

Geographical trends of soil-associated biodiversity changes due to tree plantations in South America: Biome and climate constraints revealed through meta-analysis

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Abstract

Aim: To evaluate the interaction between climate and biome structure when explaining changes in species richness of soil-associated communities due to tree plantations developed in different biomes. Compare the response of plants, soil invertebrates and soil microorganisms, and to test whether they should be considered sensitive-coupled biotas.

Location: Continental South America.

Time Period: 1996–2023.

Major Taxa Studied: Plants, soil invertebrates and soil microorganisms.

Methods: Through a meta-analysis, the change in species richness (i.e. response ratio) associated with tree plantations was evaluated in 127 points of study across South America, considering soil-associated communities of plants, invertebrates and microorganisms. The influence of biome structure (open vs. closed habitats) on the response ratio, and its interaction with the actual evapotranspiration (AET) and temperature seasonality was evaluated. Differentiated responses of different taxa were tested by comparing models with and without an interaction term referring to the taxon studied. The regional agricultural cover and plantation age were considered as anthropogenic variables.

Results: Models containing the AET were better at explaining the trend of change in species richness than those with temperature seasonality. The response of the change in species richness was oppositely related to the AET in open and closed biomes. Plants presented a higher loss in species richness than soil invertebrates and microorganisms. The three taxa were positively associated with AET, while seasonality was not relevant in any case. Both anthropogenic variables significantly lessened the change in species richness in all models.

Main Conclusions: The structural contrast between the anthropogenic habitat and the biome where it is developed is a key factor influencing the response of soil-associated communities to tree plantations. Nevertheless, its influence must be assessed together with climatic and anthropogenic variables given that their interaction can explain different geographical trends in the change in species richness across regions.

KEYWORDS

afforestation, Anthropocene, climate, diversity, energy, invertebrates, microorganisms, plants

1 | INTRODUCTION

Changes in biodiversity due to anthropogenic factors have been the focus of study in ecology for the last few decades. Recently, as the scale of study has expanded from local to planetary, the relationship between the proposed drivers and biodiversity have been found to vary in different regions of the globe (Chapin III et al., 2000; Laurance et al., 2014; Newbold et al., 2015). Global studies have described geographic patterns of biodiversity loss in which climatic and local biodiversity characteristics are key to explaining differences in the effect of large-scale anthropogenic disturbance. Newbold, Oppenheimer, et al. (2020b) showed different degrees of impact of land-use change according to the biome studied, highlighting high levels of diversity loss in tropical and Mediterranean biomes. In the same way, Murphy and Romanuk (2014) and Newbold, Bentley, et al. (2020a) found that the change in species richness varied according to the group studied. Furthermore, the degree of environmental dissimilarity between the anthropogenic habitat studied and its natural context has to be considered, as it is a key factor driving the assembly of the novel biological community in the anthropogenic habitat (Corbelli et al., 2015; Filloy et al., 2010; Santoandré et al., 2019). In this study, we aim to explain the geographical variation in the change in species richness when a particular land use is studied (tree plantations in this case) at a continental scale, by considering the role of climate, the environmental characteristics of different biomes, and different taxonomic groups.

Geographical variation in the change in species richness of biological communities (defined here as the change in species richness between the natural and the anthropogenic habitat) can be explained by environmental conditions that are associated with energy flow in the ecosystems and the ecological niche of species (Evans et al., 2005; Newbold, Oppenheimer, et al., 2020b). On the one hand, environmental energy is related with high metabolic rates and the surplus of resources, what allows bigger populations and faster recovery of disturbances (Evans et al., 2005). In this way, high actual evapotranspiration (AET), taken as a proxy for environmental energy (Willmott & Matsuura, 2001), would allow biological communities to recover faster after anthropogenic disturbances. Therefore, under the hypothesis of environmental energy, we expect less change in species richness after anthropogenic disturbance in habitats with higher temperature and water availability (high evapotranspiration) than in habitats with low evapotranspiration. On the other hand, climate seasonality was proposed to decrease the change in species richness due to land-use change (Newbold, Oppenheimer, et al., 2020b). Temperature seasonality is linked to seasonal variation in resources and environmental conditions, which often leads to habitats with species with broader ecological niches (Saupe et al., 2019; Vázquez & Stevens, 2004). In this case, wider ecological niches would increase the ability of species to better cope with environmental changes associated with land-use. Under this hypothesis, we expect to find less change in species richness in temperate biomes than in tropical ones. When considering the two hypotheses we find a crossroads, since AET and seasonality are distributed in

opposite ways. Thus, one would expect opposite geographic patterns of change in species richness along the latitudinal gradient. In this study, we set out to test both hypotheses to shed light on the predominant causes of species loss due to land-use change at a continental scale.

