



Review paper

Diversity Storage: Implications for tropical conservation and restoration



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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,

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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 ($< 1 \text{ ha}^{-1}$) 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, pre-occupation 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

biodiversity in highly altered agricultural landscapes must expedite dispersal processes for birds and mammals and the tree species that they disperse to ensure that such changes take place, rather than leave current dominants trapped in environments in which they are unlikely to survive.

The key problem is that much of the ecology of existing tropical communities is the ecology of common species, which arguably are those best adapted to current climatic conditions. Over time scales of centuries, millennia and longer, species move, evolve or disappear with changing environments. As in the past, natural climate change alone will result in no-analog communities unlike those that exist today (Millar and Brubaker, 2006; Williams et al., 2007). In a future in which human influences on rates of climate change are compounded by human domination of landscapes, priorities for conservation and restoration must adapt. Changes in temperature, precipitation and seasonality in agricultural landscapes may even preview conditions projected over much of Africa, Asia and Central and South America by the end of this century (e.g. scenarios RCP 4.5 and RCP 8.5, IPCC, 2013, p. 89). Fragmented forests of the present may become nurseries of relic or incipient species that can better coexist with human-dominated landscapes of a hotter future than common species of the present. For most, that future will be aborted if dispersal agents are not present to carry seeds across landscapes.

3. Species abundances

Species-abundance distributions of tropical trees are highly skewed, with a few common and many infrequent or rare species (e.g. McGill et al., 2007). Skewed species-abundance distributions are general, occurring from dry-deciduous forests in southern India with 26 tree species ha^{-1} to rainforests in Bornean Malaysia and Amazonian Ecuador with >600 species ha^{-1} (Condit et al., 2004a). In hyperdiverse forests, common species are often very common (>20 ha^{-1}), but many species are rare or very rare (<1 or $\ll 1 \text{ ha}^{-1}$; e.g. Hubbell, 2013 and Pitman et al., 2001). Most of the diversity in tropical forests can be attributed to rare species.

An unprecedented inventory in the Amazon illustrates skew in relative abundances of tree species (ter Steege et al., 2013). In 1170 sampling sites of $\sim 1 \text{ ha}$ each across the Amazon Basin, 227 tree species, 1.4% of an estimated 16,000 tree species >10 cm diameter at breast height (dbh at 1.3 m), account for half of the individual trees. Tree species best known to science are likely to be those and other common, easily-studied species. “Hyperdominants”, each estimated to number 370,000,000 or more individuals, do not face imminent extinction in likely climate-change scenarios (IPCC, 2013). They are widespread enough to migrate to or remain in habitats with cooler local climates, and they are genetically diverse or physiologically plastic enough to acclimate to or adapt to some change. Much less attention is accorded the vastly greater number of infrequent and rare species in densities <1 ha^{-1} . In the Amazon samples, 13% of trees identified to species level are undescribed “morphospecies” (ter Steege et al., 2013). The authors estimate that about 10,000 species remain un-identified and not sampled, 6000 with populations <1000 individuals. These are at risk of extinction from human interference or chance with or without climate change (Hubbell et al., 2008). These unknowns may be relics adapted to climates past or incipient species that will respond positively to future change. Or they may be doomed.

The question of why some tree species are common while others are rare cannot be resolved here, but interpretations are worth mention. One view is that tropical tree species exist where they do because they are adapted to particular edaphic, seasonal or demographic niches, and displace competing species that are not as well adapted (e.g. Ricklefs, 2004). This framework integrates a role of history in determining which species equilibrate in a region, but the theme is that resources in time and space are finely partitioned. The other extreme is neutral theory, which posits that tree distributions and abundances reflect random processes, with no need to consider adaptation to particular edaphic niches or important interactions among species (Hubbell, 2001). Like changes in frequency of alleles under weak and fluctuating selection, neutral theory posits that associations of trees with environmental variables are difficult or impossible to distinguish from random (Holt, 2006; Lewontin, 1974). Subtle associations may exist, but are undetectable, leaving neutrality as the operational null hypothesis.

Issues of chance and determinism have implications for conservation. If seeds of all species are dispersed to all possible sites, and species differ markedly in use of resources, competition among seedlings, saplings or adults favors the best-adapted species. Chance plays a minor role. Conservationists can protect environments with known features with some confidence that species of interest will remain, and restorationists know what species should thrive within a given set of physical parameters. If chance plays a large role, the task of conservation biologists is more complicated, but the challenges for restorationists diminish. Most species should have wide tolerances.

