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Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research

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ABSTRACT

Old-growth tropical forests are being extensively deforested and fragmented worldwide. Yet forest recovery through succession has led to an expansion of secondary forests in human-modified tropical landscapes (HMTLs). Secondary forests thus emerge as a potential repository for tropical biodiversity, and also as a source of essential ecosystem functions and services in HMTLs. Such critical roles are controversial, however, as they depend on successional, landscape and socio-economic dynamics, which can vary widely within and across landscapes and regions. Understanding the main drivers of successional pathways of disturbed tropical forests is critically needed for improving management, conservation, and restoration strategies. Here, we combine emerging knowledge from tropical forest succession, forest fragmentation and landscape ecology research to identify the main driving forces shaping successional pathways at different spatial scales. We also explore causal connections between land-use dynamics and the level of predictability of successional pathways, and examine potential implications of such connections to determine the importance of secondary forests for biodiversity conservation in HMTLs. We show that secondary succession (SS) in tropical landscapes is a multifactorial phenomenon affected by a myriad of forces operating at multiple spatio-temporal scales. SS is relatively fast and more predictable in recently modified landscapes and where well-preserved biodiversity-rich native forests are still present in the landscape. Yet the increasing variation in landscape spatial configuration and matrix heterogeneity in landscapes with intermediate levels of disturbance increases the uncertainty of successional pathways. In landscapes that have suffered extensive and intensive human disturbances, however, succession can be slow or arrested, with impoverished assemblages and reduced potential to deliver ecosystem functions and services. We conclude that: (i) succession must be examined using more comprehensive explanatory models, providing information about the forces affecting not only the presence but also the persistence of species and ecological groups, particularly of those taxa expected to be extirpated from HMTLs; (ii) SS research should integrate new aspects from forest fragmentation and

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landscape ecology research to address accurately the potential of secondary forests to serve as biodiversity repositories; and (iii) secondary forest stands, as a dynamic component of HMTLs, must be incorporated as key elements of conservation planning; i.e. secondary forest stands must be actively managed (e.g. using assisted forest restoration) according to conservation goals at broad spatial scales.

Key words: biodiversity conservation, ecosystem services, forest recovery, landscape structure, landscape restoration, land-use transformation.

CONTENTS

I. Introduction	2
(1) Purpose and structure of review	4
II. Secondary forest dynamics in human-modified landscapes	4
(1) Proximate and ultimate forces driving forest succession	5
(2) Regenerating driving forces and plant life histories	6
(3) Potential successional pathways in HMTLs	6
(4) The (neglected) role of chronic human disturbances and its societal drivers	8
III. The conservation importance of secondary forests	9
IV. Conclusions	11
V. Acknowledgements	11
VI. References	12

I. INTRODUCTION

Rapid human population growth (8–10 billion by 2050; United Nations, 2011) and increasing demand for agricultural land have promoted land conversion from tropical forest landscapes to agricultural landscapes, and the last tracts of old-growth forests have been converted into archipelagos of forest remnants (Hansen *et al.*, 2013). Yet nearly one-third of old-growth forests cleared in the Neotropics undergoes secondary succession (SS) annually (Aide & Grau, 2004; Aide *et al.*, 2013), and there has been a global increase in secondary forest cover (0.25 million square kilometres of tropical forest gain between 2000 and 2012; Hansen *et al.*, 2013). Secondary forests therefore represent a frequent or even dominant type of natural vegetation in many human-modified tropical landscapes (HMTLs; Wright & Muller-Landau, 2006; Chazdon *et al.*, 2009a; Gardner *et al.*, 2009), thus emerging as a potential repository for tropical biodiversity and a source of essential ecosystem functions and services (Barlow *et al.*, 2007; Perfecto, Vandermeer & Wright, 2009; Melo *et al.*, 2013; Ferraz *et al.*, 2014; Gilroy *et al.*, 2014b).

Although SS has been a key research topic in tropical ecology for nearly half a century (Bazzaz & Pickett, 1980; Finegan, 1984), the current scenario of rapid global land-use change has increased the interest in SS among ecologists and conservationists. Unfortunately, despite this research effort, the intermingled biophysical and societal factors and drivers that govern the probability of abandoned private lands experiencing SS are often complex and poorly understood (Lambin & Meyfroidt, 2011; Aide *et al.*, 2013; Ellis, 2013). Also, the role played by secondary forests in biodiversity conservation is not clear (Prach & Walker, 2011; Melo *et al.*, 2013; van Breugel *et al.*, 2013; Chazdon, 2014),

largely because it depends on successional pathways, i.e. on the particular series of temporal changes experienced by regenerating forest stands in vegetation composition and structure, community types, system states, and other parameters of populations and communities. While forest regeneration appears to proceed rapidly and accumulate species at high rates in some tropical forests (e.g. Letcher & Chazdon, 2009; Norden *et al.*, 2009; Lebrija-Trejos *et al.*, 2010a), other forests experience arrested regeneration (e.g. Schnitzer, Dalling & Carson, 2000; Mesquita *et al.*, 2001; Suazo-Orduño *et al.*, 2015) and retain impoverished assemblages (Corlett, 1992; Turner *et al.*, 1994; Clark, 1996; Slocum *et al.*, 2004; Tabarelli, Lopes & Peres, 2008). Understanding the factors that promote or arrest SS is therefore urgently needed to evaluate properly the potential conservation importance of secondary forests in HMTLs and to identify areas where restoration interventions are required.

Over the last few years, an increasing number of studies have monitored forest regeneration and successional processes over time, combining chronosequence and dynamic approaches (Chazdon *et al.*, 2007; Lebrija-Trejos *et al.*, 2010b; Norden *et al.*, 2011, 2015; Moro *et al.*, 2015; Rozendaal & Chazdon, 2015). These studies have repeatedly shown that even nearby abandoned fields with the same fallow age, soil type, and climate conditions do not necessarily follow a single and predictable route to the old-growth forest stage, but can follow multiple successional pathways (Chazdon *et al.*, 2007; Norden *et al.*, 2011, 2015; but see Terborgh, Foster & Núñez, 1996; Lebrija-Trejos *et al.*, 2010a). Within the same landscape, some stands may show rapid regeneration rates and fairly smooth successional pathways, while others exhibit erratic pathways and/or slow regeneration rates (Norden *et al.*, 2011, 2015; Cole, Bhagwat & Willis, 2014; Jakovac *et al.*, 2015). A substantial fraction of

