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Diversity of Tiphiidae (Insecta: Hymenoptera) in the fragmented Brazilian semi-deciduous Atlantic Forest

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Abstract The Atlantic Forest is one of the most important areas of biodiversity in the world, but it has been largely replaced with agropastoral areas and at the present only 12.5 % of the original cover remains. Despite the ecological importance of insects, few studies have been used in conservation approaches for the Atlantic Forest, mainly due to a great taxonomic impediment. A group quite ecologically important but deeply neglected includes parasitoid wasps that control a great number of invertebrates, like tiphiid wasps that are parasitoids of underground coleopteran larvae. The present study aimed to estimate Tiphiidae species richness and diversity in 15 patches of a highly fragmented Atlantic Forest region, using factors that drive the diversity pool from a metacommunity, such as immigration and speciation probabilities. The parameters were estimated using the Neutral Biodiversity Theory, which is based on the total ecological equivalence of species at the same trophic level. Diversity values were molded to the area size, the immigration probabilities, and/or the speciation probability. Eight genera and 460 individuals of Thynninae, Myzininae and Tiphiinae were collected. Variation in species richness, estimated by both rarefaction and first-order jackknife methods, was explained by patch size and by immigration and speciation probabilities. These variables also explained the variation in Shannon diversity and species evenness. Variations in species richness and diversity of Tiphiidae are strongly associated with neutral processes, but they are also influenced by forest fragmentation and intensive agricultural activities.

Introduction

The Atlantic Forest is the second largest forest biome in South America (Ribeiro et al. 2009, 2011), and it is considered a hotspot of biodiversity since Meyer (1988), who first defined and described ten tropical forests as hotspots. Nowadays, 35 biodiversity conservation hotspots are recognized and the Atlantic forest is one of the most species rich areas on the planet (Ribeiro et al. 2011). The original cover of this biome was approximately 150 million hectares under highly heterogeneous environmental conditions, encompassing different habitats including deciduous and rain forests, mangroves, swamps, sand vegetation (*restingas*), inselbergs, high-altitude grasslands (*campo rupestre and campo de altitude*), and mixed Araucaria pine forests (Scarano 2002; Câmara 2003 in Ribeiro et al. 2011). However, currently, only 12.5 % of the original cover remains (Fundação SOS Mata Atlântica and INPE 2002, 2014; Ribeiro et al. 2009).

Massive areas of Atlantic Forest are being reduced to an archipelago of small, widely separated forest fragments (Ranta et al. 1998), with approximately 97 % of Atlantic Forest fragments having areas smaller than 250 ha (Ribeiro et al. 2009). Despite a dramatic reduction in Atlantic Forest deforestation since 2008, more than 60,000 ha were lost

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between 2010 and 2013 (Fundação SOS Mata Atlântica and INPE 2014). The main cause of Atlantic Forest deforestation is agricultural expansion (Dean 1997), as in other tropical forests worldwide (Kaimowitz and Angelsen 1998; Sodhi et al. 2004; Pirard and Treyer 2010; Kissinger et al. 2012; Adu et al. 2012; FAO 2014). The resultant agro-mosaics now represent the predominant landscape type in formerly forested lands across the world (Sodhi et al. 2004; Tabarelli et al. 2010).

Forest fragmentation may be understood based on the basic conceptual model provided by island biogeography theory although this model has limitations and it cannot explain the dynamic that is greatly amplified in fragmented habitats (Haila 2002; Laurance 2008; Mendenhall et al. 2014). The island biogeography theory explains variation in species richness as a balance between immigration and extinction rates (MacArthur and Wilson 1963, 1967; Schoener 2010), which are also key components of the unified neutral theory of biodiversity and biogeography proposed by Hubbell (1997, 2001). The neutral theory treats the organisms of the same trophic level from a metacommunity[1] as essentially identical in their individual probability of birth and death, immigration and speciation (Hubbell 2001; Mangel 2002; Bell 2001; Chave 2004). In addition, the neutral theory assumes that species are under no differential selection pressures (Hubbell 2001; Hubbell and Lake 2003), which means that species do not have different competitive ability and the diversity of a meta-community is given stochastically by immigration, speci-ation, birth and death (Hubbell 2001; Mangel 2002; Chave 2004; Economo and Keitt 2008; Rosindell et al. 2011, 2012; Matthews and Whittaker 2014). Furthermore, it can robustly encompass the predictions of island biogeography theory, like species-area relationships (Rosindell et al. 2011).

The ratio between local births and immigration has an effect (decreasing or increasing) on the number of species coexisting in disturbed communities, which is important for ecosystem management and conservation (Dornelas 2010), whereas disturbance can increase the extinction rate and favor the dominance by a single species (Gardner and Engelhardt 2008). In this way, the neutral theory can be extended to explain patterns of species responses to dis-turbance (Kadmon and Benjamini 2006). The application of this theory in conservation approaches has the advan-tages of not requiring species-specific details, which are often lacking, and the inclusion of more intrinsic biological information linked to relative abundances rather than the extrapolation of species-area relationships (Rosindell et al. 2012).

A great number of species remain unknown to science, especially those from hotspot biomes (Joppa et al. 2011) such as the Atlantic Forest. The insect fauna is a good example of that, despite of recent efforts to characterize it, our knowledge on its diversity remains incipient (Lewin-sohn and Prado 2002; Lewinsohn et al. 2005; Rafael et al. 2009; Diniz-Filho et al. 2010) and many groups, such as the Tiphiidae wasps (Genise and Kimsey 1991; Kimsey 1991, 1992), have been neglected (Marinoni and Peixoto 2010). Tiphiidae is a cosmopolitan and diverse family (Pate 1947) of solitary and fossorial ectoparasitoid wasps of soil-dwelling beetle larvae (Brothers and Finnamore 1995; Pate 1947; Potter and Rogers 2008). The family includes more than 1500 described species representing 120 genera (Brown 2005). In Brazil, 102 species representing 19 genera have been described (Justino and Santos 2016). Tiphiidae wasps are mentioned as flower visitors and may be involved in pollination (Kevan 1973); furthermore, some species of Thynninae in Australia have a strong relationship with orchids as showed by Alcock (2000), Brown (1998), Handel and Peakall (1993), Mant et al. (2002, 2005), Peakall and Beattie (1996), Peakall et al. (2010) and Stoutamire (1983). Santos and Brandão (2011) and Santos et al. (2014) carried out the first characteriza-tions of Tiphiidae diversity in the Atlantic Rain Forest, but the tiphiid fauna of Atlantic Semi-deciduous Forest is as yet largely unknown. Recent collections in patches of Semi-deciduous Forest have resulted in new records (Jus-tino et al. 2013).

