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Riparian forest restoration as sources of biodiversity and ecosystem functions in anthropogenic landscapes

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Abstract

1. Restoration of tropical riparian forests is challenging, since these ecosystems are the most diverse, dynamic, and complex physical and biological terrestrial habitats. This study tested whether biodiversity can predict ecosystem functions in a human-impacted tropical riparian forest.
2. We explored the effects of several biodiversity components (taxonomic or functional groups) on different ecosystem functions associated with restored riparian forests
3. Overall, 49% of the biodiversity components showed positive effects on ecosystem functions, each component to a different degree. In general, our results showed that both taxonomic and functional biodiversity had strong effects on ecosystem functions indicating that floral and faunal biodiversity enhanced the multifunctionality of these restored riparian tropical forests.
4. These findings indicate that in restored riparian forests, recovery of biodiversity is followed by improvement in important ecosystem functions that are the basis for successful restoration. Future research and policy for restoration programs must focus on restoring elementary faunal and floral components of biodiversity in order to promote ecosystem multifunctionality.

Key-words: Cerrado, ecological synthesis, ecosystem process, land-use, multifunctionality

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1 Introduction

The process of habitat loss and fragmentation is the main driver of the current worldwide decline in biodiversity (Fahrig, 2003). Alterations in biodiversity and ecosystem services, largely driven by global environmental change, are also contributing to this decline (Foley et al., 2005). As a result, the number and persistence of many species will depend not only on habitat protection but also on habitat restoration, defined as the process of facilitating recovery of ecosystems following disturbance (Pedrini et al., 2020).

Tropical forests have many unique properties related to their high rates of primary productivity and biodiversity, which distinguish them ecologically from other ecosystems worldwide (Brockerhoff et al., 2017). These properties include the development of biological structures in vertical and horizontal layers of living and dead plants, a complex process at multiple vertical levels, the ability for self-renewal in the face of constant land-use changes and anthropogenic disturbances, restoring ecological functions (Martins et al 2017). These forests are comprised of multiple ecological functions that are driven by variable environmental conditions and operate at multiple spatial scales (Gardner et al., 2009). For instance, patches of forest, especially riparian forests, have a strong influence on micro- and regional climates (Allen, 2016; Burdon et al., 2020).

Natural terrestrial ecosystems are valued for their ability to simultaneously maintain multiple functions and services, i.e., ecosystem multifunctionality (Allan et al., 2013). Biodiversity is by no means the only, or even the primary driver of ecosystem functioning, which is also influenced by many biotic and abiotic environmental factors that operate at different scales (Cardinale et al., 2011), but maintenance of biodiversity is a fundamental strategy for enhancing ecosystem services (Cardinale et al., 2011). For this reason, it is essential to understand how biodiversity affects different ecological processes and ecosystem functions in order to successfully restore patches of disturbed habitats (Allan et al., 2013).

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The relationship between biodiversity and ecosystem functioning (hereafter BEF) has emerged as one of the most exciting and controversial research areas in ecology over the last two decades (see Manning et al., 2018 for a review). Faced with the prospect of a massive and irreversible loss of biodiversity, ecologists have begun to investigate the potential consequences of current land-use changes on biodiversity and the functioning of natural and managed-novel ecosystems (Loreau et al., 2002). Biodiversity can substantially alter the structure and functioning of ecosystems and BEF studies has suggested that biodiversity loss may impair the functioning of natural ecosystems, diminishing the number and quality of services they provide (Balvanera et al. 2013; Cardinale et al. 2006, Cardinale et al. 2011, Hooper et al. 2012).

While research in the last few decades has provided many insights into BEF relationships, our current understanding of how biodiversity loss influences ecosystem functions and services amid myriad anthropogenic disturbances is neither precise nor complete (Cardinale et al., 2012; Hooper et al., 2012; Naeem et al 2012). To extend the BEF theory to restoration, researchers must gather data on ecological attributes that are easy to obtain, cost effective, and easily applicable, such as land use and canopy height, usually used to evaluate wildlife support (Palmer & Filoso, 2009). Still, no study has shown that species richness of planted trees directly increases long-term functional benefits in ecologically restored riparian forest sites (i.e., without weeding and replanting). As restored plant communities mature, their BEF relationships could be affected by trait-based changes in composition and abundance that cannot be evaluated in short-term experiments. Thus, to evaluate the success of forest restoration projects, understanding the long-term relationships between BEF is essential, insofar as it affects the ability of ecosystems to simultaneously provide multiple functions and services, in other words, the ecosystem multifunctionality (Hector & Bagchi, 2007).

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The scales at which experimental research is conducted to understand which mechanisms underpin BEF relationships fail to match the scales at which biodiversity changes occur (i.e., local and landscape levels). However, models developed in short-term local studies could then be embedded into spatially explicit meta-community and ecosystem models that incorporate habitat heterogeneity, dispersal, and abiotic drivers to predict relationships between BEF at the landscape level (Hooper et al., 2012). Another fruitful approach may be to use data from BEF experiments to assign parameters from local models of species interactions, based on functional traits, that predict how biodiversity has an impact on broader scales of ecosystem processes. Real-world experiments assessing different biotic and abiotic variables and ecosystem functions at different scales appears to be a better and more robust approach to disentangle the complexity involved in ecosystem multifunctionality (Steur et al., 2020).

Tropical riparian forests are among the most diverse, dynamic, and complex biophysical habitats in terrestrial environments (Burdon et al., 2020). As interfaces between terrestrial and aquatic systems, they encompass sharp environmental gradients, complex ecological processes, and unique communities (Little et al., 2015; Pollock & Beechie, 2014). Riparian forests are recognized as important sources of “ecosystem services”, as they support watershed protection, wildlife enhancement, and ecosystem maintenance (Surasinghe & Baldwin, 2015). These forests usually support higher biodiversity and structural complexity than their surroundings (Bunnell & Houde, 2010). Consequently, deforestation of riparian areas may cause a significant decay in habitat quality in adjacent ecosystems (Surasinghe & Baldwin, 2015). Additionally, re-establishment of disturbed riparian forests is currently considered the “best management practice” for restoring aquatic ecosystems to their natural or semi-natural states (Sweeney et al., 2002).

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To assess whether BEF analyzed at different scales (taxonomic biodiversity, functional biodiversity) might predict ecosystem multifunctionality (decomposition; leaf and miscellaneous litter production; nitrogen and phosphorus content in the litter; pH and phosphorus content of the soil; and litter and soil fertility), we studied restored fragments of tropical riparian forest, within a highly heterogeneous landscape. We tested the effect of (1) animal and plant species richness, abundance, and diversity (taxonomic biodiversity level); (2) richness and abundance of functional groups (functional biodiversity level).

2 Materials and Methods

2.1 Study sites and restoration overview

The study was conducted in five patches of riparian forest that represent a chronosequence of restoration. The patches are in different areas (hereafter referred as sites) surrounding the reservoir of the Volta Grande hydroelectric power plant (HPP) on the Rio Grande River in southeastern Brazil (20°01'54" S, 48°13'17" W) (Table S1). The region has a tropical climate with dry winters and rainy summers - AW following Köppen classification (Alvares et al., 2013), with a well-defined dry season between May and October and a rainy season from November to April. The mean annual temperature ranges from 22 °C to 24 °C and the mean annual precipitation reaches 1,500 mm.

