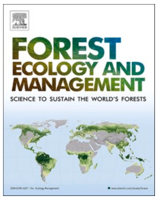
Forest Ecology and Management 553 (2024) 121592

Contents lists available at ScienceDirect

Forest Ecology and Management

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



Eucalyptus plantation reduces diversity and disrupts predator-prey correlations of soil invertebrates within Atlantic Forest

Felipe Martello[a,b,*], Wesley Dáttilo[c,1], Débora Rodrigues Souza-Campana[d,2], Hugo Reis Medeiros[a], Rogério R. Silva[e,3], Milton Cezar Ribeiro[a,f], Maria Santina C. Morini[d,4]

[a] Spatial Ecology and Conservation lab (LEEC), Department of Biodiversity, Institute of Biosciences, São Paulo State University - UNESP, Rio Claro, São Paulo, Brazil
[b] Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK
[c] Red de Ecoetología, Instituto de Ecologia (INECOL), Xalapa, Veracruz, Mexico
[d] Laboratório de Mirmecologia do Alto Tietê (LAMAT), Universidade de Mogi das Cruzes, Avenida Dr. Cândido Xavier de Almeida Souza, 200, Centro Cívico, Mogi das Cruzes, São Paulo, Brazil
[e] Museu Paraense Emílio Goeldi (MPEG), Coordenação de Ciências da Terra e Ecologia, Av. Perimetral 1901, CEP 66077-830 Belém, PA, Brazil
[f] Environmental Studies Center (CEA), São Paulo State University - UNESP, Rio Claro, São Paulo, Brazil

ARTICLE INFO

Keywords:
Silviculture
Multi-taxon approach
Trophic groups
Biodiversity
Brazil

ABSTRACT

Human activities in the Anthropocene have led to the conversion of a significant area of the Earth's surface to agroecosystems, including tree plantations such as eucalyptus. Brazil, as the largest producer of eucalyptus timber, faces the challenge of preserving its rich biodiversity, particularly in the Atlantic Forest biome, which is one of the world's most threatened and diverse. This study aimed to assess the impact of eucalyptus plantation on soil invertebrate communities compared to that of native forest remnants. We sampled ants, beetles, springtails, and spiders as model groups to evaluate the alpha diversity and composition of soil invertebrates in these forests. We also examined trophic interactions between springtails and their potential natural enemies (spiders, ants, and beetles) in both environments. Our results revealed that the abundance and richness of ants and beetles were higher in native forests than in eucalyptus plantations, whereas springtails exhibited a negative response to eucalyptus plantation in terms of abundance, and spiders showed higher richness in eucalyptus plantations. Furthermore, the composition of soil invertebrate communities, with the exception of springtails, was significantly different between eucalyptus plantations and native forests.The correlations between the abundance of springtails and their potential predators (spiders and beetles) were significantly reduced in eucalyptus plantations compared with native forests. Our findings highlight the negative impact of eucalyptus plantation on soil invertebrate diversity and community composition, potentially disrupting predator-prey relationships and emphasizing the importance of preserving native forests to safeguard invertebrate biodiversity and ecological processes.

1. Introduction

Human activities in the Anthropocene have led to the conversion of a significant area of the Earth's surface into agroecosystems (Ellis et al., 2012; Johnson et al., 2017). Plantations tree (i.e., eucalyptus and pinus) are among the land uses that are growing at a constant rate, replacing natural environments in several megadiverse global regions (FAO - Food and Agriculture Organization of the United Nations, 2020). Brazil is the largest producer of eucalyptus trees in the wood and pulp production industry (Silva et al., 2020) and is one of the major threats to native forests (Pereira et al., 2012; Valduga et al., 2016). For instance, in the Atlantic Forest, a biodiversity hotspot and one of the most threatened

---

* Corresponding author at: Spatial Ecology and Conservation lab (LEEC), Department of Biodiversity, Institute of Biosciences, São Paulo State University - UNESP, Rio Claro, São Paulo, Brazil.
E-mail address: felipemartello@gmail.com (F. Martello).

[1] 0000-0002-4758-4379
[2] 0000-0002-2107-6261
[3] 0000-0002-0599-2155
[4] 0000-0002-1823-6703

https://doi.org/10.1016/j.foreco.2023.121592
Received 2 September 2023; Received in revised form 13 November 2023; Accepted 15 November 2023

and diverse biomes of the world, 11% of its original area is converted into silviculture and regions where the native remnants are immersed in the eucalyptus monoculture plantations (Galindo-Leal and Câmara, 2003; Mittermeier et al., 2004; Marques et al., 2020). In such fragmented landscapes, the long-term conservation of tropical forests may need to involve ecological concepts in the management and planning of different land uses (Zhang and Fu, 2009), although anthropic environments (e.g., urban areas and plantations) are rarely considered in biodiversity conservation policies (Barlow et al., 2008).

Tree plantations can provide environmental conservation services in tropical forests due to its structural similarity to native forests, such as canopy cover and vertical stratification, which may support certain wildlife species and ecosystem functions. (Zhang and Fu, 2009; Valduga et al., 2016). In terms of biodiversity conservation, tree plantations may facilitate the movement of organisms across the landscape matrix and provide suitable habitats for forest-dependent species (Lindenmayer et al., 2006; Lyra-Jorge et al., 2010; Pestana et al., 2023). For example, the preservation of native understory and tree regeneration inside tree plantations provides food and refuge for birds (Zurita et al., 2006) and ants (Falcão et al., 2015), and is essential for the conservation of fruit-feeding butterflies (Barlow et al., 2008). However, the regular spatial distribution of trees in plantations and the loss of structural components of pristine forests reduced richness and changed the composition of species assemblages of different taxa (birds: Zurita et al., 2006; fruit-feeding butterflies: Barlow et al., 2008; ants: Suguituru et al., 2011; edaphic macrofauna: Lo Sardo and Lima, 2019), including phylogenetic (Liu et al., 2016) and functional (Martello et al., 2018) diversity. The eucalyptus plantations can also change trophic structure of invertebrate communities, as it can benefit certain predatory species, such as birds and spiders (Filloy et al., 2023), and parasitoid insects (Dall'Oglio et al., 2016).

For invertebrates, eucalyptus plantations may harbor a limited number of forest-dependent species, although more studies are necessary to better understand the relationship between organisms and environmental variables that are amenable to management (Barlow et al., 2007, 2008; Martello et al., 2018). This duality of plantation trees value for biodiversity conservation highlights the need to carry out studies on multiple taxa, exposing the range of different responses of biodiversity to environmental changes. In this sense, multitaxa studies allow investigation of the relationship between different taxonomic groups, unraveling how environmental changes affect the interaction between these groups (Le Provost et al., 2021). These interactions are important because of the interdependence between adjacent trophic groups, which may lead to the loss of biodiversity and ecological processes that depend on these interactions (i.e., population regulation and pollination) (Valiente-Banuet et al., 2015). Moreover, relationships between taxonomic groups also have an applied character, since these relationships between taxonomic groups are criteria for identifying environmental bioindicators based on the premise that highly interacting groups respond similarly to environmental variations (Manning et al., 2015).