Regarding all of the aspects presented above, the present study aimed to answer the following questions: (1) How diverse is the Tiphiidae fauna in the Atlantic Semi-decid-uous Forest? (2) Are the species richness and diversity of Tiphiidae affected by fragmentation of the Atlantic Forest fragmentation ? (3) Is the metacommunity structure of Tiphiidae driven by stochastic processes that underpin the unified neutral theory of biodiversity and biogeography, such as immigration and speciation?

Materials and methods

Study area and collection methodology

The present study was conducted in 15 forest fragments of different sizes (Table 1) from northwestern São Paulo State (Fig. 1). The landscape in this region consists of an agri-cultural matrix, which includes cane, citrus and coffee crops, and pasture (Table 1). Forest patches in northwest-ern São Paulo have been characterized as Semi-deciduous Seasonal Forest with different stages of ecological suc-cession (Necchi Jr. et al. 2012). The climate in the region is defined as Temperate, with two distinct seasons (i.e., dry

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[1] Metacommunity consists of all trophically similar individuals and species in a regional collection of local communities.

Table 1 Characteristics of the study area forest fragments: geographic coordinates, total size and surrounding matrix

Area	Latitude	Longitude	Size (ha)	Surrounding matrix
Barretos	20°29′05″S	48°49′21″W	885.5	Pasture/sugarcane crops
Bebedouro	20°53′06″S	48°32′26″W	397	Pasture/sugarcane crops
Macaubal	20°44′34″S	49°55′45″W	66.8	Pasture/sugarcane crops
Magda	20°28′25″S	50°17′36″W	1656.2	Pasture/sugarcane crops
Matão	21°37′14″S	48°32′14″W	2189.6	Citrus crops/coffee crops
Novo Horizonte	21°31′15″S	49°17′41″W	635	Sugarcane crops
Palestina	20°17′18″S	49°30′01″W	116.3	Sugarcane crops
Planalto	21°00′05″S	49°58′26″W	207.5	Pasture/sugarcane crops
Pindorama	21°13′12″S	48°55′04″W	107.8	Pasture
Sales	21°24′17″S	49°30′01″W	1799.6	Pasture/sugarcane crops
Taquaritinga	21°24′08″S	48°41′14″W	55.6	Citrus crops
Turmalina	20°00′13″S	50°26′02″W	108.3	Pasture
União Paulista	20°55′16″S	49°55′34″W	230.4	Pasture/sugarcane crops
Vicentinópolis	20°55′34″S	50°20′55″W	128.2	Pasture/sugarcane crops
Votuporanga	20°30′52″S	50°05′12″W	112.6	Pasture/sugarcane crops

Fig. 1 Study area showing the locations of the 15 semi-deciduous forest patches. The *lower left panel* shows South America; *circles within the boxed region* represent the semi-deciduous forest patches. The *upper right panel* shows São Paulo state and the locations of the 15 semi-deciduous forest patches. The *gray lines* represent rivers

winters and rainy hot summers), and temperatures higher than 22 °C (Peel et al. 2007).

The Tiphiidae fauna was sampled using a standardized sampling protocol that included placing two Malaise traps in each fragment from June of 2007 to November of 2009 (Table 1) totaling 60 samples from each fragment (30 days per trap). Bottles used in the Malaise traps were filled with 70 % alcohol and some drops of detergent to break the surface tension. The first trap was placed inside the patch 50 m from the edge, whereas the second trap was placed 50 m from the first, 100 m from the patch's edge. All of the specimens were pinned for identification by specialists and later deposited in the Hymenoptera collection of the Instituto de Biociências, Letras e Ciências Exatas da

Universidade Estadual Paulista "Júlio de Mesquita Filho", Brazil. The number of specimens and species collected were counted for each sample and in total.

Data analyses

To describe the spatial variation in tiphiid diversity in the fragmented Atlantic Forest, some traditional parameters were estimated for each forest patch. Species richness was estimated by rarefaction and first-order jackknife methods, species evenness was estimated using Pielou's index (J'), and species diversity was estimated using the Shannon index (H'). The Shannon index (Log base = 2), was chosen because it incorporates both species richness and evenness, and due to this it is possible to understand the influence of these two components on the species diversity. In addition, parameters of the neutral theory (Hubbell 2001), such as the Biodiversity Fundamental Number (θ, see Hubbell (2001) for details), immigration probability (m) (probability of the individual immigrating from a metacommunity, see Hubbell (2001) for details), and point-mutation peciation probability (v) [probability of a new species arising in the local community, using the simplest speciation model, see Hubbell (2001), Etienne et al. (2007) and Kopp (2010) for more information], were estimated for each fragment using the classic neutral model that is characterized as being spatially implicit, since the exact spatial location of each individual was not considered (see Etienne and Olff 2005; He 2005; Etienne 2005; Rosindell et al. 2011, for details). The relationships of the parameter estimates with patch size were modeled using simple and multiple Generalized Additive Mixed Models (GAMMs). In the multiple models, m and v were treated as explanatory variables on a logarithmic scale. In addition, to model the variation in θ, species richness and evenness were regarded as explanatory variables. Spatial correlation was included in all of the models, testing the five most used correlation structures: exponential, gaussian, linear, spherical, and rational quadratic. Moreover, the type of surrounding matrix was regarded as a random effect in all the models, i.e. possible influences of the surrounding matrix were eliminated to have more control on the relationships between the dependent and independent variables.

