LETTER

REPLY TO CANNON AND LERDAU: Maintenance of tropical forest tree diversity

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We thank Cannon and Lerdau (1) for their interest in our article (2) and for raising several related issues. At the outset, they express doubt that the Janzen–Connell mechanism is "sufficient for the long-term maintenance of diversity." The statement is made without reference to any feature of our model and can thus be regarded as an expression of opinion. Our results suggest that the Janzen–Connell effect, with otherwise neutral dynamics, can sustain diversity maintenance on evolutionary timescales; our simulations show that Janzen–Connell can permit long-term persistence in communities of up to 1,000 species on modestly sized landscapes, consistent with the most hyperdiverse natural tree communities. However, we did not discount other contributing processes that could either enhance or degrade diversity.

Cannon and Lerdau (1) raise the specter of Allee effects as potentially threatening species persistence for rare tropical tree species and suggest that that "participation of trees in networks of partially interfertile and closely related species, commonly called syngameons" offer a "relatively simple" mechanism for the maintenance of diversity (3). Because our model does not assume pollen limitation, or Allee effects of any kind, this point is tangential to the Janzen–Connell mechanism. However, adding Allee effects to a neutral model will degrade diversity even faster than drift, and reproductive assurance via syngameons could, at most, bring diversity up to neutral expectations (also note that hybridization can lead to extinctions due to reproductive interference). Thus, we see no plausible pathway for this mechanism to maintain observed levels of tropical tree diversity.

Further, there are empirical reasons to expect Allee effects to be weak in tropical forests. One might expect strong selection for selfing were Allee effects ubiquitous, yet nearly all tropical forest tree species are thought to be obligate outcrossers (4). Long-lived plants have many opportunities to reproduce, and there are no studies showing that pollen limitation actually scales up to influence the population dynamics of long-lived plants such as trees (5). Therefore, even if the syngameon phenomenon could maintain observed levels of tropical forest tree diversity, it is not empirically supported in tropical forests. In contrast, the Janzen–Connell mechanism is supported by hundreds of studies worldwide (6).

Virtually the entire literature on hybridization between tree species is based on temperate models, often at range boundaries or on steep environmental gradients. Moreover, it is not clear that the occurrence of hybridization, even when substantiated, as in oaks (*Quercus*) in the United States, alters the numbers of species counted in morphologically based species inventories of forest stands (7). The occurrence of hybridization in tropical forest trees remains a little-investigated, open question. A trickle of hybridization could help infuse adaptive genetic variation, which could continue to fuel Red Queen arms races, so syngameons could be important, even if they do not directly enhance diversity above neutral expectations. We therefore thank Cannon and Lerdau (1) for their comments while respectfully dissenting from their claims about our results.

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