

Neotropical rainforest restoration: comparing passive, plantation and nucleation approaches

Fernando C. Bechara^{1,2} · Sara Jo Dickens² · Emily C. Farrer² ·
Loralee Larios^{2,3} · Erica N. Spotswood² · Pierre Mariotte^{2,4} ·
Katharine N. Suding^{2,5}

Received: 17 April 2016 / Revised: 5 June 2016 / Accepted: 25 July 2016
© Springer Science+Business Media Dordrecht 2016

Abstract Neotropical rainforests are global biodiversity hotspots and are challenging to restore. A core part of this challenge is the very long recovery trajectory of the system: recovery of structure can take 20–190 years, species composition 60–500 years, and reestablishment of rare/endemic species thousands of years. Passive recovery may be fraught with instances of arrested succession, disclimax or emergence of novel ecosystems. In these cases, active restoration methods are essential to speed recovery and set a desired restoration trajectory. Tree plantation is the most common active approach to reestablish a high density of native tree species and facilitate understory regeneration. While this approach may speed the successional trajectory, it may not achieve, and possibly inhibit, a long-term restoration trajectory towards the high species diversity characteristic of these forests. A range of nucleation techniques (e.g., tree island planting) are important restoration options: although they may not speed recovery of structure as quickly as plantations, their emphasis on natural regeneration processes may enable greater and more natural patterns of diversity to develop. While more work needs to be done to compare forest restoration techniques in different environmental contexts, it appears that nucleation and, at times, passive restoration may best preserve the diverse legacy of these forested systems (both with lower costs). An integrated approach using both plantation productivity

Communicated by Peter Ashton.

✉ Fernando C. Bechara
bechara@utfpr.edu.br

¹ Division of Forest Engineering, Universidade Tecnológica Federal do Paraná, Dois Vizinhos, PR, Brazil

² Department of Environmental Science, Policy, & Management, University of California, Berkeley, CA, USA

³ Division of Biological Sciences, University of Montana, Missoula, MT, USA

⁴ Centre for Carbon, Water and Food, University of Sydney, Camden, NSW, Australia

⁵ Department of Ecology & Evolutionary Biology, University of Colorado, Boulder, CO, USA

but also the natural functions associated with nucleation may develop composition and diversity trajectory desired in Neotropical conservation efforts.

Keywords Tropical forest · Biodiversity · Succession · Assembly · Regeneration

Introduction

Deforestation continues to remain a threat in the Neotropics (Brook et al. 2006; Laurance et al. 2006; Asner et al. 2009; FAO 2010; Gibson et al. 2011). In the past, the focus of conservation has been protecting pristine and old-growth forests, however, efforts have increasingly focused on restoring degraded areas to increase the area of lands with high biodiversity value and ecosystem services (Díaz et al. 2006; Kaimowitz and Sheil 2007; Carpenter et al. 2009; Rey Benayas et al. 2009; Bullock et al. 2011; Suding 2011).

Neotropical forests have a notoriously variable rate of recovery: some stands recover structure rapidly and without human intervention within a couple of decades, but in other cases may take even centuries. On the other hand, to recover pre-disturbance species composition forests may take from one century up to thousands of years (Terborgh 1992; Bush and Colinvaux 1994; Pitman et al. 2005; Liebsch et al. 2008).

When forests undergo succession, their trajectories do not always follow deterministic pathways: site resilience and species performance interact with landscape and disturbance histories to dictate the successional trajectory of a forest plot (Pardini et al. 2010; Brudvig 2011; Chazdon 2012, 2014). Both stochastic and deterministic processes drive the composition of secondary forests (Dent et al. 2012). Stochastic processes such as chance dispersal can interact with deterministic processes including niche availability, local competition with early arriving species, and density dependent build-up of predators and pathogens, resulting in unpredictable changes in the species composition (Young et al. 2001, 2005; Suding and Hobbs 2009).

Practitioners are regularly faced with the challenging problem of quantifying resilience in a highly diversified forest system that operates on a so extended timescale (Chazdon 2008a; Prach and Hobbs 2008; Suding and Hobbs 2009; Holl and Aide 2011; Suding 2011; Elliott et al. 2013). When it has been determined that active restoration is necessary, the next challenge is to select a cost-effective restoration approach. The goal of active restoration should be to push the system over a particular threshold and reinitiate “auto-genic recovery” (King and Hobbs 2006), fundamental to reinforce feedbacks and reestablish critical functional groups (Clewett and McDonald 2009). Spatial and temporal pattern of active interventions will influence the course of community trajectories (Palmer et al. 1997).

Although human interventions might be able to drive forest community assembly to reach the looked-for endpoint (Stanturf et al. 2014), we argue that a greater understanding of the time scales associated with recovery stages of—(1) structure; (2) species diversity; and (3) rare and endemic species composition—is critical to restoration techniques decision making. Regarding to what legacy of restored forests do we want to leave for the next generations, we compare passive, plantation and applied nucleation approaches, when an important question emerge: How trajectories imposed by active methods could affect the endpoint of restoration projects in Neotropical forests?

How long does it take to restore Neotropical moist, rain and wet forests through passive restoration?

Revoking agriculture or cattle farming in deforested areas in the tropics has revealed the inherent capacity of these systems to naturally recover and highlights the importance of considering passive restoration in management plans (Clewell and McDonald 2009; Holl and Aide 2011). However, tropical forest natural regeneration can be stalled if the system has crossed an ecological threshold resulting in a new stable, degraded state (Lamb et al. 2005) and in highly degraded landscapes passive restoration may not occur at all (Chazdon 2013).

The rate of recovery of Neotropical forests varies greatly, and there are stories of both successes (Arroyo-Mora et al. 2005) and failures using passive restoration to restore both composition and structure (Uhl et al. 1988; Letcher and Chazdon 2009; Holl and Aide 2011). Norden et al. (2009) showed in a Costa Rica chronosequence study that secondary forests were undergoing reassembly of canopy tree composition through the successful recruitment of seedlings, saplings, and young trees of mature forest species. The sites had a high abundance of generalist species from the regional flora, high levels of seed dispersal, and the presence of near-by old-growth forest remnants. In these situations plant species richness quickly increased within the first few decades, especially for species with smaller-sized stems (Guariguata and Ostertag 2001; Norden et al. 2009), and later there was a clear convergence with mature forest community composition, supporting an equilibrium model of succession (Norden et al. 2009). However, some degraded tropical ecosystems may remain in a state of arrested forest succession (Sim et al. 1992; Chapman and Chapman 1999; Hooper et al. 2005; Goldsmith et al. 2011; Ortega-Pieck et al. 2011; Chazdon 2014). Under high disturbance conditions, as mining areas, for example, where soil removal, compaction or degradation has occurred, a site may never return to a state similar to original conditions (Gómez-Pompa et al. 1972; Uhl et al. 1988; Martínez-Garza and Howe 2003; Chazdon 2008b) but instead cross a threshold into a disclimax or emerge as a novel ecosystem (Hobbs 2006). Degraded grasslands and aquatic ecosystems can reassemble to alternative stable states as a result of threshold crossing regime shifts (Hobbs and Norton 1996; Suding et al. 2004; Suding and Hobbs 2009), and these same theories should be applied when assessing tropical forest space and time recovery in addition to succession theory (Young et al. 2001).