In addition to the hypothetical mechanisms acting at broad scales, the Anthropocene challenges us to consider a space intervened by human activity (Ellis, 2011; Graham et al., 2017; Valiente-Banuet et al., 2015). In that sense, considering the level of anthropogenic disturbance at a regional scale (here the agricultural cover) is a key factor when studying land-use effects on richness in anthropized landscapes. The change in species richness has been described to be lessened in highly modified landscapes, as the regional pool of species is already affected by land-use and presents a higher proportion of species that can cope with anthropogenic disturbance (Newbold et al., 2015). At a local scale, the magnitude of the effect of land-use change on species richness also depends on the degree of the environmental dissimilarity between the anthropogenic and the natural habitat (environmental filtering effect) (Kraft et al., 2015). As physiognomic characteristics of the vegetation (from here on, structure) typically vary across biomes, we expect differential influences on biodiversity for the same land use when broad scales are assessed. Considering closed biomes as forests, and open biomes as grasslands, savannas and stepes, as defined by Pausas and Bond (2020), we expect greater effects of tree plantations in biomes with open habitats than in closed ones. Therefore, by considering the structural contrast at a local scale, and the agricultural cover at a regional scale, we will intend to address the influence of anthropogenic variables in the variation in the change in species richness across South America.

Commercial tree plantations are expanding around the world and efforts are being made to understand their impacts on biodiversity (Bremer & Farley, 2010; Wang, Zhang et al., 2022). Bremer and Farley (2010) described that tree plantations have differential effects according to the structure of the disturbed biome and that it is also partly explained by the plantation age. While in grasslands the plantation age was associated with a decrease in species richness, as it grows progressively different to the natural, in forests it did not show a clear association. With this in mind, we will consider this structural contrast given by plantation age and biome structure at the local scale as the basic driver of plantation impact. Therefore, by incorporating regional agricultural cover and climatic variables, we aim to explain the geographic variation that is not explained by the structural contrast on its own.

Geographical patterns of biodiversity and their response to land use have been previously described for above-ground macroorganisms, such as plants and animals (Buckley & Jetz, 2007; Kier et al., 2005), but only recently the scope has been focused on belowground invertebrates and microorganisms (Decaëns, 2010; Goss-Souza et al., 2017; Sylvain & Wall, 2011). Soil ecosystems and their biota are relevant as they are involved in several ecosystem processes and services (Delgado-Baquerizo et al., 2016). The functioning of soil ecosystems depends on complex interactions

between multiple taxa such as plants, soil invertebrates and microorganisms (Lavelle et al., 2006; Thakur et al., 2019). Therefore, to address the effect of land-use change on soil ecosystems, efforts must be made to include soil-associated communities (both above- and belowground) through a multi-taxa approach. Despite being part of close ecological interactions, these taxa do not usually respond together to anthropogenic disturbance (Le Provost et al., 2021; Wang & Tang, 2019). In this study, we will compare the response of plants, soil invertebrates and soil microorganisms, and test whether there are generalities or they should be considered uncoupled biotas when responding to land-use change.

Our aim was to assess the influence of climate and biome structure on the response of communities highly dependent on soil conditions (soil-associated from herein) to tree plantations across South America. Throughout bibliographic research and meta-analysis our goals were to (i) Detect a general response of soil-associated communities of plants, arthropods and microorganisms to commercial tree plantations along South America, and compare the responses between taxa; (ii) Explore the influence of biome structure on the change in species richness due to tree plantations taking into account other potential drivers (i.e. AET/climate seasonality, regional agricultural cover, plantation age); (iii) Identify potential geographical trends of change in species richness of above- and below-ground communities to tree plantations in South America. Commercial plantations are monoculture stands that imply a great disturbance for their initiation, with simplified strata when matured (Pauro et al., 2021; Santoandré et al., 2019). Thus, we predict an overall negative effect of commercial plantations on species richness. As tree plantations are forests, albeit highly simplified, we expect lower loss of species richness when tree plantations are developed in forest biomes than when they are developed in biomes with an open structure, such as grasslands, steppes and savannas. However, we expect variation in the change in species richness across the continent that could be explained by climatic factors interacting with the structural contrast between forest plantations and the natural habitat where they developed.

