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Biodiversity and Ecosystem Functioning in Tropical Habitats — Case Studies and Future Perspectives in Atlantic Rainforest and Cerrado Landscapes

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<http://dx.doi.org/10.5772/59042>

1. Introduction

Currently, environmental changes can be seen as an intrinsic feature of ecosystems, once finding ecosystems that do not suffer of anthropogenic pressures, either direct or indirect, is rare [1]. Such pressures come from the continuous and exponential human population growth, which propels urbanization, activities and processes directly linked to the use of fossil fuels, mining, agriculture and cattle growth. The maintenance of current human population growth implies in the supply of a huge demand for food and technology, resulting in rising pollution and loss of habitats and entire ecosystems [2-5].

Anthropogenic impacts alter the physical environmental characteristics, climate, temperature, soil and water quality, and biogeochemical cycles, interfering directly on the biota [6-11]. The immense resource consumption exerted by the human population demands an ongoing exploitation of natural resources. This causes a constant increase of greenhouse gas emissions and, consequently, the temperature around the globe, also generating an intense conversion of soil use [12,13]. The shift from natural environments into cultivated soils became noteworthy in several countries mainly after the Green Revolution, and together with the frequent use of fertilizers, have changed or destroyed natural habitats, decreasing biodiversity directly or indirectly [9,14]. In addition to these factors, species overexploitation and species invasion

have contributed to the decline of biodiversity [15]. Current data indicates that almost 30% of known species in the World became extinct or are endangered due to anthropogenic pressures.

The loss of biodiversity itself is not the only problem associated with human disturbance, as such habitat changes may have a harmful cascade effects that alter other environmental properties. Every biodiversity loss may be translated into a loss of functional diversity [16], which is related to the characteristics of organisms that allow them to perform different function in the ecosystem [16,17]. These functions, such as seed dispersal [18,19], pest and weed biological control [20], pollination [21], nutrient cycling [22], and the decomposition of organic matter, among others, are essential to ecosystem functioning maintenance. Ecosystem functioning include biogeochemical and ecosystem processes [23], responsible by matter cycling and energy flow, being directly related to resource dynamics and ecosystem stability [17]. Generally, the ecosystem functioning can be estimated as the magnitude and dynamics of ecosystem processes resultant from the interactions within and between different levels of biota [24].

Traditionally, the main parameters used for estimate ecosystem functioning are linked to plant communities, such as primary productivity and biomass stability [25-27]. Processes mediated by other organisms, including arthropods, have seldom been used for such estimates [28,29], regardless their crucial role. Arthropods are very diverse organisms, abundant everywhere, highly successful and spread across the globe. They represent more than 80% of all described biodiversity and, among them, insects are the most abundant [30]. Arthropods perform several functions in ecosystems, at different levels. These organisms inhabit from the underground soil layers to the top of tress, are engaged in several trophic levels, and interfere in the occurrence and distribution of several other organisms through intricate interactions such as predation, competition, herbivory and mutualism. Arthropods perform soil bioturbation [31], pest, weed, parasite and disease control [32-34], pollination [35,36], seed dispersal [18,37], dung and carrion removal [37], and act in decomposition and nutrient cycling [22,38,39]. Thus, it is expected that changes in the diversity of arthropods can also trigger changes in the ecosystem functioning.

Functional features of species may influence how ecosystem functioning will be altered with biodiversity loss [40]. Different species may be redundant in the functions they play in the ecosystem, and in this case species loss would be compensated by another one that performs the same function. Hence, biodiversity loss would not necessarily cause decrease on ecosystem functioning, as well as it would not increase if new species were added (redundancy hypothesis, or null hypothesis). Alternatively, some species may be singular or unique in the functions they play within the ecosystems, and their loss would eventually result in a decrease of ecosystem functioning (linearity hypothesis). Finally, the effect of species loss or gain on ecosystem functioning may be dependent on the conditions (community species composition or soil fertility, for instance) under which these biodiversity alterations occur, and the outcome would be unpredictable (idiosyncrasy hypothesis) [40].

The linearity hypothesis is a pattern frequently reported in studies carried out in temperate regions [41], while in the tropics the null hypothesis seems to be the most common. This difference in the reported patterns may be linked to higher biodiversity levels found in the

tropics, suggesting a possible functional redundancy among species, which does not seem to occur in temperate regions. Notably, tropical regions harbor the highest World biodiversity [42,43], once 16 of the 25 biodiversity hotspots are located in these regions [43,44]. Conversely tropical regions also exhibit the highest rates of species loss due to human activities [45,46]. Among the main human alterations that cause biodiversity loss is land use change [47-49] and, according to estimates, it will remain as the main activity during the next 100 years [50]. Several tropical biomes have experienced high biodiversity loss due to land use change and, in Brazil, the Atlantic Forest and the Cerrado (Brazilian savanna) may be highlighted [8,51-53].

The Atlantic Forest originally covered ca. 150 million hectares along the Brazilian coast [52], occurring in tropical and subtropical regions, and including sites with large altitude variation, humidity, temperature and rainfall regimes. Such a variation in abiotic conditions allowed the differentiation of several phytophysiognomies, high endemism and the occurrence of numerous rare species, harboring ca. of 8% of Worlds' biodiversity. However, recent estimates indicate that more than 90% of its vegetation cover has been lost, and the Atlantic Forest is nowadays composed by forest fragments, mostly smaller than 250 ha, immerse in a landscape of different human modified habitats [52]. The effects of habitat loss due to human activities are extensively reported in the literature concerning the Atlantic Forest [8,54-56], but the effects of biodiversity decrease on the processes related to ecosystem functioning still need more consistent information. The Brazilian Cerrado is the second larger biome of the country, occupying originally approximately 22% of its area [57], and stands out by its high biodiversity and endemism. The Cerrado is currently suffering an elevated degree of human exploitation, and nowadays remains less than 30% of its original area [43]. High fragmentation and conversion in pasture or agriculture areas, cause biodiversity loss, soil erosion, arrival and establishment of invasive species, and shifts on fire regimes, carbon cycles and climate [51-53].

In this chapter we aimed to evaluate the relationship between biodiversity and ecosystem functioning in the tropical biomes Atlantic Forest and Cerrado. We report here three case studies that investigate different ecosystem processes modulated by arthropods: litter decomposition, seed dispersal and protection against herbivores. In these studies we seek to understand the relative importance of species richness and of the presence of keystone species on the studied ecosystem functions.