The study sites are in a highly anthropogenic matrix formed mainly by grassland and sugarcane plantations. Four of the five sites have been reforested and have different ages (10 and 20 years) and widths (30 and 100 m), and one site is a 30-year-old, 400-m-wide and naturally restored secondary forest, here considered as a reference site. Most of the original riparian vegetation in the study area was removed and flooded during the construction of the reservoir in 1974. Between 1994 and 2004, 10-month-old nursery-grown seedlings of 35 tree species, raised from seeds obtained in nearby forest remnants, were planted in a single replanting project along the shores of the reservoir, with a spacing of 3 × 2 m.

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2.2 Experimental design

At each of the five sites, we installed four randomly plots, each 1600 m^2. Biodiversity and environmental samplings were performed monthly between March 2013 and January 2014. Details of sampling methods for plants, vertebrates, invertebrates, and ecological processes can be found in the Supplementary Material.

The selected ecosystem functions, all of which are important for ecosystem multifunctionality (Maes et al., 2012), included: litter (leaf and miscellaneous) production and decomposition; litter nitrogen and phosphorus concentrations; soil pH and available phosphorus; and indexes of litter-quality and soil-fertility. Details for sampling of ecosystem functions can be found in the Supporting Information.

To disentangle the effects of distinct predictors on ecosystem functions, we divided them into two levels: taxonomic biodiversity (animal and plant species richness, including seed rain; abundance; and diversity) and functional biodiversity (animal and plant functional groups), for a total of 67 variables (Figure 1).

2.3 Statistical Analysis

2.3.1 Site dissimilarities according to land use and biodiversity

In order to understand the degree of dissimilarity of the study sites in terms of biodiversity components, we performed principal components analyses (PCA) with the package *vegan* for software R (R Development Team, 2016). In these analyses, sites were ordinated in relation to: (1) richness and abundance of animals and plants, (3) animal and plant diversity (Shannon and evenness indexes), and (4) richness and abundance of functional groups (for animals and plants). Prior to the PCA, we ran correlation analyses for each of the four groups (with the package *pych* for R) and removed the variables that were highly correlated ($r > 0.8$).

2.3.2 Ecosystem multifunctionality analysis

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To understand whether ecosystem functions can be predicted by biodiversity and environmental features, we fitted two models, structured according to different levels of sampling (Figure 1): taxonomic biodiversity and functional components.

Because of the large number of predictor variables, we performed a variable-selection procedure that identifies the most important variables and minimizes prediction risk, resulting in a highly interpretable model to predict forest multifunctionality under a restoration scenario. We utilized the least absolute shrinkage and selection operator analysis (*lasso*; Tibshirani (1996), a shrinkage method that applies the L_1 penalty to least-squares regression, thereby performing a subset selection. First, we determined how the variables varied along the coefficients; in this step, the variables that did not change were eliminated. Then, we selected the minimum *lambda* to obtain the mean cross-validated error and the coefficient for each variable. The resulting fitted model minimizes prediction error, making it useful for both inference and planning. The *lasso* analysis was executed with the package *glmnet* for R (Friedman et al., 2010). We conducted all statistical analyses using the R programming language (R Development Team, 2016).

3 Results

3.1 General results for biodiversity

During the sampling period, we captured 58,858 individual animals of 268 species, including 16 mammals, 122 birds, 23 amphibians and reptiles, 28 species of cavity-nesting bees and wasps, 79 species of ants, and 451 morphospecies of soil invertebrates. We sampled 127 tree species for a total of 1006 individuals. From these taxa, we classified 24 functional groups including richness and abundance of carnivores, herbivores, frugivores, granivores, invertebrate and vertebrate insectivores, decomposers, nectarivores, pioneer and secondary trees, and floral syndromes.

3.2 Site dissimilarities according to land use and biodiversity

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Site dissimilarities were well defined by the differences in land use (SFigure 1a). Altogether, the richness and abundance of different biodiversity groups explained 69% of site dissimilarities (SFigure 1a). Diversity effects strengthened with time as a consequence of restoration. Overall, sites 1 (30 years old), 2 and 3 (20 and 10 yo, respectively) were related to higher richness and abundance of trees, seeds, and birds (axis 2). In contrast, sites 4 (20 yo) and 5 (10 yo) were associated with decreases in the richness and abundance of invertebrates (e.g., wasps) and vertebrates (e.g., mammals) (axis 2). Site dissimilarities according to the Shannon diversity and evenness of general groups (SFigure 1b) suggested that sites 1 and 2 are more similar to each other, while sites 3, 4, and 5 are closer to each other.

The richness and abundance of functional groups explained 69% of site dissimilarities (SFigure 1c). In general, sites 1, 2 and 3 were related to increases in the richness and abundance of pioneer and secondary trees, frugivores, and omnivores on axis 2 (42% explanation). On the other hand, sites 4 and 5 were more similar to each other, being related to decreases in richness and abundance of the functional groups, on both axes.

3.3 Ecosystem multifunctionality analysis

A total of 56 (out of 118) predictor variables influenced at least one of the nine ecosystem functions analyzed. Around 40% of were positive. This percentage of explanation varied for each ecosystem function and scale of sampling. For instance, leaf-litter production and the contents of nitrogen and phosphorus in litter were, on average, positively affected by more than 50% of the predictor variables, on all scales of sampling. Litter decomposition rate and litter quality were positively affected by 48% and 42% of the predictors, respectively. The remaining four ecosystem functions (pH, miscellaneous litter production, litter quality, and soil fertility) were positively explained by less than 40% of the predictors, e.g., soil fertility was explained by only 28% of the predictor variables.

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The summary results for the *lasso* analyses are presented in Figures 2 and 3, distinguished according to the two fitted models. In these figures, the x axis displays the *lasso*-selected predictor variables, and the y-axis represents the coefficient estimates for each variable. Only those coefficients with values different from 0 were displayed on the plot next to the coefficient estimate point. A negative coefficient implies a negative effect on the response variable (i.e., the ecosystem function), and a positive coefficient, a positive effect. Below, we described each model fitted according to the scale of sampling.

3.4 Effects of biodiversity model on ecosystem functions

In general, the species richness and abundance of distinct taxonomic groups had 50% positive effects on ecosystem functions. The taxonomic biodiversity variables with the most positive effects on the ecosystem function were richness of trees and wasps, affecting six of the nine ecosystem functions. The Shannon index of above-ground invertebrates negatively affected eight of the nine ecosystem-function variables.

Of the 22 predictor variables selected by *lasso* in the taxonomic biodiversity model, 12 had a positive effect on litter decomposition rates (Figure 2). Evenness of vertebrates, abundance of birds, and richness of soil arthropods had the three most-positive effects on decomposition. On the other hand, the abundance of bees, frogs and wasps and the richness of vertebrates (for example) negatively affected litter decomposition (Figure 2).

Overall, the richness and abundance of different taxa (Figure 2) showed positive effects on leaf litter and miscellaneous litter production. Therefore, 55% of the predictors of taxonomic biodiversity components showed a positive effect on leaf and miscellaneous litter production. On the other hand, some taxonomic-biodiversity predictors (e.g., richness of birds, frogs and bees, and abundance of bees) had small influences on leaf and miscellaneous litter production. On average, the Shannon diversity and evenness of below-ground invertebrates had a positive effect on the rates of leaf and miscellaneous litter production,

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while the Shannon diversity of above-ground invertebrates had only a small effect on litter production (Figure 2).

