Title Natural regeneration and biodiversity: a global meta-analysis and implications for spatial planning

Authors: Agnieszka E. Latawiec[1,2,3,4*], Renato Crouzeilles[1,4], Pedro H.S. Brancalion[5], Ricardo R. Rodrigues[6], Jerônimo B.B Sansevero[1,7], Juliana Silveira dos Santos[1], Morena Mills[8], André Gustavo Nave[9], Bernardo B.N. Strassburg[1,4]

1 – International Institute for Sustainability, Estrada Dona Castorina 124, 22460-320, Rio de Janeiro, Brazil

2 – Opole University of Technology, Department of Production Engineering and Logistics, Luboszycka 5, 45-036 Opole, Poland

3 – University of East Anglia, School of Environmental Science, Norwich, NR4 7TJ, United Kingdom

4 – Rio Conservation and Sustainability Science Centre, Department of Geography and the Environment, Pontifícia Universidade Católica, 22453900, Rio de Janeiro, Brazil

5 – Department of Forest Sciences, "Luiz de Queiroz" College of Agriculture, University of São Paulo, 13418-900, Av. Pádua Dias, 11, Piracicaba, São Paulo, Brazil

6 – Department of Biology, "Luiz de Queiroz" College of Agriculture, University of São Paulo, 13418-900, Av. Pádua Dias, 11, Piracicaba, São Paulo, Brazil

7 – Universidade Federal Rural do Rio de Janeiro (UFRRJ). Instituto de Floresta (IF), Departamento de Ciências Ambientais (DCA). BR 465, Km 07, 23890-000, Seropédica, Rio de Janeiro, Brazil

8 – Centre of Excellence for Environmental Decisions, University of Queensland, Australia

9 – Bioflora, Rod. Piracicaba – Tupi, Km 18, 13420-280, Piracicaba, São Paulo, Brazil

Agnieszka E. Latawiec and Renato Crouzeilles contributed equally to this article.

Abstract

Natural regeneration offers a cheaper alternative to active reforestation and has the potential to become the predominant way of restoring degraded tropical landscapes at large scale. We conducted a global meta-analysis and quantified the relationships between both ecological and socioeconomic factors and biodiversity responses in regenerating areas. To do so, biogeographic realms, past disturbance and the human development index (HDI) were used as the explanatory variables that affect biodiversity responses. In addition, we present a case study of large-scale natural regeneration in the Brazilian Atlantic Forest and identify areas where different forms of restoration would be most suitable. Natural regeneration was predominantly reported within: i) the Neotropical realm, ii) areas that were intensively disturbed, and iii) countries with medium HDI. We also found that biodiversity will be more similar to old-growth forests in: i) countries with either low, high HDI or very high HDI; ii) less biodiverse realms; and iii) areas of less intensive past disturbance. The benefits of natural regeneration seemed to respond to the environmental Kuznets curve. Our case study from Brazil showed that the level of forest gain resulting from environmental legislation, in particular the Brazilian Forest Code, has been reduced but remains substantial. Complementary market incentives and financial mechanisms to promote large-scale natural regeneration in human-modified agricultural landscapes are also needed. Our analysis provides insights into the factors that promote or limit the recovery of biodiversity in naturally regenerating areas, and aids to identify areas with higher potential for natural regeneration.

1. Introduction

Ecological restoration is critical to reverse biodiversity decline, restore ecological processes and supply ecosystem services in disturbed or degraded lands throughout the world (Lamb *et al*. 2005, Chazdon *et al*. in press, Crouzeilles *et al.* in press). Spurred by international and local momenta, a range of initiatives has arisen in different parts of the world to restore native systems. For example, The Aichi Targets 14 and 15 of the United Nations Convention on Biological Diversity (Janishevski *et al*. 2015) aim to restore the ecosystems that provide essential services and restore at least 15 % of degraded ecosystems, respectively. The "Bonn Challenge", a global restoration initiative, set a goal of restoring 150 million hectares of deforested and degraded forests by 2020 (WRI, 2012). Other examples are the result of the 2014 New York Climate Summit – the New York Declaration on Forests – which promotes restoration of 350 million hectares globally by 2030, and the recent 20x20 initiative to restore 20 million hectares of forests by 2020 in some Latin American and Caribbean countries, launched at the COP 20 in Peru. Examples can also be found at the country and biome level. At the country level: the Green Belt Movement in Kenya (de Aquino *et al*. 2011) restored over 51 million trees in watersheds of major mountain ecosystems since 1977[1]. At a biome level, the Brazilian Atlantic Forest Restoration Pact, gathers more than 250 members, including environmental organizations, research institutes, private companies, and government agencies, and aims to restore 15 million hectares of forest by 2050 (Melo *et al*. 2013).

