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Meta-analysis of carbon stocks and biodiversity outcomes across Brazilian restored biomes

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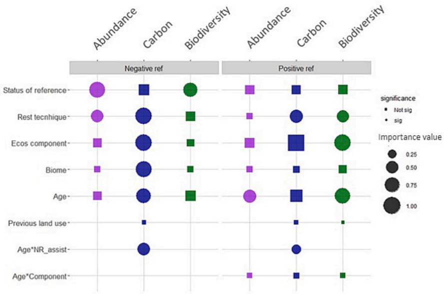
HIGHLIGHTS

- Restoration initiatives are more effective in improving degraded areas than attaining full recovery.
- Abundance is restored more easily, then carbon, then species biodiversity.
- Recovery occurs at different paces for plants, animals and soils.
- Assisted natural regeneration shows higher success than spontaneous natural regeneration and tree planting, across biomes.

GRAPHICAL ABSTRACT



Restoration of abundance, carbon and diversity in restoration initiatives across Brazilian biomes.

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ABSTRACT

Ecosystem restoration strategies vary widely in the techniques applied and ecological contexts. We conducted a meta-analysis to evaluate how restoration success varies across socio-ecological contexts, taxonomic groups and

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biomes. Restoration success is quantified as the percentage of each ecological metric value attained in the restoration site compared to the reference systems. We show that restoration success is different for plants, animals, and soils and across ecological indicators. Abundance of individuals is easier to restore than carbon stocks, which are easier than species diversity. However, abundance may be a poor indicator of ecosystem recovery because there is no unidirectional trend over time, and abundance often fails to distinguish restored from degraded areas. We also found that carbon stocks in the soil and in the vegetation are restored at analogous paces, but the recovery of soil carbon stocks is less variable than plant stocks across sites. Our results demonstrate that different restoration techniques are effective in recovering diversity and carbon stocks, but assisted natural regeneration showed a slightly higher success compared to other strategies. However, there is a considerable difficulty in restoring converted and degraded areas to achieve conditions similar to the original ecosystems. It is critical and timely to investigate benefits and effectiveness of ecosystem restoration techniques to biodiversity and carbon recovery different ecosystem types to improve the restoration effectiveness.

1. Introduction

In the last century, the Earth has gone through large landscape transformations that resulted in a rapid decline in biodiversity and ecosystem services (Lamb et al., 2005; Steffen et al., 2015). About three-quarters of land surface, previously under native vegetation cover, has been significantly altered by human activity (Bongaarts, 2019), of which one to six billion ha are considered converted or degraded (Gibbs and Salmon, 2015). Restoring these lands can bring multiple benefits for biodiversity, climate change mitigation and poverty alleviation (Brancalion et al., 2019; Strassburg et al., 2017; Strassburg et al., 2020). The need for restoration has motivated international agreements such as the Bonn Challenge and the New York Declaration on Forests, where the parties committed to bring 350 Mha of degraded and deforested lands into restoration by 2030. Achieving restoration targets requires the design of restoration strategies that are effective for different ecosystems across multiple socio-ecological contexts (McDonald et al., 2016; Strassburg et al., 2020).

Ecosystem restoration strategies vary widely in the techniques applied and associated management costs (Holl and Aide, 2011; Chazdon and Uriarte, 2016; Strassburg et al., 2016; Rohr et al., 2018). Spontaneous natural regeneration consists of abandoning fields and protecting them from disturbances (e.g., fencing out cattle and fire protection) to allow natural recovery (Shono et al., 2007; Zahawi et al., 2014; Crouzeilles et al., 2017). Assisted natural regeneration consists in applying additional management practices to speed up and increase the diversity of natural regrowth, such as controlling invasive species and planting native ones. On the other end, and at higher costs, active restoration strategies consist of applying soil amendments, planting seeds and/or saplings, and actively caring after the plantings during the first years (Shono et al., 2007; Zahawi et al., 2014).

Both spontaneous and assisted natural regeneration are usually more cost-effective strategies than active restoration in landscape contexts of low previous land-use intensity and duration, and high amounts of native vegetation cover (Holl and Aide, 2011; Jakovac et al., 2015; Chazdon and Uriarte, 2016; Crouzeilles et al., 2020). In such contexts, spontaneous natural regeneration and active restoration can deliver similar biodiversity and carbon benefits (Jones et al., 2018). In contexts of high of degradation levels (e.g. mining areas), however, there are major impediments for regrowth and active restoration will deliver more benefits and provide higher chances of restoration success (Meli et al., 2017). Restoration success can be measured by the level of ecological outcomes (or benefits) it delivers and by indicators of ecosystem recovery. The effectiveness of ecosystem restoration success depends on the goal, targeted benefits and on interactions between restoration technique and socio-environmental contexts. The decision on which restoration technique to apply takes into account a number of criteria such as the potential to deliver ecosystem services, financial resources or the ultimate goal of the restoration project (Morrison and Lindell, 2011; Strassburg et al., 2018). Strategies that introduce useful species and crops, for example, such as assisted natural regeneration and active restoration, can generate higher revenues than spontaneous natural regeneration and be preferred when socio-economic benefits are a major goal (Vieira et al., 2009; Garcia et al., 2015; de Oliveira and Carvalhaes, 2016; FAO, 2017; Miccolis et al., 2019; Badari et al., 2020).

When the goal is ecosystem restoration, indicators of restoration success usually include metrics that cover three ecological outcomes: structure, biodiversity, and ecological processes (Ruiz-Jaen and Aide, 2005). These ecological outcomes, or benefits, can be quantified by different metrics. Most common metrics are individuals′ abundances and amount representing structure, number of species and taxonomic and functional diversity representing biodiversity, and biomass or carbon stocks representing a key ecological process that is productivity (Ruiz-Jaen and Aide, 2005; Wortley et al., 2013). The recovery of these three ecosystem components is also associated with ecosystem services such as soil protection against erosion, biodiversity conservation and carbon sequestration, and therefore are highly relevant for ecosystem restoration programs.

