Research Article

Annual and Seasonal Changes in the Structure of Litter-Dwelling Ant Assemblages (Hymenoptera: Formicidae) in Atlantic Semideciduous Forests

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We surveyed ant fauna in the leaf litter in an Atlantic Semideciduous forest in the State Park of Rio Doce (PERD). The work aimed to produce basic information about habitat effects on diversity, as well as about how the ant fauna in a such buffered forest habitat, as the litter layer, could respond the climate variation in a short and long term. We sampled two years in two distinct forest physiognomies, which respond to different geomorphologic backgrounds, in dry and rainy seasons. Species composition, richness and abundance of these forests were distinct. However, both forests hosted similar numbers of rare and specialized, habitat demanding species, thus suggesting both are similarly well preserved, despite distinct physiognomies. However, the lower and more open forest was, more susceptible to dry season effects, showing a steeper decline in species numbers in such season, but similar numbers in the wet seasons. The pattern varied between years, which corroborates the hypothesis of a strongly variable community in response to subtle climatic variation among years. The present results are baselines for future long term monitoring projects, and could support protocols for early warnings of global climatic changes effects on biodiversity.

1. Introduction

Species richness and composition respond to different habitat variables and abiotic factors that influence climate, seasonality, humidity, topography, and lithology [1–4]. The construction of the concept of "habitat components" is based on the interactions between abiotic and biotic variables, which result in the parameters on which the niches of species evolve [5]. One habitat component which is hardly studied is its temporal variance, due to the fact that it is highly unpredictable [6].

Forest litter is a crucial habitat compartment for mineral cycling, humidity retention, and, greatly, to biodiversity

maintenance [7, 8]. Conversely, the insect fauna that dominates the litter is a fundamental factor for its transformation. In a whole tropical forest, ants and termites are the most important animals in relation to biomass and relative abundance. Ants are found in virtually all strata of forests, playing a key role in structuring ecological communities in tropical ecosystems [9]. They are responsible for processes of soil mineralization due to its extensive bioturbation activity [10], promoting changes in physical environments [7], and, consequently, a vast movement of nutrients [8, 11]. Furthermore, an ant assemblage responds positively to natural succession [12–14], causing feedback responses, such as plant species dispersal and seed collecting [15–17]. They are also responsible for important predation rates on tropical forests (e.g., army ants) [11].

For ant assemblages, the negative effects of low temperature [18], intense rainfalls (daily and cumulative), plus the positive effects of high relative humidity of the understorey and forest ground, influence directly the foraging and nesting [19]. The effect of intense rainfall may occur due to interference in the communication process between individuals, by literally washing down the worker's chemical trails, or by flooding areas with soils less susceptible to drainage [20]. Thus, these factors affect many phenological activities in the colonies [20, 21] and are crucial parameters in structuring ground-dwelling ant assemblages in tropical forests [18–20]. Additionally, it may have confounding positive effects with the rainfall, such as increasing humidity or increasing the litter volume [22], thus resulting in a difficulty to evaluate the real effects on the ants assemblages.

Therefore, the way how seasons and years (namely general weather conditions) should affect ant species parameters along time must be highly variable and unpredictable. Campos et al. [23] have shown that arboreal ant assemblage in an Atlantic semideciduous forest, in the State Park of Rio Doce, responded as strongly to host trees as to time passing, and more significantly than to seasonality. Further, the authors observed that changes in ant fauna was not affected by the host plant habitat specificities, such as being in a forest artificial border, within the forest, or in a natural lake ashore. In other words, ant species composition and relative density may respond to more subtle components of the environment.

In the present study, we aimed to evaluate the effects of habitats and temporal variation on the litter-dwelling ant species richness, abundance, and composition in this same semideciduous Atlantic forest. In order to investigate the hypothesis that temporal variation may have stronger effect than habitat specificities, we sampled in two contrasting forest physiognomies, in two different geomorphologic backgrounds.