All of the statistical analyses were performed using the packages *vegan* version 2.2-1 (Oksanen et al. 2015), *untb* version 1.7-2 (Hankin 2015), *mgcv* version 1.8-4 (Wood 2014), and *nlme* (Pinheiro et al. 2015) for the program R version 3.0.1 (R Development Core Team 2013).

Results

In total, 460 individuals were collected in the 15 sampled fragments. They were from eight genera, 14 morphospecies and three subfamilies: Myzininae, Tiphiinae and Thynninae. Myzininae contains the third largest number of genera in the Tiphiidae (Kimsey 1991), Tiphiinae has a worldwide distribution (Allen 1972), Thynninae is distributed in the Neotropics and Australasia (Kimsey 1992, 2004) and is the largest subfamily in terms of the numbers of genera and species (Kimsey 1991).

The most abundant genus was *Scotaena* Klug (Thynninae), with 240 specimens collected. *Upa* Kimsey (Thynninae) and *Myzinum* Latreille (Myzininae) were the richest genera, represented by three species and morphospecies, respectively. Thynninae was the family with the most genera and species collected: *Aelurus brasilianus* Kimsey; *Eucyrtothynnus* Turner, *Rostrynnus tarsatus* Klug; *Scotaena* Klug, with possibly two different species; and three species of *Upa* Kimsey: *U. nasuta* Kimsey 1996, *U. porteri* Kimsey 1996, *U. tridentata* Kimsey 1996. Only one individual of *Eucyrtothynnus* was collected in União Paulista, and only one individual of *Rostrynnus tarsatus* was collected in Sales. (Online Resource 1).

The rarefied species richness (RSR) was strongly related to the patch size and the immigration (m) and speciation (v) probabilities (Table 2; Fig. 2). Based on the Akaike Information Criterion (AIC), the best-fitting model for the total species richness (TSR), as estimated by the first order jackknife, included only m as an explanatory variable. In contrast, the ANOVA that was applied to this model and to the second best-fitting model, which includes the area, m and v, indicated no differences between them (*Likelihood Ratio* = 5.541; $P = 0.236$), and due to this the most complete model (tsr ~ area + log(m) + log(v)) was preferred, since it explained almost 89 % of the variation in the TSR (Table 2; Fig. 2).

Similar results were obtained from modeling the variation in Shannon diversity (H'). The model with the lowest AIC included only m and v (Table 2), but ANOVA revealed no significant difference between this model and the most complete one, that include area, m, and v as explanatory variables (*Likelihood Ratio* = 0.8477; $P = 0.6545$). Moreover, the most complete and second-best-fitting model explained more of the variation in H' (92.2 %) than did the best-fitting model (83.7 %), and because of this the most complete model was preferred (Fig. 3). For species evenness, the model that included both m and v best explained 79.9 % of the variation in this parameter (Table 2; Fig. 3). Additionally, the Fundamental Biodiversity Number (θ) was best modeled by the combination of patch size, species richness, species evenness, and immigration probability (Table 2; Fig. 4). Variation in the immigration and speciation probabilities was unrelated to the patch size variation (Table 2). The choice of the best-fitting spatial correlation structure was based solely on the AIC values (Online Resource 2).

Table 2 Diagnostic parameters of models explaining variations in species richness, diversity, and evenness (J'); immigration probability (m); and speciation probability (v)

RV ~ EVs	R^2	DF	Estimate	P	Random effect Intercept (residual)	Spatial correlation	AIC
RSR ~ s(Area) + te(log[m]) + te(log[v])	0.986	10	Intercept: 2.507; s(Area): 4.596; te(log[m]): 2.901; te(log[v]): 3.168	Intercept: <0.001*; s(Area): 0.006*; te(log[m]): <0.001*; te(log[v]): 0.005*	7.77×10^{-85} (0.100)	0.2206	33.163
RSR ~ s(Area) + te(log[m])	0.968	11	Intercept: 2.507; s(Area): 25.59; te(log[m]): 304.66	Intercept: <0.001*; s(Area): <0.001*; te(log[m]): <0.001*	8.30×10^{-18} (0.163)	0.0935	41.476
RRSR ~ s(Area) + te(log[v])	0.551	11	Intercept: 2.508; s(Area): 1.000; te(log[v]): 2.919	Intercept: <0.001*; s(Area): 0.631; te(log[v]): 0.0074*	1.87×10^{-13} (0.654)	0.0935	51.552
RSR ~ te(log[m]) + te(log[v])	0.775	11	Intercept: 2.508; te(log[m]): 1.000; te(log[v]): 1.988	Intercept: <0.001*; te(log[m]): <0.001*; te(log[v]): 0.0204*	6.07×10^{-6} (0.468)	0.0004	37.836
RSR ~ s(Area)	−0.024	12	Intercept: 2.310; s(Area): 1.000	Intercept: <0.001*; s(Area): 0.274	4.91×10^{-7} (1.033)	0.1914	54.508
RSR ~ te(log[m])	0.613	12	Intercept: 2.508; te(log[m]): 1.000	Intercept: <0.001*; te(log[m]): <0.001*	1.27×10^{-14} (0.640)	0.0938	41.194
RSR ~ te(log[v])	0.59	12	Intercept: 2.471; te(log[v]): 3.124	Intercept: <0.001*; te(log[v]): 0.006*	1.40×10^{-5} (0.657)	0.1260	47.768
TSR ~ te(Area) + te(log[m]) + te(log[v])	0.872	10	Intercept: 4.342; te(Area): 2.494; te(log[m]): 3.856; te(log[v]): 1.000	Intercept: <0.001*; te(Area): 0.029*; te(log[m]): <0.001*; te(log[v]): 0.002*	4.54×10^{-7} (0.660)	8.803×10^{-5}	71.467
TSR ~ te(Area) + te(log[m])	0.391	11	Intercept: 4.104; te(Area): 1.000; te(log[m]): 1.764	Intercept: <0.001*; te(Area): 0.094; te(log[m]): 0.058*	1.83×10^{-6} (1.458)	0.1777	70.076
TSR ~ te(Area) + te(log[v])	0.239	11	Intercept: 3.999; te(Area): 1.000; te(log[v]): 1.461	Intercept: <0.001; te(Area): 0.075; te(log[v]): 0.190	3.53×10^{-5} (1.619)	0.1903	72.179
TSR ~ te(log[m]) + te(log[v])	0.394	11	Interept: 4.187; te(log[m]): 1.881; te(log[v]): 1.000	Intercept: <0.001*; te(log[m]): 0.091; te(log[v]): 0.396	1.95×10^{-7} (1.523)	0.1481	72.487

