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Corresponding author:
Mariane Aparecida Nickele;
Email: nickele.mariane@gmail.com

Assessing forest restoration effectiveness in the Seasonal Semideciduous Forest in the Upper Paraná Atlantic Forest ecoregion using epigaeic ant assemblages

Mariane Aparecida Nickele[1], Wilson Reis Filho[2], Susete do Rocio Chiarello Penteado[3], Elisiane Castro de Queiroz[4], Luis Cesar Rodrigues da Silva[5], Thiele Sides Camargo[1], Alexandre Casadei-Ferreira[1,6], Rodrigo Machado Feitosa[1] and Marcio Roberto Pie[7]

[1]Universidade Federal do Paraná, Curitiba, PR, Brazil; [2]Epagri/Embrapa Florestas, Colombo, PR, Brazil; [3]Embrapa Florestas, Colombo, PR, Brazil; [4]Funcema, Curitiba, PR, Brazil; [5]Itaipu Binacional, Foz do Iguaçu, PR, Brazil; [6]Biodiversity and Biocomplexity Unit, Okinawa Institute of Science and Technology Graduate University, Onna, Okinawa, Japan and [7]Department of Biology, Edge Hill University, St Helens Road, Ormskirk, Lancashire L39 4QP, UK

Abstract

Itaipu Hydroelectric Power Plant initiated a large reforestation programme after the expropriation of the areas destined for the formation of the reservoir. This study aimed to evaluate the effectiveness of forest restoration of the Seasonal Semideciduous Forest in the Upper Paraná Atlantic Forest ecoregion, Brazil, using epigaeic ant assemblages as bioindicators, by comparing ant species richness and composition in the Reservoir Protection Strip with adjacent areas, such as the primary forest of the Iguaçu National Park and the Permanent Preservation Area located on a rural property and agricultural areas. In total, 171 ant species were identified. Ant species richness was higher in forest than in agricultural areas and did not differ among forest areas. However, ant species composition in forest areas, regardless of the restoration technique used, was not similar to the primary forest, possibly due to variation in forest recovery time. This study highlights the great value of the Iguaçu National Park as a conservation unit. Also, it reveals that the efforts for the creation and maintenance of the Reservoir Protection Strip, which remains without anthropic interventions for years, might indeed lead to a complete recovery of the ant species composition over time, reinforcing their great importance for biodiversity conservation.

Introduction

The last few centuries have been marked by a major conversion of tropical forests into mosaics of habitats altered by human action, driven mainly by the human population growth and socio-economic pressures (Gascon *et al.* 2002). The Atlantic Forest is the second largest tropical rain forest on the American continent, which originally stretched continuously along the coast of 17 Brazilian states, extending into the east of Paraguay and northeastern Argentina in its southern portion. Considered a global centre of endemism, the Atlantic Forest of South America is among the most diverse tropical forests. However, after centuries of exploitation, this forest has lost more than 93% of its area, placing it among the world's highest priorities for conservation (Galindo-Leal & Câmara 2003, Myers *et al.* 2000). Forest loss and degradation have led to widespread biodiversity loss (Solar *et al.* 2016), which generate concern and awareness regarding the need of natural resource conservation (Malhi *et al.* 2014).

The Upper Paraná Atlantic Forest ecoregion is the largest among the 15 ecoregions identified in the Atlantic Forest biome, with the Seasonal Semideciduous Forest as the dominant vegetation type (Di Bitetti *et al.* 2003). The Iguaçu National Park stands out as the largest integral protection conservation unit of the Upper Paraná Atlantic Forest ecoregion, located in the western region of the State of Paraná, in southern Brazil (Di Bitetti *et al.* 2003), adjacent to the Iguazú National Park, in Argentina. This region includes the Itaipu Binacional Hydroelectric Power Plant, on the Paraná River, at the border between Brazil and Paraguay. The dam was built by the two countries between 1975 and 1982. Since 1979, after the expropriation of the areas destined for the formation of the reservoir, Itaipu developed the largest reforestation programme ever conducted by a hydroelectric power plant in the world. Today, more than 99% of the Permanent Preservation Areas, which currently consist of the so-called Reservoir Protection Strip, are restored (Itaipu 2015).

Forest restoration is a strategy to reverse forest loss and degradation, recovering the same or very close conditions of the original forest. It is mainly carried out through active revegetation, natural regeneration or mixed techniques, which can be carried out by planting seedlings of native and/or exotic species, natural regeneration, assisted natural regeneration, or even the establishment of agroforestry systems (Stanturf *et al.* 2014a, b). And, environmental indicators can provide useful information for monitoring management practices, aiming to rehabilitate degraded ecosystems. The use of bioindicators can provide evidence of the development level of an environment in different stages of reconstitution, which can be evaluated by the structure of certain species and/or the composition of species present in each environment (Majer 1983, Ribas *et al.* 2012).

Ants are ecologically important components of natural and disturbed ecosystems, providing a variety of ecological functions in almost all trophic levels, given their diversity and behavioural plasticity in nesting habits, feeding spectrum, and association with numerous species of plants and animals (Elizalde *et al.* 2020, Folgarait 1998). Several studies documented how ant community composition is influenced by plant diversity and vegetation physiognomy and therefore can serve as an indicator taxon for the invertebrate fauna, as well as soil conditions (e.g., Costa-Milanez *et al.* 2014, Segat *et al.* 2017 and Solar *et al.* 2016). Ant assemblages can change over the course of plant succession. That is, ant diversity tends to increase with increasing diversity of plant communities, the availability of micro-habitats, and consequently a greater availability of food and shelter resources (Majer 1983, Mauda *et al.* 2018, Solar *et al.* 2016). In particular, epigaeic ants are the most sensitive ant assemblages to forest recovery (Schmidt *et al.* 2013), and they were more efficiently sampled with pitfall traps (a rather simple and cheap survey method) than other sampling methods, such as Winkler (Donoso, 2017, Parr & Chown 2001).

Epigaeic ant assemblages have not been studied to date in the Iguaçu National Park, and in the Reservoir Protection Strips of the Itaipu, on the Brazilian side, even though they are considered important species source sites for biodiversity conservation. This study aimed to evaluate the effectiveness of forest restoration of the Seasonal Semideciduous Forest in the Upper Paraná Atlantic Forest ecoregion, Brazil, using epigaeic ant assemblages, comparing ant species richness and composition in the Reservoir Protection Strips of the Itaipu, with adjacent areas, such as the primary forest of the Iguaçu National Park, and disturbed areas, such as Permanent Preservation Areas located on a rural property and agricultural areas. Our hypothesis is that forest restoration techniques used in the Reservoir Protection Strips, which remain without anthropic interventions for approximately 35 years, were effective and ant richness and composition may be more similar to primary forest than highly disturbed areas.

Materials and methods

Study area

The research was carried out in the western portion of the State of Paraná, Brazil, in the municipalities of Foz do Iguaçu, PR, Santa Terezinha de Itaipu, PR, and São Miguel do Iguaçu, PR (Figure 1). According to the global classification of Köppen, the climate is of the Cfa type, characterised as humid subtropical temperate, with well-defined winter and summer seasons, where rainfall is equally distributed throughout the year. The local temperature varies between maximum 40° C and minimum 3° C, with an annual maximum average of 26° C and minimum of 15° C. The average annual rainfall is 1,700 mm, with a predominantly high relative humidity, rarely below 80%, even in the driest periods of the year. The average altitude is 192 m, and the predominant vegetation is the Seasonal Semideciduous Forest (Ibama 1999).