We performed the first case study in a secondary forest fragment, in the Atlantic Forest biome. In this study we test the relationship between litter decomposition and the biodiversity of several functional groups of soil and litter arthropods. We performed the second case study in the Cerrado biome, testing the effect of ants biodiversity that visit extrafloral nectaries on the protection of these plants against herbivores and herbivory.

Lastly, in the third case study, carried out in the same region of the first one, we analyzed the effect of ant biodiversity on seed removal, comparing secondary forests and *Eucalyptus* crops. In this study we test the direct effect of land use change on the relationship between biodiversity and functioning. From the analysis of these three case studies we concluded this chapter presenting some future perspectives of studies on this subject, to solve some knowledge gaps related to the biodiversity and ecosystem functioning relationship in tropical ecosystems.

2. Case study 1

Decomposition is the process that transforms nutrients retained in organic matter into their inorganic form, making them available in the soil to the primary producers [58,59], and is therefore a key supporting process for the functioning of ecosystems. This process is ruled by three main factors: the physicochemical environment, the quality of the decomposing material and the soil and litter fauna [58,60-63]. These factors present different interaction routes [64] and the relative importance of each component changes in different time and spatial scales [65].

The physicochemical environment is related to the climate, or microclimate, mainly humidity and temperature [66,67]. Abiotic conditions may indirectly affect decomposition, altering litter characteristics, or directly, controlling the activity of decomposers [66,68]. Litter quality is usually associated to foliar material degradability [69], as the concentration of some nutrients has been frequently associated to its palatability to organisms [70]. Usually a higher initial nitrogen concentration reflects in a higher organic matter quality to decomposers. Finally, organisms living in litter and soil are crucial for decomposition processes and nutrient release [60,71-73]. These organisms revolve, mix, break and digest the detritus, metabolizing the litter constituents [58]. Among the components of the soil community, fungi and bacteria are the main decomposing agents. Nevertheless, the micro and mesofauna of soil and litter arthropods have an important role in the decomposition process, through fragmentation of organic matter, through the mixing and vertical movement of organic matter [74]. The existence of an abundant and diversified arthropod fauna is expected, then, to favor an enhanced nutrient cycling [75] and a subsequent faster plant growth [76].

The abundant arthropod fauna composing soil and litter communities can be categorized into different guilds or functional groups, according to their activities, which may affect the microbial community by several ways [77]. Fungivores and bacteriovores consume exclusively the microorganisms, decreasing their abundance. Moreover, they can decrease their prey species richness, through an intense predation, or else an increase of this species richness, through the top-down control of the more competitive species, mediating their coexistence. Detritivores, on the other hand, consume part of organic matter together with the film of microorganisms, releasing the broken and partially digested organic matter in their faeces. As a result, besides their negative effects on microorganisms due to predation, detritivores may increase litter fragmentation, resulting in more decomposing surface and higher decomposer abundance and species richness. These organisms interact in complex food webs and therefore diversity and abundance changes of a given functional group or guild may alter abundance, diversity and functioning of another group [78,79]. It is important hence the investigation of the functional groups role on the decomposition process, as different guilds may interfere more than others.

The process of litter decomposition, as well as the intricate relationships among the diverse components of the edaphic fauna associated to the litter, offers an excellent study system of the relationship between biodiversity and ecosystem processes, mainly in tropical environments with their huge diversity. In this study case we verify how soil and litter arthropod biodiversity affects litter decomposition in a tropical habitat. Our hypothesis is that increasing

arthropod abundance and species richness cause higher decomposition rates, and that some functional groups may have stronger roles in this process.

2.1. Methods

We carried out this study from July 2008 to February 2009, in a ca. 300 ha secondary forest in Viçosa, Minas Gerais, Southeast Brazil (20°45'S e 42°55'W). The main vegetation is composed by Semidecidual Seasonal Atlantic Forest, located within the domain of the Atlantic Forest [80]. In the study area we set two 75m parallel transects, apart 5 m from each other. Along each transect we delimited 15 1m² squares, 5m distant from each other, in a total of 30 sampling points. We collected approximately 200g of freshly fallen leaves from predominant tree species in each sampling point. These leaves were mixed and oven-dried at 60°C for 72 hours. Dried leaves were weighted and separated in groups of 5g, which were placed into litter bags, measuring 15 x 15 cm, with a mesh of 2 mm [81,63]. In each sampling point we set 15 litter bags and, after 30 days we started to remove them. Litter bags were removed fortnightly along 225 days. At the end of the experiment we took a 20 cm deep soil sample in each sampling point, which were taken to soil analyses. The soil analyses were performed at the Soil Lab analyses of the Federal University of Viçosa, and consisted of organic matter content and macroporosity, variables that could interfere in the decomposition process.

After removal, we placed litter bags in Berlese funnels for 48 hours, to extract the arthropods. After their identification, arthropods were sorted according to their feeding habits: detritivores, fungivores and predators [82-86]. The arthropods that we cannot sort in the above categories, because we could not identify feeding habits, were classified as “other arthropods”, and were considered only in the analyses that included all arthropods.

After the arthropod extraction, litter was oven-dried at 60°C for 72 hours and weighted to compare with the initial weight (5g). We considered litter weight loss as the difference between initial and final weight (after 225 days), and we used this as an estimate of decomposition in each sampling point.

2.2. Statistical analyses

To test the hypothesis that more arthropod richness and abundance leads to a higher litter decomposition rate we used a model selection approach [87,88]. The response variable was litter weight loss, and explanatory variables were: total abundance and richness of arthropods, abundance and richness of fungivores, detritivores and predators, as well as macroporosity and soil organic matter. Before structuring the model, we carried out a correlation test among the explanatory variables, using the package “psych”, and whenever two variables presented a correlation higher than 0.7 we removed the variable considered biologically less relevant [89]. Variables that presented correlation higher than 0.7 were: total arthropod species richness and predator species richness (0.73) and total arthropod abundance and detritivore abundance (0.94). We opted, then, to remove predator species richness and total arthropod abundance, as the former represents a possible action of organisms distant from the focal process of decomposition and the latter because it is an estimate more general than detritivore abundance.

The procedure of model selection involved the “MuMIn” package [90], that allows the construction of all possible models starting from the global model containing all variables. For each model, the procedure calculates model weight, based on the Akaike Information Criteria–AICc(ω). After doing so, it ranks all models and the best models are those containing lower AICc and higher weight values. We standardized and centralized all explanatory variables [91], using the package “arm” and the models were built with these transformed variables prior to model selection. All models within $\Delta\text{AICc} < 2$ bounds were considered to obtain a good evidence of support [87]. In the case of more than one model, we averaged the models to obtain only one final model with averaged model coefficients, including their respective confidence interval. Parameters for which the confidence interval crossed zero were considered non-significant [88]. All analyses were performed under the platform R [92].