Table 2 continued

RV ~ EVs	R^2	DF	Estimate	P	Random effect Intercept (residual)	Spatial correlation	AIC
TSR ~ te(Area)	0.093	12	Intercept: 3.755 te(Area): 1.000	Intercept: <0.001* te(Area): 0.020*	2.26×10^{-7} (1.886)	0.7541	70.337
TSR ~ te(log[m])	0.423	12	Intercept: 4.178 te(log[m]): 2.023	Intercept: <0.001* te(log[m]): 0.019*	3.35×10^{-5} (1.550)	0.1532	69.009
TSR ~ te(log[v])	0.218	12	Intercept: 4.072 te(log[v]): 1.400	Intercept: <0.001* te(log[v]): 0.096	4.18×10^{-5} (1.805)	0.1715	71.704
J ~ s(Area) + te(log[m]) + te(log[v])	0.749	10	Intercept: 0.563 s(Area): 1.000 te(log[m]): 1.000 te(log[v]): 2.162	Intercept: <0.001* s(Area): 0.035* te(log[m]): 0.016* te(log[v]): <0.001*	4.96×10^{-8} (0.142)	0.2869	1.840
J ~ s(Area) + te(log[m])	0.115	11	Intercept: 0.544 s(Area): 1.000 te(log[m]): 1.000	Intercept: <0.001* s(Area): 0.822 te(log[m]): 0.050●	2.82×10^{-19} (0.288)	0.511	19.646
J ~ s(Area) + te(log[v])	0.726	11	Intercept: 0.545 s(Area): 1.000 te(log[v]): 1.620	Intercept: <0.001* s(Area): 0.133 te(log[v]): <0.001*	1.99×10^{-6} (0.154)	0.203	2.213
J ~ te(log[m]) + te(log[v])	0.799	11	Intercept: 0.544 te(log[m]): 2.103 te(log[v]): 1.000	Intercept: <0.001* te(log[m]): 0.044* te(log[v]): <0.001*	2.08×10^{-9} (0.132)	0.266	0.086
J ~ s(Area)	−0.073	12	Intercept: 0.270 s(Area): 1.000	Intercept: <0.001* s(Area): 0.834	2.63×10^{-16} (0.321)	0.093	20.435
J' ~ te(log[m])	0.184	12	Intercept: 0.543 te(log[m]): 1.000	Intercept: <0.001* te(log[m]): 0.051	1.21×10^{-10} (0.280)	0.081	16.275
J' ~ te(log[v])	0.720	12	Intercept: 0.544 te(log[v]): 1.424	Intercept: <0.001* te(log[v]): <0.001*	1.90×10^{-6} (0.164)	0.105	0.567
H' ~ s(Area) + te(log[m]) + te(log[v])	0.922	10	Intercept: 0.324 s(Area): 3.248 te(log[m]): 1.000 te(log[v]): 2.446	Intercept: <0.001* s(Area): 0.033* te(log[m]): <0.001* te(log[v]): <0.001*	6.72×10^{-7} (0.052)	0.001	−11.448
H' ~ s(Area) + te(log[m])	0.579	11	Intercept: 0.324 s(Area): 1.000 te(log[m]): 1.000	Intercept: <0.001* s(Area): 0.789 te(log[m]): <0.001*	6.62×10^{-21} (0.130)	0.094	−2.667
H' ~ s(Area) + te(log[v])	0.411	11	Intercept: 0.324 s(Area): 1.000 te(log[v]): 1.000	Intercept: <0.001* s(Area): 0.955 te(log[v]): 0.0034*	1.80×10^{-16} (0.154)	0.094	2.370