Most of the taxonomic-biodiversity predictors (13 of 24; 54%) had a positive effect on nitrogen content in leaf litter. These predictors included the richness of vertebrates, reptiles and frogs and the abundance of trees, wasps, birds, and soil arthropods, among others. In contrast, we observed small effects of the richness of wasps, ants, trees, and reptiles on nitrogen content in litter, as well as the abundance of frogs, bees and mammals, and the Shannon diversities of invertebrates and below-ground invertebrates on nitrogen content in litter (Figure 2).

Additionally, we found that 14 (of 27; 52%) of the predictor variables at the taxonomic biodiversity level had positive effects on phosphorus content in litter. Among these, the richness of vertebrates, trees, reptiles, and frogs showed higher β-values. On the other hand, the abundance of birds, Shannon diversity, and evenness of below-ground invertebrates, and the richness of ants showed small effects on phosphorus content in litter (Figure 2).

Only six predictors of taxonomic biodiversity (of 25; 24%) had a positive effect on soil pH. The Shannon index of invertebrates, the abundance of reptiles, and the evenness of vertebrates had the most positive impact on the pH. In contrast, the abundance of trees had the most negative impact (Figure 2).

For the phosphorus content in soil, 11 of 25 (44%) of the taxonomic predictors had positive effects (e.g., richness and abundance of mammals, diversity of invertebrates, and overall diversity of animals). Otherwise, the Shannon diversity of trees and abundance of vertebrates had negative effects on the phosphorus content in the soil (Figure 2).

In general, soil fertility and litter quality were affected by taxonomic-biodiversity predictor variables (Figure 2). Thus, the richness of trees had a larger effect on litter quality

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than on soil fertility. The richness of soil arthropods, wasps, and frogs had positive effects on soil and litter quality. The abundance of birds, trees, vertebrates, mammals, frogs, and overall animals also had positive effects on soil and litter quality. The Shannon diversity of invertebrates and below-ground invertebrates, and the Shannon diversity of overall animals positively affected soil fertility. The evenness of vertebrates, trees, and above- and below-ground invertebrates also had positive effects on soil fertility and litter quality.

3.5 **Functional-biodiversity effects on ecosystem functions**

Of the 22 predictors of functional biodiversity selected to explain decomposition, we found that 95% had a positive effect on at least two functions (from 2 to 7 of the 9) (Figure 3). The abundance of functional groups, such as pioneer and secondary trees, floral syndromes, herbivores, and insectivorous invertebrates had positive effects on decomposition (Figure 4). Also, the richness of decomposers, frugivores, granivores, nectarivores, and of seeds in seed rain had positive effects on decomposition. The abundance of some functional groups, such as granivores, omnivores, and frugivores had low values, suggesting small effects on decomposition (Figure 3).

The majority of the predictor variables at the functional biodiversity level (14 of 25) had positive effects on litter production, and half (11 of 22) on miscellaneous litter production, although the sizes of their effects differed. For example, the abundance of vertebrate insectivores had a stronger effect on leaf production than on miscellaneous litter production. Conversely, the abundance of insectivorous invertebrates had a positive effect on miscellaneous litter production and a negative effect on leaf-litter production. Also, the richness of granivores and frogs, the abundance of insectivorous invertebrates, and the Shannon diversity of vertebrates had positive effects on leaf litter, but negative effects on miscellaneous litter production. In contrast, lower rates of miscellaneous litter production

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were associated with deviations in the Shannon diversity of invertebrates, evenness of below-ground and above-ground invertebrates, and richness of secondary trees (Figure 3).

Many of the functional-group predictors (10 of 19) had positive effects on nitrogen content in litter (SFigure2). The abundance of herbivores, insectivorous vertebrates, invertebrates, frugivores, granivores, and pioneer trees as well as the richness of seeds, herbivores, pioneer trees, and insectivorous invertebrates had positive effects on nitrogen content in litter. On the other hand, the abundance of decomposers and the richness of secondary trees, nectarivores, and granivores had small effects on nitrogen in litter. For phosphorus content in litter, nine of 21 (43%) predictors had a positive effect. Thus, the abundance of granivores, pioneer trees, floral syndromes, nectarivores, and omnivores and the richness of insectivorous vertebrates, herbivores, and decomposers had positive effects. In contrast, the abundance of secondary trees and decomposers and the richness of secondary trees, among other predictors, had small effects on phosphorus in litter (Figure 3).

Increases in the abundance of omnivores, frugivores, and granivores, as well as the richness of carnivores, decomposers, insectivorous invertebrates, frogs, seed rain, floral syndrome, and wasps, and the evenness of invertebrates had positive effects on phosphorus content in soil. In contrast, the richness of secondary trees, nectarivores, birds, omnivores, and herbivores had small effects on soil pH and phosphorus content (Figure 3).

The abundance of nectarivores, carnivores, decomposers, omnivores, vertebrate insectivores, and secondary and pioneer trees showed positive effects on soil fertility and litter quality. Likewise, the richness of seeds, carnivores, vertebrate and invertebrate insectivores, granivores, frugivores, herbivores, and omnivores positively influenced soil fertility and litter quality. The richness of most functional groups had a small or null effect on soil fertility and litter quality (except for the groups listed above, which showed positive effects). Additionally,

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the Shannon diversity of animals, evenness of above-ground invertebrates, and evenness of trees had positive effects on litter quality (Figure 3).

4 Discussion

Our results showed that biodiversity effects seem to be remarkably consistent across different groups of organisms and among trophic levels and functional groups. This consistency indicates the existence of general underlying principles that dictate how the organization of biological communities' influences ecosystem functioning (Hooper et al., 2012). We found exceptions to this pattern for some BEF; however, there was substantial variability in the response of ecosystem functions under different environmental conditions. In general, we found that for each sampling scale, half of the predictors, on average, had strong positive effects on the ecological processes studied, while the other half caused small or null effects. According to (Turnbull et al., 2016), positive BEF relationships arise from phenotypically and genetically based differences or trade-offs in species characteristics, as no one species or only a few species perform or contribute to different ecosystem functions in the same way. These findings offer opportunities to explore the boundaries that constrain biodiversity effects on ecosystem multifunctionality.

4.1 Dissimilarities in study sites according to different scales of diversity

The richness and abundance of different biodiversity groups were important predictors to define the similarities of ecosystem functions between reforested sites (e.g., tree density and the size and age of sites). The restored sites are located in areas with diverse land uses, including monocultures of sugarcane, soybean, and rubber trees, which in many cases are the dominant matrices. Previous studies in the same area, have suggested that landscape configuration has a strong effect on the local biodiversity and consequently on some ecosystem functions (Araújo et al. 2018; Londe et al. 2020).

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Studies including planting experiments have demonstrated that larger and older areas have experienced persistent positive diversity–productivity relationships (Tilman et al., 2006; Van Ruijven & Berendse, 2010), while smaller and younger reforested patches have commonly lost this relationship, or it is considerably weakened (Roscher et al., 2012). In restored plant communities, however, species loss and gain are non-random, and changes in composition can be more critical for ecosystem function than loss or gain in species richness per se (Zavaleta et al., 2010).

Our findings indicated that many important ecosystem functions were highly affected by the presence of different groups at the levels of taxonomic biodiversity and functional biodiversity, which may indicate that the community shows complementarity in functional redundancy. At present, we know little about the biological mechanisms that are responsible for complementarity among species, besides, some studies showed that species loss has adverse effects on a range of ecosystem functions and services (Balvanera et al., 2006; Cardinale et al., 2006), but that relatively few species are needed to sustain the overall health of the environment (Cardinale et al., 2006), suggesting a high degree of functional redundancy (Schoolmaster et al., 2020).