Soil invertebrates are highly diverse group, comprising more than 93% of soil animal species (Decaëns et al., 2006) and they are often soil ecosystem engineers because they influence the characteristics of a large volume of soil (Lavelle, 2002). In addition they are involved in multiple interactions with other organisms and through a series of chemical, physical, and biological processes (De Deyn et al., 2003; Decaëns, 2010; Menta and Remelli, 2020). Soil invertebrates also have a high diversity trophic groups that respond differently to habitat modification and provide multiple ecosystem services, including biological pest control and nutrient cycling (Majer, 1983; Jansen, 1997; Uehara-Prado, 2009; Lo Sardo and Lima, 2019). Consequently, soil invertebrates are often used as bioindicators to monitor restoration projects and environmental aspects that affect tree plantation productivity. For instance, they are positively correlated with improved forest management practices, such as adding legume shrubs, but negatively correlated with management intensity, such as understory removal (Zhao et al., 2013). They can also be important indicators of soil quality (for example, springtails diversity is related to soil mineralization and humidification), forming oftenly been part of comprehensive soil quality index (Stork and Eggleton, 1992). Given the importance of invertebrates in ecological processes and associated ecosystem services, assessing the impact of tree plantations on invertebrate assemblages may assist in management programs aimed at preserving the environment (Brown et al., 2015; Lo Sardo and Lima, 2019).

This study aimed to investigate how managed eucalyptus plantations affects soil invertebrate communities compared to native forest remnant communities. We used ants, beetles, springtails, and spiders as model groups to compare the alpha diversity and composition of soil invertebrates in eucalyptus plantations and native forests. We also estimated the influence of each environment on the trophic interactions between springtails and their potential natural enemies (spiders, predatory ants, and beetles). Although eucalyptus plantations are structural forests, they differ from Atlantic Forest in that they are agricultural crops in which chemical products (such as fertilizers and herbicides) are used, they are monocultures with low plant diversity and density, and they are structurally simpler, without understory vegetation (Tavares et al., 2019). Therefore, we expected that forest remnants would support the highest diversity of ants, beetles, springtails, and spiders than managed eucalyptus plantations (Câmara et al., 2012, Aslam et al., 2015). Finally, we expected that the abundance correlations between trophic groups (predator-prey) would be weaker in eucalyptus plantations because land use intensity tends to strongly reduce the relationship between adjacent trophic groups (Le Provost et al., 2021).

2. Material and Methods

2.1. Study area

The study was carried out in 10 forest remnants and 10 eucalyptus plantations (hereafter named as sampling sites) in São Paulo state, southeast Brazil (to verify the location of each sampling site see Supplementary Material). The study region is composed of small and isolated forest remnants immersed in a mosaic of urban areas and farmlands, where eucalyptus plantations, pastures, and sugarcane monocultures are the main crops. Eucalyptus plantations are usually harvested every seven years, creating a mosaic of plantations of different ages. The ten studied forest patches are remnants of the Ombrophilous Dense Forest, which is a megadiverse ecosystem of the Atlantic Forest biome (Colombo and Joly, 2010). This ecosystem is characterized by evergreen phanerophytes up to 15 m tall and a dense understory that includes palms, lianas, epiphytes, and ferns (Tomasulo and Cordeiro, 2000; Oliveira et al., 2006). The ten studied eucalyptus plantations were monocultures of *Eucalyptus saligna* close to the logging stage. Distances between sampling sites within the same treatment ranged between 264 m (native forest) and 1.8 km (eucalyptus plantation).

2.2. Invertebrate sampling

Each sampling site was sampled once in 2010 and 2011 during the rainy season (between September and December), as this is the period with the highest invertebrate activity (Moço et al., 2005). At each sampling site, we established six sampling points at 50 m intervals along a 250-m transect (Kaspari et al., 2000). When the distance between neighboring sampling sites was small, transects were established to maximize the distance between the sampling points. We collected leaf litter from an area of 0.5 m^2 in each of the six sampling points in each transect. The litter was transferred to a Berlese funnel for seven days to collect invertebrates. Over this period, the invertebrates that dropped out of the Berlese funnel mesh sack were collected in plastic cups with moist sponges and later transferred to 80% ethanol vials (Bestelmeyer et al., 2000). At each sampling site, all samples from different years and sampling points were aggregated into a single sample, aiming to enhance the representativeness of each sample while concurrently avoiding spatial and temporal pseudoreplication, resulting in a total of 20 samples, 10 in the Atlantic forest and ten in eucalyptus plantations.

Spider (Araneae), beetle (Coleoptera), and springtail (Collembola) specimens were identified at the family level by specialists (see Acknowledgements). We identified Formicidae specimens at the morphospecies or species level, based on Suguituru et al. (2015). We used taxonomic-level families for spiders, beetles, and springtails due to taxonomic and logistical constraints and because most of these specimens were immature, making identification at a more specific level impossible. The identification of individuals at coarser taxonomic levels, such as family, has been used as a strategy to reduce the cost and time required for identification without significant loss of information. (Pik et al., 1999; Souza et al., 2016). Several studies have documented that a broader taxonomic level (family or genus) can serve as a useful bioindicator of the human impact of environmental changes on soil invertebrates (Zhao et al., 2013; Timms et al., 2013; Caruso and Migliorini, 2006; Gerwing et al., 2020), including springtails (Potapov, 2016), spiders (Lovell et al., 2007), and beetles (Báldi, 2003). All vouchers were deposited at the Myrmecology Laboratory at the University of Mogi das Cruzes, Brazil.

2.3. *Diversity analysis*

To investigate the effects of eucalyptus plantations on invertebrate diversity, we used abundance and richness as alpha diversity measures. We defined the abundance of spiders, beetles, and springtails as the total number of individuals collected (at the family level), whereas for ants, we calculated the species occurrence in samples as a proxy of abundance because the number of individuals is typically not used as an indicator of abundance, as it depends on nest size, foraging behavior, and nutritional status of colonies (Silvestre and Brandão, 2000; Gotelli et al., 2011). For spiders, beetles, and springtails, we calculated the richness of families, whereas for ants, we calculated the richness of species.To estimate the effects of eucalyptus plantation on invertebrate diversity, we used two sample T-test, comparing the indices of diversity between the two environments (forest remnants or eucalyptus plantations). Prior to this we performed Shapiro-Wilk test to assess normality and F-test to assess variance homogeneity. We performed the Mann-Whitney U test, instead of the T-test, whether variables did not have normal distribution or homogeneity of variance (Siegel and Castellan, 1988).