2.3. Results and discussion

2.3.1. Litter arthropod fauna

We sampled 2,284 individual and 198 arthropod species, from seven classes: (i) Arachnida, (ii) Malacostraca, (iii) Symphyla, (iv) Chilopoda, (v) Diplopoda, (vi) Entognatha and (vii) Insecta. The class with more orders was Insecta (10 orders), followed by Arachnida (four), Entognatha (three), Malacostraca, Symphyla, Chilopoda and Diplopoda (one order each). The most abundant arthropods in our sampling were Acari and Collembola, which are usually described as more abundant in soil and litter [93]. Besides, high abundance of these two groups had already been reported by [94] and [95], who studied forest fragments in the same region. Oribatid mites were the most representative group in all sampling, and these mites have an important role in decomposition process, as most are detritivore [93]. Collembola also presented high abundance and species richness in the samples. These organisms are fungivores and their trophic activity includes both the direct consumption of microorganisms and organic matter fragmentation [96]. Besides, they constitute an important source of food to predatory organisms, being very important in food webs to soil and litter [97].

2.3.2. Arthropod biodiversity and ecosystem functioning

Opposed to what we expected, there was no effect of arthropod species richness and abundance on decomposition rates, both considering total arthropods and when they were sorted by their feeding habits. Although our final model presented soil macroporosity and detritivore species richness as explanatory variables, their 95% confidence interval includes zero, and were considered non-significant (Table 1).

Our results contrast with others, which reported a positive effect of species richness on ecosystem processes [98-103]. The lack of relationship in our study may have occurred due to a high functional redundancy among arthropod species [40,104]. Accordingly, we infer that the studied community is composed by species with similar functions, thus species loss does not cause changes on ecosystem functioning. However, this possible redundancy assumed in this case study does not necessarily exclude another hypothesis to explain the biodiversity-

Response variable	Explanatory variables (parameters)	Estimate	SE	Lower CI	Upper CI
Decomposition (litter weight loss)	Intercept	1.7027	0.0882	1.5297	1.8756
	Macroporosity	0.0977	0.0953	-0.0777	0.2732
	Detritivore species richness	-0.0920	0.0897	-0.2679	0.0838

Table 1. Summary of model averaging results, detailing the explanatory variables present in the final average model. Parameters estimates were obtained from standardized variables.

functioning observed: the linearity hypothesis. Two curves may be generated by these two hypotheses: a linear relationship (Type I curve) in the case of singular species and an asymptotic curve (Type II curve) in the case of redundant species [105]. Therefore, both hypotheses may be explained by the same curve, depending on the scale data was sampled. Linearity, then, would be a component of redundancy curve, but that would only be expected in cases with low diversity. From a given species richness a saturation of the functions would occur, with species playing similar roles. Data obtained in the present study would fit into this latter diversity scale. To test such assumption one can manipulatively reduce arthropod abundance and richness, studying a broad range of species richness, and effectively testing the redundancy hypothesis in tropical environments.

Another possible explanation to the absence of relationship between arthropod diversity and litter decomposition is the similar litter constitution across all sampling points. It is known that the chemical and physical composition of litter has an effect on decomposition rates [61,62,70,106,107]. The manipulation of litter diversity and composition in litter bags may lead to the establishment of different arthropod communities, according to leaf degradability. The manipulation of species richness and composition of plants under decomposition may lead to different responses of arthropod species richness, which might mirror variation in decomposition rates.

Furthermore, in this study we evaluated only the role of arthropod diversity of the soil-litter system. It is known, however, that fungi and bacteria (the microflora) are the decomposers and responsible for organic matter mineralization [58,60,71]. Conversely arthropods act indirectly on decomposition and, even though they facilitate the action of true decomposers, detecting their action on decomposition may be less straightforward.

The absence of relationship between litter decomposition and arthropod species richness and abundance must be evaluated with caution, because assuming functional redundancy among species may be uncertain. Such outcome may lead us to the wrong conclusion that species loss does not affect ecosystem functioning at all, and this early, which may be wrong as discussed above.

Our conclusion is that litter decomposition process in the tropics and other hyper diverse habitats may be more complex than it is for the well known temperate habitats. Studying only one component may not give a precise response, due to the immense assembly of components in complex habitats and their equally complex interactions. Manipulative experiments,

microbial activity estimates, as well as manipulation of litter diversity and composition should give us a more precise knowledge of the biodiversity role on ecosystem key processes.

3. Case study 2

Besides the ecosystem processes, as decomposition and nutrient cycling, species interactions are also important in the maintenance of ecosystem stability. The importance of predation and competition in community structuring is well studied [108-110], although mutualism may also have a central role in species distribution in ecosystems [111,112]. Ants may establish a wide variety of mutualistic associations with plants [113,114]. Plants may offer resources like shelter, food, or both, that may be used by ants in several ways. The mutualistic interactions between ants and plants vary from diffuse, such as secondary seed dispersal [115] and use of extrafloral nectaries (EFNs) by generalist species [116], to more specialized interactions, such as domatia colonization by *Azteca* sp. [117-119]. On the other hand, ants may also be beneficial to plants, increasing seed dispersal or reducing herbivory, for example [120].

EFNs, are nectar producing structures associated to plant vegetative organs, as leaves or petioles [121]. Extrafloral nectar is a liquid resource, composed by glucose, sucrose and fructose, and containing sometimes amino acids and proteins [122]. EFN-bearing plants are more visited by ants than plants without them [123], and ants that use extrafloral nectar as a resource may establish a generalist association of protection in exchange for food [114,119]. Therefore, the benefits arising from this interaction may explain its success [124]. The interaction between ants visiting EFNs and the plants has been the subject of several studies, although there are some divergences among the obtained results. Several studies relate advantages for EFN-bearing plants, such as decreasing the herbivory and the abundance of herbivores, or even positive effects on plant fitness [120,121,123,125-127]. However, some studies did not spot beneficial effects of visiting ants [128,131,132], indicating that in some cases ants may not be efficient in reducing herbivory [128]. The outcome of the interaction between ants and plants may depend on feeding habits of the herbivores, due to the interaction between ants and sap-feeding insects. Several authors [123,130-134] suggest that generalist ants feeding on their honeydew protect these insects from predators and competitors over chewing insects [130]. Moreover, plant protection may be related to ant species composition, as different ant species present varied behavior and defensive characteristics [129].