2. Materials and Methods

2.1. Study Sites. Samples were taken in the State Park of Rio Doce (PERD-IEF), Marliéria, Minas Gerais. This is approximately 36,000 ha of protected forests and lakes, comprising part of the municipalities of Timóteo, Marliéria, and Dionísio—between the parallels $19^{\circ}48'18''-19^{\circ}29'24''$ S and meridians $42^{\circ}38'30''-42^{\circ}28'18''W$. The park is bound in the East by the Doce River and Piracicaba River to the North [24]. The vegetation is characterized as lower montane Atlantic semideciduous forest, with a percentage of deciduous trees between 20 and 50% [25, 26]. The forest varies greatly in physiognomy and soil conditions from north to south. Also, the park preserves the largest natural lake system in the Atlantic rainforest domain (10% of its area) that resulted from geological movements around the old Doce river and affluents during the Pleistocene [27].

The climate is tropical humid mesothermal [28]. The wet season occurs from October to March and the dry



FIGURE 1: Map showing the location of the PERD and the study sites in relation to the surrounding region. Star at the north showing the location of Macuco's IMA (TM) and at the south showing the Gambazinho's IMA (LG) (Source: [22].)

season from April to September [29]. Samples were taken in August (dry season) and November (rainy season) in the years of 2005 and 2006, in two different areas: the Lagoa do Gambazinho's IMA (Integrated Monitoring Array) (hereafter LG) (southern PERD) and the Trilha Macuco ou Juquita's IMA (hereafter TM) (northern PERD) (Figure 1).

The LG is composed by a secondary, edaphically constrained low forest vegetation (10–15 m high) [30] in an area with irregular topography, varying from hills to lowlands, with permanent and temporary swamps [31]. In the TM, there is a predominance of high and medium forest in the lowlands and medium forests in the slopes and crests, with little topographic variation, but the presence of alternating hills and lowlands. The whole area of the TM is in an old alluvial terrace, the paleochannel of the Belem River (tributary of Doce River), while LG has a distinct geological unit, and this entire area lies on a unit called litostatigragphic Mantiqueira Complex [31].

2.2. Sampling Design. The study areas are two permanent plots of 100 ha (IMA) produced during the Rio Doce TEAM Project, a long-term project coordinated by the Conservation International through the TEAM (Tropical Ecology, Assessment, and Monitoring) Initiative network [32]. The samples used in this work are part of Rio Doce TEAM Project—Ant Protocol [33]. The chosen areas are permanent plots set to attend several projects, and transects were easily set in a full random design due to the existence of open narrow research paths. Eight transects were sampled per season in both areas,