2.4. *Species composition analysis*

To evaluate whether there were differences in composition between invertebrate communities located in forest and eucalyptus plantation for each group of invertebrate we performed a PERMAVOVA analysis (9999 permutations) based on a Jaccard distance (using presence or absence data), conducted in R environment (R Core Team, 2023) using “vegan” package (Oksanen et al., 2022).

2.5. *Invertebrate interactions at community level*

To evaluate whether eucalyptus plantations affect the interspecific interactions between springtails and their potential natural enemies (spiders, ants, and beetles), we calculated the coefficient of correlation between the abundance of prey-predator groups (i.e., spider-springtail, beetle-springtail, and ant-springtail) separately in forest and eucalyptus plantations. For this analysis, we used all families of spiders, however only the genus of ants and families of beetles that include predatory or omnivores species were selected, which included 23 genus of ants (*Acanthognathus, Basiceros, Brachymyrmex, Camponotus, Carebara, Cerapachys, Crematogaster, Dyscothyrea, Ectatomma, Gnamptogenys, Heteroponera, Hylomyrma, Hypoponera, Lachnomyrmex, Linepithema, Megalomyrmex, Monomorium, Myrmelachista, Nylanderia, Odontomachus, Oxypoecus, Pachycondyla, Paratrechina*) and five families of beetles (Carabidae, Histeridae, Elateridae, Scydmaeninae, and Staphylinidae). These ant genera and beetle families are known to encompass predatory species that provide biological control services in both natural and agroecosystems (Achiano and Giliomee, 2005; Zhang et al., 2008; Echegaray et al., 2015; Jałoszyński, 2018; Cividanes, 2021). We tested whether each correlation between prey-predator groups in each environment were different from zero by using the One-Sample T-Test.

Finally, we tested for each prey-predator group whether the differences in correlation coefficients between environments were different from a random population of correlation coefficients. Thus, we compared the observed difference in correlation coefficient between the environments to a population of simulated differences between coefficients where the environment type was randomized ($n = 9.999$). We considered that the observed differences in correlation coefficient between environments were different from a random population of correlation coefficient differences whether the probability of the observed value belonging to the simulated values is less than or equal to 5% ($p < =0.05$).

3. Results

We sampled 3046 individuals, of which 1516 were springtails, 713 were ants, 542 were spiders and 275 were beetles. Twenty-one spider families and 342 individuals were sampled in native forests and 25 families and 200 individuals in eucalyptus plantations. We sampled 22 beetles families and 244 individuals in native forests and only one family and 31 individuals in eucalyptus plantations. We sampled eight families and 995 individuals of springtails in native forests and seven families and 521 individuals in eucalyptus plantations. We sampled 61 species and 430 individuals of ants in native forest and 37 species and 283 individuals in eucalyptus plantation (for more information see Supplementary Material).

Comparing alpha diversity between eucalyptus plantations and the native Atlantic Forest, the abundance and richness of ants and beetles were higher in native forests than in eucalyptus plantations. Similarly, springtail abundance was higher in native forests than in eucalyptus plantations, but richness did not differ between environments. Conversely, for spiders, the richness was higher in eucalyptus plantations than in native forests, while abundance did not differ between environments. (Fig. 1).

For composition both beetles, spiders and ant communities in the native forest were different from those in eucalyptus plantations, while for springtails there was no differences between communities. (Table 1 and Supplementary Material).

The correlations between the abundance of springtails and their predators invertebrate groups varied from -0.275 to $+0.777$ and only correlations between springtails-beetles, and springtails-spiders in the native forest were significantly higher than zero (Fig. 2). For these two pairs of correlations the eucalyptus plantation significantly changed the correlation between the trophic groups (sprintails-spiders $p = 0.013$ and springtails-beetles $p = 0.016$) and in both cases the relationship between abundance changed from positive (in the native forest) to null (in the eucalyptus plantations). The correlation between springtails and ants was not different from zero in both environments and there was no significant change in the correlation between the environments either ($p = 0.161$).

4. Discussion

Our results show the impact of eucalyptus plantations on different groups of soil invertebrates, in comparison to native Atlantic Forest, either by decreasing alpha diversity, altering community composition, or weakening the relationship between some predator-prey groups. Corroborating our hypotheses, eucalyptus plantations had a negative effect on the alpha diversity of invertebrates, except for spiders, which

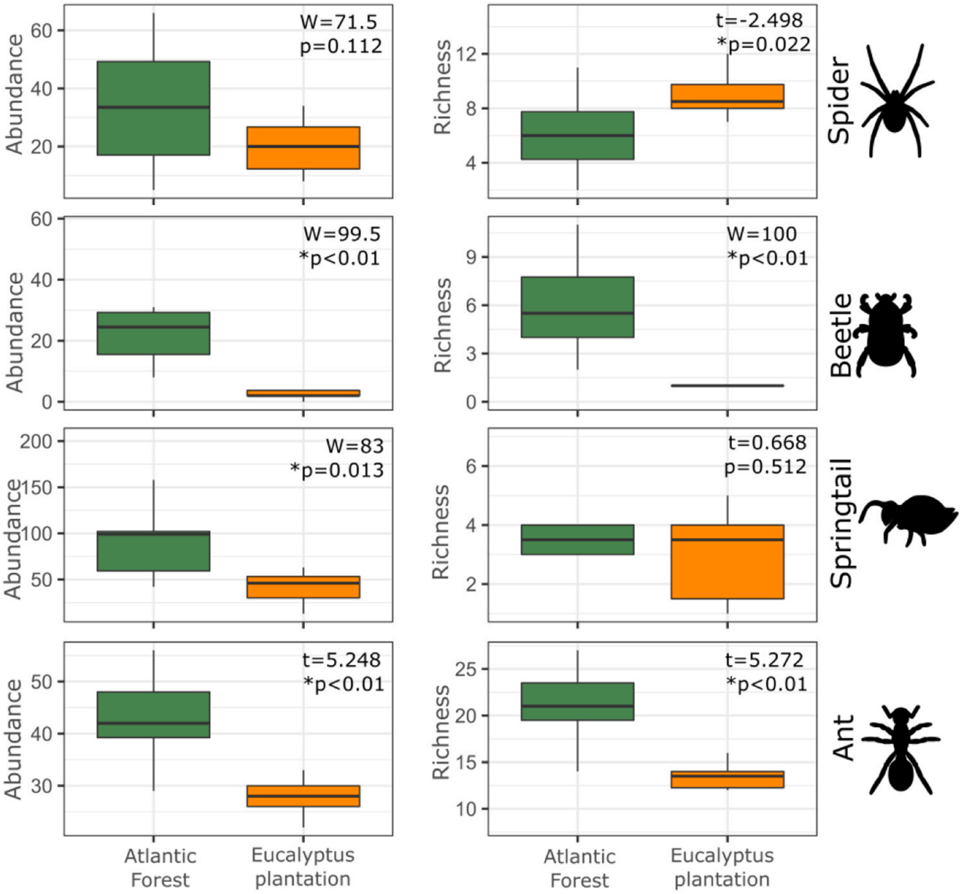


Fig. 1. Effect of eucalyptus plantations on the biodiversity of four invertebrate taxa. "p" values indicate the significance of a hypothesis test (T-test or Mann-Whitney U test) of the comparison between diversity in areas of Atlantic Forest and eucalyptus plantation. Asterisks indicate significant differences in diversity between the environments.

