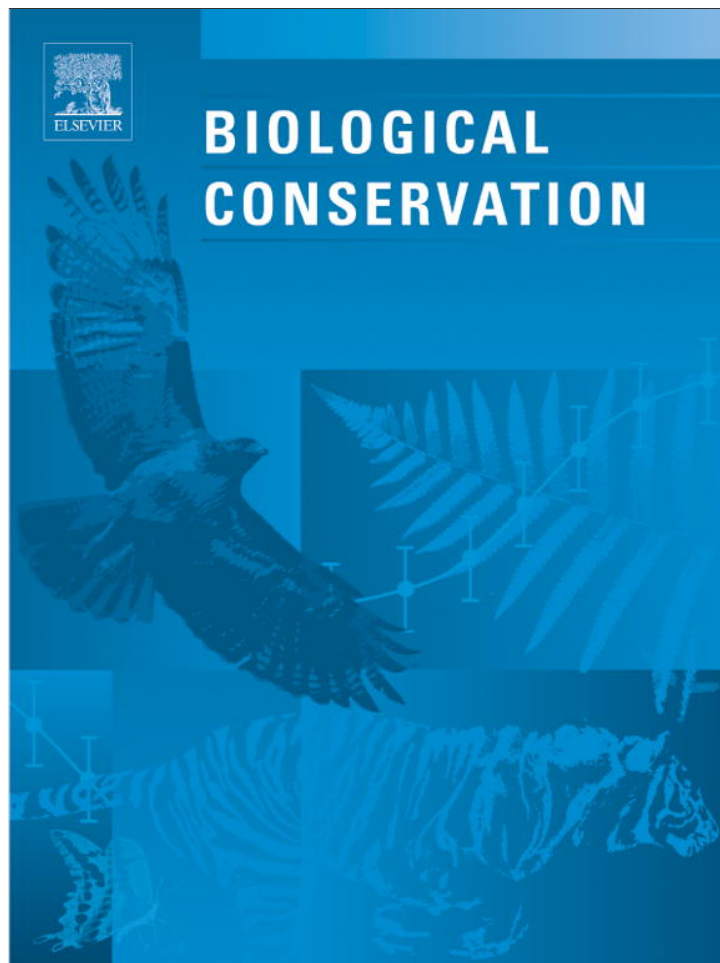


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Perspective

The 'few winners and many losers' paradigm revisited: Emerging prospects for tropical forest biodiversity

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ABSTRACT

Despite its relevance to contemporary biodiversity conservation, the ecological mechanisms controlling nonrandom species replacements and biotic homogenization of native biotas remain poorly understood. Here, we advocate for the widespread occurrence of a pattern of winner–loser species turnover exhibited in tropical forest floras: the replacement of old-growth tree species by a small set of pioneer or successional tree species across edge-dominated habitats in hyper-fragmented landscapes. A growing body of evidence on biotic reassembly in human-degraded forest sites suggests that winner–loser replacements are often advanced by native rather than exotic plant species, leading to taxonomic homogenization at multiple spatial scales (i.e. from local to regional assemblages). This process does not rely on biological invasions and associated shifts in geographic ranges of nonindigenous species. Moreover, this form of biodiversity erosion is not limited to restricted-range and endemic species but can include any species of many ecological groups that are apparently intolerant to highly modified habitat conditions, such as desiccated/illuminated forest edges and fire-degraded forest fragments persisting in open-habitat matrices. This unidirectional pattern of species turnover is expected to set in motion devastating cascading effects onto higher trophic levels that will eventually disrupt the structure of the entire forest ecosystem. Our framework not only reaffirms the winner–loser replacement paradigm, but also contends that the proliferation of disturbance-adapted native organisms has a pivotal role in sealing the fate of tropical biodiversity in particular contexts.

