Title
Riparian forest recovery following a decade of cattle exclusion in the Colombian Andes

Authors
Calle, Alicia
Holl, Karen D

Publication Date
2019-11-01

DOI
10.1016/j.foreco.2019.117563

Peer reviewed

Forest Ecology and Management 452 (2019) 117563

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Riparian forest recovery following a decade of cattle exclusion in the Colombian Andes

Alicia Calle[a,b,*], Karen D. Holl[a]

[a] Environmental Studies Department, University of California Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA
[b] Fundación CIPAV – Centro para la Investigación en Sistemas Sostenibles de Producción Agropecuaria, Cali, Colombia

ARTICLE INFO

Keywords:
Forest and landscape restoration
Forest recovery
Human-managed landscapes
Silvopastoral systems
Tropical forest

ABSTRACT

To meet their large-scale forest and landscape restoration targets, countries must find ways to accommodate areas for conservation alongside agricultural production. In some pasture-dominated regions of Latin America, intensive silvopastoral systems (SPS) are being promoted to increase cattle productivity on certain lands while facilitating the removal of cattle from marginal areas for forest restoration. However, the recovery of these forests and their contribution to the overall conservation value of the landscape has not been assessed rigorously. We evaluated forest structure and composition in 20 sites in a region of the Colombian Andes where a decade ago farmers transitioned to SPS and fenced off riparian areas to enable forest recovery. We compared these restored forests to a reference model based on the remaining riparian forest across the region, all of which has been subjected to human management. We found that woody species richness was higher in restored than in reference forests, and the proportion of large-seeded, later successional, animal-dispersed species were similar in both forest types. Whereas we found a similar suite of dominant tree species in restored and reference forest, *Guadua angustifolia*, a native giant bamboo was more abundant in the reference forests due to human management. Total tree basal area was higher in restored forests due to a small number of very large trees likely present in the pastures at the time of site protection. These findings highlight (1) the potential for recovery of diverse forests in riparian sites despite previous grazing use and (2) the role of remnant trees in facilitating natural succession. Overall, rapid forest recovery with minimal intervention in previously farmed lands is good news for conservation in a region that still harbors significant biodiversity despite high levels of fragmentation and the influence of human management.

1. Introduction

In response to large-scale international initiatives such as the Bonn Challenge (http://www.bonnchallenge.org), many tropical countries have made ambitious forest and landscape restoration commitments, pledging to restore multifunctional landscapes for both ecological integrity and human well-being (Mansourian and Vallauri, 2005; IUCN and WRI, 2014). However, in regions where people rely largely on agriculture for their livelihoods, sustaining food production while simultaneously conserving biodiversity and maintaining the flow of ecosystem services is a challenge (Bullock et al., 2011; Rey Benayas and Bullock, 2012). Some management practices, such as the addition of live fences, retention of trees in pastures, and use of agroforestry and silvopastoral systems (SPS), can enhance the delivery of key services and increase the conservation value of agricultural landscapes without compromising production (Harvey et al., 2008; Perfecto and Vandermeer, 2010; Mendenhall et al., 2014). Payments for environmental services and other incentive schemes are increasingly being used to promote the adoption of such land management practices. Nonetheless, the long-term conservation impacts of such programs have rarely been evaluated (Pattanayak et al., 2010; Salzman et al., 2018).

There is no question that biodiversity conservation benefits are maximized where large areas of primary and secondary forest are protected (Chazdon et al., 2009; Lira et al., 2012; Gilroy et al., 2014), but the reality of many agricultural regions is one of highly fragmented landscapes with only small forest patches, often heavily impacted by human activities and surrounded by open areas. In this context, restoring secondary forests is important to reconnect existing fragments and to facilitate species movement and persistence in the landscape (Chazdon et al., 2009; Newmark et al., 2017). In particular, riparian forests have substantial conservation benefits relative to their small footprint. They contribute to stream water quality by retaining

* Corresponding author at: Environmental Studies Department, University of California Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA.
E-mail address: lcalle@ucsc.edu (A. Calle).

https://doi.org/10.1016/j.foreco.2019.117563
Received 5 August 2019; Received in revised form 16 August 2019; Accepted 19 August 2019

sediments and filtering contaminants; provide habitat, resources, and corridors for the movement of many species; and often harbor species not found elsewhere in the landscape (Sabo et al., 2005; Gillies and St. Clair, 2008; Lees and Peres, 2008; Dybala et al., 2019).

Whereas the conservation value of remnant riparian forests in fragmented landscapes is well documented, few studies have evaluated how these forests recover on abandoned agricultural lands over time, and what their importance is for conservation. Suganuma et al. (2014) studied a chronosequence (4–53 years) of 26 riparian forests undergoing restoration in the Brazilian Atlantic Forest and concluded that time is the key factor determining the extent of recovery. Forest structure is the first attribute to be regained, triggering successional processes that eventually lead to the recovery of species richness over several decades (Liebsch et al., 2008; Norden et al., 2009; Lebrija-Trejos et al., 2010; Dent et al., 2013; Suganuma and Durigan, 2015). Initial site conditions such as dense grass cover or the presence of remnant trees, which are often the legacy of previous agricultural uses, play an important role during these early stages and may explain the highly variable rates of recovery across sites (Meli et al., 2015; Holl et al., 2018). Recovery of floristic composition, on the other hand, is unpredictable (Liebsch et al., 2008; Arroyo-Rodríguez et al., 2013; Dent et al., 2013; Suganuma and Durigan, 2015), and particular functional groups such as large-seeded or shade-tolerant species may be underrepresented or entirely missing (Liebsch et al., 2008; Arroyo-Rodríguez et al., 2013; Santo-Silva et al., 2013; Holl et al., 2017), thereby compromising the conservation value of these forests.

Additionally, in many human-managed landscapes the absence of undisturbed forests, the loss or proliferation of forest species for cultural reasons, and the lack of historical data can make it impossible to identify a minimally degraded analogue ecosystem that serves as benchmark to evaluate forest restoration progress. In such cases, acknowledging that pre-degradation conditions are no longer attainable and defining a reference model based on the co-evolution of plants, animals and humans under past, present and future environmental conditions may be the only option (Higgs et al., 2014; McDonald et al., 2016). Regardless, defining a reference model at the outset is crucial to evaluate recovery following an intervention (Aronson et al., 1995; McDonald et al., 2016), as long as its limitations are acknowledged.

The goal of this study was to evaluate the conservation value of regenerating riparian forests in a highly biodiverse but intensively managed agricultural landscape. We measured forest recovery in 20 riparian sites permanently retired from use for cattle grazing over a decade ago in the Colombian Andes. A spatial analysis of the study region (Calle, 2019) shows significant gains in total tree cover on these farms following the implementation of silvopastoral practices. Here we compare forest structure and composition in the restored sites to an earlier dataset of 88 secondary riparian forest fragments in this region. We anticipated that relative to the remnant fragments, restored riparian forests would have higher stem density, lower basal area, lower species richness, and a species assemblage dominated by pioneer, small-seeded, wind-dispersed species.