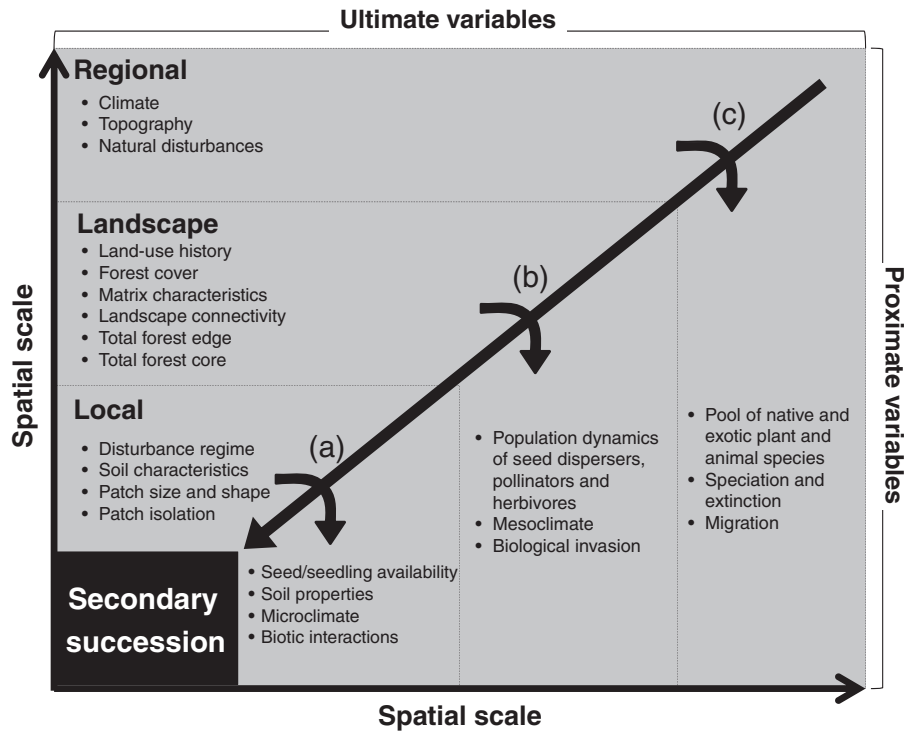


Fig. 1. Forest succession is influenced by a myriad of ultimate (indirect) and proximate (direct) variables operating simultaneously across multiple spatial scales, including the patch (a), landscape (b) and regional (c) scales. These variables can interact among scales (represented by arrows), potentially resulting in important synergistic outcomes that can alter forest regeneration. Within each spatial scale we show patterns and processes operating at different timescales. Although the ‘landscape scale’ may depend on the habitat requirements, behaviour and vagility of the focal organism, as well as on the ecological process of interest (Brennan *et al.*, 2002), we use the term ‘landscape’ in a broad sense, to refer to a spatially heterogeneous land area (typically varying in size from hectares to several square kilometres) containing a mosaic of land cover patches (e.g. forest patches, agricultural lands, vegetation corridors, and human settlements) (Turner, 1989). There are also many different interpretations of the term ‘region’, but from an ecological point it can be defined by natural features such as ecosystems, biomes, drainage basins, mountain ranges and soil types, as well as by the socio-cultural context, and is typically larger than the landscape scale (above several square kilometres; Bailey, 1996).

such ‘unexplained variation’ may result from limited study designs rather than from natural stochasticity (Norden *et al.*, 2011). For example, most studies on SS are performed at a local or stand-level spatial scale (e.g. Chazdon, 2003, 2008, 2014; Castro-Luna, Sosa & Castillo-Campos, 2007; Peña-Cuellar *et al.*, 2012; Bonner, Schmidt & Shoo, 2013), and include fallow age as the main (or even the single) explanatory variable into the study models (reviewed by Pickett, Collins & Armesto, 1987; Guariguata & Ostertag, 2001; Chazdon, 2003, 2008, 2014; Lohbeck *et al.*, 2015). Thus, they do not assess (nor control for) the effects of other key local, landscape, and regional variables that can shape successional pathways (Fig. 1).

In this context, although many ecological factors affecting animal and plant populations and communities may operate at local scales (e.g. habitat structure, resource availability, vegetation biomass) (e.g. Lohbeck *et al.*, 2015), evidence from forest fragmentation and landscape ecology research have demonstrated the importance of examining patterns and processes at the landscape and regional scales (e.g. Dunning, Danielson & Pulliam, 1992; Ricklefs, 2004; Ewers & Didham, 2006; Lindenmayer *et al.*, 2008; Tschamtko *et al.*, 2012;

Fahrig, 2013; Villard & Metzger, 2014; Jakovac *et al.*, 2015). For example, species’ extinctions within secondary forest patches and the colonization of empty patches may be driven by patch size and isolation (MacArthur & Wilson, 1967; Hanski, 1999). Based on the ‘habitat amount hypothesis’ (Fahrig, 2013), however, the patch size and isolation effects are probably driven by one single factor – the total amount of habitat (forest cover in our case) in the ‘local landscape’ surrounding a secondary forest site. This is because there will be more individuals, and thereby more species, in local landscapes with more forested area (i.e. sample area effect; Fahrig, 2013). The distribution and abundance of species in secondary forests can also depend on source–sink dynamics and the neighbourhood effect (reviewed by Dunning *et al.*, 1992). For example, young secondary forests are known to be less suitable (i.e. sinks) than old-growth forests for many shade-tolerant plant species (Tabarelli, Peres & Melo, 2012; Chazdon, 2014) and for forest-dependent animal species (Dunn, 2004; Harris & Pimm, 2004; Castro-Luna *et al.*, 2007; Peña-Cuellar *et al.*, 2012; Carrara *et al.*, 2015). Thus, the arrival and persistence of these species in secondary forest patches may depend on sources of immigrants

from old-growth forests (Pickett *et al.*, 1987; Dunn, 2004; Gardner *et al.*, 2008). In fact, based on the neighbourhood effect, a species' abundance in a given patch is expected to depend more strongly on characteristics of contiguous patches than on more distant patches within the landscape (Dunning *et al.*, 1992). Tschamtkke *et al.* (2012) describe other relevant theoretical models of how the landscape moderates biodiversity patterns and processes in HMTLs. Among them, the 'landscape-moderated insurance hypothesis' is particularly relevant for SS, as it postulates that landscape complexity can provide higher resilience and stability of ecological processes in HMTLs, thus offering spatial and temporal insurance. For instance, both landscape connectivity and beta diversity are expected to be higher in complex-structured landscapes (Tschamtkke *et al.*, 2012), potentially favouring SS through the arrival of a higher number of species.

Although further empirical studies are needed to test these hypotheses accurately, these theoretical models suggest that both the successional pathways and the conservation importance of secondary forests must be evaluated beyond the traditional forest-regeneration research agenda and its stand-level-based investigative approach (Pickett *et al.*, 1987; Chazdon *et al.*, 2009b; Meiners *et al.*, 2015). Because SS is a complex process affected by variables operating at multiple scales (Fig. 1), we require new multi-scale approaches to tropical forest succession to guide effective management and conservation programs in HMTLs (Ricklefs, 2004; Gardner *et al.*, 2009; Perfecto *et al.*, 2009; Melo *et al.*, 2013; Meiners *et al.*, 2015).

(1) Purpose and structure of review

In this review, we first update SS knowledge by incorporating concepts, methodological approaches and findings emerging not only from forest succession ecological theory (e.g. Bazzaz & Pickett, 1980; Finegan, 1984; Pickett *et al.*, 1987; Chazdon, 2008), but also from emerging disciplines such as landscape ecology (e.g. Lindenmayer *et al.*, 2008; Tschamtkke *et al.*, 2012; Mendenhall *et al.*, 2014), and forest fragmentation research (e.g. Fischer & Lindenmayer, 2007; Didham, Kapos & Ewers, 2012; Villard & Metzger, 2014). We assess both plants and animals, but focus on plants because they represent key structural and functional elements of forest ecosystems, and exhibit multiple pathways at the community level. Furthermore, they support food webs and represent a substantial proportion of tropical biodiversity (Slik *et al.*, 2015). Also, they determine most of the aboveground biomass and related ecosystem services (see Gilroy *et al.*, 2014b; Lohbeck *et al.*, 2015).

