Reply to Ferrarini: Strengths and weaknesses of simple competition models

In our work (1), we showed how a largely overlooked mechanism of coexistence based on intransitive competitive relations could be widespread in nature and improve our understanding of biodiversity maintenance. We outlined the basic mechanism, providing a simplified model that can be expanded in several directions. In his comment, Ferrarini (2) raises four points that he believes weaken our approach. Here, we show that these arise from a misunderstanding of our framework, and it is not clear that any of these points would change our fundamental results.

First, he stresses how our approach is rooted in zero-sum dynamics and focuses exclusively on competitive relations, reported as (−,0). We presented two equivalent mathematical formulations: one based on classic game-theory and the other using replicator equations. Note that replicator equations work with relative frequencies, which are necessarily “zero-sum” (the frequencies must sum to 1) regardless of the underlying population dynamics. Similarly, our representation of competition (−,−) is based on the substitution of individuals, and is thus represented by (−,+), analogous to predator-prey relations, and not (−,0) as stated by Ferrarini (2). This is evident, given that the replicator equations we used can be rewritten as a lower dimensional Lotka–Volterra predator-prey system. Although many types of interaction can occur between species, given our focus on diversity maintenance within a trophic level, we concentrated on competitive and neutral interactions (1).

Ferrarini (2) states that we do not consider the internal dynamics of the interacting species. However, we did treat intraspecific dynamics implicitly. Because we are dealing with relative frequencies, each species is clearly bounded by monodominance, and as a species drops to low frequency, it increasingly interacts with heterospecics relative to conspecifics. One could extend the framework to more sophisticated models, including density dependence (e.g., 3), but this would break the simple analytical results we presented. We have shown that these analytical results yield a deeper understanding compared with simulation approaches.

Ferrarini’s third concern is that interactions are pairwise (2). Although this is common in models of species interaction, we did discuss this very issue in the Supporting Information for our paper in PNAS (1) and in an article by Rojas-Echenique and Allesina (3), modeling multiple simultaneous competitors in a spatial context.

Fourth, Ferrarini (2) is concerned that time is “ill-defined” in the model and that pairwise interactions are temporally constant. We first note that time is by no means ill-defined: In the replicator equations, all individuals potentially interact at the same time (as in any mean-field system of ordinary differential equations), whereas the game-theoretical formulation can be coupled to the results obtained with differential equations using Gillespie’s algorithm (4). We also note that all our results pertain to the asymptotic behavior at $t\to\infty$, such that the speed of dynamics plays no role in our theory. Finally, although we did define a superior competitor for each pair of species at the beginning of the experiment, we discussed a relaxation of this assumption in the Supporting Information for our paper (1).

We conclude that although our simplified model necessarily has several limitations, these are not those outlined by Ferrarini (2).

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