

The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests

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ABSTRACT

Secondary forests are increasingly important components of human-modified landscapes in the tropics. Successional pathways, however, can vary enormously across and within landscapes, with divergent regrowth rates, vegetation structure and species composition. While climatic and edaphic conditions drive variations across regions, land-use history plays a central role in driving alternative successional pathways within human-modified landscapes. How land use affects succession depends on its intensity, spatial extent, frequency, duration and management practices, and is mediated by a complex combination of mechanisms acting on different ecosystem components and at different spatial and temporal scales. We review the literature aiming to provide a comprehensive understanding of the mechanisms underlying the long-lasting effects of land use on tropical forest succession and to discuss its implications for forest restoration. We organize it following a framework based on the hierarchical model of succession and ecological filtering theory. This review shows that our knowledge is mostly derived from studies in Neotropical forests regenerating after abandonment of shifting cultivation or pasture systems. Vegetation is the ecological component assessed most often. Little is known regarding how the recovery of belowground processes and microbiota communities is affected by previous land-use history. In published studies, land-use history has been mostly characterized by type, without discrimination of intensity, extent, duration or frequency. We compile and discuss the metrics used to describe land-use history, aiming to facilitate future studies. The literature shows that (i) species availability to succession is affected by transformations in the landscape that affect dispersal, and by management practices and seed predation, which affect the composition and diversity of propagules on site. Once a species successfully reaches an abandoned field, its establishment and performance are dependent on resistance to management practices, tolerance to (modified) soil conditions, herbivory, competition with weeds and invasive species, and facilitation by remnant trees. (ii) Structural and compositional divergences at early stages of succession remain for decades, suggesting that early communities play an important role in governing further ecosystem functioning and processes during succession. Management interventions at early stages could help enhance recovery rates and manipulate successional pathways. (iii) The combination of local and landscape conditions defines the limitations to succession and therefore the potential for natural regeneration to restore ecosystem properties effectively. The knowledge summarized here could enable the identification of conditions in which natural regeneration could efficiently promote forest restoration, and where specific management practices are required to foster succession. Finally, characterization of the landscape context and previous land-use history is essential to understand the limitations to succession and therefore to define cost-effective restoration strategies. Advancing knowledge on these two aspects is key for finding

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generalizable relations that will increase the predictability of succession and the efficiency of forest restoration under different landscape contexts.

Key words: ecological filter, human-modified landscapes, secondary succession, natural regeneration, resilience, forest restoration, tropical forests, ecosystem functioning

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I. INTRODUCTION

Across the tropics, large extents of forests have been converted to other land uses, mainly agriculture and pastures. Once agricultural and pastoral use cease and fields are abandoned, they can be covered by natural forest regeneration giving place to secondary forests (also called regrowth or successional forests). Successional forests are increasingly widespread in tropical regions, estimated to cover *ca.* 600 million hectares around the world, together with selectively logged forests (Brown & Lugo, 1990; Pan *et al.*, 2011). Immersed in human-modified landscapes, secondary forests can maintain important ecosystem services including carbon sequestration (Chazdon *et al.*, 2016; Poorter *et al.*, 2016), nutrient cycling (Powers & Marín-Spiotta, 2017), hydrological regulation (Ziegler *et al.*, 2009), biodiversity recovery (Strassburg *et al.*, 2016; Rozendaal *et al.*, 2019), and connectivity between forest fragments (Stouffer *et al.*, 2006; Arroyo-Rodríguez *et al.*, 2017). Secondary forests may also deliver direct resources to local populations such as timber, firewood, non-timber forest products (NTFPs) (Junqueira, Shepard & Clement, 2011), as well as sustaining crop productivity in swidden-fallow systems (Silva-Forsberg & Fearnside, 1997; Junqueira *et al.*, 2011; Jakovac *et al.*, 2016b). Regrowth is gaining importance also in

restoration initiatives where natural forest regeneration is being considered as a low-cost alternative to tree planting and a promising means to foster large-scale restoration (e.g. Lamb, 2014; Chazdon & Guariguata, 2016; Crouzeilles *et al.*, 2017; Chazdon *et al.*, 2020). The success of natural regeneration as a strategy to restore ecosystems, however, is very variable (Crouzeilles *et al.*, 2019) and depends on having favourable socio-economic and biophysical conditions for regrowth (Holl & Aide 2011, Crouzeilles *et al.*, 2017, Meli *et al.*, 2017, Chazdon *et al.*, 2020). The rate at which different vegetation attributes recover and the capacity of successional forests to attain levels similar to old-growth forests is highly variable. Within a successional pathway, differential recovery of vegetation attributes is related to the complexity of underlying processes. For example, biomass recovers around three times faster than species richness (Poorter *et al.*, 2016; Rozendaal *et al.*, 2019), because the later depends on the re-establishment of more complex biotic interactions. Across successional pathways, differences in recovery rates of vegetation attributes can indicate differential resilience, i.e. capacity to recover to old-growth forest levels (Mesquita *et al.*, 2001; Norden *et al.*, 2015; Arroyo-Rodríguez *et al.*, 2017). Some pathways can have extremely slow recovery of all vegetation attributes and be considered in an arrested successional stage (Mesquita *et al.*, 2015). While part of this

variation is driven by idiosyncratic and stochastic processes, successional pathways are strongly influenced by biophysical conditions, landscape context and how the land was used prior to its abandonment for regrowth (hereafter called previous land-use history). Climatic and edaphic conditions best explain differences in successional pathways at regional and continental scales (Moran *et al.*, 2000; Poorter *et al.*, 2016), while landscape context and previous land-use history largely drive successional pathways at local and landscape scales (Mesquita *et al.*, 2015; Martínez-Ramos *et al.*, 2016; Arroyo-Rodríguez *et al.*, 2017). At local scales, management practices affect the legacies from former vegetation such as seeds, roots and stumps, and modify soil conditions and biotic interactions (Hooper, Legendre & Condit, 2004; Styger *et al.*, 2007). At regional scales, land use modifies landscape context, i.e. composition and configuration, affecting the seed rain and environmental conditions (e.g. temperature, moisture and wind) under which succession can proceed (Nepstad *et al.*, 1996; Arroyo-Rodríguez *et al.*, 2017). The effects of previous land-use history on succession will also depend on the intensity, spatial extent, frequency, and duration of land use (Turner, 2010; Chazdon, 2014). Therefore, what is broadly called ‘land-use effects’ is actually a complex combination of processes and mechanisms acting on different ecosystem components and at different spatial and temporal scales. Understanding the ecological processes and mechanisms underlying land-use effects on succession is crucial for predicting the potential for natural regeneration as a forest restoration strategy, and for designing practices to assist succession and enhance its ecological quality and economic benefits for landowners (Forero-Montaña *et al.*, 2019).

In this review we synthesize knowledge on how land-use history affects tropical forest succession in human-modified landscapes. We focus on succession after clear cut, and therefore do not include studies evaluating regeneration after logging or in degraded forest fragments. The main aim is to elucidate the mechanisms underlying the divergence of successional pathways in human-modified landscapes, and to discuss the implications for ecosystem functioning and forest restoration based on natural regeneration. This study complements previous reviews that focused on successional processes (Chazdon, 2014), on specific regions (e.g. Martínez-Ramos *et al.*, 2016) and on landscape context (Arroyo-Rodríguez *et al.*, 2017), by providing a comprehensive overview of descriptors of land-use history and their effects on different ecological components in secondary forests across the tropics.

II. A FRAMEWORK DESCRIBING SUCCESSIONAL PATHWAYS

This review is organized following a framework that summarizes the main drivers of successional pathways in human-modified landscapes (Fig. 1, solid grey boxes). The framework is founded on previous studies on the hierarchical basis of succession (Pickett, Collins & Armesto, 1987), community assembly rules (Grime, 1998; Lortie *et al.*, 2004; Peterson & Carson, 2008)

and on models describing succession in human-modified landscapes (e.g. Chazdon, 2014; Mesquita *et al.*, 2015; Martínez-Ramos *et al.*, 2016; Arroyo-Rodríguez *et al.*, 2017).

This framework illustrates the idea that a combination of socio-economic and biophysical factors defines where and when regrowth will occur, i.e. site availability to succession (Fig. 1, arrow 1). These factors also define (and are partly defined by) land-use patterns and landscape context (Fig. 1, arrow 2). Ecological processes governed by characteristics of the landscape and by management practices associated with land-use history define filtering processes that act upon species availability (Fig. 1, arrow 3) and species establishment and performance (Fig. 1, arrow 4), finally shaping successional communities. In an interactive process, we use the outcomes of this review to complement the framework with the major processes underlying the effects of land-use history on succession (Fig. 1, white boxes).

