Small-scale area effect on species richness and nesting occupancy of cavity-nesting bees and wasps

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ABSTRACT**.** Small-scale area effect on species richness and nesting occupancy of cavity-nesting bees and wasps. The research was conducted in an urban forest remnant in southeast Brazil. We tested the predictions of the following hypotheses: (1) larger areas present higher species richness of bees and wasps, (2) solitary bees and wasps occupy more nests in larger areas, (3) rare species occupy more nests in smaller areas. We sampled Aculeate bees and wasps using trap nests from February to November 2004. We placed trap nests in sampling units (SU) with different size (25, 100 and 400 m^2) located in 6 ha of secondary mesophytic forest. One hundred and thirty-seven trap nests were occupied by seven species of bees and four species of wasps. We found an increase in wasp, but not bee species richness following increase in SU size. Hymenoptera richness (*i.e.* bees plus wasps) was also greater in larger SU. Both the number and density of occupied nests increased with SU size. The wasp *Trypoxylon lactitarse* responded significantly to area size, larger SU having more occupied nests. The same pattern was exhibited by the wasp *Auplopus militaris*, the *Megachile* bee species, and the bee *Anthodioctes megachiloides*. Only *Trypoxylon* sp. was not affected by SU size. Our results show that cavity-nesting bee and wasps respond differently to the area effects. Such findings must be complemented by information on the frequency and dynamics of area colonization and nest occupancy by species of solitary Hymenoptera.

KEYWORDS. Aculeata; Brazil; forest remnant; solitary bee and wasps; trap-nests.

RESUMO. Efeito de área em pequena escala sobre a riqueza e comportamento de nidificação de abelhas e vespas solitárias. Este trabalho foi realizado em fragmento florestal urbano localizado na região sudeste do Brasil. Foram testadas as predições das seguintes hipóteses: (1) áreas maiores apresentam maior riqueza de espécies de abelhas e vespas que nidificam em cavidades pré-existentes, (2) espécies de abelhas e vespas que nidificam em cavidades pré-existentes ocupam mais ninhos em áreas maiores, (3) espécies raras ocupam mais ninhos em áreas menores. Estes insetos foram amostrados por meio de ninhos-armadilha de fevereiro a novembro de 2004. As armadilhas foram dispostas em unidades amostrais com diferentes tamanhos (25, 100 e 400 m^2), alocadas em um fragmento de floresta mesofítica de 6 ha. Cento e trinta e sete armadilhas foram ocupadas por sete espécies de abelhas e quatro espécies de vespa. Observamos um aumento na riqueza de vespas associado a uma maior área amostral; não observamos o mesmo para abelhas. A riqueza de espécies de Hymenoptera (abelhas e vespas, em conjunto) foi maior em áreas maiores. Tanto a abundância quanto a densidade de ninhos ocupados por abelhas e vespas aumentou com o aumento da unidade amostral. *Trypoxylon lactitarse* ocorreu mais frequentemente em áreas maiores. O mesmo padrão foi observado para *Auplopus militaris*, espécies do gênero *Megachile* e *Anthodioctes megachiloides*. Apenas *Trypoxylon* sp. não foi afetada pelo tamanho da unidade amostral. Os resultados do estudo mostram que abelhas e vespas solitárias respondem de maneira diferente ao tamanho de área. O entendimento dessas relações deve ser complementado por informações sobre a frequência e dinâmica de ocupação de ninhos e colonização de áreas por abelhas e vespas solitárias.

PALAVRAS-CHAVE. Abelhas e vespas solitárias; Aculeata; Brasil; fragmento florestal; ninho-armadilha.

Increasing species richness with increasing area of investigation is one of the most confirmed generalizations in Ecology (Schoener 1976; Lawton 1999; Lomolino 2000). Numerous studies describe and interpret the underlying mechanisms of species–area relationships for different taxa, and for scales ranging from local forest remnants to the entire Globe (Connor & McCoy 1979; Williamson 1988; Rosenzweig 1995; Drakare *et al.* 2006).