Ecosystem services provided by restoration as well as the major ecological components associated with ecosystem recovery vary with ecosystem type. Forest restoration and tree planting schemes offer significant potential for carbon sequestration and storage in aboveground biomass, while grasslands restoration has a great potential of storing carbon in the soil and belowground biomass (Overbeck et al., 2015; Koch et al., 2022). Therefore, understanding how different ecological components can be restored by distinct restoration strategies in different biomes is of outmost importance in order to improve restoration effectiveness.

We conducted a meta-analysis to quantify ecosystem restoration success across the six Brazilian biomes. Specifically, we aimed to answer three research questions: i) how successful are different restoration strategies in restoring biodiversity, abundances and carbon stocks across biomes?; ii) How restoration success varies between different ecosystem components (plant, animals and soil components)?; and iii) which factors influence the restoration of abundance, diversity and carbon across biomes? This synthesis study will help advance on the understanding of how hard is the restoration of different ecosystem components across biomes, and provide directions for increasing the effectiveness of ecosystem restoration in multiple biomes.

2. Methods

2.1. Data collection

We searched the scientific literature to identify studies that provided quantitative data of individual's abundance, species diversity, and carbon stocks in both restored and reference systems. We included studies from all six biomes in Brazil, including wet forests (Amazon, Atlantic Forest), dry forests (Caatinga), savannah (Cerrado), grasslands (Pampa) and wetlands (Pantanal). We considered as ‘restored systems’ those where active or passive restoration techniques have been applied. Reference systems were classified as ′positive′ and ′negative′ references. Positive reference systems included the original ecosystem which had experienced no or low disturbance (as indicated in the study). Negative reference systems included the alternative land uses such as bare soil, pasture, agriculture, and post-mining areas.

The search was conducted in international online databases: Web of Science, Scopus and Science Direct, as well as in Brazilian databases such as Scielo and Periódicos Capes. Publications until December 2018 were included, without restriction of starting year. We applied a Boolean search in English and Portuguese for the title, topic and abstract, including a combination of keywords related to restoration techniques, attributes, and biomes (Supplementary material, Table S1). This search returned 833 articles. Additionally, we used snowball approach to include the references cited in two recent reviews on restoration and agroforestry systems in Brazil (Crouzeilles et al., 2016; Santos et al., 2019) (Table SI1, Fig. SI1), adding 69 studies.

To be included in the meta-analysis, studies had to meet all following criteria: i) have been carried out in Brazil, ii) provide quantitative measurements of biodiversity recovery and/or carbon stock in both restored and reference systems (positive or negative reference systems), and iii) have multiple sampling sites (replicates) for both restored and reference systems (Fig. SI1). After checking the abstracts and eliminating duplicates, 201 studies were selected to have their full text checked. Finally, after analysing the entire articles, we retained 104 studies that met the inclusion criteria and then retrieved standardized information as described next (Table SI1).

We gathered the following information from the selected studies: i) geographic region, ii) latitude and longitude, iii) year of data collection, iv) age of the restored system (years elapsed since restoration began), v) total area restored (hectares), vi) land-use history, vii) biome, viii) type of reference (positive or negative), ix) status of the reference system, xx) restoration technique, xi) ecological metric (abundance, diversity, carbon), xii) type of ecological metric (e.g. Shannon diversity index, species richness), xiii) quantitative value of the ecological metric, xiv) and the ecosystem components (soil, animal or plant).

The information extracted from the studies was reclassified for the analysis as follows. Restoration technique was classified into three groups: spontaneous natural regeneration, assisted natural regeneration (includes agroforestry systems based on natural regeneration and assisted secondary succession), and active restoration (plantations of native or non-native species meant for ecosystem restoration) (Shono et al., 2007, Morrison and Lindell, 2011; Holl and Aide, 2011; FAO, 2017). Given the low number of studies in the non-rainforest biomes, those were grouped under the category ‘OTHER’, and the remaining were categorized under ‘Amazon’ or ‘Atlantic forest’. Ecological metrics were classified as abundance (e.g. density of individuals, total number of individuals, cover), diversity (e.g. Shannon index and evenness (J’), species richness, rarefied species richness), and carbon stock (total carbon in the soil, soil microbial biomass, aboveground and belowground biomass, soil organic matter and soil CO_2 efflux). Each ecological metric was represented by three ecosystem components: plant, animal and soil. Previous land-use history was classified into six groups: i) agriculture (conventional agriculture); ii) shifting cultivation (i.e., swidden agriculture, swidden-fallow agriculture, slash-and-burn agriculture); iii) pasture (i.e. cattle or buffalo ranching, cultivated grassland); iv) mining; v) clear-cut (no land use after the native vegetation was cut and immediate start of regrowth/restoration); iv) multiple previous land uses (underwent multiple land uses, usually agriculture and cattle ranching or silviculture). Reference systems were further classified by their status, i.e. their disturbance history or land-use type. Positive references were classified into ‘disturbed’ (for native ecosystems that were subjected to low disturbance, e.g. selective logging) or ‘mature’ (for non-disturbed native ecosystems). Negative references were classified into agriculture, pasture, or degraded areas (i.e., mined areas, degraded abandoned pasturelands). The list of variables and subcategories retrieved from the articles and used in this study is provided in Table S2-1.