The interaction among ants, EFN-bearing plants and herbivores is very common in the Brazilian Cerrado. This biome is composed by herbs, shrubs and small trees that vary in density, composing different phytophysiognomies [135]. These physiognomies are usually divided in three groups, characterized by fields, savannas and forests [136]. *Qualea grandiflora* (Vochysiaceae) is among the several EFN-bearing plant species of Cerrado, which are medium to large-sized trees that reach 30 meters [137]. It is very studied in the Cerrado as it has a large distribution and abundance, and also because it attracts several ant species to their EFNs, placed at the basis of the petioles, near to leaf insertion [138].

This case study evaluates whether the ants foraging on *Qualea grandiflora* protect these plants against herbivory. We tested the hypotheses that increased ant species richness and abundance (i) decreases herbivore species richness and abundance, and (ii) changes the proportion of herbivore guilds in Cerrado.

3.1. Methods

Sampling was carried out in Panga Ecologic Station (PEE), situated in Minas Gerais, Brazil (19°09'20"-19°11'10" S, 48°23'20"-48°24'35" W). The area is a 409 ha of Cerrado, with several phytophysiognomies [139, 140]. Climate is Aw, tropical with a rainy summer and dry winter [141]. The average temperature during winter is 18°C and during summer is 23°C, and monthly rainfall is 60 mm during winter and 250 mm during summer.

Insects were sampled during January 2013, during the rainy season. We chose 90 individuals of *Qualea grandiflora*, 30 in each phytophysiognomy: *Cerradão* (Forest), *Cerrado Stricto Sensu* (Dense Savanna) and *Campo Cerrado* (Field Savanna). As it is known that ant species richness and abundance may vary with tree density in Cerrado [142], we expect that sampling in three different plant densities would produce a higher range of variation on ant community parameters. We sampled herbivores by beating, using an entomological umbrella of 1 m² [143, 144]. We did 10 beatings in each tree, and all insects were collected. All herbivores were counted, identified up to the family level, and sorted into two groups (guilds): leaf chewing insects and sap-sucking insects. Ants were sampled by pitfall traps, placed in the trunk of trees at 1.5 meters above ground level. In each tree we installed four pitfalls, to maximize ant sampling. Pitfall traps remained open for 48 hours, and ants were identified to the lower level as possible (genus or species). When identification up to species level was not possible, we asserted the individuals into morphospecies. Herbivores eventually collected in the pitfall traps were added to the beating sampling.

3.2. Statistical analyses

To test whether an increase of ant species richness and abundance decreases herbivore species richness and abundance, we carried out an ANCOVA (analysis of covariance), with Poisson distribution, considering phytophysiognomies as covariates. To test the hypothesis that increasing ant species richness and abundance decreases the proportion of leaf chewing insects and increases sap-sucking insects, we carried out an ANCOVA to one of the herbivore guilds, using a binomial distribution, corrected for overdispersion. Only one analysis is needed in this case, as the two response variables (proportion of each guild) are complementary. All analyses were carried out in R platform and models were simplified by removing non-significant variables and obtaining the minimal adequate model [145].

3.3. Results and discussion

We sampled 2,597 ants, from 150 species, 25 genera and seven subfamilies. The most abundant subfamily was Formicinae (1,293 individuals), followed by Myrmicinae (737), Dolichoderinae (426), Pseudomyrmecinae (110), Ectatomminae (22), Ponerinae (eight) and Heteroponerinae

(one). The subfamily with the highest species richness was Myrmicinae (55 species), followed by Formicinae (40), Pseudomyrmecinae and Dolichoderinae (20 species each), Ectatomminae (three), Ponerinae (two) and Heteroponerinae (one). We sampled 233 herbivore insects, and Coleoptera was the most abundant order (141 individuals), followed by Hemiptera (75), Lepidoptera (11) and Orthoptera (six). Herbivores were sorted in 97 species, and the order with highest species richness was Coleoptera (62 species), followed by Hemiptera (24), Orthoptera (six) and Lepidoptera (five).

Ant species richness did not affect both herbivores abundance and species richness. As the studied plant species is a mirmecophile, it was not expected to maintain obligatory associations with ant species, being visited by generalist ant species foraging both during the day and the night. Several species in a given community may have a redundant role in some ecological functions, such as predation [146]. Moreover, as mirmecophytes are usually visited by several ant species, species richness may not contribute effectively for herbivore decrease. Therefore, ant species richness visiting EFN-bearing plants may not contribute to herbivore decrease because (i) they may be highly redundant, and/or (ii) they encompass non-aggressive ant species.

Nevertheless, we observed a decrease of herbivore abundance with the increase of abundance of ants in the trees of *Cerradão* and *Campo Cerrado* ($\chi^2=0.7$; $p=0.02$) (Figure 1). The higher number of ants present in a given site gives a higher probability of encounters between them and herbivores, decreasing the number of herbivores [147]. Some ant species may present aggressive behavior, or efficient recruitment ability, and if the most frequent ants have these attributes, there would be a higher chance of herbivore attack and decreasing.

Conversely, we also observed that herbivore abundance increased with the abundance of ants in *Cerrado Stricto Sensu* ($\chi^2=1.7$; $p=0.05$) (Figure 1). Another interesting result regards a higher sap-sucker insect abundance in *Cerrado Stricto Sensu*, in comparison with the other two phytophysionomies (Figure 2). This latter result may explain the positive relationship between ant and herbivore abundance, because most of the herbivores belong to sap-sucking insects, and the positive association between them and ants is well known. As there are more sap-sucking insects in the *Cerrado Stricto Sensu*, ants may be consuming more sugars from the honeydew than from the EFNs [148], possibly leading to a dominance of more aggressive, abundant and frequent ants [149]. Therefore, the association between ants and EFN-bearing plants may shift from mutualistic to antagonistic when sap-sucking insects are present. When there is high resource competition on the plants, ants have a tendency to consume more honeydew than nectar [150], protecting sap-sucking insects and harming the plants.

Although the above scenario may arise from the three trophic level interaction mentioned above, it has been suggested that ants may also repel chewing insects by consuming honeydew, decreasing their abundance and activity on plants [133]. The different responses of herbivores to abundance of ants found in our study suggest that the effect of ants on herbivores is dependent of herbivore feeding habits. Several studies have reported non-obligatory interactions between ants and sap-sucking insects [123,130-134]. In this interaction, ants feed on the honeydew and protect the insects against predators and competitors [130]. Such an interaction may produce an explanation for the above results, because most ants participating in this

interaction are generalists, consuming both honeydew and nectar from EFNs. Therefore, both sap-sucking insects and plants may be protected by the ants, as both provide resources to them. In this scenario, leaf chewing herbivores would be repelled or predated by the foraging ants.