2. Methods

2.1. Study site

We conducted this study in the La Vieja River watershed, which spans the states of Quindío and Valle del Cauca on the western slope of Colombia's central cordillera (Fig. 1). Study sites are located on gently to steep undulating terrain ranging in altitude from 950 and 1400 m.a.s.l., within the Tropical Premontane Moist and Dry Forest life zones (Espinal, 1977). Mean annual temperature is 21 °C and mean precipitation is 1750 mm distributed bimodally, with peaks in April and October. Most of the original forest cover was cleared in recent decades, and only sparse forest fragments remain, most of them in riparian areas and none of them free of human influence. Today the region is a densely populated agricultural mosaic of cash crops (e.g., coffee, plantain, citrus) and primarily cattle pastures, which occupy 33% of the total area (DANE, 2014). Pastures usually consist of monocultures of exotic grasses with < 5% tree cover, managed with fertilizers and herbicides (Giraldo et al., 2011). Nevertheless, the region is part of the tropical Andes biodiversity hotspot known for its extraordinary biodiversity and endemism and high risk of species extinction (Myers et al., 2000; Brooks et al., 2002).

From 2003 to 2008, the Center for Research in Sustainable Agricultural Production Systems (CIPAV) implemented a project to promote the adoption of silvopastoral practices in 104 cattle farms across this region (World Bank, 2008). The project paid farmers to implement management practices and land use changes that supported biodiversity and/or carbon sequestration. While the new systems and practices aimed to increase productivity in the best grazing areas, farmers were also encouraged to remove cattle from the less productive steep slopes and from riparian areas considered critical for conservation, and to fence them off permanently to eliminate grazing and allow forest recovery. However, riparian area protection was entirely voluntary and farmers were not obliged to keep protections in place during or after the project. At the time of initial site protection, conditions varied by farm from 100% pasture cover, pasture with some herbaceous cover or early successional vegetation, to pasture with scattered remnant trees or occasionally a sparse canopy. Where a narrow riparian forest already existed, farmers moved the fence to expand the area under protection. Farmers used different approaches to restore the newly fenced sites: some planted fast-growing species and controlled pasture growth for a few months initially, but more often they relied entirely on natural regeneration. Over the years, riparian forest management varied by farm, from continuous protection with well-maintained fences to a more hands-off approach with less strict site supervision.

Based on monitoring data from the silvopastoral project, Google Earth images and farm visits, we identified sites where riparian areas had been initially protected during the project (2003–2008) and remained protected in 2017. Only sites with no signs of ongoing or recent grazing (e.g., fence in good condition and presence of early regeneration) were included, although isolated incidents of cattle breaking into a plot or occasional tree harvesting cannot be ruled out in the context of an actively farmed landscape. The final sample consisted of 20 protected riparian forests (hereafter 'restored') located on 16 cattle farms; all forests were ≥100 m long and ≥15 m wide, and were separated by ≥100 m.

2.2. Sampling design

We sampled vegetation in the restored riparian forests in 2016–2017, 10–14 years after the sites were initially protected from grazing. At each site we established one 100 × 10 m (0.1 ha) plot running parallel and immediately adjacent to the water, where we measured the diameter of all trees ≥ 2.5 cm DBH (hereafter 'restored'), and the height of all tree seedlings ≤2.5 cm DBH and ≥10 cm tall (hereafter 'restored seedlings'). We excluded one species, *Guadua angustifolia* (giant bamboo), from the seedling counts because it is usually planted by farmers rather than dispersed naturally and mostly propagates vegetatively. In two cases the vegetation became impassable so we divided the plot and continued sampling further downstream. We recorded average canopy cover every 10 m by taking densiometer measurements in four directions and recorded ground cover every 4 m using the point-intercept method.

As a reference model for comparison, we used data from 88 riparian forest plots gathered in the mid-2000s by another team who used the same methods to sample in the same municipalities across the same altitudinal range (Calle and Méndez, 2009). Their dataset included only trees ≥ 2.5 cm DBH (hereafter 'reference'), but not seedlings < 2.5 cm. These data were collected specifically to serve as a reference model for future assessments of riparian forest recovery in the region. The sample

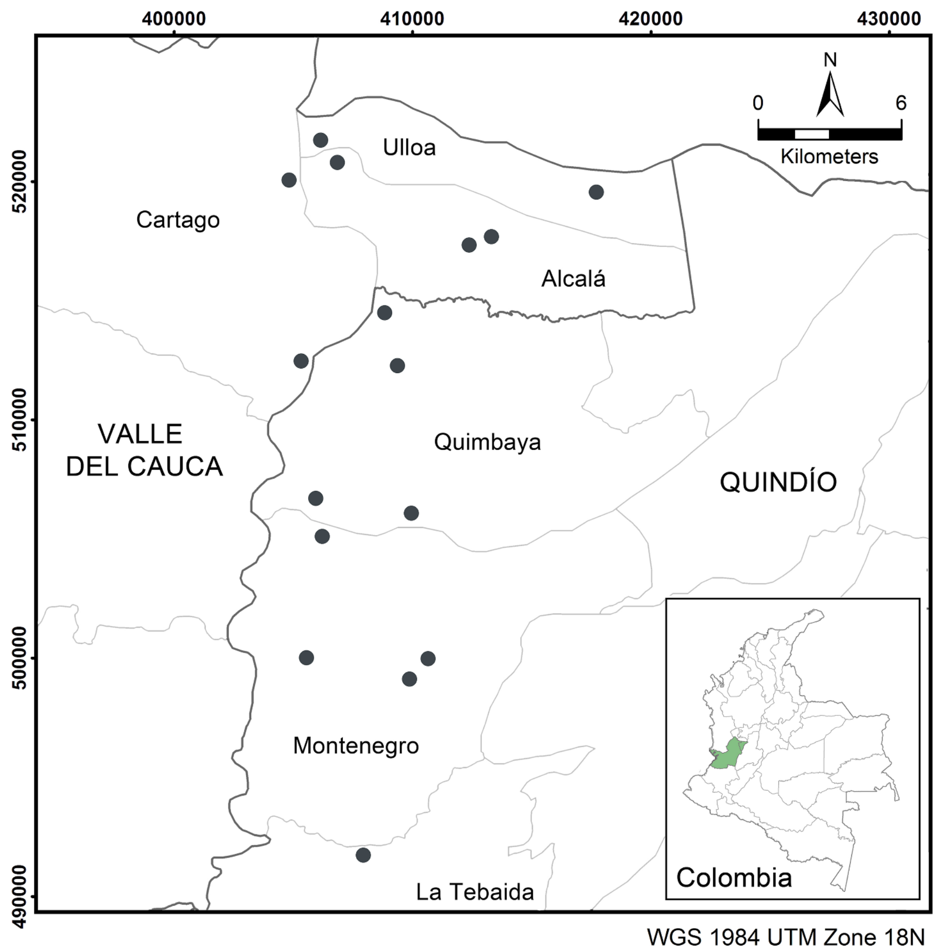

Fig. 1. Location of the 16 farms where 20 protected riparian sites were sampled in the states of Quindío and Valle del Cauca, Colombia.

consisted of riparian plots located on private farms, all of which had a closed canopy and no signs of recent logging or grazing at the time of sampling, but likely had a history of previous disturbance or management (Calle and Méndez, 2009). Given the absence of undisturbed riparian forests or historical data about these forests, this dataset represents the most intact reference system available for a landscape under intense human influence.