2.2. Data analyses

From the 104 studies selected, we calculated 1987 response rations (RR) hereafter referred to as samples (Fig. 1). The RR was calculated as the natural logarithm of the ratio between the mean value for biodiversity, abundance or carbon stock within the restored system ($\bar{X}_E$) and the reference system ($\bar{X}_C$) within the same study, $RR = \bar{X}_E / \bar{X}_C$. RRs were calculated separately relative to positive or negative reference systems. The same study may present comparisons with both reference systems, and based on more than one ecological metric, so for each study often multiple RRs were calculated. A positive RR means that a given site has a higher value of biodiversity, abundance or carbon stock in the restored system than in the reference system of the same study site, while a negative RR means the opposite.

Approximately 70 % of the samples ($n = 1334$; $N = 76$ studies) had complete information on ecological metrics, biome, restoration technique, reference system status, age of restoration, and previous land-use type. After eliminating outliers, the dataset contained 1281 samples (76 studies).

We used a multi-model inference approach to identify the drivers of RR variation across studies and quantify their effects sizes on the recovery (i.e. RR) of species diversity, abundance and carbon stocks compared to reference systems (Burnham and Anderson, 2002). This approach consisted in, for each response variable, first running the model with all variables, second running a stepwise model selection and third averaging the best models to retrieve the average model parameters, as we describe in detail below.

First we built eight generalized linear mixed effect models (GLMM) in which RR was the response variable, the study ID was the random factor and the following variables were fixed factors: ecological metric, restoration technique, age of the restoration system, previous land use, biome, reference status, and the ecosystem components (see details in Table S2-1). Each model contained different sets of the data. The two first models run contained all samples with positive references and the other one including samples with negative references. These two models were named global model for positive reference and global model for negative reference (see Table S2-1 and 2). In these models, we included all possible two-way interactions between pairs of fixed factors that did not have a singularity. Because both global models indicated significant interactions with ecological metrics (Table SI2-1), we then ran separate GLMM for the subset of samples containing each ecological metric (abundance, diversity, and carbon) and reference system (positive or negative). Numeric variables such as the response variable “RR” and the fixed factor “age” were centred using the function *scale* of the nlme package for R. GLMM were fitted using the lme function from the nlme package for R (Pinheiro et al., 2021).

Second, for each of the eight GLMM, we applied a stepwise model selection procedure using the *dredge* function of the MuMIn package for R, which generates all combinations (subsets) of fixed effect terms and returns a list of models ranked based on the Akaike Information Criteria (AIC) (Bartón, 2015). When collinearity was detected between pairs of variables, we kept only the variable with the largest effect size.

Third, for each of the eight GLMM, we calculated an average model based on all models within a delta AIC ≤ 2 (Burnham and Anderson, 2002) (Table S2-2), using the *model.avg* function from the MuMIn package for R (Bartón, 2015). We extracted the conditional-averaged-model estimates, confidence intervals, and relative importance of each variable kept in the average model. The relative importance of each variable is measured as the sum of the AIC weights over all models in which that variable appears and is calculated independently for each average model (Burnham and Anderson, 2002). Additionally, we reported the explanation coefficient (marginal R_m^2 and conditional R_c^2) of the best models used in the averaged models, to provide a measure of variance explained (following Burnham and Anderson, 2002).