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1. Introduction

McKinney and Lockwood (1999) compiled evidence suggesting that as the relentless process of human disturbance increases in spatial extent and intensity, few highly resilient species ('winners') gradually come to dominate ecological communities at the expense of native species that cannot tolerate human-induced disturbances

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('losers'). 'Winners' are usually portrayed as exotic, cosmopolitan ruderal species rapidly expanding their geographic ranges, whereas 'losers' are usually represented by endemic or narrowly distributed native species (Spear and Chown, 2008; Qian and Guo, 2010; Shaw et al., 2010). This ubiquitous and rarely reversible global pattern of biotic reassembly has unequivocally propelled the issue of biological invasions as the main driver of 'winner–loser replacements' (hereafter, WLRs) and the ensuing process of biotic homogenization (i.e. reduced beta-diversity or increased species similarity) experienced by emergent ecosystems (Olden and Rooney, 2006). The ex-

tent to which unique native biotas become both impoverished and compositionally homogenized in response to WLRs may be highly variable, but is clearly affected by the invader capacity to either out-compete native populations or take advantage of their decline and local extirpation.

However, biotic homogenization may result from ecological processes other than local substitution of 'losers' by invasive 'winners' because native biotas can also be rearranged in response to the establishment of human-modified landscapes (Lôbo et al., 2011). In fact, previous research addressing species replacements and community reorganization has primarily focused on biological invasions facilitated by intentional or accidental introductions of nonindigenous species, thereby failing to consider that native, disturbance-adapted species can also proliferate at multiple spatial scales (see Santos et al., 2008; Tabarelli et al., 2010b). Disturbance-tolerant native species in human-modified habitats can therefore exhibit patterns of community mono-dominance that so far have been considered to be exclusive of exotic species spearheading successful invasions (Guo and Ricklefs, 2010).

A growing body of evidence supports the rearrangement of native biotic assemblages subjected to human-induced disturbances and, consistent with ecological theory, it is unsurprising that some species may benefit from either natural or anthropogenic disturbances, while others are detrimentally impacted (Lewis et al., 2009). This implies that any native biota – potentially harboring both 'winner' and 'loser' species – can be intrinsically vulnerable to WLRs and biotic homogenization in response to anthropogenic perturbation. In other words, native biotas exposed to pervasive disturbances, such as deforestation and forest fragmentation, may experience an endogenous process of biotic homogenization driven by the hyper-proliferation of some indigenous *r*-strategists, rather than replacements of native by hyperabundant alien species (Tabarelli et al., 2008; Lôbo et al., 2011).

In fact, pioneer tree species (mostly ecologically-plastic and generalists) are apparently proliferating in many fragmented or edge-dominated landscapes, particularly in the Amazon and Atlantic forest region (Laurance et al., 2006a; Santos et al., in press). Proliferation has been documented in both 'old' and newly fragmented landscapes dominated by an open-habitat matrix (Laurance et al., 2006b; Michalski et al., 2007; Tabarelli et al., 2008). In this landscape context, vast tracts of tropical forests may experience a form of WLRs that is primarily driven by native species, yet this also results in locally impoverished and increasingly homogenized tree assemblages (Santos et al., 2008; Tabarelli et al., 2010a). The species composition of these forests tend to converge at the landscape scale both taxonomically and in terms of functional groups (Santos et al., 2010), thereby contributing to the taxonomic homogenization of tree assemblages/floras at regional scales (Lôbo et al., 2011). Although we are unable to examine to what extent proliferation of native pioneers translates into local extinction of native species, as potentially driven by biological invasions, there is little doubt that this phenomenon is widely catalyzed by human-induced homogenization of abiotic conditions and that this can easily rival or outpace biological invasions in terms of the extent to which biological communities are reassembled (see Tabarelli et al., 2010b).

Here, we point out the occurrence of a particular type of WLR experienced in some tropical forest biotas that is mainly driven by native species leading to both species loss and biotic homogenization from local to regional scales. More explicitly, we examine the widespread replacement of the old-growth tree flora by a small subset of pioneer or successional tree species across edge-dominated habitats in hyper-fragmented landscapes dominated by open habitats, such as pastures and crop lands. We use emerging evidence of tree community reassembly in both historical and recently fragmented landscapes to revisit the winner–loser paradigm and

highlight the role of large-scale rearrangements of the native flora driven by the proliferation of a few indigenous species. Although the extent to which this phenomenon applies to other moist tropical forest regions remains unknown, we put forward some basic predictions for species persistence in tropical biotas and argue for a more comprehensive understanding of WLRs as a central paradigm in tropical conservation ecology.