We are particularly interested in the forces driving the shifts in biotic assemblages as succession proceeds and in understanding the causes of the multiple successional pathways experienced by regenerating stands. We then examine the potential implications of such an integrated understanding of succession to determine the importance of secondary forests for biodiversity conservation. Finally, we propose a future research agenda focused on key

topics that will further help understand which the main drivers of successional pathways in dynamic HMTLs are. Although previous studies have recognized the role played by landscape configuration on key processes (e.g. seed dispersal) and patterns (e.g. species availability) for SS (Pickett *et al.*, 1987; Meiners *et al.*, 2015), to our knowledge no attempts have been made to combine emerging knowledge from tropical forest succession, forest fragmentation and landscape ecology research to offer an integrated framework on the main ecological driving forces that shape successional pathways at multiple spatial scales. Admittedly, most of the ecological factors shaping SS are indirect consequences of proximate (e.g. economic activity, policy, road culture, social institutions, governance) and underlying societal (e.g. population density, percentage of economically active population) drivers (e.g. Ostrom, 2009; Aide *et al.*, 2013; Quezada *et al.*, 2014). However, herein we concentrate on the ecological factors directly shaping SS because a proper assessment of the interplay between the indirect societal and biophysical factors and drivers underlying them is outside the scope of this review.

II. SECONDARY FOREST DYNAMICS IN HUMAN-MODIFIED LANDSCAPES

Secondary succession research has already identified a complex suite of variables affecting the regeneration potential of secondary forests (e.g. disturbance type, extent, intensity and frequency, propagule availability, and the condition of the local and the surrounding landscape), particularly at the stand scale (Pickett *et al.*, 1987; Wijdeven & Kuzee, 2000; Chazdon, 2003, 2008; Dunn, 2004; Lawrence, 2005; Powers & Pérez-Aviles, 2013; Cole *et al.*, 2014; Réjou-Méchain *et al.*, 2014). Fragmentation research and landscape ecology have identified additional variables affecting the dynamics of populations and communities in HMTLs (e.g. landscape forest cover, connectivity, matrix composition, forest edge density), with important implications for forest regeneration at the landscape and regional scales (Ricklefs, 2004; Fischer & Lindenmayer, 2007; Putz *et al.*, 2011; Didham *et al.*, 2012; Tschamtkke *et al.*, 2012; Fahrig, 2013; Ferraz *et al.*, 2014; Villard & Metzger, 2014). Considering that succession is modulated by processes operating at multiple scales (e.g. Meiners *et al.*, 2015), combining these three approaches may offer a unified view of SS through two levels of integration. The first level integrates proximate and ultimate biophysical variables that influence regeneration across multiple scales (Fig. 1). The second level integrates these complex variables and their impacts on plant life histories (Fig. 2). Addressing SS as a process responding to the interplay of local, landscape and regional factors may unravel the ecological causes behind a variety of successional pathways and enable one to predict the importance of secondary forest stands as repositories of tropical biodiversity, and also as a source of essential ecosystem functions and services in HMTLs.

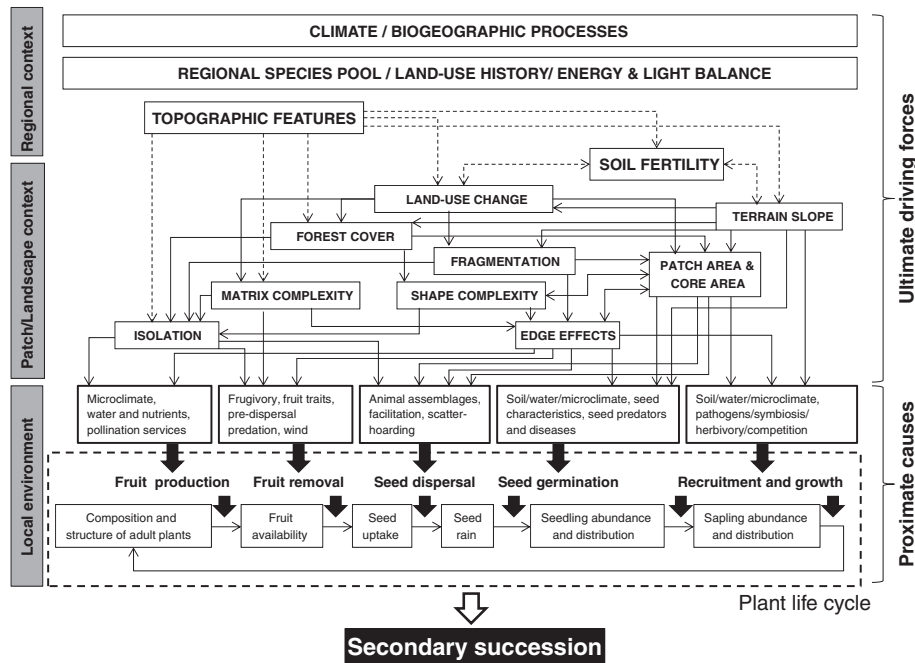


Fig. 2. Conceptual model highlighting potential relationships between different regeneration driving forces (both direct and indirect) operating at multiple spatio-temporal scales in human-modified tropical landscapes. The processes (in bold) generating the patterns (boxes) within the plant life cycle (dotted box; *sensu* Wang & Smith, 2002) are influenced by numerous local factors, which together represent the main proximate causes of forest regeneration. Such patterns and processes are, at the same time, determined by patch attributes (e.g. size, shape and isolation), which also depend on the landscape and regional contexts. For clarity, not all direct and indirect pathways are shown, but only some important paths are highlighted based on empirical and theoretical studies (e.g. Ewers & Didham, 2006; Fischer & Lindenmayer, 2007; Didham *et al.*, 2012; Fahrig, 2013). We also simplified the model by excluding synergistic interactions across scales, and direct associations between regional features and local patterns and processes (e.g. in terms of species diversity; Lawton, 1999).

(1) Proximate and ultimate forces driving forest succession

At the local scale (i.e. a small patch of abandoned land or stand), soil and microclimate conditions, as well as antagonistic (e.g. competition, predation, herbivory, parasitism and diseases) and mutualistic (e.g. mycorrhizal and nitrogen-fixing bacterial symbiosis, pollination, seed dispersal) biotic interactions are proximate factors determining which species arrive and establish in regenerating forest stands (Pickett *et al.*, 1987; Moran *et al.*, 2000; Chazdon, 2003; Norden *et al.*, 2011; Silva *et al.*, 2012; Réjou-Méchain *et al.*, 2014; Meiners *et al.*, 2015; a in Fig. 1). The relative roles played by each of these abiotic and biotic factors may change depending on landscape composition. At one extreme, in landscapes dominated by forested matrices, variation in SS pathways observed across secondary forest stands is mainly associated with local variation in environmental factors, such as substrate quality and microclimate. This is because propagule availability is expected to be relatively high, thus reducing seed limitation pressures (Meiners *et al.*, 2015). Conversely, in landscapes that have suffered intensive and extensive land-use changes with low remaining forest cover, SS will additionally depend on numerous factors operating at the landscape (b in Fig. 1) and regional (c in Fig. 1) scales, particularly those affecting the production, dispersal

and predation of propagules, and intense herbivory of regenerating assemblages.

