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Review paper

Diversity Storage: Implications for tropical conservation and restoration

Henry F. Howe *

Biological Sciences (m/c 066), University of Illinois at Chicago, Chicago, IL 60607, United States

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ABSTRACT

The future of tropical biodiversity in human-dominated landscapes will be conservation and restoration of processes of seed dispersal by birds and mammals. Here the Diversity Storage Hypothesis posits that immense biological diversity resides within skewed species-abundance distributions of tropical trees, and further predicts that many species will adjust to increases of 1.5–3.0 °C anticipated from climate change by 2100. Common and widespread tropical trees (>100,000,000 individuals) may shift ranges but are unlikely to face extinction. Many rare species (e.g. <1000 individuals) have a more precarious future. The latter may be declining species bound for extinction, incipient species adjusting to environmental changes, or relics of past warmer and more seasonal climates that will be resurrected if processes of seed dispersal allow them to persist and spread. In fragmented agricultural landscapes, preserved or planted corridors, buffers and stepping-stone habitat patches around and between forest remnants are more vital than efforts to preserve or create contemporary forest compositions, dominance relations, and species-abundance distributions. An implication of Diversity Storage is that it is more important to facilitate migration into and out of changing landscapes to allow inherent diversity to adjust and coexist with agricultural economies than to resist change.

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1. Introduction

Changes in land management and climate will have profound effects on ecosystems worldwide (Diffenbaugh and Field, 2013; Parmesan and Yohe, 2003). With widespread conversion of tropical forests to agriculture over the last 150 years,

* Tel.: +1 630 202 7276.
E-mail address: hfhowe@uic.edu.

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conservation of dwindling protected areas is insufficient insurance for maintaining tropical biodiversity, or for ensuring regeneration of diverse forests if land is eventually released from agriculture. The challenge is especially acute in more than half of the land areas in tropical biomes that have been cleared for agriculture, logged repeatedly, or intensively hunted (e.g. Garcia et al., 2014). The best hope in degraded landscapes is to strategically preserve forest remnants (Ekroos et al., 2014; Melo et al., 2013; Rudel et al., 2009), and to determine where and how vegetation can be restored with assisted or unassisted secondary succession (Chazdon, 2008a, 2014). Efforts should emphasize preservation or creation of mixed-species corridors, planted-tree buffers and stepping-stone habitat patches that permit movement of plant populations in response to environmental change. Because most tropical trees are dispersed by animals, conservation and restoration of the 21st Century must emphasize protection or reintroduction of birds and mammals that actually mediate tree dispersal on local scales, and allow tree migration on regional scales. For long-term resilience of landscapes that remain under cultivation or grazing, it is more important to maintain or create patches and corridors of forest cover and encourage the dispersal agents that use them than to attempt to re-establish contemporary forest composition, as defined by dominance and species-abundance distributions, that are or will soon become ecologically obsolete.

Implications of processes and consequences of species turnover for both conservation and ecological restoration do not receive the attention they deserve. The Diversity Storage Hypothesis proposes: (1) tropical communities will change dramatically in species composition as land use and climates change, (2) for projected increases of 1.5–3° C this century, some or even many taxa in species-rich communities will respond positively to climate change, and (3) others will not. One unusual emphasis in this paper is in suggesting rare tree species, the source of most tree diversity in the tropics, as potential sources of species capable of responding positively to climate change. Another unusual emphasis is that the successful migration of common tree species and expansion of adapting species to new sites requires protection or re-introduction of dispersal agents responsible for tree movement across landscapes.

Turnover could result in net loss of taxa to landscape or global extinction, or replacement or even increases in richness due to range shifts and – in the longer term – speciation (e.g. Ellis et al., 2012; Parmesan and Yohe, 2003; in decades, Dornelas et al., 2014, in millennia or longer, Jaramillo et al., 2010). Positive responses may occur among widespread and abundant species with high genetic diversity, as well as spread of incipient species that by chance are pre-adapted, or are continually adapting, to developing conditions. It is uncertain what the future role of currently rare species (<1 ha^{-1}) will be. Because they comprise most tree species in diverse contemporary tropical forests, their fates are important (Hubbell, 2013; Pitman et al., 2001; ter Steege et al., 2013). Rare tree species that are relics of past climate regimes may be resurrected by return of conditions to which they are adapted. Or, lacking the genetic diversity of more common species with much larger populations, rare species may become extinct. Whether by range shifts, speciation, or resurrection in situ, species fortunes over centuries in a given landscape are virtually certain to reflect competitive gains by many species and ultimately genera that are now infrequent or rare, at the expense of those that are now common.

The Diversity Storage Hypothesis is developed for tropical trees. This is feasible because quantitative inventories exist for relative tree abundances at multiple scales in multiple tropical sites (e.g. Losos and Leigh, 2004; Pitman et al., 2001; ter Steege et al., 2013), and paleobotanical records calibrated with geological and biogeochemical proxies are the basis of ecological interpretations of climate change in the past (e.g. Davis et al., 2005; Jaramillo et al., 2010; Metcalfe and Nash, 2012). Diversity Storage is directly relevant to other species-rich taxa that are strongly associated with trees, such as herbivorous insects. Relevance is indirect for taxa with few species, including vertebrates that pollinate flowers or disperse seeds.

This Diversity Storage Hypothesis predicts that strong positive responses by a subset of currently common, infrequent or rare tree species will reflect adaptive responses to changes in land use or climate. This is not the storage effect of rare species in some community-drift models in which frequency-dependent advantages for rare species occur if density-dependent mortality of seedlings reduces abundances of common species (Hubbell, 2008). Rare-species advantages exist (e.g. Wills et al., 2006), but density-dependent seedling mortality may not be involved. On Barro Colorado Island (BCI) in Panama, for instance, survival of seedlings of 180 tree species shows that density-dependent mortality among conspecifics varies widely among species, but is much more pronounced in rare than common species (Comita et al., 2010). For most species in that sample, proximity of heterospecifics has a negligible effect on growth and mortality, suggesting that rare species may hold on, but are maladapted to current biotic or abiotic conditions. Diversity Storage predicts replacement of taxa that are now common with relic or novel species better adapted to or by chance more tolerant of environments as they change, not because of community drift reflecting random processes.

2. Short and long view

Conservation and restoration planning must accommodate both the short term of decades and the longer term of centuries or more. Imminent threats to tropical forests remain hunting, deforestation, forest fragmentation and complications of fire (Brodie et al., 2012; Laurance et al., 2012; Siegert et al., 2001). Deforestation affects local weather, often resulting in higher temperatures, decreased humidity and lower soil moisture tens to hundreds of meters inside fragment edges (Laurance et al., 2011). Fragmented forests in agricultural landscapes are not small-scale replicas of their former selves; they are developing communities adjusting to changing biotic and abiotic realities. For reasons that will become apparent, preoccupation with preservation of forest integrity defined by contemporary tree-species composition and dominance relations will become increasingly counterproductive with time in "permanent" agricultural landscapes. Forest composition and dominance will change with local, regional and global climates, as *they always have*. Long-term resilience of tropical