Psyche

		20	005						
Species	LG		TM		LG		ТМ		Frequency (%)
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	
Solenopsis (Diplorhoptrum) sp1	27	26	23	27	34	36	3	26	63.13
Pyramica denticulata (Mayr, 1887)	21	16	1	15	27	22	19	19	43.75
Brachymyrmex australis Forel, 1901	12	22	12	28	4	22	13	18	40.94
Strumigenys elongata Roger,1863	13	9	6	12	21	13	16	18	33.75
Hypoponera trigona (Mayr, 1887)	16	1	8	9	13	15	24	19	32.81
Pheidole diligens Smith F., 1858	1	7	11	15	11	21	15	24	32.81
Odontomachus meinerti Forel, 1905	12	11	8	19	19	7	15	12	32.19
Solenopsis (Diplorhoptrum)sp5	29	7	24	6	13	3	11	4	30.31
<i>Hypoponera distinguenda</i> Emery, 1890	13	12	1	11	18	19	12	7	29.06
Pheidole cf. flavens Roger, 1863	5	14	3	1	18	16	16	9	25.63
Crematogaster longispina Emery,1890	1	4	13	5	17	5	17	8	21.88
Wasmannia auropunctata (Roger,1863)	9	6	6	4	26	1	11	1	20.00
Strumigenys cf. silvestrii Emery, 1906		13	11	11	2		9	16	19.38
Pheidole cf. dimidiata (Emery, 1894)	1	6	2	1	6	17	5	18	17.50
Pheidole midas Wilson, 2003	7	11	2	5	1	9	9	11	17.19
Carebarella sp1	5	2	2	8	11	4	14	8	16.88
Sericomyrmex cf. bondari Borgmeier, 1937	14	5	1	9	5	12	6	1	16.56
Apterostigma gp. pilosum Mayr, 1865	6	8		1	11	4	13	3	14.38
Solenopsis (Diplorhoptrum) sp2	4	7	5	13	3		6	8	14.38
Brachymyrmex longicornis Forel, 1907		1	13	9			9	12	13.75
Pachycondyla gp. harpax (Fabricius,1804)	9	4	6		2	5	3	3	10.00
Solenopsis sp4	1		1	11			7	11	9.69
Pheidole cf. minutula Mayr, 1878	1		5	8	4		1	11	9.38
<i>Brachymyrmex</i> sp3	15	1			8	5			9.06
Pyramica crassicornis (Mayr,1887)	6	5	1	3		4	1	9	9.06
<i>Cyphomyrmex tranversus</i> Emery, 1894	1	1	1		4	5	7	8	8.44
Octostruma iheringi (Emery,1888)	2	1	1	1	2	7	5	7	8.13
Crematogaster (Orthocrema) sp6	3		7	4	5	2	1	3	7.81
Hylomyrma reitteri (Mayr,1887)	3	5		2	3	9		3	7.81
Solenopsis cf. terricola Menozzi, 1931	4	5		3	2	3	3	5	7.81
Octostruma rugifera (Mayr, 1887)		4		5		5		8	6.88
Hypoponera sp6	3	5	1	1	1	9		1	6.56
Pyramica eggersi (Emery,1890)		1			1	11	5	2	6.25
Crematogaster nigropilosa Mayr, 1887	6	7		5		1		1	6.25
Mycocepurus smithii Forel, 1893	1	3	1	3	3	2	2	4	5.94
Carebara panamensis (Wheeler, 1925)	2	2			1	4	4	5	5.63
Rogeria besucheti Kluger, 1994	2	1			4	2	4	5	5.63
Discothyrea sexarticulata Borgmeier,1954	1	2		5			4	5	5.31
Megalomyrmex modestus Emery, 1896	2	3	1	3			2	6	5.31
Crematogaster limata Smithi F., 1858	3	4		6		1	1	1	5.00
Paratrechina sp4	1			1	7	2	4		4.69
<i>Ectatomma permagnum</i> Forel, 1908	3	1	1	3	2		3	1	4.38
Brachymyrmex heeri Forel, 1874	6	5	1	1					4.06
Octostruma cf. balzani (Emery, 1894)		2		4		6	1		4.06
Carebara urichi (Wheeler, 1922)	1	1		2	1	1	1	5	3.75

TABLE	1: Continued.	

Species		20	005						
	LG		TM		LG		TM		Frequency
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	(79)
Dolichoderus imitator Emery, 1894	4		4		3		1		3.75
Acromyrmex subterraneus brunneus Forel, 1912	2	2	2	1	1		3		3.44
<i>Camponotus (Tanaemyrmex) punctulatus andigenus</i> Emery, 1903		1	3		3	1	2	1	3.44
Hylomyrma sp2		2		1	1	3		4	3.44
Pyramica sp5	1	5				5			3.44
Strumigenys perparva (Brown, 1958)	1		1		1	1	5	1	3.13
Megalomyrmex drifti Kempf, 1961	3	4	1	1			1		3.13
Pheidole sp9						4		6	3.13
Brachymyrmex sp5	3	6							2.81
Ectatomma tuberculatum (Olivier,1792)	2		1	1	3		2		2.81
Pachycondyla venusta Forel, 1912	1		2	1	1	1		3	2.81
Pyramica alberti (Forel, 1893)				3			6		2.81
Pyramica brevicornis (Mann, 1922)		1	1	2	3	1	1		2.81
Brachymyrmex cf. pictus Mayr, 1887	2		1		1		4		2.50
Ectatomma suzanae Almeida, 1986	3			1			3	1	2.50
Hypoponera foreli (Mayr, 1887)	3	1	1		1		2		2.50
<i>Hypoponera</i> cf. <i>punctatissima</i> (Roger 1859)				2			6		2.50
Prionopelta antillana Forel, 1909	1			1	2		2	2	2.50
Pvramica subedentata (Mayr, 1887)	2			1	1		2	2	2.50
Trachvmvrmex cornetzi Forel, 1912	1		1		1	3	1	1	2.50
Hypoponera sp8		3	2		2				2.19
Odontomachus haematodus (Linnaeus, 1758)	1		3		1		1	1	2.19
Wasmannia cf. sigmoidae (Mayr, 1884)							7		2.19
Acanthognathus ocellatus Mayr, 1887		1	1	1				3	1.88
Brachymyrmex sp7	5				1				1.88
<i>Myrmicocrypta sauamosa</i> Smith E. 1860	-	1		2	2	1			1.88
Pachycondyla gilberti Kempf, 1960		1		-	1	1	1	2	1.88
Pheidale sp13		3		2	-	1	-	-	1.88
Pvramica mavnei (Forel 1916)		3		2		2		1	1.88
Salenapsis sp16		5	1	3	2	2		1	1.88
Strumigenvs precava (Brown 1954)	1	2	1	5	2		2	1	1.88
Acropyga gaeldii Forel 1893	1	1					2	1	1.56
Apterostiama sp5		1			3		2	4	1.50
Brachumurmer sp4	А				5	1	2		1.50
Camponotus (Tanaemvrmer) melanoticus Emery	4					1			1.50
1894	1	1			1	2			1.56
Megalomyrmex goeldii Forel, 1912		5							1.56
Pheidole sp12	5								1.56
Solenopsis sp6	2	3							1.56
Linepithema pulex Wild, 2007	1		1	1	1			1	1.56
Wasmannia sp3	1	1	2						1.25
<i>Cryptomyrmex longinodus</i> Férnandez & Brandão, 2003		2				2			1.25
Amblyopone lurilabes Lattke, 1991				1		2		1	1.25
Crematogaster acuta (Fabricius,1804)		4							1.25