Our first question was whether taxonomic biodiversity had any effect on ecosystem functioning in reforested riparian areas. We expected that an increase in biodiversity would have a positive effect on the ecosystem functions. We found that an increase in overall animal (of all the taxonomic groups sampled) and tree species richness and abundance, the diversity index, and evenness had positive effects on 54% of the ecosystem functions. For example, richness and abundance of mammals, abundance of birds, richness of arthropods in the soil, and richness of trees all had positive effects on a minimum of five and a maximum of six of the nine ecosystem functions studied. However, there were exceptions, where some

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biodiversity taxa had minimal or null effects (e.g., bird richness, overall vertebrate abundance, and bee abundance).

We found that plant species richness and abundance had positive effects on a large number of processes in the restored ecosystems, although they did not show any effect on nitrogen and phosphorus in litter or on soil fertility. This could be explained by the more dystrophic soil of the forest patch with the highest species richness and abundance, compared with the reforested patches (Szefer et al., 2017). There is growing evidence that the quality of leaf litter is related to the ecological role played by functional groups of species (Szefer et al., 2017) and to variation in soil N and P availability (Kozovits et al., 2007; Hobbie, 2015). Several soil physical parameters can affect the relationship between soil fertility and plants, such as the percentage of clay minerals, soil aggregate stability, and soil compaction (Bardgett et al., 2014). All these physical parameters influence soil hydrological regimes and consequently the exchange of chemical elements (Horn & Gra, 1998; Cheng & Heidari, 2019), especially P and N, which are directly related to floral parameters; and can affect the productivity of the ecosystem. On the other hand, soil fertility was positively affected by a few components of the biodiversity level, such as the richness of mammals, the abundance of decomposers, and the richness of seeds in seed rain.

The association of vegetation structure indicates a possible relationship between soil chemical characteristics and the rapid decomposition of organic matter in tropical riparian forests (Soares et al., 2020). In fact, the effects of biodiversity on decomposition seem to be remarkably consistent across different groups of organisms, among trophic levels, and across the various ecosystems that have been studied. When we evaluated the effects of biodiversity on the rate of organic-matter decomposition in litter, we found considerable variation in the predictive power of different taxonomic groups. However, as expected, the trend was more pronounced for certain taxa. For example, the abundance of birds, richness of soil arthropods,

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and richness and abundance of trees were positively related to the litter decomposition rate. This consistency indicates that there are general underlying principles that dictate how the organization of communities influences this function in the restored forests studied here. According to (Cardinale et al., 2011), limited evidence suggests that, on average, a decline in plant diversity may reduce decomposition rates and the efficiency by which biologically essential elements are recycled back into their inorganic forms. The lack of a direct and strong relationship between the tree diversity and soil processes such as decomposition may also be a result of oversimplifying the data analysis. Trees support other components of diversity in the system, such as understory herbaceous plants and soil microorganisms, among other actors that mediate the litter decomposition process. Explanatory models that include multitaxonomic diversity reveal a significant indirect effect of trees on decomposition (Fujii et al., 2017).

Another important ecosystem function, the amount of litterfall produced by forests, also could be increased by augmenting biodiversity, since litterfall has components of both plant and animal origin. However, in this study, the composition of the taxonomic groups that most affected the components in litterfall (the quantity of leaves and fruits, seeds, branches, etc.) did not show large differences between positive and negative effects, which is consistent with other studies (Fayle et al., 2015; Oliver et al., 2015; Huang et al., 2017). This pattern was expected, since the different groups that comprise biodiversity exhibit behaviors and participate in functional groups that relate differently to the resources offered by the forest. Therefore, some groups will be more related to leaves and other groups will be more related to branches, fruits, and seeds. However, in our study, the variables that explained litter production, at the biodiversity level, showed some unexpected results, with essential components explaining little or almost nothing of ecological processes (e.g., richness and abundance of invertebrates and trees).

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The general effect of species richness differed amongst the studied functions and biogeochemical cycles (such as phosphorus and nitrogen content). Certain taxa seemed to be more important in explaining BEF. For example, the positive relationship of mammal and tree species richness with nitrogen and phosphorus concentrations in soil was expected, but the null effect of decomposer richness on these two elements was not. Balvanera et al. (2006), in a meta-analysis of biodiversity effects on ecosystem function, did not find similar results for biogeochemical cycles, which may occur if complementarity, facilitation, and insurance effects increase the community-level use of limiting resources (Hooper et al., 2012). The presence of certain groups such as legume trees may be more determinant for nutrient cycling than is species richness (Vitousek & Howarth, 1991). However, changes in vegetation composition may cause a discrepancy between biogeochemical cycles (Pasut et al., 2020). Animal bodies, feces, and fruits processed by animals are available to become soil organic matter along with litter directly produced by plants. Also, large-bodied seed dispersers such as peccaries and primates ingest, digest, and defecate large amounts of fruit pulp and seeds, as well as grasses and leaves (Fragoso & Huffman, 2000; Stevenson & Guzmán-Caro, 2010), moving plant matter across the landscape and processing it in ways that make it available to a wider range of invertebrates, fungi, and microorganisms.

The richness of soil arthropods was another biodiversity component that was positively related to litter production. Many arthropods that nest in forest soil, such as ants, termites, and coleopterans, use the forest canopy as a substrate for foraging (Souza-Campana et al., 2017; Dambros et al., 2018). A large part of the soil fauna, in our study, was composed of leaf-cutting ants and termites, as is typical in neotropical forests (Fujii et al., 2017), which could be acting to increase the quantity and quality of some organic material in the litter. Other components of biodiversity, such as bird and bee richness, were also strongly associated with litter production. This could be an indirect result, since the richness of birds

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and bees is linked with forest structure, with more-structured forests supporting more bird species (Casas et al., 2016; Rhoades et al., 2018). Litter production in more-structured forests exceeds that in less-structured forests (Capellesso et al., 2016; Souza et al., 2019). This result may reflect the success of the restoration process at the sites evaluated here. Also, birds are predators of invertebrates that consume litter, and predation on these invertebrates can increase the amount of litter (Stratford & Şekercioğlu, 2015). At the study sites, various species of insectivorous birds (ground, understory, and canopy) were recorded (Mafia & de Azevedo, 2020). As expected, the abundance of plants was directly proportional to leaf litter production.

The number of taxonomic-biodiversity variables related to pH and phosphorus content in the soil was smaller than expected. For pH, only the diversity of invertebrates is among those expected to affect pH, since many are decomposers. We expected that plant diversity would affect pH, but we failed to find such an effect, probably because the soil of the most mature and diverse forest is more dystrophic and acidic than the eutrophic soil in the restoration patches. This weak association of biodiversity with soil pH has been reported previously. Dawud et al., (2017) found a positive effect of diversity and a negative effect of species composition on topsoil pH. Soil pH is an important factor in maintaining nutrient cycling (such as N) and is related to the activity of soil biota (Malý et al., 2014; Fujii et al., 2017). Also, pH in topsoil is regulated by the input, quality, and decomposition of litter (Vesterdal et al., 2008). Indeed, some authors have suggested that functional groups of trees are more important than biodiversity per se (Dawud et al., 2017) and have emphasized the importance of additive effects of diversity on the abundance and community structure of soil microbial and macrofaunal communities (Scheibe et al., 2015; Wandeler et al., 2016). While these studies reported only weak or absent effects of species diversity on pH or nutrients in

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the soil, they supported strong relationships between tree diversity and soil fauna (Fujii et al., 2017).