Relative roles of chance and determinism are difficult to distinguish in theory or practice (Chazdon, 2008b; Clark, 2012; Leigh et al., 2004). Seed-fall observations and seed-addition experiments in Panama show that seeds of many common tropical species fail to arrive in sufficient numbers to occupy most sites, even where dispersal agents are common (e.g. Harms et al., 2000; Muller-Landau et al., 2008; Svenning and Wright, 2005). Priority has a large component of chance, not necessarily reflecting traits physiologically “best-adapted” to a site. Intensive seedling inventories in Panama, Ecuador and French Guiana find that most tree species are poorly represented in the seedling layer (Comita et al., 2007a; Metz, 2012; Norden et al., 2009, respectively). Even for abundant species, demonstrating habitat affinities is difficult. On BCI in Panama, Comita and colleagues (2007b) find that shrub and tree habitat associations (high plateau, low plateau, slope, streamside, swamp) are detectable at a small tree stage (<1 cm dbh) for 19 of 80 common tree species, and at a larger sapling or tree stage ($\geq 1 \text{ cm}$ dbh) for 18 of the 80 species. Five have the same habitat association as both smaller and larger trees. For about half, habitat affiliations are not obvious at either life stage. An exhaustive study of 1400 tree species in forest dynamics plots in Panama,

Ecuador and Colombia shows that 36%–51% of tree species have strong associations with soil-nutrient distributions (John et al., 2007). The unsettling news is that 49%–64% do not.

Rarity itself is a challenge. Species may be common in some places and rare elsewhere, common somewhere not yet sampled, rare everywhere, or have very limited geographical ranges. Hubbell (2013) uses power-law relationships of number with nearest-neighbor distances of common species to estimate that rare tree species often occupy extremely restricted ranges, frequently <15 km². With that reasoning, both intensive 25–52 ha samples at 15 sites across the tropics and 1 ha samples over vast areas of the Amazon Basin miss the majority of rare species. Where forests have been cleared for agriculture, many rare species are almost certainly already extinct (Pitman et al., 2002; Hubbell et al., 2008). Hubbell and colleagues predict that species with populations <1,000,000 are in danger of extinction from deforestation. Applied to terSteege and colleagues' (2013) sample, >10,000 tree species face extinction under plausible land-use scenarios in the Amazon alone, without climate change in the mix.

4. Species origin and extinction

Species formation and extinction mean different things in paleoecology, phylogenetics, and plant population biology (Rabosky, 2013). Plant macrofossils show change in morphological structure over millions of years (e.g. Soltis et al., 2005). Phylogenetics show relatedness of extant species based on sequence similarity, with criteria for species or “evolutionarily significant units” varying among investigators and phylogenies according to assumed rates of base-pair substitution (e.g. Rull, 2008). Whether substitution rates are assumed to be fixed or varied within phylogenies, the choice of what to analyze with fossil or molecular evidence usually depends on initial identification of taxonomic units identified by morphology.

Alternatively, for cryptic species that look alike but represent divergent lineages, species-level status is indicated by agreed-upon amounts of divergence (e.g. mitochondrial sequence differences in fig wasps of 4.2%–6.1%, implying divergences over 1.5–5.1 million years; (Molbo et al., 2003). More dramatic differences among species that are morphologically indistinguishable occur in tropical frogs in Southeast Asia, where disparities range from 9.95%–16.12% for one morphological species described as *Odoranna livida* (Stuart et al., 2006). Molecular analyses of some widely-sampled tree species do show cryptic genetic structure of morphologically similar populations (e.g. *Symphonia globulifera* L. f. [Clusiaceae] in South America, Dick et al., 2003; several Central American trees, Poelchou and Hamrick, 2013), but do not show genetic structure that might reflect speciation over small spatial scales. The role of cryptic speciation in tropical trees is not yet established, much less clear.

Broad molecular phylogenies do not detect such variation. They may isolate evolutionary differences between historical periods, for instance origination in the Miocene as compared with Pleistocene, or periods of relative stasis contrasted with bursts of radiation broadly contemporaneous with orogeny and glaciation (e.g. Fine and Kembel, 2011; Rull, 2011; Vegas-Vilarrúbia et al., 2011). Such studies indicate that the estimated number of generations required to produce species-level status is coarse in fossil and broad phylogenetic analyses. With few exceptions (e.g. *Homo sapiens*), species differences defined by fossil morphology or base-pair substitutions rarely are detected on time scales <100,000 years.