In Section III we provide an overview of knowledge on the socio-economic drivers of regrowth, aiming to contextualize where, when and for how long regrowth is allowed in current human-modified landscapes. In Section IV.1, we provide a literature review on studies that explicitly investigated the role of land-use history on secondary succession. The aim was to: identify the descriptors used to characterize land-use history (Section IV.1); describe successional pathways associated with land-use history (Section IV.2); and present the mechanisms underlying the effects of land-use history on successional communities (Sections IV.3 and IV.4). We used the databases *Web of Science* and *Scopus* using the search strings “land use” AND “succession*” AND “tropic*” in the title, abstract and key words. We did not restrict the search by publication date, returning 565 published studies up to November 2020. We screened the title and abstract to select only studies that explicitly addressed the role of variation in previous land-use history on tropical secondary forests. Studies that addressed only temporal changes over succession or comparisons of secondary forests solely with old-growth forests were not included [see Chazdon (2014) for a comprehensive review]. After eliminating non-relevant articles and complementing with references cited therein, a total of 196 articles were assessed for full content. Results of this search are presented in Section IV and provided as online supporting information (Table S1). We discuss these results in the context of the implications for ecosystem functioning and for forest restoration based on natural regeneration in Section V.

III. THE SOCIO-ECONOMIC DRIVERS OF SITE AVAILABILITY TO SUCCESSION

The occurrence, distribution and permanence of secondary forests are driven by complex interactions between ecological, environmental, socio-cultural, economic and political factors operating at different spatial, temporal and organizational scales (Perz & Almeyda, 2010; Latawiec *et al.*, 2016) (Fig. 1, arrow 1). Forest regrowth typically occurs when pressure on land diminishes, which may happen as a consequence of

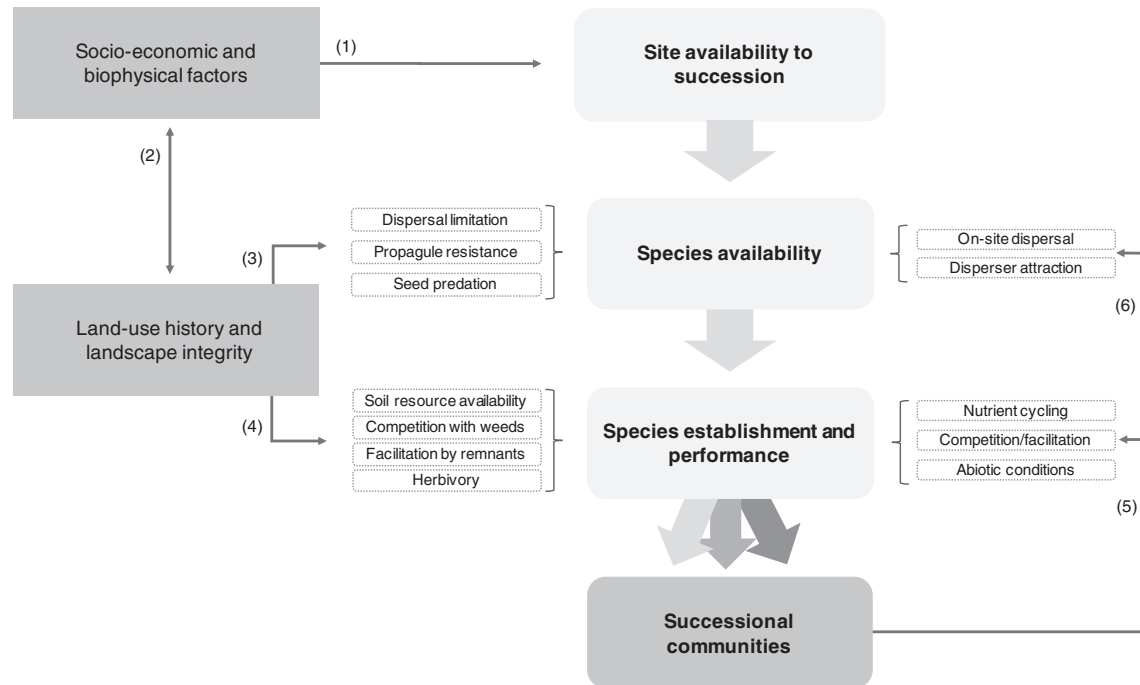


Fig 1. Main pathways through which land-use structures successional communities in human-modified landscapes. Socioeconomic and biophysical factors determine the abandonment of agricultural fields and availability of space for succession to proceed (1), as well as land-use patterns that define landscape integrity and management practices (2). Land use affects species availability (3) and species establishment and performance (4) through direct effects of landscape integrity and management practices and indirect effects of modified resources availability and biotic interactions. Land-use-mediated ecological filters reduce the set of species available in the seed and sprouts bank and seed rain (3), constrain the species able to establish successfully (4) and, combined with species life history, determine which species will perform best and dominate. The established plant community will then feed back (5, 6) the successional process by modifying on-site seed rain, environmental conditions and biotic interactions in the understorey. The resulting successional communities can follow different successional pathways.

rural–urban migration (e.g. Aide & Grau, 2004; López *et al.*, 2006; Schmook & Radel, 2008; Rudel *et al.*, 2009; Hecht *et al.*, 2015), changes to other production systems and increased availability of off-farm labour (e.g. Rudel, 2010) or, most often, the (temporary) abandonment of agricultural lands and pastures (e.g. Arroyo-Mora *et al.*, 2005; Wright & Muller-Landau, 2006; Chazdon *et al.*, 2020). ‘Marginal’ areas for agriculture such as steep slopes (Helmer *et al.*, 2008; Asner *et al.*, 2009; Crk *et al.*, 2009; Rudel *et al.*, 2009), low-fertility soils (Chinaea, 2002; Arroyo-Mora *et al.*, 2005; Helmer *et al.*, 2008) and/or poorly accessible areas are more likely to be permanently abandoned and to develop forest regrowth (Thomlinson *et al.*, 1996; Daniels, 2010, but see Sloan, Goosem & Laurance, 2015). In other contexts, young secondary forests dominate the landscape, driven for example by the intensification of shifting cultivation agriculture (Metzger, 2002; Jakovac *et al.*, 2017).

Besides their occurrence, the permanence of secondary forests in the landscape is also a product of socio-economic drivers. Recent studies have shown that most regrowth in human-modified landscapes is allowed to proceed for only two decades or less (Chazdon *et al.*, 2016; Schwartz *et al.*, 2017, 2020; Reid *et al.*, 2019; Nunes *et al.*, 2020; Schwartz *et al.*, 2020). The permanence of regrowth is higher in landscapes with lower accessibility, population density and demand for agricultural production (Metzger, 2002; Jakovac *et al.*, 2017). At the governance sphere,

land-use regulations and subsidies for agriculture also influence the decision on allowing regrowth to proceed (Díaz *et al.*, 2011; Chazdon *et al.*, 2020). Although decisions on where and when to abandon land are essentially taken at the household level, these decisions are also triggered by drivers operating at larger scales, such as regional and national policies (Vieira *et al.*, 2014), land opportunity cost (Crk *et al.*, 2009; Hecht *et al.*, 2015; Chazdon & Guariguata, 2016), land tenure (McClellan *et al.*, 2018), market fluctuations (Aide & Grau, 2004; Walsh *et al.*, 2008), conservation initiatives (Harvey *et al.*, 2008), and economic and political changes (Rudel, 2012; Chazdon, 2014). Most often, the trigger is an interaction of socio-economic and biophysical factors operating at multiple spatial and temporal scales. The example of forest transitions in Puerto Rico in the last 50 years illustrates these interactions: rapid economic development after the Second World War led to a shift away from agricultural activities, leading to an overall increase in forest cover; at local scales, biophysical factors such as topography ultimately influenced the areas that were actually abandoned and where forest regeneration took place (Rudel, Perez-Lugo & Zichal, 2000; Brandeis, Helmer & Oswalt, 2007; Yackulic *et al.*, 2011). Despite our growing understanding and recognition of the relevance of forest regrowth, the environmental and socioeconomic factors – and the complex interactions between them that influence the

likelihood of forest regeneration – are not yet fully understood (Aide *et al.*, 2013). This is a promising and necessary pathway for future research to support the design of governance strategies for forest restoration (Guariguata & Brancalion, 2014).

IV. HOW LAND-USE HISTORY DEFINES SUCCESSIONAL PATHWAYS

The majority of studies evaluating the effects of previous land-use history on succession were conducted in Neotropical

rainforests and evaluated vegetation attributes (Fig. 2A, B, E). The literature review shows that most of our knowledge comes from succession in abandoned pastures, shifting cultivation systems, and cropping fields (Fig. 2D). Most studies evaluated the effects of differential previous land-use history using same-age comparisons and chronosequences (Fig. 2F). Details regarding the 196 articles reviewed are provided in Table S1.

