ORIGINAL PAPER

Interactive effects of habitat fragmentation and microclimate on trap-nesting Hymenoptera and their trophic interactions in small secondary rainforest remnants

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Abstract The combined effects of habitat fragmentation and climate change on biodiversity and biotic interactions are poorly understood. In the context of ongoing deforestation and agricultural intensification in the tropics secondary rainforest fragments might contribute to biodiversity conservation and mitigation of climate warming. This study investigated the interactive effects of habitat fragmentation and microclimate on the abundance and biotic interactions of trap-nesting bees and wasps in secondary forest fragments in the northwestern lowlands of Costa Rica. Fragment size did not affect hymenopteran abundance, parasitism and mortality rates, but all variables differed between edge and interior locations in the forest fragments. Interactive effects between size and location indicate higher mortality rates at interior locations in larger fragments. Microclimatic differences at edge and interior locations led to significant effects on all tested response variables. Abundance at interior locations was significantly higher with increasing temperatures. Mortality rates at interior location increased at lower mean temperatures, whereas higher temperatures at edges marginally increased mortality rates. Our results indicate that edge effects, mediated by altered microclimatic conditions, significantly change biotic interactions of trap-nesting hymenopterans in small secondary fragments.

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Introduction

Different aspects of global environmental change endanger species persistence, alter species distributions and lead to changes in antagonistic and mutualistic interactions (Barlow et al. 2007), whereas logging of rainforests results in landscapes consisting of patchily distributed forest fragments in a matrix of pastures and plantations (Vitousek et al. 1997; Tilman et al. 2001). Deforestation and resulting fragmentation are regarded as a major threat to biodiversity (Davies et al. 2000; Fahrig 2003) due to habitat loss and edge effects and can result in reduced species richness, population declines (Donovan and Flather 2002), loss of genetic diversity (Gibbs 2001) and disruption of trophic interactions such as predation and parasitism (Turner 1996; Kruess and Tscharntke 2000; Laurance et al. 2002; Klein et al. 2006). Moreover regional estimates of extinctions from deforestation are probably worse than previously thought, because studies neglected extinction debts and assumed that persisting forest was contiguous (Hanski et al. 2013; Kuussaari et al. 2009).

In addition to fragmentation, climate change and consequent changes in microclimatic conditions can also affect insect communities. Species adapted to forest conditions and living in constant shade cannot easily adapt to higher temperatures and lower air moisture in open habitats and do not have many options to escape from rising temperatures (Deutsch et al. 2008; Ruibal 1961). This is especially true for lowland forest species of bees and wasps with narrow thermal optima (Deutsch et al. 2008; van Berkum 1988). The situation for them becomes even harsher when they are additionally confronted with habitat loss and fragmentation (Tewksbury et al. 2008). Until now only a few studies have investigated the influences and interactions of more than one threat (e.g. Gibson et al. 2013; Hill et al. 2006; Opdam and Wascher 2004).

Solitary bees and wasps colonizing trap nests have been used as bio-indicators, because they are sensitive to land use change and habitat fragmentation (Tscharntke et al. 1998; Klein et al. 2006; Tylianakis et al. 2006). Bees and wasps fulfill important tasks in ecosystem functions. Bees are the most important pollinator group of plants (Didham et al. 1996; Kremen et al. 2007) and wasps are important predators and parasitoids, with considerable economic and agricultural relevance (Penagos and Williams 1995; Tylianakis et al. 2005). Their variety of functional niches makes insects and other invertebrates important for the maintenance of vital ecosystem processes (Didham et al. 1996). In studies conducted in native Neotropical forests trap-nesting bees are considered more sensitive to habitat fragmentation, preferring continuous forest and natural gaps, whereas wasps seem to prefer small forest remnants and cleared areas (Morato and Campos 2000). Both groups depend on nesting sites (Potts et al. 2005), materials for nest constructions (Taki et al. 2008) and pollen or arthropod food resources (Tscharntke et al. 1998). The nesting frequencies of trap-nesting Hymenoptera are also known to respond to climate factors such as temperature, precipitation, humidity and sun-exposure (Thiele 2005).

