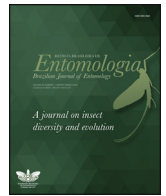




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Review

Diversity of wasps (Hymenoptera: Aculeata: Vespidae) along an altitudinal gradient of Atlantic Forest in Itatiaia National Park, Brazil

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ABSTRACT

Surveying the diversity of stinging wasps (Hymenoptera: Aculeata) provides an important information base to assist in biodiversity conservation and the management of forest reserves, as wasps depend on and maintain the population balance of several other groups of insects. In accordance, this paper presents an altitudinal survey of wasps (Hymenoptera, Aculeata, Vespidae) in Itatiaia National Park, Brazil, which is a protected area covered by Atlantic Forest in a mountainous landscape, with altitudes ranging between 540 and 2791 metres above sea level. Six altitudinal zones were sampled with entomological net, and the abundance and diversity of the species were indicated by zones. Field sampling took 288 h of discontinuous activity, which was randomly conducted from December 2012 to December 2013. A total of 398 individuals belonging to 29 species and two subfamilies (Eumeninae and Polistinae) were sampled. Eight species are new records for the state of Rio de Janeiro. We found a monotonic decrease in wasp diversity in relation to altitude, and the number of captured individuals differed significantly between the low and high altitudes.

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Introduction

Biodiversity hotspots are threatened areas that are home to a total of more than 60% of all terrestrial species on the planet. The Brazilian Atlantic Forest is one of the 34 biodiversity hotspots in the world and is a priority area for conservation (MMA/SSBF, 2002). It is the most devastated and seriously threatened biome in Brazil and has a long history of colonization and exploitation of resources, which have already eliminated most of its natural ecosystems, leaving less than 8% of the original forest extent (Pinto and Brito, 2005).

The richness and abundance of invertebrate species provide a vast information base to assist in biodiversity conservation and forest reserve management (Pyle et al., 1981; Lewinsohn et al., 2005). Among insects, aculeate wasps (either social, solitary or parasitoids) exhibit great variations in structure, physiology and behaviour and are of special interest for conservation, as they are considered predominant predators in terrestrial ecosystems, as they control the populations of several other organisms (Lasalle and Gauld, 1993; Cirelli and Penteado-Dias, 2003). Lawton (1983) and Santos et al. (2007) have shown that environments with a more

complex structure make the establishment and survival of more species of social wasps possible.

The relevant role in terrestrial ecosystems played by wasps makes any effort to know and preserve them highly justifiable (Amarante, 1999). In this context, biological inventories are basic tools for the initial survey of biological biodiversity, as well as for monitoring changes in different components of this biodiversity, whether under different environmental conditions in response to impacts of natural processes or human activities.

This work aimed to determine the richness and abundance of the Vespidae in Itatiaia National Park, Brazil, and determine the variation in composition of this community along an altitudinal gradient in the Atlantic Forest. The question to be answered is whether different species may respond differently to environmental variations along this altitudinal gradient.

Materials and methods

Study area

The Itatiaia National Park (Parna Itatiaia) (Fig. 1) is included in the Atlantic Forest Biome and is located in south-eastern Brazil in the Serra da Mantiqueira region (44°34'–44°42'W and 22°16'–22°28'S), among the municipalities of Resende and Itatiaia

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Fig. 1. Delimitation of the Itatiaia National Park in the states of Rio de Janeiro and Minas Gerais, Brazil, indicating the collection points and their respective altitudes.

in north-western Rio de Janeiro, and Alagoa, Bocaina de Minas and Itamonte in southern Minas Gerais. It was the first Conservation Unit in Brazil that was created on June 14, 1937 through Federal Decree No. 1713 (IBDF, 1982) and has an area of 300 km².

The marked altitudinal gradient (540 masl in the southern limits of the park up to 2000 masl on the plateau in the north) and climatic variation provide several ecosystems in the Atlantic Forest in Itatiaia that shelter several endemic species of flora and fauna. The relief is an influencing factor for the climate in the Itatiaia region (IBDF, 1982). According to the Köppen–Geiger classification system (Alvares et al., 2013) this region present the climate C (humid subtropical zone), and the climate varies with the altitude into two types: Cwb in the highest parts above 1600 masl (mesothermic with mild, rainy summers and dry winters) and Cfb in the low parts of the mountain slopes (mesothermic with temperate summers and no well-defined dry season).

The variation of the vegetation is highly conditioned by the relief, altitude and climate. Barros (1955), and Brade (1956) highlighted the significant difference in the floristic compositions between the northern and southern faces of the Mantiqueira Range due to climatic differences related to the orientation of the slopes, continentality and altitude.