Population biologists, on the other hand, consider speciation to be a matter of reproductive isolation of similar populations. Reproductive isolation may involve much or little genetic change (Rieseberg and Willis, 2007; Templeton, 1981). Hybridization, chromosomal duplication, chromosomal re-arrangement, and strong selection in the presence of gene flow play more prominent roles in plant and invertebrate speciation than in terrestrial vertebrates, where species formation in allopatry appears to be the rule (Coyne and Orr, 2004). An important point for Diversity Storage is that tree speciation may create partial or full reproductive isolation among populations with little genetic change. Cryptic divergence by fig wasps referenced above probably involved reproductive isolation in much less than 1.5 my. With rapid environmental change, one expects strong selection among incipient species in diverse and widespread taxa, producing shifts in species-abundance distributions through range shifts and speciation without great change in dominant genera or families. Over millennia or longer, evolution from diverse taxa and currently rare taxa, perhaps derived from rare resurrected “relics” of past climates or new species capable of expanding in changing environments, produces different generic or familial compositions of non-analog communities.

Distinguishing relic from incipient species would be enlightening. Ecological applications of phylogenetics are promising (Morlon, 2014; Mouquet et al., 2012), but require samples from just these extremely parochial relic or incipient species, if they exist. Some endemic plants may be relics of previous climates, now restricted to microrefugia or “holdout” populations (e.g. Hannah et al., 2014; Rull, 2009; Stewart et al., 2010). Or, rare tropical trees may be incipient species forming under continuous, protracted speciation, beginning with point mutations that spread slowly by selection or drift among close relatives in a limited geographic area (Rosindell et al., 2010). Examples might include geographically limited herbs, vines, shrubs and small trees of the species-rich genus *Piper* (Paul and Tonsor, 2008). The argument for Diversity Storage assumes that populations diverge from surrounding or nearby parent populations as a consequence of selection from rapid environmental change. Divergence need not be allopatric if strong selective differentials create reproductive isolation. This could happen with little or much genetic change, for instance, if selection on some alleles pulls along linked loci, or quantitative genetic differentiation reinforces selection against hybrids (Feder et al., 2012; Via, 2012). Without episodes of strong favorable selection, small populations of a few to a few hundred individuals are likely to be quickly selected, or drift, to extinction.

Diversity Storage could provide fuel for pulses of speciation and migration across regions *only if migration is possible*. Species could arise from common or rare taxa. It now appears that speciation in trees is proportional to abundance of species-level taxa in forest-dynamics sites (Etienne et al., 2007), consistent with the general observation that ecological speciation is often diversity-derived, if not “diversity-driven” (Rundle and Nosil, 2005; Rabosky, 2013). Patterns most consistent with Diversity Storage as used here would be environmentally-driven bursts of species formation and extinction acting on incipient species over time, or on older taxa available for resurrection by returning conditions. Alternatively, Diversity Storage likely includes taxa that shift ranges as conditions change. The assumption in either case is that species with the capacity to move as environments change will move, replacing competitors that cannot keep pace (see Corlett and Wescott, 2013). For Diversity Storage to contribute to conservation and restoration in human-dominated habitats, migration must be possible across fragmented landscapes.

5. Species composition and climate change

Shifts in composition of communities at a given site have been the rule over almost any substantial period of time. In the Amazon, southern boundaries of the Basin shifted to dry woodland or savanna during the last glacial cycle ~20,000–50,000 years ago (Whitney et al., 2011). The central Amazon remained wooded, but pollen records show shifts in the composition of vegetation, with some areas now occupied by rainforest in more seasonal forest (Cowling et al., 2001; Bush and Metcalfe, 2012). Tropical rainforest persisted near the coast of West Africa, but not in most of the Congo Basin (Anhufo et al., 2006). Jagged edges of plots of isotope, pollen and sea- and lake-level proxies indicated that African climates were not stable for long during the Pleistocene, or even in the Holocene (Cowling et al., 2008; Nash and Meadows, 2012). Dynamism reflected in geological records have shown that it would be remarkable if the same hyperdominant tropical tree species of this century were as dominant in the same locations 20,000 years ago, or will be 20,000 years into the future. At current rates of environmental change, they may not be dominant in 200 years.