Although a myriad of restoration methods is available, restoration has normally been grouped into two main approaches: passive (leaving areas for natural regeneration) and active restoration (human intervention in order to accelerate and influence the successional trajectories) (Holl & Aide 2011). Many studies in different tropical regions have explored the factors and mechanisms facilitating natural regeneration in abandoned agricultural areas or in areas of low agricultural productivity at a local scale (Cramer *et al*. 2008). Natural regeneration has been shown to depend on:

[1] http://www.greenbeltmovement.org/what-we-do/tree-planting-for-watersheds

i) isolation from source forests (Pereira *et al*. 2013, Curran *et al*. 2014, Crouzeilles & Curran 2016), ii) frequency of recurrent fire (Hooper *et al*. 2004), iii) type of soil seed bank (e.g. composed by native species; Lamb *et al*. 2005), iv) intensity of land degradation (Guariguata & Ostertag 2001), v) time since deforestation started (years vs. decades; Lamb *et al*. 2001, Crouzeilles *et al.* in press), and vi) climate (Vieira *et al*. 2006, Poorter *et al.* 2016). Although socioeconomic factors have often been overlooked in restoration studies (Wortley *et al*. 2013), ultimately the success of natural regeneration (i.e. return to a reference condition) depends on socioeconomic attributes, and direct and indirect benefits to landholders and local communities (Cairns & Heckman 1996, Sayer *et al.* 2004, Lamb *et al*. 2005). Cost is an important factor when considering restoration, and natural regeneration has been shown to be the most cost-effective restoration approach for increasing native vegetation cover at large scale (Chazdon 2014). Rural-urban migration can result in the abandonment of poor quality agricultural land, leading to an increased quantity of land available for restoration (Aide & Grau 2004, Rezende *et al.* 2015). Within rural properties that are not abandoned, financial incentives can encourage restoration, especially within areas that are not currently used for agriculture or that have low productivity (Wunder 2006, Brancalion *et al*. 2012). Recent international market mechanisms or policies (e.g. certification systems, Kyoto Protocol) can instigate restoration by government (Wuethrich 2007) or private landholders.

Despite research effort, both ecological/biophysical and socioeconomic factors that influence the likelihood of abandoned lands to regenerate are complex and not entirely understood (Aide *et al*. 2013). As a consequence, it is still being debated where large-scale natural regeneration should occur. Some studies suggest that land for natural regeneration can be made available through the coupling of sustainable intensification of agricultural production with land sparing (Phalan *et al.* 2016). Sustainable intensification, in a nutshell, means producing more from current agricultural lands that are being used below their potential, while respecting biophysical constraints to avoid adverse impacts from over intensification (Foresight 2011). Phalan *et al.* (2016) presents mechanisms that harness the potential of yield increases to make space for nature at large scales. Strassburg *et al*. (2014) shows that the current productivity of Brazilian pasturelands is only about 30% of its sustainable potential. Increasing productivity to 70% of its sustainable potential, could accommodate agricultural production of main products (meat, soybean, sugarcane and maize; including for exports) and release 36 million hectares for restoration of natural systems (Strassburg *et al*. 2014). The same could be true for other places worldwide (Strassburg *et al*. 2014), and not only for pasture but also for other agricultural products (Krolczyk *et al*. 2014, Krolczyk & Latawiec 2015). Nevertheless, even if within the same landscape matrix, some areas could be used for sustainable intensive agriculture and other for natural regeneration, a successful land-sparing approach depends on relevant legislation and its enforcement and is limited by landowners preferences.

In this paper we aim to answer two key questions: i) how do different ecological, biophysical and socioeconomic factors correlate with the success of natural regeneration? And ii) where and how can we find potential areas for natural regeneration at large scale? These questions explore the driving factors of regeneration success in a global perspective, focused in regions where Forest Transition has occurred. To these ends, we first conducted a global meta-analysis to quantify the effects of socioeconomic, biogeographic, and ecological factors on biodiversity responses in natural regenerating areas. The success of natural regeneration can be measured using three ecosystem attributes: biodiversity, vegetation structure and ecosystem processes (Ruiz-Jaen & Aide 2005, Sansevero & Garbin 2015). In this study we used ecological metrics as abundance, richness, diversity and similarity as biodiversity response and the human development index (HDI), biogeographic realms (according to Olson *et al*. 2001) and past disturbance as the measured explanatory variables affecting biodiversity. Second, we present a case study of large-scale natural regeneration in the Brazilian Atlantic Forest and identify areas where different forms of restoration would be most suitable. The case study shed light onto the role of restoration regulations on the expansion of natural regeneration in agricultural regions, where most of native vegetation loss has been observed and its potential future gain is expected to happen. We hypothesized that the farm size is positively associated to the proportion of its area that has to be mandatorily restored, as a consequence of the mechanisms established by the Brazilian Forest Code to reduce the allocation of land to restoration in small- and medium-sized farms (Soares-Filho *et al*. 2014). This paper contributes to current knowledge on the impacts of natural regeneration within different socioeconomic and ecological/biophysical contexts, and provides insight to the factors that promote or limit natural regeneration of tropical forests at a global scale. To our knowledge, this is the first study that presents a global meta-analysis of how different socioeconomic, ecological and biophysical factors affect biodiversity in naturally regenerated areas.