For example, the extirpation of key mutualistic (e.g. seed dispersers, pollinators) and antagonistic (e.g. seed predators) animal groups and the proliferation of generalist herbivores (e.g. leaf-cutting ants) at the local and landscape scales alter ecological processes that are critical for forest recovery (Urbas *et al.*, 2007; Dirzo *et al.*, 2014; Leal, Wirth & Tabarelli, 2014b). The composition of the anthropogenic matrix and the spatial structure of the remaining forest (e.g. percentage of forest cover, connectivity, forest edge density, and forest core areas) affect the functions of pollinators, seed dispersers, seed predators, and herbivores (Janzen, 1971; Howe & Smallwood, 1982; Bawa, 1990; Coley & Barone, 1996; Meyer *et al.*, 2013). Changes in the landscape spatial pattern influence other proximate causes affecting forest regeneration, such as the mesoclimatic conditions, fire incidence, biological invasions, plant harvesting, and browsing by livestock (b in Fig. 1). At a regional scale, land-use history determines the number and sizes of old-growth forest patches in the region (Ewers *et al.*, 2013), which operate as sources of native species (c in Fig. 1). Also, the regional climate, geomorphology, edaphology, and patterns of speciation, species extinction and migrations determine the ecological nature of the regional species

pool (e.g. disturbance-adapted *versus* disturbance-sensitive species), directly influencing the ecological profile of the colonizing flora (Ricklefs, 2004). Thus, forest regeneration is determined by a complex set of ecological processes and mechanisms that interact within and among scales (Pickett *et al.*, 1987; Chazdon, 2014; Meiners *et al.*, 2015).

(2) Regenerating driving forces and plant life histories

Forest regeneration depends directly on the patterns and processes involved in the plant life cycle (Wang & Smith, 2002; Fig. 2). This cycle is composed of a series of transitional stages whereby ovules are fertilized and become seeds, seeds are moved away from the parental plants and are deposited in a given spot. Then, the surviving seeds may germinate giving rise to seedlings, and these may ultimately develop into reproductive plants which, in turn, influence seed availability for following generations. Each of these stages is affected by numerous local conditions (e.g. microclimate and soil characteristics) and biotic processes (e.g. pollination, seed dispersal, herbivory, animal movements, and plant–soil, plant–plant and plant–animal interactions), which collectively drive forest regeneration in HMTLs (e.g. Pickett *et al.*, 1987). However, such direct causes depend on numerous indirect driving forces that act at the patch (e.g. patch size and isolation, edge effects), landscape (e.g. forest cover, connectivity, matrix complexity) and regional scales (e.g. climate, regional species pool, topography) (Figs 1 and 2).

For example, seed dispersal, seed germination and seedling recruitment are conditioned by different interconnected drivers, such as topography, landscape forest cover, isolation, and matrix complexity (Fig. 2). Likewise, plant growth and reproduction respond to soil and microclimatic characteristics conditioned by topography, as well as by patch (e.g. size, shape and isolation) and landscape characteristics (e.g. forest cover, connectivity, matrix complexity), which directly determine the intensity of edge effects, such as levels of habitat desiccation, light intensity and wind turbulence (Saunders, Hobbs & Margules, 1991; Murcia, 1995; Laurance *et al.*, 2002; Ewers & Didham, 2006). From a plant's perspective, these driving forces may represent regenerative barriers that act as dispersal-limitation agents (e.g. lack of vertebrate seed dispersers) or ecological filters (e.g. seed/seedling predation by generalist herbivores, competition with exotic and disturbance-adapted species; Tabarelli *et al.*, 2012). Integrating plant life cycles into SS, these same driving forces directly affect the taxonomic profile of successional plant and animal assemblages, and their regeneration rates, by differentially affecting the population dynamics of participating species. These multi-scale and interacting forces are also expected to govern the occurrence of alternative successional pathways within and across landscapes (Laurance *et al.*, 2007; Tschardtke *et al.*, 2012; Arroyo-Rodríguez *et al.*, 2013; Norden *et al.*, 2015; Reyer *et al.*, 2015). In synthesis, the structure of biotic assemblages inhabiting secondary forest patches in HMTLs and their

development (the pathways) is determined by a suite of driving forces across multiple scales (Gardner *et al.*, 2009; Tabarelli *et al.*, 2012; Meiners *et al.*, 2015).

(3) Potential successional pathways in HMTLs

In tropical wet forests, SS occurs mainly in areas of high human population density, where forests have been extensively transformed into agricultural landscapes under the effect of societal drivers (e.g. increasing global demand for food), but where migration of people has led to the abandonment of lands (Aide *et al.*, 2013). Land abandonment is a complex phenomenon that is mostly driven by socioeconomic factors, such as migration to areas where new life opportunities are offered to rural people (e.g. Rey Benayas *et al.*, 2007). SS can also occur in areas with relatively low productivity, such as those present at high elevations (e.g. cooler temperatures, steeper slopes), that are not appropriate for large-scale mechanized agriculture (Aide *et al.*, 2013). Whatever the societal causes of SS, HMTLs can be highly heterogeneous (Ellis, 2013), depending on the type, extent, frequency and intensity of human disturbances, ranging from relatively conserved landscapes to strongly degraded ones (*sensu* Melo *et al.*, 2013). The former scenario is typical from recently human-colonized landscapes, and is characterized by a high old-growth/secondary forest ratio and low coverage of edge-affected habitats. In the latter scenario, typical from landscapes with a long history of human occupation and anthropogenic land use, remaining old-growth forest patches are very small (with small core areas, strongly affected by edge effects and highly isolated from each other), embedded in anthropogenic matrices dominated by naturally regrowing forests, agroforestry production systems, pasturelands and/or annual crops. As described below, with increasing land-use intensity, both the successional pathways of secondary forests and their predictability are altered (Fig. 3).

Generally, the capacity of the ecosystem to recover from human disturbances, i.e. ecological resilience, is expected to be higher and more predictable in recently modified landscapes, with higher remaining forest cover, where remnant trees and seed and seedling banks composed of native species persist, and where well-preserved biodiversity-rich native forests are still present in the landscape (Folke *et al.*, 2004; Hooper, Legendre & Condit, 2004; Lamb, Erskine & Parrotta, 2005; Lawrence, 2005; Gilroy *et al.*, 2014a; Jakovac *et al.*, 2015; Reyer *et al.*, 2015; a in Fig. 3). In agreement with this idea, secondary forests in recently cleared landscapes with higher remaining forest cover and less human disturbance converge relatively quickly to the community attributes of nearby reference forests (e.g. Terborgh *et al.*, 1996; Sheil, 1999; Norden *et al.*, 2009, 2011; Dent, DeWalt & Denslow, 2013; Jakovac *et al.*, 2015). Nevertheless, such convergence is particularly evident for stand structure (e.g. tree basal area, stem density and species richness) and animal species richness compared to species composition, as even under such relatively favourable scenarios for forest regeneration, significant differences in species composition between secondary forests and reference areas have been commonly

