

Effects of habitat fragmentation on trap-nesting bees, wasps and their natural enemies in small secondary rainforest fragments in Costa Rica



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„Wenn du lange genug in den Abgrund blickst, blickt der Abgrund auch in dich hinein.“

Friedrich Nietzsche

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Summary (English)

I. Human induced global change threatens biodiversity and trophic interactions. Fragmentation is considered as one of the major threats to biodiversity and can cause reduced species richness, population declines, loss of genetic diversity and disruption of trophic interactions such as predation and parasitism. However forest fragmentation effects can be eclectic due to species specific traits. Specialist species with narrower niches or at higher trophic levels may be in danger of extinction whereas generalist species with less specific habitat requirements may even profit from fragmentation. In the tropics, known as “the” terrestrial biodiversity hotspots, even biodiversity inventories are often lacking, especially in forest canopies. Ongoing deforestation and resulting fragmentation in tropical regions are expected to heavily affect ecosystem functions by changes in biodiversity, community compositions and disruption of trophic interactions. It is even less unknown in what extent different global change drivers for example climate change and fragmentation interact. It is unlikely that deforestation will end, so that small secondary forest fragments will be important habitat elements that must be investigated to optimize their potential contribution to biodiversity conservation.

This dissertation aimed to disentangle the effects of forest fragmentation on trap-nesting bee and wasp communities in small secondary forest fragments addressing the following main questions:

- 1) Are there interactive effects between microclimate and fragmentation on the abundance of bees and wasps, their mortality - and parasitism rates (Chapter II)?
- 2) How does fragmentation affect bee biodiversity from canopy to the understory with considerations of single species patterns (Chapter III)?
- 3) How is fragmentation affecting diversity and community composition of different trophic levels between understory and canopy with emphasis on the host-antagonist relation? (Chapter IV).

II. A variety of global change drivers affect biodiversity and trophic interactions. The combined effects of habitat fragmentation and climate change are poorly understood and with ongoing deforestation and agricultural intensification secondary rainforest fragments might contribute to biodiversity conservation and mitigation of climate warming. This chapter 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 Northeastern lowlands of Costa Rica.

Habitat area did not affect hymenopteran abundance, parasitism and mortality rates, but tree location- from the forest border to the forest center- influenced all variables. Interactive effects were found such as in the higher mortality rates at interior locations in larger fragments. Mean temperature at edge and interior locations led to significant effects on all tested variables and interactive effects between temperature and tree locations were found. Abundances at interior locations were 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.

III. This chapter focusses on the vertical distribution of bees, their parasitism and mortality rates as well as single species patterns in relation to fragment size and edge effects in secondary rainforest remnants.

No size effects on bee abundance, bee diversity and on parasitism- and mortality rates were found. Bees were least abundant at the intermediate height and were most abundant in the understory; whereas the highest diversity was found in the canopy. Tree location had no effect on bee abundance, but on bee diversity since most species were found in the forest interior. The cuckoo bees *Aglaomelissa duckei* and *Coelioxys* sp. 1 only partly followed the patterns of their hosts, two *Centris* species.

Edge effects greatly influenced the bee community, so that the amount of edge habitat in secondary forest fragments will influence the conservation value for bees.

IV. In this section the effects of habitat fragmentation on biodiversity, on community structure of hosts and natural enemies as well as the relation of hosts and antagonists were investigated from the understory to the canopy. The results stress the importance to monitor biodiversity, community composition and trophic interactions from the understory to the canopy. The higher trophic level of the antagonists was found to be more sensitive to fragment size compared to their hosts. Again edge effects were found to be the dominant driver since both host and antagonist richness, as well as community compositions were strongly affected. Ongoing fragmentation and increased amount of edge habitat could favor few abundant disturbance-adapted species over the rare and more diverse forest-adapted

species. A positive-density dependent parasitism rate was demonstrated, as well as an increase of the parasitism rate not only with antagonist abundance but also diversity.

Small secondary forest fragments surely can contribute to the conservation of biodiversity and trophic interactions, but increase of edge habitat will have negative consequences on above-ground nesting Hymenoptera, so that important interactions such as pollination, predation and parasitism could be disrupted. Therefore small forest fragments could contribute to biodiversity conservation but will not be able to compensate for the loss of large areas of primary forests.

V. This dissertation contributes to the understanding of habitat area - and edge effects as well as the interaction of those with microclimatic conditions in small secondary rainforest fragments. As study system trap nests inhabited by solitary above-ground nesting bees, wasps and their natural enemies were chosen because they allow to study trophic interactions along their whole vertical distribution from the understory to the canopy. The effect of fragment size was rather weak, however, larger sizes affected the diversity of natural enemies positively, proofing the hypothesis that higher trophic levels react more sensitive to habitat loss. Edge effects heavily affected the abundance, diversity and community composition of hosts and their natural enemies as well as parasitism and mortality rates. Increased edge conditions resulting from ongoing fragmentation and deforestation will therefore negatively affect bees, wasps and their trophic interactions with natural enemies. Those changes affect important processes such as pollination, predation and parasitism, which could result in changes of ecosystem functioning. This study showed the importance to include all strata in biodiversity monitoring since height did matter for the trap-nesting communities. Diversity was shown to be higher in the canopy and community composition did change significantly. To conclude we could show that secondary forest fragments can sustain a trap-nesting bee and wasp community, but the amount of interior habitat is highly important for the conservation of forest-adapted species. Probably the conservation of large primary forest in combination with a high habitat connectivity, for example with small secondary forest fragments, will help to sustain biodiversity and ecosystem functioning better than the mere presence of small forest fragments.