2. Methods

Literature review and meta-analysis on biodiversity responses to natural regeneration

We conducted an extensive analysis of all recorded studies in the database used by Crouzeilles & Curran (2016) and Crouzeilles *et al.* (in. press), which investigated the scale of effect of forest cover on restoration success and the main ecological drivers of forest restoration success, respectively, both for biodiversity and vegetation structure at the global scale. This database is the most comprehensive gathered to date on restoration success (i.e. return to a reference condition; Crouzeilles & Curran 2016, Crouzeilles *et al.* in. press). It was constructed based on seven key reviews on either biodiversity responses or ecological succession of forest structures in degraded and/or restored ecosystems (Dunn 2004, Ruiz-Jaen & Aide 2005, Bowen *et al*. 2007, Benayas *et al*. 2009, Gibson *et al*. 2011, Wortley *et al*. 2013, Curran *et al*. 2014). The inclusion criteria used in Crouzeilles & Curran (2016) and Crouzeilles *et al.* (in. press) selected studies that were carried out in forested ecosystems and had multiple sampling sites (replicates) to measure biodiversity (mammals, birds, invertebrates, herpetofauna and plants) and/or vegetation structure (cover, density, height, biomass and litter) in both reference (old-growth forests) and degraded or restored systems. We used a subset of this database by considering only studies that: i) had comparison of reference forests (old-growth or less disturbed forests) vs. natural regenerated forests (i.e. data on degraded and active restoration systems were excluded); ii) were conducted in tropical regions; iii) had information on past disturbance for each natural regenerated forest; and iv) had comparison for biodiversity (i.e. data on vegetation structure were excluded).

We also gathered information on socioeconomic, biogeographical and ecological factors for each selected study. Socio-economic factors were represented by Human Development Index (HDI), which aims to assess the development of country and takes into account indicators of life expectancy, education and income per capita (UNDP 2014). We gathered this information for the exact location and year in which the selected study was conducted. When this information was unavailable, we considered the HDI value for the country which the study was carried out and/or the nearest study's year. For example, if there was no HDI value for 1979 and 1970, and the value for 1980 was the closest one, we used this HDI value in the analysis. The HDI values were obtained from either the United Nations Development Programme or the Human Development Report. They contain HDI values ranging from 1980 to 2013 and 2000 to 2013, respectively, with different intervals of years between the released data. We classified the HDI values in four classes according to the United Nations Development Programme criteria: i) very high (values ≥ 0.8), ii) high (≥ 0.7 and < 0.8), iii) medium (≥ 0.55 and < 0.7), and iv) low (< 0.55).

Biogeographical factors were represented by the biogeographic realms proposed by Olson *et al.* (2001). This is the broadest biogeographic division in the Earth's land surface, clustering ecoregions that may contain several habitat types, but have strong biogeographic patterns, such as climate conditions (temperature and precipitation), and distribution of terrestrial organisms (e.g. higher taxonomic levels). Such taxonomic diversity occurs as organisms evolved relatively isolated over long-term due to natural barriers, such as large mountains and oceans. Despite this broad division, the next classification level encompasses more than 80 different ecoregions, which would preclude our analysis. Thus, here we used studies across the four biogeographic realms included in the tropical region: i) Indo-Malay, ii) Afrotropic, iii) Australasia, and iv) Neotropic. The coordinate systems of each study landscape and either the HDI values or the biogeographic realms were overlapped using the software ArcGis 9.3 (ESRI 2008).

Land classes indicating the type and intensity of disturbance prior to the forest recovery in a given area can be used to understand the ecological effects of the past disturbance on restoration success (Dent & Wright 2009, Curran *et al*. 2014). We gathered information on land classes from the studies included in the original database used by Crouzeilles & Curran (2016) and Crouzeilles *et al.* (in. press). When there was different past disturbance types for each natural regenerating area, these were considered as different treatments. We classified the past disturbance in four classes according to Dent & Wright (2009): i) Extensive transformation – areas that were little transformed and remained under occupation for short-term (e.g. not completely cleared forests); (ii) Extensive occupation – areas that were little transformed and remained under occupation for long-term (e.g. agroforestry and shaded plantations); (iii) Intensive transformation – areas that were heavily transformed and remained under occupation for short-term (e.g. clear cut and burning), and; (iv) Intensive occupation – areas that were heavily transformed and remained under occupation for long-term (e.g. plantation, pasture and agriculture).

In order to quantify the effects of socioeconomic, biogeographic, and ecological factors on biodiversity (see below), we used a meta-analysis metric called response ratio (Hedges *et al*. 1999). It measures the standardized mean effect size of each comparison of biodiversity between reference forests and natural regenerated forests within the same assessment. The response ratio is measured as ln($\bar{x}$natural regenerating forest/$\bar{x}$reference forest), where $\bar{x}$ is the mean value for a quantified measure of biodiversity within all sampling sites (replicates) in a study landscape. Response ratio ranges from negative to positive values, with values around zero considered as the desired outcome of restoration (i.e. success in bringing biodiversity in natural regenerated forest back to the reference forest). Negative values mean that biodiversity is lower in natural regenerated forests compared with reference forests, while the opposite holds for positive values.