(1) Descriptors of land-use history

Evaluating the effects of land-use history on succession requires assessing the disturbance regimes, which refer to

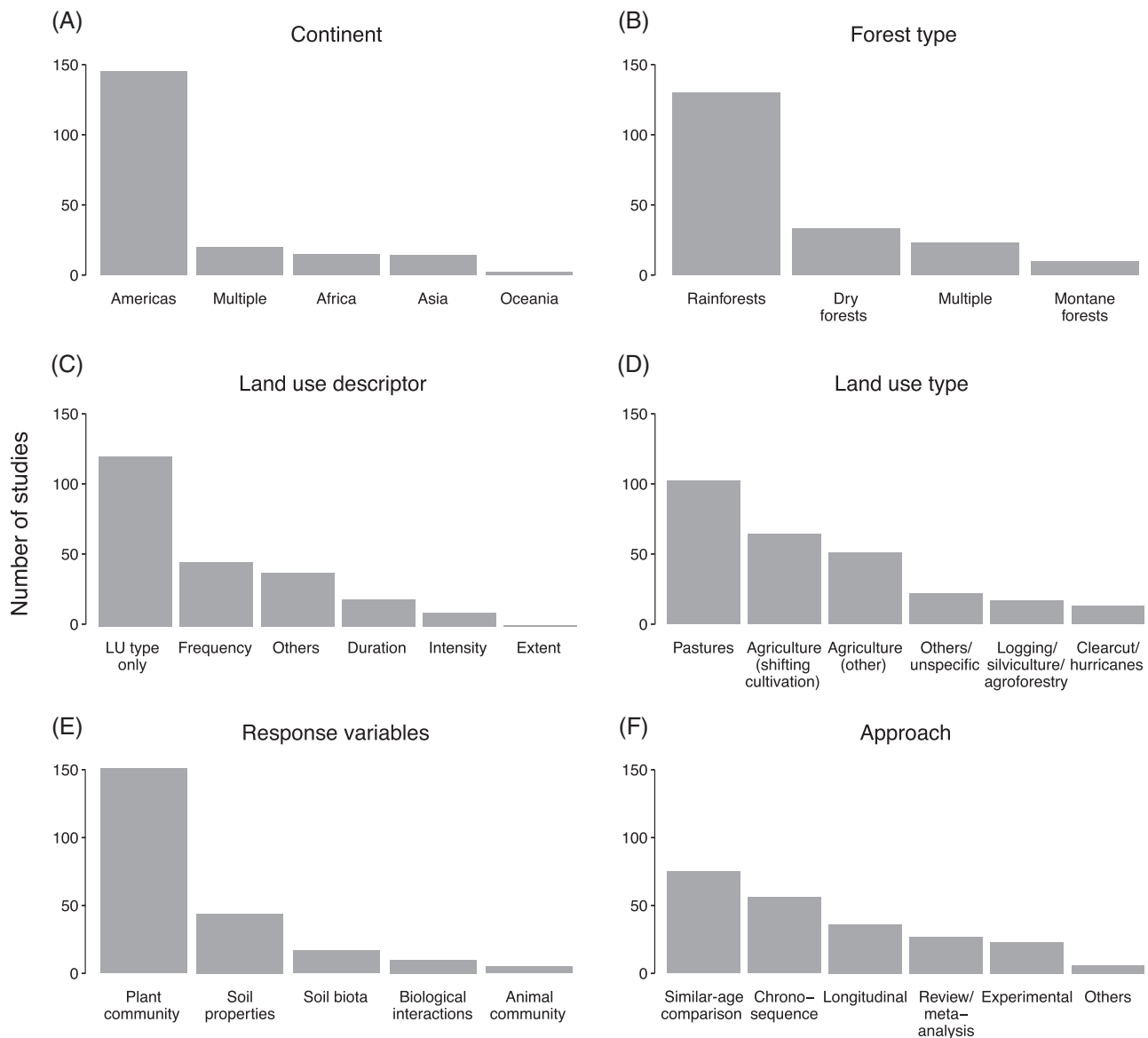


Fig 2. Quantitative description of reviewed studies according to: Continent (A) and forest type (B) where the study was conducted, the descriptors of previous land-use (LU) history assessed (C), the type of previous land use (D), the response variables analysed (E), and the study approaches used (F; similar-age comparison refers to comparisons across land-use histories with control for age during sampling, chronosequence refers to sampling using space-for-time substitution, longitudinal refers to temporal monitoring of successional patch(es), review/meta-analyses refer to studies that used results from other studies, experimental refers to studies that explicitly manipulated factors, and others refers to modelling, remote sensing and assessment of multiple drivers).

the spatial and temporal dynamics of events that disrupt the structure of an ecosystem, community or population, and change the resource availability or the physical environment (Turner, 2010). In anthropogenic contexts, disturbance regimes are also defined by qualitative descriptors, such as management practices and crop type. Assessing previous land-use history, therefore, is challenging and ideally requires a combination of field data and remote-sensing approaches (e.g. Dias *et al.*, 2016; Dutrieux *et al.*, 2016).

Most studies on secondary succession only reported the type of previous land use (61%) but did not assess other descriptors (Fig. 2C, Table S1). The type of land use is easy to identify, usually correlates with one or more disturbance descriptors (Zermeño-Hernández *et al.*, 2015), and is commonly used as a proxy for land-use intensity or the severity of the impact on succession (see Section IV.2). A few articles (10%) explicitly used land-use type as a proxy for land-use intensity (e.g. Aragón & Morales, 2003; Lakshmipathy, Balakrishna & Bagyari, 2012; Ding *et al.*, 2012b; Prieto *et al.*, 2015; Fig. 2C, Table S1). It is important to note that succession studies often refer to land-use intensity as a synonym for severity referring to the overall ecological effects on successional communities rather than to the actual amount of energy or input implied in the disturbance (Turner, 2010). This definition differs from those used in agronomic and land-use studies (see Erb *et al.*, 2013).

When indicated, the main land-use descriptors were the number and frequency of burning events or cropping cycles (e.g. Lawrence, 2004; Zarin *et al.*, 2005; Jakovac *et al.*, 2015; Fig. 2C), the length of the previous fallow period (27 studies; e.g. Dalle & de Blois, 2006), and the duration of continuous land use (e.g. Moran *et al.*, 2000; Erb *et al.*, 2013; Table S1). Few studies (19%) assessed other management practices, such as weeding frequency, soil amendment, machinery use, and type of crop to describe previous land-use history (Fig. 2; Table S1). Three studies used vegetation attributes as proxies for previous land-use impact, such as the identity of dominant species, the abundance of remaining crops and canopy cover (Table S1). As indicated by the incomplete information provided by most studies, assessing the complete land-use history is not trivial and may not always be possible. Acquisition of such information depends on interviews with long-term local inhabitants or remote-sensing analysis of time series, both of which have limitations and can be time consuming. Therefore, identifying correlations among descriptors and finding proxies that are easy to acquire will allow more studies to incorporate the effects of previous land use in understanding regrowth patterns and in predicting the potential for natural regeneration as a restoration strategy.

Correlations among descriptors were often identified. The longer the duration of land use, the higher the frequency of fire, and the larger the extent of the transformed landscape (Rossi *et al.*, 2010; Zermeño-Hernández *et al.*, 2015). Land-use intensity has been described in different ways including fire intensity (e.g. de Rouw, 1993), grazing intensity (e.g. Carpenter *et al.*, 2001; Marinho *et al.*, 2016) and combinations of frequency, duration, and management practices

[see Jakovac *et al.* (2015) and Zermeño-Hernández *et al.* (2015)]. The number of burning events has been used as a proxy for the frequency and intensity of previous land use (e.g. Nepstad *et al.*, 1996; Zarin *et al.*, 2005; Jakovac *et al.*, 2015). Time since deforestation started is usually positively correlated with land-use intensity and duration (Zermeño-Hernández *et al.*, 2015; Arroyo-Rodríguez *et al.*, 2017; Jakovac *et al.*, 2017). Duration of land use is often positively correlated with frequency of disturbance and distance to forest remnants (Zermeño-Hernández *et al.*, 2015) and negatively correlated with the amount of forest in the landscape (e.g. Moran *et al.*, 2000; Robiglio & Sinclair, 2011).

Because descriptors of landscape cover are easier to assess than land-use history itself, further research should investigate correlations among those in different contexts to establish proxies for land-use history. Such proxies could be retrieved from maps and satellite images in areas where information on land-use history is not available. Accounting for descriptors of landscape context and land-use history (Table 1) will increase our capacity to predict successional pathways (Norden *et al.*, 2015; Arroyo-Rodríguez *et al.*, 2017) and consequently contribute to the design of restoration practices to enhance natural regeneration (see Section V.2). Therefore, we encourage future studies to assess both local and landscape factors and to try to identify how they are linked and their relative roles in defining successional pathways and the potential for natural regeneration.

(2) Vegetation patterns defined by previous land-use history

Studies show that different types of previous land-use history lead to distinct rates of recovery of vegetation structure and biodiversity. The rates of recovery of biomass and species diversity in early secondary forests tend to be lower on fields previously used as pasturelands and subject to mechanized agriculture than on fields in shifting cultivation and low-input agriculture (e.g. Ding *et al.*, 2012b; Martínez-Ramos *et al.*, 2016). Biomass recovery rate in Amazonian rain forests, for instance, was 40–50% slower on abandoned pastures than on clear cuts (Zarin *et al.*, 2005; Mesquita *et al.*, 2015) and 70% slower on mechanized agriculture than on shifting cultivation systems (Moran *et al.*, 2000). Succession in non-mechanized agricultural fields had a twofold higher diversity of native species and half the percentage of exotic species than bulldozed fields (China, 2002). Species richness was lower or similar in forests regenerating on abandoned pastures compared to low-input agricultural fields, while species composition was consistently divergent (Mesquita *et al.*, 2015; Martínez-Ramos *et al.*, 2016).