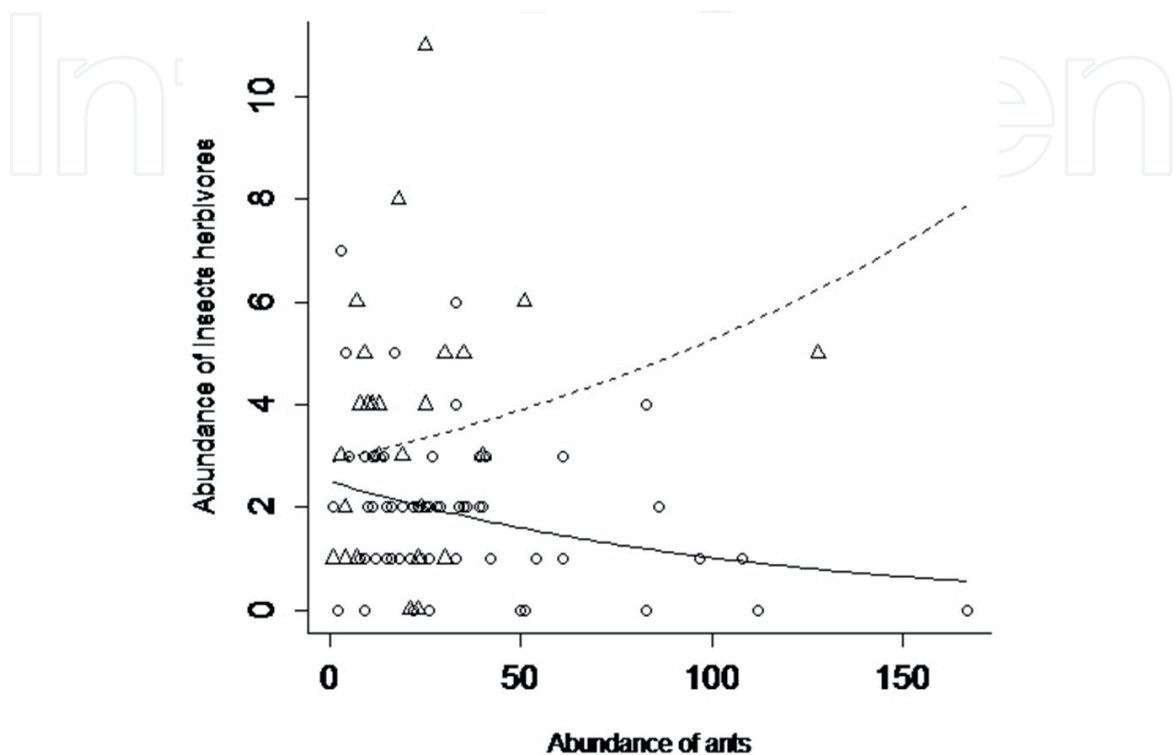


Figure 1. Relationship between abundance of ants and abundance of herbivore insects in the three studied phytophysiognomies. The continuous curve (circles) represent the decrease of herbivores in *Cerradão* and *Campo Cerrado* ($\chi^2=0.7$; $p=0.02$), and the dashed line (triangles) the increase of herbivores in *Cerrado Strictu Senso* ($\chi^2=1.7$; $p=0.05$).

However, ant species distribution and their consequent effect on interactions may be modulated by habitat type and conditions [151]. Habitats with larger resource availability may facilitate the coexistence of ant species [131]. As Cerrado is composed by vegetation types with different tree abundances [136], the relationships among organisms may also vary accordingly. EFN-bearing plants were found to be more frequent in the Forest formations of Cerrado (*Cerradão*) than in other phytophysiognomies, which indicates more extrafloral nectar in this vegetation type [152]. As tree density and species richness influences ant species richness due to higher resource availability to generalist and specialist species [142], mutualistic interactions may be dependent of resource amount and distribution. More heterogeneous habitats may generate diverse resource availability, promoting the found differences among the phytophysiognomies studied here. As there are more resources in the *Cerradão*, ant foraging may be more opportunistic, resulting in a less effective protection against herbivory by chewing insects. Additionally, as there are more resources provided by EFNs, associations between sap-sucking insects and ants may be less effective, decreasing their abundance.

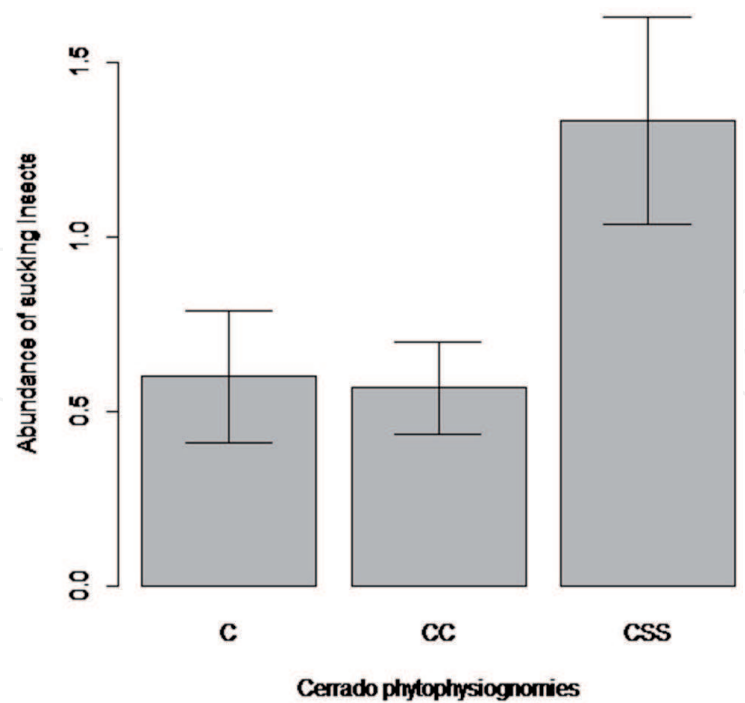


Figure 2. Relationship between SAP-sucking insects in the three phytophysiognomies. C – *Cerradão*, CC – *Campo Cerrado*, CSS – *Cerrado Stricto Sensu*. C and CC did not differed statistically.