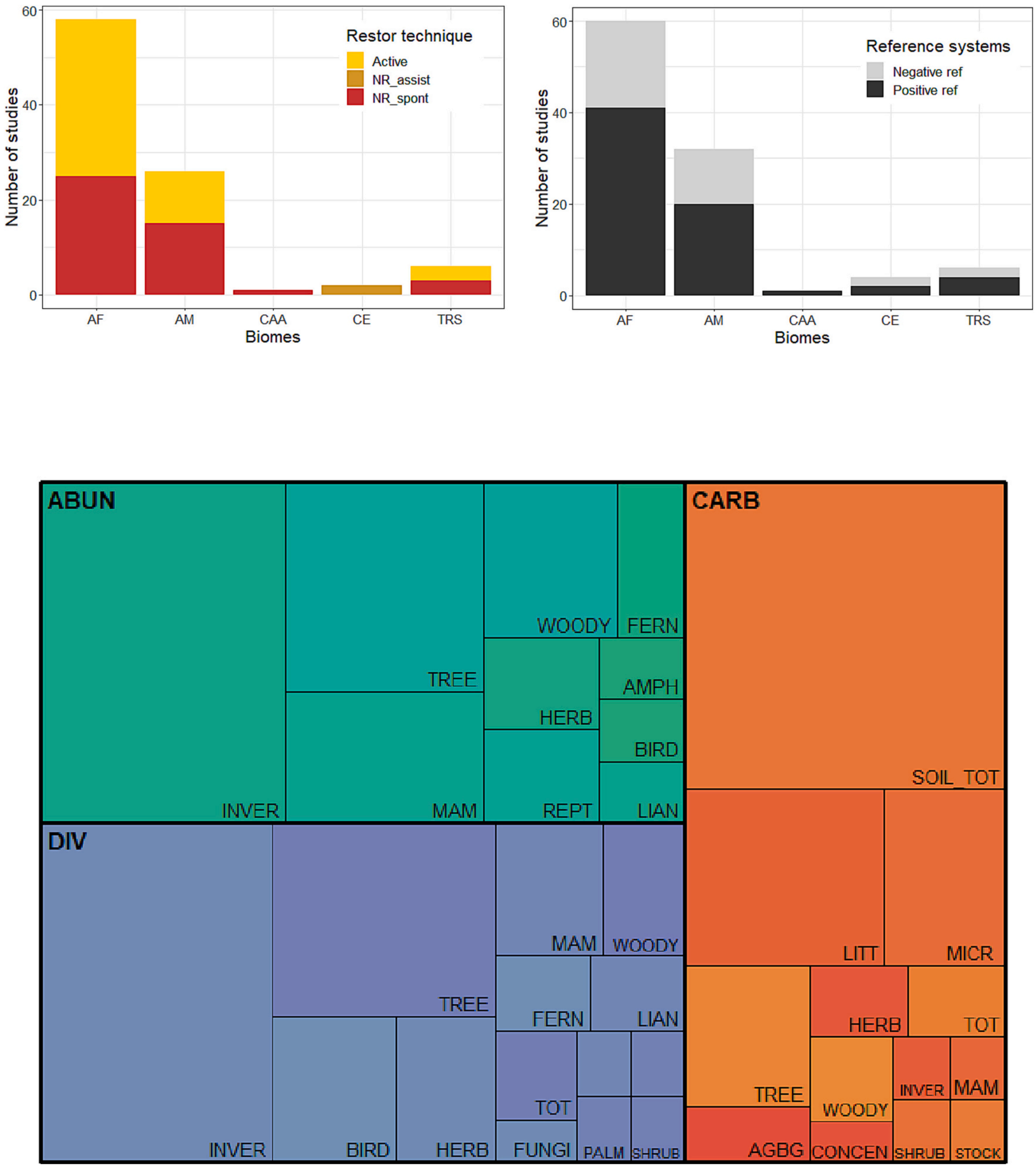

Fig. 1. Distribution of data across restoration techniques (A), type of reference system (B), and ecological metrics (C). In Fig. A, restoration techniques are Spontaneous Natural regeneration – NR_spont, Assisted Natural regeneration – NR_assist and Active restoration – Active. Biomes are Atlantic Forest – AF, Amazon – AM, Caatinga – CAA, Cerrado – CE and Transitions between the Amazon or Atlantic Forest and the Cerrado – TRS. In Fig. B, reference systems are areas before restoration (negative references) and original natural ecosystems (positive reference). In Fig. C, the size of squares represents the proportion of studies in the analysed literature that report information on each ecosystem components (e.g. Plants, soil, invertebrates, vertebrates, etc.) within each ecological metric of individuals ́ abundance (ABUN), species diversity (DIV) and carbon stocks (CARB).

3. Results

From the 1281 samples (76 studies) used in the analyses, 541 (42.2 %) refer to carbon metrics, 517 (40.4 %) to diversity metrics and 223 (17.4 %) to abundance metrics. Most studies (92 studies; 86 %) were conducted in wet forest biomes (Amazon and Atlantic Forest), while dry biomes (Cerrado and Caatinga) were represented in only 12 studies (14 %) (Fig. 1). There were no studies conducted in the Pantanal wetlands nor in the Pampa grasslands that matched the selection criteria. The number of samples and studies for each ecosystem component (plant, animal, soil) and response metric (diversity, carbon, abundance) is provided in the supplementary material (S2-2).

The recovery of restored areas is represented here by the response ratio (RR) calculated in relation to positive and negative references. When compared to the positive ecosystem (n = 777 samples, N = 68 studies), most systems under restoration showed lower values (negative values of RR) (Fig. 2-A), showing they still didn't attain the same values as the original ecosystem. When compared to the negative reference (n = 504 samples, N = 35 studies), most systems had higher RR values, represented by positive RR values (Fig. 2-B), suggesting that restoration is moving the system away from the degraded condition. Regarding the restoration technique, assisted natural regeneration showed higher RR values for carbon and diversity compared to spontaneous natural regeneration and active restoration, when comparing to both positive and negative references (Fig. 3). For abundance metrics, assisted natural regeneration yielded higher values when comparing to the negative

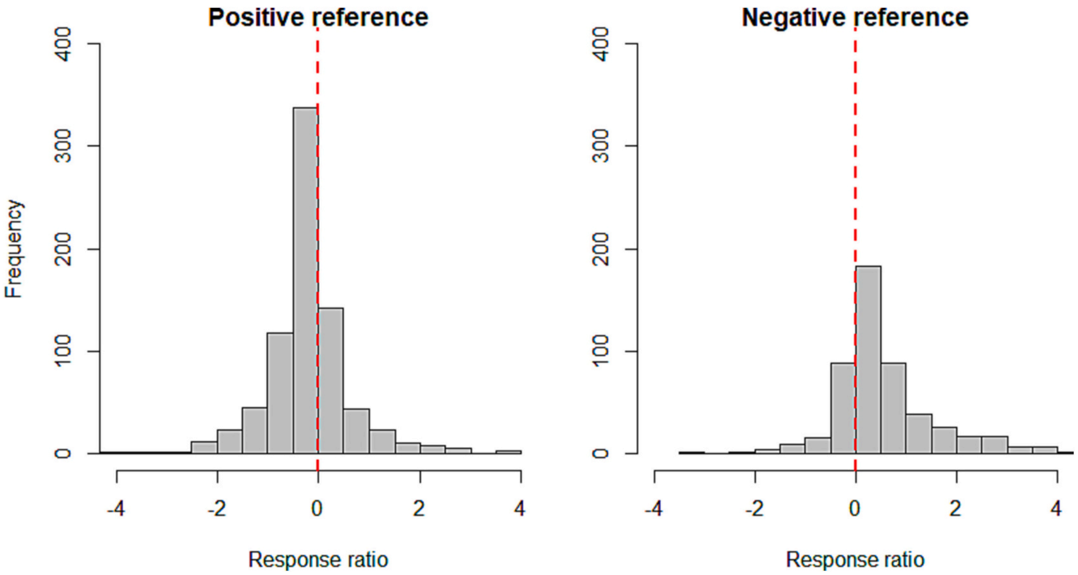

Fig. 2. Distribution of response ratios calculated based on the comparison between restored areas and positive (left) and negative (right) reference systems. The vertical red line indicates when restored systems have equal values to reference systems. All metrics for diversity, abundance and carbon are included.

reference, but restoration techniques didn't yield significant differences when compared to the negative references (Fig. 3).