Information on biodiversity of Hymenoptera in tropical rainforests is scarce, but there is even less knowledge of species interactions (Godfray et al. 1999). Trap nests are a valuable system to obtain information on biodiversity and abundance, but also on community

parameters such as mortality and parasitism rates (Tscharntke et al. 1998). Higher trophic levels, for example parasitoids, are more affected by drivers such as climate warming and higher temperatures or habitat modification (Thomson et al. 2001; Valladares et al. 2006; Fenoglio et al. 2012), due to a higher susceptibility of interactions to phenological de-synchronization and host population dynamics (Suttle et al. 2007).

There is much uncertainty about the combined effects of climate change (with resulting microclimatic changes) and habitat fragmentation on tropical forest organisms and their trophic interactions (Laurance et al. 2011; González-Varo et al. 2013; Wimp et al. 2011).

Secondary forest fragments and tree plantations can be important for biodiversity (Turner and Corlett 1996), as their coverage is rapidly expanding and protected areas are limited (Barlow et al. 2007). They can enhance landscape connectivity, but they are much more vulnerable than previously thought (Gibson et al. 2013). There is a lack of studies done inside tropical forests, since most studies have investigated influences of tropical forests in adjacent agro-ecosystems (Klein et al. 2002, 2006) or along land-use gradients (Tylianakis et al. 2005, 2006). There are very few reference studies conducted in tropical forest, such as those done in a dry forest in Costa Rica (Frankie et al. 1988) or in forest remnants in Brazil (Morato and Campos 2000). The conservation value of secondary forest fragments has rarely been addressed despite the probability that in many regions only these will remain for biodiversity conservation and maintenance of ecosystem services for agricultural areas.

In conclusion, there is a lack of studies investigating the possible interactive effects of habitat fragmentation and climate change on solitary hymenopterans and their trophic interactions in tropical secondary forest fragments. Therefore, we assessed the abundance and trophic interactions of trap-nesting Hymenoptera at three tree locations in different sized secondary forests in the Sarapiquí region of Costa Rica. This was done in order to answer the following questions:

(1) Does the abundance of solitary bees and wasps differ with the interactive effects of fragment size, tree location and temperature?
(2) How do parasitism- and mortality rates change with fragment size, tree location and temperature?
(3) What is the conservation value of secondary forest fragments for above-ground nesting Hymenoptera?

Materials and methods

Study region and study sites

This study was carried out during a 12 months period between February 2011 and February 2012 in the Sarapiquí region in Heredia province, Costa Rica in the vicinity of La Vírgen. The average annual temperature was 25.3 °C with an average annual precipitation of 3,777 mm. According to Holdridge life zone system, Sarapiquí belongs to the "tropical moist forest" (Holdridge 1967). The landscape consists mostly of forest remnants, cattle pastures and farmlands producing pineapple, ornamental plants and banana. In a region of ca 30 × 40 km, we selected twelve different sized forest fragments (average 5.4 ha ± 4.86; range 0.9–16.62 ha), at least 2 km between each, and a similar amount of forest (ap. 30 %) in a 2 km circle. The forest fragments consisted of secondary forest with no recent management activities and were located between 49 and 413 m above sea level.

Study design and sampling

In each of the 12 study sites 27 trap nests were placed. Three trees were selected along a transect line, one tree in the forest center, one at an intermediate distance and the last one at the forest edge. A package of three trap nests was installed at each of the three heights (2, 10, 20 m) on each tree. In total 324 trap nests were analyzed. Each trap nests consisted of a PVC tube filled with different diameters of about 120 reed internodes (*Phragmites australis*) cut to 20 cm length (Tscharntke et al. 1998). At 10 m height on every tree a temperature logger (iButton DS1921G-F5) was installed to measure the temperature every hour for the total sampling period. The mean temperature per tree was calculated for statistical analyses.

Occupied internodes, defined as those that were closed with soil or plant materials indicating completed nest construction (Krombein 1967), were replaced during regular inspections (1–2 months).