Table 1

Permutal Analysis of Variance (PERMANOVA) of the effect of eucalyptus plantations on invertebrate assemblage composition and pairwise PERMANOVA comparison of invertebrate assemblages. Numbers in bold represent significant differences between assemblages. “R^2” represents determination coefficient and “p” is the value of significance.

Group	R^2	F	p
Spider	**0.0922**	**1.822**	**0.024**
Springtail	0.092	1.835	0.141
Beetle	**0.342**	**9.384**	**< 0.001**
Ant	**0.279**	**6.955**	**< 0.001**

exhibited greater richness of families in the eucalyptus plantations. Despite contradicting our initial hypotheses, studies have shown a mixed effect of eucalyptus plantations on soil invertebrate biodiversity, wherein other factors, such as litter characteristics, leaf composition, and the presence of understory vegetation, also play a significant role in influencing invertebrate biodiversity (Câmara et al., 2012). Considering the taxonomic composition, the results indicated that eucalyptus plantations had a different community composition of soil invertebrates, with the exception of springtails. Finally, our results indicate that the correlations between some prey-predator groups were disrupted in eucalyptus plantations, indicating that, rather than reducing the diversity of soil invertebrates, eucalyptus plantations change the interaction between trophic groups and, consequently, the ecological processes arising from these interactions. The negative impacts of eucalyptus plantations on the local environment are well known and are among the main causes of soil invertebrate biodiversity loss. Eucalyptus plantations tend to cause soil degradation because of the high demand for nutrient uptake (Harrington and Ewell, 1997), although there may also be an increase in soil fertility due to the increased litter content in degraded and treeless lands (Zhang and Fu, 2009; Yitaferu et al., 2013). Furthermore, the allelopathic properties of eucalyptus trees, which are influenced by oils and phenolic compounds in their leaves, result in increased resistance to insects and render them unpalatable to grazers (Zhang and Fu, 2009). These properties also lead to a reduced decomposition rate (Pozo et al., 1997) and negatively affect the seed germination and seedling growth of native plant species (Duarte et al., 2006; Zhang and Fu, 2009). Consequently, these factors have been identified as the mechanisms driving biodiversity impoverishment in eucalyptus plantations.

Beetles, characterized in our study by high taxon diversity in the native rainforest, were more severely affected by eucalyptus plantations: only a single family of Coleoptera occurred in eucalyptus plantations. This family is Staphylinidae, an extremely highly diverse group that has a global distribution, owing to its high range of habitats and feeding habits (Beutel and Leschen, 2016), and is a common beetle family of litter and soil fauna (Bohác, 1999). Many beetle families absent in eucalyptus plantations perform essential roles in ecosystem functioning, such as dung beetles (Scarabaeinae), an important group for nutrient cycling that actively contributes to the soil through the burial of decomposing organic matter in the construction of galleries for nesting within soil (Nichols et al., 2007). Beetles are a megadiverse invertebrate group that reflects a wide variety of nesting, feeding, and behavioral habits (Nichols et al., 2007). Environmental homogeneity and degradation caused by eucalyptus plantation alters the environment and reduces the availability of resources to beetles. For example, compared

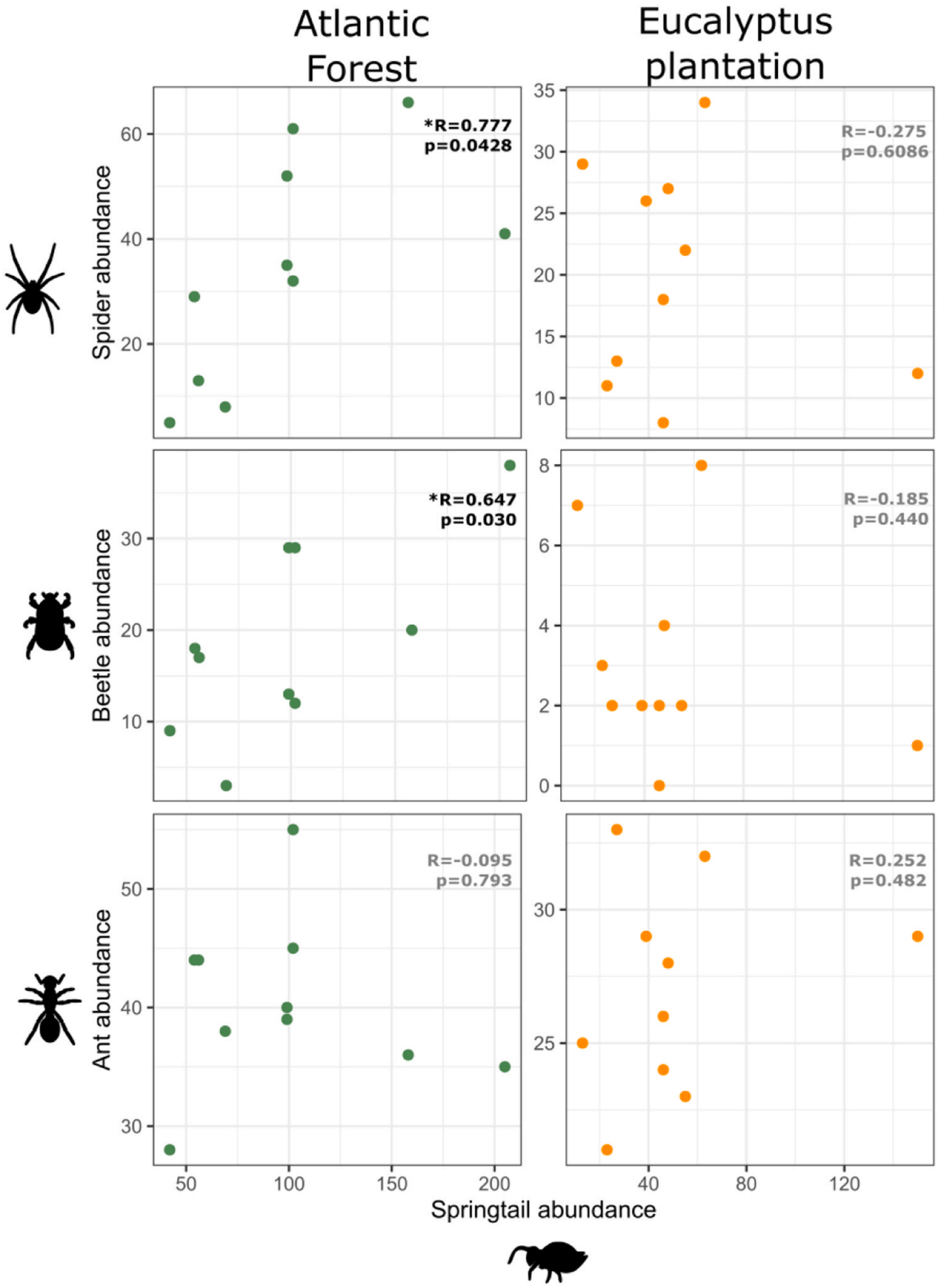


Fig. 2. Correlation between the abundance of soil invertebrate prey (springtails) and predators (spider, beetle, and ant). R values represent correlation coefficients, and p values indicate whether correlation coefficients are significantly different from zero by One-Sample T-Test. Bold R and p-values indicate correlation coefficients that are significantly different from zero.