The two average global models showed significant differences across ecological metrics and significant interactions between metric, biome and restoration technique (Table S2-1). Compared to positive references, restored systems tend to have higher RR with increasing restoration age, and higher RR for abundance than for carbon and diversity, for animals than soil biota and plants (Table S2-2). Compared to negative references, RR was higher for carbon stocks and diversity than for abundance (Table S2-3). To further investigate the significant interactions between metric, biome and restoration technique, we rerun the analyses and calculated average models for each metric separately.

Diversity RR were calculated from 46 studies and 517 samples. The diversity of animals was mainly derived from studies with invertebrates (65 % of studies), the diversity of plants was predominantly from trees (43 % of the studies) and of the soil biota is entirely from fungi (Fig. 1; see Table S2-1 for the number of studies and samples). The average model for diversity metrics comparing restored systems with positive references (n = 402; N = 43) explained 36 % of the data variation (R^2_m = 0.14 - only fixed effects, R^2_c = 0.36 – fixed and random effects) and showed significant effects of restoration age, ecosystem components, restoration technique, biome and status of the reference system (Fig. 4). The RR of diversity increased with restoration age, being lower for plants then animals and higher for assisted natural regeneration than for spontaneous natural regeneration (Fig. 5, Table S2-2). When compared with the negative references (n = 115; N = 18), only the status of the reference system was significant, with pasture showing higher RR than agriculture, suggesting that restored systems are more different from pastures than from agricultural fields in terms of species diversity.

Carbon RR were calculated from 38 studies and 541 samples. Carbon stocks and biomass measures for animals were available only for invertebrates (67 % of studies) and mammals (33 %), for plants they were predominantly from dead biomass in the litter (38 % of the studies) and from trees and woody vegetation (34 % of the studies). For the soil component, carbon stocks were mainly from total carbon stocks (90 % of the studies) (Fig. 1, Table S2-1).

For carbon metrics, the significant factors in the average model for positive reference (n = 201; N = 33) were assisted natural regeneration that was higher than spontaneous natural regeneration and the interaction between restoration age and assisted natural regeneration (Fig. 4), suggesting a higher recovery of carbon stocks with time in assisted compared to spontaneous natural regeneration systems. Such values did not differ from active restoration. Compared with negative references (n = 340; N = 24), the Atlantic Forest showed lower RR than the Amazon and higher RR than the other biomes. RR of carbon for plants was higher than for soils, and higher in assisted than in spontaneous natural regeneration (Fig. 4).

Abundance RR were calculated from 35 studies and 223 samples. Animals abundance was predominantly from invertebrates (62 % of studies) followed by mammals (13.5 %), plants abundance was predominantly from trees and woody vegetation (70 % of the studies) and abundance of the soil biota was entirely from fungi (Fig. 1, Table S2-1). For abundance metrics, no factor was significant when compared with positive references (n = 174; N = 33; Fig. 4). When compared to negative references (n = 49; N = 10), RR was marginally higher in assisted than in spontaneous natural regeneration and higher for degraded lands than for pastures or agriculture (Fig. 4).

Across the six average models presented above for each metric (Fig. 4), restoration technique showed the highest effect size, followed by the reference system's status, biome, restoration age and ecosystem components. These factors also had the highest relative importance and therefore were retained in several average models (Fig. 5, Table S2-1). Since previous land-use had lower importance than all other variables, and was not retained in any average model, we excluded this variable and rerun all models. This allowed the inclusion of studies previously eliminated from the analysis for missing this information. The larger dataset containing n = 1539 samples and N = 91 studies confirmed the patterns described above and are not presented here.

4. Discussion

Our results demonstrate that restoration success is highly variable and depends on the monitored metric, the restoration technique applied and on the biome. We also found that most restoration initiates result in considerable improvement compared to degraded areas but may still be far from full recovery. These results, therefore, suggest that there is a considerable difficulty in restoring converted and degraded areas to achieve conditions similar to the original ecosystems and that diversity is the hardest component to restore. While restored areas, regardless of the restoration technique, show higher values of carbon and diversity metrics when compared with degraded areas, such as agricultural lands and pastures, restored areas tend to have lower diversity and carbon