The key point is that tropical environments have been dynamic over the evolutionary history of plant genera alive today (see Rull, 2008, 2011). Six major glaciations of the last million years were preceded by dozens of lesser but detectable warm and cold spells (Millar and Brubaker, 2006). These were in turn preceded by dramatic shifts in climate, including glaciation, in the Eocene (34 mya; Tripathi et al., 2005), which since the end of the Cretaceous in South America interacted with the rise of the Andes (Hoorn et al., 2010). Extensive glaciation occurred as far back as the Late Paleozoic (Montañez and Poulsen, 2013). Most important for genera alive today, global temperatures reached or exceeded the 1.5–3° C increase predicted by intermediate climate scenarios by the year 2100 (IPCC, 2013, p. 1114) early in the current interglacial, during the last interglacial, and over the million years preceding the Pleistocene, as well as during the Paleocene–Eocene Thermal Maximum 56–51 mya (Willis and MacDonald, 2011; IPCC, 2013, p. 389). Abrupt climate changes on the scale of decades have occurred repeatedly (Alley et al., 2003). The point is that contemporary plant communities almost certainly include many species with the genetic capacity to withstand 1.5–3° C increase in temperature, with associated changes in precipitation and seasonality, even if these species are not widely abundant in the early 21st Century (e.g. Feeley and Silman, 2010). Rates of change in temperature and precipitation may exceed these intermediate projections (IPCC, 2013, scenario RCP 8.5, p. 1114), in which case plants and animals will face more immediate imperatives to acclimate, evolve or move.

A practical issue in an era of change is that much less is known about rare than common species. For instance, currently common and charismatic nutmegs (Myristicaceae) are well known from studies of pollination and dispersal (e.g. Kitamura and Poonswad, 2013; Ratiarison and Forget, 2013; Sharma and Armstrong, 2013 and references therein). Two common *Virola* species on BCI in Panama that are hyperdominant in the Amazon Basin offer insight into likely responses to climate change. On BCI, *V. sebifera* and *V. surinamensis* saplings and adults are sensitive to drought (Condit et al., 1995), as are *V. surinamensis* seedlings (Engelbrecht and Kursar, 2003). Both species now occupy vast ranges, but with drying and more seasonal climates over 50–100 years predicted for Central and northeastern South America (IPCC, 2013, RCP 4.5, pp. 1338–1344), ranges may shrink. Were these *Virola* species to disappear, fruit resources for a coterie of birds and monkeys that are important for dispersal of other tree species would disappear with them. No one knows how 71 other *Virola* species will increase or decrease in numbers if forests become drier or wetter. Of 73 *Virola* accorded species-level status (<https://ctfs.arnarb.harvard.edu/webatlas/neotropicaltree>), 35 are incompletely described morphospecies of unknown affinities, physiological capacities or geographical distributions.

Other species-rich genera will have winners and losers by the end of this century. *Inga* (Fabaceae) has hundreds of species (<http://www.tropicos.org/NameSearch.aspx?name=Inga>). Based on existing inventories and drought response in Panama, at least *Inga fagifolia*, *I. laurina*, *I. vera* and an undescribed *Inga* on BCI will do well in a drying climate, even if up to 50 congeners across the Isthmus disappear or persist only in moist havens (see Condit et al., 1996, 2004b, 2011). More of hundreds of *Inga* species in the Amazon, many undescribed, will likely persist in drying regions, but their relative drought sensitivity is unknown.

Species-poor genera may or may not respond positively to projected climate changes. For the monotypic rainforest tree *Poulsenia armata* (Moraceae), a hyperdominant in South America, the breeding population is enormous. However ecological studies suggest that the vast current range will probably contract. In a 50-ha plot in Panama, *P. armata* experienced 7% mortality during a strong El Niño drought, and 4%–5% mortality in other years (Condit et al., 1996). With no congeners, and some unknown block to speciation, the genus may become far less common or disappear from much of its range in Mesoamerica and northeastern South America.