Occupied internodes were opened in the lab, nests were identified, brood cells were counted and parasitized and dead cells were noted to calculate parasitism and mortality rates. Nests were then placed in pieces of transparent plastic tube and closed with cotton at both ends. When the adults emerged, they were killed for later identification. All wasps, bees and parasitoids were at least identified to genus level.

Statistics

For every response variable (number of brood cells, mortality rate, parasitism rate) linear mixed effects models containing all interactions of fragment size, tree location and temperature were calculated with the statistical program R (R Development Core Team VS R 3.0.3). All models contained the random terms "fragment" and "height" to account for the nested design. The model, which explained most of the variance, was chosen according to the lowest AIC. A correction term for overdispersion was included in all final models.

As the response variable "number of brood cells" consisted of count data, a Poisson distribution was used. In the case of the parasitism and mortality rate linear models with binomial distribution were used (Crawley 2002).

We did not separate the data into functional groups, for example bees and wasps, as we were interested into the response of the trap-nesting community. However the separate analyses can be found in the supplementary material.

Results

Bees, wasps and natural enemies

During 12 months 22,101 brood cells were constructed by solitary bees and wasps. The community consisted of 38 hymenopteran genera comprising seven nonparasitic and two parasitic bee genera and 15 nonparasitic and 14 parasitic wasp genera (Table 1). The majority of brood cells (89.3 %) were constructed by wasps, whereas only 10.7 % were constructed by bees. In total 3,714 cells were attacked by natural enemies, and of these, 332 were bee cells (8.9 %) and 3,382 were wasp cells (91.1 %). In total 3,480 cells showed mortality due to other causes, and of these, 459 were bee cells (13.1 %) and 3,025 were wasp cells (86.9 %).

Table 1 Number of brood cells per location (tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center) of all genera or morpho-species

Species	Tree 1	Tree 2	Tree 3
Anthophoridae			
Centris labrosa	120	311	206
Centris analis	148	57	43
Aglaomelissa duckei	1	5	26
Megachilidae			
Megachile sp. 1	27	0	9
Megachile sp. 2	4	7	67
Megachile sp. 3	7	0	0
Megachile sp. 4	7	0	7
Duckeanthidium thielei	0	0	4
Anthodioctes gualanense	23	0	31
Coelioxys sp. 1	3	11	27
Coelioxys sp. 2	0	0	1
Coelioxys sp. 3	1	0	0
Coelioxys sp. 4	0	0	1
Coelioxys sp. 5	0	0	2
Colletidae			
Hylaeus sp. 1	20	9	89
Apidae			
Tetrapedia maura	107	4	17
Sphecidae			
Ampulex	2	6	8
Liris	3	47	78
Nitela	2	9	13
Penepodium	1	0	0
Pison	53	121	145
Podium	442	549	852
Trigonopsis	1	0	4
Trypoxylon	6,493	3,185	4,000
Pompilidae			
Ageniella	2	0	0
Auplopus	650	237	588
Dipogon	3	0	4
Priocnemella	49	28	35
Eumenidae			
Montezumia	14	0	2
Pachodynerus	40	50	105
Zethus	18	40	75
Chalcidoidae			
Brachymeria sp. 1	0	0	3
Leucospis sp. 1	15	5	23
Melittobia	179	48	40
Perilampidae sp. 1	1	1	0

Table 1 continued

Species	Tree 1	Tree 2	Tree 3
Chrysididae			
Caenochrysis	133	35	57
Chrysis	5	0	4
Exochrysis	22	22	33
Ipsiura	1	3	5
Neochrysis	15	0	3
Pleurochrysis	2	1	10
Ichneumonidae			
Ichneumonidae sp. 1	1	0	0
Ichneumonidae sp. 2	0	6	2
Ichneumonidae sp. 3	2	1	2
Ichneumonidae sp. 4	2	0	0
Ichneumonidae sp. 5	1	0	0
Mutillidae			
Spaeropthalmina	18	16	9
Coleoptera			
Tetraonyx sexguttata	12	7	8
Bruchidae	1	0	0
Dermestidae	16	1	0
Nitidulidae	0	0	1
Diptera			
Anthrax	15	5	11
Dolichopodidae	550	575	680
Sarcophagidae	37	9	13
Arachnida			
Acari	28	13	9
Lepidoptera			
Lepidoptera	14	5	9

Fragments and microclimate

We tested the effects of fragment size and tree location on the mean temperature. Mean site temperature did not vary with fragment size ($p = 0.654$), but did vary with tree location. At the inner trees, we found a significantly lower temperature (tree 2: $p < 0.001$, tree 3: $p < 0.001$) compared to trees at the edge.