Zusammenfassung (German)

I. Die weltweite Umweltveränderung, die durch den Menschen verursacht wird, gefährdet die Artenvielfalt und die trophischen Wechselbeziehungen zwischen Organismen. Fragmentierung gilt als eine der Hauptbedrohungen für die Biodiversität und kann weitreichende Konsequenzen haben wie zum Beispiel verminderte Artenvielfalt, Rückgang von Populationen, Verlust von genetischer Diversität und auch die Unterbrechung von trophischen Interaktionen, z.B. Prädation und Parasitierung. In Waldökosystemen können Fragmentierungsauswirkungen vielfältig sein. Spezialisierte Arten mit engen natürlichen Nischen, die zum Beispiel in höheren trophischen Ebenen zu finden sind, könnten vom Aussterben bedroht sein, während generalisierte Arten mit weniger spezifischen Habitatansprüchen sogar profitieren könnten. In den Tropen, „den“ terrestrischen Biodiversitäts-Hotspots, fehlen oft sogar grundlegende Bestandsaufnahmen von Flora und Fauna, insbesondere für die Kronen der Regenwälder. Die fortschreitende Abholzung in tropischen Regionen und die dadurch verursachte Fragmentierung wird die Funktion des Ökosystems durch Veränderung der Artenvielfalt, der Zusammensetzung von Artengemeinschaften und der Unterbrechung von trophischen Interaktionen in hohem Maße beeinflussen. Besonders das Zusammenwirken von verschiedenen Facetten des globalen Umweltwandels, z. B. Klimawandel und Fragmentierung, ist nahezu unbekannt.

Da es unwahrscheinlich ist, dass die Abholzung von Regenwäldern eingestellt wird, ist es äußerst wichtig den Wert von kleinen Sekundärwaldfragmenten für den Schutz der Artenvielfalt zu untersuchen.

Diese Dissertation trägt dazu bei verschiedene Aspekte der Fragmentierung auf die Artengemeinschaft von nisthilfenbewohnenden Hymenopteren in kleinen Sekundärwaldfragmenten zu untersuchen und behandelt dabei die folgenden zentralen Fragen:

- 1) Wirken Fragmentierung und mikroklimatische Bedingungen interaktiv auf die Abundanz von Bienen und Wespen sowie deren Mortalitäts- und Parasitierungsraten (2. Kapitel)?
- 2) Wie beeinflusst Fragmentierung die Artenvielfalt von Bienen vom Unterholz bis zur Krone und wie reagieren einzelne Arten darauf (3. Kapitel)?
- 3) Wie beeinflusst Fragmentierung die Biodiversität und die Artengemeinschaften verschiedener trophischer Ebenen vom Unterholz bis zum Kronendach unter besonderer Berücksichtigung der Wirts-Antagonist-Beziehung (4. Kapitel)?

II. Eine Reihe von Faktoren des weltweiten Umweltwandels beeinflusst die Artenvielfalt und trophische Interaktionen. Die Auswirkungen von Fragmentierung und Klimawandel, die sich gegenseitig beeinflussen könnten, sind nahezu unverstanden. Außerdem könnten Sekundärwaldfragmente zum Erhalt der Artenvielfalt und der Abschwächung der Auswirkungen des Klimawandels sowie der anhaltenden Abholzung und der Intensivierung der Landwirtschaft dienen. Dieser Abschnitt untersucht mögliche Wechselwirkungen zwischen Fragmentierung und Temperatur auf die Abundanz und trophische Interaktionen von nisthilfenbewohnenden Bienen und Wespen in kleinen Sekundärwaldfragmenten im Nordosten Costa Ricas.

Die Fragmentgröße hatte keinen Einfluss auf die Abundanz, die Parasitierungs- und Mortalitätsraten der Hymenopteren, während der Baumstandort- vom Waldrand zur Waldmitte immensen Einfluss auf alle untersuchten Variablen hatte. In größeren Fragmenten war die Mortalitätsrate innerhalb des Waldes verglichen mit kleineren Fragmenten höher. Die mittlere Temperatur beeinflusste alle untersuchten Variablen und hatte je nach Standort des Baumes unterschiedliche Auswirkungen. Die Abundanzen im Waldinneren stiegen signifikant mit höheren Temperaturen an. Die Mortalitätsraten im Waldinneren nahmen mit niedrigeren Temperaturen zu, während höhere Temperaturen am Waldrand zu höheren Mortalitätsraten führten. Unsere Ergebnisse zeigen, dass Randeffekte, die auch durch Temperaturunterschiede zustande kommen, biotische Interaktionen von nisthilfenbewohnenden Bienen und Wespen in kleinen Sekundärwaldfragmenten ändern.

III. Dieses Kapitel konzentriert sich auf den Einfluss der Fragmentgröße und der Randeffekte auf Bienen und deren Parasitierungs- und Mortalitätsraten vom Unterholz bis zu den Kronendächern in kleinen Sekundärwaldfragmenten. Dabei wurden auch die Muster von einzelnen Arten näher untersucht.