Because of both site-specific factors and dispersal-driven effects, it is difficult to predict the timescales of successional trajectories in secondary tropical forests (Guariguata and Ostertag 2001; Potts et al. 2002). Some commoner species relative abundance can be predicted (Potts et al. 2002), but the rate of recovery varies greatly for sites, as the number of species becoming structurally important over this time can vary (Letcher and Chazdon 2009). Biomass in moist and wet Neotropical abandoned pastures can converge with that of old-growth forests in 20–30 years, but to reach species richness and composition comparable to the original forest, may take at least 80 years (Brown and Lugo 1990; Pascarella et al. 2000; Marín-Spiotta et al. 2007; Letcher and Chazdon 2009; Norden et al. 2009). Aide et al. (2000) reported that a 40 year interval is necessary for recovery of mature tropical forest structure and richness in abandoned pastures of Puerto Rico, but more than 60 years to reach similar species composition to the original forest. In Southern Brazilian Atlantic forests, even though diversity increased after 15–30 years (up to 95 woody species.ha⁻¹), only a small number of species become structurally important over this time, suggesting that these communities will need many more decades to recover their

original structure (Siminski et al. 2011). Klein (1980) estimated more than 90 years to recover the climax diversity and Suganuma and Durigan (2015) projected up to 270 years to recover the proportion of slow growth tree individuals of these ecosystems in Brazil. Chazdon (2014) overview predicted 100–180 years depending on soil quality. Saldarriaga et al. (1988) estimated 190 years for a previously cultivated site to reach mature tropical forest basal area and biomass values. Still other studies suggest longer successional time frames are necessary. Depending on the soil degradation and other disturbances, recovery of pre-disturbance structure and original species composition could take 100–500 years (Uhl et al. 1988; Corlett 1995; Chazdon 2003; Liebsch et al. 2008; Dent et al. 2012; Suganuma and Durigan 2015). In Guatemala, areas of tropical rainforests cleared by the Maya and abandoned 1200 years ago still have anomalously low plant diversity (Terborgh 1992).

Evaluating the success of natural regeneration based on diversity alone can be misleading (Corlett 1995). Firstly, in some of these studies the high plant diversities recorded reflect the presence of long-lived pioneer species, which are normally absent in the primary forest, instead of the presence of rare primary forest species. Second, reports of high secondary forest species richness frequently refer to small plot sizes (typically <0.5 ha). The relative uniformity of secondary forests and the small size of regional pioneer floras mean that species-area curves rise more slowly and reach a plateau more quickly than in primary, undisturbed forests, where larger plots could present much higher richness (Schilling and Batista 2008).

Different types of tropical forest species recover at vastly different rates. In a secondary Southern Brazilian Atlantic Forest, sites cleared after slash-and-burn, pastures or agriculture, Liebsch et al. (2008) estimated 65 years to recover the proportion of animal-dispersed species (80 % of the species), 157 years to reestablish the proportion of non-pioneer species (90 % of the species) and 167 years for restitute understorey species (50 % of the species; especially Rubiaceae and Myrtaceae). These authors verified an increasing number of animal dispersed, non-pioneer and understorey species with time after disturbances. However, they estimated 1–4 thousand years to reach original endemism levels (40 % of the species occur just in Atlantic forests), consisting of several rare species (i.e., with one or less than one individual per hectare). This rarity generally encompasses 30–50 % of the tree species in tropical forests (Lepsch-Cunha et al. 2001). Thomas et al. (2008) recorded that 39 % of species were represented by only one individual in Brazilian Atlantic tropical forest in a one hectare plot. But in the Peruvian Amazon, 63 % of tree species were represented by a single individual and 85 % represented by less than two individuals (>10 cm dbh) per hectare (Gentry 1988). Remarkably, 55 % of tropical tree species that are likely to support highly vulnerable functions are rare (Mouillot et al. 2013).

An understanding of the magnitude of Neotropical floristic diversity is essential to establish a reference for restoration projects. In the Neotropics the number of tree species (~22,500) is about 1.6 and 3.5 times higher than in Asian and African tropics, respectively (Fine et al. 2008). Finally, including plant life forms other than trees in assessments substantially increases diversity in Neotropical forests. For example, in the moist and wet forests of Costa Rica, Ecuador and Panama, trees (including large shrubs) comprise only 31–35 % of the plant species registered in complete florulae (Gentry and Dodson 1987). In these forests, 33–36 % of the species are herbs (including subshrubs), 16–20 % climbers, 11–22 % epiphytes and 1 % parasites. This high diversity of species and life forms of Neotropical forests must be taken into consideration when determining restoration goals.

Tree plantations: a critic view

The most popular active restoration approach in tropical forests is definitely the establishment of plantations in order to establish a canopy covers and catalyze native forest succession (Lugo 1992; Guariguata et al. 1995; Parrotta et al. 1997; Wunderle 1997; Holl et al. 2000; Montagnini 2001; Carnevale and Montagnini 2002; Chazdon 2003; Cusack and Montagnini 2004; Lamb 2011; Elliott et al. 2013). High-diversity plantations create greater heterogeneity of habitats for animals and microsites for germination and plant recruitment, facilitate reproduction with conspecific remnant trees and reduce the synchronicity of canopy death (Carnevale and Montagnini 2002; Chazdon 2008a; Rodrigues et al. 2009, 2011).