Biodiversity data can represent different taxonomic groups (plants, birds, mammals, herpetofauna, and invertebrates). These biodiversity data included different ecological metrics, abundance, richness, diversity and similarity: abundance was represented by number, proportion, frequency and density of individuals, equitability; richness by observed, estimated, rarefied richness, species density; diversity by Shannon index, Simpson index, Margalef index, Fisher alpha, evenness; and species similarity by Sorenson index, Morisita-Horn index, ANOSIM, PCA, MDS, Mantel, Jaccard index, Bray Curtis and Euclidean distances.

There can be more than one comparison of biodiversity between reference forests and natural regenerated forests (i.e. many response ratios) for the same study landscape, if for example, there was more than one: i) study in the same study landscape, ii) taxonomic group studied, and/or iii) ecological metric (e.g. abundance, richness, diversity and similarity) measured. To avoid spatial pseudo-replication, we resampled any given biodiversity dataset with replacement (10,000 bootstraps) and used only one comparison per study landscape to generate the median effect size and 95% confident intervals (e.g. Gibson *et al.* 2011, Curran *et al*. 2014, Crouzeilles *et al.* in. press). Thus, we quantified the effects of socio-economic, biogeographic, and ecological factors on biodiversity via a bootstrapped meta-analysis for a pooled dataset that includes response ratio of different taxonomic groups and ecological metrics (e.g. Rey Benayas et al. 2009). Consideration of different taxonomic groups facilitates a deeper understanding of biodiversity responses to restoration. Lack of data for each taxonomic group and ecological metric precluded individual analysis. Nonetheless, different taxonomic groups and ecological metrics can be pooled in the same meta-analysis as the response ratio is calculated as log natural of a ratio (ln(natural regenerating forests/reference forests)), i.e. the differences are standardized. Outliers were removed to assure normally distributed residuals, which were checked by plotting residuals (Crawley 2007). Difference among classes of a factor (HDI, biogeographic realm or past disturbance) may be driven by the time since natural regeneration started. So we tested it performing one-way ANOVA, which we ran 10,000 times for each factor, with one comparison per study landscape to avoid spatial-replication. We presented the results in terms of percentage of time which there was difference among the classes of a factor (i.e., p value ≤ 0.05). This dataset was smaller than those used in the meta-analysis as not all selected studies provided information on the time since natural regeneration started, thus we preferred to perform meta-analysis only for the same "full" dataset. Meta-analysis and ANOVA were conducted in R 2.12 (R Development Core Team 2010).

Case study - The role of Brazil's Forest Code to catalyze natural regeneration at large scale in the Atlantic Forest

The new version of the Brazilian Forest Code (established in 2012) provides a comprehensive example of how legislation may foster forest gain in agricultural regions. Compliance with this law may result in the restoration of 21 million hectares of native vegetation in private farms during the next 20 years (Soares-Filho *et al*. 2014). Restoration should occur in Areas of Permanent Preservation (APPs – pre-determined areas where land use is restricted and native vegetation has to be conserved or restored; e.g. riparian buffers, mountain tops and steep slopes), and Legal Reserves (LRs – percentage of the farm area that must be covered by native vegetation, without a pre-determined location and depending on the farm size and in which biome the farm is located – e.g. 20% and 80% in the Atlantic Forest and Amazon, respectively) (for further details, see Garcia *et al.* 2013). In addition, farmers are obliged to include their landholdings in the on-line federal Environmental Registry System (CAR, the acronym in Portugese), in which they have to delineate areas that will be protected or restored to ensure environmental compliance. The new Forest Code established mechanisms to favor legal compliance of farms driving a historical deficit of native vegetation, and these mechanisms focus on small- to medium-sized landholdings and affected 90% of all farms in Brazil (Soares-Filho *et al*. 2014). Examples of these mechanisms are the reduction of the width of riparian buffers to be restored and the permission to farm within APPs where native vegetation was already converted (restoration amnesty in APP), the removal of restoration requirements of LRs in small- and medium-sized farms (restoration amnesty in RLs), and amnesty of fines for those who engage in a restoration plan.

We assessed the restoration planning of 284 medium- to large-sized farms (214 ±183 ha each), totaling 63,338 hectares, in eight municipalities (Alcobaça, Caravelas, Ibirapuã, Mucuri, Nova Viçosa, Porto Seguro, Prado, Teixeira de Freitas, and Vereda) of Bahia state, in the Atlantic Forest region of northeast Brazil (Fig. 1). The landscape is predominantly composed by commercial Eucalyptus plantations and cattle ranching, and remaining native forest cover is low (< 10%). Although the states from Northeast Brazil has lower income and social development compared to south and southeastern states, the specific region where the assessment was made has higher revenues from land use as consequence of the large-scale, industrial production of Eucalyptus, reflecting the socioeconomic and ecological context of Northern Espírito Santo and Southern Bahia states. This region may represent the overall context in which large-scale restoration programs will be implemented in Brazil and in other tropical countries where new legal instruments and market regulations have fostered land use reorganization to protect and restore native ecosystems within farms (Rodrigues *et al.* 2011, Nepstad *et al.* 2014).