Die Fragmentgröße hatte keinen Einfluss auf die Bienenabundanz, die Artenvielfalt oder die Parasitierungs- und Mortalitätsraten. Die höchste Bienenabundanz wies das Unterholz auf, während die höchste Diversität im Kronendach gefunden wurde. Der Gradient vom Waldrand bis zur Waldmitte hatte keinen Einfluss auf die Bienenabundanz, wohingegen die Diversität zum Waldinnern hin anstieg. Die Kuckucksbienen *Aglaomelissa duckei* und *Coelioxys* sp. 1 folgten nur zum Teil den Mustern ihrer Wirte, zwei *Centris* Arten.

Randeffekte hatten großen Einfluss auf die Bienengemeinschaften, so dass der Anteil von Waldrändern bzw. die Form der Sekundärwaldfragmente über den Nutzen für die Erhaltung der Bienenartvielfalt bestimmt.

IV. In diesem Kapitel wurden die Fragmentierungsauswirkungen auf die Biodiversität, die Gemeinschaftszusammensetzung von Wirten und ihrer natürlichen Feinde als auch die Beziehung zwischen den Wirten und ihren natürlichen Feinden vom Unterholz bis zum Kronendach untersucht. Die Ergebnisse zeigten, dass es äußerst wichtig ist die Biodiversität, die Zusammensetzung der Artengemeinschaft als auch die trophischen Interaktionen in den verschiedenen Straten des Regenwaldes zu untersuchen. Die natürlichen Feinde, die auf einer höheren trophischen Ebene stehen, reagierten empfindlicher auf die Größe der Fragmente. Randeffekte waren der einflussreichste Faktor, weil die Diversität der Wirte und der natürlichen Feinde, sowie deren Artengemeinschaften stark beeinflusst wurden. Fortschreitende Fragmentierung und der damit einhergehende erhöhte Flächenanteil des Randhabitats könnte daher wenige häufige Arten bevorzugen, die gestörtes Habitat tolerieren können, wohingegen die seltenere aber artenreichere Gemeinschaft, die das Waldinnere bevorzugt, benachteiligt wird. Es konnte außerdem eine positiv-dichteabhängige Parasitierungsrate sowie ein positiver Zusammenhang zwischen der Abundanz und Diversität von natürlichen Feinden und der Parasitierungsrate gezeigt werden. Kleine Sekundärwaldfragmente können sicherlich helfen die Artenvielfalt und die trophischen Interaktionen zu erhalten, aber die Erhöhung des Anteils von Randhabitat wird nachteilige Folgen für solitäre Hymenopteren haben. Dies kann zur Unterbrechung von wichtigen Interaktionen wie Bestäubung, Prädation und Parasitierung führen. Kleine Sekundärwaldfragmente können daher zwar hilfreich zur Erhaltung der Biodiversität sein, aber niemals große Primärwaldflächen, die von unschätzbarem Wert sind, ersetzen.

V. Die vorliegende Doktorarbeit trägt zum Verständnis der Auswirkungen der Habitatgröße und von Randeffekten als auch deren Wechselwirkungen mit mikroklimatischen Bedingungen in kleinen Sekundärwaldfragmenten bei. Benutzt wurden Nisthilfen, die von solitären Bienen, Wespen und ihren natürlichen Feinden besiedelt werden, da hierdurch auch trophische Interaktionen vom Unterholz bis zum Kronendach aufgenommen werden können. Die Fragmentgröße hatte keine weitreichenden Auswirkungen. Größere Fragmente wiesen allerdings eine höhere Vielfalt von natürlichen Feinden auf, was die Hypothese der höheren Empfindlichkeit von höheren trophischen Ebenen bestätigt. Randeffekte hingegen haben sowohl die Bienen und Wespen als Wirte als auch deren natürliche Feinde in ihrer Häufigkeit, Artenvielfalt und Artenzusammensetzung in hohem Maße beeinflusst. Eine Erhöhung des Anteils von Randhabitaten, die mit fortschreitender Abholzung und Fragmentierung einhergeht, wird daher einen negativen Einfluss auf diese Hymenopteren

haben, was sogar die Funktion des Ökosystems beeinflussen könnte, da dadurch auch wichtige Interaktionen, zum Beispiel Bestäubung, Prädation und Parasitierung beeinträchtigt werden. Außerdem konnte diese Doktorarbeit zeigen, dass es unbedingt notwendig ist die Fauna des gesamten Regenwaldes unter Berücksichtigung aller Straten aufzunehmen. Die Artenvielfalt in der Kronenschicht war höher und auch die Zusammensetzung der Artengemeinschaften war signifikant verschieden zwischen dem Unterholz und den Kronendächern.

Diese Doktorarbeit zeigt, dass kleine Sekundärwaldfragmente zwar Lebensraum und Ressourcen für eine Gemeinschaft von solitären Bienen, Wespen und deren natürlichen Gegenspielern bieten kann, dass jedoch die Form und damit der Anteil von Innenhabitat ausschlaggebend für den Erhalt von spezialisierten Waldarten ist. Der Erhalt von großen Flächen von Primärwald ist daher unabdingbar, jedoch könnten Sekundärwaldfragmente zur Erhöhung der Vernetzung beitragen, um so ein stabiles, artenreiches und einzigartiges Waldökosystem zu erhalten, was allein durch kleine Sekundärwaldfragmente nicht möglich sein wird.