with the native Atlantic Forest, eucalyptus plantations have lower canopy cover and understory density (Tavares et al., 2019) and and changes in environmental characteristics that may decrease beetle diversity (Hopp et al., 2010). Similar to beetles, the richness and abundance of ants were also reduced in eucalyptus plantations. Ants are insects that dominate the edaphic macrofauna (Lach et al., 2010), and in a previous study (Martello et al., 2018), we have shown that not only alpha diversity, but also functional diversity and beta diversity, are affected by management type, including abandoned eucalyptus plantations. Such differences can be explained when we evaluate the occurrence of species in different environments; for example, specialized food diets, such as *Neocerapachys splendens*, *Cyphomyrmex transversus*, and *Strumigenys appretiata* occurred only in the native forest.

Among the studied groups, spiders were the only group that positively responded to the presence of eucalyptus plantations, exhibiting higher family richness when compared to areas of the native Atlantic forest. Additionally, the composition of spider communities in these two environments was significantly different, suggesting that the environmental changes associated with eucalyptus plantations affect spider community, probably due to the increasing in the number of spider families in eucalyptus. Spiders feed on a wide range of organisms and are a major component of generalist predator communities (Agustí et al., 2003). Moreover, spider prey includes invertebrates that can be favored by eucalyptus plantations, such as Diptera, Isoptera, Orthoptera (Câmara et al., 2012), which may explain the increase in its diversity in eucalyptus plantations. Many of these generalist and opportunistic species may be non-native species in forest environments, as eucalyptus plantations can act as an intermediate environment between natural and anthropic environments (Tavares et al., 2019).

In our study, we observed a higher abundance of springtails in forested areas compared to eucalyptus plantations, underlining the sensitivity of springtails to eucalyptus plantation. Springtail are known to be highly sensitive to soil conditions, and eucalyptus plantations can lead to shifts in soil pH, reduced organic matter content, and changes in nutrient availability, which can directly impact springtail population (Sousa et al., 2000). In addition, the homogenization and low quality of leaf litter of eucalyptus plantations reduces the quantity and quality of food resources, which may also affect springtail populations (Chauvat et al., 2014; Ribeiro et al., 2018). Despite the effects on abundance, our results showed no significant differences in the richness or composition of springtail families in eucalyptus plantations compared to forest. Although it is common for studies to show a negative impact of eucalyptus plantations on the richness and composition of springtail (Sousa et al., 2000),it is not uncommon for no difference to be found between the diversity of springtails in eucalyptus plantation and natural areas (Ribeiro-Troian et al., 2009; Cifuentes-Croquevielle et al., 2020). Springtails could also show tolerances to environmental fluctuations, including physico-chemical changes due to agriculture, and may respond in different ways to anthropogenic changes (Chauvat et al., 2011). Thus, our results suggest that the greatest impact of eucalyptus plantations on the springtail community is at the population level (reducing the number of individuals), without significant changes in the wealth and composition of families.

Aligned to the negative impact of the eucalyptus plantations on springtail abundance, we found remarkable shifts in correlations with their potential predators. While in forest the abundance of springtails correlates positively with spiders and beetles, in eucalyptus plantations these correlations are negative, although not significantly different from neutral correlations. Eucalyptus plantations may lack specialist predator species found in Atlantic forests and are often characterized by a greater prevalence of generalist and omnivore species that may extend their diet to prey other than springtails (Mori et al., 2015; Martello et al., 2018). Moreover, in eucalypt plantations, springtails exhibit functional traits associated with defence against predators, such as repugnant glands, which may reduce their association with potential predators (Jorge et al., 2023). These shifts in the relationships between springtails and predatory vertebrates suggest that the ecological dynamics in eucalyptus plantations may be disrupted compared to natural forest habitats. Spiders and beetles are important predators of springtails (Kuusk and Ekbom, 2010; Jelaska et al., 2014), and the loss of correlation between springtails and beetles/spiders could lead to a restructuring of the community, resulting in a less diverse and more generalist ecosystem. Such changes may affect the balance of the soil, as these invertebrates play a crucial role in feeding the soil microbiota, including fungi, algae and bacteria, and participate in nutrient cycling through the decomposition of organic matter (Bellini and Zeppelini, 2009). It is important to highlight that the correlation analysis performed here is only an evidence of changes in the predator-prey interaction of invertebrate communities. Analysis of trophic interaction networks, both through field experiments and genetic or isotopes analysis, can provide new perspectives, as food web approaches are essential for analyzing the consequences of human activities and for the sustainable management of natural resources (Sabatté et al., 2021).

5. Conclusions

In conclusion, our study sheds light on the effects of eucalyptus plantations on soil invertebrate diversity, particularly in comparison with areas of native Atlantic forests. First, we found that ants, beetles, and springtails exhibited greater abundance and/or species richness in the native Atlantic Forest than in eucalyptus plantations, suggesting that the presence of eucalyptus has a negative impact on the diversity of these invertebrate groups, which are crucial components of the soil ecosystem. Community composition of spiders, ants, and beetles displayed distinct community compositions in the two environments, indicating that the establishment of eucalyptus plantations triggered substantial changes in these communities, mainly to differences in richness between environments, which could have far-reaching consequences for the functioning and stability of the ecosystems. The positive predator-prey relationships observed in the native forest between springtails and their predators, such as spiders and beetles, were disrupted in the eucalyptus plantations, indicating a potential disturbance in ecological processes, such as predation dynamics, which are essential for regulating population sizes and maintaining ecosystem balance. In light of these findings, it is crucial to consider conservation strategies that prioritize the preservation of native Atlantic forests to safeguard the rich diversity of invertebrates and the ecological processes that they support. Maintaining intact forest ecosystems can enhance the stability and resilience of ecological interactions and ultimately contribute to the overall health and sustainability of the environment. Our study underscores the significance of informed decision making in land-use planning and management practices, seeking a harmonious balance between human needs and the preservation of biodiversity and ecosystem functioning.