Psyche

1890

		20	005			Frequency			
Species	LG		ТМ		LG		TM		
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	(%)
Gnamptogenys porcata (Emery,1896)		1					1	2	1.25
Paratrechina steinheili (Forel, 1893)		1	3						1.25
Pheidole sp14	1			1				2	1.25
Pheidole sp16			1					3	1.25
Wasmannia rochai Forel, 1912			1	1		1		1	1.25
Amblyopone cf. armigera Mayr, 1897	1						1	1	0.94
Brachymyrmex sp8					1	2			0.94
<i>Camponotus (Mymocladoecus) latangulus</i> Roger, 1863		2		1					0.94
Camponotus (Myrmophaenus) novogranadensis Mayr, 1870	1	1		1					0.94
Crematogaster sp3	2					1			0.94
Cyphomyrmex peltatus (Kempf, 1966)		1					2		0.94
Eurhopalothrix prox. bruchi Santischi, 1922		1		1			1		0.94
Gnamptogenys gracilis (Santischi, 1929)	1							2	0.94
Octostruma sp4				1		1		1	0.94
Paratrechina sp6					1		2		0.94
Solenopsis sp14				2				1	0.94
Trachymyrmex prox. relictus Borgmeier, 1934			1		1		1		0.94
Azteca cf. alfari Emery, 1893	1	1							0.63
<i>Camponotus femoratus</i> (Fabricius,1804)		1						1	0.63
Cephalotes pusillus (Klug,1824)	1		1						0.63
Crematogaster curvispinosa Mayr, 1862	2								0.63
Hylomyrma sp3	1						1		0.63
<i>Hypoponera</i> sp12	1	1							0.63
Megalomyrmex silvestrii Wheeler W.M., 1909				1		1			0.63
Mycocepurus goeldii Forel, 1893	2								0.63
Myrmelachista (Hincksidris) sp2			1		1				0.63
Pachycondyla verenae (Forel, 1922)	1					1			0.63
Pheidole sp4					1			1	0.63
Pseudomyrmex tenius (Fabricius, 1804)			2						0.63
Rogeria microma Kempf, 1961	2								0.63
Solenopsis sp3						2			0.63
<i>Stegomyrmex olindae</i> Feitosa, Brandão & Diniz, 2008							2		0.63
Wasmannia cf. lutzi Forel, 1908	2								0.63
Acanthognathus prox. rudis Brown & Kempf, 1969		1							0.31
Acropyga smithii Forel, 1893						1			0.31
Anochetus diegensis Forel, 1912				1					0.31
Brachymyrmex sp9					1				0.31
<i>Camponotus (Tanaemyrmex) balzani</i> Emery, 1894		1							0.31
Camponotus (Myrmoclaedocus) bidens Mayr, 1870			1						0.31
<i>Camponotus (Mymocladoecus) crassus</i> (Mayr, 1862)			1						0.31
Camponotus (Mymocladoecus) rectangularis Emery,	1								0.31

TABLE 1: Continued.