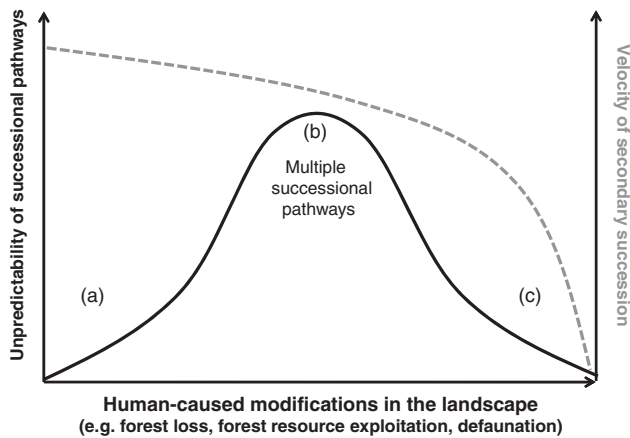


Fig. 3. Conceptual diagram showing the hypothesized relationship between disturbance intensity in human-modified tropical landscapes and the level of predictability of successional pathways (continuous line) and the velocity of secondary succession (dashed line). SS is expected to be relatively fast and more predictable (i.e. convergent with the vegetation of nearby old-growth forests, dominated by old-growth forest species) where the land has been used for a short time, and where well-preserved biodiversity-rich native forests are still present in the landscape (a). Because of the increasing variation in landscape spatial configuration and matrix heterogeneity in landscapes with intermediate levels of disturbance, successional pathways will become highly variable, and hence less predictable (b). With further increasing human disturbance, however, the landscape will become more homogenous (e.g. dominated by open areas, with limited availability of old-growth forest remnants) and biologically impoverished, thus decreasing successional recovery and increasing the predictability of successional pathways (e.g. hyper-dominance of disturbance-adapted species, biotic homogenization) as the variation in potential pathways is strongly reduced. In fact, we predict that there must be a threshold of disturbance intensity (e.g. topsoil loss, reduction in soil fertility, extinction of seed dispersers and/or dominance of grasses, lianas or invasive ferns) above which the system may be abruptly driven towards a slow or arrested succession state (see Mesquita *et al.*, 2001; Lamb *et al.*, 2005; Tabarelli *et al.*, 2008; Putz *et al.*, 2011; Jakovac *et al.*, 2015).

shown in plants (e.g. Chazdon *et al.*, 2007; Lebrija-Trejos *et al.*, 2010a; Dent *et al.*, 2013; Sandor & Chazdon, 2014) and animals (Moutinho, 1998; Shankar-Raman, Rawat & Johnsingh, 1998; Vasconcelos, 1999; Dunn, 2004; Gardner *et al.*, 2008; Hernández-Ordóñez, Urbina-Cardona & Martínez-Ramos, 2015).

With increasing human-driven modifications in the landscape, however, the heterogeneity of HMTLs also increases, resulting in a mosaic of land-cover types (e.g. old-growth forest patches, secondary forests, agricultural lands, and human settlements) with different spatial configuration (Fahrig *et al.*, 2011; Ellis, 2013; Mendenhall *et al.*, 2014; Villard & Metzger, 2014). This heterogeneity is expected to reduce predictability of the successional pathways in particular locations for several reasons (b in Fig. 3). First, as forest cover decreases in the

landscape, successional patches change from being surrounded by forested areas towards being immersed in heterogeneous matrices, with variable availability and arrival of old-growth forest species (Tabarelli *et al.*, 2010; Melo *et al.*, 2013; Gilroy *et al.*, 2014a; Mendenhall *et al.*, 2014). Second, the landscapes with intermediate forest cover (i.e. 20–50% remaining forest cover) show greater variability in the degree of fragmentation (e.g. number of forest patches) and in total forest edge, thus increasing the relative impact of surrounding landscape spatial configuration on ecological patterns and processes (Villard & Metzger, 2014 and references therein). For example, the impact of landscape configuration (e.g. forest patch size) on the abundance and richness of birds (Martensen *et al.*, 2012) and small mammals (Pardini *et al.*, 2010) can be relatively higher in landscapes with intermediate forest cover than in landscapes with high (>50%) or low (<30%) remaining forest cover. Thus, ecological processes such as pollination, seed dispersal and seed predation can be highly variable among forest patches, depending on the amount of forest cover in the local landscape. Finally, differences in disturbance regimes can promote the taxonomic differentiation (i.e. increasing beta-diversity) of plant (Arroyo-Rodríguez *et al.*, 2013) and animal (Gardner *et al.*, 2008; Püttker *et al.*, 2015) assemblages among forest patches. These effects feed the ‘landscape-divergence hypothesis’ (Laurance *et al.*, 2007) stating that secondary forests developed in sites with contrasting biotic and abiotic environmental settings and located in landscapes differing in spatial structure can exhibit increasing levels of taxonomic differentiation and divergent successional pathways (b in Fig. 3). Therefore, differences in landscape structure and land-use dynamics may result in contrasting biotic and abiotic conditions among regenerating stands (Fig. 2), differentially driving the regeneration into diverse successional pathways (Steininger, 2000; Mesquita *et al.*, 2001; Laurance *et al.*, 2007; Tschardt *et al.*, 2012; Martin, Newton & Bullock, 2013; Jakovac *et al.*, 2015; Norden *et al.*, 2015).

Human disturbance above a certain threshold is expected to limit, and even interrupt, the ecological resilience of the system (Folke *et al.*, 2004; Lawrence, 2005; Banks-Leite *et al.*, 2014; Cole *et al.*, 2014; Gilroy *et al.*, 2014a; Jakovac *et al.*, 2015; Reyer *et al.*, 2015). This strongly decreases successional recovery and increases predictability as the variation in potential pathways is strongly reduced (c in Fig. 3). Landscapes with long land-use histories have experienced persistent modifications and mostly high levels of resource exploitation, which has led to (quasi-) permanent changes in environmental conditions, resource degradation, defaunation, and proliferation of disturbance-adapted species such as pioneer plants and generalist herbivores (e.g. Shankar-Raman *et al.*, 1998; Martorell & Peters, 2005; Bihn *et al.*, 2008; Tabarelli *et al.*, 2008; Meyer, Leal & Wirth, 2009; Melo *et al.*, 2013). Such old agricultural landscapes clearly contrast with newly agricultural frontier areas. Most of these old landscapes have lost the largest

patches of old-growth forests that operate as source areas for the old-growth flora (Melo *et al.*, 2013), guilds of animal dispersers (Silva & Tabarelli, 2000), and natural enemies of proliferating herbivores (e.g. moisture-loving phorid flies – a specialist parasitoid of leaf-cutting ants: Almeida, Wirth & Leal, 2008). With the loss of old-growth forest cover, the habitat, as well as the ecological and landscape connectivity (*sensu* Fischer & Lindenmayer, 2007) can also be reduced (see Fahrig, 2013), limiting the interchange of seeds and species among regenerating stands (Silva & Tabarelli, 2000; Didham *et al.*, 2012; Gilroy *et al.*, 2014a). In many cases, the environmental conditions in the landscape have greatly changed (e.g. by increasing edge-effects and persistent use of agrochemicals, heavy machinery, fire and or cattle-ranching activities), with negative implications for forest regeneration, such as increased tree mortality, inhibited arrival, establishment and growth of old-growth species, intense herbivory of regenerating assemblages, invasion by disturbance-adapted species, and altered soil and microclimatic conditions (e.g. Laurance *et al.*, 2002; Hooper *et al.*, 2004; Urbas *et al.*, 2007; Santos *et al.*, 2008; Tabarelli *et al.*, 2008; Chazdon *et al.*, 2009b; Meyer *et al.*, 2009; Leal *et al.*, 2014b).