Sampling design

Collections were carried out at 6 points at different altitudes (Table 1; Fig. 2) in Itatiaia National Park during nine expeditions from December 2012 to December 2013. Two points were alternated over periods of 4 days/month with daylight from 9 h to 17 h. A total of 18 samples were collected for a total of 36 days of sampling, and each sample corresponding to 2 days (16 h) of work per point. The sampling effort in each area was completed after 48 h, for a total of 288 h of fieldwork.

Data analysis

The metrics between the observed and expected values are based on the individual rarefaction technique (gamma log function) of Krebs (1989). The abundance data for the species were adjusted to the log normal model using the octave abundance class method (Magurran, 1988; Lobo and Favila, 1999). The dominance analysis was calculated according to the Simpson index with ranges

from 0 (all taxa are equally present) to 1 (one taxon dominates the community completely) (Simpson, 1949). The similarities between the abundance data of the different sample areas are indicated by the Bray Curtis similarity index, and the replacement of the taxa between the different altitudinal ranges was measured according to the beta diversity index ($S/\alpha - 1$), where S = total number of species and α = average number of species (Whittaker, 1972). The software programmes PAST v. 2.16 (Hammer et al., 2005), Dives (Rodrigues, 2005) and R Core Team (2015) were implemented for the analyses.

Results

A total of 398 specimens from 14 genera and 29 species of Vespidae belonging to the subfamilies Eumeninae (8 genera and 9 species) and Polistinae (6 genera and 20 species) were sampled (Table 2). The following 8 species are new records for the state of Rio de Janeiro and are listed below with their previously known distribution among Brazilian states (Bohart and Stange, 1965; Giordani Soika, 1990; Garcete-Barrett, 2011; Souza and Zanuncio, 2012; Garcete-Barrett and Hermes, 2013): *Polybia jurinei* (Saussure, 1854) [MG, AM, MS, PA, and SP]; *Mischocyttarus socialis* (Saussure, 1854) (Plate 1) [AM, MG and SP], *Ancistrocerus flavomarginatus* (Brèthes, 1906) [RS, PR and SC], *Hypodynerus archavaletae* (Brèthes, 1903) (Plate 2) [RS, PR and SP], *Pachymenes ater* (Saussure 1852) (Plate 3) [RS, PR, SC and SP], *Pseudodynerus subapicalis* (Fox) (Plate 4) [ES, GO, MT, RO, SC and SP], *Stenosigma allegrum* (Zavattari 1912) [RS, SC and SP], *Zethus brasiliensis brasiliensis* (Saussure, 1852) [RS, SC, PR and SP].

The distribution pattern of abundances by octaves presented a high percentage of rare species in the community (Fig. 3). The differences in the abundance at different altitudes (P1, P2 and P3) and (P4, P5 and P6) were highly significant (Kruskal–Wallis test: $X^2 = 49.93$, $gl = 1$, $p < 0.001$). Sample P1 had the highest species richness in relation to the other points and the lowest dominance index, while point 5 had the lowest richness and the highest dominance index (Fig. 4). The individual rarefaction curve shows the taxonomic differences between the sampled points (Fig. 5). The similarity and species turnover among the sampled areas are indicated in Table 3.

Table 1
Geographic coordinates of the sampled areas, altitudes and periods working in Itatiaia National Park.

Samples	Coordinates	Altitudes	Periods
1	22°27'11.80"S–44°36'27.40"W	630 m	December/2012; October–December/2013
2	22°27'02.62"S–44°36'38.50"W	840 m	February–April–July/2013
3	22°25'42.91"S–44°37'10.25"W	1.200 m	March–August–September/2013
4	22°20'03.22"S–44°42'38.31"W	1.730 m	February–July–October/2013
5	22°21'57.62"S–44°44'44.84"W	1.965 m	December/2012; April–September/2013
6	22°24'29.96"S–44°39'03.99"W	2.204 m	March–August–December/2013

**Fig. 2.** View of sampled areas in the Itatiaia National Park, Brazil.

Discussion

The variation of species richness along environmental gradients has been investigated in different geographic areas and with different taxa in the search for ecological patterns (e.g., bees and wasps: Carpenter, 1993, Marques, 2011, Perillo et al., 2017; Vespoidea: Santos et al., 2014; butterflies: Fleishman et al., 1998; flies: Devi and Jauhari, 2004; spiders: Chatzaki et al., 2005, Almeida-Neto et al., 2006, and Purcell and Avilés, 2008; beetles: Escobar et al., 2005; isopods: Sfenthourakis et al., 2005; moths: Beck and Chey, 2008; birds: Kattan and Franco, 2004; mammals: Geise et al., 2004, McCain, 2004, 2005, 2007a, and Remonti et al., 2009; plants: Bhattarai and Vetaas, 2006, and Lovett et al., 2006). Merrill et al. (2008) discuss that the altitudinal gradients of species diversity result from a combination of ecological and evolutionary processes rather than a single effect.