Table 2 continued

RV ~ EVs	R^2	DF	Estimate	P	Random effect Intercept (residual)	Spatial correlation	AIC
$H' \sim te(\log[m]) + te(\log[v])$	0.837	11	Intercept: 0.324 $te(\log[m])$: 1.000 $te(\log[v])$: 2.108	Intercept: <0.001* $te(\log[m])$: <0.001* $te(\log[v])$: 0.002*	7.46×10^{-10} (0.080)	0.094	−14.603
$H' \sim s(\text{Area})$	−0.048	12	Intercept: 0.324 $s(\text{Area})$: 1.000	Intercept: <0.001* $s(\text{Area})$: 0.543	2.54×10^{-14} (0.213)	0.093	7.901
$H' \sim te(\log[m])$	0.609	12	Intercept: 0.324 $te(\log[m])$: 1.000	Intercept: <0.001* $te(\log[m])$: <0.001*	3.09×10^{-7} (0.130)	8.00×10^{-7}	−6.587
$H' \sim te(\log[v])$	0.456	12	Intercept: 0.305 $te(\log[v])$: 1.000	Intercept: <0.001* $te(\log[v])$: 0.003*	2.06×10^{-9} (0.155)	0.175	−2.285
$\theta \sim s(\text{Area}) + s(\text{RSR}) + te(J') + te(\log[m])$	0.996	9	Intercept: 1.007 $s(\text{Area})$: 5.256 $s(\text{RSR})$: 0.998 $te(J')$: 3.842 $te(\log[m])$: 0.994	Intercept: <0.001* $s(\text{Area})$: <0.001* $s(\text{RSR})$: <0.001* $te(J')$: <0.001* $te(\log[m])$: <0.001*	4.24×10^{-18} (0.034)	0.093	4.595
$\theta \sim s(\text{Area}) + s(\text{RSR}) + te(J')$	0.621	10	Intercept: 1.012 $s(\text{Area})$: 1.000 $s(\text{RSR})$: 1.000 $te(J')$: 1.000	Intercept: <0.001* $s(\text{Area})$: 0.041* $s(\text{RSR})$: <0.004* $te(J')$: 0.231	1.67×10^{-10} (0.486)	0.494	29.229
$\theta \sim s(\text{Area}) + s(\text{RSR}) + te(\log[m])$	0.959	10	Intercept:1.007 $s(\text{Area})$: 4.628 $s(\text{RSR})$: 1.001 $te(\log[m])$: 1.000	Intercept: <0.001* $s(\text{Area})$: <0.001* $s(\text{RSR})$: <0.001* $te(\log[m])$: <0.001*	2.49×10^{-14} (0.128)	0.093	18.322
$\theta \sim s(\text{Area}) + te(J') + te(\log[m])$	0.483	10	Intercept: 0.926 $s(\text{Area})$: 1.000 $te(J')$: 1.000 $te(\log[m])$: 1.000	Intercept: <0.001* $s(\text{Area})$: 0.081* $te(J')$: 0.001 $te(\log[m])$: 0.566	4.23×10^{-8} (0.430)	0.658	34.653
$\theta \sim s(\text{RSR}) + te(J') + te(\log[m])$	0.795	10	Intercept: 1.008 $s(\text{RSR})$: 1.000 $te(J')$: 2.999 $te(\log[m])$: 1.000	Intercept: <0.001* $s(\text{RSR})$: <0.001* $te(J')$: 0.100 $te(\log[m])$: 0.038*	6.12×10^{-11} (0.299)	0.168	29.845
$\theta \sim s(\text{Area}) + s(\text{RSR})$	0.588	11	Intercept: 1.045 $s(\text{Area})$: 1.000 $s(\text{RSR})$: 1.000	Intercept: <0.001* $s(\text{Area})$: 0.080 $s(\text{RSR})$: <0.001*	2.53×10^{-5} (0.540)	0.5291	26.821

Table 2 continued

RV ~ EVs	R^2	DF	Estimate	P	Random effect Intercept (residual)	Spatial correlation	AIC
$\theta \sim s(\text{Area}) + te(J')$	0.541	11	Intercept: 0.941 s(Area): 1.000 te(J'): 1.000	Intercept: <0.001* s(Area): 0.009* te(J'): <0.001*	3.55×10^{-9} (0.431)	0.625	31.000
$\theta \sim s(\text{Area}) + te(\log[m])$	0.131	11	Intercept: 0.942 s(Area): 1.000 te(log[m]): 1.000	Intercept: <0.001* s(Area): 0.086 te(log[m]): 0.231*	2.40×10^{-8} (0.646)	0.453	42.799
$\theta \sim s(\text{RRSR}) + te(J')$	0.575	11	Intercept: 1.029 s(RSR): 1.000 te(J'): 1.000	Intercept: 0.0013* s(RSR): 0.002* te(J'): 0.634*	2.75×10^{-12} (0.598)	0.526	30.029
$\theta \sim s(\text{RSR}) + te(\log[m])$	0.678	11	Intercept: 1.005 s(RSR): 1.000 te(log[m]): 1.000	Intercept: <0.001* s(RSR): <0.001* te(log[m]): 0.040*	1.14×10^{-10} (0.448)	0.421	25.771
$\theta \sim te(J') + te(\log[m])$	0.430	11	Intercept: 0.963 te(J'): 1.000 te(log[m]): 1.000	Intercept: <0.001 te(J'): 0.005* te(log[m]): 0.841	1.82×10^{-12} (0.503)	0.174	36.865
$\theta \sim s(\text{Area})$	0.065	12	Intercept: 0.912 s(Area): 1.000	Intercept: <0.001* s(Area): 0.091	1.66×10^{-8} (0.670)	0.187	41.588
$\theta \sim s(\text{RSR})$	0.581	12	Intercept: 1.040 s(RSR): 1.000	Intercept: 0.001* s(RSR): <0.001*	2.01×10^{-7} (0.600)	0.523	26.283
$\theta \sim te(J')$	0.470	12	Intercept: 0.959 te(J'): 1.000	Intercept: <0.001* te(J'): 0.001*	2.34×10^{-8} (0.505)	0.1770	32.909
$\theta \sim te(\log[m])$	0.104	12	Intercept: 0.967 te(log[m]): 1.000	Intercept: <0.001* te(log[m]): 0.119	4.30×10^{-12} (0.668)	0.2593	41.702
$\log[m] \sim s(\text{Area})$	−0.053	12	Intercept: −1.639 s(Area): 1.000	Intercept: <0.001* s(Area): 0.523	9.66×10^{-7} (1.158)	0.1613	58.645
$\log[v] \sim s(\text{Area})$	−0.010	12	Intercept: s(Area): 1.104	Intercept: s(Area): 0.312	2.69×10^{-14} (2.614)	0.5517	81.549

RV = response variable; Evs = explanatory variables; RSR = rarefied species richness; TSR = total species richness; RSR = rarefied species richness (estimated by first-order jackknife); H' = species diversity as estimated by the Shannon index; θ = biodiversity fundamental number; Area = patch size; log[m] = immigration probability on a logarithmic scale; log[m] = speciation probability on a logarithmic scale; s = smoothing term for GAMM; te = smoothing full tensor for GAMM

Discussion

The present study explored the variation in species richness and diversity as a function of patch size and variables that can be influenced by forest fragmentation, such as m and v. The immigration rate is regulated by a neutral speciation-extinction process, whereas the probability of speciation reflects the rate at which a new species arises per individual propagation event (Hubbell 2001; Economo and Keitt 2008). Most studies based on neutral theory involve simulations, and few include empirical data.

