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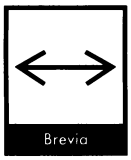

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The utility of covariances: a response to Ranta et al.

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In an earlier publication (Houlahan et al. 2007) we reviewed trends in population covariances within communities across a range of long-term empirical data sets. We used these results to argue that compensatory dynamics are rare in natural communities. Ranta et al. (2008) explored interspecific interactions in a simulated environment and showed that 'negative community covariance can be absent even in strongly competitive communities and can be found present in communities without competitive interactions'. On this basis they conclude that 'the negative community covariance method ... is of limited practical value when attempting to detect the presence of interspecific interactions among species in a community, or the relative importance of competition and environment in driving population fluctuations.'

There are three closely related points to consider here: first, exactly what is shown by demonstrating an absence of negative community covariance in some strongly competitive communities; second, what is shown by demonstrating negative community covariance in the absence of competition; and third, what these results say about the general utility of the community covariance method.

Getting the right argument

It is critically important to note that an absence of negative covariance is not the same as the presence of strong, positive covariance. As indicated in Table 1, the presence of positive covariance offers an unambiguous outcome about the importance of processes that cause negative or neutral covariance. In addition, negative covariances in communities without competitive interactions are expected because if the population were on a random walk, the probability that the sum of covariances is negative should be approximately equal to the probability that the sum of covariances is positive. Because our results indicated that positive covariation in real-world communities is far more common than negative covariation, we could safely conclude that interspecific competition is not as important as processes that cause positive covariation. The obvious consistency of our results suggests that covariances can indeed be a useful tool for exploring the relative importance of different influences on population dynamics.

Expanding the arguments

Ranta et al. are correct that negative community covariance can be absent in communities where strong competition is occurring, but only if the processes that cause populations to co-vary negatively (including competition) are not as important as processes that cause species to co-vary positively (Table 1). The logic is not symmetrical; if we see negative covariances, it does not mean that competition is important (although it is consistent with the hypothesis), but if we see positive covariances it is evident that competition is not as important as processes that cause species to co-vary positively. Ranta et al. showed that when competition was strong, negative covariances were seen unless there were other, more important, processes that caused positive covariance, such as a common response to the environment or interactions among positive temporal autocorrelation, intraspecific competition and interspecific competition (Ripa and Ives 2003).

Ranta et al. are also correct that negative community covariance can be present even in the absence of competition. However, the question is not whether we observe negative covariance in 'one' community (because there is about a 0.5 probability of seeing that when populations are

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Table 1. Decision table for the use of covariances.

Importance of Process	Processes driving positive covariance	Processes driving negative covariance	Interpretation
High importance	Natural populations should co-vary positively more than expected by chance	Natural populations should co-vary negatively more than expected by chance	Strong support for either result allows exclusion of the other
Low importance	Natural populations should co-vary negatively or as much as expected by chance	Natural populations should co-vary positively or as much as expected by chance	Ambiguous about the presence of a process but does exclude hypotheses of high importance

on random walks) but whether we see more negative or positive covariances than we would expect by chance across many communities. It is important that the distribution of covariances rather than any single covariance is used as a diagnostic. Ranta et al.'s results were consistent with this assertion by showing that, in the absence of competition among species, there were never more negative sums of covariances than would be expected by chance. That is, more than 50% negative covariances were only seen in the presence of strong competition. Note once again, as we did in the original paper, there are clearly mechanisms other than interspecific competition that can induce negative pairwise covariances in abundance, so negative covariation alone is not diagnostic of interspecific competition. And as Ranta et al. have shown, the absence of negative covariance does not alone provide support for the hypothesis that competition is absent in a particular population. However, the issue is not whether interspecific competition occurs (clearly it does), whether it can cause negative covariance (clearly it can), or whether it can occur in the absence of negative covariance (clearly it can, as demonstrated by Ranta et al. 2008); the issue is whether interspecific competition is an important determinant of population dynamics, and more specifically, whether, in nature, interspecific competition plays an important role in dampening fluctuations in community abundance (i.e. compensatory dynamics). Our results suggest that it is not and it does not.

We were explicit in our paper that we could make strong conclusions about positive and negative covariances from correlative analysis, but not about the mechanisms that caused them. For example, our main conclusion was that 'positive covariance among species is far more common in nature than negative covariance'. In fact, our concluding sentence was that 'variability in community abundance appears to be driven more by processes that cause positive covariation among species (e.g. similar responses to the environment) than processes that cause negative covariation among species (e.g. the direct effects of competition for scarce resources)'. We used specific processes as examples but were explicit that there are many possible processes that can cause populations to co-vary positively or negatively. In the final analysis, our results speak for themselves; the unambigously high prevalence of strong, positive covariance in real-world natural communities provides strong support for the argument that compensatory dynamics are rare in natural communities.

Future research

Ranta et al. suggest that ecologists should incorporate more biological realism into studying the relative importance of competitive versus external driving forces of community dynamics and that we should use more powerful statistical tools to answer this important question. While we agree wholeheartedly with this statement, one important impetus for using the covariance technique was the lack of either knowledge of these important biological drivers for particular systems, or the lack of consistent measurement of these important drivers at the necessary time scales in multiple communities. This problem was also recognized by Ranta et al. (2008): "Little is known about environmental forcing and its equivalence for species present". However, the detailed simulation study by Ranta et al. provides some interesting hypotheses that can be further tested. Their simulations suggest that the proportion of negative covariances is increased by low population growth rates, low degrees of environment equivalences, positively autocorrelated environmental variation and a high degree of community interaction. Relating these system traits of either the species within the communities or the environment to the sign and magnitude of the community covariances could help us to detect the mechanisms that are driving positive covariance among species across these systems.

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