Finally, fecund populations with sufficient genetic variation may evolve in response to strong selection (Davis and Shaw, 2001). This clearly occurs in some temperate trees on the scale of millennia, with a possibility of much more rapid change in these and other organisms with high fecundity (Davis et al., 2005). For a tropical example, in apparent response to land management over a period of 100 years, the widespread palm *Euterpe edulis* (Arecaceae) has adjusted to loss of large toucans (*Ramphastos*) as dispersal agents in fragments of the Atlantic Forest of Brazil through evolution of smaller fruits that are accessible to smaller birds (Galetti et al., 2013). Variation in seed size and the ratio of aril to seed mass occurs within species, probably reflecting variable selective pressures on fruits traits in space and time (Howe and Vande Kerckhove, 1980; Russo, 2003). However, the compelling evidence that *Euterpe* palms have adapted to local selection for seed dispersal in a matter of decades is remarkable.

6. Diversity Storage: conservation and restoration priorities

Targets of conservation and restoration are unsustainable if they are defined by species assemblages that are environmentally obsolete. The pace of change in land use and climate ensure that existing species *compositions* are or will soon be ecologically obsolete where they now exist (see Wright, 2010; Corlett, 2011). Wide recognition exists of the importance of large tracts of undisturbed tropical forests as refuges for endangered flora and fauna, and as sources of plant and animal colonists of surrounding areas (e.g. Gibson et al., 2011). Over centuries to millennia, the most important contributions of large reserves will not be preservation of tropical forests as we now know them. A realistic hope is that large reserves will retain enough variety to maximize odds that common or rare taxa will respond to changing conditions through replacement of existing dominants (for re-framing of the realized niche, see Sax et al., 2013). Ecological obsolescence presents immediate challenges to >50% of former tropical forest land area degraded by clear-cut logging, fragmentation, intensive hunting, and conversion to pasture and crops. Even if tolerant species prosper or evolve, reduced connectivity impedes their movement and accelerates extinction.

Conservation and restoration efforts now and in the future tropics must stress dispersal processes, not existing species compositions. Neither conservation nor restoration of biodiversity can be effective unless opportunities exist for dispersal of plants and animals across changing landscapes (Corlett and Wescott, 2013; McConkey et al., 2012). Plantations, field crops and pastures exacerbate negative effects of climate change because inhospitable habitats withdraw options for forests to grow, inhibit or preclude seed dispersal, and accelerate changes in temperature, relative humidity, soil moisture and wind exposure in forest fragments (e.g. Cordeiro et al., 2009; Laurance et al., 2011, 2012; Feeley and Rehm, 2012). Drying remnants could be nurseries of species capable of surviving drier and more seasonal climates of the future, but survivors cannot spread from isolated fragments without dispersal agents and avenues for migration. The most important single challenge in highly altered tropical landscapes is to conserve forest cover that permits tree migration and provides cover and food for the animals that make plant migration possible. The forest cover need not look like pristine old-growth; it needs to exist, and support guilds of agents of seed dispersal in all seasons of the year.

7. Uncertainty with optimism

Some caveats are necessary. Ecological methods that estimate the existence of a huge pool of rare, geographically-limited tree species are compelling (Hubbell, 2013; ter Steege et al., 2013), but existence of the pool has yet to be demonstrated. Ecological applications of phylogenetics make tests of the Diversity Storage Hypothesis possible in principle (see Mouquet et al., 2012), and presumably representative taxa can be studied. However the expense of finding and testing genetic affinities of thousands of rare species, or cryptic species within recognized taxa, may prove prohibitive.

Moreover, climate predictions are uncertain. Past changes in climate of the predicted magnitude of 1.5–3.0 °C have caused upheaval in biological communities. However projected scenarios of change in this century are based on averages of dozens of models (e.g. 42 each for RCP 4.5 and 8.5, IPCC, 2013, p. 1069). If the most pessimistic climate projections prove accurate for the RCP 8.5 models, Amazonian rainforest will contract by 70% with or without massive changes in land use. Additionally, ultimate changes in climate depend on rates of production and residence times of greenhouse gasses. Models predict that 20%–35% of CO₂ added to the atmosphere remains there for 200–2000 years; the residual is drawn down over 3000–7000 years (Archer et al., 2009). On a time scale of human civilizations, elevated CO₂ is permanent. While the IPCC (2013) averages many models for prediction of climate change to a rhetorically expedient end of this century, fewer predict changes to year 2300, and very few to year 3000. The future of biodiversity on already-altered landscapes depends on control of greenhouse gasses, and which models for CO₂ residence and climate response best predict the future.