Fragment size, tree location and temperature effects on abundances

Contrary to our expectations, fragment size alone had no influence on the abundance of bees and wasps ($p = 0.25$). However, fragment size did influence the number of brood cells in interaction with tree location (tree 2: $p < 0.001$, Fig. 1a; Table 2). The abundance at the intermediate tree was significantly lower in larger fragments compared to smaller ones, whereas abundance at the forest center and the edge increased slightly with larger fragment sizes. Furthermore, independent of fragment size, inner trees showed a lower
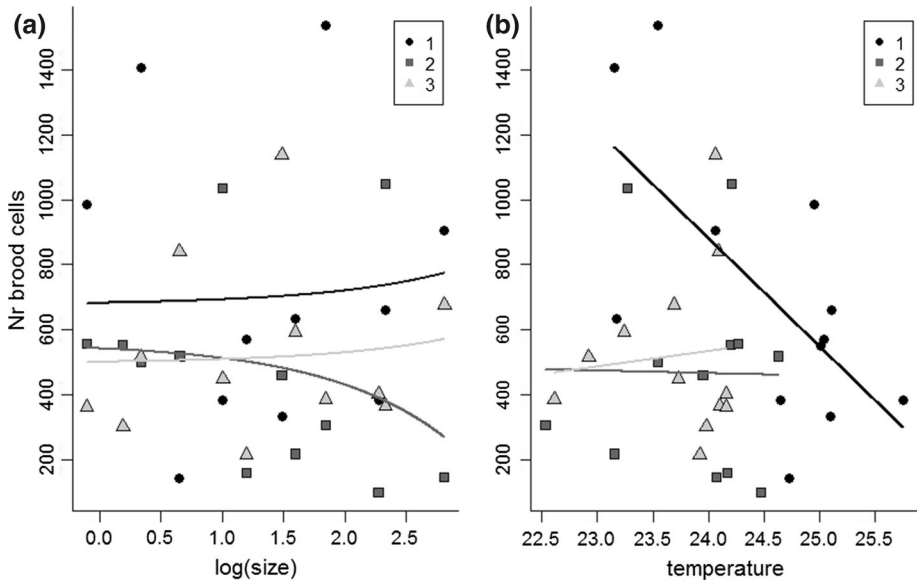
Fig. 1 Effects of **a** the interaction between size and location respectively **b** temperature and location on the abundance of trap-nesting hymenopterans (location: tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center)

abundance of hymenopterans (tree 2: $p = 0.0132$, tree 3: $p = 0.0042$) compared to the forest edge with a higher abundance.

A rise in temperature negatively affected the abundance of trap nesting hymenopterans ($p < 0.001$), but the influence of temperature also depended on tree location. The high abundance at the edge was negatively affected by a rise in temperature, whereas higher temperatures at the inner trees led to similar or slightly higher abundances (tree 2: $p = 0.014$, tree 3: $p = 0.005$, Fig. 1b).

Fragment size, tree location and temperature effects on mortality rates

Fragment size alone had no influence on mortality rates (Table 2). However, it was interesting that larger fragments had higher mortality rates inside the forest (tree 2: $p = 0.00317$, tree 3: $p = 0.00868$, Fig. 2a) compared to the forest border.

The mortality rates responded differently at edge and center locations. The negative slope of the mortality rates at both inner locations (tree 2 × temperature: $p = 0.025$, tree 3 × temperature: $p = 0.036$) with increasing temperature was significantly different from the slightly positive increase at edge trees (Fig. 2b).