Litter nutrients are important for maintaining ecological processes and are strongly related to biodiversity, as the primary and secondary decomposition of organic material and the primary productivity are dependent on plants and animals (Kerdraon et al., 2020). We found positive effects for most predictor variables of taxonomic biodiversity, such as richness and abundance of trees, for both nutrients (P and N) and soil arthropods, which were good predictors for nitrogen content in litterfall. Among the positive effects, we first discuss the role of the faunal diversity in decomposition and nutrient (N and P) content in both the litter and the soil. The overall richness and abundance of animals and trees had strong positive effects on phosphorus in soil. The principal forms of phosphorus in soils are associated with calcium (Ca) or magnesium (Mg) in phosphates (relatively unweathered environments), and with clays and iron (Fe) and aluminum (Al) oxides, in old, highly weathered tropical landscapes (Spain et al 2018). The low solubilities of these phosphates and oxides make P a relatively immobile element in its inorganic form. Thus, the concentration of exchangeable phosphorus in highly weathered P-depleted soils is determined mostly by biological recycling processes, especially those related to organic-matter degradation (Tiessen, 2015). Tree diversity, in part, is important for maintaining the nitrogen and phosphorus pools in restored tropical forest (Zeugin et al., 2010), although this relationship depends on the initial site conditions (Redondo-Brenes & Montagnini, 2006) which makes robust generalizations difficult.

Plant species richness can increase fine-root biomass and length, facilitating P uptake from the different soil layers. Tree species richness also has a positive effect on soil organic carbon and litter decomposition, increasing the bioavailable P content (Wu et al., 2019). The acquisition of P in neotropical forests also seems to be favored by the presence of N-fixing

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legume trees, even in the N-richer but P-limited soils (Houlton et al., 2008). It has previously been observed that the activity of phosphatases is favored by increasing N availability in the soil. Furthermore, the amount and rate of nutrient cycling are partly affected by herbivores through litterfall dung (Fonte & Schowalter, 2005). Insect herbivores can increase soil N and P fluxes by as much as 30% in tropical rainforests, through their fragmentation activity (Schowalter et al. 2011). Defecation by monkeys and other vertebrate herbivores, with further processing by dung beetles, contributes to improving soils and ultimately affects nutrient storage in these forests (Neves et al., 2010). Soil fertility depends on nutrient mineralization, and soil organic matter increases with plant richness; the expected richness of tree species determined, in this study, the greater fertility of the soil and the amount of litter produced. The richness and abundance of other animal groups such as nectarivores also had positive effects on soil fertility.

Shannon diversity and evenness also positively affected the ecosystem functions. We found positive responses and some consistency for BEF. For example, the diversity index of the overall fauna was a good predictor of important ecosystem functions, such as decomposition, N in litter, and P in soil. Moreover, Shannon diversity of the overall animal group and below-ground animals improved different ecosystem functions by more than 50%. Although we had expected that the diversity of trees (Shannon index) would have a positive effect on litter decomposition, the effect was small. The lack of a direct and strong relationship between tree diversity and soil processes such as litter decomposition may also be a matter of oversimplifying the data analysis. Trees are important in supporting other components of diversity in the system, such as understory herbaceous plants and soil microorganisms, among other actors that mediate the litter decomposition process. When explanatory models include multitaxonomic diversity, a significant indirect effect of trees on decomposition is revealed (Fujii et al., 2017). A modeling study by (Loreau & Hector, 2001)

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demonstrated a negative effect of plant litter diversity on litter decomposition, as a larger number of litter types should increase the probability that decomposers will not consume at least part of them. The same model predicted a positive effect of decomposer diversity on decomposition rates, due to partitioning of resources between different decomposers. Nevertheless, we found only a small effect of below-ground invertebrates on litter decomposition, although the diversity of the overall invertebrates positively influenced it.

4.2 Functional-diversity effects on ecosystem multifunctionality

We found that specific functional groups of organisms were essential to maintain the functions in the restored sites. Carnivores, herbivores, and pioneer trees positively affected most of the ecosystem functions (six of nine). Likewise, decomposers, insectivorous vertebrates, and nectarivores showed a positive effect on five of the nine ecosystem functions. Numerous well-known studies have posited that species identity and biodiversity are surrogates of functional-trait effects on ecosystem functioning (see Hättenschwiler et al, 2018; Szefer et al., 2017). However, according to (Schoolmaster et al., 2020), these surrogates should not be assumed to be “causal” although significant biodiversity–ecosystem function correlations are spurious associations that arise from common-cause confounding in mis-specified trait-based ecosystem function models. Residual effects of species identity, while causally related (i.e., elements of species composition), also indicate incomplete trait information.

We observed that functional-group diversity had strong effects on certain ecosystem functions, in particular those associated with litter decomposition, litter quality, and N and P cycling. Our results agreed with several BEF experiments that have shown that functional-group diversity is a good predictor of ecosystem multifunctionality (Temperton et al., 2007; Fujii et al., 2017). For example, we found a positive effect of the richness of carnivorous and herbivorous animals on litter quality and litter-P. Most measures of nitrogen increased with

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the abundance of pioneer trees, since many of them are legumes, able to fix atmospheric nitrogen and therefore increase nitrogen stocks (Houlton et al., 2008; Oelmann et al., 2007; Temperton et al., 2007). Indeed, we found positive effects of the richness and abundance of pioneer trees on N and P contents in the litter, as well as a positive effect of the abundance of secondary trees. Likewise, important functional groups such as herbivores and decomposers had positive and strong effects on almost 70% of the functions. According to (Dawud et al., 2017), functional groups are important in ecosystem multifunctionality, indicating that supporting a large degree of heterogeneity in specific characteristics of some taxonomic groups (those that can be captured by functional-trait diversity) may enhance ecological functions.

Increasing evidence shows that the critical means by which species influence ecosystem functions is through their functional traits (e.g., phenotypic attributes that represent niche exploitation; (Díaz et al., 2007). While functional diversity may theoretically increase with species richness in some contexts (Hooper et al., 2005), measures of taxonomic biodiversity (particularly species richness) have proved to explain little of the variance in ecosystem functions compared to indices of functional traits. Indeed, we found that certain functional groups had stronger effects on certain BEF. These components included the presence or relative abundance of certain functional trophic groups, such as herbivores, carnivores, and pioneer trees (i.e., legumes), and also an element that encompasses a functional-trait value or importance to the BEF (e.g., pollination syndromes). These are hereafter jointly termed (variation in) functional composition.

We found important effects of certain functional groups that clearly affect litterfall production. The abundance of insectivorous and nectarivorous vertebrates and seed eaters that travel through the canopy and manipulate parts of the plants contribute to the fall of leaves, seeds, and branches. Also, the abundant herbivores such as ants, termites, and beetles have a

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similar role as the above functional groups. However, here, the functional groups that determined soil fertility were less abundant than the groups that determined litter quality.