The number of species used in high diversity plantations varies greatly. Holl et al. (2013) used only four species (two fast-growing and N-fixing species and two long-lived species) to facilitate recovery rather than try to plant several of the original species. Lamb (2011), using the “framework species method” and Chazdon (2012) suggested 20–30 species as the reference number; but Lamb (2011), in the “method of maximum diversity” recommended 80–100 species for highly degraded landscapes. Rodrigues et al. (2009) considered the planting of less than 30–50 species as insufficient for Brazilian forests and recommended the use of 85–110 species (“filling and diversity species method”). There is no “one size fits all” number of species for tropical forest restoration; instead, such a number should be determined according to the landscape, local conditions and potential restoration logistics (Durigan et al. 2010). Moreover, tropical forest restoration may be governed more by the diversity of functional groups (e.g., nitrogen fixers, slow- and fast-growing, canopy architecture and fauna attracting) than simply the number of tree species used in a plantation (Lamb et al. 2005; Young et al. 2005). Planting a higher diversity of trees species does not necessarily lead to higher diversity of regenerating trees in the understory (Butler et al. 2008; Chazdon 2014). Overall, a reference number of tree species that should be reintroduced in large-scale high diversity plantations with a goal of restoring the original biodiversity requires further studies using cost-benefit analysis (Rodrigues et al. 2009).

Reintroducing endangered species may be reasonable, although this approach still needs further study regarding specific population genetic considerations (McKay et al. 2005), and is generally not feasible in most restoration projects (Durigan et al. 2010). When practitioners restoring at large scales use seedlings from non-locally collected seed, the result may be higher diversity of unsuitable species, seedling mortality and endogamy, or even “genetic pollution” (McKay et al. 2005).

Restorations by plantations result in a standard trajectory, predictable for most attributes of structure, richness, and functional guilds, but floristic composition is not predictable (Suganuma and Durigan 2015). Most practitioners consider planting high density of trees in total area a tried-and-true method, but plantations can also be expensive and ecologically insufficient in many environmental contexts (Murcia 1997; Souza and Batista 2004; Sampaio et al. 2007; Rey Benayas et al. 2008) since they still relies on natural processes, for example, the recovery of pollinators (Dixon 2009), seed dispersers, consumers and mycorrhizae (Ruiz-Jaen and Aide 2005; Brudvig 2011; Morrison and Lindell 2012). More than creating vegetative cover, the success of habitat restoration depends on the arrival of these wildlife colonists (Wunderle 1997; Scott et al. 2001; Bowen et al. 2007; Pinotti et al. 2012; Chazdon 2014; Peña-Domene et al. 2014).

When used unnecessarily or inappropriately, plantations on a large scale can actually hinder the recovery processes or redirect it to a state quite different from the previous forest (Holl 2012). Some managers rely on tactics that can rapidly transform the structural components of tropical degraded forests, providing an ephemeral “quick fix” (King and Hobbs 2006) in two or three years, dismissing the necessity for gradual recovery of ecological processes vital to forest structure. As a result, many projects aim toward achieving short-term goals, which may unintentionally inhibit long-term ecosystem restoration (Holl and Cairns 2002). This is especially common for large-scale projects in the Neotropics for which a baseline environmental diagnosis is lacking or, as a result of intentional efforts to increase the profit margin with higher silvicultural inputs and services. Although passive restoration is cheaper and may achieve higher quality restoration than plantings in many cases, “it does not fit an industrial model of production and does not provide corporate profits” (Chazdon 2014, p. 310). Under such policies, it is common to implement expensive “overrestoration” projects, as named by Clewell and McDonald (2009) (Fig. 1).

Plantations still have complex implications that are not well understood for the structure and composition of future forests, landscape, fauna, and genetic diversity (Chazdon 2003, 2014). The high densities of particular tree species in plantation restorations can increase secondary forest productivity but may also slow ecosystem recovery by having too strong influence on successional trajectories (Guariguata and Ostertag 2001; Holl 2007; Holl and Aide 2011). According to Chazdon (2003, 2008a), when millions of seedlings are planted, usually the selection process involves human decision making rather than an evolutionary process. In fact, the issue of whether plantations should be considered a type of tropical forest is contentious (Putz and Redford 2010), and given these limitations, there is a considerable need for more research and new restoration approaches.

Nucleation: a new approach

Tropical forest regeneration in abandoned pastures frequently follows a nucleation model of succession starting around “key microsites” that facilitate wood species recruitment foci that spread and coalesce (Peterson and Carson 2008; Chazdon 2014). The usage of nucleation approach was born from field observations where remnant trees acted as “nurse plants” facilitating a sphere of regeneration over time (Reis et al. 2003; Schlawn and Zahawi 2008; Chazdon 2014). In a review of system patchiness, it was determined that “scattered trees” act as keystone structures capable of increased landscape connectivity and function as restoration nuclei (Manning et al. 2006). *Araucaria* pine trees that establish in Brazilian grasslands can attract bird species known to disperse seeds of forest species (Duarte et al. 2006). Slocum (2001) described similar patterns with the formation of “tree islands” in abandoned pastures from “focal trees” in Costa Rica. Nepstad et al. (1991) noticed that scattered trees, after clearing in Amazonian forest, generated “tree islands” that expand and coalesce over time, as has Janzen (1988) in Costa Rican pastures. Additionally in Costa Rica, the “matrix discontinuity hypothesis” confirmed that rotting logs and steep slopes microsites significantly enhance nucleation (Peterson et al. 2014).

The use of nuclei patches as nurse patches to facilitate restoration has been around since the early 1990s. In 1988, Janzen suggested a “vertebrate-generated forest initiation” through the planting of “nuclear trees”. Nepstad et al. (1991) proposed the planting of “catalyzing trees” or “island-forming trees” in short intervals leading to forest fragments.

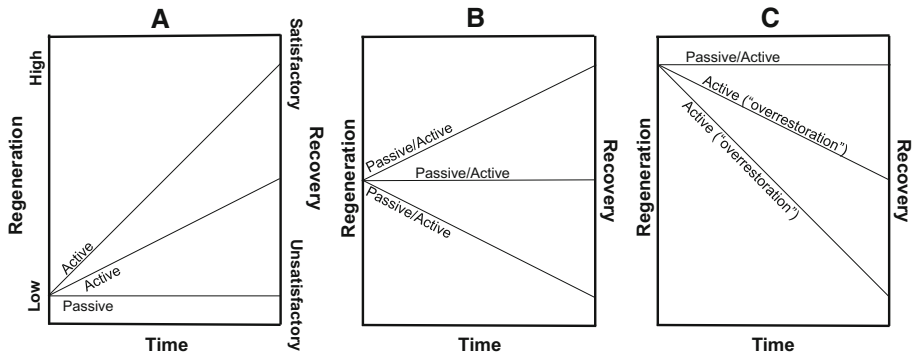


Fig. 1 Possible outcomes of restoration decisions based on regeneration potential of the site. “Satisfactory Recovery” means a return similar or close to the original old-growth forest structure and composition attributes. **a** In a low regeneration condition, where passive restoration may fail and different levels of active restoration may result in a more preferred recovery condition, satisfactory or not. **b** In an intermediate regeneration situation, it is difficult to estimate future trajectories and, to some degree, restoration will be a gamble. **c** In a high regeneration state, any kind of restoration could be effective. However, the use of active restoration techniques with high levels of intervention can present side effects, leading the community to an excessively different pathway and lower degree of natural recovery (“overrestoration”)