CRediT authorship contribution statement

Felipe Martello: Writing – original draft, Conceptualization, Formal analysis; **Wesley Dáttilo:** Conceptualization, Formal analysis, Writing – review & editing; **Débora Rodrigues Souza-Campana:** Data curation, Investigation, **Hugo Reis Medeiros:** Writing – review & editing; **Rogério R. Silva:** Data curation, Conceptualization, Formal analysis; **Milton Cezar Ribeiro:** Writing – review & editing, Conceptualization; **Maria Santina C. Morin:** Methodology, Project administration, Funding acquisition, Supervision, Data curation Investigation Writing – review & editing.

Declaration of Competing Interest

As per the submission guidelines, on behalf of all authors, I declare that there are no financial and personal relationships with other people or organizations that could inappropriately influence this research.

I also affirm that there is no interference from any external or internal influences that might compromise the objectivity, credibility, or impartiality of the research findings presented in the article.

Data Availability

Data will be made available on request.

Acknowledgements

The authors would like to thank the professionals who helped identify invertebrate families: Angelico Ansejo and Gabriel Biffi (Coleoptera), Antônio Brescovit (Araneae) and Maria Lúcia Jardim Macambira (Collembola). MSCM receives research grants from FAPESP (#10/50973-7 and #10/50294-2). MCR also thanks FAPESP (#2021/10639-5; #2022/10760-1), National Council for Scientific and Technological Development (#313016/2021-6; #440145/2022-8) and PROCAD/CAPES (project #88881.068425/2014-01) for their financial support. The National Council for Scientific and Technological Development supported RRS through the Programa de Capacitaç ão Institucional (PCI) (#170097/2016-1) and DRSC (# 300690/2019-3).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2023.121592.

References

Achiano, K., Giliomee, J., 2005. Biology of the house fly predator Carcinops pumilio Erichson) Coleoptera: Histeridae). Biocontrol 50, 899–910. https://doi.org/10.1007/s10526-005-3632-4.

Agustí, N., et al., 2003. Collembola as alternative prey sustaining spiders in arable ecosystems: prey detection within predators using molecular markers. Mol. Ecol. 12, 3467–3475. https://doi.org/10.1046/j.1365-294X.2003.02014.x.

Aslam, T.J., Benton, T.G., Nielsen, U.N., Johnson, S.N., 2015. Impacts of eucalypt plantation management on soil faunal communities and nutrient bioavailability: trading function for dependence? Biol. Fertil. Soils 51, 637–644.

Báldi, A., 2003. Using higher taxa as surrogates of species richness: a study based on 3700 Coleoptera, Diptera, and Acari species in Central-Hungarian reserves. Basic Appl. Ecol. 4 (6), 589–593.

Barlow, J., et al., 2007. The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. J. Appl. Ecol. 44, 1001–1012. https://doi.org/10.1111/j.1365-2664.2007.01347.x.

Barlow, J., et al., 2008. Diversity and composition of fruit-feeding butterflies in tropical Eucalyptus plantations. Biodivers. Conserv 17, 1089–1104. https://doi.org/10.1007/s10531-007-9240-0.

Bellini, B.C., Zeppelini, D., 2009. Registros da fauna de Collembola (Arthropoda, Hexapoda) no Estado da Paraíba, Brasil. Rev. Bras. Entomol. 53, 386–390. https://doi.org/10.1590/S0085-56262009000300012.

Bestelmeyer, B.T., et al., 2000. Field techniques for the study of ground-living ants: an overview, description, and evaluation. In: Agosti, D., Majer, J.D., Tennant, A., de Schultz, T. (Eds.), Ants: Standard Methods for Measuring and Monitoring Biodiversity. Smithsonian Institution Press, Washington, pp. 122–144.

Beutel, R.G., Leschen, R.A., 2016. Handbookof Zoology. Arthropoda: Insecta. In: Coleoptera, Beetles, Volume 1. Morphology and Systematics. de. Gruyter, New York, Berlin.

Bohác, J., 1999. Staphylinid beetles as bioindicators. Agric. Ecosyst. Environ. 74, 357–372. https://doi.org/10.1016/S0167-8809(99)00043-2.

Brown, G.G., et al., 2015. Biodiversidade da fauna do solo e sua contribuição para os serviços ambientais. In: Parron, L.M., Garcia, J.R., Oliveira, E.B., Brown, G.G.;, Prado, R.B. (Eds.), Serviços ambientais em Sistemas Agrícolas e Florestais do Bioma Mata Atlântica, 2015. Embrapa, Brasília, pp. 122–154.

Câmara, R., et al., 2012. Effects of eucalyptus plantations on soil arthropod communities in a Brazilian Atlantic forest conservation unit. Biosci. J. 28, 445–455. ⟨http://www.seer.ufu.br/index.php/biosciencejournal/article/view/13450/9590⟩.

Caruso, T., Migliorini, M., 2006. Micro-arthropod communities under human disturbance: is taxonomic aggregation a valuable tool for detecting multivariate change? Evidence from Mediterranean soil oribatid coenoses. Acta Oecol. 30 (1), 46–53.

Chauvat, M., et al., 2011. Assemblages of Collembola across a 130-year chronosequence of beech forest. Soil Org. 83, 405–418.

Chauvat, M., Perez, G., Ponge, J.F., 2014. Foraging patterns of soil springtails are impacted by food resources. Appl. Soil Ecol. 82, 72–77.

Cifuentes-Croquevielle, C., Stanton, D.E., Armesto, J.J., 2020. Soil invertebrate diversity loss and functional changes in temperate forest soils replaced by exotic pine plantations. Sci. Rep. 10 (1), 7762.

Cividanes, F.J., 2021. Carabid beetles (Coleoptera: Carabidae) and biological control of agricultural pests in Latin America. Ann. Èntomol. Soc. Am. 114 (2), 175–191.

Colombo, A.F., Joly, C.A., 2010. Brazilian Atlantic Forest lato sensu: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. Braz. J. Biol. 70, 697–708. https://doi.org/10.1590/S1519-69842010000400002.

Dall'Oglio, O.T., Ribeiro, R.C., Ramalho, F.D.S., Fernandes, F.L., Wilcken, C.F., Assis Júnior, S.L.D., Zanuncio, J.C., 2016. Can the understory affect the hymenoptera parasitoids in a eucalyptus plantation? Plos One 11 (3), e0151165.

De Deyn, G.B., Raaijmakers, C.E., Zoomer, H.R., Berg, M.P., de Ruiter, P.C., Verhoef, H. A., van der Putten, W.H., 2003.). Soil invertebrate fauna enhances grassland succession and diversity. Nature 422 (6933), 711–713.

Decaëns, T., 2010. Macroecological patterns in soil communities. Glob. Ecol. Biogeogr. 19, 287–302. https://doi.org/10.1111/j.1466-8238.2009.00517.x.

Decaëns, T., Jiménez, J.J., Gioia, C., Measey, G.J., Lavelle, P., 2006. The values of soil animals for conservation biology. Eur. J. Soil Biol. 42, S23–S38.