Fragment size, tree location and temperature effects on parasitism rates

Parasitism rates varied between 2 and 28 % and did not increase with fragment size. However the parasitism rates depended on tree location since parasitism was higher at the intermediate locations compared to the forest edge and center (tree 2: $p < 0.001$, Table 2).

Moreover, we found that temperature affects parasitism rates differently at the tree locations. At the edge and the center the parasitism rates were not influenced by temperature, but increasing temperatures led to lower parasitism at intermediate trees (Fig. 3).

Table 2 Results of generalized linear mixed effects models relating hymenopteran abundance, mortality rate and parasitism rate to the explanatory variables fragment size, location (tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center) and temperature respectively their interactions

	Explanatory variables	z value	p value
Abundance	Size	1.163	0.244945
	Tree 2	−2.475	**0.013331***
	Tree 3	−2.845	**0.004439****
	Temperature	−3.439	**0.000585*****
	Size × tree 2	−4.64	**3.48e−06*****
	Size × tree 3	−0.364	0.716166
	Tree 2 × temperature	2.464	**0.013736***
	Tree 3 × temperature	2.774	**0.005535****
Mortality rate	Size	−0.87	0.38408
	Tree 2	2.126	**0.03351***
	Tree 3	1.993	**0.04629***
	Temperature	0.754	0.45097
	Size × tree 2	2.95	**0.00318****
	Size × tree 3	2.625	**0.00867****
	Tree 2 × temperature	−2.249	**0.02450***
	Tree 3 × temperature	−2.099	**0.03582***
Parasitism rate	Size	−0.393	0.694632
	Tree 2	3.354	**0.000796*****
	Tree 3	0.213	0.8312
	Temperature	−1.153	0.248861
	Size × tree 2	−3.117	**0.001827****
	Size × tree 3	−0.477	0.63337
	Tree 2 × temperature	−3.37	**0.000751*****
	Tree 3 × temperature	−0.248	0.803816
	Size × temperature	0.385	0.700339
	Tree 2 × size × temperature	3.113	**0.001854****
	Tree 3 × size × temperature	0.508	0.61126

Results of final models are shown *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

In addition we found interactive effects of size, location and temperature on parasitism rates (Fig. 4). Temperature did not influence the response of the parasitism rates to size at the edge and the forest center, but did so at the intermediate tree ($p = 0.002$). There, temperature changed the response direction of the parasitism rates to fragment sizes. With increasing fragment sizes parasitism rates decreased with temperatures in the lower and middle range, but increased strongly with higher temperatures.