In 1997, Wunderle suggested the use of “archipelagos” of small restoration patches or “islands” less than 50 m across scattered within dominant open degraded areas to reduce isolation and promote adequate seed rain. Other authors recommended plantings in “clumps” or “tree islands” to promote spatial heterogeneity, alter soil and microclimate, trap wind-dispersed seeds and serve as perches and cover for disperser animals (Harrington 1999; Robinson and Handel 2000; Zahawi and Augspurger 2006). Rey Benayas et al. (2008) proposed the densely-planted “woodland islets” (tens to hundreds of m²), well-spaced (tens to hundreds of m² apart) occupying 1 % of a field, to increase heterogeneity and biodiversity using an intermediate degree—between passive restoration and plantations—of intervention and consequently costs.

Recently, the nucleation theory (Yarranton and Morrison 1974) has been applied in different Neotropical forests specially in Brazil and Costa Rica (Boaneres and Azevedo 2014), but specifics of methods and justifications differ among these countries. In Brazil, the named “nucleation techniques” take an integrated approach that combine several techniques, including artificial shelters for fauna, artificial perches, seed bank and seed rain sod block nuclei, ground-covering shrub/herbaceous nuclei, and the planting of native trees and bromeliads in dense nuclei (Reis et al. 2003, 2010; Vogel et al. 2015, 2016). Multiple techniques are then applied together in several small nuclei (1–12 m²), which can be applied randomly or in mowed systematic strips in the middle of pastures on large scale (Vogel et al. 2015), producing key microsites that occupies 10–33.3 % of the restoration area (Fig. 2). These nucleation techniques have been recommended and applied by managers, scientists, governmental agencies and forestry companies of Brazil (Ivanauskas et al. 2007; Wuethrich 2007; Rodrigues et al. 2009; Brancalion et al. 2010; Vogel et al. 2015); however, large-scale and long-term data are still needed to evaluate their effectiveness.

In Costa Rica, “islands” of greater size and distance apart have been tested experimentally, where patches of “plantation islands” with 50–100 m² are spaced about 8 m apart and occupy 20 % of the total restoration area (Fink et al. 2009; Cole et al. 2010; Celentano et al. 2011; Holl et al. 2011, 2013; Zahawi et al. 2013). This technique was

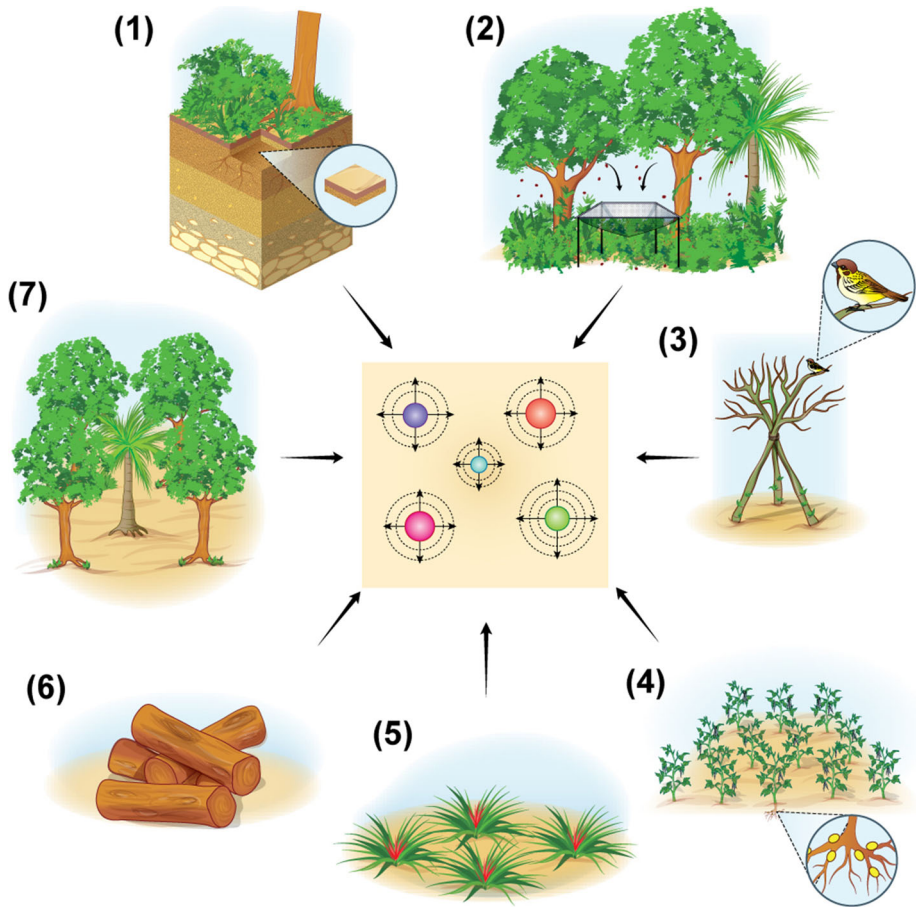


Fig. 2 Brazilian nucleation techniques use the establishment of restoration nuclei of different sizes (represented by *central circular areas*) within a degraded area (*square*) aimed to increase heterogeneity of sites that may interact, irradiate and coalescence along the time. Nucleus types include: 1 Topsoil seed bank (plus litter and edaphic fauna) from closest natural remnants. 2 Seed rain translocation from closet natural remnants: seed traps collect propagules that introduce several life forms. 3 Artificial perches. 4 Cover crop: use of annual legume nodulation plants. 5 Terrestrial tank epiphytes islets. 6 Artificial shelters for animals. 7 Trees islets: planting pioneer trees nuclei that provide shade to central non-pioneer plants

previously tested in Honduras (Zahawi and Augspurger 2006) and recently reviewed and named “applied nucleation” by Corbin and Holl (2012). Although plantations foster greater bird abundance and compositional similarity to old-growth forest than applied nucleation designs (Reid et al. 2014; Vogel et al. 2015), Vogel et al. (2015) showed that Brazilian nucleation techniques facilitated exclusive species with higher richness and abundance (in disagree with Reid et al. 2014). Overall, it is argued that applied nucleation facilitates pollinator visitation and tree recruitment to a similar degree as plantations, but with lower costs (Holl et al. 2013; Lindell and Thurston 2013; Zahawi et al. 2013).