2.3. Data analysis

We used t-tests to compare structural attributes (i.e., tree density and basal area) in reference and restored forests, with and without including the dominant species, *G. angustifolia*. When needed, we used a natural-log transformation to meet the assumption of normality and homoscedasticity.

To compare species dominance in the overstory of reference and restored plots, we calculated the Importance Value Index (IVI), an average of relative tree density, frequency and basal area. To compare species richness between forest types, we created sample-based rarefaction and extrapolation curves and plotted the 95% confidence intervals (iNEXT v. 2.0.18; cran.r-project.org/packages/ iNEXT) for the reference, restored and restored seedling plots. Curves were based on 50 randomized bootstrap replications, and extrapolations were based on the Chao estimator (Gotelli and Chao, 2013).

To visualize similarities in tree species composition between reference and restored overstories, we used non-metric multidimensional scaling (NMDS). We tested for differences among group centroids (means) using permutational analysis of variance (PERMANOVA) (vegan v.2.3–2; cran.r -project.org/packages/vegan). We used Bray-Curtis and Morisita-Horn (abundance-based) distance with similar results, and we report the latter. Species for which we recorded only one individual in the total sample were removed from this analysis.

An expert botanist classified each species by seed size (< 5 mm, 5–10 mm, > 10 mm), primary dispersal mode (abiotic vs. vertebrate), successional stage (pioneer vs. late), and threat status (not threatened vs. threatened —local, regional or International Union for the Conservation of Nature (IUCN) threat). We used Chi-squared tests to compare the proportions of species belonging to each of these groups in the reference, restored and restored seedling plots. We also compared the proportion of individuals of these groups in the reference and restored plots.

3. Results

3.1. Overview

We recorded an average of 1305 trees and 2600 seedlings ha^{-1} in the restored plots, whereas there were an average of 1928 ha^{-1} trees in the reference plots. The total IVI for the 20 most important tree species was similar in reference (81%) and restored forests (72%), and 13 of these species were shared by both forest types (Table 1). *Guadua angustifolia* was by far the dominant canopy species in both forest types, but its IVI in the reference plots was more than twice (54%) that of restored sites (25%). The next most important species included *Cupania americana, Cecropia angustifolia, Cinnamomum triplinerve, Croton magdalenensis* and other typical early successional trees, as well as *Inga edulis* and *Erythrina poepiggiana*, which are commonly planted for coffee shade (Table 1). Excluding *G. angustifolia*, the remaining 19 most

Table 1
Importance Value Index (IVI) expressed as percent for the top 20 tree species in reference and restored plots. Species in bold are in the top 20 of only one forest type.

Reference forest	IVI %	Restored forest	IVI %
Guadua angustifolia	53.8	*Guadua angustifolia*	25.2
Cupania americana	3.0	*Cupania americana*	6.0
Erythrina poeppigiana	2.4	*Inga edulis*	5.9
*Anacardium excelsum**	2.1	*Cecropia angustifolia*	3.5
Cecropia angustifolia	2.0	*Oreopanax cecropifolius**	3.4
Inga edulis	1.7	*Croton magdalenensis*	3.3
*Oreopanax cecropifolius**	1.5	*Cinnamomum triplinerve*	2.9
Sorocea trophoides	1.5	*Anacardium excelsum**	2.8
Croton magdalenensis	1.4	*Erythrina poeppigiana*	2.7
Cinnamomum triplinerve	1.3	***Trichilia pallida****	2.0
Tetrochidium rubrinervium*	1.3	*Ocotea macropoda**	1.9
Guarea guidonea	1.3	*Brosimum alicastrum*	1.9
Trophis caucana	1.2	*Ficus insipida*	1.8
Ficus insipida	1.2	***Trichanthera gigantea***	1.7
Aiphanes horrida*	1.1	***Albizia caribaea****	1.7
Brosimum alicastrum	1.0	***Zanthoxylum rhoifolium***	1.4
Lacistema aggregatum	1.0	*Guarea guidonea*	1.3
Inga marginata	0.9	***Cordia alliodora***	1.3
Ocotea macropoda	0.9	***Nectandra lineata*****	1.3
Nectandra turbacensis*	0.8	***Machaerium capote****	1.3

* Species identified by a local expert as locally threatened.
** Species exclusive to the specific forest.

important species account for less than one third (28%) of the total IVI in the reference sites, and almost half (48%) of the total IVI in the restored sites. Both forest types had a small number of important species and a large number of species represented by only one or few individuals.

3.2. Forest structure

Tree stem density was significantly higher in reference than restored plots ($t_{23.6} = 2.17$, $p = 0.040$, Fig. 2a), whereas basal area was similar in both forest types ($t_{27.2} = 0.86$, $p = 0.395$, Fig. 2b). When *G. angustifolia* was removed from the analysis, however, restored plots had both higher stem density ($t_{21.5} = -3.74$, $p = 0.001$, Fig. 2c) and higher basal area (14.6 ± 2.4 vs. $8.0 \pm 1.4\,m^2\ ha^{-1}$; $t_{88.9} = -5.28$, $p < 0.001$) than reference plots (Fig. 2d). The difference in stem density was driven by the higher abundance of smaller diameter trees, mostly bamboo, in the reference plots (Fig. 2a, c). The difference in basal area was due to the higher abundance of large (≥40 cm DBH) trees in restored plots (Figs. 2b, d and 3), which were likely present before the sites were protected from grazing. In restored plots, large trees accounted for 1.4% of stems and 37.8% of the basal area, whereas in reference plots 0.6% of stems and 21.8% of the basal area were in the largest size class. Average canopy cover in restored plots was 89% and average ground cover was 77% of which < 5% was pasture grass

3.3. Species richness

We recorded a total of 108 tree species across all 88 reference plots, 89 species in the 20 restored plots, and 95 species in the 20 restored seedling plots (Table S1). Fifty-two species were common to both forest types, 38 were exclusive to reference forests, and 46 were exclusive to restored forests; 13 tree species were only recorded as seedlings in the restored plots. Average tree species density per plot, which corrected for the four times greater number of reference sites, was higher in restored forests both for seedlings (19.0 ± 1.7 species ha^{-1}) and trees (16.1 ± 1.6 species ha^{-1}) as compared to the reference plots (8.5 ± 0.7 species ha^{-1}). Observed species richness per plot was also significantly higher in restored and restored seedling plots than in reference forests (Fig. 4).

3.4. Community composition

The NMDS and PERMANOVA indicated a separation in the mean compositional difference of the reference and restored communities, despite some overlap among individual sites (Fig. 5). The main separation along Axis 1 was driven by *G. angustifolia*: reference plots, most of which had abundant *G. angustifolia,* fell further to the right while restored plots, most with little or no *G. angustifolia,* were located to the left.

Despite these differences, the reference and restored plots, and the restored and restored seedling plots, all had similar percentages of small, medium and large-seeded species, abiotically and vertebrate-dispersed species, pioneer and late successional species, and species with some level of threat (local, regional, IUCN) (Table 2). The percentage of individuals belonging to different functional groups was also similar in the reference and restored plots with the exception: the percentage of individuals of late successional species was significantly higher in restored plots.