At the time of the reservoir formation, a study carried out by Itaipu in the Brazilian territory revealed that 23% of secondary forests, 24.7% of highly exploited forests undergoing natural rehabilitation and 50.3% of agricultural areas were restored. Itaipu also made possible the establishment of the Santa Maria Ecological Corridor, which connects the riparian forests of the reservoir and other protected areas, with the Iguaçu National Park, extending through the Private Reserve of Natural Heritage of the Santa Maria Farm. This corridor allowed the connection between two of the most extensive conservation areas in Southern Brazil, the Iguaçu and Ilha Grande National Parks, maintaining genetic exchange among different populations (Itaipu 2015).

Then, the following study sites were selected: (1) Iguaçu National Park **primary forest** (INP_PF): area with primary vegetation cover of Seasonal Semideciduous Forest (25°32'42"S, 54°24'56"W); (2) Reservoir Protection Strip formed by **secondary forest** (RPS_SF): permanent preservation area with remaining vegetation cover from Seasonal Semideciduous Forest (25°14'54"S, 54°26'49"W); (3) Reservoir Protection Strip formed by **natural regeneration** (RPS_NR): permanent preservation area with vegetation cover resulting from natural processes, composed of regenerating plants (25°22'12"S, 54°23'57"W); (4) Reservoir Protection Strip formed by **reforestation** (RPS_RF): area that was agriculture in the past, but with the formation of the reservoir, it was predominantly reforested with a mix of native species of the Mata Atlantica biome (25°22'51"S, 54°27'11"W); (5) Permanent Preservation Area located on rural property (PPA_RP): permanent preservation area formed by **secondary forest located on a rural property** between the Iguaçu National Park and the Reservoir Protection Strip, where is the Santa Maria Ecological Corridor (25°27'43"S, 54°21'19"W); and (6) **Agriculture** (AGR): soybean or corn monoculture area (25°22'17"S, 54°25'22"W).

The Reservoir Protection Strips have been without human intervention for 35 years. Secondary forest located on a rural property until now suffers from anthropogenic disturbances. However, all forest areas selected for the study are surrounded by agricultural areas.

Sampling ants

We established 12 transects of 125 metres in each area, separated by at least 500 m. In total, we sampled 72 transects (sampling units). We sampled ants in three transects per season of 2017, using epigaeic pitfall traps. Pitfall traps consisted of plastic recipients (8 cm diameter and 11 cm height) half filled with 300 ml of liquid solution of water, glycerol (5%), and salt (5%), which collected and killed the ants. Traps were buried so that they were flush with the soil and remained in the field for 48 h (Martins *et al.* 2021, Schmidt *et al.* 2013, Solar *et al.* 2016). Along each transect, we installed five epigaeic pitfall traps spaced by 25 m. The first trap was placed 25 m away from the edge in each area. A pitfall trap was also placed in each transect in the transition between forest areas and agriculture, totalling 420 epigaeic pitfall traps.

We sorted, mounted and identified the ants to genus level using available taxonomic key in Baccaro *et al.* (2015). For species identification, comparisons were made with material deposited at the Padre Jesus Santiago Moure Entomological Collection (DZUP)

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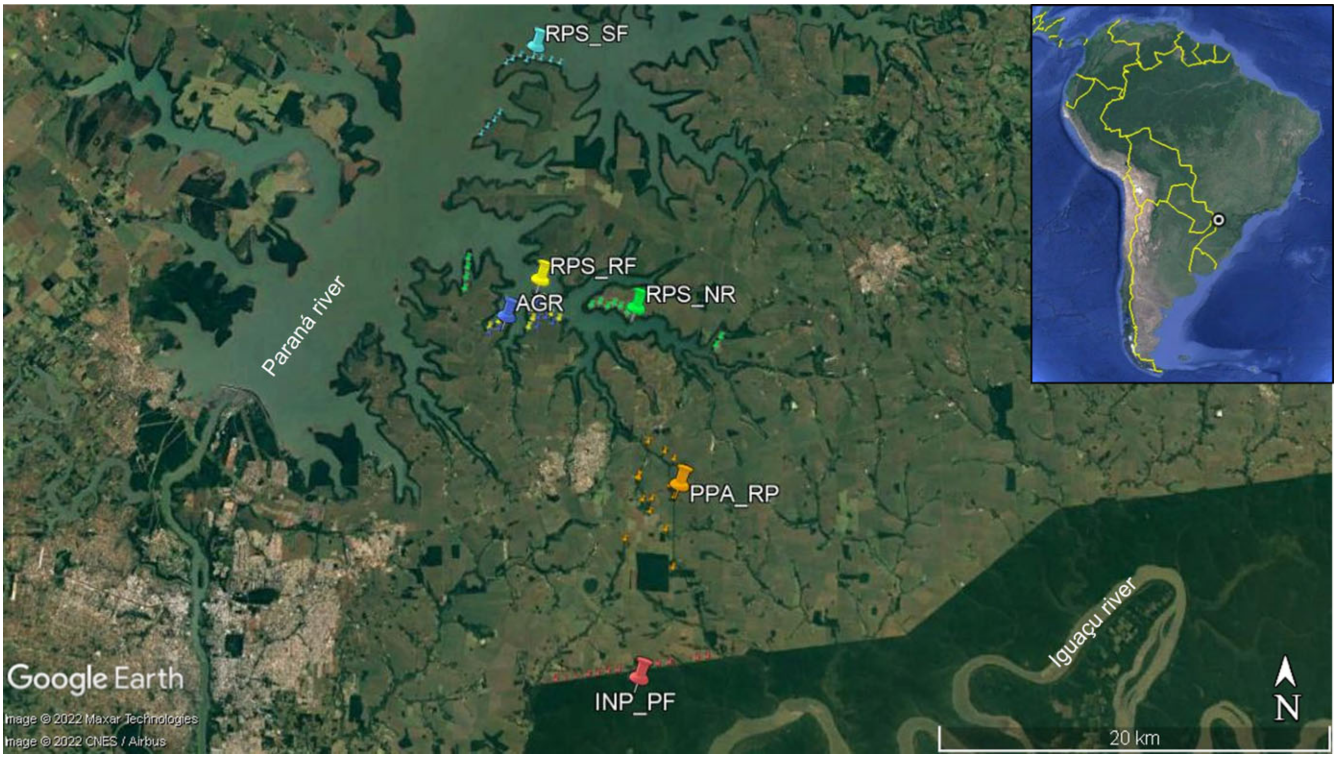

Figure 1. Study site locations. INP_PF: Iguaçu National Park Primary Forest; RPS_SF: Reservoir Protection Strip formed by secondary forest; RPS_NR: Reservoir Protection Strip formed by natural regeneration; RPS_RF: Reservoir Protection Strip formed by reforestation; PPA_RP: Permanent Preservation Area located on rural property; AGR: Agricultural area. Source: Google Earth Pro v. 7.3.4.8642, 25°21′04.08″S, 54°18′12.84″W, elev 280 m, eye alt 66.25 km. Data SIO, NOAA, US Navy, NGA, GEBCO. Image Landsat/Copernicus. © Google Earth. Imagery date: 12 May 2022 (accessed 21 June 2022).

in the Universidade Federal do Paraná, Curitiba, PR, Brazil, where vouchers were deposited. We also applied species names using updated taxonomic revisions for some of the ant genera recorded here. Taxonomic sources for species identification included *Acromyrmex* (Gonçalves 1961), *Anochetus* (Brown 1978), *Carebara* (Fernández 2004), *Crematogaster* (Longino 2003), *Ectatomma* (Kugler & Brown 1982), *Gnamptogenys* (Camacho *et al.* 2020), *Labidus* (Watkins 1976), *Linepithema* (Wild 2007), *Megalomyrmex* (Brandão 1990), *Odontomachus* (Brown 1976), *Neoponera* and *Pachycondyla* (Mackay & Mackay 2010), *Pheidole* (Wilson 2003), *Prionopelta* (Ladino & Feitosa 2020), *Strumigenys* (Bolton 2000) and *Wasmannia* (Longino & Fernández 2007). Morphospecies were assigned number codes that apply only to this study.