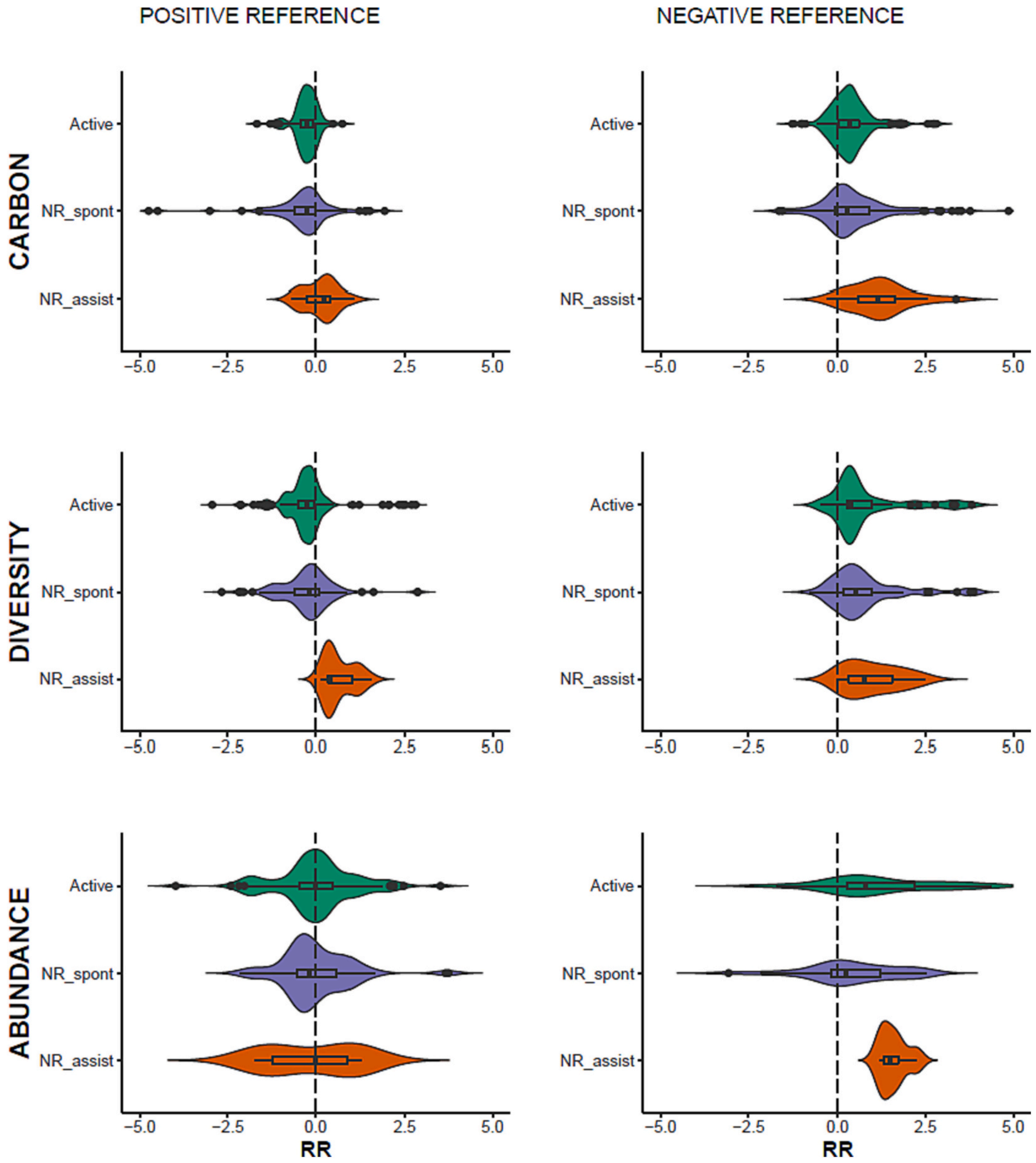

Fig. 3. Recovery levels across restoration techniques (active, spontaneous natural regeneration and assisted natural regeneration), metrics (carbon stock, diversity and abundance) and reference systems (positive and negative references). The graphs show the distribution of response ratios (RR). Boxplots show the median and 95 % quantiles. RR equals to zero means the restored system has similar values to the reference systems. RR tend to be negative when compared to the positive reference and positive when compared to the negative reference.

stocks than the positive reference systems, even when the latter comprises disturbed natural vegetation. It is important to note that most restoration initiatives analysed here are <20 years old. In naturally regenerating secondary forests, carbon and biodiversity take >20 years to attain levels similar to original systems in forest biomes (Poorter et al., 2016; Rozendaal et al., 2019). Another study on six major ecosystems (forest, grasslands, wetlands, rivers, lakes and marine ecosystems) compared reference to recovering ecosystems, indicating that the latter have annual deficits of 46–51 % for organism abundance, 27–33 % for species diversity and 32–42 % for carbon (Moreno-Mateos et al., 2017). It also suggests that disturbed ecosystems might still do better than young restoration in terms of diversity and carbon stocks, highlighting their conservation value and their role in landscape restoration initiatives.

Nevertheless, restoration initiatives have been able to significantly improve degraded areas especially comparing to pastures or mining (Fig. 4), which hold extremely low levels of biodiversity. RR values of restored areas showed a larger variation in comparison to agriculture than to pastures, probably because of the wide sort of agricultural management approaches. The use of chemical inputs and mechanized techniques can result in high levels of soil degradation, but small-scale and shifting cultivation systems might allow higher levels of biodiversity in the cropping fields (Padoch and Pinedo-Vasquez, 2010; Edivaldo and Rosell, 2020; Mukul et al., 2020). Therefore, land use systems offer different starting points for restoration. Evaluating this starting point and the potential for natural regeneration in each situation is the first step for increasing the efficiency of restoration initiatives (Shono et al., 2007; Rohr et al., 2018).

4.1. Recovery of ecosystem components

Our results show that ecological recovery occurs at different paces for each metric and ecosystem component. Abundance is easier to restore than carbon stocks, which are easier than species diversity, as