Land-use types such as agroforestry systems can have opposing effects on the recovery of vegetation structure and diversity. Studies in Central America and the Caribbean found that the recovery of basal area and biomass is faster after the abandonment of agroforestry systems based on coffee or cacao than after pastures or palm plantations (*Bactris gasipaes*) (Fernandes & Sanford, 1995; Pascarella *et al.*, 2000; Rivera, Zimmerman & Aide, 2000; Marcano-Vega, Aide &

Báez, 2002). The crop trees remaining from the agroforestry system contributed to the more rapid recovery of biomass and basal area. However, the shaded environment under their canopies constrained the regeneration of native species, leading to lower stem density and species richness of native species when compared to pastures (Pascarella *et al.*, 2000; Rivera *et al.*, 2000; Marcano-Vega *et al.*, 2002).

Besides land-use type, variations in intensity, frequency and duration of previous land use play an important role in defining recovery rates and successional pathways. Historically, shifting cultivation was considered a low-intensity land-use system serving as a model to describe successional processes in tropical forests (e.g. Uhl & Jordan, 1984; Uhl, 1987; Guariguata & Ostertag, 2001). Recent studies, however, depicted that even slight increases in management intensity and cut-and-burn frequency result in strong changes in plant communities and recovery rates of tropical dry and rain forests, potentially leading to secondary forests with similar characteristics to those found in pasturelands (e.g. Gehring, Denich & Vlek, 2005; Lawrence *et al.*, 2007; Styger *et al.*, 2007; Ding *et al.*, 2012a; Jakovac *et al.*, 2016a). In systems managed with short fallow periods (<5 years), the basal area and canopy height of secondary-forest fallows are reduced by *ca.* 14% after each additional cropping cycle (Jakovac *et al.*, 2015). Also, studies suggest that fields used for more than 4–6 cropping cycles may converge to arrested successional states where rates of change in structure, diversity and composition are extremely low (Lawrence, 2005a; Styger *et al.*, 2007; Jakovac *et al.*, 2016a).

Variations in land-use history within land-use types generate variation in the rates of recovery of vegetation structure. Increased intensity, frequency, spatial extension and duration of previous land use leads to reduced regrowth rates of tree biomass, basal area, canopy height and species richness (Hughes, Kauffman & Jaramillo, 1999; Lawrence, 2004; Gehring *et al.*, 2005; Lawrence *et al.*, 2007; Styger *et al.*, 2007; Williams-Linera *et al.*, 2011; Jakovac *et al.*, 2015; Zermeno-Hernández *et al.*, 2015; Villa *et al.*, 2018; Cabral-Gomes *et al.*, 2020). It also leads to lower plant density (Williams-Linera *et al.*, 2011; Zermeno-Hernández *et al.*, 2015; Sanchez-Tapia *et al.*, 2020) but higher density of stems (e.g. Pascarella *et al.*, 2000; Gehring *et al.*, 2005; Longworth *et al.*, 2014; Sanchez-Tapia *et al.*, 2020). This apparent contradiction is probably a result of the impoverishment of the soil seed bank and increased dependency on resprouters, as suggested by the increased proportion of multi-stemmed trees and lianas (Gehring *et al.*, 2005; Jakovac *et al.*, 2015; Sanchez-Tapia *et al.*, 2020). The few studies that found no significant effects of land-use history on regrowth rate or species diversity (Zimmerman *et al.*, 1995; Peña & Duque, 2013; Derroire *et al.*, 2016b; Poorter *et al.*, 2016; Wood, Rhemtulla & Coomes, 2017) attributed these results to the lack of detailed information on previous land-use history or to narrow variation in its descriptors.

Land-use history not only affects vegetation structure, but also regulates the variation of species composition among pathways. With increasing intensity, frequency or duration of previous land use, there is a slower species turnover (Peterson & Carson, 2008; Klanderud *et al.*, 2009; Mwampamba &

Schwartz, 2011; Ding *et al.*, 2012b; Longworth *et al.*, 2014) and differential species composition (e.g. Mesquita *et al.*, 2001; Lawrence, 2005b; Styger *et al.*, 2007; Jakovac *et al.*, 2016a). Additionally, studies show an increase in the relative abundance of herbs, invasive ferns, shrubs and lianas at early stages of succession (e.g. Buschbacher, Uhl & Serrao, 1988; Rivera *et al.*, 2000; Lawrence, 2005b; Dalle & de Blois, 2006; Styger *et al.*, 2007; Vieira & Proctor, 2007; Klanderud *et al.*, 2009; Hogan *et al.*, 2016; Sanchez-Tapia *et al.*, 2020). Concomitantly, the species composition of understorey herbs (Bergman *et al.*, 2006; Styger *et al.*, 2007; Ribeiro, Bruna & Mantovani, 2010) and the identity of the canopy-dominant tree species change with previous land-use intensity (Zimmerman *et al.*, 1995; Pascarella *et al.*, 2000; Rivera *et al.*, 2000; Boucher *et al.*, 2001; Mesquita *et al.*, 2001; Thompson *et al.*, 2002; Lawrence, 2005b; Franklin *et al.*, 2006; Chai & Tanner, 2011; Wallenfang *et al.*, 2015; Hogan *et al.*, 2016). Studies in rain forests found that after intensive land use, succession is initiated by long-living pioneers such as *Vismia* spp. in Central Amazon (e.g. Mesquita *et al.*, 2015; Jakovac *et al.*, 2016a), *Byrsonima* spp. in Mexico (Martínez-Ramos *et al.*, 2016), *Moquimastrum polymorphum* in the Atlantic forest (Sanchez-Tapia *et al.*, 2020) and *Psidium* spp. shrubs in Madagascar (Styger *et al.*, 2007) instead of the classical short-lived pioneers, like *Cecropia* spp., *Trema* spp. in the Americas and *Harungana* spp. and *Musanga* spp. in Africa. Indicator species associated with different levels of land-use impact have been reported (Chinea, 2002; Styger *et al.*, 2007; Jakovac *et al.*, 2016a), and could be used together with other metrics to classify the ecological integrity of successional pathways and identify the need for restoration actions to foster regrowth and species diversity.

Different frequencies of fire also lead to divergence in functional traits in secondary forests regenerating in pastures (Fernandes Neto *et al.*, 2019; Sanchez-Tapia *et al.*, 2020; Sansevero *et al.*, 2020). In Central Amazon, fire-managed pastures gave place to secondary forests with higher wood density, and lower leaf dry matter content and seed mass than those following clear cut (Fernandes Neto *et al.*, 2019). In the Atlantic Forest, increased frequency of fire led to communities with lower wood density and leaf area index and higher bark thickness and seed mass (Sanchez-Tapia *et al.*, 2020). More studies are needed to verify how land-use history affects functional composition in other biogeographic and landscape contexts.

The reviewed studies show that previous land-use history is strongly associated with vegetation structure, diversity and composition of moist and dry secondary forests. Overall the studies support that longer and/or more intensive previous land-use history leads to secondary forests with reduced recovery rates, an impoverished plant community and a characteristic species taxonomic and functional composition.

(3) Land-use effects on species availability to succession

(a) Seed dispersal limitation

Dispersal limitation defines the quantity and quality of seed rain in successional fields (Fig. 1). According to reviewed

studies, dispersal limitation is one of the most important constraints to regeneration in pastures and agricultural fields (e.g. Holl *et al.*, 2000; Hooper *et al.*, 2004; Palomeque *et al.*, 2017). The conversion of native vegetation into different types of land use inevitably modifies the sources of seed rain by transforming landscape configuration and composition through forest fragmentation, reduction of forest cover, expansion of young secondary forests and the presence of isolated trees in the agricultural matrix (Lawrence, Peart & Leighton, 1998; Metzger, 2002; Robiglio & Sinclair, 2011; Arroyo-Rodriguez *et al.*, 2017; N'Guessan *et al.*, 2019). The amount of forest cover in the landscape and the distance of forest remnants to successional patches influences the seed rain in successional fields.