Ant collections were authorised by the licence 55313-1 (Brazilian Biodiversity Information and Authorization System – SISBIO). Access to the genetic heritage was also registered by the record number ACDFB38 (National Management System of the Genetic Heritage – SisGen).

Environmental variables

Vegetation cover was used as an estimate of resources available for epigaeic ants. The percentage of vegetation cover was measured using digital images taken with a camera at the height of 1.3 m, with the lens facing up and next to where the epigaeic trap was placed. We also recorded richness and composition of plant species in all forest strata. To determine the number of plant species, 10 x 20 m plots were delimited in five transects from each forest area for the identification and measurement of tree and shrub individuals taller than 1.0 m and/or with more than 3 cm in circumference at breast height, measured at 1.30 m above ground. The plant species identification was carried out with the help of The Plant List platform (version 1.1, 2013).

Statistical analyses

Ant species accumulation curves and extrapolated sample-based rarefaction curves were obtained considering presence/absence data and incidence data in each sampling unit, reducing a potential bias caused by rarely sampled species (Chao *et al.* 2014). To assess whether ant species richness differs among treatments, a one-way analysis of variance (ANOVA) was performed, considering the data normality that was analysed by the Shapiro–Wilk test. In addition, a non-metric multidimensional scaling (NMDS) analysis was performed to test for changes in ant species composition among areas. The ordering was based on a species presence–absence data matrix and Jaccard's dissimilarity index. After a visual inspection of the data, a PERMANOVA was performed to test for significant clustering of the areas. In order to test the significance of possible differences in ant species composition among areas, the distribution of similarities between each pairwise area was also compared through an ANOSIM similarity analysis. By ANOSIM similarity analysis, high R-values mean high dissimilarities among the areas.

The value of each ant species as an indicator of each area was calculated using the Indicator Value (IndVal) method of Dufrêne and Legendre (1997). This index combines a measure of the habitat specificity of a species to a level of disturbance, or a disturbance state, with its fidelity within that state. Species with high specificity

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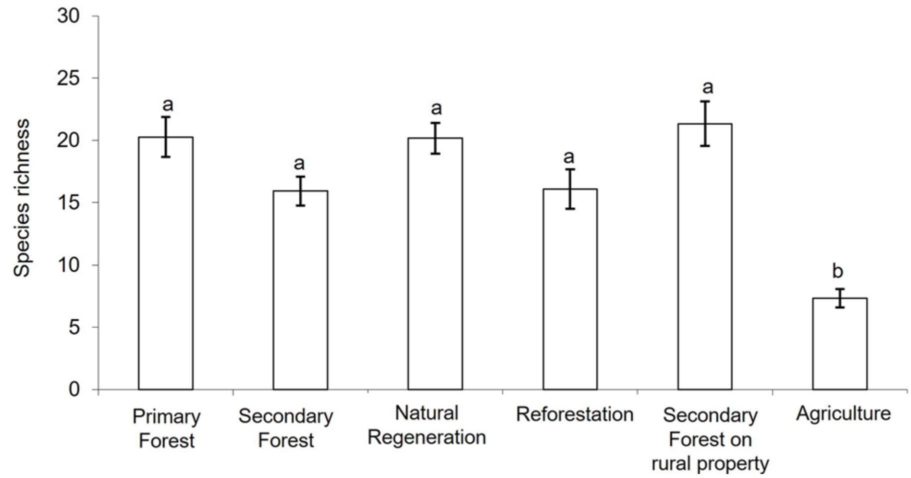

Figure 2. Average ant species richness per transect in each area. Different letters indicate significant differences among treatments ($p < 0.001$). Bars are standard errors.

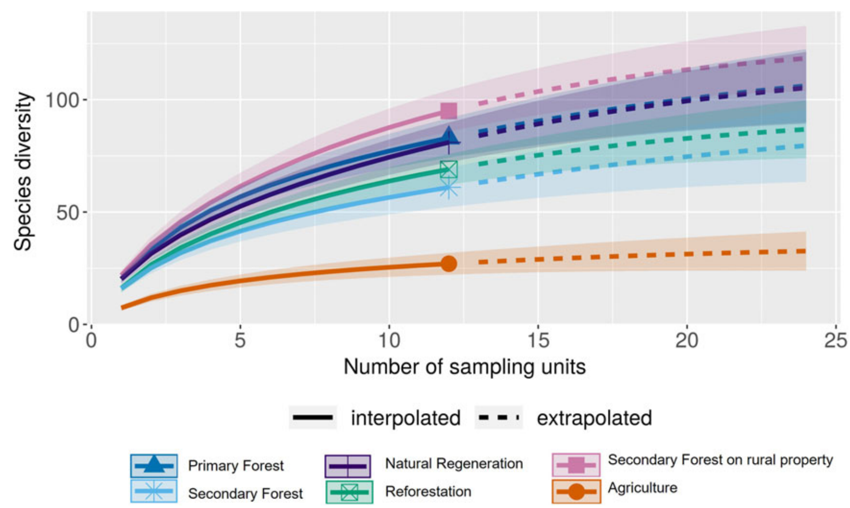

Figure 3. Interpolation and extrapolation ant species accumulation curves per area, with 95% confidence intervals.

and fidelity within an area will have a high indicator value. Significance was tested using the Monte Carlo test with 10,000 permutations.

To assess plant species richness and the percentage of forest cover among areas, a one-way ANOVA and Shapiro–Wilk test were performed. And the NMDS analysis was also performed to assess differences in tree composition. To analyse plant species composition, we selected only species with more than 10 cm in diameter at breast height.

Ants collected in the transition between forest areas and agriculture were not included in the analyses, as there was only one pitfall in the transition per transect, but they were included in the taxonomic list. Also, agricultural areas were not included in the analysis of the environmental variables, since they were either soybean or corn monocultures. All analyses were performed using the R software environment (R Core Team 2019), except interpolation and extrapolation curves performed in the iNEXT online (Chao *et al.* 2016).

Results

Ant species richness and composition

Overall, we sampled 171 ant species from 45 genera and 8 subfamilies (Appendix 1). Myrmicinae was the richest subfamily (92 species), followed by Formicinae (36), Ponerinae (17), Dolichoderinae (10), Dorylinae (6), Ectatomminae and Pseudomyrmecinae (4 species each), and Amblyoponinae (2). The most species-rich genera were *Pheidole* (40 species), *Camponotus* (24), *Solenopsis* (13), *Hypoponera* (10) and *Brachymyrmex* (9). In this study, we sampled three ant species new to science: *Pheidole* sp. n. 1, sampled only in the secondary forest located on a rural property; *Pheidole* sp. n. 2, sampled in all study areas; and *Pheidole* sp. n. 3, sampled only in the secondary forest (Appendix 1).

The secondary forest located on a rural property accumulated the largest number of species (94), followed by the primary forest (87), but ant species richness did not vary within forest areas (Figure 2, $F_{5,66} = 13.74$, $p < 0.001$). However, ant species richness was significantly higher in forest areas, irrespective of the rehabilitation technique used, than in agricultural areas. The interpolation and extrapolation ant species accumulation curves also showed that the agricultural area accumulated the lowest ant species (Figure 3). In the transition between forest areas and agriculture, 86 ant species were sampled in total, with 9 being sampled only in the transition. (Appendix 1).