Discussion

Bees, wasps and natural enemies

In this study the abundance and diversity of wasps in small secondary forest remnants was much higher than that of bees. Previous studies in the Central Amazon and Northern Brazil
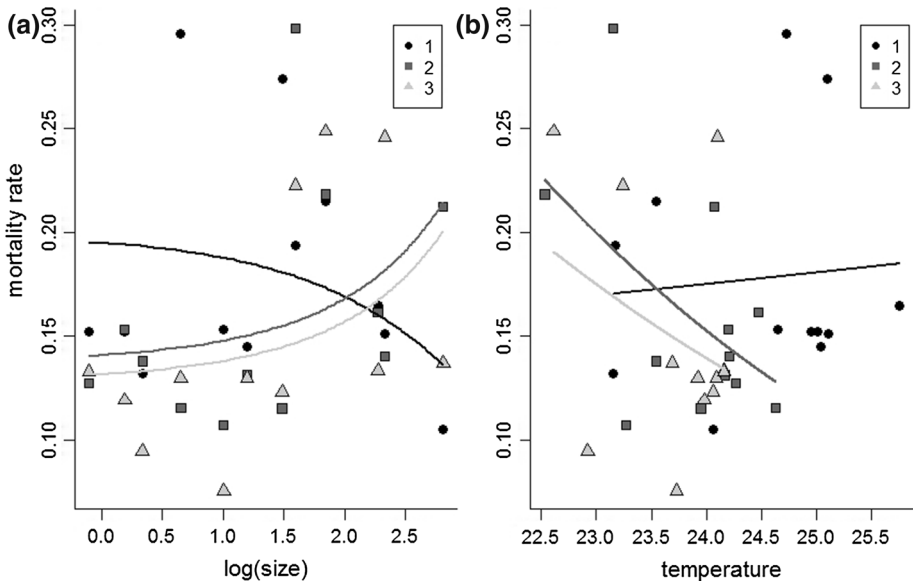
Fig. 2 Effects of **a** the interaction between size and location respectively **b** temperature and location on the mortality rate of trap-nesting hymenopterans (location: tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center)
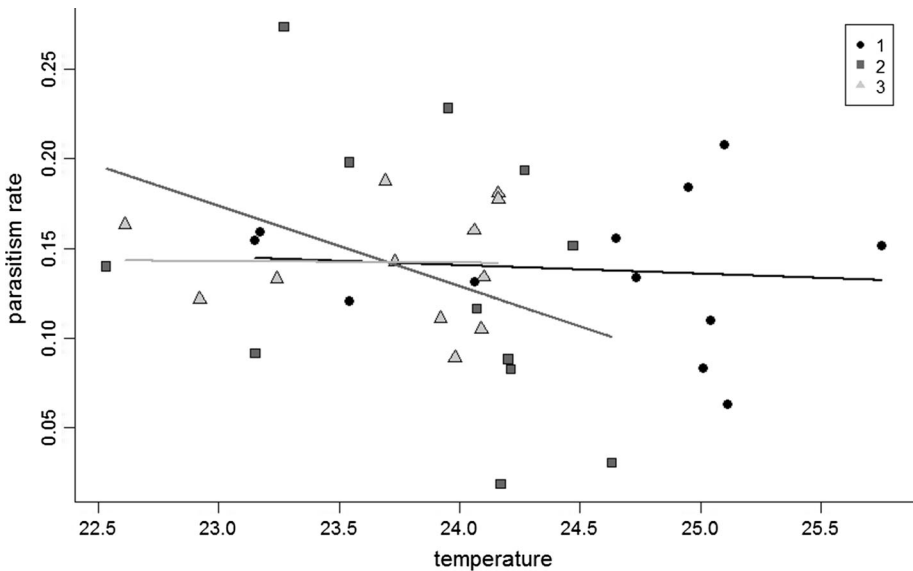
Fig. 3 Effects of temperature and location on the parasitism rate of trap-nesting hymenopterans (location: tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center)

(Batista Matos et al. 2013; Morato and Campos 2000) also found a higher abundance of wasps compared to bees. Bees seem to be more vulnerable to habitat fragmentation because they were more often found in continuous forests and natural gaps, whereas wasps
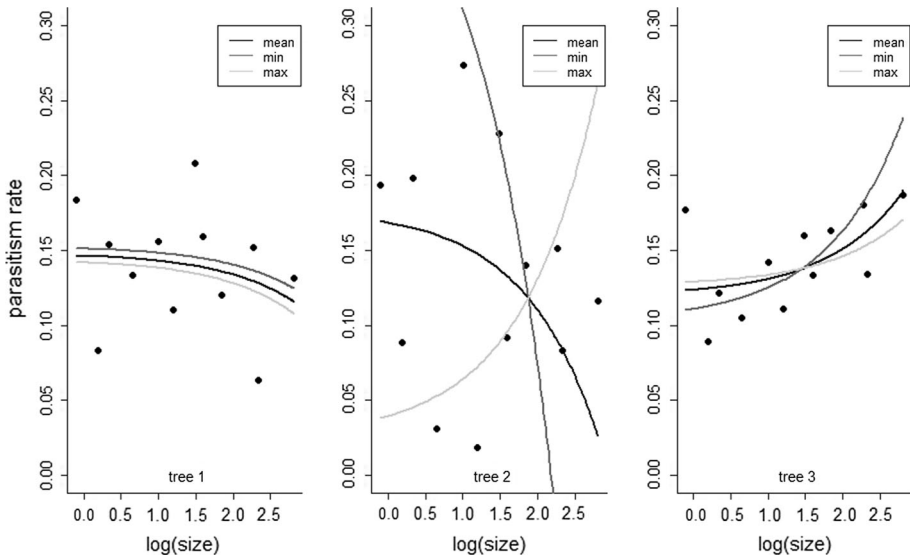
Fig. 4 Size effects on the parasitism rate for three different temperatures (mean, minimal and maximal temperature at the forest border (tree 1) at intermediate distance (tree 2) in the forest center (tree 3)

were more often found in small forest remnants and cleared areas (Morato and Campos 2000).