TABLE 1: Continued.

		20	005						
Species	LG		ТМ		LG		TM		Frequency (%)
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	
Camponotus (Myrmobrachys) trapezoideus Mayr, 1870		1							0.31
Carebara pilosa Férnandez, 2004								1	0.31
Cephalotes maculatus (Smith F., 1876)	1								0.31
Cerapachys splendens Borgmeier, 1957		1							0.31
Crematogaster sp8								1	0.31
Dolichoderus lutosus Smith F., 1858				1					0.31
Eciton burchelli (Westwood, 1842)		1							0.31
Gnamptogenys sp3					1				0.31
Heteroponera angulata Borgmeier, 1959		1							0.31
<i>Hypoponera</i> sp10					1				0.31
Hypoponera sp13		1							0.31
Hypoponera sp17							1		0.31
Labidus coecus (Latreille, 1802)		1							0.31
Linepithema iniquum (Mayr, 1870)			1						0.31
<i>Myrmelachista</i> sp1	1								0.31
<i>Myrmelachista</i> sp3							1		0.31
Neivamyrmex sp1						1			0.31
Nesomyrmex spininoidis Mayr, 1887	1								0.31
Nesomyrmex wilda Smith M.R., 1943			1						0.31
Pachycondyla ferruginea Smithi F., 1858		1							0.31
Pachycondyla villosa inversa Smith F., 1858							1		0.31
Pheidole fallax Mayr, 1870							1		0.31
Pheidole sp17					1				0.31
Pseudomyrmex gp. pallidus Smith F., 1855			1						0.31
Pyramica appretiata (Borgmeier, 1954)		1							0.31
Rogeria scobinata (Kluger, 1994)		1							0.31
Solenopsis (Euophthalma) globularia Smith F., 1858				1					0.31
Solenopsis sp15								1	0.31
Strumigenys sublonga Brown, 1958							1		0.31
Strumigenys schmalzi Emery, 1905		1							0.31
Wasmannia villosa Emery, 1894					1				0.31

thus 16 per year, with 10 samples of 1 m^2 litter per transect, using the apparatus of Mini-Winkler [34], equidistant 10 m one from another, summing up 320 samples on two years. Each transect had its exact position previously sorted using random numbers and a plotted map of the transect, thus assuring a fully random sampling design.

Ants were taken to the lab, sorted, and identified to genera. Species confirmations were achieved in collaboration with the Myrmecological laboratory of CEPLAC, Bahia. The collection is saved in both CEPLAC and in the collection of the Laboratory of Evolutionary Ecology of Canopy Insects, in DEBIO/ICEB/UFOP.

2.3. Data Analysis. In order to evaluate the effect of accumulation of species in each sampling unit and for all observed

data, we made species accumulation curves (Coleman method), which devise the expected richness for random subsamples of the data set grouped [35, 36]. Calculations were made using the computer program EstimateS version 8 [35]. The Coleman curve is essentially the same to a rarefaction curve and more efficient computationally [37, 38]. The Abundance-based Coverage Estimator (ACE) was used as estimator of species richness [35, 39], because the coefficient of variation (CV) was larger (CV = 0.519) than abundance distribution. When the CV was larger than CV > 0.5, Chao [39] and Colwell [35] recommend Chao 1 and ACE as the best estimates for abundance-based richness.

A nonsmetric multidimensional scale analysis (NMDS) was used to demonstrate overall differences in species composition between the two areas. The ordination was carried

out for the data on species presence and absence in each plot, using the Jaccard index. We used analysis of similarities (ANOSIM) [40] to test for differences in species composition between areas. In order to investigate patterns of similarity between the ant communities in both areas, we used the relative differences between *R*-value of the ANOSIM test [41]. These analyses were performed using the software PAST [42].

Factorial analysis of variance (ANOVA) models [43], with Poisson distribution of data (which is automatically logtransformed in the model in order to best fit the distribution) [44], were used to analyse the results. The statistical package GLZ-Generalized Linear/Nonlinear Models (Statsoft Statistica 7.0 software) was used when generating analyses of the frequency of occurrence of ants (number of records) and the total number of species for each sample (transect) in different areas, seasons, and between years. Wald's test was used to verify the true parameter value based on the sample estimate, assuming that the value of P < 0.05 is significant. The measures of relative abundance (frequency of species per transect) were based on the number of occurrences of species per point (each 1 m² of the transect), summing up 10 possible occurrences of each species per transect, or 40 per season/IMA.