Ant species composition also varied among areas. NMDS revealed that ant species composition differed in forest and agricultural areas (Figure 4, PERMANOVA $F_{5,66} = 6.63$, $p < 0.001$). ANOSIM revealed greater similarity within forest

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Table 1. Dissimilarity (R-values) among the areas obtained by ANOSIM analysis for ant species composition. High R-values mean high dissimilarities among the areas

	Primary forest	Secondary forest	Natural regeneration	Reforestation	Secondary forest on rural property
Secondary forest	0.52 (***)				
Natural regeneration	0.51 (***)	0.12 (*)			
Reforestation	0.54 (***)	0.27 (***)	0.11 (*)		
Secondary forest on rural property	0.49 (***)	0.38 (***)	0.18 (**)	0.21 (***)	
Agriculture	0.88 (***)	0.91 (***)	0.88 (***)	0.85 (***)	0.92 (***)

***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

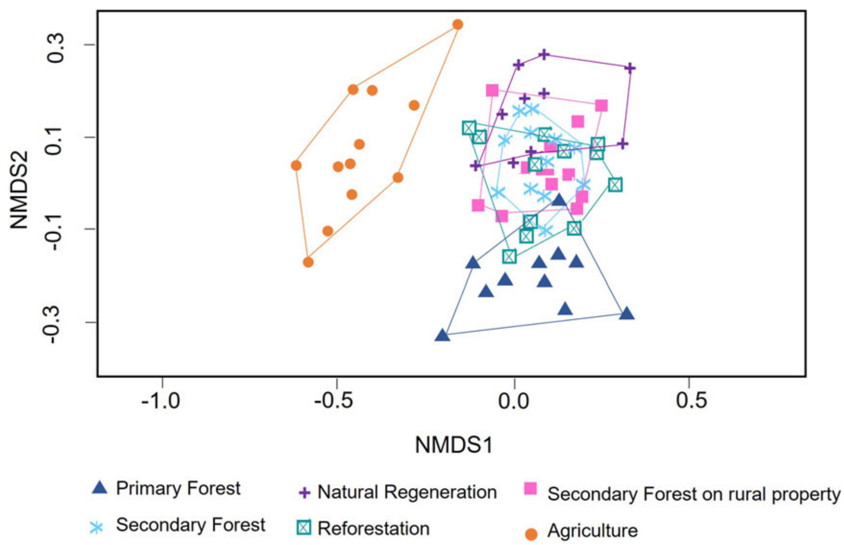

Figure 4. Non-metric multidimensional scaling (NMDS) analysis plot of ant species composition.

areas than agricultural areas. However, there are differences in ant species composition evenly among forest areas (Table 1). For all combinations, the R values were significant, but there was a greater similarity in ant species composition between the secondary forest and the natural regeneration area. In addition, there was a greater similarity between the natural regeneration and the reforestation area (Table 1).

The IndVal results showed a total of 11 significant indicator species for the primary forest, 1 species for the secondary forest, 2 species for the reforestation area, 2 species for the secondary forest located on a rural property, and 4 species for the agricultural area (Table 2).

Environmental variables

We sampled 110 plant species belonging to 82 genera and 34 families. Of these, 45 species were arboreal with more than 10 cm diameter at breast height (Appendix 2).

There were no differences in the plant richness among forest areas (Figure 5; ANOVA $F_{4,55} = 1.31$, $p = 0.27$). However, there were dissimilarities in arboreal plant species composition among forest areas, especially in relation to the Iguaçu National Park (Figure 6, PERMANOVA $F_{4,55} = 1.03$, $p < 0.001$). Finally, only the natural regeneration area showed vegetation cover significantly lower than other forest areas (Figure 7, ANOVA $F_{4,55} = 11.29$, $p < 0.001$).

Discussion

Through monitoring ant communities in regenerating forested areas, it is possible to evaluate the methodologies and the effectiveness of revegetation techniques in maintaining local diversity and, consequently, the self-sustainability of these environments (Pereira *et al.* 2007). Ant species richness did not differ among forested areas in our study. The structural complexity of the habitat is one of the main factors driving species richness and composition on a regional scale. The main factors that contribute to the high diversity of ants in forested areas are forest cover, the diversity of nesting sites, the amount of food available, the foraging area and interspecific competition (Braga *et al.* 2010, Coelho *et al.* 2009, Mauda *et al.* 2018, Ribas *et al.* 2011, Solar *et al.* 2016). A minimum of established forest conditions is sufficient for ants to colonise a forest regardless of its age, causing species richness to be similar among the forest remnants with different recovery times, although species composition could differ (Schmidt *et al.* 2013).

Ant species richness in forest areas is significantly greater than in agricultural areas. The lower species richness in agricultural areas is expected since agricultural areas have less structural diversity, a fact observed in several studies (e.g., Falcão *et al.* 2015, Martello *et al.* 2018, Solar *et al.* 2016). Deforestation, mainly for agricultural development, pastures or forest monoculture plantations, is widely recognised as the most serious anthropogenic threat to terrestrial biodiversity (Sala *et al.* 2000). Degraded environments or environments with low plant diversity (e.g., monocultures)

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Table 2. Ant species indicators of each area according IndVal analyses. Only significant indicator species are shown

Species	Area	Indval	p
Linepithema angulatum Emery (1894)	Primary forest	0.75	0.011
Pheidole sp.6	Primary forest	0.67	0.021
Pheidole gertrudae Forel (1886)	Primary forest	0.66	0.009
Pheidole cf. *schwarzmaieri* Borgmeier (1939)	Primary forest	0.64	0.003
Linepithema pulex Wild (2007)	Primary Forest	0.63	0.002
Holcoponera striatula (Mayr 1884)	Primary forest	0.63	0.001
Acromyrmex aspersus Smith (1858)	Primary forest	0.58	0.024
Camponotus cingulatus Mayr (1862)	Primary forest	0.5	0.019
Camponotus lespesii Forel (1886)	Primary forest	0.5	0.019
Pheidole sp.8	Primary forest	0.47	0.003
Pheidole sp.4	Primary forest	0.42	0.027
Pheidole cf. *radoszkowskii* Mayr (1884)	Secondary forest	0.47	0.001
Acromyrmex subterraneus (Forel 1893)	Reforestation	0.45	0.045
Pheidole leonina Wilson (2003)	Reforestation	0.36	0.019
Pheidole sigillata Wilson (2003)	Secondary forest on rural property	0.48	0.017
Wasmannia auropunctata (Roger 1863)	Secondary forest on rural property	0.43	0.007
Solenopsis sp.5	Agriculture	0.73	0.001
Dorymyrmex brunneus Forel (1908)	Agriculture	0.5	0.014
Solenopsis invicta Buren (1972)	Agriculture	0.48	0.046
Pheidole cornicula Wilson (2003)	Agriculture	0.46	0.014

IndVal: indicator value. p – probability, resulting of the permutation test.

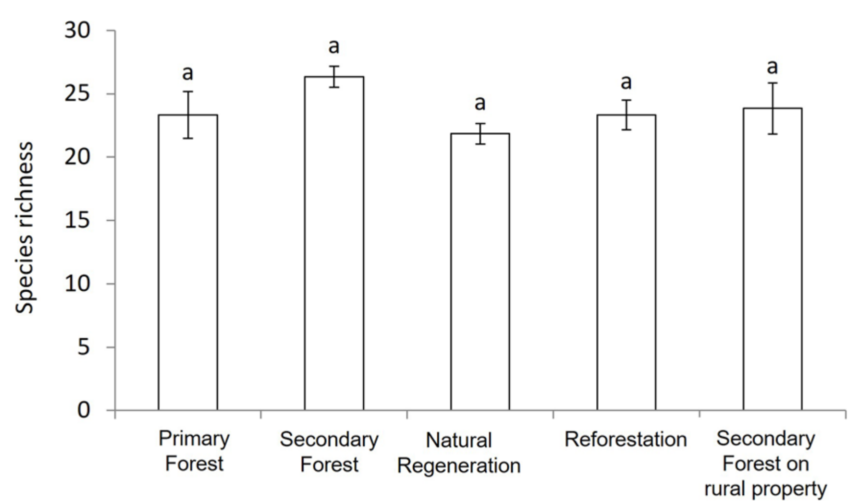

Figure 5. Average plant species richness per transect in each area. Treatments underneath the same letter are not statistically different ($p > 0.05$). Bars are standard errors.

present limitations to the organisms due to the lack of resources provided by these environments. Thus, in these areas, ant communities may present low species diversity (Pereira *et al.* 2007). In these conditions, most ant species are usually generalist species that can nest in several nest sites and use varied food sources, such as some *Pheidole* and *Solenopsis* species found in the present study (Braga *et al.* 2010, Diehl *et al.* 2004). In addition, the lower ant diversity in agricultural areas can be attributed to the application of pesticides for the control of pests, diseases and weeds, the level of soil compactness caused by human intervention in these areas, the absence or low amount of litter, which possibly decreases the quantity and quality of available resources, and the exposure of species to high thermal amplitude (Dias *et al.* 2008, Lapola & Fowler 2008).