Studies show that the density and diversity of regenerating trees decreases sharply with distance from the forest edge (e.g. Guariguata *et al.*, 1997; Martínez-Garza & González-Montagut, 1999; Holl *et al.*, 2000; Mesquita *et al.*, 2001; Benítez-Malvido *et al.*, 2005; Jakovac *et al.*, 2015). Studies suggest that most seed dispersal in human-modified landscapes occurs within 300 m of the forest border towards open areas (e.g. Cubiña & Aide, 2001; Hooper *et al.*, 2004; Lawrence, 2004). The rate of seed arrival and the composition of the seed rain at different distances from the forest will depend on dispersal modes and the niche of dispersers. Most animal-dispersed seeds reach shorter distances from the forest edge (e.g. average 4 m in Cubiña & Aide, 2001) than wind-dispersed seeds (e.g. average 250 m in Holl, 1998). Overall, generalist dispersers can reach longer distances than forest frugivorous vertebrates (Howe & Smallwood, 1982; Holl *et al.*, 2000; Benítez-Malvido, Martínez-Ramos & Ceccon, 2001; Robiglio & Sinclair, 2011). As a consequence, the proportion of late-successional species and the density of seed rain declines with distance to the forest (Lawrence, 2004). Studies found that the seed rain in agricultural fields and pastures is mainly from early-successional species (>85%), which are mostly dispersed by wind or generalist birds and bats (Benítez-Malvido *et al.*, 2001; Martínez-Garza *et al.*, 2011; Wieland *et al.*, 2011). In dry forests, the prevalence of wind dispersal over animal dispersal (Vieira & Scariot, 2006) makes the plant community less affected by dispersal limitations than in moist forests (Lebrija-Trejos *et al.*, 2010; Griscom & Ashton, 2011).

Dispersal limitation can be reduced by the management practice of allowing isolated trees in pastures and cropping fields. Remnant trees left in the fields increase the rate of biomass recovery (N'Guessan *et al.*, 2019), and provide perches for dispersers, enhancing the seed rain dispersed by frugivorous bats and birds (e.g. Vieira, Uhl & Nepstad, 1994; Otero-Arnaiz *et al.*, 1999; Benítez-Malvido *et al.*, 2001; Guevara, Laborde & Sanchez-Rios, 2004), thus increasing the diversity and density of seeds from tree species (Guevara *et al.*, 2005). The morphological and phenological characteristics of the remnant trees affect the abundance and species composition of the seed rain below their crowns (Sandor & Chazdon, 2014), due to differential attraction of dispersers (Guariguata, Rheingans & Montagnini, 1995; Duncan &

Chapman, 1999; Slocum, 2001; Guevara *et al.*, 2004; Hooper *et al.*, 2004).

The landscape composition, i.e. the distribution of land-use types in the landscape, also affects the amount and composition of the seed rain in successional fields. Agricultural fields and pastures immersed in the landscape contribute with seeds from pioneer herbs, shrubs, climbers, potentially invasive species and from a few bat-dispersed species typical of disturbed areas (Dupuy & Chazdon, 1998; Duncan & Chapman, 1999). Secondary forest patches immersed in agricultural landscapes mostly contribute early-successional species to regenerating sites (Hooper *et al.*, 2004; Nascimento *et al.*, 2006). The age distribution of such patches in the landscape, however, will influence the composition of the seed rain as it is related to species turnover over time (Lawrence, 2004; van Breugel *et al.*, 2013). The floristic composition across the landscape also defines the availability and species composition of animal dispersers (Bobrowiec & Gribel, 2010). Additionally, the dominant tree species in these secondary forests will influence the composition of dispersers and potentially feed back in the composition of the successional plant community (Bobrowiec & Gribel, 2010). Post-dispersal by cattle and insects play a minor role in redistributing seeds across open fields but may contribute to changes in the species composition of regrowth (Esquivel *et al.*, 2008; L.C. Leal, Andersen & Leal, 2014b).

(b) Seed and sprout resistance to management practices

The seed and sprout bank in the soil is a result of the accumulated seed rain and of the legacies of the original forest left after disturbance, such as seeds, sprouts and seedlings, and is the other main source of species in tropical forest succession (Uhl *et al.*, 1981; Cubiña & Aide, 2001; Klanderud *et al.*, 2009; Sousa *et al.*, 2017). The composition and density of soil seed banks, however, depends not only on legacies from the previous forest but also on the arrival of species dispersed from surrounding sources, either from forest fragments or from other types of land use. The viability of recalcitrant seeds from late-successional species, which are often legacies from the previous forest, is reduced with the duration of land use (Garwood, 1989; Cubiña & Aide, 2001), while the seed bank from herbs and shrubs is boosted (Guevara, Moreno-Casasola & Sanchez-Rios, 2005).

Management practices during land use also impact the legacies by reducing the viability of seeds and sprouts and by differentially favouring certain species (Fig. 1, arrow 4). In large-scale agriculture, bulldozing and repeated ploughing eliminate stumps and sprouting roots (China, 2002). In small-scale low-input agriculture, field management usually relies on manual weeding, which has a lower impact on regenerating sources than machinery, but still eliminates species with a transient seed bank or low sprouting ability (e.g. Uhl *et al.*, 1981; de Rouw, 1993; Jakovac *et al.*, 2016b), and favours the persistence of native tree species that are useful for farmers (Junqueira, Shepard & Clement, 2010).

Recurrent cutting and burning is a common practice in tropical agricultural fields and pasturelands that gradually selects for fire-resistant species (Vieira *et al.*, 1994; Holl *et al.*, 2000; Hooper *et al.*, 2004; Kalaba *et al.*, 2013; Sanchez-Tapia *et al.*, 2020), and along with grazing and weeding selects for strong sprouters and clonal species (Uhl *et al.*, 1981; de Rouw, 1993; Aide & Cavelier, 1994; Pascarella *et al.*, 2000; Hooper *et al.*, 2004; Lawrence, 2005*b*; Dalle & de Blois, 2006; Klanderud *et al.*, 2009; Williams-Linera *et al.*, 2011; Massad *et al.*, 2013; Jakovac *et al.*, 2016*a*). The presence of sprouters has been shown to facilitate the recovery of species composition in dry forests (Williams-Linera *et al.*, 2011).

(c) Seed predation

The environment transformed by land use favours seed predators and pathogens, reducing the rate of seed survival by 30–90% (Alvarez-Buylla & Martínez-Ramos, 1990; Martínez-Garza & González-Montagut, 1999). This significantly constrains the accumulation of forest species in the soil seed banks of pastures and agricultural fields, reducing species availability for succession (Nepstad *et al.*, 1996; Holl, 1998; Cubiña & Aide, 2001). A higher number of seeds tend to be lost to predation than to pathogens (Myser, 2003), but the role of pathogens has received less attention and remains unclear (Dalling *et al.*, 2011). Studies in the Neotropics show that 42–80% of woody species from the seed bank of pastures and shifting cultivation fields are consumed by predators such as ants, grasshoppers and small rodents (Alvarez-Buylla & Martínez-Ramos, 1990; Aide & Cavelier, 1994; Nepstad *et al.*, 1996; Wijdeven & Kuzee, 2000). The rate of seed predation varies with plant and predator species (Uhl, 1987; Aide & Cavelier, 1994; Myser, 2003), possibly leading to differential success of successional plant species in abandoned fields. The magnitude of such impacts on successional pathways, however, remains unclear – and may be context-dependent – and should be investigated further.

(4) Land-use effects on species establishment and performance

Once a species has arrived at a site, its establishment success and performance will depend on the species' life-history strategies combined with resource availability and biotic interactions (Pickett *et al.*, 1987), which are both influenced by management practices and landscape context (Fig. 1, arrows 3 and 4).

(a) Modified soil chemical and physical properties

Conventional agriculture and cattle ranching gradually reduce soil fertility due to nutrient losses by different practices (Sommer *et al.*, 2004; Bruun, Mertz & Elberling, 2006; Styger *et al.*, 2007; Wallenfang *et al.*, 2015). Burning volatilizes organic matter, carbon, nitrogen (N) and sulfur (Holscher *et al.*, 1997; Certini, 2005). Harvesting, leaching

and erosion reduces the concentration mainly of N, potassium and phosphorus (P) in the topsoil (Arnason, 1982; Jordan *et al.*, 1983; Holscher *et al.*, 1997; Runyan, D'Ondorico & Lawrence, 2012). Leaching and erosion become more important with extended cropping period (Kleinman, Pimentel & Bryant, 1995), in permanent cultivation systems and pastures (Buschbacher *et al.*, 1988; Holscher *et al.*, 1997), and in areas with steep slopes (Ramakrishnan & Toky, 1981). Bulldozing and repeated burning eliminate dead logs, which are important long-term sources of cations and soil carbon (Jordan *et al.*, 1983; Uhl & Jordan, 1984; Buschbacher *et al.*, 1988; Ribeiro-Filho, Adams & Murrieta, 2013). The longer the duration of continuous land use, the lower the levels of organic matter and nutrients in the soil, and the higher the degradation of soil structure, including reduced porosity, aeration, soil carbon content and water infiltration capacity. Studies suggest that pastures result in larger changes in the soil nutrients pool than small-scale agriculture or agroforestry systems (Moreira *et al.*, 2009).

Land-use practices could potentially improve soils and enhance regrowth, but in general soil improvements during land use do not last for long (but see Glaser & Birk, 2012). Although fertilization increases nutrient availability in the short term (Buschbacher *et al.*, 1988; MacDonald, Bennett & Taranu, 2012; Ribeiro-Filho, Adams & Murrieta, 2013), nutrients are rapidly taken up by the crops or regrowing vegetation (Abadin *et al.*, 2002), adsorbed to clay particles and metal (hydr)-oxides, and gradually lost by leaching and erosion (Holscher *et al.*, 1997; MacDonald *et al.*, 2012).