Fragments and microclimate

Temperatures were lower inside the forest when compared to the forest border and fragment size had no influence on the temperature.

Tree locations are partly characterized by temperature differences, making it difficult to strictly separate edge- and temperature effects. However other factors also characterize edge and center locations, such as light conditions, humidity, wind speed and interactions with other organisms (Ewers et al. 2007, 2009). Forest borders frequently have reduced humidity, increased light and greater temperature variability (Hunter 2002; Laurance and Williamson 2001; Saunders et al. 1991). But since temperature explained much of the variability in the models, we decided to include this important factor.

Fragment size, tree location and temperature effects on abundances

Fragment size did not have a significant influence on the hymenopteran abundance. Some studies have demonstrated that habitat loss leads to a loss of biodiversity (Debinski and Holt 2000), whereas patterns for abundance-area relationships are more variable (Connor et al. 2000). It could well be that more specialized and strict forest species have disappeared and have been replaced by species that profit from habitat edges (Connor et al. 2000; Laurance et al. 2002; Ewers et al. 2009). Species with small area requirements, which tolerate matrix and edge habitats are the least vulnerable (Gascon et al. 1999; Offerman et al. 1995), whereas forest-specialized bees and wasps are quite sensitive to environmental changes (Batista Matos et al. 2013). Therefore, small secondary forest remnants may already suffer from a reduction of forest specialists. For example, the vast

majority (approx. 50 %) of wasps belong to the genus *Trypoxylon,* a genus known to occupy trap nests in more open areas with lower tree circumference (Morato and Campos 2000; Tylianakis et al. 2005) and nearly all bees belong to the genus *Centris* (see Table 1). With a higher percentage of habitat generalists species interactions may already have changed and could have led to reduced pollination and higher herbivory rates through changes in the relative abundance of predators and parasitoids (Klein et al. 2006).

The abundance of bees and wasps was higher at the edge compared to the forest interior, probably because they obtain access to complementary resources such as nesting materials or nutrients (Ries and Sisk 2004) and probably profit from the higher light availability and the resulting greater cover of understory plants at the edge (Fye 1972). The higher hymenopteran abundance at the edge supports the hypothesis that species composition in our fragments shifted in favor of disturbance adapted species. The higher humidity and lower temperatures inside the forest can negatively influence the activity of bees and wasps because of their limited ability to thermoregulate (Loyola and Martins 2006).

Temperature was included in our analysis in order to investigate the combined effects of habitat fragmentation and climate change. Higher temperatures resulted in lower abundances, which may give cause for concern, that solitary bees and wasps will not only be harmed by habitat loss and fragmentation, but also by rising temperatures.

The influence of higher temperatures depended on the tree location. At the edge, where we found the highest abundance, higher temperatures had a highly negative impact on bees and wasps. Higher mean temperatures are correlated with higher fluctuations of temperatures at sites with direct sun expose, with temperature extremes above 40° and more intensive radiation (Murcia 1995). More thermo-sensitive bee and wasps species presumably cannot further compensate for such steep temperature fluctuations (Fye 1972). However, higher temperatures inside the forest led to an increased breeding activity of bees and wasps, presumably because bees and wasps try to avoid the high temperatures at the edge and nest inside the forest. At least wasps are known to markedly respond to relative humidity, which is related to temperature (Batista Matos et al. 2013).

With the highest abundance at the edge in small secondary fragments, a continued temperature rise will negatively influence trap-nesting bees and wasps in high temperature tropical lowland habitats, but it is not known to what extent even those hymenopterans adapted to disturbed conditions can compensate for projected climate warming (Buckley et al. 2013).