In the present study, the sampled species richness (RSR) as estimated by rarefaction showed greater variation with respect to patch size, whereas the total species richness (TSR), as estimated by the first order jackknife, was more sensitive to m and v than to patch size. Some studies have demonstrated that v and the dispersal distance affect species-area relationships (Durrett and Levin 1996; Zillio et al. 2005; Rosindell et al. 2011; Campos et al. 2012). Rosindell et al. (2011) proposed that m is related to the mean dispersal distance, and Campos et al. (2012) noted that species-area relationships are less sensitive to v in more fragmented habitats, suggesting that ecological drift is the mechanism underlying the generation of biodiversity in such habitats. According to Hubbell (2001), a community under ecological drift without immigration should gradually lose species over time because of local extinction.

One of the most recognized diversity patterns in ecology is that larger habitats support more species than do smaller ones (Rosenzweig 1995; Connor and McCoy 2001). However, the largest area of the present study presented a very low RSR, whereas some of the smaller areas showed high RSR and TSR values (Fig. 2). In contrast, the largest area showed a high TSR. Some studies have recorded an inverse relationship between species richness and the area of the forest fragment for different taxa (Carvalho and Vasconcelos 1999; Gascon et al. 1999; Ewers et al. 2007; Zipkin et al. 2009). Didham et al. (1998a, b) reported that the observed species richness and abundance of beetles (which are hosts to tiphiids) are equally high in small and large fragments and that they increase towards the forest edge, although rarefied species richness remains constant following fragmentation. Lövei et al. (2006) also found an inverse relationship between the species richness of beetles and forest area as a result of the edge effect. Didham et al. (1998a) noted that the edge effect on the species richness of beetles depends on individual density. Many parasitoids also show host density dependence, affecting their spatial distributions (May et al. 1981; Walde and Murdoch 1988; Rohani and Miramontes 1995; Hassell 2000). Price (1991) noted that host–parasitoid specificity is related to forest complexity, concluding that several species of idiobiont parasitoid per individual host can be found in forests of greater structural complexity because such forests can support a greater diversity of generalist species and impart stronger host density dependence, as is observed at forest edges compared to the forest core (Yahner 1988).

The positive consequences of the edge effect for community structure, including species richness, have been observed for different taxa (Carvalho and Vasconcelos 1999; Harper et al. 2005; Ewers et al. 2007; Zipkin et al. 2009). Consequently, the high species richness observed in some small fragments in the present study could be a result of the edge effect, as smaller forest patches suffer more from edge effects because of the higher ratio of edge per unit area (Didham et al. 1998a, b; Barbosa and Marquet 2002; Ewers et al. 2007). Edge effects are important drivers of change in many fragmented landscapes and depend on several abiotic and biotic factors that can be combined in different ways, characterizing the forest edge as an environment that is highly variable in space and time (Laurance et al. 2007).

In contrast, the low RSR observed in the largest area may be the result of pesticide application. This area is surrounded by a matrix that includes citrus and coffee crops, which commonly receive extensive applications of insecticides due to the large numbers of pests (Moguel and Toledo 1999; Belasque Jr. et al. 2010; Soares et al. 2013). Several studies have demonstrated that the use of such pesticides significantly reduces the regional biodiversity of invertebrates in natural ecosystems (Berendse et al. 2004; Beketov et al. 2013; Goulson 2013). In northwestern São Paulo State, insecticides are sprayed by airplanes, which can enlarge their area of action and strongly affect nearby natural ecosystems. In contrast, biological control has been used in sugarcane crops with desired efficiency and no negative impact in areas nearby (Parra 2014). Therefore, the low RSR observed in the largest area of the present study is potentially the effect of pesticide application in the surrounding matrix, although we do not have direct evidences for this. Clearly, this aspect should be considered in future studies.