2. Winners and losers in degraded tropical forests

Several faunal taxa have already been identified as 'losers' in tropical forests, such as large-bodied mammals (Peres and Palacios, 2007), understory birds (Lees and Peres, 2006) and specialized dung beetles (Nichols et al., 2009), but there is virtually no evidence that these ecological groups have been outcompeted or otherwise replaced by exotic counterparts that are expanding their ranges in response to human disturbances. In fact, few exotic species have successfully invaded continental tropical forest regions and pushed endemic species to extinction (Sodhi et al., 2008) as predicted by the classic notion of WLRs driven by biological invasions (sensu McKinney and Lockwood, 1999). Biological invasions are undoubtedly a major driver of species extinctions and homogenization in insular habitats and continental water bodies, but the strength of their influence in biotic reassembly of continental forests remains virtually unknown. Conversely, there is ample evidence on the negative effects of habitat disturbance on tropical floras and the extent of these effects is surely global (Laurance et al., 2011).

For woody plants, the concomitant hyper-proliferation of pioneer plants and collapse of the shade-tolerant/old-growth flora in several neotropical fragmented forest landscapes (including Amazonia and the Atlantic Forest) comprises a case of widespread substitution of a wide range of native 'losers' by a few native 'winners'. Put briefly, in the immediate aftermath of forest edge creation by deforestation, several groups of shade-tolerant/old growth tree species become disadvantaged and are gradually replaced by a small set of light-demanding pioneer/successional tree species at multiple spatial scales (Laurance et al., 2006b; Tabarelli et al., 2008; Aguiar and Tabarelli, 2010). In these terms, 2–20-fold increments in pioneer abundance have been documented in edge-dominated habitats (Laurance et al., 2006a; Tabarelli et al., 2010b; Lôbo et al., 2011; Santos et al., 2012), without detectable shifts in species geographic ranges. Such WLRs result in locally impoverished tree assemblages (Oliveira et al., 2004; Laurance et al., 2006b; Santos et al., 2010), that converge at the landscape scale both taxonomically and in terms of functional traits (Michalski et al., 2007; Santos et al., 2008), thereby contributing to biotic homogenization of tree floras at the regional scale (Fig. 1). For example, local floras in the Brazilian Atlantic Forest, have experienced a 20–40% increase in species similarity in response to the proliferation of small-seeded, short-lived pioneer species exhibiting wide geographic distributions (Lôbo et al., 2011).

Such triumphant species, however, apparently simply take advantage of vacant sites and resources released by declining plant populations, rather than directly displace/outcompete the old-growth flora across edge-affected habitats. This nonrandom winner–loser reshuffling of strictly native floras is therefore best described as a form of local density compensation 'by default' involving little or no contests with encroaching exogenous species. For instance, winner species may be favored by edge-mediated shifts in microclimate and elevated resource availability, such as light and soil nutrients (Laurance et al., 2006a; Tabarelli et al., 2008) resulting from population collapse of functional groups typical of old-growth forest, such as emergent trees (Oliveira et al., 2008). Additionally, high mortality rates of large trees due