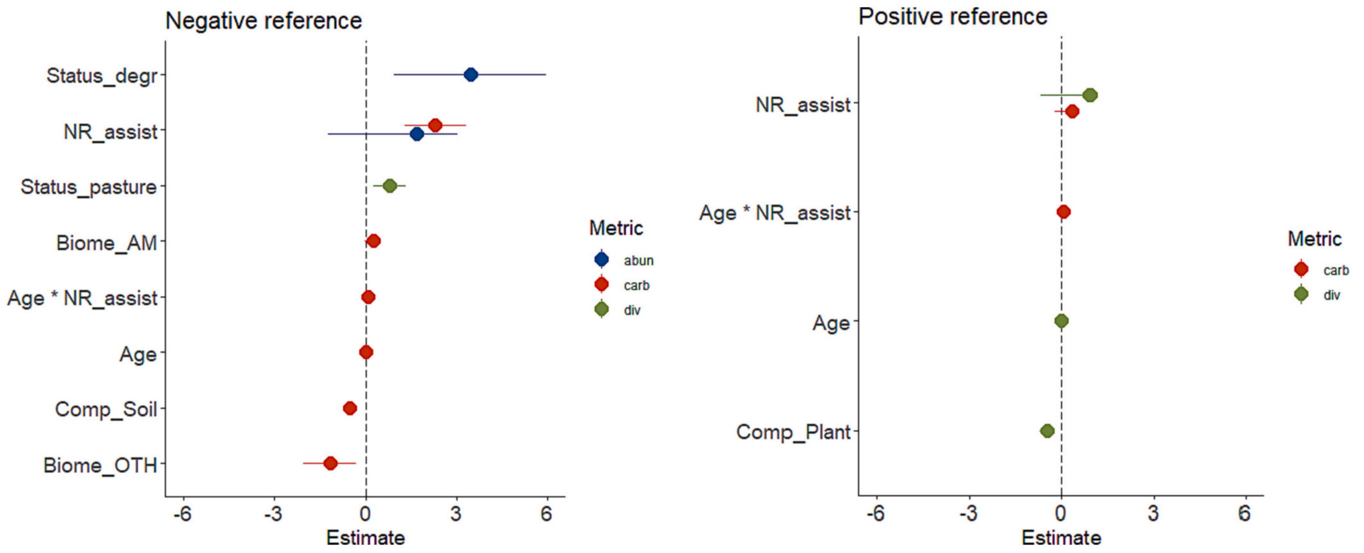

Fig. 4. Conditional effect sizes of significant variables retained in the average models for positive reference (left) and negative references (right). The average effect sizes and confidence intervals are shown only for the significant predictors in the average models. Variables are: Status_degr (reference is degraded area), NR_assist (Assisted natural regeneration), Status_pasture (reference is pasture), Biome_AM (Amazon biome), Comp_Soil (Soil component), Biome_OTH (class other biomes), Comp_Plant (Plant component).

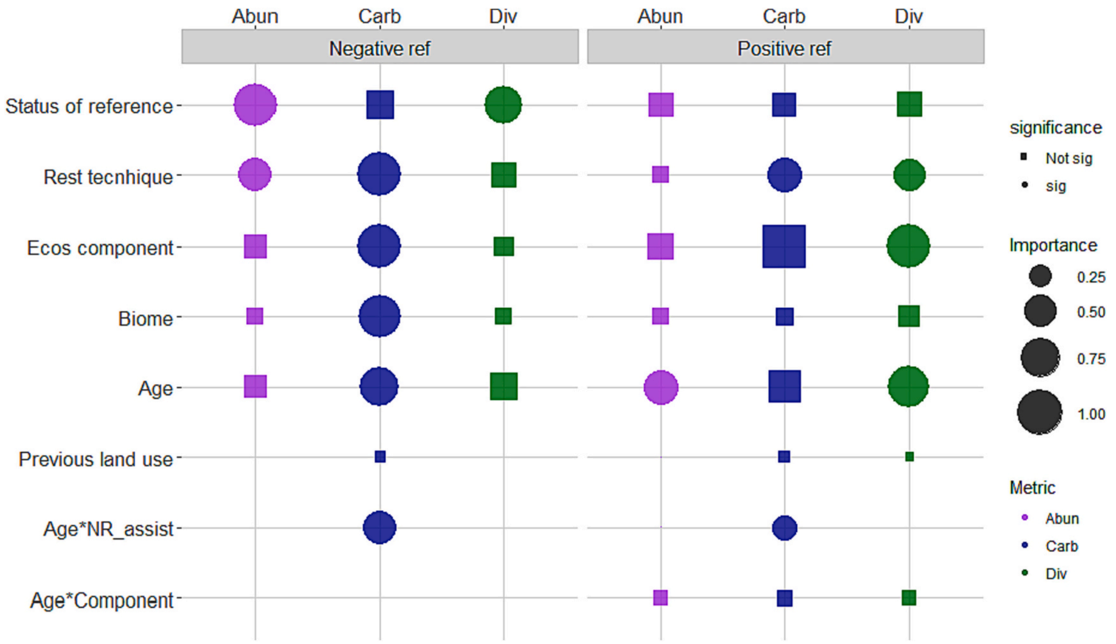

Fig. 5. Variables importance values in response ratios models. Variable's importance across the average models testing the effects of different factors (rows) on the response ratio of abundance (purple), carbon (blue) and diversity (green) in relation to the negative and positive references. Each column represents one model. Rows refer to each variable retained in the average model with its respective importance value and significance level (circle symbols refer to significant variables and squares to non-significant ones). Variable importance varies from zero to one and are represented by the size of circles.

shown by the negative estimates in Table SI2-2. However, abundance may be a poor indicator of ecosystem recovery status as abundance levels in restored areas often equal or surpass the values in positive reference systems (Fig. 3). In forest biomes, for example, abundance of plant species peaks at intermediary stages of succession before it is reduced as a consequence of competition, showing a hump shape variation over time (Peet and Christensen, 1987; Burkhart and Tomé, 2012; Vospernik and Sterba, 2015; Cardoso de Oliveira et al., 2019). Also, abundance levels in restored systems often do not differ from those found in pastures and agricultural lands (Fig. 3), providing little information on the system's recovery status. Therefore, abundance may not be a good indicator of restoration success because there is no unidirectional trend over time, and it often fails to distinguish restored from degraded areas.

On the other hand, diversity and carbon levels tend to increase with restoration age and vary between ecosystem components. Our results suggest that carbon stocks in the soil and vegetation are restored at analogous paces, but the recovery of carbon stocks in the soil is less variable than in plants. This is supported by previous studies that showed that soil organic carbon stocks can recover quickly after disturbance and remain largely unchanged in the first decades of restoration (Sierra et al., 2012; Martin et al., 2013; Wang et al., 2017).

We also found that values of soil carbon stock are more similar to negative references than plant carbon stocks, suggesting that soil carbon stocks are relatively higher than in vegetation. This agrees with previous studies showing that pastures may retain high soil carbon content, facilitating the restoration of carbon stocks (Martin et al., 2013) but not necessarily of biodiversity (Fig. 4).