The relationship between species diversity and area was similar to that observed between RSR and area, whereas species evenness showed a slight inverse linear relationship with area, decreasing with increasing area (Fig. 3). Considering that the Shannon index incorporates both species richness and evenness (Magurran 2004; Gotelli and Chao 2013), our results suggest that the faunistic heterogeneity in the study area is established primarily by the species richness. Metzger (1997) verified that species richness in the Semi-deciduous Atlantic Forest was correlated with fragment shape and connectivity, whereas species evenness was highly related to landscape composition and to the
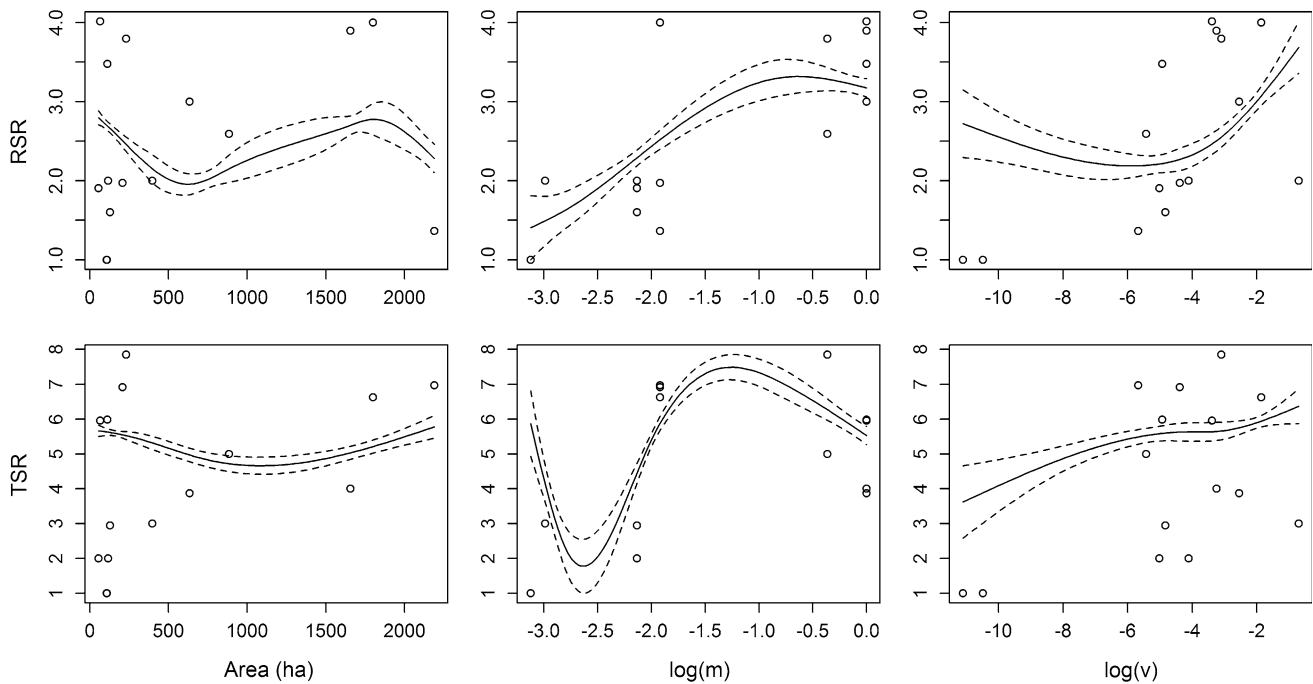
Fig. 2 Relationships of both sampled species richness (RSR) as estimated by rarefaction and the total species richness (TSR) as estimated by the first order Jackknife with patch size, log(immigration probability) and log(speciation probability)
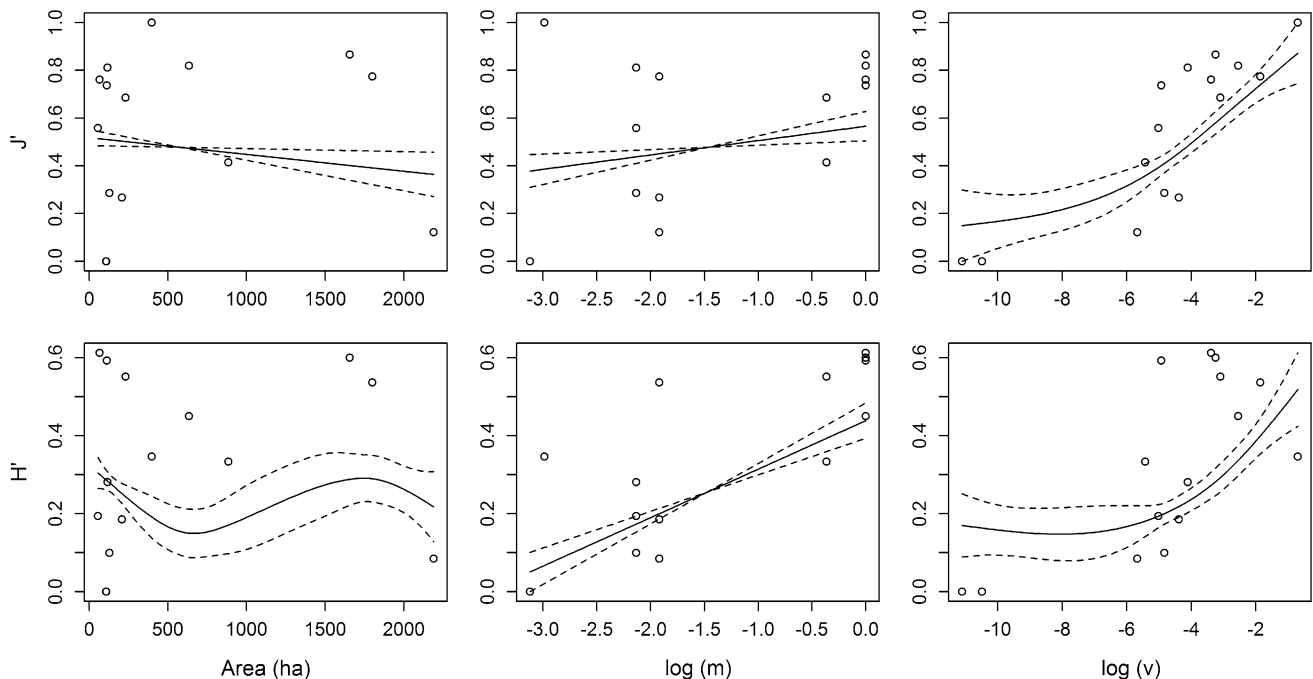

Fig. 3 Relationships of species evenness as estimated by Pielou's index and diversity as estimated by the Shannon index with patch size, log(immigration probability), and log(speciation probability)

spatial arrangement of forests, primarily the boundary complexity, and corridor and small patch (up to 0.72 ha) densities. Corridors are a significant component of effective biodiversity conservation systems, promoting the

connectivity among fragments and allowing species immigration among formerly isolated patches (Mech and Hallett 2001; Tewksbury et al. 2002; Ayres et al. 2005; Rouget et al. 2006; Santos et al. 2008; Gilbert-Norton et al.
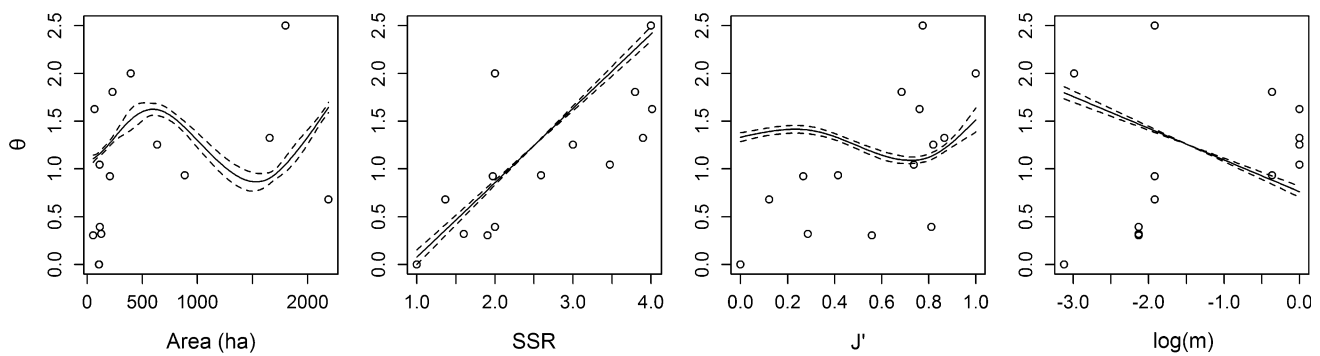
Fig. 4 Relationships of fundamental biodiversity number (θ) with patch size (Area), sampled species richness (RSR), log(immigration rate) and species evenness