4. Discussion

We anticipated that after only a decade of recovery, restored forests would have lower species richness and only a subset of the species present in the remnant forest fragments in the landscape. Instead, both the trees and woody seedlings in recovering forests were surprisingly diverse and hosted a similar proportion of later successional species, vertebrate-dispersed species, and regionally threatened species as the reference forests. In addition, there was evidence of structural recovery; most plots had a closed canopy and low grass cover, and stem density and basal area of species other than *G. angustifolia* were similar to reference forests. These findings contrast with previous studies showing that forest recovery on agricultural lands, especially pastures, can be slow (Uhl et al., 1988; Aide et al., 1995; Meli and Dirzo, 2013; Mesquita et al., 2015) or subject to ecological filters that result in an impoverished community from which large-seeded, vertebrate-dispersed, or shade-tolerant species are often absent (Aide et al., 2000). Whereas these riparian forests are unlikely to recover the species diversity of the forests that were originally cleared, their ability to recover with minimal intervention is good news for conservation in a part of the Colombian Andes that still harbors significant biodiversity despite high levels of fragmentation (Vargas, 2002; Gilroy et al., 2014).

Local and landscape factors may help explain the relatively rapid recovery of these riparian areas despite their previous grazing use. At the local scale, the presence of large (≥40 cm DBH) remnant trees at restored sites likely facilitated forest regrowth. Our results show that a small number of large trees comprised the majority of above-ground basal area in most restored sites demonstrating their important role in biomass accumulation. These are likely primarily remnant trees that were present at the sites when they were protected, although differential tree growth rates make this is difficult to state with certainty. Remnant trees are common in some agricultural landscapes, especially in pastures where farmers retain them for a number of reasons, mostly shade, timber, and fruit (Harvey and Haber, 1999; Garen et al., 2011). Faced with little competition outside the forests, these trees can grow very large, both isolated and in groups. Many previous studies have shown the importance of remnant trees in facilitating forest recovery: they serve as stepping stones for seed dispersers moving across open areas and therefore are foci for seed deposition (Guevara et al., 2004); mitigate soil temperatures and increase nutrient availability facilitating seed germination and establishment (Belsky et al., 1989; Rhoades et al., 1998; Derroire et al., 2016); and themselves are sources of propagules to recolonize abandoned pastures (Esquivel et al., 2008; Griscom and Ashton, 2011; Pignataro et al., 2017; Prevedello et al., 2018). The most common remnant tree species at our sites, *Inga edulis, Erythrina poeppigiana,* and *Croton magdalenensis,* provide important resources for a variety of animals, and therefore likely served as nuclei for the

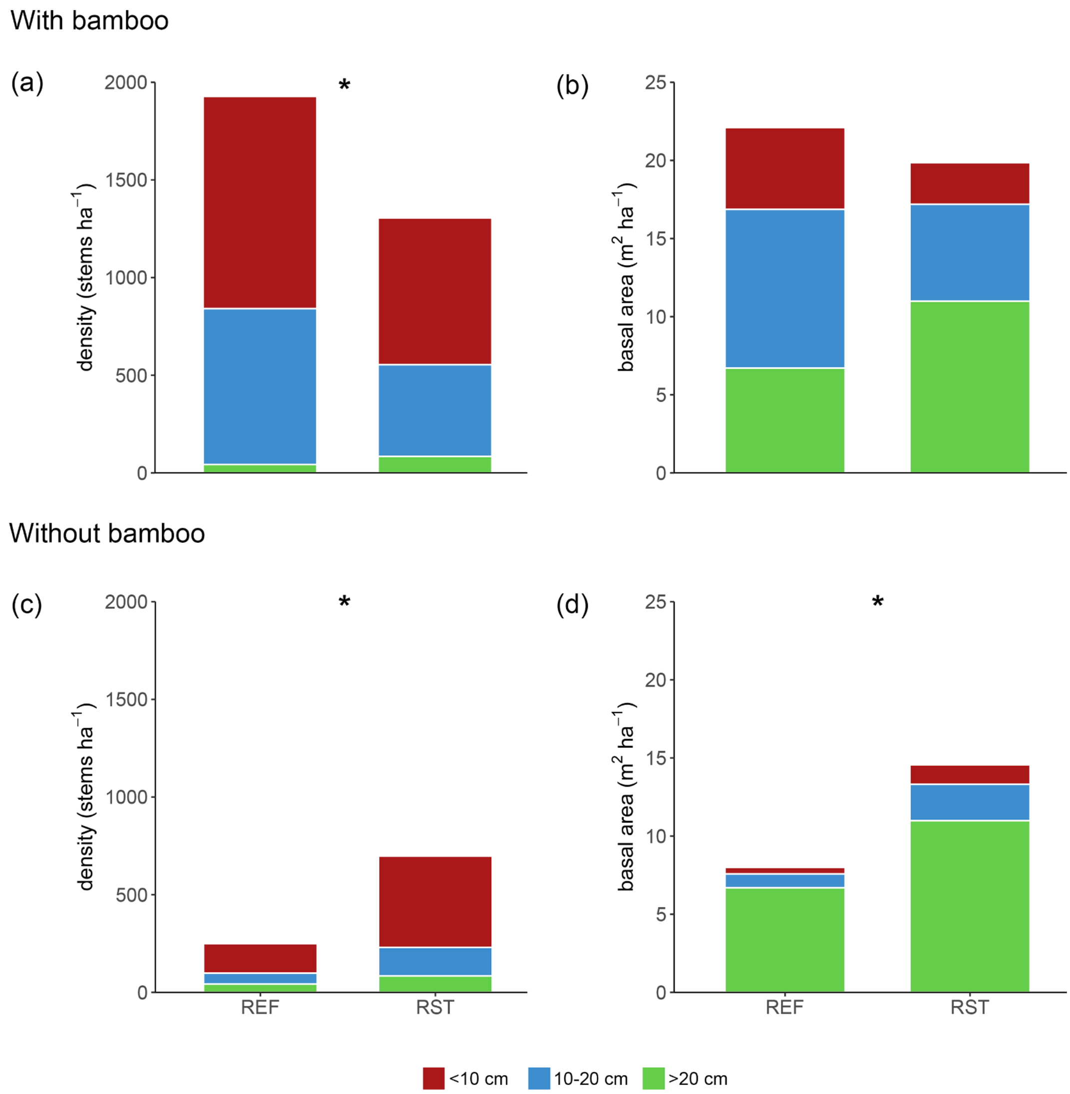

Fig. 2. Comparison of stem density and basal area in reference (REF, n = 88) restored (RST, n = 20) forests. Colors represent different diameter classes for stems ≥ 2.5 cm DBH. Total stem density with (a) and without bamboo (c); and total basal area with (b) and without bamboo (d). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

expansion of natural regeneration following the removal of cattle grazing (Rey Benayas et al., 2008; Zahawi et al., 2013).