2 | MATERIALS AND METHODS

2.1 | Data acquisition

Data acquisition consisted of a literature search using the main peer-reviewed articles databases and obtaining environmental data rasters from online repositories. We search peer-reviewed articles in English, Portuguese, and Spanish using Web of Science, SCOPUS and Google Scholar, following the Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) protocol (Moher et al., 2015; Page et al., 2021) (Appendix S1, Figure S1.1). The search initially produced 3261 articles, from which one person selected articles that fulfil the following criteria: (1) were not repeated; (2) sampling was carried out between 1990 and 2023; (3) compared species richness between a commercial tree plantation and a nearby natural

area; (4) the taxa studied were plants, soil invertebrates, or soil microorganisms (see search string in Appendix S1); (5) the study area had no experimental manipulation; (6) the article included species richness (S) per treatment or the species list per site, and the number of sites studied (N); (7) studies with geographical coordinates of sampling points; (9) a minimum of two replicates per treatment. The temporal range of the studies was fixed to compare the values of climate and agricultural cover provided by the rasters. The final data set included 81 original articles (Appendix A, data sources) and 127 points of comparison between commercial tree plantations and a nearby natural habitat (Figure 1a). To explore the distribution of the data across south American biomes, each study was mapped according to the mean annual temperature and the mean annual precipitation in a diagram based on the Whittaker biome classification (Whittaker, 1975), using the package “plotbiomes” in R (Figure 1b).

From each article, we retrieved coordinates of the sampling point, the structure of the biome of reference (i.e. open for grasslands, steppes, and savannas, or closed for forests), taxa studied (i.e. plants, soil invertebrates, or microorganisms), the plantation age (time since the site is forested), the species richness and its standard deviance, and the number of replicates for each treatment. Species richness was obtained from the text, tables, species lists per site, figures, or article supporting information. When richness was obtained from figures, its value and standard deviance were obtained via the software ImageJ (Abramoff et al., 2004). If the mean species richness was reported together with a Standard Error or the Confidence Interval, their values were converted to Standard Deviation (SD). In the case there was no information about the variability in the data (4 cases out of 103), the missing data was obtained based on the predictive mean matching (Beckmann et al., 2019), using the package “mice” in R (Van Buuren & Groothuis-Oudshoorn, 2011).

To test the stated hypotheses, the AET was used as a proxy of environmental energy (Willmott & Matsuura, 2001), as energy can be considered both by the metabolic pathway (temperature) or resource (water availability). To account for seasonality, data on the annual deviation of temperature was retrieved from BIOCLIM (Fick & Hijmans, 2017). In addition, the level of regional disturbance was considered using a worldwide raster of agricultural cover, considering the percent of the cover of a five-minute cell (Ramankutty & Foley, 1999). To retrieve the value of the variables for each point, the mean was estimated for a 0.5-degree buffer around each point of study with the QGIS 3.6 software (Qgis 2018, <http://qgis.osgeo.org>), overlapping the coordinates of each study and the variable rasters. Based on the agricultural cover raster, the data ranged from regions with <1% to 93% of agricultural cover.

2.2 | Data analysis

To assess the change in species richness between tree plantation and natural habitat, it was calculated as the response ratio (RR). The response ratio was calculated considering the difference between the species richness in an anthropogenic habitat (*S_{lu}*) and a nearby

