the question about logseries versus negative binomial, rather than lognormal.

Alonso and Pascual also bring these analytical questions into the arena of community ecology, recalling the original intent of MacArthur (4). The interpretation we present here suggests a way in which the lognormal, negative binomial, and logseries may eventually be seen as part of the same general theory, the lognormal (or perhaps the gamma) being the expected final state, but either the negative binomial or logseries as the transient expectation. How this may relate to other recent theories of community structure (9–12) remains to be explored.

## References and Notes

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