3. Results

In total 2851 individuals, 48 genera and 160 morphospecies were identified and recorded, belonging to 11 subfamilies: Amblyoponinae, Cerapachyinae, Dolichoderinae, Ecitoninae, Ectatomminae, Formicinae, Heteroponerinae, Myrmicinae, Ponerinae, Proceratiinae, and Pseudomyrmicinae. Most of species and genera found belong to the subfamily Myrmicinae, followed by Formicinae and Ponerinae. Only four of the 11 subfamilies of ants were not common to the two areas: Cerapachyinae, Ecitoninae, and Heteroponerinae were found only in the TM, while Pseudomyrmicinae was found only in LG.

The number of genera occurrences was very similar between the two sites. LG showed 40 genera, being four habitatspecific genera: *Cephalotes, Myrmelachista, Pseudomyrmex,* and *Stegomyrmex.* TM had 44 genera, eight habitat-specific genera: *Acropyga, Anochetus, Cerapachys, Cryptomyrmex, Eciton, Heteroponera, Labidus,* and *Neivamyrmex* (Table 1). In both areas, we found typical litter-forest genera (*Stegomyrmex* in LG, *Cerapachys* and *Cryptomyrmex* in TM), typical forest species or species only recently described, for example, *Wasmannia villosa* and *Stegomyrmex olindae* in LG, and the typical soil ant *Cerapachys splendens* and *Cryptomyrmex longinodus* in TM. New species for science, being in process of description, were also found, as *Hylomyrma* sp2 (MZUSP).

Species richness did not reach stabilized at the end of the sampling, even after combining all samples (n = 32; Figure 2). The total species richness of the ant community per transect (1 ha) was estimated to be around 200 species, and rare-faction curve was reached to be around 160 species (Coleman's method) (Figure 2). For both IMA,



FIGURE 2: Accumulation curve of species richness (obtained by Coleman's method) for all sampling (solid black line), for Lagoa Gambazinho (dashed grey line), and for Trilha Macuco (thin black line). The overall species richness for both IMAs was estimated with Chao 2.



FIGURE 3: NonMetric Dimensional Scale (NMDS) ordination of species composition of the ant community in both IMA as sampled by Mini-Winkler.

species richness was similar (rarefied species richness for 122 occurrences Coleman method = 4.22 ± 1.63 for LG and 4.27 ± 1.53 for TM, Figure 2). However, differences in species composition were detected among areas, as revealed by NMDS (ANOSIM, R = 0.23, P < 0.001; Figure 3).

Regardless seasonal and yearly variations, species richness was very similar between both areas (Factorial ANOVA, Wald $X^2(1) = 1.06$, P = 0.30). The LG had 126 species, 36 of these habitat-specific species, and the TM showed 124 species and 35 habitat-specific species (Figure 4 and



FIGURE 4: Diagram representing the number and distribution of ant species in both IMA (Lagoa Gambazinho and Trilha Macuco) and in two seasons (dry and wet). Separation criteria were unique to each of the IMA and weather stations (large circles), collected in both IMA (intersections of top and bottom), collected in two seasons (intersections of left and right), and collected in two IMA and in two seasons or in at least one weather station (central circle).

Table 1). However, the species richness found were quite different between the dry period (42 species) and the rainy season (24 species), and this difference was due to a strong reduction of species in LG, the low and more open forest, during the dry periods (Figure 5(a)). It is worth to notice that there were more species in common between the areas during the dry season than in rainy season. Species such Azteca cf. alfari, Brachymyrmex cf pictus, B. sp5, Camponotus (Tanaemyrmex) balzani, Paratrechina steinheili, Hypoponera sp12, Solenopsis sp5, and Wasmannia sp3 were found only in the dry season, while Brachymyrmex sp8 and Pheidole sp4 were found only in wet season (Figure 4 and Table 1). Species richness declined in the LG in the dry season, when compared to TM or to itself in the rainy season, but only for 2006 (Factorial ANOVA, Climatic Season*Year, Wald $X^{2}(1) = 6.81, P = 0.009$; Figure 5(a)). The inconsistency of this decline in 2005 resulted in a lack of significant differences in species richness between areas (Factorial ANOVA, Wald $X^2(1) = 0.46, P = 0.50$; Factorial ANOVA, IMA * Climatic Season * Year, Wald $X^2(1) = 0.50$, P = 0.48) (Figure 5(a)).