Although varying economic activities are developed in these farms, all of them produce Eucalyptus in partnership with two large Brazilian pulp companies, which provide technical assistance and resources for the establishment, maintenance, and harvesting of Eucalyptus plantations, while farmers sell the timber according to pre-determined contractual conditions. Since these companies need forest certification for exports and must comply with environmental laws, they support restoration planning and implementation within partnering farmers. In particular, the 301 farms included in this study were part of a large compliance agreement established between these two pulp companies and the state environmental legislators. All of the farms included in the compliance agreement were evaluated in this work. The environmental diagnosis was performed as part of a consultancy project developed by the Laboratory of Forest Ecology and Restoration (LERF), of the University of São Paulo, Brazil, following the legal frameworks of the Environmental Registry System and Project for the Recovery of Degraded and Altered Lands, as part of the new Forest Code.

We assessed the proportion of different restoration methods prescribed for APPs and LRs in each of the 301 farms we studied. Restoration methods consisted of: i) active restoration: seedling plantation or direct seeding in the entire restoration area; and ii) passive restoration: isolating the sites from further human-mediated disturbances; assisting spontaneously regenerating seedlings by controlling invasive grasses around then and, when necessary, planting new seedlings or sowing seeds in the patches not covered by regenerating seedlings. We first evaluated the total restoration area established by legislation for all farms included in our dataset and explored how the recent changes in the law would affect restoration area. Then, we analyzed the influence of farm size in: i) the percentage of farm area to be restored, ii) the proportion of active restoration in APPs, and iii) the proportion of active restoration in LRs, using linear regressions. Based on previous observations of restoration planning in Southeastern Brazil, in which large farms producing sugarcane were distributed in more fertile soils and flat terrain, thus with more intense historical land use (Rodrigues *et al.* 2011), we hypothesized that the proportion of active restoration in APPs and LRs will increase with farm area.

3. Results

Meta-analysis on the biodiversity responses to natural regeneration

During the literature review, we selected 123 studies including 1,389 quantitative comparisons of biodiversity between reference and natural regenerated forests across 117 study landscapes. These studies were spread across the four biogeographic realms (Indo-Malay, Afrotropic, Australasia, Neotropic) found in the tropical regions (Fig. 2A). Data in these studies was collected in the field between 1984 and 2008. The time since natural regeneration began ranged from 0.5 to more than 200 years. In general, these studies were widely spread across all the classes of biogeographic realms and HDI (Fig. 2). The predominant type of area selected given the criteria described here was: areas characterized with the medium HDI (36%, n = 44; Fig. 3A) in the Neotropic realm (n = 63, 51%; Figure 3B), and with intensive occupation as the past disturbance (51%, n = 63; Fig. 3C).

Biodiversity response ratios in naturally regenerated forests were lower than in reference forests for all classes of socioeconomic, biogeographic and ecological factors, i.e. the biodiversity is more depleted in naturally regenerated forests when compared with reference forests (Fig. 4). For HDI, biodiversity responses ratio in natural regenerated forests were more similar to reference forests in countries with either low, high or very high HDIs (median effect size of -0.14, -0.16, -0.19, respectively; Fig. 4A). Countries with medium HDI were characterized with lower biodiversity response ratios in regenerating forests (median effect size of -0.23) (Fig. 4A). Regarding biogeographic realms, biodiversity responses in natural regenerated forests were more similar to reference forests in Australasia realm (-0.12), while it was more distinct for Neotropic and Indo-Malay realms (-0.18 and -0.19, respectively) (Fig. 4B). Areas with extensive occupation as the past disturbance (represented by agroforestry and shaded-plantation) showed higher biodiversity responses in natural regenerated forests than in reference forests (0.19) (Fig. 4C). For every other class of past disturbance, biodiversity responses in regenerated forests were lower than in reference forests (Fig. 4C) with biodiversity response more similar to reference area in extensively transformed areas (-0.1), while in intensively occupied areas it was lower (-0.23) (Fig. 4C). These differences in biodiversity responses among classes of HDI, biogeographic realms and past disturbance were not influenced (or at least were low influenced) by the time since natural regeneration started as only in 0.06, 0.002, and 0.35% of the 10,000 bootstraps the ANOVA was significant (i.e., p *value* ≤ 0.05), respectively. Analyzing intensive occupation separately, our results show that Afrotropic realm presents higher biodiversity response ratio in naturally regenerated forests as compared to others realms (Supplementary Fig. 1A). In addition, biodiversity response ratio in areas of intensive occupation was highest in countries with low HDI (Supplementary Fig. 1B).

