Secondary forests as biodiversity repositories in human-modified landscapes: insights from the Neotropics

Florestas secundárias como repositórios de biodiversidade em paisagens antrópicas: evidências dos neotrópicos

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Abstract: In this essay we examine some of the processes affecting the composition and structure of tree species assemblages and, consequently, what we can expect from secondary-forest stands as an element of human-modified landscapes and as an opportunity for biodiversity persistence in this ecological context. Based on the available information, it is reasonable to predict that in some landscapes or biotas: (1) small forest remnants degenerate and support plant assemblages with attributes similar to those observed in early and intermediate-aged regenerating stands, while secondary-forest stands move from initial to more advanced successional stages; (2) collectively, remnant/stand attributes and landscape integrity define the pace through which degeneration proceeds, but also the potential for regeneration; (3) at the landscape spatial scale, remnants and stands tend to converge in terms of structure, but also in terms of taxonomic and functional composition. In other words, remnants degenerate and secondary-forest stands regenerate toward a sort of 'climax community', which is conditioned by the physical and biological integrity of both patch and landscape. Considering secondary forests in the conceptual, ecological and spatial framework of human-modified landscapes may help us to understand and maximize the conservation services provided by this habitat as it proliferates through human-modified landscapes.

Keywords: Biological conservation. Forest fragmentation. Forest regeneration. Succession. Land use.

Resumo: Neste artigo, examinamos alguns dos processos que determinam a composição e a estrutura das assembleias de plantas e o que podemos esperar das florestas secundárias como elemento das paisagens antrópicas na conservação da biodiversidade neste contexto ecológico. Baseando-nos na informação disponível, podemos esperar que em algumas paisagens ou biotas: (1) remanescentes de floresta original se degenerem e tendam a compor assembleias de plantas com atributos similares às de áreas de regeneração em estágios iniciais ou intermediários de sucessão, enquanto que os *stands* de floresta secundária se movem de estágios iniciais em direção a estágios mais avançados a partir do abandono da terra, (2) o conjunto das características dos fragmentos/*stands* e as de integridade da paisagem definem a intensidade/velocidade da degeneração, mas também o potencial/velocidade de regeneração, e (3) na escala da paisagem, fragmentos e *stands* tendem a convergir do ponto de vista de estrutura, de composição taxonômica e funcional. Portanto, fragmentos e *stands* tendem a compor uma 'comunidade clímax', que é determinada tanto por atributos dos fragmentos/*stands* quanto da paisagem. Olhar as florestas secundárias no contexto conceitual, ecológico e espacial das paisagens antrópicas pode nos auxiliar a entender e maximizar os serviços de conservação prestados por este tipo de habitat.

Palavras-chave: Conservação biológica. Fragmentação florestal. Regeneração florestal. Sucessão. Uso da terra.

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INTRODUCTION

Old-growth tropical forests have been converted into archipelagos of small remnants and regenerating forest patches, which become gradually embedded in a harsh matrix of human-managed habitats, such as pastures and croplands, hereafter referred as human-modified landscapes (Tabarelli *et al*., 2010b). In this ecological context, secondary forests represent an important and persistent element (Brown & Lugo, 1990) as this sort of habitat may appear immediately after deforestation (FAO, 2011) or after the abandonment of areas devoted to economic activities, such as agriculture or livestock farming (Lugo, 2009; Gardner *et al*., 2009). The mitigation of environmental liabilities and the compliance with environmental laws frequently results in the establishment of secondary forest stands through assisted regeneration or restoration (ITTO, 2002; Rodrigues *et al*., 2009). It has also been argued that many tropical regions have experienced a process of forest transition characterized by an increase in forest cover via forest regeneration since agriculturally marginal lands are abandoned and rural populations move to urban areas (Aide & Grau, 2004).

As secondary forests continue to proliferate globally, biodiversity persistence in human-modified landscapes is likely to be effectively affected by the presence of secondary-forest stands (Chazdon *et al*., 2009), what has renewed the scientific interest for forest regeneration and the profile of secondary forest habitats, particularly in the Neotropics (see Quesada *et al*., 2009). It is not coincidence that identifying the potential for biodiversity persistence in the secondary-forest habitat and its conditioning factors have become an urgent task and knowledge about this sort of conservation service must be translated into practical guidelines relative to land-use regulation and habitat management in human-modified landscapes (Harvey *et al*., 2008; Dent & Wright, 2009; Gardner *et al*., 2009).