2010; Tabarelli et al. 2010). Forest reduction has more dramatic consequences at high species dominance, decreasing it and altering the coexistence of species, so that species richness in an area increases with evenness whereas species dominance reduces the number of species (He and Legendre 2002; Green and Ostling 2003; Hillebrand et al. 2008). Pereira et al. (2007) also found an increase in species evenness of plants with increasing severity of Atlantic Forest fragmentation. The relationship between species evenness of Tiphiidae and habitat fragmentation is conditioned by the immigration and, mainly, speciation probabilities (Table 2). This result corroborates the correlation between species evenness and corridor density found by Metzger (1997). High evenness arising from anthropogenic pressure will affect the magnitude and importance of intra-versus interspecific interactions as well as community dynamics or processes that depend on the distribution traits in a community (Hillebrand et al. 2008).

Species evenness shows non-linear relationships between the Biodiversity Fundamental Number (θ) and area (Fig. 4). Moreover, based on the present results, θ is strongly and positively influenced by species richness and shows an inverse correlation with m. Even the largest area with low RSR showed relatively high values of θ, whereas the smaller areas with relatively high RSRs presented low θ under the influence of m and species evenness. According to Hubbell (2001), θ is determined as a function of community size and v and represents the equilibrium between species richness and relative species abundance in a metacommunity. When individuals in a local community die, they are immediately replaced by offspring of other local individuals or by immigrants from the regional species pool, and the replacement probability by an immigrant is proportional to the abundance of each species in the metacommunity (Etienne and Olff 2005). Wilson and Hassell (1997) noted that the demographic stochasticity of host–parasitoid populations, as predicted by the neutral theory and incorporated in θ, is established because slower

dispersing parasitoids are unable to fix themselves in one precise location related to the host population; therefore, they go extinct because recolonization is unlikely, particularly when the metacommunity includes spatially isolated populations.

In the spatially implicit model, the diversity of a metacommunity is largely controlled by θ, whereas the diversity of a local community is controlled by θ, the local community size, and the immigration rate (Economo and Keitt 2008). Menz et al. (2013) verified that the more abundant and widespread species of Thynninae show shorter migration distances than do the less abundant and widespread species. The integrated use of the neutral and niche perspectives has been suggested as the best way to understand metacommunity dynamics (Leibold and McPeek 2006; Rosindell et al. 2012; Matthews and Whittaker 2014).

Wilson and Hassell (1997) described three stochastic factors that can influence the spatial dynamics of parasitoid metacommunities: (1) random dispersal by individuals, (2) random host encountering within a patch, and (3) a random number of individuals emerging from each host. These influences correspond to those predicted by the neutral theory. The random number of parasitoids emerging from each host and generation is inherent to the biology of the parasitoid species, and host encounters depend on random dispersal, as highlighted by Wilson and Hassell (1997). Dispersal rates are influenced by the proximity of localities, and spatial interactions between hosts and parasitoids assume a complete mixing of the dispersing individuals of both populations (parasitoid and host) such that the local instability of the host–parasitoid associations is established by asynchrony in extinctions and colonizations (Hassell 2000). The probability of extinction is directly linked with the relationship between hosts and parasitoids and distribution of the hosts among the patches (Comins et al. 1992). Concerning colonization, Elzinga et al. (2007) verified that colonization capacity is positively correlated with foraging

distance. According to Hawkins and Gross (1992), parasitoids of root feeders, such as species of Tiphiidae, show a low colonization rate compared to species that attack more exposed herbivorous hosts.

Phillips et al. (2010) and Menz et al. (2013) verified that Thynninae males, the most representative group in the present study, undergo short foraging distances in response to sexually deceptive plant species. Females of this subfamily are wingless and spend much of their time underground (Ridsdill Smith 1970a, b; Osten 1999), and their mobility over long distances likely depends on the flying males, which transport and feed females during coupling (Ridsdill Smith 1970a; Osten 1999). As a result, the dispersal rate of Thynninae is correlated with and regulated by the food resources provided by flowers and the density of beetle larvae (Osten 1999; Menz et al. 2013). Moreover, the dispersal rate can be influenced by relationships with sexually deceptive plants, as observed in some Australian thynnines (Ridsdill Smith 1970a; Phillips et al. 2010; Menz et al. 2013).

In conclusion, the local species richness and diversity of the Tiphiidae in the fragmented Atlantic Semi-deciduous Forest of northwestern São Paulo State are, on average, slightly lower than the Atlantic Rain Forest's fauna, which was studied by Santos et al. (2014). Besides that, both species richness and diversity of Tiphiidae are strongly influenced by neutral processes as well as forest fragmentation and intensive agricultural activities. However, the spatial structure of the metacommunity is partially eroded due to fragmentation and patch isolation, which hamper individual dispersal. The use of corridors connecting fragments could potentially increase the dispersal rates of both hosts and parasitoids and consequently allow a stronger influence of stochasticity on habitat dynamics. Ecological corridors have been proposed as a key component of conservation planning as they can help maintain important ecological processes that play essential roles in biodiversity (Rouget et al. 2006). One of the main difficulties in the implementation of ecological corridors is that forest fragments often occur within private landholdings (Tabarelli et al. 2004; Rouget et al. 2006; Ribeiro et al. 2009), such that corridor implementation depends on agreements among landholders (Margules and Pressey 2000; Rouget et al. 2006). Our results show the importance of conservation of the remaining areas of Atlantic Forest that even in regions where the fragmentation level is high it concentrates a great diversity of species that are barely known. Most modern conservation strategies require the management of entire landscapes, including areas that are allocated to both production and protection (Margules and Pressey 2000; Shackelford et al. 2015). As discussed above Tiphiidae wasps can show close and important relationship with plants and other insects. Improving the knowledge in the richness and diversity of these wasps is essential to guarantee and help the conservation of the Atlantic Forest.

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