In synthesis, we predict that land-use intensification reduces the resilience of secondary forests, potentially driving the system towards a slow or arrested succession state that holds a lower potential to deliver ecosystem services (Mesquita *et al.*, 2001; Tabarelli *et al.*, 2008, 2012; Lôbo *et al.*, 2011; Putz *et al.*, 2011; Leal *et al.*, 2014b; Gilroy *et al.*, 2014b; Jakovac *et al.*, 2015; c in Fig. 3). Common examples reviewed by Lamb *et al.* (2005) occur when degradation leads to topsoil loss and a reduction in soil fertility, or when the areas become dominated by grasses, lianas or invasive ferns (e.g. Schnitzer *et al.*, 2000; Hooper *et al.*, 2004; Jakovac *et al.*, 2015; Suazo-Orduño *et al.*, 2015). In both cases, the re-colonization of these sites by many of the original species can be difficult, if not impossible (Hooper *et al.*, 2004; Lamb *et al.*, 2005; Suazo-Orduño *et al.*, 2015). Thus, substantial differences in taxonomic and functional composition of plant and animal assemblages between secondary forests and nearby reference areas can persist even centuries after abandonment (Corlett, 1992; Clark, 1996; Finegan, 1996; Shankar-Raman *et al.*, 1998; Chazdon *et al.*, 2007; Bihn *et al.*, 2008). This is particularly evident for old-growth forest specialists, such as many epiphytes (Martin *et al.*, 2013; Woods & DeWalt, 2013), frugivorous and nectarivorous-insectivorous birds (Shankar-Raman *et al.*, 1998), large carnivorous bats (Peña-Cuellar *et al.*, 2012) and dietary-specialist hypogeic ants (Bihn *et al.*, 2008). The loss of both species and ecological processes in long-deforested and fragmented landscapes also reduces variation in possible successional trajectories with increased pathway predictability (Tabarelli *et al.*, 2008). In particular, in highly human-disturbed landscapes the taxonomic/functional similarity across successional pathways will increase, leading to biotic homogenization in the landscape, especially resulting from proliferation of disturbance-adapted species that are widespread throughout

multiple landscapes (Lôbo *et al.*, 2011; Tabarelli *et al.*, 2012; Leal *et al.*, 2014b; Püttker *et al.*, 2015).

(4) The (neglected) role of chronic human disturbances and its societal drivers

Emerging interdisciplinary studies have shed light on the complex interplay between dynamics of humans and biodiversity in HMTLs (Ellis, 2013; Melo *et al.*, 2013; Laurance, Sayer & Cassman, 2014). Understanding why, how and to what extent people use land or natural resources is essential to assess SS (Gardner *et al.*, 2013). Acute disturbances are those large-scale disturbances that cause massive forest loss, mainly associated with growing global population, increasing *per capita* wealth, and the increasing global demand for agricultural land (Lambin & Meyfroidt, 2011; Sodhi *et al.*, 2011; Aide *et al.*, 2013; Ellis, 2013).

Soon after the establishment of human populations, several disturbance factors arise that do not result in forest loss and fragmentation, but that have negative impacts on the biological integrity of tropical biota (Singh, 1998; Laurance & Peres, 2006; Ribeiro *et al.*, 2015). Well-known examples are continuous poaching, extraction of firewood and non-timber forest products, and the damage caused by livestock, which overall result in a subtle but constant removal of small fractions of forest biomass (Martorell & Peters, 2005; May-Tobin, 2011; Leal, Andersen & Leal, 2014a; Ribeiro *et al.*, 2015). These disturbances can be regarded as ‘chronic’ because they extend over relatively long time periods, and have cumulative effects on biodiversity in HMTLs (Sodhi *et al.*, 2011; Ellis, 2013; Melo *et al.*, 2013; Leal, Andersen & Leal, 2015; Ribeiro *et al.*, 2015).

The consequences of chronic disturbances for forest succession are relatively easy to predict, but difficult to assess. For example, harvesting of timber and fuelwood is likely severely to limit seed source availability for forest succession, particularly for those species that are being harvested (Specht *et al.*, 2015). Hunting can also reduce the seed movement of zoochorous species and affect mainly large-seeded tree species because large-bodied fauna tend to be preferred by hunters due to cost–benefit trade-offs (Stoner *et al.*, 2007; Parry, Barlow & Peres, 2009; Parry *et al.*, 2010). But even ant assemblages can be altered due to chronic disturbances limiting the provision of ecosystem services, such as seed dispersal (Leal *et al.*, 2014a) and plant protection against herbivores (Leal *et al.*, 2015). Overgrazing by livestock also imposes a continuum of vegetation degradation, including reduced biomass, simplification of seedling and sapling communities, and ultimately may lead to complete desertification (Leal *et al.*, 2005; Papachristou & Platis, 2011; Ribeiro *et al.*, 2015). Biological invasions involving plant and animal species in HMTLs are likely to take place as long as chronic disturbance prevails because humans tend to introduce domesticated plants and animals (Ellis, 2013).

In summary, despite the reduction in the annual net loss of old-growth forests observed in several tropical developing countries (Aide & Grau, 2004; Aide *et al.*, 2013; Hansen *et al.*,

2013), the frequency and intensity of chronic disturbances are expected to intensify and alter successional pathways of the remaining forest patches. Even areas embedded in large tracts of forest can be severely altered by management techniques, although the overall human impact is lower. In Brazil, for example, the management of forest for production of fruits of *Euterpe oleracea* (commercially known as ‘açai’) has been shown to cause floristic impoverishment with perceivable consequences for forest succession (Freitas *et al.*, 2015). The use and modification of remaining natural habitats by people that depend on natural resources may therefore create ‘novel ecosystems’ (*sensu* Hobbs, Higgs & Harris, 2009) that differ from their ‘pristine’ counterparts not only in terms of species composition but also in successional trajectories (Collier, 2015).

Chronic disturbances are more likely to be driven by density of human population in HMTLs and its degree of dependency on natural resources, as demonstrated across the world (Ostrom, 2009). Human dependency on natural resources is mostly governed by a context-dependent combination of availability and accessibility to natural resources and economic vulnerability (Barrett, Travis & Dasgupta, 2011). Therefore, SS in HMTLs should be drastically influenced by the socio-economic factors governing the intensity of chronic disturbances (Ostrom, 2009). Most of the world’s land experiencing SS is private, and therefore, subject to the rules of land market and laws operating in each country. The long-lasting permanence of the SS in private lands depends upon the benefits owners may receive or the enforcement of laws aimed to protect forests in private lands (Aronson *et al.*, 2011; Chazdon, 2014). Creating economic incentives and well as law enforcement must be the main policies to promote forest regrowth worldwide.