Positive species-area relationships are commonly observed in the field. Two explanations for such positive response include the habitat diversity hypothesis (Rosenzweig 1995) and the hypothesis of demographic colonization-extinction dynamics (MacArthur & Wilson 1967). Species-area relationships have been used to compare species-richness values of different areas and extrapolating species richness (*e.g.* Colwell & Coddington 1994), and for producing biodiversity maps (*e.g.* Kier *et al.* 2005). They have also been applied in the context of conservation biogeography for identifying hotspots for species richness (*e.g.* Fattorini 2007), for systematic conservation planning (*e.g.* Desmet & Cowling 2004), for predicting species loss after habitat destruction (*e.g.* Ulrich 2005) and for evaluating human impacts on biodiversity (*e.g.* Tittensor *et al.* 2007).

As the number of species, the population density of animals can also increase with the size of a particular area. However, there are few studies on this aspect of insect population (Connor *et al.* 2000; Julião *et al.* 2004). Few authors examined simultaneously the area and habitat fragmentation effects on different taxonomic groups (Robinson *et al.* 1992). Others focused on vertebrates such as large mammals (Peacock & Smith 1997) and birds (Schmiegelow *et al.* 1997), and only few were targeted at invertebrates, in particular to butterflies (Cappuccino & Martin 1997; Sutcliffe *et al.* 1997). Small-scale experimental studies on the area effect on less conspicuous animals are still more scarce (but see Zschokke *et al.* 2000; Gonzalez & Chaneton 2002; Braschler *et al.* 2003).

Given that habitat fragmentation does not affect every species on a similar way (Davies *et al.* 2000; Becker *et al.* 2010), it can alter community structure and important ecological processes, such as predation and pollination, which can suffer considerable disturbances. Further, it is known that species at high trophic levels, mutualists, habitat specialists and host plants are likely to go extinct first from the diminishing size of the habitat (Holt *et al.* 1999; Rathcke & Jules 1993; Steffan-Dewenter & Tscharntke 2002). This assumes particular importance for cavity-nesting bees and wasps given that how pollinators, predators and parasitoids (the major functional groups these insects fit in) respond to area size is still obscure (Didham *et al.* 1996; Harrison & Bruna 1999; Debinski & Holt 2000) as well as our knowledge on how this component of insect diversity respond to such habitat alterations (but see Morato & Campos 2000; Steffan-Dewenter 2002; Loyola & Martins 2006, 2008, 2009).

Here we investigate the effects of area size, at a local scale, on the species richness, as well as in the number and density of occupied nests in a mosaic area composed by Atlantic Forest remnants surrounded by a matrix of cerrado vegetation. In particular, we tested the predictions of the following hypotheses, related to area effects and passive sampling: (1) larger areas present higher species richness of solitary bees and wasps, (2) larger areas present a higher number of nests occupied by these species, and (3) rare species occupy a higher number of nests in smaller areas.

MATERIAL AND METHODS

Study Area. We conducted the study in a protected area at the Federal University of Minas Gerais, Belo Horizonte, Brazil (19°52'S, 43°58'W), from February to November 2004. In the region there are two well-defined seasons: the cold dry season receiving less than 50 mm mean monthly rainfall (April through September), with temperatures ranging from 19 to 21°C; and the hot rainy season receiving 300 mm mean monthly rainfall (October-March), with mean temperature of 23.9°C. The area has been protected since 1969, and has several types of vegetation, including cerrado, and swamps at an altitude of 830 m a.s.l. (Martins & Antonini 1994; Loyola & Martins 2006). Nesting activity of solitary bees and wasps in Brazil is higher in the wet season.

Experimental design. Trap-nests have been widely used to sample solitary bees and wasps (Krombein 1967). Their use improves biological data acquisition on species that build their nests on pre-existing cavities (Koerber & Medler 1958). Some studies used these species to evaluate the impact of parasite action (Scott *et al.* 2000) and also to describe nest building process and structure (Camillo *et al.* 1993; Pereira *et al.* 1999; Alves dos Santos *et al.* 2002; Loyola & Martins 2006).