The most traditional approaches for addressing this topic refer to (1) long-term studies that monitor forest regeneration and species accumulation as regeneration proceeds, and (2) species surveys in regeneration chronosequences (i.e., stands at different ages) in contexts of different land-use regimes or landscape configurations with known disturbance history (Uhl, 1987; Brown & Lugo, 1990; Guariguata & Ostertag, 2001; Chazdon *et al*., 2007; Piotto *et al*., 2009; Norden *et al*., 2011). In these traditional views, patterns of species composition and richness are frequently assumed as indicators/proxies of forest resilience and biodiversity persistence in secondary-forest habitats (see Bihn *et al*., 2008). However, chronosequences, particularly those with known disturbance history, are frequently rare and natural variation among regeneration stands tends to limit generalizations.

An alternative way to infer about the potential of secondary forests (1) as repositories of biodiversity, (2) its conditioning factors, and (3) practical implications for land use and management consists of identifying the relationships between the ecological drivers operating in human-modified landscapes and those that significantly affect the regeneration process and the structure of secondary forest stands. In the present essay we briefly assess and summarize some of the processes influencing tree assemblage structure and composition in forest remnants and secondary forest stands in order to identify opportunities for biodiversity persistence in secondary forests. Note that throughout the text, the term stand is used only to differentiate regenerating forest patches following land abandonment from forest remnants, which consist of forest patches that remained in the human-modified landscape without experiencing clear-cut.

Specifically, we incorporated some concepts from landscape ecology and findings informed by the fragmentation research, particularly from neotropical forests, to address or even anticipate the potential of secondary forest as repository of biodiversity in human-modified landscapes.

THE NATURE OF TREE ASSEMBLAGES IN HUMAN-MODIFIED LANDSCAPES

In tropical forests, conversion of natural landscapes into human-modified landscapes results in habitat loss but also modifies the spatial configuration of natural habitats, including an increment in the number of forest remnants, creation of forest edges and reductions on forest structural connectivity at landscape scale (Fischer & Lindenmayer, 2007). Other disturbances that result from the constant presence of human populations include hunting, logging, plant collection, and frequent fires (Tabarelli *et al.*, 2004). In general, all these disturbances are not independent from each other as they may interact, resulting in amplified (i.e., synergistic) negative impacts on biodiversity (Tabarelli *et al.*, 2004; Ewers & Didham, 2006). For example, species isolated in forest remnants can be more susceptible to climate changes, diseases, hunting, and logging (Tabarelli *et al.*, 2004; Ewers & Didham, 2006).

For instance, the creation of forest edges has been considered to impose microclimatic alterations, such as increased light incidence and wind turbulence, temperature extremes, and habitat desiccation (abiotic edge effects *sensu* Murcia, 1995). In parallel and in part as a result of these abiotic changes some pioneer plants and generalist herbivorous insects may proliferate in edge habitats (Michalski *et al.*, 2007; Santos *et al.*, 2008; Wirth *et al.*, 2008; Laurance *et al.*, 2011). These effects can be translated in terms of environmental filters for (1) tree species with large trunks susceptible to wind turbulence (Oliveira *et al.*, 2008; Laurance *et al.*, 2011); (2) shade-tolerant seedlings, with slow growth and low capacity to compensate for the attack by herbivores and pathogens (Benítez-Malvido & Lemus-Albor, 2005; Meyer *et al.*, 2011); and (3) individuals susceptible to competition with either native pioneer plants (e.g., lianas) or invasive species with fast growth and massive seed production (Laurance *et al.*, 2001, 2011). In addition to edge effects acting as filters, defaunation and loss of structural connectivity at the landscape scale may reduce seed flow/delivery between forest remnants, leading several plant populations to face dispersal limitation as their seeds are not able to reach safe sites for germination and recruitment (Melo *et al.*, 2006, 2007, 2010; Costa *et al.*, 2012).