III. THE CONSERVATION IMPORTANCE OF SECONDARY FORESTS

Over the last decades, forest succession, forest fragmentation and landscape ecology research have contributed complementary information on some key drivers of SS in HMTLs. Such knowledge can be used to assess the potential of secondary forests as biodiversity repositories in HMTLs. Although it is clear that secondary forest stands can be suitable habitats for many species (Lindell, Chomentowski & Zook, 2004; Barlow *et al.*, 2007; Castro-Luna *et al.*, 2007; Harvey *et al.*, 2008; Chazdon *et al.*, 2009b; Gillies & St. Clair, 2010; Woods & DeWalt, 2013), we still do not know if vulnerable species are able to maintain viable populations in secondary forests (Prach & Walker, 2011) or to what extent the long-term persistence of species in secondary forests relies on supplements of individuals coming from nearby old-growth forest patches operating as source areas (i.e. source–sink dynamics: Dunning *et al.*, 1992). For example, there is evidence that many rare and habitat-specialized bats are absent in young successional stages close to old-growth forests (Castro-Luna *et al.*, 2007;

Peña-Cuellar *et al.*, 2012). Also, studies of birds indicate that the percentage of secondary forests in the landscape is negatively related to the diversity of forest specialist and generalist species (Carrara *et al.*, 2015), and that the ability of species to use secondary habitats in the tropics does not reduce their risk of becoming locally extinct as a result of deforestation (Harris & Pimm, 2004). Thus, some key questions for biodiversity conservation in HMTLs are: (i) how much biodiversity can secondary forests retain in the long term as compared to old-growth forests, or (ii) to what extent do secondary forests represent suitable habitat for old-growth forest-dependent species and for those already recognized as sensitive to human-disturbances (Barlow *et al.*, 2007; Chazdon *et al.*, 2009b; Prach & Walker, 2011; Woods & DeWalt, 2013)? In line with this, we also know little about how demographic rates of plants are altered in secondary *versus* old-growth forest patches. These questions are particularly relevant because local extinction in HMTLs is not a random process but focuses on particular groups of plants (e.g. large trees, species with large seeds, those pollinated by specialized agents and those exhibiting supra-annual reproduction) and animals (e.g. species with small population sizes, specialized habitat requirements and food resources, and/or with large home-range requirements) (Laurance *et al.*, 2006; Bihn *et al.*, 2008; Santos *et al.*, 2008; Filgueiras, Iannuzzi & Leal, 2011; Leal *et al.*, 2012; Peña-Cuellar *et al.*, 2012; Tabarelli *et al.*, 2012; Woods & DeWalt, 2013; Dirzo *et al.*, 2014).

In this sense, two contrasting views promote the current debate on the conservation importance of secondary forests. First, some studies suggest that succession is a predictable process governed by niche-assembly rules, conferring high resilience to tropical forests after disturbance, both in terms of structure and species composition (Finegan, 1996; Terborgh *et al.*, 1996; Letcher & Chazdon, 2009; Norden *et al.*, 2009). If so, secondary forests could serve as biodiversity reservoirs for old-growth forest species (Aide & Grau, 2004; Wright & Muller-Landau, 2006; Chazdon *et al.*, 2009b). Others, however, suggest that human-impacted forests are doomed because their original functioning has been disrupted and species composition will never return to its original state (Turner *et al.*, 1994, 1996, 1997; Brook *et al.*, 2006). Although much of this discussion depends on how broadly the ‘original state’ is defined and also on the timescale involved (Scheffer, 2009), it is clear that many secondary forest stands can only provide suitable habitat for disturbance-adapted plant and animal species, and that they cannot be colonized by many old-growth forest species without direct intervention (Turner *et al.*, 1994; Barlow *et al.*, 2007; Gardner *et al.*, 2008; Tabarelli *et al.*, 2008; Martin *et al.*, 2013; Woods & DeWalt, 2013; Chazdon, 2014; Leal *et al.*, 2014b).

Such contrasting perspectives reflect in fact the multiple pathways that succession may follow (Fig. 3). In other words, the conservation role played by secondary forests is context-dependent as they are affected by a myriad of variables operating simultaneously and at multiple scales (Figs 1 and 2). Context-dependency, however, does not

imply idiosyncrasy, but rather a multifactorial phenomenon which, to be properly described and predicted, must be addressed by more comprehensive modelling approaches that include more detailed information about the secondary stands studied (Meiners *et al.*, 2015; Norden *et al.*, 2015). To increase predictability, ecological research must therefore identify the environmental conditions provided by secondary forests that are suitable for different groups of species, particularly for old-growth forest species and/or for species recognized as disturbance-sensitive. Of course, we should not underrate the importance of generalist species that occur in both old-growth and secondary forests, as these species are often abundant, and when present, can contribute to the rapid recovery of species composition and forest structure (Norden *et al.*, 2009).

From this perspective, our unified view predicts the occurrence of two general possibilities, which represent the two extremes of a gradient of ecological conditions or opportunities through which SS occurs in HMTLs (Fig. 3). First, succession is likely to proceed rapidly and support more diversified and convergent plant assemblages, from early- to late-successional stands, in the presence of: (i) non-degraded soils; (ii) abundant sources of propagules for plant regeneration, including allochthonous (i.e. out-patch) seeds, soil seed bank, seedling bank and sprouts; and (iii) reduced filtering imposed by site conditions, edge effects and resource exploitation by human populations (Terborgh *et al.*, 1996; Sheil, 1999; Hooper *et al.*, 2004; Lamb *et al.*, 2005; Chazdon *et al.*, 2009b; Norden *et al.*, 2011). These requisites are better met in those landscapes experiencing low-intensity land use and thus exhibiting (i) large remnants of old-growth forests and their quasi-intact animal community operating as pollinators, seed dispersers, herbivores, and parasites at the landscape scale; (ii) high percentages of remaining forest cover and high habitat and ecological connectivity; and (iii) heterogeneous matrices and reduced exploitation of forest resources (Primack & Miao, 1992; Holl, 1999; Wright *et al.*, 2000; Melo *et al.*, 2013; Dirzo *et al.*, 2014). In such a landscape context, seed dispersal limitation, ecological filtering and antagonistic biotic interactions do not offer significant constraints to many species to reach the regenerating forests (Leal *et al.*, 2014b; Meiners *et al.*, 2015).

Second, there must be a threshold of disturbance intensity in HMTLs above which the conservation importance of secondary forests decreases because of the increasingly impoverished assemblages they are able to retain (Turner *et al.*, 1994; Folke *et al.*, 2004; Slocum *et al.*, 2004; Tabarelli *et al.*, 2008; Banks-Leite *et al.*, 2014). This is particularly true when land use results in (i) intense soil degradation (loss of soil fertility and structure, high pollutant levels); (ii) reduced forest cover and high levels of habitat fragmentation; (iii) extirpation of the pollinator and frugivorous fauna; (iv) strong edge effects and degradation of secondary forest stands *via* fire, logging, plant harvesting, intense herbivory of regenerating assemblages and/or proliferation of disturbance-adapted species (Lamb *et al.*, 2005; Tabarelli *et al.*, 2008, 2012; Chazdon *et al.*, 2009b; Putz *et al.*, 2011; Leal *et al.*, 2014b).

Thus, it is not surprising that in severely deforested regions, such as in Singapore, where 99.8% of the old-growth forest has disappeared, secondary forests appear to accrete plant diversity very slowly, even if they are contiguous to relatively intact old-growth forest areas (Turner *et al.*, 1994). Slow rates of regeneration have also been reported in south-eastern Asia, in sites with higher landscape forest cover, but due to low soil fertility and the regional species pool (poor dispersal ability of dipterocarps) (Brearley *et al.*, 2004). Thus, not only the presence of intensive land use, but also seed dispersal limitation, ecological filtering and antagonistic biotic interactions represent significant constraints to the majority of the flora in secondary forests (with the exception of disturbance-adapted species).