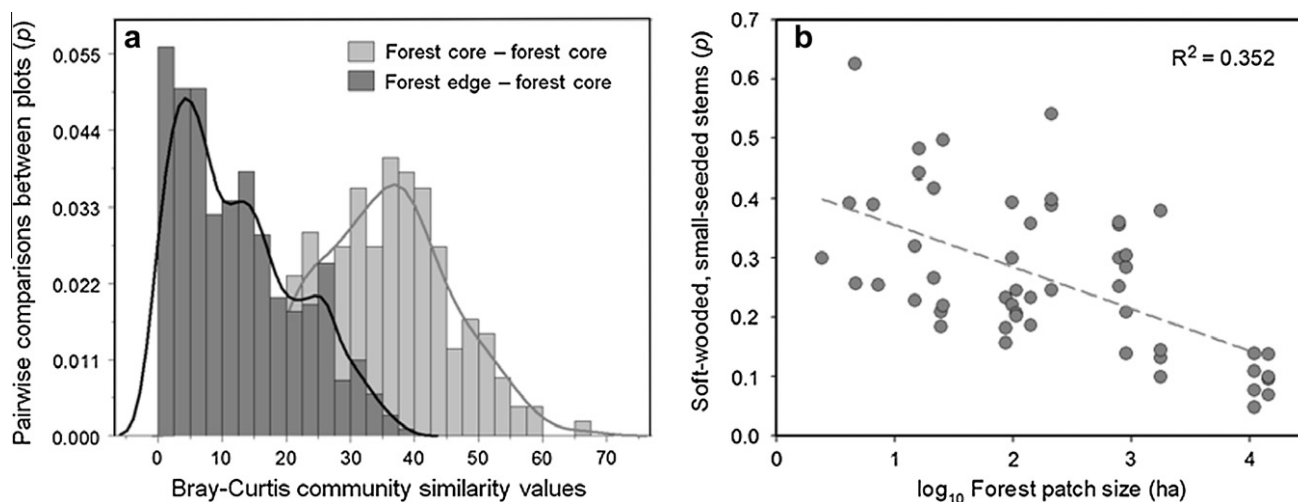


Fig. 1. Patterns of taxonomic and functional divergence between tree plots arrayed across varying distances to forest fragment edges at two neotropical landscapes of the northern Atlantic Forest and the southern Amazon: (a) floristic community similarity between 0.1-ha plots in either forest interior and forest edge conditions ($N = 400$ pairwise comparisons) or between different forest interior plots ($N = 190$ comparisons) sampled throughout the Serra Grande landscape, Alagoas, Brazil (data from Santos et al., 2008); (b) proportional representation of light-wooded, small-seeded pioneer species within 52 quarter-hectare tree plots sampled within 21 variable-sized forest patches in Alta Floresta, Brazil (data from Michalski et al. (2007)). Although illustrated by different metrics, floristic assemblages of edge-dominated sites in both of these landscapes exhibit similar patterns of species turnover and functional convergence at the expense of the species-rich flora typical of core old-growth forest conditions.

to increased wind turbulence and physiological stress (Laurance et al., 2000), and elevated failure in seedling recruitment due to both biotic and abiotic factors (Laurance et al., 2006; Norden et al., 2009; Aguiar and Tabarelli, 2010) indicate that many plant groups are unable to flourish or even persist in edge-affected habitats within landscapes dominated by nonforest areas (see Tabarelli et al. (2010b) for an Atlantic Forest review). Timber harvesting and surface fires may also increase canopy gap fracture and further depress old-growth tree populations, thereby facilitating the proliferation of light-demanding and disturbed-adapted plant species (Barlow et al., 2003; Barlow and Peres, 2008).

Relative to biodiversity persistence, this pattern of old-growth/pioneer tree species permutation is likely to involve at least two waves of species loss across hyper-fragmented landscapes dominated by open-habitat matrices. In the first instance, a highly diversified set of old-growth species are substituted by a small set of ecologically redundant, but phylogenetically unrelated native r -strategist species leading to a species-poor tree assemblage at any spatial scale (Santos et al., 2010; Tabarelli et al., 2010b). The second wave of extinctions includes the extirpation of faunal attendants of the declining old-growth flora, such as large frugivorous vertebrates (Silva and Pontes, 2008), specialized pollinators (Girão et al., 2007; Lopes et al., 2009), and specialist herbivores (Arnold and Asquith, 2002; Wirth et al., 2008). As a result, trophic interactions in highly degraded tropical forests are often mainly comprised of generalist-generalist mutualisms (Aguilar et al., 2006). In the Atlantic Forest, pioneer plants are mostly comprised of small-seeded annual species pollinated by a diverse set of small insects (Lopes et al., 2009; Melo et al., 2010). Conversely, large-seeded plants dispersed by large-bodied frugivores, typically exhibit supra-annual reproduction (often mast fruiting), and are pollinated by vertebrates and specialized vectors. These large-girthed emergent trees are disproportionately prevalent among the gradually declining old-growth flora (Melo et al., 2006; Girão et al., 2007; Lopes et al., 2009; Tabarelli et al., 2010a). In other words, an important fraction of the old-growth tropical fauna is likely to rely on both trophic and structural resources frequently provided by loser species. Even non-trophic interactions, such as epiphytism and provisioning of nesting sites, are likely to be disrupted resulting in cascading extinction events. For example, at least a quarter of