The nucleation approach may assist the natural assembly processes which should govern recovery (Corbin and Holl 2012; Holl et al. 2013; Reis et al. 2010). According to Bechara et al. (2007) Brazilian nucleation techniques were around 30 % cheaper than

plantations, in the same Neotropical site conditions. Anyway, it's a fact that nucleation is gaining momentum as a promising approach to high biodiversity restoration because it is cheaper than establishing tree plantations (Chazdon 2014).

Methods comparison

Various “If you build it, they will come” approaches have failed to support desired assemblies (Brudvig 2011). Clewell and McDonald (2009) stated “ecological restoration is not analogous to civil engineering, where all materials are assembled and all processes are controlled from start to finish”. Technical reclamation, based on engineering and mechanical approaches, can produce monotonous, uniform stands, where structural and functional diversity is reduced compared to passively restored sites (Sampaio et al. 2007; Prach and Hobbs 2008). Needless interventions overwhelm an ecosystem's inherent recovery capacity, deflecting the successional trajectory toward an undesirable altered state or even a “synthetic ecosystem”, comprising conditions and combinations of organisms that never before existed (Odum 1962).

In comparison to larger-scale plantations, some authors hypothesize that nucleation requires more time to reach a desired endpoint, but produces an intermediate “natural” restoration by allowing natural succession processes to dominate the recovery process (Reis et al. 2010; Corbin and Holl 2012; Holl et al. 2013), as we illustrated in Fig. 3.

Comparing diversity outcomes with the various restoration models in a long-term basis in different ecosystems is still a research gap. There are very few controlled experiments with sufficient replication comparing plantation, nucleation and passive restoration. The majority of studies have evaluated the successes of plantations without comparison to other methods in the same site conditions. There is also a lack of studies comparing low and high diversity plantings in the same space and time. In addition, the Brazilian nucleation

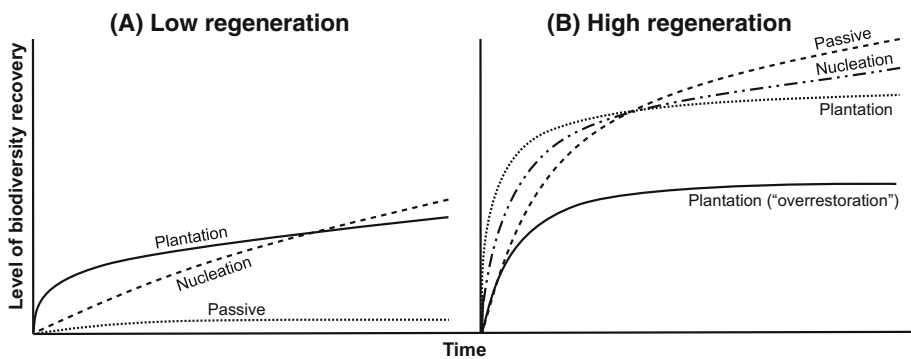


Fig. 3 Hypothetical model comparing different technologies to restore tropical forests. “Level of biodiversity recovery” refers to a return similar or close to the original old-growth forest structure and composition attributes. In highly degraded landscapes and sites (a), where passive restoration would fail to recover a forest, plantations provide recovery of the ecosystem, but nucleation may produce reassembly resulting in forest is more similar to original structure and composition in the long-term. In sites with high regeneration capacity (b), plantations would speed the recovery (especially in its understory), but could alter the natural succession trajectory, resulting in lower overall system natural recovery. In the same scenario, nucleation and passive restoration in the long term would result in higher system recovery. Under passive restoration, system recovery may take longer; therefore, the better choice for a practitioner will depend on project goals and budget

techniques still have no experimental data published in international scientific magazines, although these techniques are already well-known in the national academic circles, laws and commercial fields. Applied nucleation studies have not been evaluated in different ecosystems, and may be less effective in temperate ecosystems where seed dispersal by vertebrates is less important than in tropical ecosystems.

The oldest controlled research plantations for biodiversity restoration in Neotropical forests are now about 30 year-old, and are still far from the 60–100 years that is necessary to reestablish pre-disturbance species composition. Nucleation experiments are much younger, and on average only 5–10 years-old. While we cannot wait for long-term results to begin restoration, government and international institutions should plan to establish permanent demonstration projects that can be used to compare techniques long-term in the diverse ecosystems of tropical countries.

Conclusion

Nucleation presents an intermediate level between passive and plantation methods, considering inputs, costs and divergence with natural processes; but also in recovery speed, predictability and resistance. While the choice of restoration method will depend on site characteristics and project goals, we suggest considering both plantation and lower costs nucleation strategies. An integrated approach, e.g., islands of nucleation inside a plantation, or vice versa, to have both high and rapid plantation productivity but also the natural functions associated with nucleation would increase the likelihood of developing the composition and diversity trajectory most widely desired in Neotropical conservation efforts.

Acknowledgments We are especially grateful to Karen Holl who greatly improved the paper. We thank Richard Hobbs, Alexandre Buttler, Lauren Hallett, Dylan Chapple, Joan Dudney and Rapichan Phurisamban for helpful comments. F.C. Bechara Postdoctoral Scholarship was supported by CAPES (Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior; “Programa Ciência sem Fronteiras” #2551/13-6) and Fundação Araucária de Apoio Científico e Tecnológico do Paraná. E. Farrer was supported by a USDA-NIFA Postdoctoral Fellowship #2012-67012-19840. L. Larios was supported by the NSF Postdoctoral Research Fellowship in Biology Award #1309014, and P. Mariotte by the Swiss NSF Advanced Postdoctoral Fellowship #PBELP 3146538.