For some functional groups, the effect on BEF proved to be a cross-effect, for example the richness of floral syndromes, which can be related to the richness of plants. Other functional groups, where a positive effect on BEF was expected, had negative effects, such as the abundance of decomposers and decomposition. The functional groups that were more positively related to pH and phosphorus content in soil were the abundance of decomposers (as a result of organic-matter degradation processes), the richness of pioneer trees, abundance of frugivores (manipulation of the fruits that fall to the ground, while at the same time these frugivores may defecate while eating the fruits). These functional groups were consistent and expected. Several investigators have reported correlations between soil properties, such as pH or phosphorous content, with forest properties, such as above-ground biomass or species distributions (Condit et al., 2013; Schaik & Mirmanto, 2013). Pioneer trees may grow several meters in a year, improving soil fertility by accelerating soil organic-matter accumulation, enhancing P concentration, and lowering pH (Diemont et al., 2006; Vleut et al., 2013). The abundance of frugivores (animal feces; seeds and fruits that may fall to the ground) may increase the supply of nutrients and organic-matter content to the soil, leading to more favorable soil physical and chemical conditions for environmental restoration.

5 Conclusion

Restored patches must meet two broad conservation objectives: representativeness and persistence (Noss et al., 2012). The first objective attempts to represent the variety of populations, species, or ecosystem functions of each region; while the second attempts to promote the persistence of these elements over the long term (Margules & Pressey, 2000). Our findings indicate that the restored sites represents the natural variation in taxonomic biodiversity that was almost as important for ecosystem functioning as the natural variation in

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functional biodiversity, but each component display specific responses. Therefore, estimating if taxonomic biodiversity is a better predictor than functional biodiversity for ecosystem functions is worth evaluating. In our study, both these approaches were essential in explaining the ecosystem multifunctionality. However, the relative importance of taxonomic biodiversity versus functional composition depended strongly on the type of ecosystem function.

The scales at which we conduct experimental research to understand the mechanisms that underpin BEF relationships fail to match the scales at which biodiversity changes actually occur (in landscapes and local-level ecosystems). Community and functional ecology will need to interface more broadly with other disciplines in order to determine how diversity relates to ecological processes over evolutionary time at ecosystem scales. Although these challenges will not be easily met, the field of BEF research now has all the necessary tools to take these next important steps.

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Ethics Statement

Trapping and handling were approved by IBAMA – Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (permissions 10717, 129311-1, 36206-1, 36206-2, 367581, 36758-2, 37067-1) and Ethics Committee of the Institute of Sciences - University Federal de

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Ouro Preto (Comissão de Ética no Uso de Animais– CEUA - http://www.ceua.ufop.br) (055/2012 and 142/2013).

AUTHOR Contribution

Y.A., A.K., C.S.A., M.R.S.P., M.C.T.B.M., M.A.F., M.G.P.L. – Design and concept of the Project, and designed the experiment; Y.A., A.K, C.S.A., M.R.S.P., M.G.P.L., M.C.T.B.M., J.P.V.M collected the data; Y.A., M.V.B., F.V.C. and M.M.W. analyzed the data. All authors contributed substantially to manuscript development.

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Figure Captions

Figure 1. Conceptual framework indicating the level of distinct studied components: biodiversity, local, and landscape predictors from which each model was fitted to explain ecosystem functions (used as response variables).

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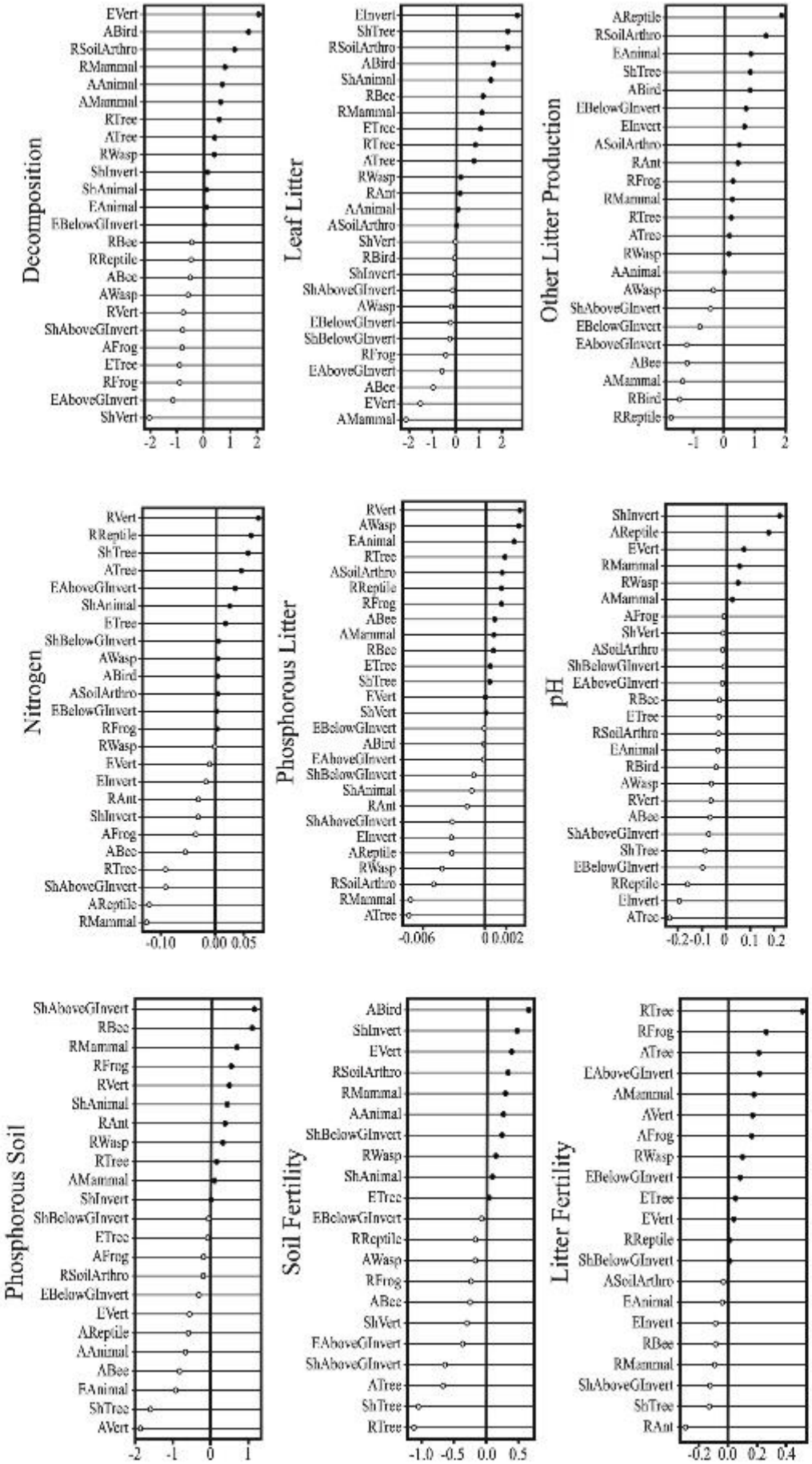
Figure 2: Taxonomic biodiversity components effects (taxonomic biodiversity model) on distinct ecosystem functions (decomposition, leaf in the litter, other litter production, Nitrogen, Phosphorous in the litter, pH, Phosphorous in the soil, soil fertility and litter fertility). W-axis represents β-coefficient from *lasso* analysis. Values greater than 0 indicate positive effect (dark circles) and lower than 0 negative effect (light circles). Central line represents 0 values.

Figure 3: Functional Biodiversity models on the ecosystem functions (decomposition, leaf in the litter, other litter production, Nitrogen, Phosphorous in the litter, pH, Phosphorous in the soil, soil fertility and litter fertility). W-axis represents β-coefficient from *lasso* analysis. Values greater than 0 indicate positive effect (dark circles) and lower than 0 negative effect (light circles). Central line represents 0 values.