Reduced soil fertility after different land-use histories has been associated with slower regrowth [Uhl & Jordan, 1984; Aide & Cavelier, 1994; Lawrence *et al.*, 1999; Kanowski *et al.*, 2003; Lawrence, 2005*a*; Villa *et al.*, 2018; but see Johnson *et al.* (2001) and Ding *et al.* (2012*b*)], lower species richness, altered species composition (Chinea, 2002; Styger *et al.*, 2007; Ding *et al.*, 2012*b*; Wallenfang *et al.*, 2015; Jakovac *et al.*, 2016*a*), and lower seedling survival and growth (Román-Dañobeytia *et al.*, 2012; Wood *et al.*, 2017). Reduced P availability due to intensive land use has been specifically linked to a decrease in regrowth rate in Central America (Arnason, 1982), Asia (Lawrence *et al.*, 2010; Runyan *et al.*, 2012) and the Amazon (Jordan *et al.*, 1983; Gehring *et al.*, 1999; Davidson *et al.*, 2004), as well as to reduced species richness and changes in species composition (Uhl, 1987; Lawrence, 2005*b*; Ding *et al.*, 2012*b*; Jakovac *et al.*, 2016*a*; Villa *et al.*, 2018).

It is difficult to disentangle the role of soils in forest regrowth in observational studies, as soil properties often correlate with management intensity, distance from the forest and soil type (e.g. MacDonald *et al.*, 2012). Fertilization experiments, on the other hand, provide direct evidence showing that regrowth in pastures is limited by N and P availability (Davidson *et al.*, 2004) and that N and P fertilization increased the biomass dominance of a few pioneer species (Gehring *et al.*, 1999) reducing community evenness and diversity (Siddique *et al.*, 2010). Such results were related to differential growth responses to fertilization among tree

species, with P limiting the growth of *Inga macrophylla* but not of *Vismia guianensis*, for example (Gehring *et al.*, 1999). Reduced soil P availability may also restrict the performance of nitrogen-fixing legumes (Gehring *et al.*, 1999; Hedin *et al.*, 2009) significantly affecting nitrogen availability and nutrient cycling during succession (Erickson, Keller & Davidson, 2001; Batterman *et al.*, 2013).

The intensity of previous land use, therefore, affects the relationship between soil and regrowth: if regrowth is allowed just after burning or after low-intensity land use there may be no nutrient limitation to native tree species (Jordan *et al.*, 1983; Uhl & Jordan, 1984; Johnson *et al.*, 2001; Lawrence, 2005b), but when regrowth occurs on intensively used cropping fields or pasturelands, it will be slower and with lower species diversity mainly due to N and P limitation (Gehring *et al.*, 1999; McGrath *et al.*, 2001; Davidson *et al.*, 2004). Current scientific knowledge supports the idea that soil conditions transformed by land use are important drivers of alternative successional pathways. More experimental studies carried out in different contexts are needed to separate the effects of nutrient limitation from management practices and landscape factors.

(b) Modified soil biology

During land use, intense tillage, continuous cropping, replacement of trees with annual species or exotic pasture grasses and lack of a litter layer all contribute to reduced soil organic matter content (McGrath *et al.*, 2001; Moreira *et al.*, 2009; Smith *et al.*, 2014; Smith, Marín-Spiotta & Balsler, 2015). Such loss along with the use of pesticides reduces the abundance and diversity of soil macro- and microbiota and changes their community composition (Templer *et al.*, 2005; Ayuke *et al.*, 2011; Smith *et al.*, 2014; Fragoso *et al.*, 2016; Birhane *et al.*, 2017; Zhou, Wang & Luo, 2018).

Changes in soil microbiota may imply a reduction in nutrient availability to plants, especially through organic P pools (Hamer *et al.*, 2013) and reduced N fixation (Gavito *et al.*, 2008; Batterman *et al.*, 2013), which may negatively affect seedling survival and growth (Gavito *et al.*, 2008; Menge & Chazdon, 2016). Moreover, infestation by arbuscular mycorrhiza can promote differential species survival during regeneration (Menge & Chazdon, 2016; Bachelot *et al.*, 2018). The few studies available suggest that recovery of soil microbial communities happens relatively rapidly, taking between 5 and 15 years after succession starts to reach similar levels to old-growth forests (Guggenberger & Zech, 1999; Templer *et al.*, 2005; Hamer *et al.*, 2013; Cai *et al.*, 2018). Higher intensity of land use can, however, reduce the recovery rates of arbuscular mycorrhizal communities [Carpenter *et al.*, 2001; but see Carrillo-Saucedo, Gavito & Siddique (2018)]. Nevertheless, there are very few studies relating soil microbiota to succession (eight studies; Fig. 2E, Table S1), which together with high spatial and seasonal heterogeneity (Lakshminpathy *et al.*, 2012; Cai *et al.*, 2018; Zhou *et al.*, 2018) may hinder generalizable

conclusions. The role of soil microbial communities in successional pathways remains unclear and deserves further investigation (for an extended discussion see Powers & Marín-Spiotta, 2017).

Among macrofauna, earthworms have received higher attention due to their importance as soil engineers that help sustain the soil microbiota and improve soil quality for plant growth (Fragoso *et al.*, 2016). Across the tropics, agriculture and pasture lead to reductions in the abundance and diversity of native earthworms, to local loss of entire functional groups and to the spread of invasive exotic species (Fragoso *et al.*, 2016; Rossi *et al.*, 2010), with consequences such as long-lasting soil compaction (Chauvel *et al.*, 1999) and reduced decomposition rate (Geissen & Guzman, 2006). Low diversity and slow recovery of native macrofauna are related to longer duration of land use, more intense soil transformation, more frequent fires, and larger extent of transformed landscape (Castaño-Meneses & Palacios-Vargas, 2003; Sánchez-de León & Zou, 2004; Rossi *et al.*, 2010). The current knowledge suggests that land-use-induced changes in soil biology might contribute to alternative successional pathways, particularly at early stages, but that this effect may vanish within the first decades of succession.

(c) Competition with weeds and invasive plants

Previous land-use practices affect seed germination, seedling establishment and the performance of tree species by strengthening biotic interactions such as competition. Recurrent fire events and continuous cultivation favour colonization by weeds, lianas and invasive species (de Rouw, 1995; Jakovac *et al.*, 2016b; Palomeque *et al.*, 2017), which rapidly cover the ground and reduce light availability at ground level. This environment may restrict the germination of many pioneer species with germination triggered by light (Alvarez-Buylla & Martínez-Ramos, 1992; Benítez-Malvido *et al.*, 2001; Bentos, Nascimento & Williamson, 2013), such as *Cecropia* and *Trema*, for example (Suazo-Ortuño *et al.*, 2015). It is important to note, though, that under extreme degradation, the presence of any vegetation cover may favour the germination of forest species as it ameliorates the harsh environmental conditions (Catterall, 2016).

After seed germination, competition for light and nutrients with climbers and invasive species reduce seedling performance of successional forest species. Climbers and bamboos (not all invasive) are usually resistant to disturbance and tolerant to high light availability, being favoured by repeated burning, and intensive and continuous land use (Gehring *et al.*, 2005; Sovu *et al.*, 2009; Jakovac *et al.*, 2015). At early stages of succession climbers can spread over tree crowns and infest >80% of regenerating trees (Kuzee & Bongers, 2005; Lawrence, 2005b; Jakovac *et al.*, 2015), reducing tree growth (Schnitzer & Bongers, 2002; Lai *et al.*, 2017; Estrada-Villegas *et al.*, 2020), and contributing to slower overall forest regrowth (Paul & Yavitt, 2011). Studies on management of secondary forests show that removing

climbers significantly increases tree growth (Villegas *et al.*, 2009; César *et al.*, 2016).

Invasive species can spread easily and densely across agricultural landscapes, competing for space, light and nutrients with native species and potentially reducing their establishment success and performance (Colón & Lugo, 2006; Catterall, 2016; Palomeque *et al.*, 2017). For instance, *Leucaena leucocephala* is a pan-tropical invasive tree native to central America, in which high resistance to fire, rapid growth rates and high continuous production of seeds allow it to outcompete native successional species in tropical rain and dry forests (Erickson, Davidson & Keller, 2002; Colón & Lugo, 2006; Wolfe & van Bloem, 2012). Other invasive species are known to hinder succession and affect species composition, such as the grass *Imperata* spp. (Styger *et al.*, 2007), the shrub *Chromolaena odorata* in Africa (Robiglio & Sinclair, 2011; Norgrove & Hauser, 2015), the fern *Pteridium* spp. in the Neotropics (e.g. Silva & Matos, 2006; Schneider & Fernando, 2010; Suazo-Ortuño *et al.*, 2015; Palomeque *et al.*, 2017) and exotic pasture grasses across the tropics (e.g. Guariguata *et al.*, 1995; Holl *et al.*, 2000; Hooper *et al.*, 2004; Palomeque *et al.*, 2017). Differential density and species composition of competitors may, therefore, contribute to the divergence of successional pathways.