For this study, we placed trap nests in nine 25–400 m^2 square sampling units (henceforth SU, fig. 1 in Loyola & Martins 2008). Distribution of SU (treatments) in the study area followed a Latin Square design with three treatments (25, 100, and 400 m^2) each replicated three times (see Loyola & Martins 2008). In such sampling design the comparisons between lines and columns are orthogonal among them and also to the treatment, *i.e.*, the comparisons between lines and columns are independent (Underwood 1997; Krebs 1998). We established SU in a 6 ha of secondary mesophytic forest, where trees are medium to large in size, reaching less than 25 m. We defined a minimum distance of 25 m from any SU, in every direction.

Trap nests were made from compact wood and wooden sticks, measuring 25×25×130 mm and 11 cm-deep canals with 6, 9, and 12 mm diameters. We arranged ten sticks of wood from each canal diameter to form a trap nest block, totaling 30 trap nests per nest block. We placed each block on a compound structure made of a 1.5 m pole, to which a platform was fixed at 1.4 m above the ground. We then placed five of these blocks in each of the SU: one in the center and the others at each square corner. Hence, we placed 150 trap nests in each SU, making a total of available 1350 nesting sites in the study area.

We inspected trap nests bi-weekly; collected those occupied by bees or wasps, took them to the laboratory, and replaced them by empty ones to keep the number of empty traps constant. In the laboratory, we placed nests individually in small tulle meshes, keeping adults until hatching. Adults were pinned and identified to species or genus (morphospecies).

Statistical analysis. We applied Analysis of Variance (ANOVA) to evaluate the area effect on mean species richness and the mean number and density (i.e., number of nest per unit area) of occupied nests by solitary bees and wasps. We excluded all species that did not occupy a minimum of ten nests during the study period. We grouped the species of the *Megaliche* genus for the analysis due to their observed common characteristics, such as nest building material, inside nest architecture and providing used material. Further, there is an inherent difficulty of species identification in this genus.

We tested ANOVA residuals for normality (Kolmogorov–Smirnov test) and for homogeneity of variance (Levene test). We used SYSTAT 10.2 (SYSTAT Software Inc. 2002) for statistical analysis, and established the $\alpha = 0.05$ significance level for all probability analyses.

RESULTS

Four wasp and seven bee species occupied a total of 137 trap nests (see Loyola & Martins 2006, for details). Wasps occupied the majority of nests (n = 103, 75%). The remaining trap nests (n = 34, 25%) were occupied by bees. Wasp species were *Auplopus militaris* (Lynch-Arribalzaga 1873) (n = 53 occupied nests), *Trypoxylon (Trypargilum) lactitarse* Saussure (n = 25), *Trypoxylon* sp. (n = 21), Sphecidae sp. (n = 4). Bees were *Megachile (Ptilosarus) bertonii* Schrottky, 1908 (n = 6), *Megachile (Austromegachile) corona* Mitchell, 1930 (n = 4), *Megachile (Pseudocentron)* sp. (n = 3), *Anthodioctes megachiloides* Holmberg, 1903 (n = 10), *Centris (Hemisiella) tarsata* Smith, 1874 (n = 8), *Xylocopa* sp. (n = 2) and *Tetrapedia* sp. (n = 1). Sampling effort was suitable for the study area (see Loyola & Martins 2008). During the study period, none of the trap nests were occupied by two or more species, and nesting frequency over the year showed consistent patterns associated to each species (Loyola & Martins 2006).

We found an increase in wasp, but not in bee species richness following the increase of SU size (Table I). Hymenoptera richness (*i.e.* bees plus wasps) was also greater in larger SU. Both the number and density of nests occupied by bees and wasp also increased with SU size (Table II). *Trypoxylon lactitarse* responded significantly to area size, larger SU having more occupied nests (Table III). The same pattern was exhibited by *A. militaris,* the *Megachile* species, and *A. megachiloides*. Only *Trypoxylon* sp. did not respond to SU variation in size.