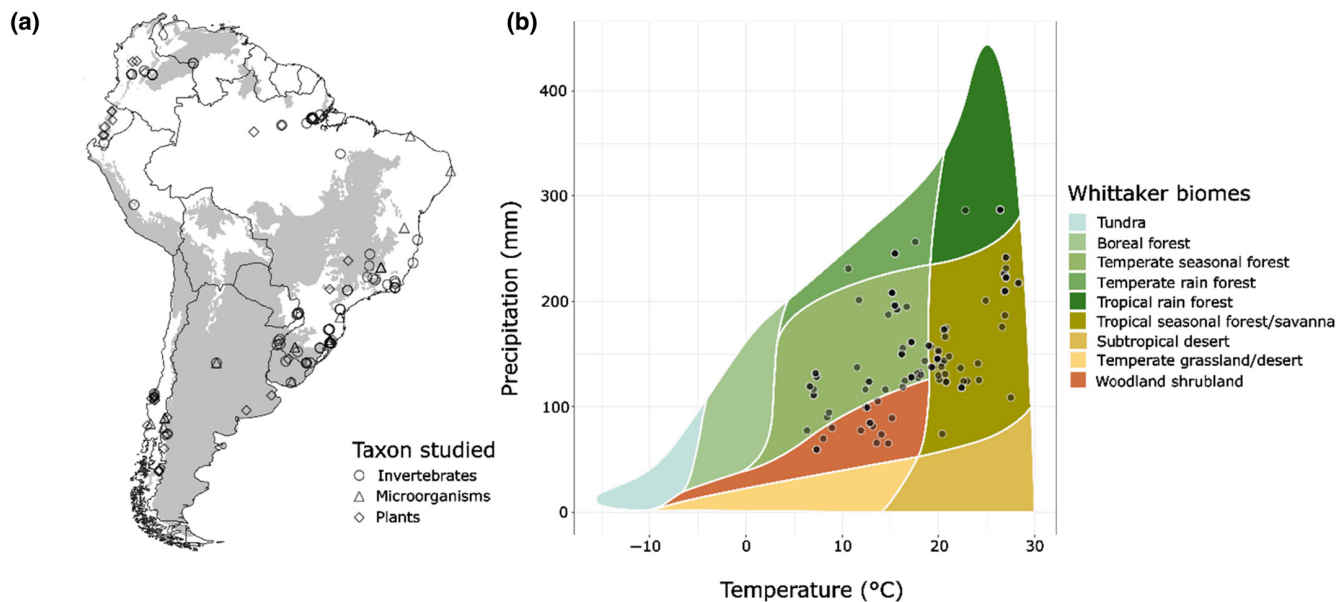


FIGURE 1 Distribution of studies across South-America and its biomes. (a) Coordinates of the studies retrieved across South America. Open structure biomes (grasslands, savannas and steppes) are painted in grey. Symbols represent the different taxa considered. (b) Distribution of studies based on the mean annual precipitation and temperature obtained from BIOCLIM, and then classified according to Whittaker's biomes distribution.

natural habitat (S_{nat}) (equation N°1). According to this equation, the more negative the value is, the more species are lost in the anthropogenic habitat. Then, the sampling error was calculated considering the mean of the species richness (\bar{X}), its standard deviance (SD) and the number of replicates (n) (equation N°2) (Koricheva et al., 2013) with the "esclac" function of the METAFOR R package (Viechtbauer, 2010)

$$RR = \ln\left(\frac{S_{lu}}{S_{nat}}\right), \tag{1}$$

$$se_{RR}^2 = \frac{SD_{nat}^2}{n_{nat}\bar{X}_{nat}^2} + \frac{SD_{lu}^2}{n_{lu}\bar{X}_{lu}^2}. \tag{2}$$

To check whether the data presented publication bias, meaning that it is more frequent to publish studies with significant effects, Egger's test was run using the function "regtest". To calculate the general response ratio of biodiversity (considering all taxa) to tree plantations, a multilevel model was made with the RR as the response variable, and the study ID and the taxa studied were included as random factors (Nakagawa & Santos, 2012).

To identify differences in the response ratio of the taxa studied, and the influence of climate and the biome structure on it, meta-regression models were made using the "rma.mv" function of the METAFOR package. In all cases, the response variable was RR, the study ID was included as a random effect factor, and the error distribution selected was gaussian (Zuur et al., 2009). To evaluate whether the response ratio varied among the taxa studied, a meta-regression model was made entering the taxa studied as the fixed factor. Differences in the response between taxa was tested by

pairwise Tukey comparison. Then, to test if the biome structure explained the RR on its own, three univariate models were run for the general RR (taxa studied as random effect factor), for plants, and soil invertebrates, with the RR as the response variable and the biome structure as the fixed factor. The effect of biome structure was not evaluated for microorganisms given that their data was unbalanced; while 19 points of study were recorded for closed biomes, only 6 were found for open biomes.

To test the influence of climate together with the structure of the biome of reference, the interaction between the biome structure and the AET or temperature seasonality was modelled. Meta-regression models of the stated hypotheses and null models were compared to determine the best explanatory model for changes in species richness. To account for the influence of different levels of regional disturbance and differences in age of the plantations, control variables of agricultural cover (AC) and plantation age (AGE) were added in all models as fixed terms. Given that the interaction between the age of the plantation and the biome structure is already documented in the literature, a first model called "Basic" containing only the interaction between these variables was evaluated. Then, based on the "Basic" model, we incorporated the agricultural cover and the interaction between the different climatic variables and the biome structure one at a time. In addition, a model only containing the intercept was evaluated as a null model. To test whether the responses differed among taxa, we compared models including taxa as a fixed factor with and without an interaction term accounting for it. In total, 13 models were run (one null model, 6 models with taxa as a main fixed effect and 6 with the additional interaction term). The best model was selected by comparing them by their Akaike information criterion (AIC). The model with the lowest AIC was

selected as the best, and it was considered more informative than its following model if their ΔAIC was bigger than two (Burnham & Anderson, 2002). The complete R code and the database were made available in the supporting information.