Ant species composition is considered the best indicator for assessing changes in habitat quality, as it changes according to variation in land use classes, from undisturbed primary forest to highly disturbed areas, such as intensive agriculture (Majer &

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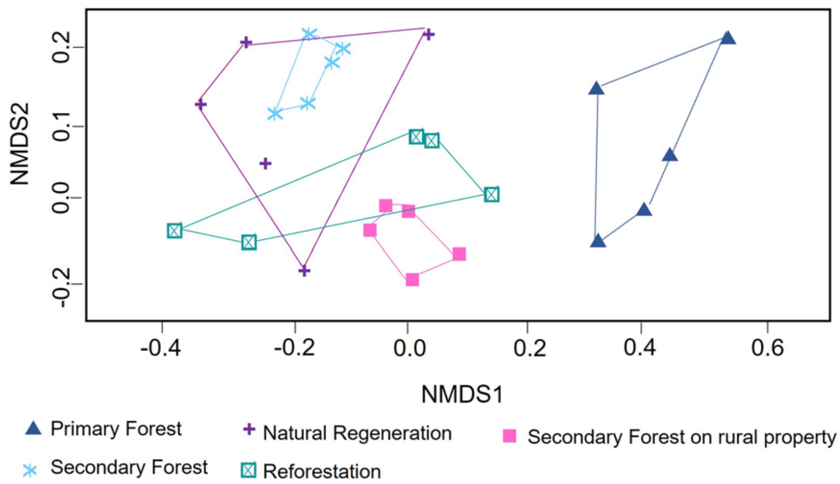

Figure 6. Non-metric multidimensional scaling (NMDS) analysis plot of arboreal plant species composition.

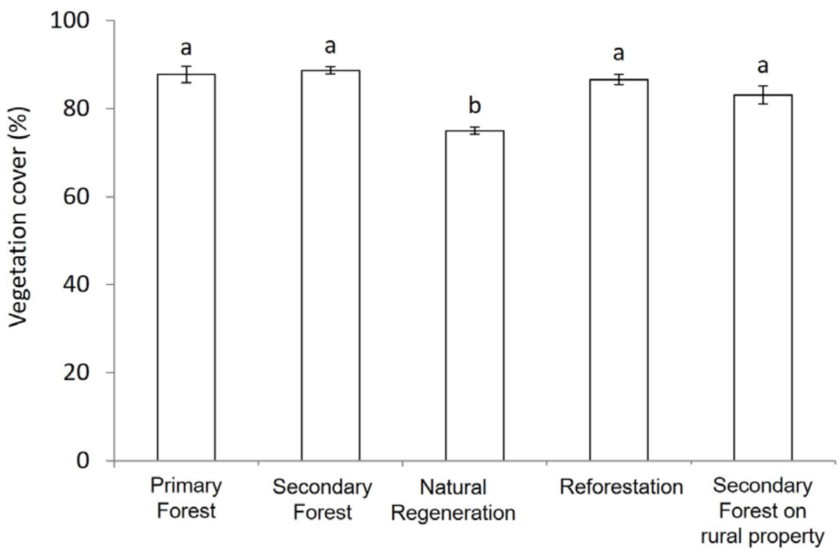

Figure 7. Vegetation cover percentage per transect in each area. Different letters indicate significant differences among treatments ($p < 0.001$). Bars are standard errors.

Nichols 1998, Ribas *et al.* 2011, Schmidt & Diehl 2008, Solar *et al.* 2016). In the present study, ant species composition in the agricultural area is different from ant species composition in the forest areas. However, among forest areas, ant species composition also differed.

After approximately 35 years of forest recovery, ant species composition in the permanent preservation areas that suffered disturbances differs significantly from the composition of the Iguaçu Nacional Park Primary Forest. Studies show after 13 (Falcão *et al.* 2015) or 25 years (Silva *et al.* 2007) of forest regeneration, the number of species and the composition profile between the primary forest and the disturbed areas still show substantial differences. In tropical forests, the complete recovery of ant species richness is estimated to occur 39 years after land abandonment. However, the recovery of species composition appears to take substantially longer than the recovery of species richness (Dunn 2004), as observed in the present study. Estimates indicate a time frame for recovery of 50 to several hundred years for a complete recovery in ant species composition in secondary forests (Bihn *et al.* 2008), since in the present study, we also observed arboreal plant composition in areas under recovery also still differ from the primary forest.

There was a greater similarity in ant species composition between the secondary forest and natural regeneration area. As the level of disturbance increased, the dissimilarities in the composition of ant species also increased compared to the secondary forest area. For example, the secondary forest located on a rural property, which still suffers from anthropogenic disturbances, such as the presence of cattle, presents greater dissimilarity in the composition of ant species than the reforestation area, which was predominantly reforested with a mix of native species of the Mata Atlantica biome and which has been without human intervention for at least 35 years. Ant communities in secondary forests might recover more quickly in areas where the forest was less disturbed at the beginning of the succession than when it was established on former pasture (e.g., Bihn *et al.* 2008). The reforestation was an agricultural area at the beginning of the reservoir's formation, so it had to be revegetated. But currently, this area is structurally similar to other forest areas in the recovery process, so there were no differences in plant species richness and percentage of plant cover due to the arboreal size of the planted species. These factors contributed to ant species richness did not differ among forest areas, despite the percentage of vegetation cover being lower in the forest area that was naturally regenerated. Similar results were

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observed in a 28-year unmanaged eucalyptus plantation, where ant species richness was similar to native forests, yet ant species composition was more similar to managed plantations (Martello *et al.* 2018).

This is the first study on epigaeic ant assemblages in forest and agricultural areas in the region between the Iguaçu National Park and the Reservoir Protection Strip of the Itaipu, on the Brazilian side. *Pheidole gigaflavens* Wilson (2003) and *Pheidole mosenopsis* Wilson (2003) were recorded for the first time in Brazil. Moreover, 16 new records to the State of Paraná were also obtained: *Camponotus balzani* Emery (1894), *Camponotus bidens* Forel, 1912, *Camponotus depressus* Mayr (1866), *Camponotus zenon* Emery (1925), *Carebara urichi* (Wheeler 1922), *Mycetomoellerius kempfi* (Fowler 1982), *P. cornicula*, *P. gigaflavens*, *P. leonina*, *Pheidole midas* Wilson (2003), *P. mosenopsis*, *Pheidole obscurithorax* Naves (1985), *Pheidole sensitiva* (Borgmeier 1959), *P. sigillata*, *Pheidole sculptior* Forel (1893) and *Pheidole synarmata* Wilson (2003) (Guénard *et al.* 2017, Janicki *et al.* 2016). Furthermore, three species are new to science (*Pheidole* sp. n. 1, 2 and 3, ACF unpublished data).