As a potential scenario, as soon as forest fragmentation occurs, some pioneer species start to proliferate in the environments impacted by edge effects, such as small forest remnants and forest edges (Tabarelli *et al.*, 2010a, 2010b). In these edge-affected habitats, populations of a large number of species typical of undisturbed/mature forests (i.e., forest-dependent species) become rare or even extinct. The accumulated result of these processes on the structure of tree assemblages may be observed at different spatial scales. At the local scale, assemblages become taxonomically and functionally impoverished (up to a 50%-drop in species richness), as several ecological groups move to rarity or local extirpation (Oliveira *et al.*, 2004; Girão *et al.*, 2007). At the landscape scale, assemblages become taxonomically and functionally more similar by converging in terms of life-history traits associated with growth and reproduction, particularly regarding to pollination system, dispersal strategy and reproductive phenology (Michalski *et al.*, 2007; Santos *et al.*, 2008; Lopes *et al.*, 2009; but see Laurance *et al.*, 2007; Tabarelli *et al.*, 2010a). These pervasive processes may operate at regional scale as pioneer proliferation advances and the extinction of forest-dependent species accumulates over time (Lôbo *et al.*, 2011; Tabarelli *et al.*, 2012). Such a permanent replacement of typical groups of mature/interior forests by colonizing species across edge-affected habitats, associated with the collapse of above-ground biomass (Laurance *et al.*, 1997; Oliveira *et al.*, 2008; Paula *et al.*, 2011), has been interpreted as degeneration or retrogressive succession. Doubtless, this sort of succession represents an important force operating in some human-modified landscapes, particularly in those dominated by edge-affected habitats (Tabarelli *et al.*, 2010b) or moving in such direction (see Laurance *et al.*, 2011).

SECONDARY FORESTS AS EDGE-AFFECTED HABITATS

Classically, it has been recognized that the regeneration process in tropical forests is greatly conditioned by (1) environmental filters for plant recruitment imposed by soil attributes (water and nutrients); (2) seed availability; (3) competitive interactions among plant species; and (4) antagonistic interactions between plant species (allelopathy), and between animals and plants, such as seed predation and seedling herbivory (Guariguata & Ostertag, 2001; Norden *et al*., 2011). Across some abandoned areas of the Brazilian Amazon, soil depletion, establishment of allelopathic ruderal plants (e.g., *Pteridium aquilinum* (L.) Kuhn), limited arrival of forest-species seeds, and predation of medium and large seeds may not only retard but also prevent regeneration from proceeding beyond initial successional stages dominated by shrubs or small trees; i.e., arrested succession (Richards, 1996; Wieland *et al*., 2011). On the other hand, if soil conditions are favorable for forest plants, forest seeds are available and seedlings are not intensively defoliated, forest regeneration proceeds and secondary-forest stands accumulate biomass, species richness/diversity increases and, after several decades without additional disturbances, stands can be considered as late-secondary forest stands (Brown & Lugo, 1990; Guariguata & Ostertag, 2001; Norden *et al*., 2011). In other words, the regeneration process and the attributes of secondary-forest stands are closely correlated to disturbance and time elapsed since the last disturbance (Uhl, 1987; Guariguata & Ostertag, 2001; Zarin *et al*., 2005).

However, in the spatial and ecological context of human-modified landscapes it is reasonable to propose that the regeneration process, as well as the composition and structure of secondary-forest stands are conditioned by (1) environmental filters imposed by soil characteristics, but also by those associated with edge effects; and (2) dispersal limitation resulting from (a) population decline experienced by vertebrate pollinators and those serving as dispersers of intermediate- and large-sized seeds, and (b) the collapse of forest structural connectivity at landscape spatial scale. Additionally, pressures created by the proliferation of seed predators and generalist herbivores on edge-affected habitats, and population declines resulting from the exploitation of forest products, as well as from other regular disturbances (fire and the use of biocides) may impose effective impacts on forest regeneration. In other words, forest regeneration is likely to be strongly influenced by the spatial configuration of secondary-forest stands (e.g., size and shape) and by some landscape-level attributes, such as primary forest cover and structural connectivity.