Case study - The role of Brazil's Forest Code to catalyze natural regeneration at large scale in the Atlantic Forest

A total of 1,990 hectares (3.1 ± 2.7% of total area of farms, mean ± SD, ranging from 0 to 20.8%) were allocated for restoration according to the diagnosis of the 284 farms in the south of Bahia. Overall, larger farms would have to restore a higher proportion of their area to comply with the law (linear regression: p *value* < 0.0001; $r^2 = 0.09$). Total restoration area included 876 hectares of restoration in APPs (1.5 ± 1.0% of total area of farms) and 1114 hectares (5.4 ± 4.4% of total area of farms obliged to restore LRs) in LRs. The APP area where agricultural activities and infrastructure could be maintained indefinitely (1537 ha), thus eligible for restoration amnesty, was almost double the area required for restoration (876 ha). The proportion of APP area eligible for restoration amnesty reduced with farm size (p *value* $= 0.005$; $r^2 = 0.02$). Only 20% of farms would have to restore LRs, and 10% of farms would have to restore more than 10 hectares to supply LR deficit. The proportion of land allocated to active restoration was not affected by farm size in both APPs (p *value* $= 0.14$; $r^2 = 0.004$) and LRs (p *value* $= 0.11$; $r^2 = 0.02$). Overall, the proportion of active restoration required was similar in APPs (59 ± 32%, mean ± SD) and LRs (48 ± 38%).

4. Discussion

Our global review shows that areas in the Neotropic realm, with medium HDI values, and with intensive occupation as the past disturbance were more studied in the last decades. In addition, our meta-analysis reveals for the first time overall patterns of biodiversity responses in natural regenerating areas across socioeconomic, biophysical and ecological factors. We found that biodiversity will be more similar to old-growth forests in: i) countries with either low or high HDI; ii) less biodiverse realms; and iii) low transformed lands occupied for a short-term. Finally, our case study shows an empirical example of how the Brazilian legislation currently shapes Forest Transition in the south of Bahia.

We found that the greater biodiversity benefits were obtained from natural restoration within countries with low and high levels of development, potentially reflecting the environmental degradation of forest as predicted by the environmental Kuznets curve (Mather 1992, Bhattarai & Hammig 2001, Dinda 2004, Meyfroidt & Lambin 2011). Countries with lower HDI values usually have a less intensive land use, more recent deforestation and more forested landscapes facilitating natural regeneration (Chazdon *et al*. 2007), and consequently a greater potential for biodiversity persistence and/or recovery. As HDI increases to medium HDIs, land use intensity increases, there is less forest area and there are other environmental impacts (e.g. high levels of hunting, pollution) that can influence the recovery of biodiversity. As HDI increases further, environmental degradation decreases due to higher sensitivity of the population to care for the environment and programs focused on recovery of degraded land increase, again facilitating natural regeneration. Additionally, the "economic development path" may also help to explain this pattern of forest recovery as increasing urbanization and economic development can promote a rural-urban migration thus promoting natural regeneration in agricultural abandoned lands. In Latin American countries, forest transition is observed within marginal lands previously occupied by extensive pastures (Grau & Aide 2008): high quality agricultural land has become monocultures of commodity crops, while steep slopes have been converted to commercial forestry or abandoned allowing vegetation recovery (Aide & Grau 2004, Rudel *et al.* 2005, Meyfroidt *et al.* 2010). Countries like Puerto Rico, Costa Rica, Ecuador, Mexico, and Honduras show a significant increase in forest cover in the last 60 years (Aide & Grau 2004). While these forest gains are not intentional but rather they were a consequence of demographic and economic changes, marginal agricultural land presents a potential opportunity for making space for natural regeneration that minimizes competition for land.

Contrasts between biogeographic realms also represent differences in terms of species richness of these tropical forests (Leigh *et al.* 2004, Slik *et al*. 2015). Indo-Pacific and Neotropics region shows high tree species richness compared to continental tropical Africa (Slik *et al.* 2015). Therefore, an initial high species richness could be one of the reasons for slow biodiversity recovery in Indo-Pacific and Neotropics. Previous studies demonstrated that vegetation structure in the Neotropics can be recovered in a few decades (Guariguata & Ostertag 2001). On the other hand, species richness and composition can take centuries (Liebsch *et al.* 2008) and past land use intensity as well as the distance to propagule sources represent important barriers to natural regeneration (Guariguata & Ostertag 2001, Crouzeilles & Curran 2016). Moreover, past land use plays an important role in the net change in local richness in the Neotropics and Indo-Malay region (see Newbold et al. 2015).

Our results, showing that areas that had suffered intensive transformation tend to have most impoverished biodiversity than those that had suffered extensive transformation (Fig. 4C) also corroborate with that of other authors (Lamb *et al.* 2005, Chazdon *et al.* 2007). Natural regeneration within areas of extensive transformation provided a higher biodiversity response as compared with the reference systems (Fig. 4C). Areas with extensive occupation as the past disturbance (represented by agroforestry and shaded-plantation) showed higher biodiversity responses in natural regenerated forests than in reference forests (Fig. 4C). This pattern can be explained by higher resource availability for species in these areas (Tscharntke et al. 2008) and may support authors that defend a land-sharing approach (Perfecto & Vandermeer 2010; Badgley & Perfecto 2007). Badgley and Perfecto (2007), using a global dataset of 293 yield ratios for plant and animal production, argue that agroecological production systems that are based on organic agriculture principles could suffice to provide enough food to global population. Green manures derived from nitrogen-fixing legumes can provide enough biologically fixed nitrogen to replace synthetic nitrogen fertilizer (Badgley & Perfecto 2007). Other authors claim that where large-scale intensive farming is not viable due to unfavorable biophysical conditions, agroforestry and other nature-friendly types of farming can contribute to increased tree cover (Fischer *et al.* 2008), which will be beneficial for some objectives (e.g. protection from erosion, carbon storage) but less effective for others (e.g. conservation of species dependent on relatively undisturbed forest).