Duarte, N.F., et al., 2006. Mixed field plantation of native and exotic species in semi-arid Brazil. Aust. J. Bot. 54, 755–764. https://doi.org/10.1071/BT05173.

Echegaray, E.A., Cloyd, R.A., Nechols, J.R., 2015. Rove beetle (Coleoptera: Staphylinidae) predation on Bradysia sp. nr. coprophila (Diptera: Sciaridae). J. Èntomol. Sci. 50 (3), 225–237.

Ellis, E.C., et al., 2012. All is not loss: plant biodiversity in the Anthropocene. PLoS One 7, e30535. https://doi.org/10.1371/journal.pone.0030535.

Falcão, J.C., et al., 2015. Efficiency of different planted forests in recovering biodiversity and ecological interactions in Brazilian Amazon. . Ecol. Manag. 339, 105–111. https://doi.org/10.1016/j.foreco.2014.12.007.

FAO - Food and Agriculture Organization of the United Nations. (2020). Global forest resources assessment 2020: Main report. Food & Agriculture Organization of the UN.

Filloy, J., Oxbrough, A., Oddi, J.A., Ramos, C.S., Ribero, M.N., Santoandré, S., Vaccaro, A.S., 2023. Understorey structural complexity mediated by plantation management as a driver of predation events on potential eucalypt pests. For. Ecol. Manag. 531, 120799.

Galindo-Leal, C., Câmara, I.G., 2003. The Atlantic Forest of South America: biodiversity status, threats and outlook. Island Press, Washington.

Gerwing, T.G., Cox, K., Gerwing, A.M.A., Campbell, L., Macdonald, T., Dudas, S.E., Juanes, F., 2020. Varying intertidal invertebrate taxonomic resolution does not influence ecological findings. Estuar. Coast. Shelf Sci. 232, 106516.

Gotelli, N.J., et al., 2011. Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis of myrmecologists. Myrmecol. N. 15, 13–19.

Harrington, R.A., Ewell, J.J., 1997. Invasibility of tree plantations by native and non-native plant species in Hawaii. For. Ecol. Manag. 99, 153–162.

Hopp, P.W., Ottermanns, R., Caron, E., Meyer, S., ROß-NICKOLL, M., 2010. Recovery of litter inhabiting beetle assemblages during forest regeneration in the Atlantic forest of Southern Brazil. Insect Conserv. Divers. 3 (2), 103–113.

Jałoszyński, P., 2018. Biology of Acarophagous Scydmaeninae. In: Betz, O., Irmler, U., Klimaszewski, J. (Eds.), Biology of Rove Beetles (Staphylinidae). Springer, Cham. https://doi.org/10.1007/978-3-319-70257-5_12.

Jansen, A., 1997. Terrestrial invertebrate community structure as an indicator of the success of a tropical rainforest restoration project. Restor. Ecol. 5, 115–124.

Jelaska, L.S., Franjevic, D., JelASKA, S.D., Symondson, W.O.C., 2014. Prey detection in carabid beetles (Coleoptera: Carabidae) in woodland ecosystems by PCR analysis of gut contents. Eur. J. Entomol. 111 (5), 631–638.

Jorge, B.C.S., Winck, B.R., da Silva Menezes, L., Bellini, B.C., Pillar, V.D., Podgaiski, L.R., 2023. Grassland afforestation with Eucalyptus affect Collembola communities and soil functions in southern Brazil. Biodivers. Conserv. 32 (1), 275–295.

Kaspari, M., 2000. A primer on ant ecology. In: Agosti, D., Majer, J.D., Alonso, L.E.,T.R., Schultz, T.R. (Eds.), Ants, standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, pp. 9–24.

Kuusk, A.K., Ekbom, B., 2010. Lycosid spiders and alternative food: feeding behavior and implications for biological control. Biol. Control 55 (1), 20–26.

Lach, L., Parr, C., Abbott, K., 2010. Ant ecology. Oxford university press,.

Lavelle, P., 2002. Functional domains in soils. Ecol. Res. 17, 441–450. https://doi.org/10.1046/j.1440-1703.2002.00509.x.

Le Provost, G., Thiele, J., Westphal, C., Penone, C., Allan, E., Neyret, M., Manning, P., 2021. Contrasting responses of above-and belowground diversity to multiple components of land-use intensity. Nat. Commun. 12 (1), 3918.

Lindenmayer, D.B., et al., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131, 433–445.

Liu, C., et al., 2016. Reorganization of taxonomic, functional, and phylogenetic ant biodiversity after conversion to rubber plantation. Ecol. Monogr. 86, 215–227.

Lo Sardo, P.M., Lima, J.S., 2019. Edaphic macrofauna as a recovery Indicator of abandoned areas of Corymbia citriodora in the Southeastern Brazil. Floram 26, e20190031. https://doi.org/10.1590/2179-8087.003119.

Lovell, S., Hamer, M., Slotow, R., Herbert, D., 2007. Assessment of congruency across invertebrate taxa and taxonomic levels to identify potential surrogates. Biol. Conserv. 139 (1–2), 113–125.

Lyra-Jorge, M.C., et al., 2010. Influence of multi-scale landscape structure on the occurrence of carnivorous mammals in a human-modified savanna, Brazil. Eur. J. Wildl. Res. (2004. Print.) 56, 359–368.

Majer, J.D., 1983. Ants: bio-indicators of minesite rehabilitation, land-use, and land conservation. Environ. Manag. 7 (4), 375–383.

Marques, M.C.M., et al., 2020. The Atlantic Forest: An introduction to the megadiverse forest of South America. In: Marques, M.C.M., Grelle, C.E.V. (Eds.), The Atlantic Forest: History, Biodiversity, Threats and Opportunities of the Mega-diverse Forest. Springer. https://doi.org/10.1007/978-3-030-55322-7.

Martello, F., et al., 2018. Homogenization and impoverishment of taxonomic and functional diversity of ants in Eucalyptus plantations. Sci. Rep. 8, 3266. https://doi.org/10.1038/s41598-018-20823-1.

Menta, C., Remelli, S., 2020. Soil health and arthropods: from complex system to worthwhile investigation. Insects 11, 54. https://doi.org/10.3390/insects11010054.

Mittermeier, R.A., et al., 2004. Hotspots Revisited. Sierra 390. https://doi.org/10.1017/CBO9781107415324.004.

Moço, M.K.S., et al., 2005. Caracterização da fauna edáfica em diferentes coberturas vegetais na região norte Fluminense. Rev. Bras. Ciênc. Solo 29, 555–564. https://doi.org/10.1590/S0100-06832005000400008.

Mori, A.S., Ota, A.T., Fujii, S., Seino, T., Kabeya, D., Okamoto, T., Hasegawa, M., 2015. Biotic homogenization and differentiation of soil faunal communities in the production forest landscape: taxonomic and functional perspectives. Oecologia 177, 533–544.