(d) Facilitation by remnant trees

Besides attracting dispersers and enhancing species availability (see Section IV.3a), remnant trees also affect species performance during succession in abandoned fields. Remnant trees shade out pasture grasses, reduce temperatures, increase humidity and improve soil nutrient availability under their crowns, consequently favouring seedling establishment and performance (Vieira *et al.*, 1994; Guariguata *et al.*, 1995; Hooper *et al.*, 2004), particularly in tropical dry forests (Guevara *et al.*, 2004; Griscom & Ashton, 2011; Mwampamba & Schwartz, 2011; Williams-Linera *et al.*, 2011). The density of remnant trees is usually reduced with intensive land use, such as in mechanized agriculture (Chazdon, 2014). Therefore, through its effects on seed rain (Section IV.3a) and on species performance, the density and composition of remnant trees may affect the density and species composition of the regenerating community at the onset of succession.

(e) Herbivory

Herbivory is an important interaction structuring plant communities in tropical forests (Coley & Barone, 1996). Agricultural fields and early successional communities harbour higher abundances of herbivores compared to natural forests (Silva *et al.*, 2009; Massad *et al.*, 2013; Hahn, Orrock & Wardle, 2016), probably due to high resource availability provided by the nutritious and/or palatable leaves of crops and pioneer species (Poorter *et al.*, 2004), facilitated host-searching in the simplified ecosystem, and high availability of suitable nesting sites (Silva *et al.*, 2009; L.C. Leal

et al., 2014b). Herbivory was shown to cause more damage to the plant community at earlier than later stages of succession (Silva *et al.*, 2009; Villa-Galaviz, Boege & del-Val, 2012; Hahn *et al.*, 2016), because of the higher digestibility of leaves from pioneer than late successional species (Poorter *et al.*, 2004), and the greater impact of herbivory on the performance of seedlings than adult trees (Massad *et al.*, 2013; Hahn *et al.*, 2016). In the Neotropics, leaf-cutting ants from the genus *Atta*, for example, prefer regenerating tree seedlings over pasture grasses and can remove 8–15% of available leaf area, significantly reducing seedling survival of certain species (e.g. nutrient-rich leaves) (Nepstad *et al.*, 1996; I.R. Leal, Wirth & Tabarelli, 2014a). The role of herbivory in seedling survival, however, will depend on plant investment in protection, which in some species may increase with physiological stress (Leal, Andersen & Leal, 2015), infestation by arbuscular mycorrhiza (Bachelot *et al.*, 2018) and exposure to fire (Massad *et al.*, 2013).

In pastures, grazing reduces the density of seedlings (Marinho *et al.*, 2016) and favours the persistence of unpalatable species (Griscom, Griscom & Ashton, 2009). A modelling exercise indicated that grazing and fire had synergistic effects causing greater reduction in regrowth when combined than the sum of their individual effects, and consequently yielding large variation depending on the intensity, frequency and extent of fire (Cantarello *et al.*, 2011). It is expected, therefore, that interactions between land-use history and herbivory will affect species performance and establishment during early colonization, altering species density, diversity and composition of successional plant communities.

V. DISCUSSION

(1) Land-use effects on ecosystem functioning

The reviewed studies show that land-use history defines successional pathways through impacts on multiple processes that define species availability to succession, species performance and local environmental conditions. Studies also show that the impacts of previous land-use history on regrowth can last for decades after land use has ceased (e.g. Zimmerman *et al.*, 1995; Mesquita *et al.*, 2015; Hogan *et al.*, 2016; Estrada-Villegas *et al.*, 2020). The integration of knowledge provided in this review suggests that land-use history alters ecosystem functioning and favours feedbacks that sustain alternative successional pathways for decades (Fig. 1, arrows 5 and 6). Initial site conditions left after land use define the early successional communities that interact with the transformed surrounding landscape to define environmental conditions and species turnover over time.

This review showed that land-use history strongly determines the assembly of early dominant species (e.g. Styger *et al.*, 2007; Martínez-Ramos *et al.*, 2016; Estrada-Villegas *et al.*, 2020), possibly affecting ecosystem functioning during succession (Fig. 1). The identity and functional characteristics

of these dominant species strongly drive ecosystem functioning (Lohbeck *et al.*, 2016; Mora *et al.*, 2017), microclimatic conditions in the understorey (Kabakoff & Chazdon, 1996; Lebrija-Trejos *et al.*, 2011), and biotic interactions (Bobrowiec & Gribel, 2010; van Breugel *et al.*, 2011). Case studies showed that species dominating after intensive land-use history hold traits such as long-lived leaves with low nutrient content (Uhl, 1987; Gomes & Luizão, 2012), differential crown architecture (Vester & Cleef, 1998), tick barks (Sanchez-Tapia *et al.*, 2020), high wood density (Fernandes Neto *et al.*, 2019) and high sprouting ability (e.g. Uhl *et al.*, 1981; Dalle & de Blois, 2006; Williams-Linera *et al.*, 2011). Traits like wood density and sprouting ability trade off with regrowth rates (Bond & Midgley, 2001; Lohbeck *et al.*, 2015; Pinho *et al.*, 2018). As a consequence, these communities might show slow nutrient cycling (Erickson *et al.*, 2002; Gomes & Luizão, 2012), as well as slow rates of change in vegetation structure, diversity and environmental conditions (Section IV.2). These successional communities and the associated environmental conditions interact with the surrounding landscape to define species turnover (Fig. 1, arrow 6): a crucial element for successional progress (Finegan, 1996; Chazdon, 2014). Therefore, cascading effects resulting from initial site conditions and landscape context lead to feedbacks that help sustain divergent communities over decades (Fig. 1, arrow 5).

The consequences of land-use history for ecosystem functioning, however, might differ between rain and dry forests because of intrinsic differences in community assembly

throughout succession (Gei *et al.*, 2018; Poorter *et al.*, 2019). For instance, dry forests might be more resilient to management practices such as cutting and burning as most species are able to resprout repeatedly compared with only a few species with these traits in rainforests (Kauffman, 1991; Bond & Midgley, 2001). On the other hand, dry forests might be less resilient to bulldozing and ploughing, given their higher dependency on local legacies (sprouts) than on dispersal from surrounding sources (Griscom & Ashton, 2011; Pulla *et al.*, 2015). Understanding of successional differences across forest types is recent and deserves additional attention in future studies.

Hence, advancing our knowledge of succession in human-modified landscapes requires a multidimensional approach that depicts ecosystem functioning in alternative successional pathways in multiple forest types. Additionally, we invite future research to evaluate the impacts of manipulating early successional communities on recovery rates (e.g. Brown & Ewel, 1987; Palomeque *et al.*, 2017). Such knowledge will be needed to support the definition of management alternatives to enhance natural regeneration in forest restoration programs.

(2) Implications for forest restoration based on natural regeneration

In this review we provide an integrated understanding of the mechanisms driving succession (Fig. 1) and defining alternative successional pathways. Here, we apply this

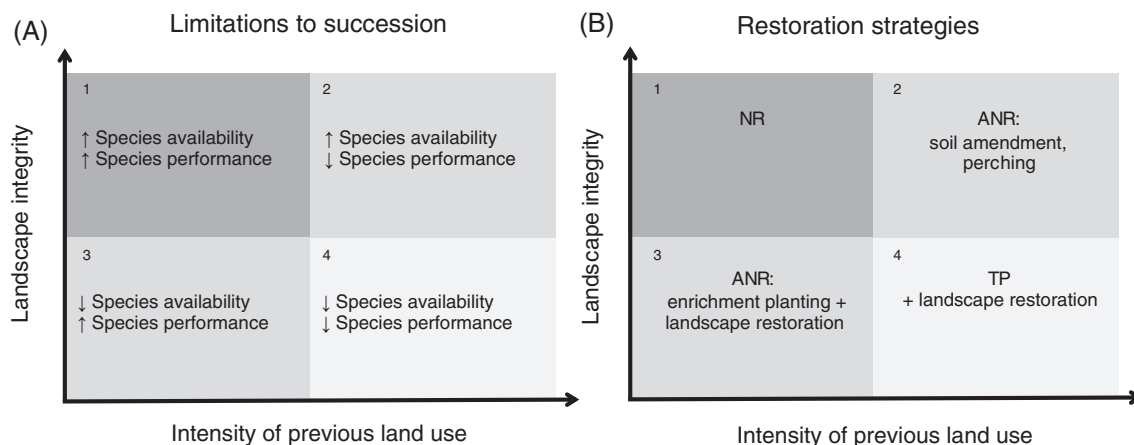


Fig 3. The interaction between landscape integrity and previous land-use history defines the limitations to succession (A), and restoration requirements (B). Here landscape integrity represents the amount and quality of sources of propagules, meaning that higher landscape integrity involves higher forest cover, lower forest fragmentation and higher tree cover in agricultural fields. The axis of intensity of previous land use summarizes an increase in the spatial extent, frequency, duration and intensity of management practices. (A) Species availability for succession is strongly reduced by reduction in landscape integrity as well as by intensive, extensive and long-term land use. Limitations to species performance increases with land-use intensity due to reduced resource availability and increased competition with invaders, for example. As a response to these driving factors, succession follows different pathways with varying rates of biomass regrowth and species turnover. (B) Along the gradients of landscape integrity and intensity of previous land use within and across human-modified landscapes, different restoration strategies will be required: unassisted natural regeneration (NR), assisted natural regeneration (ANR) or tree planting (TP). In each quadrant we provide examples of management practices that can help to overcome the limitations to succession (A) for effective restoration of ecosystem functions.