Undisturbed primary forests have a unique ant species composition, are a key driver of species richness at the landscape scale, and may be an important species source for biodiversity conservation at local and regional scales (Pacheco *et al.* 2013, Solar *et al.* 2016). In the Iguaçu Nacional Park, 87 ant species were sampled through pitfall traps in the present study. On the Argentine side, another study revealed 172 ant species in the Iguazú National Park, sampled with different methods from 1998 to 2011 (Hanisch *et al.* 2015). Our study adds 18 new records, for a total of 191 ant species to this important protection conservation unit of the Upper Paraná Atlantic Forest ecoregion.

The most significant number of indicator ant species were detected in the primary forest: five species of *Pheidole*, two species of *Camponotus* and *Linepithema* each, and one species of *Acromyrmex* and *Holcoponera*. Of these, *Holcoponera striatula* (Mayr 1884) has already been recorded as an indicator of primary forests in studies carried out in the Amazon forest (Solar *et al.* 2016, Vasconcelos & Vilhena 2006). For the other species, there are no records as indicator species, but it is worth mentioning that this is the first study using ants as bioindicators in this region. The species *Pheidole radoszkowskii* (Mayr 1884) is considered an indicator of the secondary forest. This species has already been recorded as an indicator of habitats with discreet human impact on the southeast coast of Bahia, Brazil (Delabie *et al.* 2006). In the natural regeneration area, no indicator species was determined, which can be explained by the greater similarity of this area with the secondary forest and the area that was reforested. In the reforestation, *A. subterraneus* and *P. leonina* were the indicator species. *Acromyrmex subterraneus* has already been considered an indicator in fragments of Atlantic Forest in São Paulo, Brazil (Lapola & Fowler 2008) and also in areas of eucalyptus reforestation (Marinho *et al.* 2002). *Pheidole leonina* was also recorded in areas of the Amazon Forest in Acre, Brazil (Oliveira *et al.* 2009). In the secondary forest located on a rural property, *W. auropunctata* and *P. sigillata* are considered indicators of this area. *Wasmannia auropunctata* is considered an indicator of production areas, such as pastures (Solar *et al.* 2016), but this species has also been reported as an indicator of areas with an intermediate stage of succession in the Vale do Rio Doce region, Minas Gerais, Brazil (Coelho *et al.* 2009). *Pheidole sigillata* has also been recorded in areas of urban parks and fragments of the Atlantic Forest in the state of São Paulo (Fernandes *et al.* 2018). In the AGR, *Solenopsis* sp. 5, *D. brunneus*, *S. invicta* and *P. cornicula* are considered indicators of this environment. *Dorymyrmex brunneus* and *Pheidole* sp. have already been considered indicators of agricultural areas (Pacheco *et al.* 2013). *Dorymyrmex brunneus* is also commonly found in urban environments (Farneda *et al.* 2007). *Solenopsis invicta* is common in disturbed or undisturbed areas, presenting enormous adaptive plasticity and possibly having the genic potential to exploit a great variety of environments (Diehl *et al.* 2004). In general, *Pheidole* also is a generalist genus, having species characteristic of forest environments or open environments (Braga *et al.* 2010), as observed in the present study.

In the present study, the effectiveness of the rehabilitation techniques used in the Reservoir Protection Strip of the Itaipu was evaluated, showing there were no differences in ant species richness among forest areas in the process of recovery and the primary forest of the Iguaçu National Park. It demonstrates the great importance of the Reservoir Protection Strip and the Permanent Preservation Areas in rural properties to conserve biodiversity. The discovery of three ant species new to science sampled in these areas reinforces these environments' value. However, regardless of the rehabilitation technique used, ant species composition in disturbed forest areas is not similar to the primary forest due to the short forest recovery time. This highlights the great value of the Iguaçu Nacional Park as a conservation unit within the Atlantic Forest biome, given that they represent unique biodiversity in this region. Also, the present study revealed that the efforts for the formation and maintenance of the protection strips around the Itaipu reservoir, which remain without anthropic interventions for several years, might indeed lead to a complete recovery of the composition of ant species over time, reinforcing their great importance for biodiversity conservation.

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Authors' contributions. All authors contributed to the study conception and design. MAN, WRF, SRCP, LCRS and ECQ collected field data; MAN, ECQ, TSC, ACF and RMF identified the ants; LCRS identified the plants; MAN and MRP analysed the data; MAN wrote the first draft of the manuscript; and all authors commented on previous versions of the manuscript and approved the final manuscript.

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Appendix 1: Species list of ants in Seasonal Semideciduous Forest areas, in the Alto Paraná Ecoregion, Atlantic Forest, Brazil

Species	INP_PF	RPS_SF	RPS_NR	RPS_RF	PPA_RP	AGR	Transition
Amblyoponinae							
Prionopelta amabilis Borgmeier, 1949				X			
Fulakora armigera (Mayr, 1887)					X		
Dolichoderinae							
Azteca alfari Emery, 1893			X				
Azteca sp.1					X		
Dolichoderus bispinosus Olivier, 1792	X	X	X	X	X		X
Dorymyrmex brunneus Forel, 1908	X		X			X	X
Forelius sp.1		X					X
Linepithema angulatum Emery, 1894*	X						
Linepithema gallardoi (Brethes, 1914)*	X						
Linepithema iniquum Forel, 1908	X	X	X		X		X
Linepithema micans Forel, 1908	X	X	X	X	X		X
Linepithema pulex Wild, 2007	X	X	X	X	X		X
Dorylinae							
Acanthostichus quadratus Emery, 1895				X			X
Cylindromyrmex sp.1	X						
Labidus coecus (Latreille, 1802)	X						
Labidus praedator (F. Smith, 1858)	X	X					X
Neivamyrmex sp.1	X						
Nomamyrmex esenbeckii (Westwood, 1842)				X			
Ectatomminae							
Ectatomma edentatum Roger, 1863	X	X	X	X	X		X
Holcoponera striatula (Mayr, 1884)	X	X	X		X		X
Gnamptogenys sulcata (F. Smith, 1858)				X			
Poneracantha triangularis (Mayr, 1887)				X			
Formicinae							
Brachymyrmex pilipes Mayr, 1887*	X						
Brachymyrmex sp.1	X	X	X	X	X		X
Brachymyrmex sp.2		X		X	X		X
Brachymyrmex sp.3			X				X
Brachymyrmex sp.4	X	X	X	X	X		X
Brachymyrmex sp.5	X	X	X	X	X		X
Brachymyrmex sp.6						X	
Brachymyrmex sp.7			X	X	X	X	X
Brachymyrmex sp.8	X						
Camponotus ager Smith, F., 1858*	X	X	X	X	X		X
Camponotus atriceps Smith, F., 1858	X	X	X	X		X	X
Camponotus balzani Emery, 1894			X				X

(*Continued*)

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(*Continued*)