Supporting Figure 1: Representation of the first two principal components showing sites dissimilarities according to (a) ecosystem functions and predictors variables at local and landscape levels (see hierarchies in Figure 1); (b) Richness and abundance of distinct groups (biodiversity level); (c) Shannon and Evenness diversity indexes of distinct groups (biodiversity level) and; (d) Richness and abundance of functional groups (biodiversity level) (A = abundance, Arthro = Arthropods, Carniv = Carnivores, E = Evenness Index, Frugiv = Frugivores, G = Ground, Graniv = Granivores, Herbiv = Herbivores, Invert = Invertebrates, Ominv = Omnivores, R = Richness, Second = Secondary, Sh = Shannon Diversity Index, Sindr = Syndrome, Vert = Vertebrates).

Supporting Figure2. Graphic representation of the positive effects (green arrow pointing northeast) and negative effects (red arrows pointing southwest) of biodiversity, local and landscape variables on the ecosystem functions in a restored area in Southeastern Brazil.


Decomposition
EVert
ABird
RSoilArthro
RMammal
AAnimal
AMammal
RTree
ATree
RWasp
ShInvert
ShAnimal
EAnimal
EBelowGInvert
RBee
RReptile
ABee
AWasp
RVert
ShAboveGInvert
AFrog
ETree
RFrog
EAboveGInvert
ShVert
-2 -1 0 1 2
Leaf Litter
EInvert
ShTree
RSoilArthro
ABird
ShAnimal
RBee
RMammal
ETree
RTree
ATree
RWasp
RAnt
AAnimal
ASoilArthro
ShVert
RBird
ShInvert
ShAboveGInvert
AWasp
EBelowGInvert
ShBelowGInvert
RFrog
EAboveGInvert
ABee
EVert
AMammal
-2 -1 0 1 2
Other Litter Production
AReptile
RSoilArthro
EAnimal
ShTree
ABird
EBelowGInvert
EInvert
ASoilArthro
RAnt
RFrog
RMammal
RTree
ATree
RWasp
AAnimal
AWasp
ShAboveGInvert
EBelowGInvert
EAboveGInvert
ABee
AMammal
RBird
RReptile
-1 0 1 2
Nitrogen
RVert
RReptile
ShTree
ATree
EAboveGInvert
ShAnimal
ETree
ShBelowGInvert
AWasp
ABird
ASoilArthro
EBelowGInvert
RFrog
RWasp
EVert
EInvert
RAnt
ShInvert
AFrog
ABee
RTree
ShAboveGInvert
AReptile
RMammal
-0.10 0.00 0.05
Phosphorous Litter
RVert
AWasp
EAnimal
RTree
ASoilArthro
RReptile
RFrog
ABee
AMammal
RBee
ETree
ShTree
EVert
ShVert
EBelowGInvert
ABird
EAboveGInvert
ShBelowGInvert
ShAnimal
RAnt
ShAboveGInvert
EInvert
AReptile
RWasp
RSoilArthro
RMammal
ATree
-0.006 0 0.002
pH
ShInvert
AReptile
EVert
RMammal
RWasp
AMammal
AFrog
ShVert
ASoilArthro
ShBelowGInvert
EAboveGInvert
RBee
ETree
RSoilArthro
EAnimal
RBird
AWasp
RVert
ABee
ShAboveGInvert
ShTree
EBelowGInvert
RReptile
EInvert
ATree
-0.2 -0.1 0 0.1 0.2
Phosphorous Soil
ShAboveGInvert
RBee
RMammal
RFrog
RVert
ShAnimal
RAnt
RWasp
RTree
AMammal
ShInvert
ShBelowGInvert
ETree
AFrog
RSoilArthro
EBelowGInvert
EVert
AReptile
AAnimal
ABee
EAnimal
ShTree
AVert
-2 -1 0 1
Soil Fertility
ABird
ShInvert
EVert
RSoilArthro
RMammal
AAnimal
ShBelowGInvert
RWasp
ShAnimal
ETree
EBelowGInvert
RReptile
AWasp
RFrog
ABee
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EAboveGInvert
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ATree
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-1.0 -0.5 0.0 0.5
Litter Fertility
RTree
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ATree
EAboveGInvert
AMammal
AVert
AFrog
RWasp
EBelowGInvert
ETree
EVert
RReptile
ShBelowGInvert
ASoilArthro
EAnimal
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RBee
RMammal
ShAboveGInvert
ShTree
RAnt
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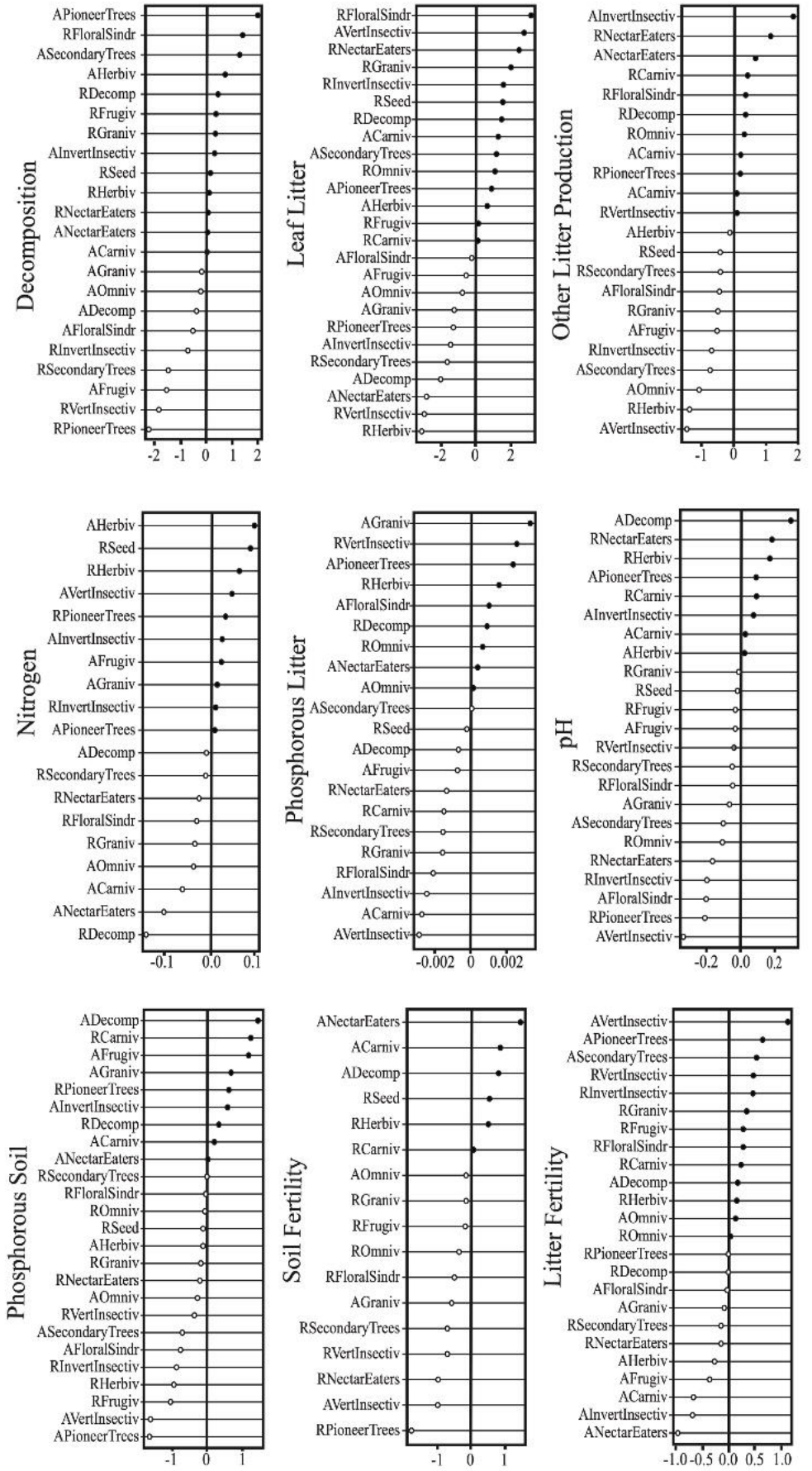