understanding to identify in which contexts natural regeneration could lead to effective forest restoration and which management practices would be required to foster restoration. This review shows that the recovery of multiple ecological attributes, i.e. the potential for natural regeneration to take place and to restore ecosystems, is context dependent and is a product of interactions between local and landscape conditions (Fig. 3). Secondary succession will proceed at higher rates where limitations to species availability, establishment and performance are lower (Fig. 3). The few studies evaluating interactions between local and landscape factors suggest that dispersal limitation is a stronger driver of species richness and turnover while local-level filtering effects mainly drive regrowth rate and species composition (Table S1; e.g. Martínez-Garza & Howe, 2003; Robiglio & Sinclair, 2011; Jakovac *et al.*, 2016a). With an increasing amount of forest in the landscape (landscape integrity), there is lower dispersal limitation and therefore higher species availability for naturally regenerating forests. With increasing intensity of previous land use, availability of species is narrowed down by filtering effects mediated by management practices, and species performance is reduced by limited soil nutrients and competition with invasive species (Fig. 3A). The limitations to succession imposed by local and landscape conditions can guide decisions on how to manage natural regeneration for effective forest restoration.

Unassisted natural regeneration will be an optimal restoration strategy in contexts of high landscape integrity and low intensity of previous land use (Fig. 3B, quadrant 1). In other contexts, assisted natural regeneration or tree planting are likely the way forward (Shono, Cadaweng & Durst, 2007; Chazdon *et al.*, 2020). Natural regeneration can be assisted by management practices appropriate to each context (Fig. 3B, quadrants 2 and 3). Where seed sources are abundant but local conditions are deteriorated (Fig. 3B, quadrant 2), practices to amend soil conditions (Allen, Allen & Gómez-Pompa, 2005), enhance seed rain (Zanini & Ganade, 2005; Toh, Gillespie & Lamb, 1999) and/or stimulate seed germination (Dupuy & Chazdon, 2008) will be needed to assist natural regeneration (Fig. 3B, quadrant 2).

Where seed sources are scarce but local conditions are not deeply transformed (Fig. 3B, quadrant 3), enrichment planting (Lascrain-Rangel *et al.*, 2019) could effectively enhance species diversity. Additional management practices might be required depending on specific biophysical conditions and on the restoration goal (Holl *et al.*, 2000; Chazdon *et al.*, 2020). Recovery rates and species turnover can be fostered through the selective removal of invasive species (Uebel, Wilson & Shoo, 2017; Palomeque *et al.*, 2017) and lianas (César *et al.*, 2016; Palomeque *et al.*, 2017) and through silvicultural treatments (Swinfield *et al.*, 2016; dos Santos & Ferreira, 2020). When economic returns are desired, possible management practices include planting or favouring the regeneration of commercial species (Fantini *et al.*, 2019; Forero-Montaña *et al.*, 2019).

In the situation where seed sources are scarce and local conditions are deteriorated (Fig. 3B, quadrant 4), recovery of

vegetation structure, diversity and composition is bound to be slow. In this context, speeding up succession would require the restoration of local and landscape conditions. An active restoration approach to improve local soil conditions and introduce species diversity (e.g. tree planting) will be required to kick-start successional processes. Additionally, improving landscape integrity will guarantee higher and more diverse seed dispersal and therefore higher restoration success (Martínez-Garza & Howe, 2003; Crouzeilles *et al.*, 2019). A landscape restoration approach, therefore, is needed especially where landscape integrity is low (Fig. 3B, quadrants 3 and 4).

It is important to note that spatial auto-correlations between local and landscape factors often result in synergistic effects. Distance to the forest is often positively correlated with the intensity, frequency and duration of previous land use (see Section IV.1). As a consequence, landscapes with higher integrity and locations closer to the forest edge promote higher natural regeneration (Goosem *et al.*, 2016), higher predictability of

Table 1. Main descriptors of land-use history influencing succession following agriculture or pasture land use, and examples of how to quantify them. One or more metrics can be used to describe previous land use; the choice of which metric to use being dependent on research question and data availability

Descriptors of previous land-use history	Metrics
Type	Pasture, shifting cultivation, conventional agriculture, agroforestry, etc. Crop(s) species/pasture grass species/livestock species
Intensity	Number of slash and/or burning events Livestock density Use of machinery, pesticides or herbicides Length of the fallow period Weeding practice (clear or selective weeding) Weeding frequency Presence of remnant trees (% cover or density) Indices combining frequency and duration
Frequency	Burning events frequency Slash-and-burn frequency Land cleaning/ploughing frequency Cropping frequency
Duration	Amount of time since old-growth forest clear cut Amount of time in continuous use (e.g. as agriculture or pasture) Average length of the cropping period over the period of land use Length of the last cropping phase previous to abandonment
Spatial extent	Size of the agricultural field or pastureland Size of the agricultural mosaic

succession (Arroyo-Rodríguez *et al.*, 2017) and higher restoration success (Crouzeilles *et al.*, 2017, 2020b). Therefore, the amount of surrounding forest and proximity to forest fragments could be easy-to-assess proxies for the potential of natural regeneration in human-modified landscapes (see Crouzeilles *et al.*, 2019, 2020a). Further studies are needed to identify the main proxies better for the potential for natural regeneration across regions.

Finally, the success of restoration initiatives based on natural regeneration will also depend on the restoration goals and on socio-economic aspects that govern the decision to allow regrowth to proceed (Section III). Environmental policies play an important role in determining the fate of regrowth and in constraining management practices (see Guariguata & Brancalion, 2014; Chazdon *et al.*, 2020). Therefore, natural regeneration can be an effective strategy to restore forest landscapes where there are lower limitations to succession (Fig. 3) and under appropriate governance systems.

VI. CONCLUSIONS

- (1) In human-modified landscapes, successional pathways are largely defined by land-use history. Although random processes contribute to define successional assemblages, land use imposes constraints on species availability and performance during regrowth. This review highlights that the most important underlying processes include dispersal limitation, ecological filtering, competition, facilitation, herbivory and tolerance to disturbance and environmental conditions.
- (2) The impact of previous land-use history on regrowth will depend on variations in the intensity, frequency, duration, extent and type of previous land use. Here we provide examples of how specific land-use practices in agricultural and pastoral fields constrain the availability of species and lead to differential species performance. Slight variations in land-use history can lead to different successional pathways within a landscape. Hence, descriptors of land-use history (Table 1) and landscape configuration and composition must be accessed in studies evaluating drivers of successional communities and predicting the potential for natural regeneration.
- (3) Within the set of species available to succession, a narrower set will be able to overcome competition for light, nutrients and space with weeds, lianas and invasive species and to establish and grow successfully. More experimental studies are needed to understand how biotic interactions lead to differential species performance and drive community assembly. Specifically, studies should evaluate how experimental removal of invasive and dominant species can affect the establishment and growth of native species.
- (4) The results of independent studies together suggest that cascading effects of land-use history on local conditions and species availability and performance may lead to differential ecosystem functioning. It remains unclear, however, how the early-successional assemblages favoured by previous land use foster or hold back further successional processes. The functional characteristics and biotic interactions of species that thrive after different land-use histories should be a research priority to advance knowledge on the impacts of land use on ecosystem functioning and to assist the design of management practices that enhance natural regeneration in forest restoration programs.
- (5) Our knowledge on succession after land use is strongly biased towards Neotropical wet forests, and low- to mid-intensity land-use history. More studies on degraded landscapes, on dry forests and covering the Paleotropics must be pursued to identify idiosyncrasies and generalities of tropical forest succession and to help define restoration strategies suited to local conditions.
- (6) Moving forward in the mechanistic understanding of succession in human-modified landscapes requires the assessment of land-use history (Table 1), long-term monitoring of successional patches, and careful experimental design to control for correlations between local and landscape factors. Special attention to variations in these factors is required when selecting secondary forest patches in chronosequence studies. The mechanistic framework proposed here on how land use drives successional pathways will help update successional theory to the current context of extensive anthropogenic influence and will support restoration science to identify key pathways to manage natural regeneration.
- (7) Finally, based on the knowledge summarized herein, we describe the potential for natural regeneration in different contexts of previous land-use history and landscape integrity (Fig. 3). Natural regeneration will be more successful where there are lower barriers to succession. In other situations, assisted natural regeneration, tree planting and landscape restoration are required.

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IX. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.
Table S1. List of articles compiled in the literature review on the effects of land-use history on secondary succession with classification of study region and study design.

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