Three basic patterns of diversity have been discussed in relation to response of altitudinal variation (Jansen et al., 1976; Wolda, 1987; McCoy, 1990; Stevens, 1992; Olson, 1994; Abrams, 1995;

Fisher, 1998; Ward, 2000; Pyrcz and Wojtusiak, 2002; Sanders et al., 2003; Colwell et al., 2004; Rahbek, 1995, 2005; McCain, 2007a,b; Grytnes and McCain, 2007): (1) The unimodal-parabolic pattern or the “bell curve distribution” indicates that the highest diversity occurs at intermediate altitudes. (2) The monotonic-decreasing pattern with altitude elevation occurs when the diversity decreases with increasing altitude. (3) The monotonic-increasing pattern with altitude elevation occurs where the diversity increases with altitude.

Several studies with Insecta communities on altitude gradients have demonstrated the existence of the parabolic-unimodal pattern (Olson, 1994; Samson et al., 1997; Fisher, 1998; Sanders, 2002; Araújo et al., 2006; Brehm et al., 2007; Geraghty et al., 2007; Merrill et al., 2008; Hackenberger et al., 2009). According to Rahbek (1995), Lomolino (2001) and Kluge et al. (2006), this pattern is observed mainly in areas close to sea level and with lower altitude gradients.

One of the probable causes for this increase in diversity at the intermediate altitudes is the mid-domain effect (Colwell and Lees, 2000; McCain, 2004, 2005; Hawkins et al., 2005; Brehm et al., 2007;

Table 2
Abundance of Vespidae species for each of the six areas sampled along an altitudinal gradient in Itatiaia National Park, Brazil.

Taxa	Areas						Total
	1	2	3	4	5	6	
Polistinae							
<i>Epiponini</i>							
<i>Agelaiia angulata</i> (Fabricius, 1804)	37	44	32	7	–	14	134
<i>Agelaiia multipicta</i> (Haliday, 1836)	5	3	2	–	–	–	10
<i>Agelaiia vicina</i> (Saussure, 1854)	28	10	12	1	–	2	53
<i>Brachygastra lecheguana</i> (Latreille, 1824)	2	5	–	–	–	–	7
<i>Polybia ignobilis</i> (Haliday 1836)	1	–	–	–	–	–	1
<i>Polybia jurinei</i> Saussure, 1854	1	–	–	–	–	–	1
<i>Polybia fastidiosuscula</i> Saussure, 1854	1	1	–	1	–	–	3
<i>Polybia flavifrons hecuba</i> (Richards, 1951)	5	–	–	9	7	14	35
<i>Polybia minarum</i> Ducke, 1906	6	–	1	–	–	–	7
<i>Polybia paulista</i> (Ihering, 1896)	1	–	1	–	–	–	2
<i>P. platycephala sylvestris</i> Richards, 1978	2	–	–	–	–	–	2
<i>Polybia punctata</i> Buysson, 1908	2	–	2	1	–	2	7
<i>Protonectarina sylveirae</i> (Saussure, 1854)	–	–	–	1	–	–	1
<i>Mischocyttarini</i>							
<i>Mischocyttarus</i> sp. 01	2	–	3	–	–	–	5
<i>Mischocyttarus</i> sp. 02	1	–	–	–	–	–	1
<i>Mischocyttarus</i> sp. 03	–	2	–	–	–	–	2
<i>M. parallelogrammus</i> Zikán, 1935	10	8	2	–	–	–	20
<i>M. socialis</i> (Saussure, 1854)	2	9	–	–	–	–	11
<i>Polistini</i>							
<i>Polistes versicolor</i> (Olivier, 1971)	29	10	–	–	–	–	39
<i>Polistes cinerascens</i> Saussure, 1857	2	1	–	–	–	–	3
Eumeninae							
<i>Ancistrocerus flavomarginatus</i> (Brèthes)	1	1	–	–	–	–	2
<i>Hypodynerus arechavaletae</i> (Brèthes, 1903)	1	–	–	–	4	–	5
<i>Omicron</i> sp.	8	–	–	–	–	–	8
<i>Pachymenes ater</i> (Saussure, 1852)	6	7	4	1	–	2	20
<i>Pseudodynerus subapicalis</i> (Fox)	1	–	–	–	–	–	1
<i>Stenosigma allegrum</i> (Zavattari, 1912)	1	1	2	–	–	–	4
<i>Stenonartonia flavotestacea</i> (Giordani Soika, 1941)	3	1	7	1	–	–	12
<i>Zethus brasiliensis brasiliensis</i> Saussure	–	1	–	–	–	–	1
<i>Zethus discoelioides</i> Saussure, 1852	–	1	–	–	–	–	1
Richness	25	16	11	8	2	5	
Total	158	105	68	22	11	34	398