I General Introduction

Tropical rainforests are the most important terrestrial biodiversity hotspots (Connell 1978; Wilson 1988) and characterized by high rates of rainfall and sun radiation leading to high primary productivity (Wilson 1988; Ghazoul and Sheil 2010). Costa Rica, the place where this dissertation was conducted, is considered as hotspot for both species richness and endemism of plants and animals (Orme et al. 2005).

Global change drivers such as climate change, land use intensification and habitat fragmentation threaten biodiversity and ecosystem functioning. In wide parts of tropical regions, deforestation goes on and leads to anthropogenic landscapes with patchily distributed forest fragments in a matrix of pastures and plantations (Vitousek et al. 1997; Tilman et al. 2001). Vertical stratification or microclimate were often not taken into account, when investigating fragmentation effects and secondary forest fragments are not well studied despite of their potential utility for biodiversity conservation.

Habitat Fragmentation

Habitat fragmentation including both habitat loss and fragmentation per se, is one of the most important threats for biodiversity (Fahrig 2003; Neame et al. 2013; Vaughn et al. 2014). Especially in the tropics, the largest reservoirs of terrestrial biodiversity, deforestation goes on and imperils global biodiversity more than any other contemporary phenomenon (Laurance et al. 2012). This results in landscapes with small forest fragments of different quality in a matrix of pastures and plantations (Vitousek et al. 1997; Tilman et al. 2001). Generally habitat loss leads to consistent negative effects on biodiversity whereas fragmentation per se has weaker effects on biodiversity and can have positive or negative consequences (Fahrig 2003; Nordén et al. 2013). Habitat fragmentation was shown to cause 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 Tschardtke 2000; Laurance et al. 2002; Klein et al. 2006). However regional estimates of extinctions from deforestation could be even worse than previously thought, because most studies neglected extinction debts and assumed that persisting forest was continuous (Kuussaari et al. 2009; Hanski et al. 2013).

Habitat fragmentation results in edge effects, so that natural habitats are affected by their surrounding matrix. Rainforest fragments are heavily influenced by the conditions of the surrounding habitats (Laurance et al. 2011a; Lippok et al. 2014). There is a gradient of temperature, humidity, tree altitude, forest structure and invasive species depending on the

structure of the forest border (Didham and Lawton 1999) and forest species are threatened by change of abiotic factors, through interactions with other species such as invasive, disturbance-adapted species (Gibson et al. 2011; Laurance et al. 2012). Therefore habitat fragmentation is affecting taxa differently depending on their needs (Huggett 2005; Lindenmayer and Luck 2005; Ewers and Didham 2006). Mobility, feeding ranges, nesting behavior as well as being member of a higher trophic level can lead to a more sensitive response to fragmentation (Ockinger et al. 2010; Williams et al. 2010; Holt et al., 1999; Rand et al., 2012).

Vertical stratification

Tropical rainforests consist of different strata, the forest floor, the understory and the canopy with outstanding emergents (Ghazoul and Sheil 2010). Every strata is characterized by abiotic factors, forest physiognomy and resource availability (Basset et al. 2003). The canopy receives nearly 100 % of the solar radiation, whereas the understory is reached by less than 1% (Parker 1995). The canopy has a higher leaf area density and abundance of young leaves, flowers and seeds compared to the understory (Parker 1995; Hallé 1998). The vertical gradient of resources and microclimatic factors create different niches, which leads to stratified communities of animals (Basset et al. 2003; Vance et al. 2007; Paniagua et al. 2009). The highest diversity of arthropods was often found to be equal or higher in the forest canopy (for example Erwin 1982; Stork and Grimbacher 2006). However due to difficulties in data assessment in the canopy, the diverse upper canopy regions of tropical forests were often ignored in the past (Basset et al. 2013). The situation changes now and some studies brought considerable progress (Basset et al. 2013; Wardhaugh et al. 2014). However studies on trophic interactions in tropical forest canopies are still missing.

Microclimate

Climate change and resulting microclimatic changes can affect insect communities. Especially 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 (Ruibal 1961; Deutsch et al. 2008). This is especially true for lowland forest species with narrow thermal optima (van Berkum 1988; Deutsch et al. 2008). The situation for these species 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 global change driver (e. g. Gibson et al. 2013; Hill et al. 2006; Opdam and Wascher, 2004). So 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 (Wimp et al. 2011; Mantyka-Pringle et al. 2012; González-Varo et al. 2013).

Secondary forest fragments

Intact primary forest contains more species per unit area than fragments (Laurance et al. 2002; Barlow et al. 2007) and is therefore irreplaceable (Gibson et al. 2011), but as deforestation rapidly goes on (Barraclough 2013), it is important to evaluate if secondary forest fragments can be helpful for biodiversity conservation (Barlow et al. 2007). Secondary forest fragments and tree plantations could help in biodiversity conservation especially of smaller taxa like arthropods (Turner & Corlett 1996), because their coverage is rapidly expanding and they could connect the limited protected areas (Barlow et al. 2007). They therefore can enhance landscape connectivity, but they were found more vulnerable than previously thought (Gibson et al. 2013). The conservation value of secondary forest fragments has rarely been addressed despite the probability that in many regions biodiversity conservation will heavily depend on them also for the maintenance of ecosystem services for agricultural areas.

Study Design and Chapter Outline

Trap-nests were used to monitor the biodiversity of above-ground nesting solitary bees and wasps and their natural enemies (Fig. 1a).