A similar interaction effect between area and year effects (Factorial ANOVA, IMA*Year, Wald $X^2(1) = 7.34$, P = 0.006) and the effects of season and year (Factorial ANOVA, Climatic Season*Year, Wald $X^2(1) = 17.70$, P = 0.00003) defined the variance in ant abundance between the areas. Likewise species richness, the ant abundance declined strongly in the dry season of 2006 and only. In the present case, the strength of this interaction was perceptible in the three levels, thus reflecting in the mean numbers of ants between areas, greater in the TM, the tallest forest (Factorial



FIGURE 5: Species richness (a) and relative abundance (b) (number of occurrences on transects) of ant species in both IMA, in two seasons (dry and wet), and in two years (2005 and 2006).

ANOVA, IMA*Climatic Season*Year Wald, $X^2(1) = 5.02$, P = 0.02; Figure 5(b)).

The overall mean abundance was also very similar between areas (Factorial ANOVA, Wald $X^2(1) = 1.46$, P = 0.23). The 10 most abundant species throughout the sampling were *Solenopsis* sp1, followed by *Pyramica denticulata*, *Brachymyrmex australis*, *Hypoponera trigona*, *Strumigenys*

elongata, Pheidole diligens, Odontomachus meinerti, H. distinguenda, S. sp5, and P. cf. flavens. However, at LG, the species B. australis and P. diligens, were not among the most abundant species. In this area, besides the other eight previously mentioned, we found Crematogaster longispina and Wasmannia auropunctata amongst the most abundant. In the TM, Solenopsis sp5 was not as abundant as the others, while P. cf. dimidiata was found among the most abundant. Regarding rare species, the LG presented 36 species, 20 of these were habitat-specific species, while in TM were 33 rare species, and also 20 habitat-specific species (Table 1).

As observed for relative abundance, there was an increase in species richness in the wet season in both areas. However, despite low species richness in the dry season, species composition varied smoothly between years in both areas. The data of the rainy season in LG, for example, showed that the total number of species increased from 67 to 72 in a year to another, and the number of rare species (singletons) decreased from 26 to 21 species (38.8% to 29.2% of species). Values of relative abundance (number of occurrences per sampling event, or 4 transects and 40 points for either season/IMA) of intermediate species (species that were neither among the 10 most abundant or among singletons) varied greatly between years (Table 1), which was related to the variation in numbers of predatory ants species richness and abundance.

4. Discussion

The global ground-dwelling ant diversity in Rio Doce was remarkably high, as well as composed of rare and habitatdemanding species and genera (see below). The ant species richness in the forest litter was substantially higher than ants or general arthropods species in the canopy of these same forests [23, 45, 46]. In addition, it was comparably as high as in other tropical forests and sometimes comparable to the species richness found and wetter and closer equatorial forests [13, 19, 36, 38].

In spite of differences in physiognomy and geomorphology found in both areas, the overall mean values of species richness and abundance were not statistically different between these forest types, although there were substantial differences in relation to species composition. However, one could expect to sample more species, especially rare predators and cryptic specialists species in TM than in the LG, due to the tree heights, a better structured understorey, apparent constancy of conditions in the former compared to the latter. These conditions should allow high availability of resources and quality of sites for feeding and nesting areas [47, 48]. The TM pristine semideciduous forest was denser in trees, which also had larger basal area than the open, apparently secondary LG [31]. Among many other ecological implications, these traits imply in greater litter biomass in TM compared to LG.

In a close wet and tall forest, there might have less variation in abiotic conditions, such as local atmospheric humidity and temperature [19], and, sometimes, as is the case of PERD, this may be further buffered by a smooth and continuous topography [31]. On the other hand, ecological variables such as increased litter production in association with the high heterogeneity of the vegetation may also happen in association to close and tall forests [49], which results in high spatial complexity, allowing diversification of conditions, thus sheltering a large number of species of ants and other invertebrates in the litter and soil [31, 45, 48, 50–52]. Other studies in tropical forests have corroborated that differences of litter ants species diversity and distribution respond to habitats with low and high structural heterogeneity [53–55].