References

- Aide TM, Zimmerman JK, Pascarella JB, Rivera L, Marcano-Vega H (2000) Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restor Ecol* 8:328–338
- Arroyo-Mora JP, Sánchez-Azofeifa GA, Rivard B, Calvo JC, Janzen DH (2005) Dynamics in landscape structure and composition for the Chorotega region, Costa Rica from 1960 to 2000. *Agric Ecosyst Environ* 106:27–39
- Asner GP, Rudel TK, Aide TM, Defries R, Emerson R (2009) A contemporary assessment of change in humid tropical forests. *Conserv Biol* 23:1386–1395
- Bechara FC, Campos Filho EM, Barretto KD, Gabriel VA, Antunes AZ, Reis A (2007) Unidades demonstrativas de restauração ecológica através de técnicas nucleadoras de biodiversidade. *Rev Bras Biocienc* 5:9–11 (in Portuguese)
- Boanares D, Azevedo CS (2014) The use of nucleation techniques to restore the environment: a bibliometric analysis. *Braz J Nat Conserv* 12:93–98
- Bowen EM, McAlpine CA, House APN, Smith GC (2007) Regrowth forests on abandoned agricultural land: a review of their habitat values for recovering forest fauna. *Biol Conserv* 140:273–296

- Brancalion PHS, Rodrigues RR, Gandolfi S et al (2010) Legal instruments can enhance high-diversity tropical forest restoration. *Rev Árvore* 34:455–470
- Brook BW, Bradshaw CJA, Koh LP, Sodhi NS (2006) Momentum drives the crash: mass extinction in the tropics. *Biotropica* 38:302–305
- Brown S, Lugo AE (1990) Tropical secondary forests. *J Trop Ecol* 6:1–32
- Brudvig LA (2011) The restoration of biodiversity: where has research been and where does it need to go? *Am J Bot* 98:549–558
- Bullock JM, Aronson J, Newton AC, Pywell RF, Rey-Benayas JM (2011) Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends Ecol Evol* 26:541–549
- Bush MB, Colinvaux PA (1994) Tropical forest disturbance: paleoecological records from Darien, Panama. *Ecology* 75:1761–1768
- Butler R, Montagnini F, Arroyo P (2008) Woody understory plant diversity in pure and mixed native tree plantations at La Selva Biological Station, Costa Rica. *For Ecol Manag* 255:2251–2263
- Carnevale N, Montagnini F (2002) Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species. *For Ecol Manag* 163:217–227
- Carpenter SR, Mooney HA, Agard J et al (2009) Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. *Proc Natl Acad Sci USA* 106:1305–1312
- Celentano D, Zahawi RA, Finegan B et al (2011) Litterfall dynamics under different tropical forest restoration strategies in Costa Rica. *Biotropica* 43:279–287
- Chapman CA, Chapman LJ (1999) Forest restoration in abandoned agricultural land: a case study from East Africa. *Conserv Biol* 13:1301–1311
- Chazdon RL (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect Plant Ecol Evol Syst* 6:51–71
- Chazdon RL (2008a) Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* 320:1458–1460
- Chazdon RL (2008b) Chance and determinism in tropical forest succession. In: Carson WP, Schnitzer SA (eds) *Tropical forest community ecology*. Wiley-Blackwell, Oxford, pp 384–408
- Chazdon RL (2012) Tropical forest regeneration. *Bol Mus Para Emílio Goeldi Cienc Nat* 7:195–218
- Chazdon RL (2013) Making tropical succession and landscape reforestation successful. *J Sustain For* 32:649–658
- Chazdon RL (2014) *Second growth: the promise of tropical forest regeneration in an age of deforestation*. University of Chicago Press, Chicago
- Clewell A, McDonald T (2009) Relevance of natural recovery to ecological restoration. *Ecol Restor* 27:122–124
- Cole RJ, Holl KD, Zahawi RA (2010) Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. *Ecol Appl* 20:1255–1269
- Corbin JD, Holl KD (2012) Applied nucleation as a forest restoration strategy. *For Ecol Manag* 265:37–64
- Corlett RT (1995) Tropical secondary forests. *Prog Phys Geogr* 19:159–172
- Cusack D, Montagnini F (2004) The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. *For Ecol Manag* 188:1–15
- Dent DH, DeWalt SJ, Denslow JS (2012) Secondary forests of central Panama increase in similarity to old-growth forest over time in shade tolerance but not species composition. *J Veg Sci* 24:530–542
- Díaz S, Fargione J, Chapin FS III, Tilman D (2006) Biodiversity loss threatens human well-being. *PLoS Biol* 4:1300–1305
- Dixon KW (2009) Pollination and restoration. *Science* 325:571–573
- Duarte LS, Dos-Santos MMG, Hartz SM, Pillar VD (2006) Role of nurse plants in *Araucaria* forest expansion over grassland in south Brazil. *Austral Ecol* 31:520–528
- Durigan G, Engel VL, Torezan JM et al (2010) Legal rules for ecological restoration: an additional barrier to hinder the success of initiatives? *Rev Árvore* 34:471–485
- Elliott S, Blakesley D, Hardwick K (2013) *Restoring tropical forests: a practical guide*. Royal Botanical Garden, Kew
- FAO—Food and Agriculture Organization of the United Nations (2010) *Global forest resources assessment*. FAO, Rome
- Fine PVA, Ree RH, Burnham RJ (2008) The disparity in tree species richness among tropical, temperate and boreal biomes: the geographic area and age hypothesis. In: Carson WP, Schnitzer SA (eds) *Tropical forest community ecology*. Wiley-Blackwell, Oxford, pp 31–45
- Fink RD, Lindell CA, Morrison EB, Zahawi RA, Holl KD (2009) Patch size and tree species influence the number and duration of bird visits in forest restoration plots in southern Costa Rica. *Restor Ecol* 17:479–486
- Gentry AH (1988) Tree species richness of upper Amazonian forests. *Proc Natl Acad Sci USA* 85:156–159