Finally, although ecological data derived from chronosequence analyses (e.g. abundance, taxonomic and functional composition, species diversity) have been frequently interpreted as proxies of diversity persistence, they cannot inform us about habitat suitability or the long-term persistence of populations in secondary forest stands (e.g. van Breugel *et al.*, 2013). Thus, SS research should integrate novel aspects from ecological theory, such as metapopulation theory, niche theory, and neutral theory, among others. Fragmentation research and landscape ecology can also be of key relevance for understanding successional dynamics. For example, secondary forest stands may operate as: (i) supplementary habitats for forest-dependent species; (ii) suitable habitats for disturbance-adapted species; and (iii) structural elements in the landscape, such as stepping stones and forest corridors, enhancing matrix permeability and landscape connectivity at multiple spatial scales (Dunning *et al.*, 1992; Ewers & Didham, 2006; Lindenmayer *et al.*, 2008; Tschamtkke *et al.*, 2012).

Taking advantage of such 'real' instead of 'potential' opportunities requires: (i) long-term, population-level research devoted to understanding population dynamics and species persistence at the landscape and regional scales; and (ii) incorporating secondary forests as key elements of conservation planning and integrated landscape management (Chazdon *et al.*, 2009a; Freeman, Duguma & Minang, 2015). Also, additional studies distinguishing the effect of forest type (i.e. secondary *versus* old-growth forest) and configuration (e.g. patch size) are required (see Ferraz *et al.*, 2014). Secondary forest patches are usually smaller than old-growth stands (see Martin *et al.*, 2013), but many studies in fragmented landscapes do not distinguish between old-growth and secondary forest patches (e.g. Morante-Filho *et al.*, 2015), thus limiting our understanding of the conservation role of secondary forests. Of course, to scale-up such understanding we also need broader scale information about secondary forest distribution and land-use patterns, as we have a relatively poor knowledge of the distribution of secondary forests globally, thus limiting our ability to assess how secondary forest distribution and landscape structure affect succession at regional scales.

Considering the landscape and regional contexts, therefore, a key issue to be considered is not whether

the secondary forest patches will recover until achieving compositional levels similar to old-growth stands, but that landscape-scale forest cover increases through secondary growth, potentially allowing the ‘payment’ of extinction debts in HMTLs (see Banks-Leite *et al.*, 2014). Both theoretical and empirical evidence suggests that biodiversity persistence in HMTLs declines sharply below approximately 30% of forest cover in the landscape (Andr en, 1994; Banks-Leite *et al.*, 2014), although this threshold may vary among regions and taxonomic groups (e.g. Morante-Filho *et al.*, 2015). Thus, the increase of secondary forests in the landscape may contribute to maintain more species through the increment of landscape-scale forest cover. Furthermore, the multiple successional pathways that secondary forests can follow implies that secondary forests contribute to an increased beta-diversity at the landscape scale, thus allowing the accumulation of a higher number of species in HMTLs (i.e. gamma diversity; Gardner *et al.*, 2008; Arroyo-Rodr guez *et al.*, 2013; P ttker *et al.*, 2015). In this sense, the ‘dominance of beta-diversity hypothesis’ (*sensu* Tschardt *et al.*, 2012) proposes that the negative effects of land cover change on local (alpha) diversity can be overridden by the increase of beta-diversity, as such increase allows the maintenance of gamma-diversity. In this sense, the discussion regarding the conservation role of secondary forests should be moved from the local to the landscape level.

In synthesis, secondary forest stands must be actively monitored and managed (e.g. using assisted forest restoration) according to conservation goals considering broad spatial scales (landscape or region; i.e. the conservation scales recommended by conservation biologists) (Lamb *et al.*, 2005; Lindenmayer *et al.*, 2008; Tabarelli *et al.*, 2010). Also, the phylogenetic and functional dimensions of biodiversity should be more deeply investigated in secondary forests, as species richness, abundance and the taxonomic approach *per se* do not fully describe biological communities (Letcher *et al.*, 2012; Santos *et al.*, 2014; Meiners *et al.*, 2015). Indeed, studying changes in phylogenetic relatedness of species and individuals within regenerating assemblages can be useful to bridge gaps between ecological and evolutionary questions during forest succession, infer mechanisms of community assembly, and determine whether the evolutionary relationships among species of an assemblage affect ecological processes and ecosystem functioning (Cavender-Bares *et al.*, 2009; Letcher, 2010; Meiners *et al.*, 2015).

IV. CONCLUSIONS

(1) Secondary forest stands are likely to persist as an important component of present and future HMTLs either qualitatively or quantitatively, while old-growth forest patches continue to be cleared (Ferraz *et al.*, 2014). In addition to natural forest regeneration, many landscapes are experiencing assisted forest restoration, increasing the area of secondary forest patches. For example, over 3000 ha of the Brazilian Atlantic forest have been already restored and other

thousands are planned, particularly in hyper-fragmented landscapes with reduced forest cover (Melo *et al.*, 2013). Like other biodiversity hotspots, the long-term persistence of Atlantic forest biodiversity requires increasing the forest cover at the landscape level (Putz *et al.*, 2011).

(2) The take-home lessons of this review can be detailed as follows: (i) in tropical landscapes SS is a multifactorial phenomenon affected by a myriad of forces operating at multiple spatio-temporal scales; (ii) succession must be examined by more comprehensive explanatory models, providing information about the forces affecting not only the presence but also the persistence of species and ecological groups, particularly of those taxa expected to be extirpated from HMTLs; (iii) SS research should integrate new aspects from forest fragmentation and landscape ecology research to address accurately the real potential offered by secondary forests as biodiversity repositories; (iv) at the landscape level, secondary forest stands provide habitats of variable quality for species, and these forests can also be useful as structuring elements of HMTLs; and (v) secondary forest stands, as a dynamic component of HMTLs must be integrated into conservation-planning approaches, such as biodiversity corridors and biodiversity-friendly landscapes (Harvey *et al.*, 2008; Lindenmayer *et al.*, 2008; Chazdon *et al.*, 2009b; Putz *et al.*, 2011; Melo *et al.*, 2013; Gilroy *et al.*, 2014b).

(3) In synthesis, we must change our scale of analysis and intervention (from local to landscape and regional; Ricklefs, 2004), actively incorporating secondary forests as a key element into conservation and research planning. We require a global network of long-term experiments addressing key topics, such as the validity of chronosequence predictions for different response variables, the functional and phylogenetic basis for successional changes, and the long-term dynamics of populations and communities in secondary forests. We refer to HMTLs instead of single protected areas supporting permanent plots, covering a wide range of land-use conditions and landscape structure, in which land-use dynamics, (meta)population dynamics, species persistence, habitat restoration and management, and other key related topics can be examined and compared (cross-site comparisons), both for the identification of general drivers and for the design of management guidelines. In the Neotropics, for example, many HMTLs have been already elected as research and conservation targets (e.g. the Lacandona rainforest in Mexico, La Selva in Costa Rica, and Manaus in Brazil), largely facilitating the examination of HMTLs and their sets of secondary stands as repositories of tropical biodiversity (see the NeoSelvas project: <http://neoselvas.wordpress.uconn.edu/>; and the PARTNERS network: <http://partners-rcn.uconn.edu/page.php>).

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