LETTER

Demography and destiny: The syngameon in hyperdiverse systems

Charles H. Cannon[a,1] and Manuel T. Lerdau[b,c]

In PNAS, Levi et al. (1) argue that near-neighbor exclusion zones of conspecifics suffice to maintain tropical biodiversity. Their argument, while supported by computer simulations, does not consider (*i*) the influence that demographic processes may have on species survival or (*ii*) the phylogenetic distribution of diversity found in tropical systems. We agree that the fine-scale spatial effects of enemies described by Levi et al. may play a role in hyperdiverse systems, but we do not believe that this effect is sufficient for the long-term maintenance of diversity.

As first detailed experimentally by Allee and Bowen (2), populations that fall below a critical size have lower growth rates because mates become the limiting resource. The Allee effect poses a fundamental demographic challenge for rare species, which are prevalent in hyperdiverse tropical systems, as noted by Levi et al. (1). Many plant taxa that exist at chronically low densities (e.g., orchids) have evolved highly specialized relationships with obligate pollinators to overcome this challenge. Most tropical trees, however, have generalized pollination. How populations of chronically rare tropical tree species overcome this demographic challenge is a central question in tropical ecology. The models developed by Levi et al. do not address this issue.

A second aspect of tropical diversity not addressed by Levi et al. (1) is the combination of high species diversity with lower-than-expected diversity at the genus level. Simple models of diversity distribution show that, for the level of species diversity that is found in hyperdiverse tropical forests, generic diversity is low (3). That is, there are fewer genera present in a forest than one might expect, given the number of species. An explanation for the maintenance of high species-level diversity should also explain the simultaneous lower-than-expected levels of diversity at the generic level.

A relatively simple explanation for the maintenance of diversity that deals directly with Allee effects and predicts the lower levels of generic diversity is the participation of trees in networks of partially interfertile and closely related species, commonly called syngameons (3). Relative species densities and the number of sympatric species determine the frequency of interspecific hybridization in this neutral model. Oaks (*Quercus*), the most diverse genus of tree in the north temperate zone, are famous for their cohesive species identities in the face of frequent hybridization and typify the sygnameon (4). There is a growing body of evidence that hybridization and species stability are common among many groups of tropical trees found in hyperdiverse systems (5–8). The syngameon model of interfertile species networks provides a significant mechanism for tropical diversity maintenance. The syngameon model is congruent with the Janzen–Connell mechanism put forward by Levi et al. (1), but only the former suffices to overcome Allee effects and predict the patterns of genus- and species-level diversity found in many tropical forests.

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[a]Center for Tree Science, The Morton Arboretum, Lisle, IL 60532; [b]Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22904; and [c]Department of Biology, University of Virginia, Charlottesville, VA 22904

Author contributions: C.H.C. and M.T.L. wrote the paper.

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[1]To whom correspondence should be addressed: Email: ccannon@mortonarb.org.