- Gentry AH, Dodson C (1987) Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* 19:149–156
- Gibson L, Lee TM, Koh LP et al (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478:378–383
- Goldsmith GR, Comita LS, Chua SC (2011) Evidence for arrested succession within a tropical forest fragment in Singapore. *J Trop Ecol* 27:323–326
- Gómez-Pompa A, Vázquez-Yanes C, Guevara S (1972) The tropical rain forest: a nonrenewable resource. *Science* 177:762–765
- Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *For Ecol Manag* 148:185–206
- Guariguata MR, Rheingans R, Montagnini F (1995) Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. *Restor Ecol* 3:252–261
- Harrington CA (1999) Forests planted for ecosystem restoration or conservation. *New For* 17:175–190
- Hobbs RJ, Norton DA (1996) Towards a conceptual framework for restoration ecology. *Restor Ecol* 4:93–110
- Hobbs RJ, Arico S, Aronson J et al (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob Ecol Biogeogr* 15:1–7
- Holl KD (2007) Old field vegetation succession in the Neotropics. In: Hobbs RJ, Cramer VA (eds) *Old fields: dynamics and restoration of abandoned farmland*. Island Press, Washington DC, pp 93–117
- Holl KD (2012) Tropical forest restoration. In: van Andel J, Aronson J (eds) *Restoration ecology*. Blackwell Publishing, Malden, pp 103–114
- Holl KD, Aide TM (2011) When and where to actively restore ecosystems? *For Ecol Manag* 261:1558–1563
- Holl KD, Cairns J Jr (2002) Monitoring and appraisal. In: Perrow MR, Davy AJ (eds) *Handbook of ecological restoration*. Cambridge University Press, Cambridge, pp 411–432
- Holl KD, Loik ME, Lin EHV, Samuels IA (2000) Tropical Montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restor Ecol* 8:339–349
- Holl KD, Zahawi RA, Cole RJ, Ostertag R, Cordell S (2011) Planting seedlings in tree islands versus plantations as a large-scale tropical forest restoration strategy. *Restor Ecol* 19:470–479
- Holl KD, Stout VM, Reid JL, Zahawi RA (2013) Testing heterogeneity-diversity relationships in tropical forest restoration. *Oecologia* 173:569–578
- Hooper E, Legendre P, Condit R (2005) Barriers to forest regeneration of deforested and abandoned land in Panama. *J Appl Ecol* 42:1165–1174
- Ivanauskas NM, Rodrigues RR, Souza VC (2007) The importance of regional floristic diversity for the forest restoration successfulness. In: Rodrigues RR (ed) *High diversity forest restoration in degraded areas: methods and projects in Brazil*. Nova Science Publishers, New York, pp 63–77
- Janzen D (1988) Management of habitat fragments in a tropical dry forest: growth. *Ann Mo Bot Gard* 75:105–116
- Kaimowitz D, Sheil D (2007) Conserving what and for whom? Why conservation should help meet basic human needs in the tropics. *Biotropica* 39:567–574
- King EG, Hobbs RJ (2006) Identifying linkages among conceptual models of ecosystem degradation and restoration: towards an integrative framework. *Restor Ecol* 14:369–378
- Klein RM (1980) Ecologia da flora e vegetação do Vale do Itajaí. *Sellowia* 32:9–389 (in Portuguese)
- Lamb D (2011) *Regreening the Bare Hills: tropical forest restoration in the Asia-Pacific region*. Springer, Dordrecht
- Lamb D, Erskine PD, Parrotta JA (2005) Restoration of degraded tropical forest landscapes. *Science* 310:1628–1632
- Laurance WF, Nascimento HEM, Laurance SG et al (2006) Rain forest fragmentation and the proliferation of successional trees. *Ecology* 87:469–482
- Lepsch-Cunha N, Gascon C, Kageyama PY (2001) The genetics of rare tropical forests: implications for conservation of a demographically heterogeneous group. In: Bierregaard RO, Gascon C, Lovejoy TE, Mesquita RCG (eds) *Lessons from Amazônia: the ecology and conservation of a fragmented forest*. Yale University Press, New Haven, pp 79–95
- Letcher SG, Chazdon RL (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in Northeastern Costa Rica. *Biotropica* 41:608–617
- Liebsch D, Marques MCM, Goldenberg R (2008) How long does the Atlantic rainforest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. *Biol Conserv* 141:1717–1725
- Lindell CA, Thurston GM (2013) Bird pollinator visitation is equivalent in island and plantation planting designs in tropical forest restoration sites. *Sustainability* 5:1177–1187

- Lugo AE (1992) Comparison of tropical tree plantations with secondary forests of similar age. *Ecol Monogr* 62:1–41
- Manning AD, Fischer J, Lindenmayer DB (2006) Scattered trees are keystone structures—implications for conservation. *Biol Conserv* 132:311–321
- Marín-Spiotta E, Ostertag R, Silver WL (2007) Long-term patterns in tropical reforestation: plant community composition and aboveground biomass accumulation. *Ecol Appl* 17:828–839
- Martínez-Garza C, Howe HF (2003) Restoring tropical diversity: beating the time tax on species loss. *J Appl Ecol* 40:423–429
- McKay JK, Christian CE, Harrison S, Rice KJ (2005) How local is local? A review of practical and conceptual issues in the genetics of restoration. *Restor Ecol* 13:432–440
- Montagnini F (2001) Strategies for the recovery of degraded ecosystems: experiences from Latin America. *Interciencia* 26:498–503
- Morrison EB, Lindell CA (2012) Birds and bats reduce insect biomass and leaf damage in tropical forest restoration sites. *Ecol Appl* 22:1526–1534
- Mouillot D, Bellwood DR, Baraloto C et al (2013) Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biol* 11:1–11
- Murcia C (1997) Evaluation of Andean alder as a catalyst for the recovery of tropical cloud forests in Colombia. *For Ecol Manag* 99:163–170
- Nepstad DC, Uhl C, Serrão EAS (1991) Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. *Ambio* 20:248–255
- Norden N, Chazdon RL, Chao A, Jiang Y, Vilchez-Alvarado B (2009) Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecol Lett* 12:385–394
- Odum HT (1962) Man and the ecosystem. *Conn Agric Exp Stn Bull* 652:57–75. <http://www.ct.gov/caes/lib/caes/documents/publications/bulletins/b652.pdf>. Accessed 27 Mar 2016
- Ortega-Pieck A, López-Barrera F, Ramírez-Marcial N, García-Franco JG (2011) Early seedling establishment of two tropical montane cloud forest tree species: the role of native and exotic grasses. *For Ecol Manag* 261:1336–1343
- Palmer MA, Ambrose RF, Poff NL (1997) Ecological theory and community. *Restor Ecol* 5:291–300
- Pardini R, Bueno AD, Gardner TA, Prado PI, Metzger JP (2010) Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. *PLoS One* 5:1–10
- Parrotta JA, Turnbull JW, Jones N (1997) Catalyzing native forest regeneration on degraded tropical lands. *For Ecol Manag* 99:1–7
- Pascarella JB, Aide TM, Serrano MI, Zimmerman JK (2000) Land-use history and forest regeneration in the Cayey Mountains, Puerto Rico. *Ecosystems* 3:217–228
- Peña-Domene M, Martínez-Garza C, Palmas-Pérez S, Rivas-Alonso E, Howe HF (2014) Roles of birds and bats in early tropical-forest restoration. *PLoS One* 9:1–6
- Peterson CJ, Carson WP (2008) Processes constraining woody species succession on abandoned pastures in the tropics: on the relevance of temperate models of succession. In: Carson WP, Schnitzer SA (eds) *Tropical forest community ecology*. Wiley-Blackwell, Oxford, pp 366–383
- Peterson CJ, Dosch JJ, Carson WP (2014) Pasture succession in the neotropics: extending the nucleation hypothesis into a matrix discontinuity hypothesis. *Oecologia* 175:1325–1335
- Pinotti BT, Pagotto CP, Pardini R (2012) Habitat structure and food resources for wildlife across successional stages in a tropical forest. *For Ecol Manag* 283:119–127
- Pitman NCA, Cerón CE, Reyes CI, Thurber M, Arellano J (2005) Catastrophic natural origin of a species-poor tree community in the world's richest forest. *J Trop Ecol* 21:559–568
- Potts MD, Ashton PS, Kaufman LS, Plotkin JB (2002) Habitat patterns in tropical rain forests: a comparison of 105 plots in Northwest Borneo. *Ecology* 83:2782–2797
- Prach K, Hobbs RJ (2008) Spontaneous succession versus technical reclamation in the restoration of disturbed sites. *Restor Ecol* 16:363–366
- Putz FE, Redford KH (2010) The importance of defining 'forest': tropical forest degradation, deforestation, long-term phase shifts, and further transitions. *Biotropica* 42:10–20
- Reid JL, Mendenhall CD, Rosales JA, Zahawi RA, Holl KD (2014) Landscape context mediates avian habitat choice in tropical forest restoration. *PLoS One* 9:1–8
- Reis A, Bechara FC, Espindola MB, Vieira NK, Souza LL (2003) Restoration of damaged land areas: using nucleation to improve successional processes. *Nat Conserv* 1:85–92
- Reis A, Bechara FC, Tres DR (2010) Nucleation in tropical ecological restoration. *Sci Agric* 67:244–250
- Rey Benayas JM, Bullock JM, Newton AC (2008) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Front Ecol Environ* 6:329–336
- Rey Benayas JM, Newton AC, Diaz A, Bullock JM (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325:1121–1124