At the landscape scale, riparian sites likely provided the best possible conditions for forest recovery within the hostile pasture context. Although the remnant forest cover in this region consists mostly of narrow and discontinuous riparian fragments, they still provide seed sources and passageways for the movement of many seeds dispersed by water and by forest specialists (Johansson et al., 1996; Gillies and St. Clair, 2008; Marczak et al., 2010). In addition, riparian areas in this region are often less valuable for farming because they are steep and difficult to access, and protected by regulations. Seeds arriving to riparian sites were therefore had higher chances to establish and grow, as they faced fewer of the factors that typically limit forest recovery in tropical pastures such as soil nutrients, moisture, or the risk of reclearing (Aide and Cavelier, 1994; Holl, 1999; Reid et al., 2017).

Our results raise questions about the conservation value of the remnant forests in this region and the ongoing efforts to promote reforestation with *G. angustifolia*. Unlike many studies showing that reference forests are more diverse than young recovering forests (Aide et al., 1995; Martin et al., 2004; Letcher and Chazdon, 2009; Dent et al., 2013), restored sites in this region have accumulated more species than the remnant secondary forests in the decade since their protection. The compositional and structural differences observed between both forest types are driven by the overdominance of *G. angustifolia* in the reference forests, which likely explain their lower species density and richness relative to restored sites. *G. angustifolia* is a native bamboo that propagates easily and grows rapidly reaching a height of 30 m in less than a decade (Young and Judd, 1992). Bamboo stands grow naturally in this region alongside mixed riparian forests, but in recent decades they have expanded as a result of intense human management due to their potential to provide ecosystem services (e.g., stream bank stabilization, water filtration, carbon sequestration) and aesthetic, cultural and economic values (Camargo et al., 2011; Muñoz et al., 2017). As a result, *G. angustifolia* has spread rapidly across the study region, sometimes encroaching on or replacing mixed forests. Bamboo species can proliferate and dominate the canopy of disturbed forests, causing shifts in light and resource availability, excessive litterfall, and displacement of important faunal seed dispersers. Such changes limit the recruitment and growth of woody species, eventually altering forest structure, reducing species diversity, and leading to long-term compositional changes (González et al., 2002; Campanello et al., 2007; Cortés-Delgado and Pérez-Torres 2011; Larpkern et al., 2011). If biodiversity conservation is a priority, then restoring mixed riparian forests while controlling the spread of *G. angustifolia* is especially important to ensure the persistence of species

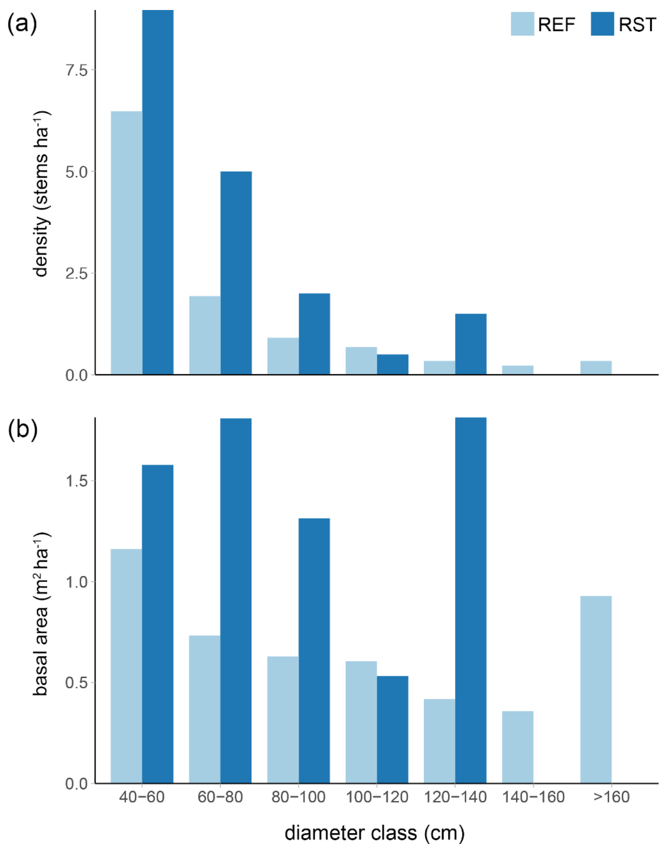

Fig. 3. Histograms of (a) stem density and (b) basal area by diameter class for trees ≥ 40 cm DBH in reference (REF, n = 88) and restored (RST, n = 20) forests.

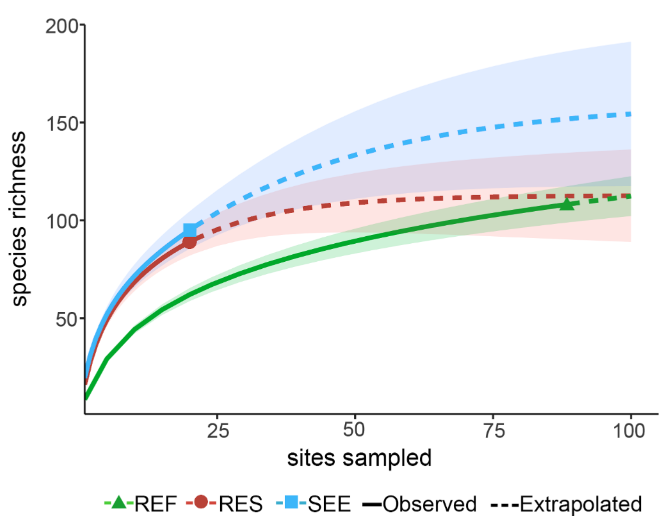

Fig. 4. Sample-based rarefaction curves for reference (REF), restored (RST) and restored seedling (SEE) plots. Solid lines are mean observed species richness, dashed lines are estimated species richness, and shaded areas represent 95% confidence intervals. Samples are 100 × 10-m plots (REF, n = 88; RST and SEE, n = 20).

in the regional pool and to prevent the further homogenization of local forests.

This study also prompts the highly debated question about what comprises an appropriate reference system in highly managed landscapes (Aronson et al., 1995; Balaguer et al., 2014; Hobbs et al., 2014): Should we use the best existing forests knowing that they may reflect an impoverished community, or aim to restore a historical reference

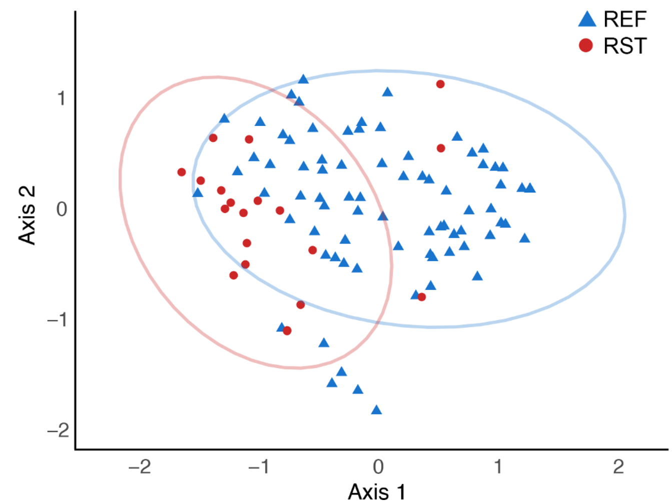

Fig. 5. Non-metric multidimensional scaling plots for community composition in reference (REF, n = 88) and restored (RST, n = 20) plots; stress = 0.15. PERMANOVA (p = 0.001) supports a significant compositional difference between site types. Three-dimensional solutions based on Morisita-Horn distance (abundance-based, robust to uneven sampling).