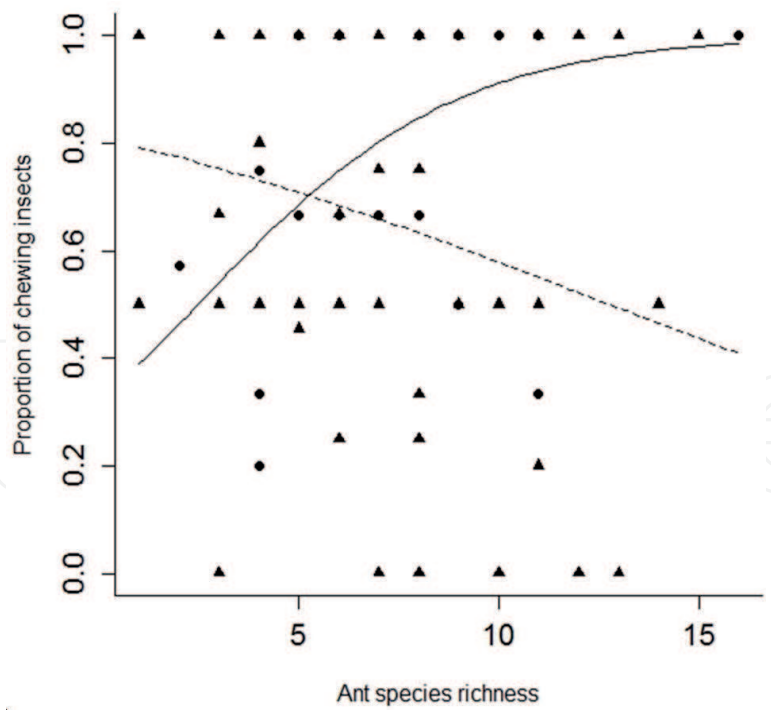


Figure 3. Relationship between the proportion of chewing insects and ant species richness. While ant species richness increased chewing herbivores in *Cerradão* (circles; continuous line), in decreases this proportion in *Cerrado Stricto Sensu* and *Campo Cerrado* (triangles; dashed line). The relationship between sap-sucking insects and ants follows a pattern contrary to the above, as these proportions are complementary.

4. Case study 3

The conversion of pristine environments into human-modified landscapes is rising around the World. Such habitat conversions may culminate in altered environmental conditions, reduction in the availability of resources and decrease in habitat heterogeneity [153]. Consequently, many authors have been warning to the existence of a biodiversity crisis [154,155]. In general the conversion of natural systems introduces newer and simplified ecosystems composed by one or few economically valuable crop species. Whereas habitat loss per se is enough to generate local extinctions [156,157], what is observed is that these habitats are usually substituted by agricultural systems as well. Therefore, most human-modified landscapes are altered by the joint action of these processes, habitat loss and conversion.

Habitat heterogeneity can be defined as the variety and the relative amount of different microhabitats available to organisms, and has been considered over the years a major variable determinant on local species richness and abundance [158-160]. Structurally more complex habitats provide more spatial niches and different types of resource exploitation, thus increasing species diversity [153,161-162], although this relationship may not be always straight [163,164]. Habitat heterogeneity reduction, for instance, can lead to lower resource availability, changes in environmental conditions and eventually species and ecosystem functions losses [165,166].

Eucalyptus crops are one of the economic activities that may lead to the above mentioned biodiversity loss in the Brazilian biomes. This culture was introduced in the country by the beginning of 19th century, and up to 2012 it is estimated to cover 5.105.246 hectares [167]. Once *Eucalyptus* is classically grown as a monoculture in Brazil, habitats are extremely simplified and homogeneous, potentially triggering the mentioned effects on biodiversity.

Several functions may be altered in *Eucalyptus* plantations, potentially due to homogenization, such as litter decomposition [97,168], nutrient cycling [169] and seed dispersal [170]. The latter is usually associated with habitat recovery, as there are several advantages for plants such as avoiding rodent predation [171,172], dispersion for nutrient-rich sites [173], protection against fire [174] and smaller competition with the parental plant [175]. Thereby, such mutualism may play a central role on local plant dynamics [176].

Seed dispersal by animals is considered a diffuse interaction, once can be performed by several generalist frugivores [177,178]. Ants are mainly reported as secondary dispersers, as they take fallen diaspores to their nests. Within the nests conditions are more suitable for the seed, because it is protected from herbivores [179-181], it is a nutrient-rich microhabitat [182,183] and free of competition with the parental plant [175,180,184].

A common observed trend is the reduction in ant species richness with habitat conversion, such as pastures [185], crops [186] and in *Eucalyptus* cultures [187,188]. Species composition is also usually altered by habitat conversion [185,189]. These changes may strongly alter seed dispersal dynamics by ants in fragmented and modified landscapes [185,190], although no mechanism was proposed to explain this correlation. In this study we tested the effect of

natural habitat conversion into *Eucalyptus* crops and the consequences for seed removal by ants. We hypothesized that higher ant species richness increases seed removal, and this relationship is more pronounced in natural forest ecosystems than in *Eucalyptus* crops. Furthermore, we hypothesized that ant species composition changes between natural and *Eucalyptus* crops, and this shift is also responsible for supposed differential seed removal rates. Finally, as we observed differential seed removal between studied habitats we tested the presence of keystone species would influence removal rates.

4.1. Methods

4.1.1. Study site

We carried out the study in Viçosa, Minas Gerais (20°45'S, 42°50'W), Brazil, during summer 2010/2011, the rainy season. The pristine vegetation in this region is within the Atlantic Forest Domain, and is classified as Seasonal Semi-deciduous Forest. From the 1930's decade an intense fragmentation process has begun, and the native vegetation was mainly substituted by coffee crops and pastures. Now days, the landscape is highly fragmented, and is composed by several secondary forest fragments, intermingled with pasture, coffee and *Eucalyptus* crop, among others. We arbitrarily chose five forest fragments and five neighboring *Eucalyptus* for our study sites.

4.1.2. Experimental design

We used *Mabea fistulifera* (Euphorbiaceae) seeds, an abundant native myrmecochorous species with elaiosome. Seeds of this species have a diplochory dispersion, primarily ballistic and secondarily mainly by ants. Seeds, collected directly from branches of several native trees, were obtained from Forest Seeds Laboratory of the Federal University of Viçosa two months before the experimental set up. Seeds had their elaiosomes preserved and were maintained in cold chamber at 20°C straight after natural dehiscence and kept until their use.