- Robinson GR, Handel SN (2000) Directing spatial patterns of recruitment during an experimental urban woodland reclamation. *Ecol Appl* 10:174–188
- Rodrigues RR, Lima RAF, Gandolfi S, Nave AG (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biol Conserv* 142:1242–1251
- Rodrigues RR, Gandolfi S, Nave AG et al (2011) Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. *For Ecol Manag* 261:1605–1613
- Ruiz-Jaen MC, Aide TM (2005) Restoration success: how is it being measured? *Restor Ecol* 13:569–577
- Saldarriaga JG, West DC, Tharp ML, Uhl C (1988) Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *J Ecol* 76:938–958
- Sampaio AB, Holl KD, Scariot A (2007) Does restoration enhance regeneration of seasonal deciduous forests in pastures in central Brazil? *Restor Ecol* 15:462–471
- Schilling AC, Batista JLF (2008) Species accumulation curve and sampling sufficiency in tropical forests. *Rev Bras Bot* 31:179–187
- Schlawin JR, Zahawi RA (2008) ‘Nucleating’ succession in recovering Neotropical wet forests: the legacy of remnant trees. *J Veg Sci* 19:485–492
- Scott TA, Wehtje W, Wehtje M (2001) The need for strategic planning in passive restoration of wildlife populations. *Restor Ecol* 9:262–271
- Sim JWS, Tan HTW, Turner IM (1992) Adinandra belukar: an anthropogenic heath forest in Singapore. *Vegetatio* 102:125–137
- Siminski A, Fantini AC, Guries RP, Ruschel AR, Reis MR (2011) Secondary forest succession in the Mata Atlântica, Brazil: floristic and phytosociological trends. *ISRN Ecol* 2011:1–19
- Slocum MG (2001) How tree species differ as recruitment foci in a tropical pasture. *Ecology* 82:2547–2559
- Souza FM, Batista JLF (2004) Restoration of seasonal semideciduous forests in Brazil: influence of age and restoration design on forest structure. *For Ecol Manag* 191:185–200
- Stanturf JA, Palik BJ, Dumroese RK (2014) Contemporary forest restoration: a review emphasizing function. *For Ecol Manag* 331:292–323
- Suding KN (2011) Toward an era of restoration in Ecology: successes, failures, and opportunities ahead. *Annu Rev Ecol Evol Syst* 42:465–487
- Suding KN, Hobbs RJ (2009) Threshold models in restoration and conservation: a developing framework. *Trends Ecol Evol* 24:271–279
- Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends Ecol Evol* 19:46–53
- Suganuma MS, Durigan G (2015) Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. *Restor Ecol* 23:238–251
- Terborgh J (1992) Diversity and the tropical rain forest. Scientific American Library, New York
- Thomas WW, Carvalho AMV, Amorim AMA, Hanks JG, Santos TS (2008) Diversity of woody plants in the Atlantic coastal forest of Southern Bahia, Brazil. *Mem NY Bot Gard* 100:21–66
- Uhl C, Buschbachert R, Serrao EAS (1988) Abandoned pastures in eastern Amazônia. I. Patterns of plant succession. *J Ecol* 76:663–681
- Vogel HF, Campos JB, Bechara FC (2015) Early bird assemblages under different subtropical forest restoration strategies in Brazil: passive, nucleation and high diversity plantation. *Trop Conserv Sci* 8:912–939
- Vogel HF, Spotswood E, Campos JB, Bechara FC (2016) Annual changes in a bird assembly on artificial perches: implications for ecological restoration in a subtropical agroecosystem. *Biota Neotrop* 16:1–9
- Wuethrich B (2007) Reconstructing Brazil’s Atlantic rainforest. *Science* 315:1070–1072
- Wunderle JM Jr (1997) The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *For Ecol Manag* 99:223–235
- Yarranton GA, Morrison RG (1974) Spatial dynamics of a primary succession: nucleation. *J Ecol* 62:417–428
- Young TP, Chase JM, Huddleston RT (2001) Community succession and assembly: comparing, contrasting and combining paradigms in the context of ecological restoration. *Ecol Restor* 19:5–18
- Young TP, Petersen DA, Clary JJ (2005) The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecol Lett* 8:662–673
- Zahawi RA, Augspurger CK (2006) Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. *Ecol Appl* 16:464–478
- Zahawi RA, Holl KD, Cole RJ, Reid JL (2013) Testing applied nucleation as a strategy to facilitate tropical forest recovery. *J Appl Ecol* 50:88–96