Species	INP_PF	RPS_SF	RPS_NR	RPS_RF	PPA_RP	AGR	Transition
Camponotus bidens Forel, 1912							X
Camponotus brasiliensis Mayr, 1862							X
Camponotus cingulatus Mayr, 1862	X	X	X		X		X
Camponotus crassus Santschi, 1922	X	X	X	X	X	X	X
Camponotus depressus Mayr, 1866					X		
Camponotus lespesii Forel, 1886	X		X	X	X		
Camponotus melanoticus Santschi, 1939					X		
Camponotus mus Roger, 1863	X						
Camponotus novogranadensis Mayr, 1870*	X	X					X
Camponotus renggeri Emery, 1894		X	X				X
Camponotus rufipes Fabricius, 1775			X		X		
Camponotus sericeiventris Guerin-Meneville, 1838	X		X		X		X
Camponotus sexguttatus (Fabricius, 1793)		X	X		X		X
Camponotus zenon Emery, 1925*	X	X	X	X	X		X
Camponotus sp.1	X		X		X		
Camponotus sp.2							X
Camponotus sp.3				X	X		X
Camponotus sp.4		X					
Camponotus sp.5							X
Camponotus sp.6							X
Camponotus sp.7	X						
Nylanderia fulva (Mayr, 1862)					X		
Nylanderia sp.1	X	X	X	X	X		X
Nylanderia sp.2	X			X			
Myrmicinae							
Acromyrmex aspersus Smith, F., 1858*	X						
Acromyrmex coronatus Fabricius, 1804	X						
Acromyrmex subterraneus (Forel, 1893)*	X	X	X	X	X		X
Apterostigma gr. *pilosum* sp. 1		X	X		X		X
Apterostigma gr. *pilosum* sp. 2	X	X		X	X		
Apterostigma gr. *pilosum* sp. 3				X	X		
Atta sexdens Linnaeus, 1758	X	X	X	X	X	X	X
Carebara brevipilosa (Fernández, 2004)	X	X	X	X	X		
Carebara urichi (W.M. Wheeler, 1922)	X	X	X	X	X		X
Cephalotes atratus (Linnaeus, 1758)							X
Cephalotes eduarduli Forel, 1921				X			
Crematogaster corticicola Mayr, 1887	X						
Crematogaster nigropilosa (Mayr, 1870)	X	X	X				X
Crematogaster quadriformis Roger, 1863						X	X
Crematogaster sp.1	X						
Crematogaster sp.2		X	X	X	X		X
Cyatta abscondita Sosa-Calvo et al., 2013		X	X				X
Cyphomyrmex minutus Mayr, 1862	X	X	X		X		X

(*Continued*)

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(*Continued*)

Species	INP_PF	RPS_SF	RPS_NR	RPS_RF	PPA_RP	AGR	Transition
Cyphomyrmex rimosus (Spinola, 1851)	X		X		X		
Mycetophylax olitor (Forel, 1893)					X		
Megalomyrmex pusillus Forel, 1912			X				
Megalomyrmex silvestrii (W.M. Wheeler, 1909)		X					
Mycetarotes paralelus Emery, 1906			X				X
Mycetomoellerius oetkeri (Forel, 1908)		X	X	X	X		X
Mycetomoellerius kempfi (Fowler, 1982)*	X		X	X	X		X
Mycetomoellerius sp.1	X	X	X	X	X		X
Mycocepurus smithii (Forel, 1893)	X	X	X	X	X		X
Myrmicocrypta sp.1		X	X	X			
Myrmicocrypta sp.2					X		
Nesomyrmex asper (Mayr, 1887)					X		
Nesomyrmex sp.1			X				
Octostruma stenognatha Brown & Kempf, 1960*	X	X	X	X			X
Pheidole aberrans Mayr, 1868		X	X	X	X	X	X
Pheidole angusta Forel, 1908					X		
Pheidole cornicula Wilson, 2003*	X		X	X	X	X	X
Pheidole fimbriata Roger, 1863	X	X	X	X			
Pheidole gertrudae Forel, 1886	X		X				
Pheidole gigaflavens Wilson, 2003					X	X	X
Pheidole leonina Wilson, 2003*	X	X	X	X	X		
Pheidole midas Wilson, 2003*	X	X	X	X	X		
Pheidole mosenopsis Wilson, 2003	X		X	X	X		X
Pheidole obscurithorax Naves, 1985						X	X
Pheidole cf. *radoszkowskii* Mayr, 1884	X	X	X	X	X		X
Pheidole risii Forel, 1892*	X	X	X	X	X		
Pheidole cf. *schwarzmaieri* Borgmeier, 1939*	X		X	X	X		
Pheidole cf. *sculptior* Forel, 1893*	X	X	X	X	X	X	X
Pheidole sensitiva Borgmeier, 1959			X				
Pheidole sigillata Wilson, 2003*	X			X	X		
Pheidole synarmata Wilson, 2003*	X	X	X	X	X	X	X
Pheidole sp. n. 1					X		
Pheidole sp. n. 2	X	X	X	X	X	X	X
Pheidole sp. n. 3		X					
Pheidole sp.1	X			X			
Pheidole sp.2	X	X					
Pheidole sp.3	X			X	X		
Pheidole sp.4	X	X	X	X	X		
Pheidole sp.5			X		X		
Pheidole sp.6	X						
Pheidole sp.7	X		X		X	X	X
Pheidole sp.8	X	X	X	X	X	X	X
Pheidole sp.9		X					

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(*Continued*)

Species	INP_PF	RPS_SF	RPS_NR	RPS_RF	PPA_RP	AGR	Transition
Pheidole sp.10		X	X	X		X	X
Pheidole sp.11	X			X	X		X
Pheidole sp.12	X			X			
Pheidole sp.13	X		X				
Pheidole sp.14					X		
Pheidole sp.15	X			X		X	X
Pheidole sp.16					X		
Pheidole sp.17							X
Pheidole sp.18					X		
Pheidole sp.19					X		
Pheidole sp.20	X						
Rogeria sp. 1					X		X
Solenopsis invicta Buren, 1972						X	X
Solenopsis sp.1	X	X	X	X	X	X	X
Solenopsis sp.2					X		X
Solenopsis sp.3		X	X		X		
Solenopsis sp.4		X	X	X	X		
Solenopsis sp.5						X	X
Solenopsis sp.6						X	
Solenopsis sp.7	X				X	X	X
Solenopsis sp.8	X						
Solenopsis sp.9							X
Solenopsis sp.10	X					X	X
Solenopsis sp.11	X		X	X	X		X
Solenopsis sp.12	X						X
Strumigenys eggersi (Emery, 1890)				X	X		X
Strumigenys elongata Roger, 1863	X						
Strumigenys xenochelyna Bolton, 2000					X		
Strumigenys aff. *schmalzi*					X		
Wasmannia auropunctata (Roger, 1863)		X	X	X	X		X
Wasmannia lutzi Forel, 1908			X	X	X		X
Ponerinae							
Anochetus bispinosus (F. Smith, 1858)			X	X			X
Odontomachus chelifer (Latreille, 1802)	X	X	X	X	X		X
Odontomachus meinerti Forel, 1905		X	X	X	X		X
Pachycondyla striata Smith, F., 1858	X	X	X	X	X		X
Pachycondyla harpax					X		
Neoponera verenae (Forel, 1922)		X			X		
Neoponera villosa Fabricius, 1804					X		
Hypoponera foreli Mayr, 1887	X	X		X	X		X
Hypoponera sp.1	X	X	X	X			X
Hypoponera sp.2	X		X	X	X		
Hypoponera sp.3						X	

(*Continued*)

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(*Continued*)

Species	INP_PF	RPS_SF	RPS_NR	RPS_RF	PPA_RP	AGR	Transition
Hypoponera sp.4	X						
Hypoponera sp.5			X		X	X	
Hypoponera sp.6	X		X		X	X	
Hypoponera sp.7			X				
Hypoponera sp.8							X
Hypoponera sp. 9		X			X		
Pseudomyrmecinae							
Pseudomyrmex gracilis (Fabricius, 1804)	X		X				X
Pseudomyrmex sp.2			X				X
Pseudomyrmex sp.3				X	X		
Pseudomyrmex sp.1					X		
Total	**87**	**64**	**82**	**71**	**94**	**27**	**86**
Unique species	**18**	**4**	**5**	**5**	**19**	**3**	**9**

INP_PF: Iguaçu National Park Primary Forest; RPS_SF: Reservoir Protection Strip formed by secondary forest; RPS_NR: Reservoir Protection Strip formed by natural regeneration; RPS_RF: Reservoir Protection Strip formed by reforestation; PPA_RP: Permanent Preservation Area located on rural property. Transition: boundary between forest and agriculture. *New records to the ant species list of the Iguaçu (Brazil) and Iguazú (Argentina) National Parks proposed by Hanisch *et al.* (2015).