To explore the response of biodiversity across South America the best model for the change in species richness was mapped calculating the predicted RR through the continent. To predict the RR across the continent, the best model was chosen. Although there were two equivalent models according to the AIC, given that the model II was nested in model V, the geographical prediction was based in model V (Burnham & Anderson, 2002). For this purpose, the raster calculator of the QGIS 3.6 software was used, entering the parameters of the best model for each case, and mapping the response with a 0.5-degree resolution. To restrict the prediction to potential tree plantation areas, the predicted area was restricted to regions inside the range of AET evaluated and with at least 1% of agricultural cover. To account for the different biomes across South America, the distribution of each biome was taken as proposed by Olson and Dinerstein (2002). A categorical value for biome structure of "OPEN" was given to grasslands, steppes and savannas, and "CLOSED" was given to forests, based on the percentage of tree cover in each biome (Woodward et al., 2004). To map the predictions of the models containing the age of the plantation, its value had to be fixed. Therefore, we predicted the RR for young and matures plantations, of 5 and 15 years since planted, respectively.

3 | RESULTS

3.1 | Meta-analysis

Considering the 127 points of comparison, the meta-analysis detected a general RR of -0.46 ($p < 0.05$), which means that, on average, tree plantations present a 36.92% reduction in species richness when compared with the natural habitat (Figure 2a). The Egger's test for publication bias did not detect funnel asymmetry in the whole dataset, (Appendix S1, Figure S2). Overall, the RR of plants was more negative than that of invertebrates and microorganisms ($p < 0.05$) but invertebrates and microorganisms did not differ ($p > 0.05$, Figure 2b). The general RR showed no association with the biome structure ($p > 0.05$). However, we did find differences in the RR between biomes with open and closed structures for soil invertebrates ($p < 0.05$). While the RR of plants did not associate with biome structure, soil invertebrates presented a more negative RR in closed biomes than in open ones, $RR = -0.41$ and $RR = -0.21$ respectively (Figure 2c,d).

3.2 | Meta-regression and geographical predictions

From the model selection process, we obtained that the best models were both the basic one plus agricultural cover and a more complex one also including the interaction between AET and biome structure

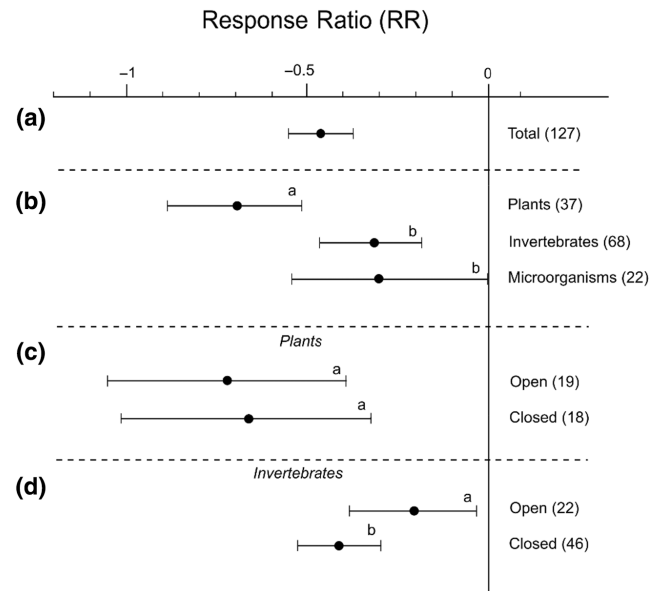


FIGURE 2 Response ratio according to different factors, different letters mean significant differences. (a) General response; (b) response for each taxon; (c) Response of plants in open and closed habitats; and (d) response of invertebrates in open and closed habitats. Bands represent 95% confidence intervals.

(Models II & V, $\Delta AIC < 2$) (Table 1). In both cases, the plantation age and the agricultural cover had a positive coefficient for both open and closed biomes (Table 2, Figures S3 and S4). In model V a significant interaction between AET and biome structure was found. AET was positively associated with overall RR in open biomes and negatively in closed ones (Figure 3). The model containing the interaction with the taxa was less informative than those considering it as a simple effect factor (Table 1).

The geographical predictions of the RR ranged from -0.91 to -0.01 for young plantations (Figure 4a), and from -0.98 to 0.48 mature plantations (Figure 4b). As plantation age had a positive effect in both open and closed biomes, the prediction for mature plantations presented more positive RR values overall. In closed biomes, the spatial prediction estimated the lower values of RR in center-east and north Brazil. In open biomes, the lower values of RR were predicted along the western South American Arid Diagonal and in southern Pampa, regions with open structure biomes and low levels of AET. The maximum values according to Model V were in the central Pampa region and the northern Cerrado region, in central Brazil.