Hence, TM should have the best conditions for more habitat-demanding ant species than LG, unless the habitat conditions in the latter are rather natural too. The region around LG has indeed a more open canopy and lower tree heights than TM, but the cause for its physiognomic pattern is subject of debate. Although the area was impacted by a fire in 1967, there would have been time enough for full recover. Soares [31] and Ribeiro et al. [46] have discussed that a great deal of the observed differences in vegetation are natural rather than result of human past disturbance. Data suggest that physiognomic differences between the two studied areas are evolutionary rather than ecological, and both may sustain equivalent levels of heterogeneity. Indeed, the geomorphologic origins of both forests ought to have stronger effect on their productivity and then on their canopy traits that relate to understorey microclimate and heterogeneity. Hence, despite apparent vulnerability of LGs and its low resistance to the dry season extreme desiccation, both forests are equivalently rich and populated with ecologically demanding species. Such pattern only could happen if both places had long enough favourable conditions for species evolution.

The occurrence of rare species of ants in the LG, for example, Stegomyrmex olindae, so far found only in humid and mature forests [56], Cryptomyrmex longinodus (first occurrence in the southeastern Brazil; Fernández, personal communication), Strumigenys sublonga (cryptic species collected by first time in tropical semideciduous forest in Minas Gerais, Castro unpublished data), Eurhopalothrix prox. bruchi, and Octostruma species, support that this forest, whatever the human impacts suffered in the past, has several ant species typical of environments with greater habitat structural complexity and a well-preserved long evolutionary history. It is quite likely that edaphic-evolving condition found in the LG forest is the best explanation for the fact. This also may explain the fact that there is not any widely distributed tall and closed forest in southern PERD as a whole.

Seasonal effects are important regulators of ecological communities in tropical forests, especially plants and invertebrates [5]. Seasonal effects were more perceptible in 2006 than in 2005, concerning both species richness and abundance. According to PERD climatic station data and our microclimatic records, the 2005 had a dry season with little rainfall, mild air temperatures, and high mean relative humidity, rising up to 80% in the winter driest days. The year of 2006 was characterized by a dry season hotter than 2005, regarding air temperature in the understorey, with abrupt changes in rainfall regimen, unlike 2005, even though we sampled exactly in the same time of the year. For instance, it rained practically every day in August 2006 (a usually very dry month), while in 2005 rainfall was recorded in only four days during the same month. In the rainy season, in relation to data of temperature and humidity, there was no significant dispatch from the expected and the understorey reached values at or near 100% relative humidity in both years. However, in November 2005, the accumulated rainfall index ranged from 312.5 to 330.61 mm (daily rain 89 \pm 4 mm), while in 2006, it ranged from 48.43 to 29.99 mm (daily rain 17 \pm 5 mm) [57].

These data suggest that in 2006, the rainy season started abnormally earlier (in August). In tropical forests, the cycle of ants colonies is synchronized with the seasonal rainfall and temperature [21], and, although the mechanism is not well known, in the more humid and hot (above 30°C and 50% of relative humidity), the faster is the development of ant colonies [20]. Nevertheless, the unpredictable start of rains may have a very negative effect in some habitats, by taking the colony not prepared for the change. On the other hand, a badly defined dry season in 2006, with subsequent early onset of the rainy season, may have provided a better partition of resources available for ant assemblage in both areas, especially preys, which could reflect the fast recovery and increasing abundance of predators in the wet season. Indeed, in 2005, some specialist predatory ants were rare or absent, as some species of the genus Strumigenys and Pyramica, known as specialist predators of Collembola, Discothyrea sexarticulata, a predator of spider eggs, and the generalist large predators as Ectatomma and Pachycondyla species, predators of insects and invertebrates with similar body size or also larger [58].

In conclusion, our results showed that contrasting forest types may have similar total ant species richness, as well as a similar amount of rare and ecologically specialized species. These similarities between these forests suggest that litterdwelling species may have high resilience, related to the litter habitat conditions, to changes and disturbances in both ecological and evolutionary times.

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