Table I. The effect of area size on species richness of cavity-nesting bees, wasps and both groups pooled together (i.e. Hymenoptera) during the study period. Degrees of freedom = df, sum of squares = SS, mean square, i.e. variance = MS. *F-ratio* is the ratio between the variance explained by the effect (area, in this case) and the unexplained variance (residual), thus $F = MS_{area}/MS_{residual}$. *P* is the probability of obtaining the observed result if the null hypothesis is considered true.

Source of variation	df	SS	MS	*F-ratio*	*P*
Wasp species richness					
Area	2	1.626	0.813	4.528	0.021
Residual	24	4.310	0.180		
Bee species richness					
Area	2	6.000	3.000	1.200	0.319
Residual	24	60.000	2.500		
Hymenoptera species richness					
Area	2	24.666	12.333	11.385	<0.001
Residual	24	26.000	1.083		

Table II. The effect of area size on the number and density of nests occupied by bees and wasps analyzed together during the study period. Degrees of freedom = df; sum of squares = SS; mean square, i.e. variance = MS. *F-ratio* is the ratio between the variance explained by the effect (area, in this case) and the unexplained variance (residual), thus $F = MS_{area}/MS_{residual}$. *P* is the probability of obtaining observed result if the null hypothesis is considered true.

Source of variation	df	SS	MS	*F-ratio*	*P*
Number of nests					
Area	2	972.667	486.333	7.984	0.002
Residual	24	1462.000	60.917		
Density of nests					
Area	2	1.270	0.635	34.770	<0.001
Residual	24	0.438	0.018		

Table III. The effect of area size on the number of nests occupied by the four most abundant Aculeate species during the study period. Degrees of freedom = df, sum of squares = SS, mean square, i.e. variance = MS. *F-ratio* is the ratio between the variance explained by the effect (area, in this case) and the unexplained variance (residual), thus $F = MS_{area}/MS_{residual}$. *P* is the probability of obtaining the observed result if the null hypothesis is considered true.

Source of variation	df	SS	MS	*F-ratio*	*P*
Trypoxylon (Trypargilum) lactitarse					
Area	2	4.427	2.213	5.090	0.014
Residual	24	10.436	0.435		
Trypoxylon (Trypargilum) sp.					
Area	2	2.186	1.093	2.751	0.084
Residual	24	9.540	0.397		
Auplopus militaris					
Area	2	170.667	85.333	6.282	0.006
Residual	24	326.000	13.583		
Megachile spp.					
Area	2	5.210	2.605	13.404	<0.001
Residual	24	4.665	0.194		
Anthodioctes megachiloides					
Area	2	18.667	9.333	4.870	0.017
Residual	24	46.000	1.917		

DISCUSSION

We showed that cavity-nesting bees and wasps respond differently to the area effect. A lack of a clear pattern could arise from different sources. First, the species-area relationship on impacted urban habitats can be altered and larger fragments do not necessarily present a higher species number, as observed for social bees (Antonini *et al.* 2000). On the other hand, the higher wasp species richness found in the larger SU confirmed that larger areas present higher wasp species richness. Similar results were found in a study comparing forested areas to forest remnants varying from 1 to 10 ha (Morato & Campos 2000). Recently, we have also shown that communities of cavity-nesting bees and wasps respond strongly to vegetation structure at a local scale and that the heterogeneity of particular habitat structure components within a given area effectively predicts cavity-nesting Hymenoptera diversity (Loyola & Martins 2008, 2009).

Second, Lomolino (2000) points out that in islands with reduced area (up to 40 ha) it is common to observe the absence of species-area relationship, the so-called “small island effects”. These effects occur in small islands where available resource level is not enough to maintain populations of most species. In these islands, habitat characteristics, stochastic disturbances, isolation, and interspecific interactions are also likely to determine how many and which species could maintain their populations (Lomolino 2000). Following this reasoning, every area size (latin squares) used in our study, would be too small to allow for a clear species-area relationship, of course. It is curious, however, that wasps in general and that certain wasps and bees species, when analyzed separately, showed a clear response to SU size. Therefore, we may assume that even at a small scale (including experimental areas) the species-area relationship still holds true, although it also depends on the particular species traits, taxonomic group and occurring habitat. Other experimental studies on the small-scale effects of habitat fragmentation have also observed this relationship for ants, butterflies, grasshoppers, gastropods, grass, forbs and vascular plants analyzed as a group (see Zschokke *et al.* 2000).