4 | DISCUSSION

In this study, we confirmed that there is variation in the influence of commercial tree plantations on species richness of soil-associated communities of plants, invertebrates and microorganisms in South America. Although an overall negative effect on species richness was detected, its variation was associated with climatic conditions (i.e. AET, as stated by the environmental energy hypothesis). However, its association depended on the structure of the disturbed

TABLE 1 Detail of the model selection process for the response of species richness ($n=127$).

Model	+ TAXA	* TAXA
	AIC	AIC
Null - Intercept AIC=188,05		
I - Basic	175.71	177.97
II - Basic+AC	173.58	178.55
III - Basic+AET*STRUCTURE	176.73	182.29
IV - Basic+TSEAS*STRUCTURE	177.97	185.31
V - Basic+AC+AET*STRUCTURE	174.47	183.13
VI - Basic+AC+TSEAS*STRUCTURE	175.74	185.22

Note: In bold letters, the lowest AIC value and the equivalents ($<2 \Delta AIC$).

Abbreviations: AC, Agricultural cover; AET, Actual evapotranspiration; AGE, Plantation age; Basic, AGE*Structure; TSEAS, Temperature seasonality.

TABLE 2 Details of the values for the parameters of models II and V.

Model	Intercept	+ AGE	+ AC	+ AET
Invertebrates				
Model II				
Open	-0.52	0.011	0.005	
Closed	-0.6	0.001	0.005	
Model V				
Open	-0.94	0.014	0.005	0.005
Closed	-0.51	0.008	0.005	-0.001
Plants				
Model II				
Open	-0.96	0.011	0.005	
Closed	-1.04	0.001	0.005	
Model V				
Open	-1.33	0.014	0.005	0.005
Closed	-0.9	0.008	0.005	-0.001
Microorganisms				
Model II				
Open	-0.53	0.011	0.005	
Closed	-0.61	0.001	0.005	
Model V				
Open	-0.95	0.014	0.005	0.005
Closed	-0.51	0.008	0.005	-0.001

Abbreviations: AC, agricultural cover; AET, actual evapotranspiration; AGE, plantation age.

biome. While tree plantations lead to higher loss of species richness in temperate open biomes (grasslands, savannas and steppes) than in tropical ones, closed biomes (forests) presented an opposite response. The anthropogenic variables, plantation age and agricultural cover, included as control proved to be of major influence in the response of the change in species richness. We found that in the

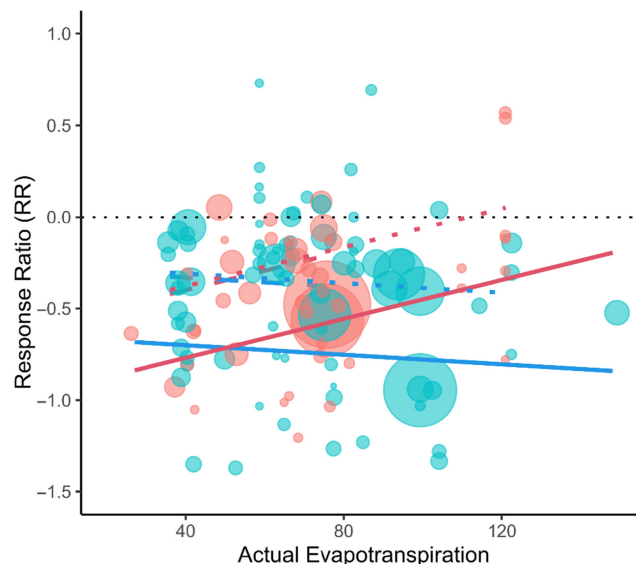


FIGURE 3 Partial regression representing the interaction of the actual evapotranspiration and the biome structure according to Model V. Open biomes are represented in red and closed biomes in blue. The response of invertebrates, microorganisms and plants are in dotted, dashed and solid lines respectively. Agricultural cover and age of the plantation were fixed in their mean value. The size of circles represents the confidence ($1/SD$) of the meta-analytical data.