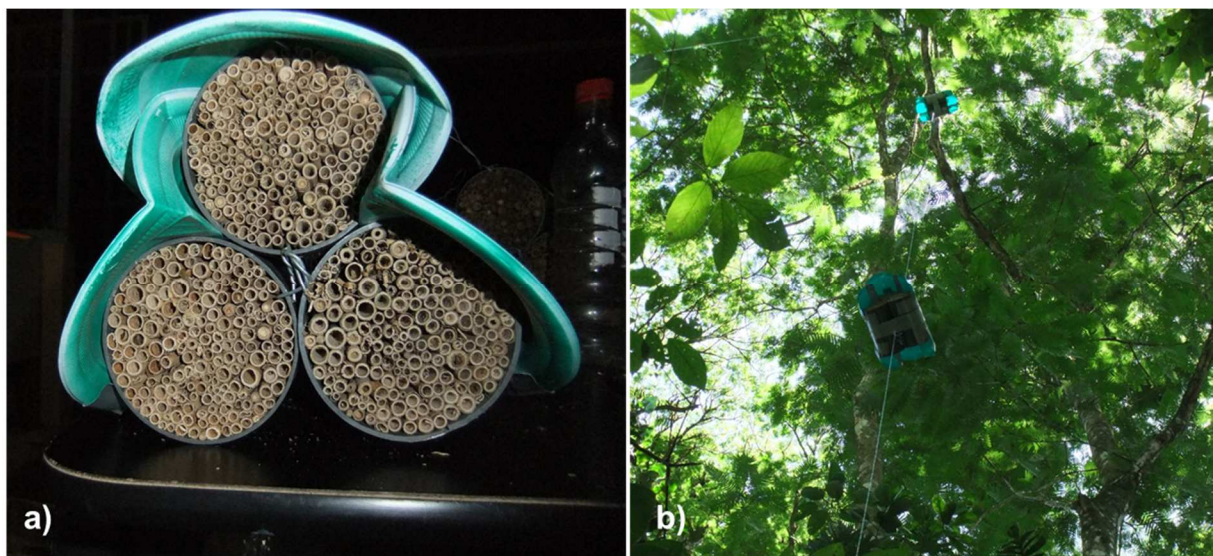


Fig. 1 a) Trap nest package with raincover b) installed trap nest packages at 10 and 20 m height, Fotos: Eva Stangler

Trap-nests are a valuable system to monitor not only abundance and biodiversity but also trophic interactions (Tschardt et al. 1998) and they have been used in a variety of studies to evaluate habitat quality or the influences of land-use (Tylianakis et al. 2005; Loyola and Martins 2006; Steckel et al. 2014). Therefore this system is well suited to investigate the differences between the strata in rainforests (Fig. 1b) as well as the effects of fragment size and edge effects on their inhabitants.



Fig. 2 The study region with forest fragments in a matrix of **a)** ornamental plants **b)** pastures **c)** pineapple plantations and **d)** banana plantations; Fotos: Eva Stangler

Bees and wasps, play important roles in ecosystem functioning. Bees are the most important pollinators (Didham et al. 1996; Kremen et al. 2007), especially for native plants in tropical forests, where animal-mediated pollination is more frequent than in temperate regions (Bawa 1990; Ollerton et al. 2011). Wasps are known to be important predators and parasitoids in natural and agricultural habitats (Penagos and Williams 1995; Klein et al. 2004). The higher trophic levels, like predators and parasitoids, are expected to be more vulnerable to environmental changes (Holt et al. 1999; Rand et al. 2012) and may act as keystone species in ecosystems (La Salle 1993). Natural enemies play an important role as they can regulate

population dynamics from the top by positive density dependent parasitism or predation (Hassel and Wilson 1997; Berryman and Turchin 2001), but knowledge on ecological interactions between hosts and natural enemies are particularly scarce (Paniagua et al. 2009).

Sarapiquí, the study region, belongs to the “tropical moist forest” according to the Holdridge’s life zone system (Holdridge 1967). Nowadays it is a typical human-dominated tropical landscape with primary and secondary forest fragments of different sizes in a matrix of pastures and plantations (pineapple, banana, ornamental plants; Fig. 2).

The study was conducted in small secondary forest fragments in order to investigate if they can sustain above-ground nesting solitary bees and wasps. 12 differently sized forest fragments were selected from 0.9 – 16.6 ha (see Fig. 3). In each of the fragments three trees were selected along a transect line from forest edge to forest center in order to measure edge effects. To account for vertical stratification three packages (each with three trap-nests) were installed at three heights at each tree, at 2 m, 10 m and 20 m (Fig. 4).