Table 2
Comparison of percent of species and percent of individuals by functional groups in reference (REF), restored (RST) and restored seedling (SEE) plots. Comparison of individuals only includes trees ≥ 2.5 cm DBH.

	Percent total species					Percent total individuals			
	REF	RST	SEE	X^2	P	REF	RST	X^2	P
Seed size[1]									
Small	20	17	12	3.38	0.50	53	52	4.24	0.12
Medium	37	35	35			36	35		
Large	43	48	54			11	13		
Primary dispersal mode[2]									
Abiotic	49	50	46	0.26	0.88	42	41		0.13
Biotic	51	50	54			58	59		
Successional stage[3]									
Pioneer	79	82	78	0.44	0.80	89	93	12.39	< 0.01*
Shade tolerant	21	18	12			11	7		
Threat status[4]									
Threat	20	32	27	3.91	0.15	29	31	1.84	0.18
No threat	80	68	73			71	69		

[1] Small (< 5 mm), medium (5–10 mm), large (> 10 mm).
[2] Abiotic (wind or gravity), biotic (birds, bats, small mammals).
[3] Pioneer (mid/early succession), shade tolerant (late succession).
[4] Threat (local, regional, or IUCN category), no threat.

system that is no longer present in the landscape? In this study, the use of the existing disturbed forests as a reference for comparison, while imperfect, provided valuable insight on two accounts. First, it evidenced the legacy of decades of human management on the remnant riparian forests and the need to take corrective actions if biodiversity conservation is a goal. And second, it highlighted the potential to restore riparian forests that may more closely resemble the historical reference system now absent from the region.

5. Conclusions

Our results demonstrate that restoring riparian forests can contribute to conservation in pasture-dominated landscapes, even in regions where the absence of undisturbed forests limits the regional species pool (Gilroy et al., 2014). Riparian sites offer suitable conditions for forest succession making natural regeneration a viable option to jumpstart the recovery process. Promoting the retention of large remnant trees in pastures and preventing the proliferation of species such as giant bamboo that may hinder forest recovery can substantially improve restoration outcomes. However, these actions require policies that stimulate and support the adoption of complex agricultural systems, improved management practices that increase connectivity in the agricultural matrix, and set-asides of lands critical for restoration and conservation (Lees and Peres, 2008; Latawiec et al., 2015; Chazdon et al., 2017). In addition, payments for ecosystem services or other financial incentives that recognize landowners' contribution to the provision of ecosystem services are needed to ensure the longevity of restored forests (Pagiola et al., 2016; Reid et al., 2017).

Acknowledgements

We thank Luis Enrique Méndez for assistance with plant identification; Alirio Bolívar for field guidance; Jack Ewel, Stacy Philpott and Paula Meli for feedback on earlier versions of this paper; and the landowners for granting us access to their farms. A. Calle received funding from the Garden Club of America Fellowship in Ecological Restoration, the Jean H. Langenheim Graduate Fellowship in Plant Ecology and Evolution, and the Heller Agroecology Graduate Student Research Fellowship.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117563.