Disturbance events have important implications for ecological resilience and ecosystem functioning of natural regenerating forests and ecosystems will present distinct recovery trajectories depending on the type, intensity and frequencies of disturbance events (Guariguata & Ostertag 2001, Colón & Lugo 2006, Jones & Schmitz 2009). These factors will greatly drive the success of forest regeneration as topsoil loss, reduction in soil fertility may diminish the survival and establishment rate of seedlings and facilitate invasion of disturbance-adapted species that compete with forest species (Guariguata and Ostertag 2001, Lamb *et al*. 2001, Scervino & Torezan 2015). A recent study in the Brazilian Atlantic Forest showed that the main variables influencing natural regeneration were soil type, topographic position, slope and distance to forest, urban areas and roads (Rezende *et al.* 2015).

Analyzing intensive occupation separately, our results show that Afrotropic realm presents higher biodiversity response ratio in naturally regenerating forests as compared to others realms (Supplementary Fig. 1A). The history of disturbance in Africa has been mentioned as a main mechanism to explain this pattern (see Cole et al. 2015). This result has important implications to increase forest cover in Africa through passive restoration, especially considering economic barriers to implementation of restoration projects. Natural regeneration is the cheapest way for the large-scale restoration (Rodrigues *et al.* 2009, Holl & Aide 2011, Brancalion *et al.* 2012). Furthermore, regeneration is significantly faster in African forests compared with those in South America and Asia (Cole *et al.* 2014) and may present an attractive alternative both for biodiversity recovery and provision of ecosystem services for both local and global population.

Programs and policies that promote sustainable increase of agricultural productivity while freeing marginal lands for forest re-growth can actively favor natural regeneration (Latawiec *et al.* 2015). In Brazil, it has been shown that land sparing for large-scale reforestation of Atlantic Forest can come from extensive cattle-ranching farms (Latawiec *et al*. 2015). Strassburg *et al*. (2014) shows that most of Brazilian pasturelands are characterized by relatively low current levels of cattle ranching productivity but with considerable potential for growth (about two thirds) which corroborates that increasing cattle productivity in these areas is a viable option to spare other areas for restoration.

Our study explored for the first time correlations between natural regeneration, biodiversity response and HDI within a global meta-analysis and future studies could complement this effort by considering other variables. It is important to highlight that it was not the aim of this study to identify the most important factors that govern natural regeneration but rather to explore biodiversity response of forest recovery and factors selected during the literature review. Other factors may affect natural regeneration, such as time since abandonment (Crouzeilles et al. *in press*) and the landscape context (amount of forest cover, proximity to other forest fragments or matrix permeability; e.g. Crouzeilles & Curran 2016), however, few selected studies had this information available (Leite *et al*. 2013, Crouzeilles & Curran 2016). In addition, the biodiversity response to natural regeneration reflects the pattern produced by ecological metrics of richness and abundance, which composed most of our dataset. The recovery of species similarity and diversity is likely to take orders of magnitude longer than abundance and richness (Dun 2004, Curran *et al.* 2014, Crouzeilles et al. *in press*).

Therefore, indicators such as similarity of species composition can misrepresent mega biodiverse areas, such as our study region, due to a high beta diversity. Secondary forests with the same past land-use, environmental and initial conditions can have significant differences for species density and successional trajectories, which reinforces the role of stochastic processes in the recovery of biodiversity (Norden *et al.* 2015). Nationally aggregated data (such as HDI index) has limitations when explaining regional and local processes, and future studies on natural regeneration could focus on finer landscape context data and other more sensitive ecological metrics of community change (e.g. similarity indices and functional diversity) (Crouzeilles et al. *in press*).

Regarding the case study considered here, the new Forest Code showed a limited impact on the available space for large-scale restoration in private farms, thus forest cover may not increase to minimum levels to support biodiversity persistence in Atlantic Forest landscapes as a result of this policy (Banks-Leite *et al.* 2014). This outcome is a direct consequence of the environmental setbacks of the new law, which authorized: i) the maintenance of agricultural land uses and infrastructure in portions of APPs and reduced their restoration requirements; ii) accounting native vegetation of APPs to reduce LR deficit, thus reducing restoration requirements of LRs; and iii) removed the obligation to restore LRs in small- and medium-sized farms (Garcia *et al.* 2013). In addition, part of the deficit of LR can be compensated by hiring or buying the LR surplus of other farms (i.e., native forest cover exceeding the 20% required), which may further reduce restoration area.