the Atlantic Forest bromeliads in northeast Brazil (consisting of over 90 species) are critically threatened because of their physical dependence on the highly illuminated crowns of increasingly rarer large emergent trees (Siqueira-Filho and Tabarelli, 2006).

Finally, it is important to mention that as a partially edge-induced phenomenon, WLRs are unlikely to exhibit the same intensity across tropical forest biotas and human-modified landscapes. Differences in terms of biogeography, natural disturbance regimes, and past exposition to human disturbances probably affect the abundance and diversity of pioneer/light-demanding species, as well as the sensitivity of the regional floras to edge effects (see Gardner et al., 2009; Arroyo-Rodríguez et al., 2012). The structural contrast between juxtaposed matrix and forest habitats also modulates both the intensity and spatial extent of edge-effects (Harper et al., 2005) and, consequently, the potential for pioneer proliferation (Nascimento and Laurance, 2002; Tabarelli et al., 2008). In the Los Tuxtlas region, for instance, the understory palm *Astrocaryum mexicanum* has proliferated across forest fragments, probably due to reduced levels of seed predation and increased light availability (Arroyo-Rodríguez et al., 2007). However, even in these edge-dominated landscapes predominantly covered by pasturelands, WLRs have not been observed in the same magnitude as in Amazonia and the Atlantic Forest (Arroyo-Rodríguez et al., 2009).

3. Winners, losers and the predicament of tropical biodiversity

Reverting to the classic paradigm, patterns of tree assemblage structure documented in human-degraded biotas at multiple spatial scales suggest that WLRs can be promoted by native rather exotic species, leading to an analogous process of biotic homogenization which does not depend on successful invasions, once critical geographic barriers have been overcome (Fig. 2). Even relatively undisturbed forest habitats will harbor refugee populations of some short-lived native pioneers that can be potentially released, to the detriment of disturbance-intolerant species, following profound habitat alteration. Moreover, nonrandom species loss is not limited to range-restricted and endemic species but includes any species of particular ecological groups that are effectively unable to deal with highly modified habitat conditions, such as desiccated/illuminated

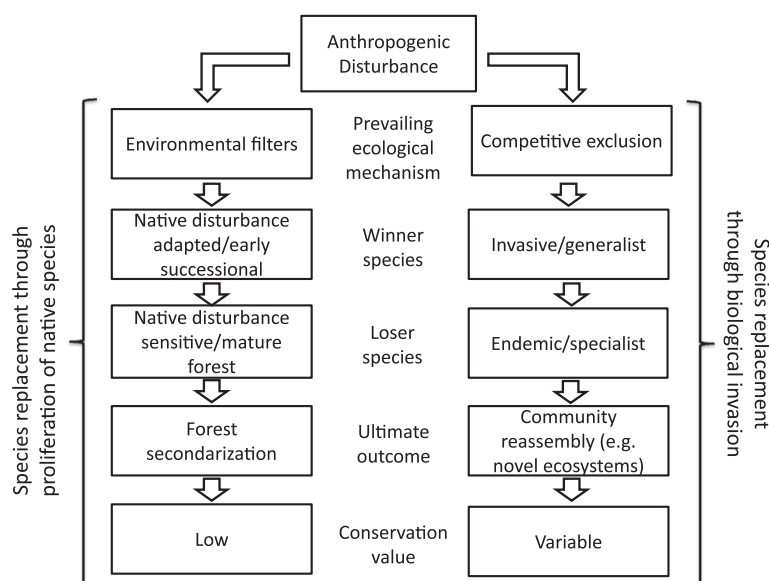


Fig. 2. Potentially alternative (but not mutually exclusive) pathways of winner–loser replacements (WLRs) experienced by tropical forest biotas in human-modified landscapes.