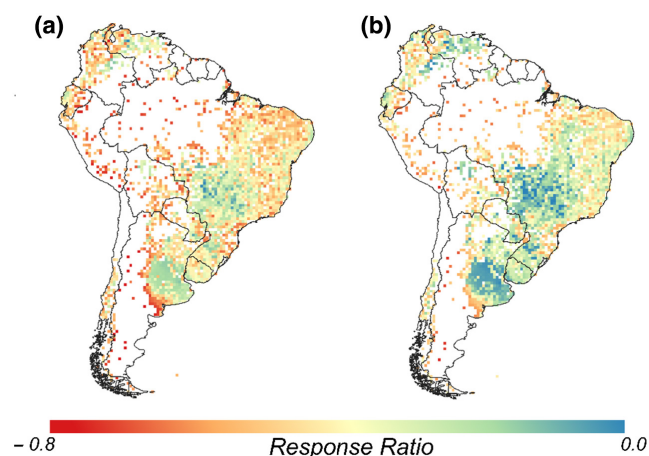


FIGURE 4 Prediction of Response ratio through South America according to model V for: (a) 5 years old plantations. (b) 15 years old plantations. The range of colours has been set between -0.8 and 0 to be able to compare the values between the two models. To comprise the three taxa, the mean of their response was plotted.

two best models, they presented a significant effect on the change in species richness. Therefore, we support that their consideration is of major relevance when studying ecological responses at large scales (Gámez-Virués et al., 2015; Gerstner et al., 2014; Newbold et al., 2015).

Although we found an overall negative response to tree plantations, we tested whether there were differences in the richness response ratio between taxa. We found that the response ratio of

plant richness was the most negative considering that of the other taxa. On the one hand, these differences may be because resources for belowground biota (soil invertebrates and microorganisms) may not be as directly affected by tree plantations as for plants (highly affected by light restrictions and allelopathic effects) (Brockhoff et al., 2003; Navarro-Cano et al., 2010; Vexetal et al., 1994). On the other hand, the slower rate of recolonization of anthropogenic habitats by plants, in comparison with the belowground biota, may also explain smaller richness of plant communities in tree plantations (de Graaff et al., 2019; Wang, Zhang et al., 2022). In the case of microorganisms, they presented high variability in their response, leading to no differentiation with soil invertebrates. As taxa of bacteria, archaea and fungi were considered as a whole group, the high diversity of life-forms included may have led to the observed pattern. In addition, the resolution at what microbial diversity was studied varied across the assessed studies, given that technologies used to study microbial diversity have improved greatly in the last decades (Nesme et al., 2016). These results confirmed that besides the trends in multi-taxa species richness loss, there are singularities for different taxa. Therefore, focusing only on general trends can lead to generalizations that may eclipse a diversity of responses in different taxa.

When testing if the structural contrast between the tree plantations and the natural habitat by its own explained variation in the change in species richness, we found that only soil invertebrates responded differently according to this variable. What is more, contrary to our prediction, loss of species richness of invertebrates was bigger in closed biomes than in open ones. Although this result is not explained by the environmental filtering hypothesis, stronger effects of tree plantations in forests than in grasslands were previously reported for multiple taxa (Corbelli et al., 2015; Filloy et al., 2010; Santoandré et al., 2019). These authors found a higher loss of taxonomic richness of multiple taxa in tree plantations developed in subtropical forests context than in a grassland context, arguing that habitat simplification in forests may be affecting microhabitat and resource availability for highly specialized species. Lastly, although all tree plantations studied were monospecific plantations for timber production, differences in the structure of the tree plantations between them could have also distorted the degree of contrast with the natural habitat. Therefore, the structural contrast between an anthropogenic habitat and a native one may not be enough to explain changes in species richness when evaluating land use effects across different biomes.

Although the biome structure was not associated with the magnitude of change in species richness for all taxa, it did affect how change in species richness associated with climatic variables. The loss of species richness due to tree plantations was oppositely related to AET in open and closed biomes across the continent. While loss of species richness was higher in temperate than tropical grasslands across the continent, that in forests responded the other way around. Based on this, the environmental energy hypothesis is only confirmed for open biomes. In biomes such as temperate grasslands and shrublands, plants are usually adapted to receive a high incidence of light, but to cope with low availability of water (Burke et al., 1998).

These characteristics might increase the loss of plant species richness in implanted forests in open biomes, where the resource of light is greatly diminished (Wang, Jiang et al., 2022). Following the loss of plant species, the overall negative effect may also reflect a cascading effect from producers to decomposers (Barnes et al., 2017; Tylianakis et al., 2008). As water availability and temperature increase (an increase of AET), plants may be able to recolonize the plantation sites, resulting in a mitigation of the change in species richness in open biomes with high AET. Higher AET may also allow soil invertebrates and microorganisms to cope with changes in environmental conditions and resources or to have faster rates of colonization, through higher metabolic rates (Gibb et al., 2015; Zhou et al., 2016). In contrast, the negative association between the change in species richness and the AET in forest biomes may be explained by a higher loss of species richness due to tree plantations in tropical forests. In this case, tree plantations may represent oversimplified habitats where the heterogeneity and abundance of resources are reduced (Holl et al., 2013). As energy is often associated with species richness, it can also be an indicator of a growing ecological specialization and rarity in species (Evans et al., 2005; Mason et al., 2008). Therefore, tree plantations may not be able to support niche overlapping and relaxed competition between specialist species from tropical forests (Bremer & Farley, 2010). Consequently, although the AET can account for broad geographical trends of change in species richness due to tree plantations, the mechanisms that determine the diversity of communities in anthropogenic habitats may be determined by the structural contrast between it and the natural habitat.