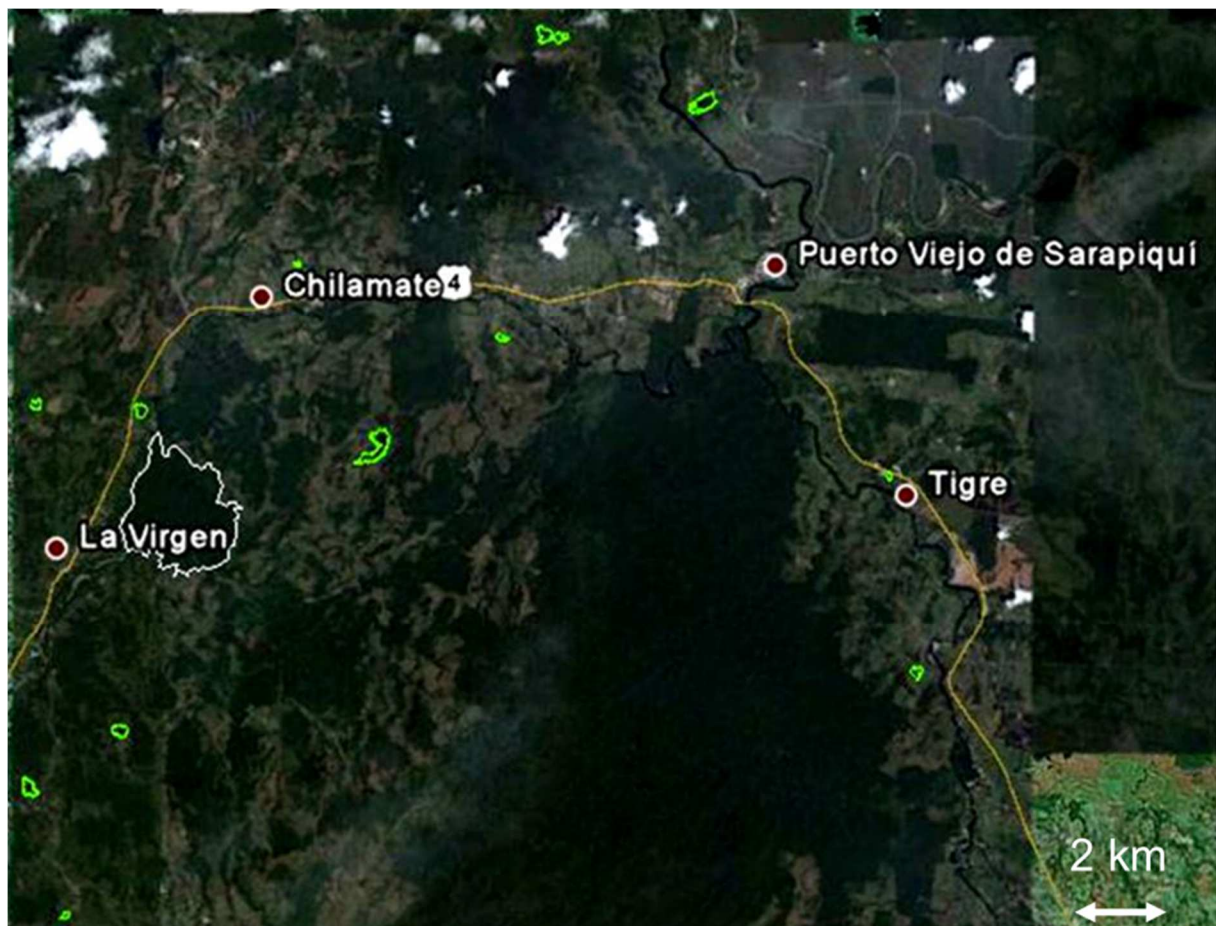


Fig. 3 The study region: Sarapiquí, Heredia, Costa Rica, with the differently sized forest fragments (bordered with light green).