Following expectations, the Forest Code revision, which reduced restoration requirements of small- and medium-sized farms to avoid losses of agricultural production and minimize investments in restoration, the proportion of APP area eligible for restoration amnesty was higher in smaller farms. Consequently, the percentage of the farm area that must be restored reduced with farm size, i.e., larger farms required a higher restoration effort than smaller farms. Given the old and intense land use of the region, active restoration predominated, a similar result obtained in regions dominated by sugarcane plantation in southeastern Brazil (Rodrigues *et al.* 2011). Given the higher proportion of flat and productive lands in large farms, where historical land use intensification would compromised the use of passive or mixed restoration, and concentration of marginal agricultural lands in smaller farms, we anticipated that the proportion of active restoration would increase with farm size. However, contrary to our hypothesis, the proportion of active restoration was not influenced by farm area both in APPs and LRs.

Our results show that the new law drastically reduced restoration requirements of individual farms, thus reducing the potential of this legislation to drive large scale natural regeneration. On one hand, the previous version of the Forest Code required more restoration, but compliance levels were very low and restricted to some few agricultural sectors more pressured by environmental sustainability standards of the market. On the other hand, the new Forest Code weakened restoration requirements, but created more effective mechanisms to support legal compliance. For instance, the Environmental Registry System establishes that every farm of Brazil has to declare, in a web-based, geospatial system, its deficit of native vegetation in APP in LR, in order to better plan financial incentives and technical support to foster restoration, and legal enforcement activities. Up to January 31th, 2016, ~2.3 million farms, which encompass an area of 263 million hectares (66% of the total land that must be registered), had already been incorporated in CAR (SFB 2016). Such positive outcomes may foster a massive involvement of farmers in restoration in the coming years, using CAR as the platform for implementing a national-wide restoration plan, mostly in tropical forests. Thus, in spite of the reduced area to be restored in each farm, the massive involvement of farms may ultimately result in a very large area to be restored in the whole country. To illustrate, if the same restoration diagnosis obtained for the 63,338 hectares of farms evaluated in this work are directly applied to the state of Bahia (6.63% of Brazil area), which has 29.581.747 hectares that must be registered in CAR, an area of almost 1 million hectares would have to be restored. If extrapolated to the whole of Brazil, it would yield an area to be restored equal to 13,5 million hectares. Interestingly, this area is very similar to the 12,5 million hectares expected by the National Plan for the Recovery of Native Vegetation (PLANAVEG, in the Portuguese acronym).

Conclusions

Factors influencing natural regeneration are heterogeneous and they depend on a range of biophysical, ecological and socioeconomic factors. On one hand, marginal lands (with low agricultural potential) offer space for natural regeneration but it is often because they are degraded and with little use for agriculture, thus their degradation can also hamper natural regeneration and biodiversity recovery. In a global perspective, we suggest that biodiversity recovery in natural regenerating forests is likely to occurs predominantly in: i) countries with either low, high HDI or very high HDI; ii) areas with less intensive past disturbance; and iii) less biodiverse realms – although it not means a good criteria to identify these areas. There is also a need to reconcile food production and taking the best areas for regeneration may sometimes be socially or politically unacceptable. Planning for natural regeneration must also take into account a range of factors: maximizing biodiversity benefits, provision of ecosystem services and landscape connectivity (e.g. Crouzeilles *et al.* 2015). Prioritization of areas for natural regeneration should also always clearly define the goals to be achieved in a landscape, including the objectives of different groups of people. Agricultural (sustainable) intensification may aid creating space for natural regeneration but it needs to be combined with policies to control rebound effect (e.g. by certification, land-use zoning). Natural regeneration is a promising way to restore degraded lands and it should always be considered as an alternative for landscape restoration. Establishing legal instruments have been considered a key strategy to foster large-scale restoration in private agricultural lands, and our case study showed that the level of forest gain potentially resulting from this strategy is still substantial, despite being severely compromised by the recent revision of the law. Complementary land sparing approaches, market incentives, and financial mechanisms are also needed to promote large-scale natural regeneration in human-modified landscapes. These implications can provide general guidelines to help policymakers and restoration practitioners regarding natural regeneration efforts in tropical forests.

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Figure captions

Figure 1. Distribution of the farms used for the case study.

Figure 2. Study landscapes (n = 119) spread across tropical biogeographic realms as proposed by Olson et al. (2001) (A) and HDI ranking for these areas (B).

Figure 3. Number of selected studies according to HDI class (A), biogeographic realm (B) and past disturbance (C).

Figure 4. Bootstrapped response ratios for biodiversity according to HDI class (A), geographic realm (B) and past disturbance (C). Zero (vertical dashed line) means no difference as compared with the reference system (old-growth forest). Therefore values closer to zero mean biodiversity in regenerated forest is similar to undisturbed forest. A negative response ratio represents more biodiversity in reference areas than restores areas, while positive response means that restored areas is characterized with more biodiversity than reference area. Lines in the box plots represent the median, first and third quartile values for 10,000 bootstraps. N = sample size, site = number of study landscapes.

Supplementary Fig. 1. Biodiversity response in areas of natural regeneration that occurred in previously disturbed areas characterized as intensive occupation classified according to geographic realm (A) and HDI (B). Values closer to zero (vertical dashed line) correspond to better biodiversity response (biodiversity in regenerated forest is similar to reference forest).

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