forest edges and fire-disturbed fragments (Fig. 2). In addition to species losses within single trophic levels, WLRs may often involve several guilds of producers and their attendant mutualists and antagonists. This likely amounts to a susceptible network of collapsed interactions comprised of many rounds of species losses, thereby extending across all levels of community reorganization via trophic cascades (Lopes et al., 2009; Tabarelli et al., 2010b). In other words, WLRs are expected to set in motion devastating cascading effects onto higher trophic levels that will eventually disrupt the structure of the entire forest ecosystem.

Spelling out the implications of these processes to biodiversity persistence across human-modified landscapes, we propose that the magnitude of species losses and reorganization experienced by contemporary tropical forest biotas rests on two basic conditions. The first one concerns the proportion of pioneer species present in the original flora of any given region. The degree of seasonality, biogeographic patterns, evolutionary exposure to natural disturbances, and land-use history are all expected to influence the diversity of pioneer or disturbance-adapted species (Gardner et al., 2009; Koh et al., 2010) and, accordingly, the ecosystem resiliency of tropical forests. The second condition refers to the spectrum of life-history traits captured by pioneer and disturbance-adapted species and the trait value distance or overlap between pioneers and the old-growth flora, which defines the range of resources available for plant attendants. The Neotropical tree flora harbors a wide diversity of trait packages that occur predominantly among old-growth tree taxa: emergent strata, slow growth rate, large seeds, floral resources associated with specialized pollinators, seed dispersal by large vertebrates, and mast-fruiting strategy (Laurance et al., 1997; Tabarelli and Peres, 2002; Tabarelli et al., 2010a). In this context, plant assemblages rearranged via either the collapse or hyper-proliferation of native species may approach those typically documented in secondary and regenerating forests (Tabarelli et al., 2008). Moving swiftly from biodiversity and species conservation value to ecosystem functioning and provision of ecological services we point out that WLRs also explain up to 50% of the above-ground biomass collapse that is eventually experienced by edge-affected habitats in the Amazon (Laurance et al., 1997), the Atlantic Forest (Paula et al., 2011), and Mesoamerica (Urquiza-Haas et al., 2007). Forest ecosystem services associated with the above and below ground phytomass, such as carbon storage, flood pulse regula-

tion, soil protection, and nutrient cycling, may be largely depleted as edge-affected habitats and pioneer-dominated WLRs encroach upon typical old-growth conditions in human-modified landscapes (Pütz et al., 2011).

In synthesis, this ubiquitous pattern of old-growth/pioneer replacement represents a form of WLR driven entirely by native species. Unlike the paradox of invaded communities, in which overall diversity is lost by gaining novel species, this pattern of species turnover can convert unique regional biotas into a collection of low-diversity assemblages. Such floristic transitions can also inform us about potential successional trajectories followed by entire biotas that are repeatedly exposed to human disturbances, particularly highly-fragmented landscapes dominated by cattle pastures and croplands. Although our arguments rely almost exclusively on recent evidence from only two Neotropical forest regions – Amazonia and the Atlantic Forest – there is no reason to believe that these reflect particular idiosyncrasies of these biotas. As an edge-induced phenomenon this pattern of WLR may be far more universal in the humid tropics but it is likely to operate at varying magnitudes in response to baseline variables and the spatial configuration of any given landscape. This perspective not only reinforces the WLR paradigm but places the hyper-proliferation of disturbance-adapted native organisms as a key area in tropical conservation science and policy. We should therefore examine both the generality of this phenomenon and its driving forces in the interest of any relict conservation value retained within anthropogenic landscapes.

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