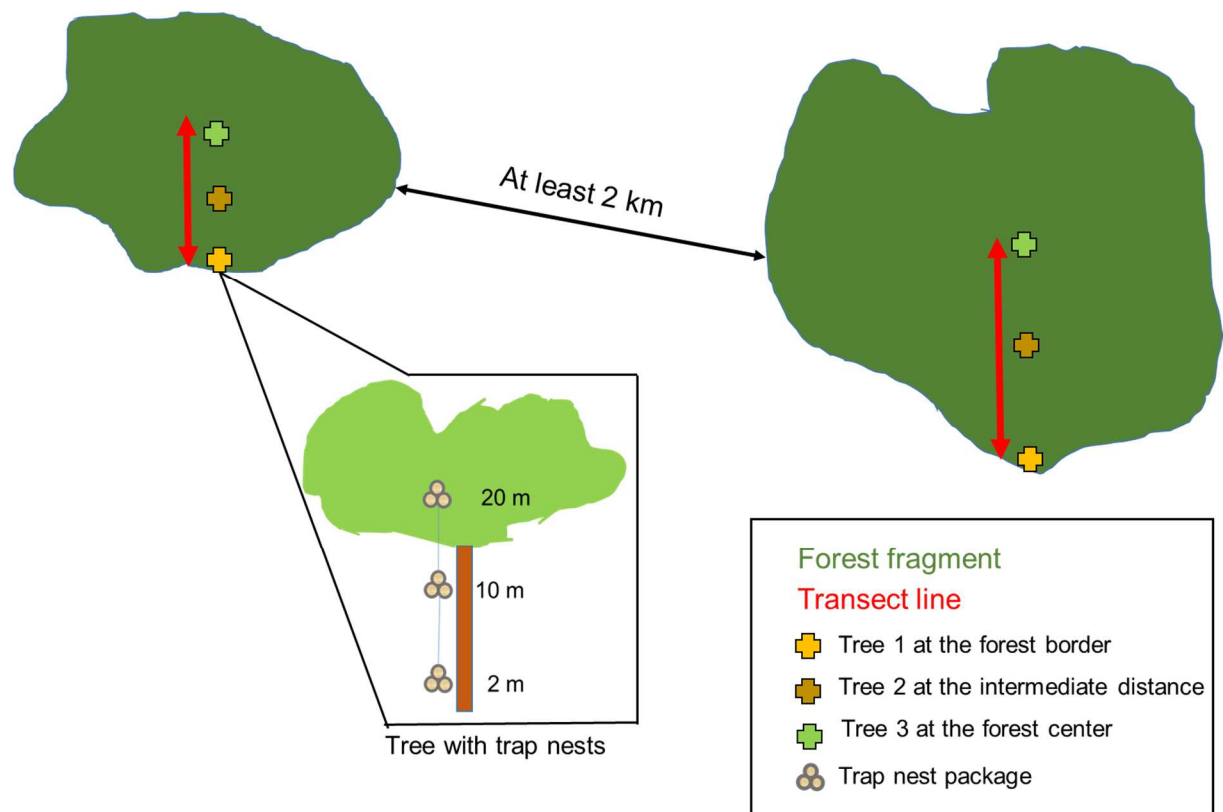


Fig. 4 Schematic study design with different sized forest fragments. At each fragment three trees were selected along a transect line, tree 1 at the forest border (yellow cross), tree 2 at an intermediate distance (light brown cross) and tree 3 at the forest center (light green cross). At each tree, three packages (each with three trap-nests) were installed at three heights, at 2 m, 10 m and 20 m.

This dissertation concentrates on the effects of fragmentation (fragment size and edge effects) on the biodiversity of above-ground nesting solitary bees, wasps and their trophic interactions with their natural enemies. The first chapter aims to contribute to the understanding of possible interactive effects of habitat fragmentation and microclimate on the abundance, the mortality and parasitism rate of trap-nesting Hymenoptera. The second chapter concentrated on the effects of habitat fragmentation on bee communities and their community parameters at different strata, including single species patterns. The last chapter asked if fragmentation affected host and antagonist communities differently and if communities changed between different strata.

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

This chapter has been published online: Stangler ES, Hanson P, Steffan-Dewenter I (2014) Interactive effects of habitat fragmentation and microclimate on trap-nesting Hymenoptera and their trophic interactions in small secondary rainforest remnants. *Biodiversity and Conservation*, 1-15.

Running title: Interactive effects of fragmentation and microclimate

Key words: area effects, edge effects, temperature, solitary bees and wasps, parasitism rate, mortality rate

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 northwestern lowland of Costa Rica.

Fragment size did not affect hymenopteran abundance, parasitism rates 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 lead to significant effects on all tested response variables. Abundance at interior locations was significantly rising with increasing temperatures. Mortality rates at interior locations were enhanced 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.

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 like predation and parasitism in food webs (Turner 1996; Kruess and Tschardtke 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 (Kuussaari et al. 2009; Hanski et al. 2013).

Not only fragmentation can affect insect communities, but also climate change and related shifts in microclimatic conditions. Species adapted to forest conditions living in constant shade cannot adapt easily to higher temperatures and lower air moisture in open habitats and have not many options to escape from rising temperatures (Ruibal 1961; Deutsch et al. 2008). This is especially true for lowland forest species of bees and wasps with narrow thermal optima (van Berkum 1988; Deutsch et al. 2008). The situation for them even becomes harsher when they are additionally confronted with habitat loss and fragmentation (Tewksbury et al. 2008). Until now only 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 (Tschardtke 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 important predators and parasitoids, with high 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 inside neo-tropical native forest trap-nesting bees are considered more sensitive to habitat fragmentation preferring continuous forest and natural gaps, whereas wasps seemed 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 (Tschardt et al. 1998). The nesting frequencies of trap-nesting Hymenoptera are also known to respond to climate factors like temperature, precipitation, humidity or sun-exposure (Thiele 2005).

Information on biodiversity of Hymenoptera is scarce in tropical rainforests, but there is even less knowledge on 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 rate and parasitism rates (Tschardt et al. 1998). Higher trophic levels, as in parasitoids, are more affected by drivers like climate warming or habitat modification (Thomson et al. 2001; Valladares et al. 2006; Fenoglio et al. 2012), due to a higher susceptibility of interactions to phenological desynchronisation 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. 2011b; González-Varo et al. 2013; Wimp et al. 2011).

Secondary forest fragments and tree plantations can be of great importance 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 tropical studies inside the forest, as most studies investigated influences of tropical forests in adjacent agro-ecosystems (Klein et al. 2002; Klein et al. 2006) or along land-use gradients (Tylianakis et al. 2005; Tylianakis et al. 2006). There are nearly no reference studies conducted in tropical forest, such as 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 been rarely addressed although 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-nesters at three locations in differently sized secondary forest in the Sarapiquí region in Costa Rica to answer the following questions:

- 1) Does the abundance of solitary bees and wasps differ with interactive effects of size, location and temperature?
- 2) How do parasitism- and mortality rates change with fragment size, location and temperature?

- 3) What is the conservation value of secondary forest fragments for above-ground nesting Hymenoptera?

Material and Methods

Study region and study sites

This study was carried out during a 12 month period between February 2011 and February 2012 in the Sarapiquí region in Heredia province, Costa Rica in the vicinity of La Virgen. The average annual temperature was 25.3°C with an average annual precipitation of 3777 mm. According to the Holdridge life zone system, Sarapiquí belongs to the zone “tropical moist forest” (Holdridge 1967). The landscape mostly consists of forest remnants, pastures for cattle and farmland producing pineapple, ornamental plants and banana. In a region of ca 30 x 40 km, twelve differently sized forest fragments (average: 5.4 ha \pm 4.86; range: 0.9 – 16.62 ha) with at least 2 km of distance between each other and a similar amount of forest (ap. 30%) in a 2 km circle were selected. The forest fragments consisted of secondary forest with no recent management activities and were located between 49 and 413 m asl.