Plate 1. *Mischocyttarus socialis* (Saussure, 1854), frontal and side view (photo: Bhrenno Trad).



Plate 2. *Hypodynerus arechavaletae* (Brèthes, 1903), frontal and side view (photo: Bhrenno Trad).



Plate 3. *Pachymenes ater* (Saussure, 1852), frontal and side view (photo: Bhrenno Trad).



Plate 4. *Pseudodynerus subapicalis* (Fox), frontal and side view (photo: Bhrenno Trad).

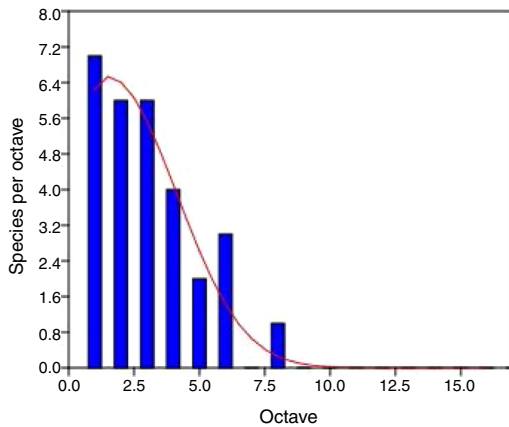


Fig. 3. Distribution of the octaves of abundances for Vespidae species (mean = 0.524, variance = 0.53, $p = 0.91$).

Colwell et al., 2009). However, according to Zapata et al. (2003), the average domain effect is a rather simplified hypothesis since it disregards several biological aspects of the species. In contrast to the parabolic-unimodal pattern, some hypotheses related to the tolerance limits of the species are used to justify the occurrence of the decreasing pattern with altitude (Stevens, 1992; Almeida-Neto et al., 2006).

Several factors can influence the altitudinal gradient, such as the effects of sampling, area, habitat complexity, productivity and climatic conditions such as temperature and humidity (Lomolino, 2001; Kluge et al., 2006; McCain, 2007b). Körner (2007) comments that there are four primary atmospheric changes associated with altitude: (i) decreasing total atmospheric pressure and partial pressure of all atmospheric gases (of which O_2 and CO_2 are of particular importance for life); (ii) reduction of atmospheric temperature, with implications for ambient humidity; (iii) increasing radiation under a cloudless sky, both as incoming solar radiation and outgoing night-time thermal radiation (because of reduced atmospheric turbidity); and (iv) a higher fraction of UV-B radiation at any given total solar radiation.

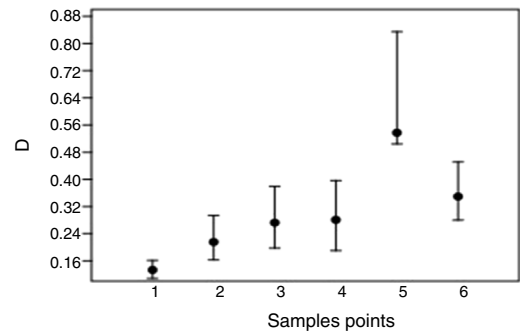


Fig. 4. Dominance analysis (Simpson index) by sampled points for the Vespidae fauna.

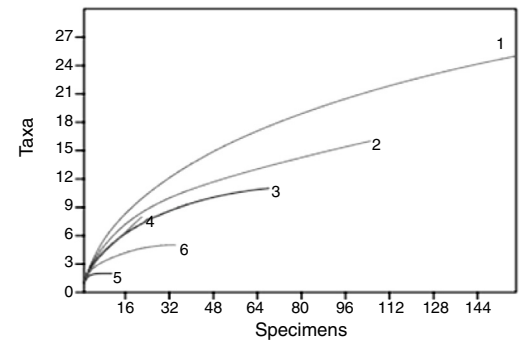


Fig. 5. Individual rarefaction curves for the 6 collection points of Vespidae in the Itatiaia National Park, RJ.