Decomposition
APioneerTrees
RFloralSindr
ASecondaryTrees
AHerbiv
RDecomp
RFrugiv
RGraniv
AInvertInsectiv
RSeed
RHerbiv
RNectarEaters
ANectarEaters
ACarniv
AGraniv
AOmniv
ADecomp
AFloralSindr
RInvertInsectiv
RSecondaryTrees
AFrugiv
RVertInsectiv
RPioneerTrees
-2 -1 0 1 2
Leaf Litter
RFloralSindr
AVertInsectiv
RNectarEaters
RGraniv
RInvertInsectiv
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ACarniv
ASecondaryTrees
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Other Litter Production
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ASecondaryTrees
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Phosphorous Litter
AGraniv
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ANectarEaters
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ASecondaryTrees
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RGraniv
RFloralSindr
AInvertInsectiv
ACarniv
AVertInsectiv
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pH
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RNectarEaters
RHerbiv
APioneerTrees
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AInvertInsectiv
ACarniv
AHerbiv
RGraniv
RSeed
RFrugiv
AFrugiv
RVertInsectiv
RSecondaryTrees
RFloralSindr
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RNectarEaters
RInvertInsectiv
AFloralSindr
RPioneerTrees
AVertInsectiv
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Phosphorous Soil
ADecomp
RCarniv
AFrugiv
AGraniv
RPioneerTrees
AInvertInsectiv
RDecomp
ACarniv
ANectarEaters
RSecondaryTrees
RFloralSindr
ROmniv
RSeed
AHerbiv
RGraniv
RNectarEaters
AOmniv
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APioneerTrees
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Soil Fertility
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ROmniv
RFloralSindr
AGraniv
RSecondaryTrees
RVertInsectiv
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AVertInsectiv
RPioneerTrees
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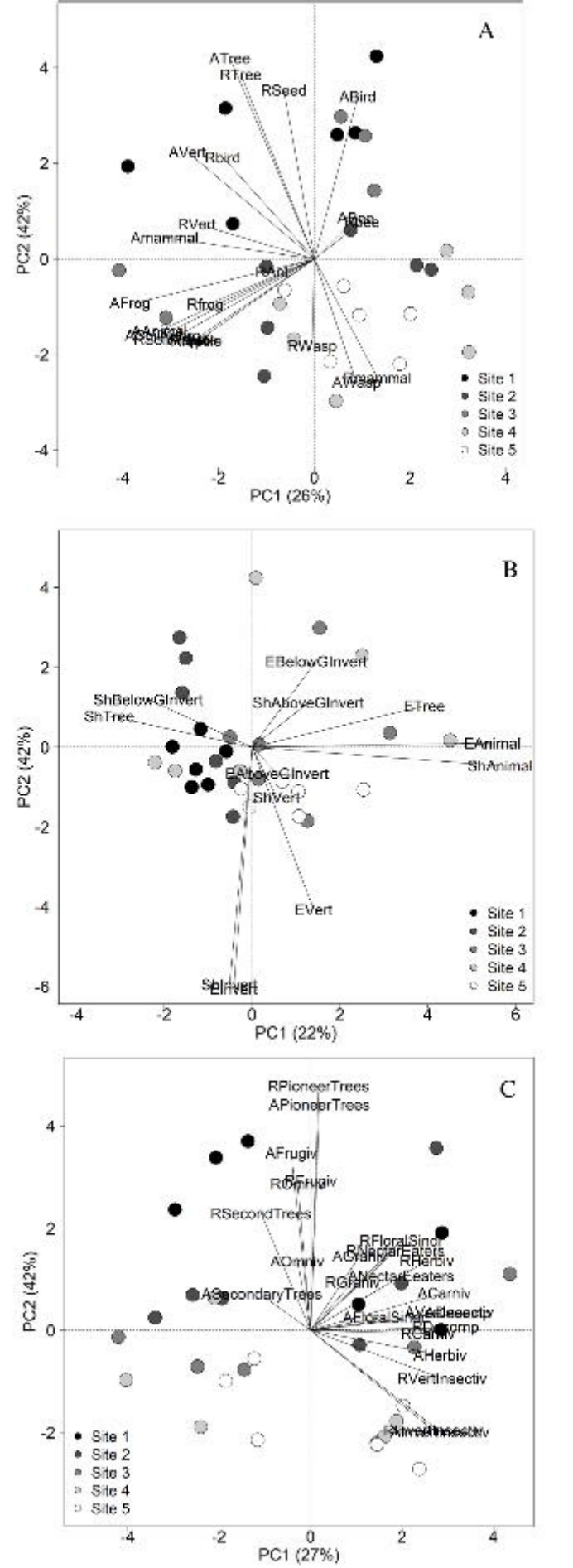
A
ATree
RTree
RSeed
ABird
AVert
Rbird
RVert
Amammal
AFrog
Rfrog
RWasp
AWasp
Site 1
Site 2
Site 3
Site 4
Site 5
PC2 (42%)
PC1 (26%)
B
EBelowGInvert
ShBelowGInvert
ShTree
ShAboveGInvert
ETree
EAnimal
ShAnimal
EAboveGInvert
ShVert
EVert
Site 1
Site 2
Site 3
Site 4
Site 5
PC2 (42%)
PC1 (22%)
C
RPioneerTrees
APioneerTrees
AFrugiv
RFrugiv
RSecondTrees
RFloralSinol
AOmniv
RHerbiv
ASecondaryTrees
ACarniv
RHerbiv
RVertInsectiv
Site 1
Site 2
Site 3
Site 4
Site 5
PC2 (42%)
PC1 (27%)

Ecosystem function (response variables)

Decomposition| Leaf Litter Production| Other Litter Production| Nitrogen Litter| Phosphorous Litter| Soil pH| Soil Phosphorus| Litter Fertility Index| Soil Fertility Index

Biodiversity level (predictor variables)

AAnimal | RAnt | ABee|RBee | ABird|RBird | AFrog|RFrog
AMammal|RMammal | AReptile|RReptile| RSeed
ASoilArthro|RSoilArthro | ATree|RTree | AVert|RVert | AWasp|RWasp

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EAnimal|ShAnimal | EAboveGInvert|ShAboveGInvert
EBelowGInvert|ShBelowGInvert | EInvert|ShInvert
Etree|ShTree | EVert|ShVert

ACarniv|RCarniv | ADecomp|RDecomp | AFloralSindr|RFloralSindr
RFrugiv|AFrugiv| AGraniv|RGraniv| AHerbiv|RHerbiv
AInvertInsectiv|RInvertInsectiv| ANectarEeaters|RNectarEaters
AOmniv|ROmniv | APioneerTree|RPioneerTree
ASecondTrees|RSecondTrees| AVertInsectiv| RVertInsectiv|