Where secondary-forest stands persist in the landscape as isolated small patches, it is reasonable to recognize such stands as edge-affected habitats; note that several edge effects penetrate more than 100 m into forest patches (Laurance *et al*., 2011). It implies that secondary stands may represent a suitable habitat only for disturbance-adapted species (see Barlow *et al*., 2007); e.g., the same flora that persists in small forest remnants as already proposed (Santos *et al*., 2008; Tabarelli *et al*., 2008). We are explicitly referring to impoverished and homogeneous assemblages dominated by proliferating native plants (Lôbo *et al*., 2011; Tabarelli *et al*., 2012), even in the lack of soil restrictions for plant establishment or in the case secondary-forest stands are protected against additional human disturbances. Transferring this ecological perspective to the taxonomic context of Neotropical forests, particularly the Amazon and the Atlantic Forest, small secondary-forest stands and forest remnants alike (both as edge-affected habitats) tend to be particularly impoverished in terms of Lecythidaceae, Chrysobalanaceae, Sapotaceae, and Myristicaceae species, among others. Several species within these families are typical of old-growth forests as they exhibit some of the following attributes: shade tolerance, slow-growing, hard wood, pollination by specialized vectors, large seeds dispersed primarily by intermediate- and large-sized birds and mammals, and edge-sensitive seedlings (Melo *et al*., 2007; Tabarelli *et al*., 2008).

SECONDARY FORESTS AND BIODIVERSITY PERSISTENCE IN HUMAN-MODIFIED LANDSCAPES

Natural landscapes are moving towards human-modified landscapes globally, and even the most remote areas of tropical forest may be converted into this type of environment dominated by edge-affected habitats (Wright, 2005; Laurance & Peres, 2006). Indeed, tropical regions could be globally divided in those dominated by aging human-modified landscapes (i.e., the old frontiers of agricultural expansion) and those composed of newly created landscapes, exposed to a recent and fast process of forest conversion and dynamic land use. Both types of human-modified landscape exhibit common elements, such as the remnants of original forest, usually small patches, and secondary-forest stands of varying ages and resulting from the abandonment of agricultural fields and pasture lands (Quesada *et al*., 2009; Tabarelli *et al*., 2010b).

However, in contrast to the old frontiers, such as the Atlantic Forest Region, the new agricultural frontiers and their landscapes still exhibit a spatial configuration that can be considered favorable to biodiversity persistence (i.e., higher landscape integrity, see below). Some landscapes modified recently (< 50 years) in Costa Rica, southern Mexico, and Central Amazon (Chazdon *et al*., 2007, 2009), still retain a significant amount of remaining mature/old-growth forest and the seed disperser fauna remains almost intact. In the other extreme of such a degradation gradient, persist the human-modified landscapes of old frontiers, in which the remaining forest habitat remains as a set of small and isolated forest remnants and secondary-forest stands, in which many groups of forest-dependent species, such as large vertebrates, have been already extirpated (Silva & Tabarelli, 2000; Canale *et al*., 2012). A classic example of highly fragmented and degraded landscapes is the Atlantic Forest of northeastern Brazil, where forest conversion for sugar cane cultivation started intensively in the XVI century (Coimbra-Filho & Câmara, 1996).

Based on studies carried out across these two contrasting fragmentation/degradation scenarios, we can predict that in some landscapes or biotas: (1) small forest remnants degenerate and support plant assemblages with attributes similar to those observed in early and intermediate-aged regenerating stands, while secondary-forest stands move from initial to more advanced successional stages; (2) collectively, remnant/stand attributes and landscape integrity define the pace through which degeneration proceeds, but also the potential for regeneration (i.e., level of resilience); and (3) at the landscape spatial scale, remnants and stands tend to converge in terms of structure (richness and diversity), but also in terms of taxonomic and functional composition.