According to Conti and Furlan (2001), only altitudes above 1000 m have special climatic conditions that are different from those in the low mountain regions. Almeida-Neto et al. (2006) investigated the variation in atmospheric temperature and relative humidity along the gradient and found no significant differences.

Because of the typical conical shape of mountains, the species–area relationship along altitudinal gradients predicts that

Table 3
Comparison between the localities sampled for Vespidae fauna in an altitudinal gradient in the Atlantic Forest. Bray–Curtis similarity analysis (normal); Wittaker Beta diversity index (in bold).

Sampled points	1	2	3	4	5	6
1	1/0	0.36	0.38	0.57	0.85	0.66
2	0.631	1/0	0.48	0.58	1	0.71
3	0.548	0.601	1/0	0.47	1	0.50
4	0.188	0.173	0.244	1/0	0.80	0.23
5	0.071	0	0	0.422	1/0	0.71
6	0.260	0.258	0.392	0.678	0.311	1/0

altitudinal zones that cover larger areas (lower altitudes) should harbour more species than those with lower mountain top extensions (Rahbek, 1997; McCain, 2007a). In addition, the reduction of the area increases the competition for resources and can cause a reduction in the number of species in this zone.

By extrapolating a hypothesis initially created for latitudinal gradients to altitudinal gradients, Stevens (1989, 1992) and Sanders (2002) proposed the “Rapoport Rule” as an explanation for the pattern of the reduction in species richness at higher altitudes. According to this hypothesis, many low-altitude species have narrower limits of occurrence and approach their maximum ranges at low altitudes, whereas higher-altitude taxa have greater climatic tolerances and can, therefore, be found in a greater range of altitudes due to the “rescue effect” of their populations at lower altitudes (Brown and Kodric-Brown, 1977; Araújo et al., 2006). Consequently, species from higher areas would inflate the species richness in lower areas, producing the well-known pattern of monotonic reduction in species richness as altitude increases (Colwell and Lees, 2000).

It is possible that a single mechanism produces different patterns of responses for each animal species (Wang et al., 2011). In this work *Protonectarina sylveirae* was influenced mainly by the phytophysiological characteristics, with an inverse environmental affinity to the closed and humid arboreal vegetation; *H. archavaletae* present direct influence from shrub vegetation and were not established in altitude meadows; *Polybia fastidiosuscula* was established in shrub vegetation and was not associated with either altitude meadows or small closed forest formations; *Polybia flavifrons hecuba* and *P. punctata* were associated with the phytophysiological characteristics of altitude meadows, small closed forest formations and shrub formations.

The temperature is also a determining factor in how long the egg and pupa stages will last (Kumar et al., 2009). Gomes and Noll (2009) observe that sunshine directly influenced the capture of the wasps, as a decrease in luminosity caused a reduction in foraging intensity. As wasps are ectothermic animals and need to maintain their body temperature above the temperature of their surroundings.

The distribution pattern of abundances by octaves presented a pattern that is typically observed for Hymenoptera (Silvestre et al., 2014), with a high percentage of rare species in the community and few species with high abundance. Polistinae specimens represented more than 85% of the total of individuals sampled and were six times more abundant than Eumeninae specimens, probably because they are social. The social wasps presented wide ecological variance, as they are able to vary their nesting habits as a function of the environmental conditions and available nesting substrates (Wenzel, 1991; Marques et al., 1993; Santos and Gobbi, 1998). However, some species exhibit restricted ecological variance limits, nesting only in sites with specific conditions (Cruz et al., 2006). The species of social wasps that nest only under certain conditions select the nest sites by the density and types of vegetation, whether open or closed, as well as the shape and arrangement of leaves and other plant structures (Machado, 1982; Wenzel, 1991; Dejean et al., 1998).

Our data suggest a pattern close to monotonically decreasing with elevation, that is, diversity decreases with increases in altitude. Perillo et al. (2017) too found a negative correlation between altitude with bee and wasp's species richness and abundance, and correlated with altitude the temperature, precipitation, water vapour pressure, and wind speed.

Future studies will be needed to investigate which abiotic and ecological factors are preponderant to determine the decrease of the wasp diversity in the high altitudes of the Atlantic forest.

Compliance with ethical standards

The specimens were collected and transported with authorization from SISBIO for activities with a scientific purpose according to article 33 of IN 154/2009, registered under number 36153-1 of the Chico Mendes Institute for Biodiversity Conservation – ICMBio, Ministry of Environment – MMA. The species vouchers are housed in MuBio-UFMG.

Conflicts of interest

The authors declare no conflicts of interest.

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