Nonetheless, the absence of a clear response by bees is a puzzle. In Central Amazon, bee species richness increased with area size, even in remnants smaller than 40 ha (Morato & Campos 2000). Ribas *et al.* (2005) observed that the total number of species in many small remnants (varying from 3.21 ha to 5.56 ha) was not significantly different from the species number in a large remnant (30.13 ha). Results were different for crickets, which had higher species richness in smaller remnants (Ribas *et al.* 2005). These results show that area and habitat fragmentation effects could indeed be observed in different scales (Loyola *et al.* 2006; Loyola & Martins 2008), and that different taxonomic groups can show diverse responses.

Solitary bees and wasps also showed a positive abundance-area relationship in the studied area. Once again, Morato & Campos (2000) observed positive abundance-area relationships for solitary wasps and bees in forest fragment and continuous forest areas in Central Amazon. Increase in population density with increasing fragment size, were also reported for Coleoptera (Burke & Goulet 1998; Didham *et al.* 1998) and specialist Lepidoptera (Steffan-Dewenter & Tscharntke 2000). Plant underground biomass is also affected by the size of the experimental areas (Dolt *et al.* 2005). In another small-scale study Aphidae density was significantly higher in larger areas (Braschler *et al.* 2003), although the small-scale experimental area size had no effect on ant nest density, when species were analyzed separately, the area effect was significant for the specie *Lasius paralienus*.

Auplopus militaris is a common species in the fragment and shows restrict ecological tolerance, restricting its nest occupation to the forest interior (Zanette *et al.* 2004). It is expected that common species in the study area (such as those nesting all over the year) should occupy a greater number of nests in larger SU because, once their populations tend to be large or there is a generation overlapping, individuals can disperse their nests more effectively in space. Dispersion can be explained not only by the species behavior, but also because species is present during longer periods in its habitat. The results found for *A. militaris* clearly confirm this hypothesis, given that this species occupied a greater number of nests in larger SU and showed a balanced nesting frequency along the study period. Further, the species' response to increasing SU size corroborates the hypothesis that habitat specialists show more evident species-area relationships (Harrison & Bruna 1999; Holt *et al.* 1999). The above explanation is equally valid for *T. lactitarse*, which occupied a greater number of nests in larger SU being also common in the studied area. Note however that *T. lactitarse* is not a species with a restricted ecological tolerance and the absence of area effect on *Trypoxylon (Trypargilum)* sp. indicates that particular species respond differently to this factor.

We also found greater nest occupancy by species of *Megachile* in larger SU. According to the same idea illustrated for *A. militaris*, *Megachile* species also disperse their nests in a spatial-temporal pattern, due to their relative abundance in the studied area (Loyola & Martins 2006). Contrastingly, rare species presenting low frequencies of nest occupancy, or presenting population dynamics with peaks in particular periods of the year, concentrate their reproductive efforts in smaller areas and place their nests close to each other (Loyola & Martins 2006). We confirmed this prediction with the results obtained for *A. megachiloides*, although this species had low frequency of occurrence in the studied area, occupying a greater number of nests in smaller areas. Another *Anthodioctes* species, *A. moratoi* established a greater number of nests in larger areas (continuous forests) than in forest remnants in Central Amazon (Morato 2001).

Conservation of solitary bees and wasps aims to guarantee the maintenance of at least two fundamental ecological processes in ecosystems: pollination and predation. Further, understanding how these groups respond to area size is essential to support decisions related to species conservation and also of vital ecological processes to the ecosystems functioning. Such understanding must be obviously complemented by information on the frequency and dynamics of area colonization and nest occupancy by species of solitary bees and wasps.

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