Species diversity levels tend to be restored more easily for animals (mainly studies on invertebrates) than for plants (mainly studies on woody vegetation). This agrees with previous studies that showed this effect is likely due to a faster recovery of invertebrate (Meli et al., 2017). In hyper diverse tropical ecosystems, as the ones included in this analysis, the full recovery of plant species diversity will depend on the arrival of forest-specialist species that usually occur at low densities and require animals to disperse their seeds, a process that can take over 50 years to be accomplished (Rozendaal et al., 2019). Hence, restoration strategies should foster the recovery of plant species through the management of natural regeneration or by planting saplings in high diversity. In defaunated landscapes, it might be necessary to reintroduce seed dispersers, in order to enhance plant diversity (Galetti et al., 2017; Genes et al., 2017).

Across biomes, we only found differences in the restoration success of carbon stocks and not for diversity or abundance. Carbon stocks in the soil and vegetation were more similar to the original systems in the dry forests of the Cerrado and Caatinga than in the wet forests of the Amazon and Atlantic Forest (Fig. 4, Table S2-2). Although diversity recovery was not significantly different across biomes (Fig. 4), dry forests under restoration were more similar (higher RR) to the positive reference and had lower variation than those in the Amazon and Atlantic forests. These analyses controlled restoration age (Fig. 4), which was retained in the final model and did not have significant interactions with biome (Table S2-2). Our data on carbon is mainly derived from aboveground tree biomass and soil carbon stocks in the soil (Table S2-2). Together, these results suggest that restoring carbon and biodiversity is easier for dry than wet ecosystems, mainly because dry ecosystems have lower values of aboveground carbon and biodiversity compared to wet systems, potentially allowing recovery in a shorter amount of time. However, dry forests and non-forests ecosystems are clearly underrepresented among restoration initiatives and among our samples (Fig. 1). Therefore, more research is needed to better understand the restoration outcomes in such ecosystems.

4.2. *Efficiency of restoration strategies*

Our analyses corroborate previous studies showing that spontaneous natural regeneration yields similar results to active restoration strategies (Meli et al., 2017; Latawiec et al., 2016). This is partly explained by the wide variation in outcomes in both approaches (Fig. 3) likely stemming from a large heterogeneity in terms of previous land use, soil conditions, and landscape context. Our results indicate that managing natural regeneration reduces such variation in restoration outcomes for biodiversity and carbon, promoting a faster recovery and diminishing chances of failure (Figs. 3, 4). These results were held when we re-run the models eliminating non-significant factors and using a larger dataset that included 50 more samples of assisted natural regeneration experiences which then included this technique in the Amazon Forest (Table SI2–2). The assisted natural regeneration systems evaluated here are agroforestry systems composed by spontaneous regeneration mixed with annual and perennial crops, in which the goal of restoring and maintaining ecosystem functions is balanced with the cultivation and management of useful products (Lima et al., 2009; Braga et al., 2012; Leite et al., 2014). It is important to recognize that most available data comes from wet forest biomes and therefore we should not generalize this results to non-forest and dry forest biomes.

The introduction and maintenance of useful plant species in the system and the management of unwanted invasive species and strong competitors may explain why assisted natural regeneration initiatives achieved higher biodiversity values than the original reference systems (Fig. 3). Interestingly, such technique was reported in the Cerrado and the Amazon, suggesting assisted natural regeneration can be a cost-effective technique for both dry and wet forests (e.g. Leite et al., 2014). On the other hand, as mentioned before, we found that soil carbon stocks recover faster in wet forest ecosystems. Previous studies showed that long-term aboveground carbon gain in wet forests may be related to interventions such as enrichment plantings, climbing cutting or liberation thinning. Thus, management of natural regeneration and restoration strategies contribute directly to the recovery of aboveground carbon stocks (Philipson et al., 2020).

4.3. *Implications for practice*

Our results have direct implications for practice, in particular by showing the importance of management for increasing restoration success. Furthermore, our analysis helps identifying adequate indicators for accessing and monitoring restoration initiatives. Ecosystem restoration based on natural regeneration can yield higher ecological benefits if regeneration is assisted. Management practices might include selective elimination of invasive and aggressive species, enrichment planting of native species and planting of fast-growing species. Additionally, the results allow identifying metrics for monitoring the development of restoration initiatives, which is essential for evaluating whether the goals are being reached. We propose that (i) biodiversity and carbon (or biomass) should be preferred indicators compared to abundance levels, (ii) different components (soils, vegetation and fauna) must be monitored because they recover at different paces and provide complementary information on restoration success. Moreover, this information can directly contribute to scaling up a robust, credible and transparent voluntary carbon market in Brazil. With biodiversity rich biomes such as the Atlantic Forest, Amazon, Cerrado and the Caatinga Forest, the country has the potential to lead global market through reforestation and forest conservation helping reduce greenhouse gas emissions, improve livelihoods and protect natural resources.

5. Conclusions

Based on the extensive dataset on restoration initiatives across multiple Brazilian biomes, our meta-analysis identified and measured the importance of different sources of variation in restoration success. Here we demonstrate how the success of restoration is measured (ecological metrics and ecosystem components), how ecosystems are restored (strategies and techniques used), the reference to which restored systems are compared (positive and negative references) and the biome in which restoration takes place. We showed that i) abundance levels are easier to restore and less informative for monitoring than species diversity or carbon stocks, ii) assisted natural regeneration increases restoration success compared to other strategies, iii) recovery occurs at different paces for plants, animals and soils, and iv) restoration success across biomes only differs for carbon stocks, which are easier to restore in dry than wet forests.

Future studies should focus on ecosystem components underrepresented in the current literature such as non-woody vegetation, carbon stocks in the below-ground biomass and species diversity of vertebrates. Improving our knowledge on these components is needed to advance our understanding on effective restoration processes.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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