In synthesis, forest regeneration and degeneration have a temporal dimension, but both processes are directly affected by the physical and biological integrity exhibited by both patch and landscape (hereafter jointly referred to as landscape integrity). In other words, remnants degenerate and forest stands regenerate toward a 'potential climax community', which is conditioned by landscape integrity (Figure 1A). As climax community we refer to those in which populations of plants and animals remain relatively stable in face of a particular environment. Note that in this model (1) the potential climax community can be described either in terms of assemblage or ecosystem attributes, and (2) landscape integrity represents an integrative variable, which incorporates both patch- (remnants/stands) and landscape-level attributes. Patch-level attributes, include: patch size, shape and isolation, and soil quality for instance. Landscape-level attributes can be arbitrarily divided into three categories: (1) quality of forest habitat – forest cover, edge density, presence of source areas, structural connectivity; (2) disturbance regime – intensity of accessory disturbances, such as hunting, fire, logging; and (3) biological integrity – seed-disperser and pollinator availability, food-web integrity, and level of biological invasion, among others. Overall, biological integrity is expected to be higher in landscapes with higher old-growth forest cover, higher landscape structural connectivity, the presence of large remnants, and lower post-fragmentation human pressures (Faria *et al*., 2007; Gardner *et al*., 2009).

According to this model, either forest sensitivity to degeneration or forest regeneration capacity (i.e., ecosystem resilience) are affected by the relative abundance of particular groups of species in the regional flora, such as pioneer/ successional, disturbance-adapted and forest-dependent species. In other words, cross-biota differences in terms of degeneration/regeneration performance depend *a priori* on historical and biogeographic factors (Tabarelli *et al*., 2008; Gardner *et al*., 2009; Rös *et al*., 2012). Biotas that evolved in the presence of intense and frequent natural disturbances, such as hurricanes, severe droughts, and volcanic eruptions, tend to contain an elevated presence of successional or disturbance-adapted species in their floras and, therefore, tend to be more resistant/resilient to contemporary human disturbances (Figure 1B). Just to give one example, the forests of Los Tuxtlas, in the Gulf of México, northern limit of the Neotropical region, apparently diversified themselves in exposure to large disturbance events/regimes and, up to the moment, there is no evidence that forest remnants have experienced an intense process of forest degeneration (Arroyo-Rodríguez *et al*., 2009, 2012). The Amazon and Atlantic Forest probably represent distinct situations, being ecosystems that originated and recently diversified in the absence of less intensive natural perturbations, such as tropical hurricanes, or disturbances by pre-Colombian human populations, at least disturbances that were not so intense and spatially pervasive as those imposed by the Mayas in Mexico and other regions of Central America (see Diamond, 2005; Barlow *et al*., 2012). With an original flora that is very rich in tree species typical of old-growth forests, it is reasonable to expect that these biotas are more susceptible to degeneration and have lower regeneration capacity in the face of increasing human impacts (Figure 1C). This perspective has been indicated by the proliferation of pioneer plants at different spatial scales in the Atlantic and Amazonian Forest (Laurance *et al*., 2006; Michalski *et al*.,