Appendix 2: Species list of plants in Seasonal Semideciduous Forest areas, in the Alto Paraná Ecoregion, Atlantic Forest, Brazil

Species	INP_PF	RPS_SF	RPS_NR	RPS_RF	PPA_RP
Acanthaceae					
Ruellia brevifolia (Pohl) Ezcurra					X
Anacardiaceae					
Mangifera indica L.*				X	
Schinus terebinthifolia Raddi			X	X	X
Annonaceae					
Annona sp.			X	X	X
Apocynaceae					
Aspidosperma polyneurum Müll. Arg.+	X				X
Tabernaemontana hystrix Steud.	X	X	X	X	X
Araliaceae					
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin+	X				X
Arecaceae					
Euterpe edulis Mart.	X				
Syagrus romanzoffiana (Cham.) Glassman+	X	X	X		X
Asparagaceae					
Cordyline spectabilis Kunth & C.D.Bouché			X		X
Bignoniaceae					
Handroanthus chrysotrichus (Mart. ex DC.) Mattos			X		
Handroanthus impetiginosus (Mart. ex DC.) Mattos				X	
Jacaranda micrantha Cham.					X

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(*Continued*)

Species	INP_PF	RPS_SF	RPS_NR	RPS_RF	PPA_RP
Boraginaceae					
Cordia americana (L.) Gottschling & J.S.Mill.+		X		X	X
Cordia trichotoma (Vell.) Arráb. ex Steud.+		X	X	X	X
Cordia sp.+	X	X	X	X	X
Caricaceae					
Jacaratia spinosa (Aubl.) A.DC.+	X				
Celastraceae					
Maytenus ilicifolia Mart. ex Reiss.				X	
Mytenus sp.		X			
Mytenus sp.+	X				X
Euphorbiaceae					
Alchornea triplinervia (Spreng.) Müll. Arg.+		X			X
Alchornea sp.			X	X	X
Sapium glandulosum (L.) Morong			X		X
Sebastiania commersoniana (Baill.) L.B.Sm. & Downs+			X		X
Fabaceae					
Adenanthera pavonina L.					X
Albizia polycephala (Benth.) Killip+		X	X		X
Apuleia leiocarpa (Vogel) J.F.Macbr.+	X				X
Bauhinia forficata Link	X	X	X	X	X
Calliandra sp.	X	X			X
Cassia sp.		X			X
Dahlstedtia muehlbergiana (Hassl.) M.J.Silva & A.M.G. Azevedo+	X				X
Gleditsia amorphoides (Griseb.) Taub.				X	
Holocalyx balansae Micheli	X	X			X
Inga virescens Benth.+	X	X	X	X	
Inga sp.		X			
Inga sp.	X			X	X
Leucaena leucocephala (Lam.) de Wit*+				X	
Lonchocarpus muehlbergianus Hassl.+	X	X			X
Machaerium brasiliense Vogel+		X			X
Machaerium stipitatum (DC.) Vogel		X	X	X	X
Machaerium sp.+	X		X		X
Myrocarpus frondosus Allemao+		X			X
Parapiptadenia rigida (Benth.) Brenan+		X	X	X	X
Peltophorum dubium (Spreng.) Taub.+	X	X	X		X
Poincianella pluviosa var. *peltophoroides* (Benth.) L.P.Queiroz				X	
Pterogyne nitens Tul.+				X	X
Senegalia polyphylla (DC.) Britton & Rose+			X	X	X
Flacourtiaceae					
Casearia sylvestris Sw.	X	X	X	X	X
Casearia sp.				X	X

(*Continued*)

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(*Continued*)

Species	INP_PF	RPS_SF	RPS_NR	RPS_RF	PPA_RP
Lamiaceae					
Vitex megapotamica (Spreng.) Moldenke		X			
Lauraceae					
Endlicheria paniculata (Spreng.) J.F.Macbr.[+]	X	X	X	X	X
Nectandra megapotamica (Spreng.) Mez [+]		X	X	X	X
Nectandra sp.[+]	X			X	
Persea americana Mill.*				X	
Magnoliaceae					
Magnolia sp.				X	
Malvaceae					
Ceiba speciosa (A.St.-Hil.) Ravenna[+]				X	
Heliocarpus popayanensis Kunth[+]		X	X		
Luehea divaricata Mart.				X	X
Meliaceae					
Cabralea canjerana (Vell.) Mart.[+]	X	X	X	X	X
Cedrela fissilis Vell.[+]	X	X	X	X	X
Guarea kunthiana A.Juss.	X				X
Guarea sp.		X			
Trichilia pallida Sw.	X	X			X
Meslastomataceae					
Tibouchina sp.					X
Não identificada sp.1		X			X
Moraceae					
Maclura tinctoria (L.) D.Don ex Steud.[+]	X		X	X	X
Morus sp.		X	X	X	
Sorocea bonplandii (Baill.) W.C.Burger, Lanj. & de Boer	X	X			X
Myrtaceae					
Campomanesia guazumifolia (Cambess.) O.Berg			X		X
Campomanesia xanthocarpa (Mart.) O.Berg	X	X		X	X
Eucalyptus sp.*[+]				X	
Eugenia involucrata DC.				X	X
Eugenia pisiformis Cambess.[+]		X	X	X	X
Eugenia sonderiana O.Berg		X		X	X
Eugenia uniflora L.				X	X
Myrcianthes pungens (O.Berg) D.Legrand	X				
Plinia sp.[+]	X				
Psidium guajava L.*			X		X
Syzygium cumini (L.) Skeels*			X		
Não identificada sp.2[+]	X			X	X
Não identificada sp.3				X	X
Piperaceae					
Piper amalago L.		X		X	
Piper sp.1			X		

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(*Continued*)

Species	INP_PF	RPS_SF	RPS_NR	RPS_RF	PPA_RP
Piper sp.2	X			X	X
Piper sp.3	X			X	X
Piper sp.4	X				
Poaceae					
Merostachys multiramea Hack.	X				
Primulaceae					
Myrsine umbellata Mart.	X	X		X	X
Rhamnaceae					
Colletia paradoxa (Spreng.) Escal.		X	X	X	X
Hovenia dulcis Thunb.*+			X	X	
Rosaceae					
Eriobotrya japonica (Thunb.) Lindl.*				X	
Prunus myrtifolia (L.) Urb.		X			X
Rutaceae					
Balfourodendron riedelianum (Engl.) Engl.	X	X		X	X
Citrus sp.1*	X	X			X
Citrus sp.2*	X	X	X		X
Citrus sp.3*					X
Helietta apiculata Benth.+				X	X
Zanthoxylum fagara (L.) Sarg.	X	X		X	X
Zanthoxylum rhoifolium Lam.+		X		X	
Zantoxyllum sp.+			X		X
Sapindaceae					
Allophylus edulis (A.St.-Hil., A.Juss. & Cambess.) Radlk.		X	X	X	X
Cupania vernalis Cambess.+		X	X	X	X
Diatenopteryx sorbifolia Radlk.+	X	X		X	
Matayba elaeagnoides Radlk.+		X	X	X	X
Sapotaceae					
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.+	X	X		X	X
Solanaceae					
Solanum sp.		X		X	
Ulmaceae					
Trema micrantha (L.) Blume			X		X
Urticaceae					
Cecropia pachystachya Trécul.+	X	X	X	X	X
Urera sp.					X
Verbenaceae					
Citharexylum myrianthum Cham.+				X	
Total	**43**	**51**	**41**	**61**	**75**

INP_PF: Iguaçu National Park Primary Forest; RPS_SF: Reservoir Protection Strip formed by secondary forest; RPS_NR: Reservoir Protection Strip formed by natural regeneration; RPS_RF: Reservoir Protection Strip formed by reforestation; PPA_RP: Permanent Preservation Area located on rural property. Transition: boundary between forest and agriculture. *Exotic species; +Species with more than 10 centimetres in diameter at breast height.

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