Fragment size, tree location and temperature effects on mortality rates

In addition to changes in abundance, changes in the mortality rate due to fragmentation or temperature effects could affect the persistence of trap-nesting hymenopterans in a changing environment. Our study showed that, within the range of our fragment sizes, there was no influence of size on the mortality rate.

The higher mortality rate at both inner trees in larger fragments and the lower mortality rate at the inner trees with higher temperatures could probably be explained through the fact that small fragments are more likely to be inhabited by disturbance adapted habitat generalists (Laurance et al. 2002). We found a high abundance at the edge, where species prefer dry conditions with more sunlight and are less adapted to humid and shady conditions, which are typically found in the center of larger fragments. They therefore respond with higher mortality rates due to, for example, mold infestation (personal observation).

Fragment size, tree location and temperature effects on parasitism rates

Higher trophic levels, for example parasitoids, experience fragmentation more severely than their hosts (Nouhuys 2005; Pimm and Lawton 1977; Ries and Sisk 2004; Tscharntke et al. 2005) and trophic interactions may be more susceptible to, for example, species abundances (Rand et al. 2006). Nevertheless there is a lack of studies investigating the combined effects of fragmentation and temperature on higher trophic levels and multi-trophic interactions (Wimp et al. 2011) in secondary rainforest fragments. With higher host abundances at edges, one could expect that the parasitism rates rise at the forest border. But curiously, parasitism rates were highest at the intermediate trees and highly variable when comparing the range of rates with the edge and center. So the question is why parasitoids cannot exploit the greater host abundance at the edge? Their high trophic position and specialization, e.g. their narrower niche, are a couple of reasons for their vulnerability (Holt et al. 1999). This could be a reason for the edge preference of hosts, since they find a lower risk of being parasitized here. Little is known about parasitoids in general and even less so in tropical rain forests, but it could well be, that they are less adaptable to the steeper temperature and humidity fluctuations nearer to the forest edge. Field data support this suggestion as parasitoids seem to be more sensitive to climatic variability than their hosts (Thomson and Hoffmann 2009) and are less able to disperse (Cornell and Hawkins 1993). But obviously one would then expect parasitoids to prefer the conditions in the forest center. A possible explanation for a higher parasitism rate at intermediate distances could be that these locations provide a compromise between climatic conditions and host abundance. This is further confirmed by our finding that at intermediate locations a rise in temperature significantly lowered the parasitism rate, presumably since parasitoids respond negatively to higher temperatures (Thomson et al. 2001). However, this pattern depended on fragment size, since the parasitism rate was lower at the intermediate trees in larger fragments compared to smaller ones. It was expected, that the parasitism rate would drop in smaller, not in larger fragments (Valladares et al. 2006). But this decrease only takes place at the intermediate locations, so that a probable explanation would be, that larger fragments support a higher percentage of specialized species in the center. Those species do not shift to the intermediate locations with more disturbed conditions, so that the parasitism rate in larger fragments is lower at the intermediate location compared to the smaller ones.

Parasitoids probably respond to smaller habitat size up to a certain critical threshold as shown by various studies (Nouhuys 2005; Pimm and Lawton 1977; Tscharntke et al. 2005). However, in our size range, this is apparently no longer true, perhaps because most of the more specialized parasitoids have already gone extinct. The results of our study are unable to document this possibility, this would be an interesting topic for future studies, since trophic interactions (such as parasitism) that involve negative feedbacks, are especially important due to their strong linkage to biodiversity, productivity and stability of ecosystems (Worm and Duffy 2003). Our results are quite worrying, because they imply that the community structure of hymenopterans is already highly altered and ecosystem functions could be harmed. This at least questions the conservation value of small secondary forest fragments, by themselves, for forest species of trap-nesting hymenopterans. For conservation a landscape-wide plan with key areas of undisturbed forests, high habitat heterogeneity and a permeable landscape (Opdam and Wascher 2004; Batista Matos et al. 2013) will probably be more valuable than the sole presence of small forest fragments.

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