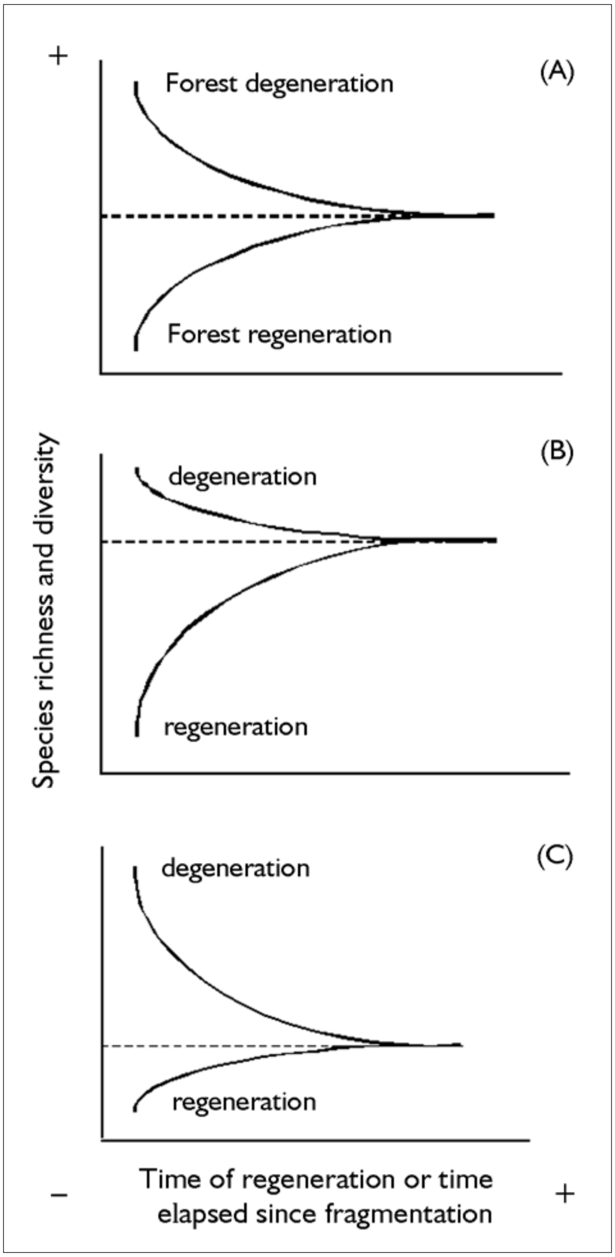

Figure 1. Degeneration of forest remnants and regeneration across secondary-forest stands in human-modified landscapes. Both processes are time-dependent (axis x) and tend to reach a potential climax community (dotted line), which is conditioned by 'landscape integrity' and exhibits corresponding attributes at community/ecosystem level (axis y), such as species richness and diversity (A). Considering the same level of landscape integrity, biotas supporting a diverse flora of pioneer or disturbance-adapted species are less susceptible to degeneration and exhibit higher levels of resilience (B) as compared to biotas supporting a higher proportion of disturbance-sensitive species, such as forest-dependent species (C).

2007; Tabarelli *et al*., 2010b; Lôbo *et al*., 2011, Santos *et al*., 2012; Tabarelli *et al*., 2012). Accordingly, landscapes with high integrity will be less susceptible to degeneration, and more suitable for regeneration, resulting in higher potential of reaching more diversified climax communities (Figure 1B), compared with landscapes with low integrity (Figure 1C), in which forest patches will be more susceptible to degeneration and, consequently, climax communities will be represented by more impoverished assemblages.

CONCLUSIONS

Translating the idea of a potential climax community into the 'secondary-forest debate' we should state that: (1) secondary-forest stands have the potential to operate as biodiversity repositories in human-modified landscapes; (2) the biodiversity spectrum able to inhabit secondary forests and maintain viable populations in this habitat depends on patch-level attributes, but also on the landscape in which they are immersed into; (3) secondary-forests stands as edge-affected habitats are not ecological equivalents of large patches of mature/old-growth forests, since a considerable proportion of tropical forest biodiversity apparently does not tolerate human-modified landscapes and their associated disturbances (e.g., forest-dependent species); and (4) as forest regeneration relies on the landscape species pool, impoverished landscapes, like many across the tropics, will result in impoverished secondary-forest stands.

To take better advantage from the opportunities offered by the presence of secondary-forest habitat in human-modified landscapes, some conceptual improvements and improved land-use regimes are needed. Secondary-forest stands represent one among several elements that compose human-modified landscape mosaics and, hence, they constitute an opportunity that needs to be incorporated into conservation plans that explicitly consider between-element complementarity. At the patch level, we should seek for shapes and sizes that minimize edge effects and the consequent proliferation of disturbance adapted-species. At the landscape scale, secondary-forest stands should remain connected, effectively protected from additional human disturbances, especially from new cycles of clear-cut what still happens across many regions (Bischoff *et al*., 2005; Teixeira *et al*., 2009). Finally, secondary-forest stands should coexist with large remnants of mature forest, not only to support assemblages dominated by disturbance-adapted species, but also to provide additional habitats and increase the chance for forest-dependent species to persist longer. Considering secondary forests in the conceptual, ecological and spatial framework of human-modified landscapes may help us to understand and maximize the conservation services provided by this habitat.

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