Taking into consideration anthropogenic variables, such as the agricultural cover and the plantation age, proved to explain an important part of the variation of change in species richness at broad scales. High agricultural cover has been described to locally benefit generalist species (endemic or exotic) and to lead to extinction of species with a highly specialized ecological niche (Newbold et al., 2018; Ramiadantsoa et al., 2018). Therefore, by modifying the regional species pool that could recolonize altered habitats, it may result in patterns of change in species richness due to land-use that are different from those expected based on climatic factors alone. On the other hand, the plantation age was positively associated with the change in species richness, meaning that older plantations presented higher species richness in comparison to young ones. Contrary to our prediction, old growth plantation may present a habitat for ecological succession rather than increase environmental filtering, in accordance with previous studies (Dejene et al., 2017; Wang, Zhang et al., 2022). This meta-analysis is constrained to changes in the species richness; including the composition of species and their functional traits would provide further evidence of the mechanisms driving species change. Human intervention at large scales creates new scenarios with novel ecological systems (i.e. Anthromes) (Ellis, 2011; Piquer-Rodriguez et al., 2021) that may present different biogeographic patterns to those observed in natural habitats.

The spatial predictions of the change in species richness to tree plantations showed differences across regions in South America. The lower values of species loss were found in the eastern part

of the Brazilian Cerrado and in the central Argentinean Pampa. Lower values of species loss in these regions may be explained by the high cover percentage of agricultural land. These two regions were described to have their biodiversity heavily affected by the 2000's (Newbold et al., 2015). Therefore, species responding to the tree plantations may have been affected by land use before, by introducing generalist species (Newbold et al., 2018). On the other hand, when evaluating regions with high values of species loss, the Atlantic Forest and the Caatinga region, together with the western South American Arid diagonal (Luebert, 2021), were detected as the more affected. Previous studies found that anthropogenic disturbance interacted with aridity variables, causing higher diversity loss in arid regions than in humid ones (Arnan et al., 2018; Peters et al., 2019). Nowadays, the agricultural cover is lower in low AET regions than in high AET ones but arid habitats will expand with climate warming and so the demand of agricultural land (Mahmoud & Gan, 2018; van der Esch et al., 2017; Zhang et al., 2023). Therefore, climatic and anthropogenic variables must be considered together to better understand the changes in species richness across regions with different environmental conditions in a changing world.

With this meta-analytical study, we aimed to describe variations in the response of multi-taxa species richness of above-ground and below-ground diversity. Although we managed to obtain several studies, particularly in an under-sampled region of the globe, our data was unbalanced between the taxa and the biomes studied. On the other hand, as land-use change is known to modify the taxonomic composition of biological communities, studying only the change in species richness may not fully detect the response of native communities. To fully understand the effect of tree plantations across different biomes, we encourage future studies to address the change in composition of biological communities, particularly that of plants and microorganisms.

In summary, we provide evidence that predictions of large-scale variation in the change in species richness due to land use change can be improved by considering already known factors, such as AET, interacting with structural dissimilarity between anthropogenic and natural habitats. In this study, tree plantations varied their effect on soil-associated biodiversity driven by AET differently in closed and open biomes. Temperate open biomes appeared to present higher loss of species richness than tropical biomes. Nevertheless, the biomes we considered do not present their original characteristics to their full extent, as human activities have greatly modified the landscape. Although AET may act as a predictor of biodiversity loss at continental scale, anthropogenic factors appear to greatly affect natural patterns of change in species richness at local scale, evidencing the consequences of land-use change. Given that current patterns of biodiversity occur in the Anthropocene, it is mandatory to integrate both natural and anthropogenic factors to shed light on the processes that shape the large-scale distribution of species.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The raw database along the R script to produce all the obtained results were made available in the supporting information.

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BIOSKETCHES

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Julieta Filloy is head of ECOMA, leading multiple projects assessing macroecological and biogeographic patterns in the Anthropocene. Main lines of research focus on diversity patterns of birds and invertebrates, among others, in natural and anthropogenic habitats across Argentina.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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APPENDIX A

Literatura used for meta-analysis

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