References

Aide, T., Zimmerman, J.K., Herrera, L., Rosario, M., Serrano, M., 1995. Forest recovery in abandoned tropical pastures in Puerto Rico. For. Ecol. Manage. 77, 77–86.
Aide, T.M., Cavelier, J., 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. Restoration Ecol. 2, 219–229 Wiley Online Library.
Aide, T.M., Zimmerman, J.K., Pascarella, J.B., Rivera, L., Marcano-Vega, H., 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. Restor. Ecol. 8, 328–338. https://doi.org/10.1046/j.1526-100x.2000.80048.x.
Aronson, J., Dhillion, S., Le Floc'h, E., 1995. On the need to select an ecosystem of reference, however imperfect: a reply to Pickett and Parker. Restor. Ecol. 3 (10.1111), 1–3. https://doi.org/10.1111/j.1526-100X.1995.tb00069.x. John Wiley & Sons, Ltd.
Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F.P.L., Santos, B.A., Tabarelli, M., Chazdon, R., 2013. Plant β-diversity in fragmented rain forests: Testing floristic homogenization and differentiation hypotheses. J. Ecol. 101, 1449–1458. https://doi.org/10.1111/1365-2745.12153.
Balaguer, L., Escudero, A., Martín-Duque, J.F., Mola, I., Aronson, J., 2014. The historical reference in restoration ecology: Re-defining a cornerstone concept. Biol. Conserv. 176, 12–20. https://doi.org/10.1016/j.biocon.2014.05.007. Elsevier Ltd.
Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R., Mwonga, S.M., 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. J. Appl. Ecol. 1005–1024 JSTOR.
Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., et al., 2002. Habitat loss and extinction in the hotspots of biodiversity. Conserv. Biol. 16, 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x. Wiley Online Library.
Bullock, J.M., Aronson, J., Newton, A.C., Pywell, R.F., Rey-Benayas, J.M., 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities. Trends Ecol. Evol. 26, 541–549. https://doi.org/10.1016/J.Tree. 2011.06.011.
Calle, A., 2019. Farmers, forests and cattle: Restoring hope in Colombia's degraded landscapes. UC Santa Cruz. doi:ProQuest ID: Calle_ucsc_0036E_11750. Merritt ID: ark:/13030/m5wx2gf4.
Calle, Z., Méndez, L.E., 2009. Estructura y composición de la vegetación arbórea en el agropaisaje del río La Vieja. In: R.M., C.J.C., N.J., P.M., A.L.M., E.A., M.L. (Eds.), Valoración de la biodiversidad en la ecorregión del Eje Cafetero. CIEBREG, Pereira, Colombia, pp. 171–182.
Camargo, J.C., Chará, J.D., Giraldo, L.P., Chará-Serna, A.M., Pedraza, G.X., 2011. Beneficios de los corredores ribereños de Guadua angustifolia en la protección de ambientes acuáticos en la Ecorregión Cafetera de Colombia. 1. Efectos sobre las propiedades del suelo. Recursos Naturales y Ambiente 53–59.
Campanello, P.I., Genoveva Gatti, M., Ares, A., Montti, L., Goldstein, G., 2007. Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. For. Ecol. Manage. 252, 108–117. https://doi.org/10.1016/j.foreco.2007.06.032.
Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E., Miller, S.E., 2009. The potential for species conservation in tropical secondary forests. Conserv. Biol. 23, 1406–1417. https://doi.org/10.1111/j.1523-1739.2009.01338.x.
Chazdon, R.L., Brancalion, P.H.S., Lamb, D., Laestadius, L., Calmon, M., Kumar, C., 2017. A policy-driven knowledge agenda for global forest and landscape restoration. Conservation Lett. 10, 125–132.
Cortés-Delgado, N., Pérez-Torres, J., 2011. Habitat edge context and the distribution of phyllostomid bats in the Andean forest and anthropogenic matrix in the Central Andes of Colombia. Biodivers. Conserv. 20, 987–999. https://doi.org/10.1007/s10531-011-0008-1.
DANE, 2014. Tercer Censo Nacional Agropecuario 2014 Tercer CNA. Bogotá DC, Colombia: Departamento Administrativo Nacional de Estadística, Gobierno Nacional.
Dent, D.H., DeWalt, S.J., Denslow, J.S., 2013. 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 (10.1111), 530–542. https://doi.org/10.1111/j.1654-1103.2012.01482.x.
Derroire, G., Tigabu, M., Odén, P.C., Healey, J.R., 2016. The effects of established trees on woody regeneration during secondary succession in tropical dry forests. Biotropica 48, 290–300. https://doi.org/10.1111/btp.12287.
Dybala, K.E., Matzek, V., Gardali, T., Seavy, N.E., 2019. Carbon sequestration in riparian forests: A global synthesis and meta-analysis. Glob. Change Biol. 25, 57–67. https://doi.org/10.1111/gcb.14475.
Espinal, S., 1977. Zonas de vida o formaciones vegetales de Colombia: memoria explicativa sobre el mapa ecológico. Bogotá, Colombia: Instituto Geográfico Agustín Codazzi IGAC.
Esquivel, M.J., Harvey, C.A., Finegan, B., Casanoves, F., Skarpe, C., 2008. Effects of pasture management on the natural regeneration of neotropical trees. J. Appl. Ecol. 45, 371–380. https://doi.org/10.1111/j.1365-2664.2007.01411.x.
Garen, E.J., Saltonstall, K., Ashton, M.S., Slusser, J.L., Mathias, S., Hall, J.S., 2011. The tree planting and protecting culture of cattle ranchers and small-scale agriculturalists in rural Panama: Opportunities for reforestation and land restoration. For. Ecol. Manage. 261, 1684–1695. https://doi.org/10.1016/j.foreco.2010.10.011. Elsevier B.V.
Gillies, C.S., Clair, C.C.St., 2008. Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. Proc. Natl. Acad. Sci. 105, 19774–19779. https://doi.org/10.1073/pnas.0803530105.
Gilroy, J.J., Woodcock, P., Edwards, F.A., Wheeler, C., Baptiste, B.L.G., Uribe, C.A.M., Haugaasen, T., Edwards, D.P., 2014. Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism. Nat. Clim. Change 4, 503–507.
Giraldo, C., Escobar, F., Chará, J.D., Calle, Z., 2011. The adoption of silvopastoral systems promotes the recovery of ecological processes regulated by dung beetles in the Colombian Andes. Insect Conservation Diversity 4, 115–122. https://doi.org/10.1111/j.1752-4598.2010.00112.x.
González, M.E., Veblen, T.T., Donoso, C., Valeria, L., 2002. Tree regeneration responses in a lowland Nothofagus-dominated forest after bamboo dieback in South-Central Chile. Plant Ecol. 161, 59–73. https://doi.org/10.1023/A:1020378822847.
Gotelli, N.J., Chao, A., 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. Encyclopedia Biodiversity 5, 195–211.
Griscom, H.P., Ashton, M.S., 2011. Restoration of dry tropical forests in Central America: A review of pattern and process. For. Ecol. Manage. 261, 1564–1579. https://doi.org/10.1016/j.foreco.2010.08.027.
Guevara, S., Laborde, J., Sánchez-Rios, G., 2004. Rain forest regeneration beneath the canopy of fig trees isolated in pastures of Los Tuxtlas, Mexico. Biotropica 36, 99–108. https://doi.org/10.1111/j.1744-7429.2004.tb00300.x.
Harvey, C.A., Haber, W.A., 1999. Remnant trees and the conservation of biodiversity in Costa Rican pastures. Agrofor. Syst. 44, 37–68. https://doi.org/10.1023/A:1006122211692.
Harvey, C.A., Komar, O., Chazdon, R.L., Ferguson, B.G., Finegan, B., Griffith, D.M., Martinez-Ramos, M., Morales, H., et al., 2008. Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. Conserv. Biol. 22, 8–15. https://doi.org/10.1111/j.1523-1739.2007.00863.x. Wiley Online Library.
Higgs, E., Falk, D.A., Guerrini, A., Hall, M., Harris, J., Hobbs, R.J., Jackson, S.T., Rhemtulla, J.M., et al., 2014. The changing role of history in restoration ecology. Front. Ecol. Environ. 12, 499–506. https://doi.org/10.1890/110267.
Hobbs, R.J., Higgs, E., Harris, J.A., 2014. Novel ecosystems: concept or inconvenient reality? A response to Murcia et al. Trends Ecol. Evol. 29, 645–646. https://doi.org/10.1016/j.tree.2014.09.006.
Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31, 229–242.
Holl, K.D., Reid, J.L., Chaves-Fallas, J.M., Oviedo-Brenes, F., Zahawi, R.A., 2017. Local tropical forest restoration strategies affect tree recruitment more strongly than does landscape forest cover. J. Appl. Ecol. 54, 1091–1099. https://doi.org/10.1111/1365-2664.12814.
Holl, K.D., Reid, J.L., Oviedo-Brenes, F., Kulikowski, A.J., Zahawi, R.A., 2018. Rules of thumb for predicting tropical forest recovery. Appl. Veg. Sci. 21, 669–677. https://doi.org/10.1111/avsc.12394.
IUCN, and WRI, 2014. A guide to the Restoration Opportunities Assessment Methodology (ROAM): Assessing forest landscape restoration opportunities at the national or sub-national level. Edited by WRI and IUCN. Gland, Switzerland: Working paper (road-test edition), IUCN.
Johansson, M.E., Nilsson, C., Nilsson, E., 1996. Do rivers function as corridors for plant dispersal? J. Vegetation Sci. 7, 593–598. https://doi.org/10.2307/3236309.
Larpkern, P., Moe, S.R., Totland, Ø., 2011. Bamboo dominance reduces tree regeneration in a disturbed tropical forest. Oecologia 165, 161–168. https://doi.org/10.1007/s00442-010-1707-0.
Latawiec, A.E., Strassburg, B.B.N., Brancalion, P.H.S., Rodrigues, R.R., Gardner, T., 2015.