In each of the 10 sampling sites (5 native forests and 5 *Eucalyptus* crops), we set 10 sampling units, which were distributed 10 meters apart from each other. Each sampling unit consisted of one ant sampling point and one seed removal spot, distanced 2 meters from each other. Ant sampling points consisted of unbaited pitfall traps (diameter 8 cm, 12 cm height), buried at soil level, and half filled with a killing solution of water, detergent and salt. Seed removal spots consisted of the provision of 10 seeds of *M. fistulifera*, which were covered by a cage with a mesh of 10 mm, to avoid seed removal by vertebrates [192]. Both pitfall traps and seeds remained in the field for 48 hours. After that, we counted the number of remaining seeds and the number and identity of ant species.

We identified ants to genera using the keys by [192], and when possible to species by comparisons with the reference collection of the Community Ecology Lab/UFV, where voucher specimens were deposited. Species identification was confirmed by a specialist.

4.2. Statistical analyses

To test the relationship between seed removal and ant species richness we used an ANCOVA, in which the response variable was the proportion of removed seeds in each site, and the explanatory variables were ant species richness and environment type (native forests or *Eucalyptus* crops). As the response variable was a ratio, we used a binomial error distribution, corrected for overdispersion when necessary. We performed this analysis in the software R [92] and we did residual analysis to check for model fit and distribution suitability.

To test whether ant species composition changes between studied habitats, we performed a NMDS (Non-metric Multidimensional Scaling), using Bray-Curtis dissimilarity index. We computed species abundances as the number of traps they occurred in each sampling site. The significance of differences was checked through PERMANOVA [193]. This analysis was performed in the package *vegan* within the software R [92]. We tested if the most frequent ant species act as keystone species [194] in seed removal by an ANOVA, in which we compared seed removal in the presence and in the absence of each species.

We removed one of the *Eucalyptus* areas a priori from all the analyses due to a heavy rain that removed all seeds, and another *Eucalyptus* area from the ANCOVA after the residual analysis as it was considered an outlier, therefore reducing our total sampling units to eight (five native and three *Eucalyptus* crops).

4.3. Results

We sampled 43 ant species, from 25 genera and seven subfamilies. From these, 23 species occurred exclusively in the native forests, five were exclusive from *Eucalyptus* and 15 occurred in both. The most frequent species were *Pheidole radoskowskii* Mayr, 1884 and *Ectatomma muticum* Mayr, 1870, which occurred in 40.24% and 30.49% of pitfall traps, respectively.

As expected, ant species richness was higher in native forest than in *Eucalyptus* crops ($\chi^2=6.93$; $p=0.008$). Moreover, seed removal rate increased with the number of ant species ($F_{1,6}=11.01$; $p=0.021$; Fig. 4), however it was higher in the *Eucalyptus* than in the native forest ($F_{1,6}=8.75$; $p=0.032$). Conversely, species composition did not differ between the two habitats (Fig. 5, PERMANOVA $F_{1,7}=1.12$, $p=0.32$). Neither the presence of *P. radoskowskii* ($F_{1,80}=0.87$; $p=0.35$), more frequent in *Eucalyptus*, nor of *E. muticum* ($\chi^2=0.94$; $p=0.33$), more frequent in native forests, influenced seed removal.

5. Discussion

Differences in species richness, abundance and composition may affect ecosystem functioning [195]. In this case study we investigated the role of these three biodiversity components on seed removal by ants in native and *Eucalyptus* forests. Concerning species richness our results confirm the general pattern of reduction in modified habitats. The main causes reported for such pattern include habitat loss, homogenization, and harshness conditions for native species [196]. In comparison with native forest, *Eucalyptus* crops may be homogeneous habitats, which

might have contributed to its lower species richness. Ant species richness is strictly related with environmental features such as higher plant species diversity, litter amount and habitat complexity [142,197-200]. From these, plant species diversity and habitat complexity decrease in *Eucalyptus* crops, which may have caused the loss of ant species that did not survive in the modified habitat. We observed the expected positive relationship between seed removal and ant species richness, both in the native forests and *Eucalyptus* crops. Nevertheless, the maximal seed removal at *Eucalyptus* was around 30% while at native forest was about 65%, which may be related to the smaller capacity of *Eucalyptus* crops of harboring species when compared to native forests. This pattern could also be attributed to keystone species (sensu [201]) at native forest, thus promoting the observed higher removal rates. However, the sole effect of potential keystone species did not explain the rates we observed, as seed removal did not change in their absence. Therefore, we have no evidence to consider the existence of some specialist seed remover species inhabiting either of the environments, reinforcing the role of ant species richness in the studied process.

On the other hand we did not find differential species composition between the two habitats types, thus we cannot assign the higher seed removal at native forest due to some keystone species. Moreover, seed removal rates at native forest did not differ when we analyzed the effects of the presence of the most abundant ant species (*E. muticum*). Therefore, we conclude that species richness is the only biodiversity component influencing the ecosystem process in the studied system. The positive relationship between ant species richness and seed removal rate may have important concerns on conservation. The maintenance of natural species richness levels can contribute to a suitable ecosystem functioning due to the role of the seed dispersal for seedling establishment and the community assembly.