Nichols, E., et al., 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. Biol. Conserv. 137, 1–19.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., Wagner, H., 2022. Vegan: Community ecology package. R. Package Version 2, 5-2.

Oliveira, F.X., et al., 2006. Comparações florísticas e estruturais entre comunidades de Floresta Ombrófila Aberta com diferentes idades, no Município de Areia, PB, Brasil. Acta Bot. Bras. 20 (4), 861–873. https://doi.org/10.1590/S0102-33062006000400011.

Pereira, H.M., et al., 2012. Global biodiversity change: the bad, the good, and the unknown. Annu. Rev. Environ. Resour. 37, 25–50. https://doi.org/10.1146/annurev-environ-042911-093511.

Pestana, L.F.A., Martello, F., Fonseca, R.C.B., 2023. Richness and composition of terrestrial mammals vary in eucalyptus plantations due to stand age. Austral Ecol. 48 (4), 743–760.

Pik, A.J., et al., 1999. Taxonomic sufficiency in ecological studies of terrestrial invertebrates. Aust. J. Ecol. 24, 555–562. https://doi.org/10.1046/j.1442-9993.1999.01003.x.

Potapov, A.A., Semenina, E.E., Korotkevich, A.Y., Kuznetsova, N.A., Tiunov, A.V., 2016. Connecting taxonomy and ecology: Trophic niches of collembolans as related to taxonomic identity and life forms. Soil Biol. Biochem. 101, 20–31.

Pozo, J., et al., 1997. Inputs of particulate organic matter to streams with different riparian vegetation. J. North Am. Benthol. Soc. 16, 602–611. https://doi.org/10.2307/1468147.

R Core Team (2023). _R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Ribeiro, F.P., Gatto, A., Oliveira, A.D., Pulrolnik, K., Ferreira, E.A.B., Carvalho, A.D., MORAES-NETO, S.D., 2018. Litter dynamics in Eucalyptus and native forest in the Brazilian Cerrado. J. Agric. Sci. 10 (11), 29–43.

Ribeiro-Troian, V.R., Baldissera, R., Hartz, S.M., 2009. Effects of understory structure on the abundance, richness and diversity of Collembola (Arthropoda) in southern Brazil. Neotrop. Entomol. 38, 340–345.

Sabatté, M.L., Massobrio, M.J., Cassani, M.T., Momo, F.R., 2021. Macro and mesofauna soil food webs in two temperate grasslands: responses to forestation with Eucalyptus. Heliyon 7 (1).

Siegel, S., Castellan, N.J., 1988. Non parametric statistics for the behavioural sciences. MacGraw Hill International,, New York, pp. 213–214.

Silva, V.E., et al., 2020. Influences of edaphoclimatic conditions on deep rooting and soil water availability in Brazilian Eucalyptus plantations. . Ecol. Manag. 455, 117673 https://doi.org/10.1016/j.foreco.2019.117673.

Silvestre, R., Brandão, C.R.F., 2000. Formigas (Hymenoptera, Formicidae) atraídas a iscas em uma "ilha" de Cerrado no município de Cajuru, estado de São Paulo, Brasil. Rev. Bras. Entomol. 44, 71–77.

Sousa, J.P., Da Gama, M.M., Ferreira, C., Barrocas, H., 2000. Effect of eucalyptus plantations on Collembola communities in Portugal: a review. Belg. J. Entomol. 2, 187–201.

Souza, J.L.P., et al., 2016. Taxonomic sufficiency and indicator taxa reduce sampling costs and increase monitoring effectiveness for ants. Divers. Distrib. 22, 111–122.

Stork, N.E., Eggleton, P., 1992. Invertebrates as determinants and indicators of soil quality. Am. J. Altern. Agric. 7 (1–2), 38–47.

Suguituru, S.S., et al., 2011. Ant community richness and composition across a gradient from Eucalyptus plantations to secondary Atlantic Forest. Biota Neotrop. 11 (1), 9. https://doi.org/10.1590/S1676-06032011000100034.

Suguituru, S.S., et al., 2015. Formigas do Alto Tietê. Bauru, SP: Canal 6 (2015), 456p. ⟨http://www.canal6.com.br/formigas/Formigas_do_alto_tiete_completo.pdf⟩.

Tavares, A., Beiroz, W., Fialho, A., Frazão, F., Macedo, R., Louzada, J., Audino, L., 2019. Eucalyptus plantations as hybrid ecosystems: implications for species conservation in the Brazilian Atlantic forest. For. Ecol. Manag. 433, 131–139.

Timms, L.L., Bowden, J.J., Summerville, K.S., Buddle, C.M., 2013. Does species-level resolution matter? Taxonomic sufficiency in terrestrial arthropod biodiversity studies. Insect Conserv. Divers. 6 (4), 453–462.

Tomasulo, P.L.B., Cordeiro, I., 2000. Composição florística do Parque Municipal da Serra do Itapety, Mogi das Cruzes. Sp. Bol. Inst. Bot. 14, 139–161.

Uehara-Prado, M., 2009. Selecting terrestrial arthropods as indicators of small-scale disturbance: a first approach in the Brazilian Atlantic Forest. Biol. Conserv. 142, 1220–1228.

Valduga, M.O., et al., 2016. Ecological impacts of non-native tree species plantations are broad and heterogeneous: a review of Brazilian research. . Acad. Bras. Ciênc. 88, 1675–1688. https://doi.org/10.1590/0001-3765201620150575.

Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., Zamora, R., 2015. Beyond species loss: the extinction of ecological interactions in a changing world. Funct. Ecol. 29 (3), 299–307.

Yitaferu, B., et al., 2013. Expansion of Eucalyptus woodlots in the fertile soils of the highlands of Ethiopia: could it be a treat on future cropland use? J. Agr. Sci. 5, 97–107.

Zhang, C., Fu, S., 2009. Allelopathic effects of eucalyptus and the establishment of mixed stands of eucalyptus and native species. For. Ecol. Manag. (7), 1391–1396. https://doi.org/10.1016/j.foreco.2009.06.045.

Zhang, Y.N., Yang, Z.Q., Huang, H.H., Fan, J.X., 2008. Cryptalaus berus (Coleoptera: Elateridae): an important predator of Monochamus alternatus (Coleoptera: Cerambycidae), the vector of pine wilt disease in China. Chin. J. Biol. Control 24 (3), 215–219.

Zhao, J., et al., 2013. Sentinel soil invertebrate taxa as bioindicators for forest management practices. Ecol. Indic. 24, 236–239. https://doi.org/10.1016/j.ecolind.2012.06.012.

Zurita, G.A., et al., 2006. Conversion of the Atlantic Forest into native and exotic tree plantations: effects on bird communities from the local and regional perspectives. For. Ecol. Manag. 235, 164–173. https://doi.org/10.1016/j.foreco.2006.08.009.