A final caveat is that seed dispersal will allow some tree species to migrate much more than others. Animal-dispersed trees with fruits eaten by birds, bats or terrestrial mammals that travel long distances (kilometers or at least hundreds of meters) in feeding bouts are much more likely to have “fat-tailed” seed dissemination (Clark, 1998) than trees with fruits eaten by more sedentary animals, or trees with seeds dispersed by ballistics, gravity alone, or large-seeded species dispersed by wind. Foraging toucans, hornbills, old-world fruit bats, and wide-ranging terrestrial fruit eaters regularly carry seeds from one feeding or resting site to another, resulting in multi-modal distributions rather monotonically decreasing seed numbers away from seed sources, as originally envisioned (Schupp et al., 2002; cf. Janzen, 1970). In such cases mean travel distances do not reflect seed distributions, offering hope that long-distance dispersal to and from remnants, restored stepping-stone

patches, or corridors can be frequent and effective. The downside is that less easily-dispersed tree species will not migrate, or will require more active management, than mobile species.

Despite caveats, there are grounds for optimism in managing human-dominated tropical landscapes. Key roles that fruit-eating birds and mammals play in tropical conservation and restoration are increasingly well-recognized (Chazdon, 2014; McConkey et al., 2012; Sekercioglu et al., 2004; Whelan et al., 2008). Recognition derives from basic research that documents consequences of seed dispersal by some animals rather than others (e.g. Howe and Miriti, 2004; Howe and Smallwood, 1982; Schupp et al., 2010), explores genetic implications of seed dispersal (e.g. Dick et al., 2008; Hardesty et al., 2006; Schroeder et al., 2014), describes roles that fruit-eating birds and mammals play in community structure (Bascompte and Jordano, 2014; Muller-Landau and Hardesty, 2005), documents consequences of loss of seed dispersal due to hunting or forest fragmentation (Cordeiro et al., 2009; Effiom et al., 2013; McConkey and Drake, 2006; Nuñez-Iturri et al., 2008; Terborgh et al., 2008), and documents different roles of dispersal agents in forest recovery (e.g. de la Peña-Domene et al., 2014; Ingle, 2003). Fragmented forests do not preserve all tropical diversity, but they preserve at least temporary holdouts for rare plants and fruit resources for animals (e.g. Arroyo-Rodríguez et al., 2009; Hernández-Ruedas, 2014; Turner and Corlett, 1996). Not all fruit-eating animals will cross open landscapes to forage, but many do (Galindo-Gonzalez et al., 2000; Hingstom et al., 2014; Laborde et al., 2008). Extirpation of regular dispersal agents is sometimes compensated by disturbance-tolerant birds, primates or other mammals that disseminate enough seeds to permit persistence of some trees and the resources that they produce (Albert et al., 2014; Sethi and Howe, 2009). Future forest patches in agricultural landscapes will not resemble pristine forests; conditions will favor those native and naturalized trees, and their dispersal agents, that can coexist with human-dominated landscapes (Ellis et al., 2012). Diversity Storage will permit somewhat diverse communities to persist if sufficient connectivity exists to allow dispersal agents to survive, and “winners” among trees to persist and migrate.

The greatest promise is promotion of landscape management that preserves or creates hospitable matrices between and buffers around existing remnants or restored habitats. Forest corridors, stepping-stone habitat islands and buffers that include species of trees that produce fruits that support populations of fruit-eating birds and mammals throughout the year have the most promise (Chazdon, 2014; Franklin and Lindenmayer, 2009; Lamb et al., 2005; Martínez-Garza and Howe, 2003; Melo et al., 2013). Such stands also serve as nuclei for later reforestation with much greater biodiversity than background crops or pastures if agriculture becomes infeasible (Corbin and Holl, 2012; Reis et al., 2010). For government agencies, corporations or community organizations with access to facilities and labor, Elliott and colleagues (2013) provide a guide to restoration of Southeast Asian forests that could be adapted elsewhere. Where such infrastructure is unavailable, programs can be initiated that protect strategic riparian habitats, ridges or marginal farmland from cattle, fire and intensive hunting, thereby hosting planted or residual fruiting plants and the animals that disperse seeds (Ekroos et al., 2014; Rudel et al., 2009). A realistic hope in the face of uncertainty is that biodiversity-friendly landscapes, as Melo and colleagues's (2013) term them, allow resilience where connectivity can be preserved or re-created. A necessary component is preservation or re-introduction of dispersal agents that permit plant movement.

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