Creating space for large-scale restoration in tropical agricultural landscapes. Front. Ecol. Environ. 13, 211–218. https://doi.org/10.1890/140052. Wiley Online Library.
Lebrija-Trejos, E., Meave, J.A., Poorter, L., Pérez-García, E.A., Bongers, F., 2010. Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. Perspect. Plant Ecol., Evol. Syst. 12, 267–275. https://doi.org/10.1016/j.ppees.2010.09.002. Elsevier GmbH.
Lees, A.C., Peres, C.A., 2008. Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals. Conservation Biol. 22, 439–449. https://doi.org/10.1111/j.1523-1739.2007.00870.x.
Letcher, S.G., Chazdon, R.L., 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica 41, 608–617. https://doi.org/10.1111/j.1744-7429.2009.00517.x.
Liebsch, D., Marques, M.C.M., Goldenberg, R., 2008. How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. Biol. Conserv. 141, 1717–1725. https://doi.org/10.1016/j.biocon.2008.04.013.
Lira, P.K., Ewers, R.M., Banks-Leite, C., Pardini, R., Metzger, J.P., Barlow, J., 2012. Evaluating the legacy of landscape history: extinction debt and species credit in bird and small mammal assemblages in the Brazilian Atlantic Forest. J. Appl. Ecol. 49, 1325–1333. https://doi.org/10.1111/j.1365-2664.2012.02214.x.
Mansourian, S., Vallauri, D. (Eds.), 2005. Forest Restoration in Landscapes: Beyond Planting Trees. Springer Science & Business Media.
Marczak, L.B., Sakamaki, T., Turvey, S.L., Deguise, I., Wood, S.L.R., Richardson, J.S., 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. Ecol. Appl. 20, 126–134. https://doi.org/10.1890/08-2064.1.
Martin, P.H., Sherman, R.E., Fahey, T.J., 2004. Forty years of tropical forest recovery from agriculture: Structure and floristics of secondary and old-growth riparian forests in the Dominican Republic. Biotropica 36, 297–317. https://doi.org/10.1111/j.1744-7429.2004.tb00322.x.
McDonald, T., Gann, G.D., Jonson, J., Dixon, K.W., 2016. International standards for the practice of ecological restoration–including principles and key concepts. Society for Ecological Restoration, Washington, DC.
Meli, P., Dirzo, R., 2013. Effects of grasses on sapling establishment and the role of transplanted saplings on the light environment of pastures: implications for tropical forest restoration. Appl. Veg. Sci. 16, 296–304.
Meli, P., Rey Benayas, J.M., Martínez Ramos, M., Carabias, J., 2015. Effects of grass clearing and soil tilling on establishment of planted tree seedlings in tropical riparian pastures. New Forest. 46, 507–525. https://doi.org/10.1007/s11056-015-9479-3.
Mendenhall, C.D., Karp, D.S., Meyer, C.F., Hadly, E.A., Daily, G.C., 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509, 213–217. https://doi.org/10.1038/nature13139.
Mesquita, R.de C.G., Massoca, P.E.dos S., Jakovac, C.C., Bentos, T.V., Williamson, G.B., 2015. Amazon rain forest succession: Stochasticity or land-use legacy? Bioscience 65, 849–861. https://doi.org/10.1093/biosci/biv108.
Muñoz, J., Camargo, J.C., Romero, C., 2017. Beneficios de los bosques de guadua como una aproximación a la valoración de servicios ecosistémicos desde la "Jerarquización y Calificación". Gestión y Ambiente 20, 222–231.
Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.
Newmark, W.D., Jenkins, C.N., Pimm, S.L., McNeally, P.B., Halley, J.M., 2017. Targeted habitat restoration can reduce extinction rates in fragmented forests. Proc. Natl. Acad. Sci. 114, 9635–9640. https://doi.org/10.1073/pnas.1705834114.
Norden, N., Chazdon, R.L., Chao, A., Jiang, Y.H., Vílchez-Alvarado, B., 2009. Resilience of tropical rain forests: Tree community reassembly in secondary forests. Ecol. Lett. 12, 385–394. https://doi.org/10.1111/j.1461-0248.2009.01292.x.
Pagiola, S., Honey-Rosés, J., Freire-González, J., 2016. Evaluation of the permanence of land use change induced by payments for environmental services in Quindío, Colombia. PLoS ONE 11, 1–18. https://doi.org/10.1371/journal.pone.0147829.
Pattanayak, S.K., Wunder, S., Ferraro, P.J., 2010. Show me the money: Do payments supply environmental services in developing countries? Rev. Environ. Econ. Policy 4, 254–274 Oxford University Press.
Perfecto, I., Vandermeer, J., 2010. The agroecological matrix as alternative to the land-sparing/agriculture intensification model. Proc. Natl. Acad. Sci. 107, 5786–5791.
Pignataro, A.G., Levy-Tacher, S.I., Aguirre-Rivera, J.R., Nahed-Toral, J., González-Espinosa, M., González-Arzac, A., Biganzoli, F., 2017. Natural regeneration of tree species in pastures on peasant land in Chiapas, Mexico. Agric., Ecosyst. Environ. 249, 137–143. https://doi.org/10.1016/j.agee.2017.08.020.
Prevedello, J.A., Almeida-Gomes, M., Lindenmayer, D.B., 2018. The importance of scattered trees for biodiversity conservation: A global meta-analysis. J. Appl. Ecol. 55, 205–214. https://doi.org/10.1111/1365-2664.12943.
Reid, J.L., Wilson, S.J., Bloomfield, G.S., Cattau, M.E., Fagan, M.E., Holl, K.D., Zahawi, R.A., 2017. How long do restored ecosystems persist? Ann. Mo. Bot. Gard. 102, 258–265. https://doi.org/10.3417/2017002.
Rey Benayas, J.M., Bullock, J.M., 2012. Restoration of biodiversity and ecosystem services on agricultural land. Ecosystems 15, 883–899. https://doi.org/10.1007/s10021-012-9552-0.
Rey Benayas, J.M., Bullock, J.M., Newton, A.C., 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Front. Ecol. Environ. 6, 329–336. https://doi.org/10.1890/070057.
Rhoades, C.C., Eckert, G.E., Coleman, D.C., 1998. Effect of pasture trees on soil nitrogen and organic matter: Implications for tropical montane forest restoration. Restoration Ecol. 6, 262–270. https://doi.org/10.1046/j.1526-100X.1998.00639.x.
Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan, J., Jani, A., Katz, G., et al., 2005. Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86, 56–62 Wiley Online Library.
Salzman, J., Bennett, G., Carroll, N., Goldstein, A., Jenkins, M., 2018. The global status and trends of payments for ecosystem services. Nat. Sustainability 1, 136–144. https://doi.org/10.1038/s41893-018-0033-0.
Santo-Silva, E.E., Almeida, W.R., Melo, F.P.L., Zickel, C.S., Tabarelli, M., 2013. The nature of seedling assemblages in a fragmented tropical landscape: implications for forest regeneration. Biotropica 45, 386–394.
Suganuma, M.S., de Assis, G.B., Durigan, G., 2014. Changes in plant species composition and functional traits along the successional trajectory of a restored patch of Atlantic Forest. Commun. Ecol. 15, 27–36. https://doi.org/10.1556/C.
Suganuma, M.S., Durigan, G., 2015. Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. Restor. Ecol. 23, 238–251. https://doi.org/10.1111/rec.12168. Wiley Online Library.
Uhl, C., Buschbacher, R., Serrao, E.A.S., 1988. Abandoned pastures in eastern Amazonia. Patterns of plant succession. J. Ecol. 76, 663–681.
Vargas, W.G., 2002. Guía ilustrada de las plantas de las montañas del Quindío y los Andes Centrales. Manizález, Colombia: Universidad de Caldas.
World Bank, 2008. Colombia, Costa Rica, and Nicaragua - Integrated Silvopastoral Approaches to Ecosystem Management Project. Washington, DC: World Bank.
Young, S.M., Judd, W.S., 1992. Systematics of the Guadua angustifolia complex (Poaceae: Bambusoideae). Ann. Mo. Bot. Gard. 737–769 JSTOR.
Zahawi, R.A., Holl, K.D., Cole, R.J., Reid, J.L., Banks-Leite, C., 2013. Testing applied nucleation as a strategy to facilitate tropical forest recovery. J. Appl. Ecol. 50, 88–96. https://doi.org/10.1111/1365-2664.12014.