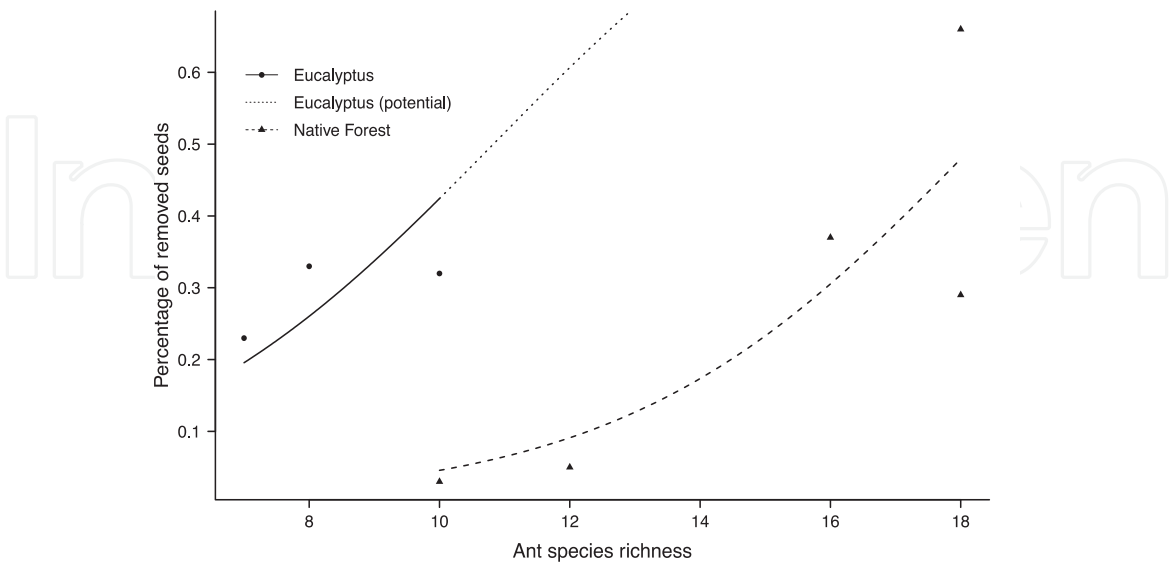


Figure 4. Seed removal rates increased with ant species richness ($F_{1,6}=11.01$; $p=0.021$), and were higher in *Eucalyptus* crop.

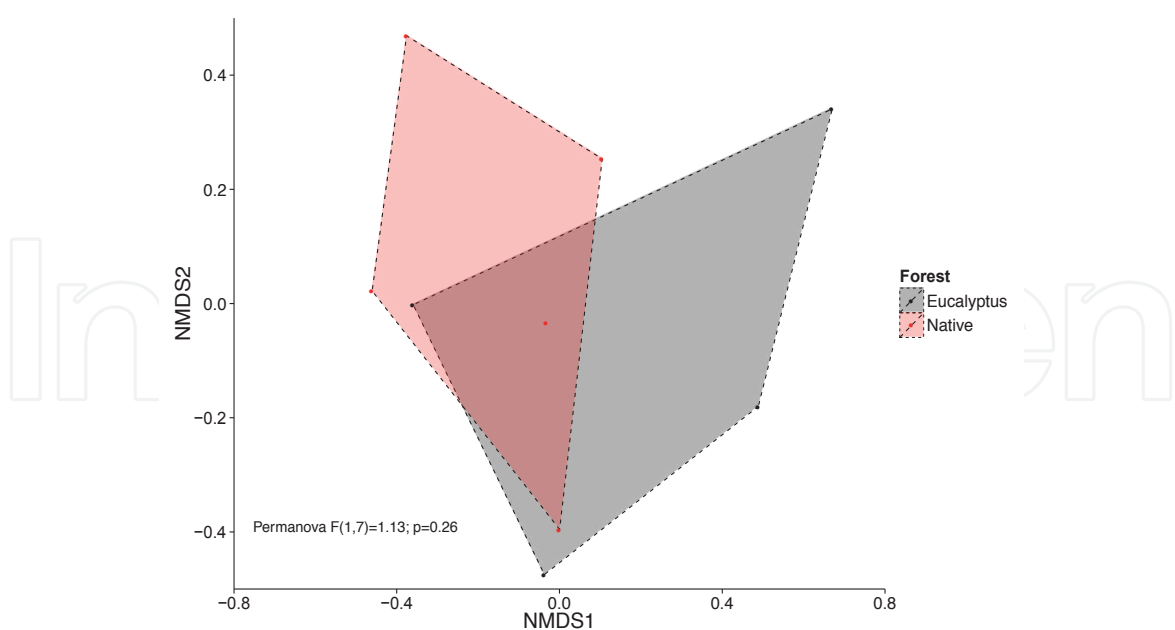


Figure 5. NMDS map of species composition according to treatment (Native or *Eucalyptus* crop). We analyzed significance by using Permanova test, which was non-significant.

6. Conclusions and perspectives

Although a positive relationship between biodiversity and ecosystem functioning is commonly reported [28, 202], we did not find such evidence from all the studies presented here. The main results presented allow us to conclude that the general effect of arthropods on ecosystem functioning is dependent on the studied process and the proximity with their agents. As more direct is the action of arthropods on the ecosystem processes, more detectable are their effects on functioning.

Arthropods contribute indirectly in the process of litter decomposition by modifying the substrate to the decomposers (the microbiota), besides acting through predation in a top-down effect on these microorganisms. Therefore, their indirect effect on litter decomposition may have produced the lack of relationship between their biodiversity and ecosystem functioning. Similarly, in the second case study we observed an absence of ant species richness and plant defense against herbivory. Nevertheless, in this study we noticed that the abundance of ants partially resulted in a decrease of the abundance of herbivore insects. The results obtained in this case study may reflect the plenty of defense mechanisms against herbivory, and ants are only a further mechanism within several others by which plants achieve a better protection. In the third case study we could evaluate a process that directly involved the importance of biodiversity on ecosystem processes, as there is a direct interaction between ants and the seeds they remove, without intermediate agents between them. Therefore, we could notice that the effect of ant biodiversity on the ecosystem process was stronger when compared to the two

previous case studies. The above rationale points that a greater proximity between the agent and process turns the relationship stronger and detectable.

Based on the studies presented here, we suggest the following steps to improve the studies of the relationship between biodiversity and ecosystem functioning. Firstly, the control of variables through manipulative approaches should be increased, as confounding variables might decrease the chance of unveiling significant relationships. Secondly, as described above, it should be investigated relationships in which the processes and their agents are more directly connected. As reported elsewhere [28], the effects on productivity decrease with the increase of the number of trophic levels between manipulated (biodiversity) and estimated (ecosystem process) elements. Finally, studies of less complex systems may produce stronger results, once in complex systems several agents may influence concomitantly a given process, decreasing the chance of detecting a relationship between biodiversity and ecosystem functioning. Our second case study is an example, as several agents may influence plant herbivory, besides the presence of a higher ant species richness and abundance. Similar conclusions have been found in a meta-analysis study involving several results obtained from different regions of the World [28]. Hence, the comparison among our results and those obtained by other authors indicate that, despite the high complexity and biodiversity found in tropical regions, the trends reported here are comparable to those found worldwide.

This chapter integrated different case studies relating biodiversity and ecosystem functioning, with varying degrees of proximity between the agents and the processes. Because human activities would certainly continue to produce loss of species, we suggest that future studies relating biodiversity and ecosystem processes consider the linkage among the agents involved in the processes, to improve the understanding of this relationship, as well as the prognosis involving changes in biodiversity.

Acknowledgements

Authors are indebted to Lucas G. Dornelas for providing his data of case study 3. Authors received grants from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq – Brazil), Fundação Capes – Brazil, and Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG).

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