Study design and sampling

In each of the 12 study sites 27 trap nests were placed. Three trees were selected on a transect line, one tree in the forest center, one in an intermediate distance and the last one at the forest edge. A package of three trap nests were installed at every of the three heights (2 m, 10 m, 20 m) on each tree. In total 324 trap nests were analyzed. 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 every tree at 10 m one 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, which were closed by 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 cells and dead cells were noted to calculate parasitism and mortality rates. Then nests were put in pieces of transparent plastic tube and closed with cotton on both sides. When the adults emerged, they were killed for later identification. All wasps, bees and parasitoids were 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 size and tree location 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” consists 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, like bees and wasps, as we were interested into the trap-nesting community responses. However the separate analyses can be found in the supplementary material.

Results

1. Bees, wasps and natural enemies

During 12 months 22101 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 3714 cells were attacked by natural enemies, and of these, 332 were bee cells (8.9%) and 3382 were wasp cells (91.1%). In total 3480 cells died of other causes, and of these, 459 were bee cells (13.1%) and 3025 were wasp cells (86.9%).

2. Fragments and microclimate

We tested the effects of size and tree location on the mean temperature. Mean site temperature did not vary with size ($p = 0.654$), but 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.

Tab. 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	species	tree 1	tree 2	tree 3
Anthophoridae				Eumenidae			
<i>Centris labrosa</i>	120	311	206	<i>Montezumia</i>	14	0	2
<i>Centris analis</i>	148	57	43	<i>Pachodynerus</i>	40	50	105
<i>Aglaomelissa duckei</i>	1	5	26	<i>Zethus</i>	18	40	75
Megachilidae				Chalcidoidea			
<i>Megachile sp.1</i>	27	0	9	<i>Brachymeria sp. 1</i>	0	0	3
<i>Megachile sp.2</i>	4	7	67	<i>Leucospis sp. 1</i>	15	5	23
<i>Megachile sp.3</i>	7	0	0	<i>Melittobia</i>	179	48	40
<i>Megachile sp.4</i>	7	0	7	Perilampidae sp. 1	1	1	0
<i>Duckeanthidium thielei</i>	0	0	4	Chrysididae			
<i>Anthodioctes gualanense</i>	23	0	31	<i>Caenochrysis</i>	133	35	57
<i>Coelioxys sp.1</i>	3	11	27	<i>Chrysis</i>	5	0	4
<i>Coelioxys sp.2</i>	0	0	1	<i>Exochrysis</i>	22	22	33
<i>Coelioxys sp.3</i>	1	0	0	<i>Ipsiura</i>	1	3	5
<i>Coelioxys sp.4</i>	0	0	1	<i>Neochrysis</i>	15	0	3
<i>Coelioxys sp.5</i>	0	0	2	<i>Pleurochrysis</i>	2	1	10
Colletidae				Ichneumonidae			
<i>Hylaeus sp.1</i>	20	9	89	Ichneumonidae sp. 1	1	0	0
Apidae				Ichneumonidae sp. 2	0	6	2
<i>Tetrapedia maura</i>	107	4	17	Ichneumonidae sp. 3	2	1	2
Sphecidae				Ichneumonidae sp. 4	2	0	0
<i>Ampulex</i>	2	6	8	Ichneumonidae sp. 5	1	0	0
<i>Liris</i>	3	47	78	Mutillidae			
<i>Nitela</i>	2	9	13	<i>Spaerophthalmina</i>	18	16	9
<i>Penepodium</i>	1	0	0	Coleoptera			
<i>Pison</i>	53	121	145	<i>Tetraonyx sexguttata</i>	12	7	8
<i>Podium</i>	442	549	852	Dermestidae	16	1	0
<i>Trigonopsis</i>	1	0	4	Nitidulidae	0	0	1
<i>Trypoxylon</i>	6493	3185	4000	Diptera			
Pompilidae				<i>Anthrax</i>	15	5	11
<i>Ageniella</i>	2	0	0	Dolichopodidae	550	575	680
<i>Auplopus</i>	650	237	588	Sarcophagidae	37	9	13
<i>Dipogon</i>	3	0	4	Arachnida			
<i>Priocnemella</i>	49	28	35	Acari	28	13	9
				Lepidoptera			
				Lepidoptera	14	5	9

3. Fragment size, tree location and temperature effects on abundances

Against our expectations size alone had no influence on the abundance of bees and wasps ($p = 0.25$). However, size did influence the number of brood cells in interaction with tree location (tree 2: $p < 0.001$, Fig. 1 a, Table 2).

At the intermediate tree, the abundance was significantly lower in larger fragments compared to smaller ones, whereas at the forest center and the edge abundance slightly rose with larger fragment sizes. Further, independent of fragment size, inner trees showed a lower 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 ($p < 0.001$), however, the influence of temperature also depended on tree location. The high abundance at the edge was negatively affected by a temperature rise, whereas higher temperatures at the inner trees lead to similar or slightly higher abundances (tree 2: $p = 0.014$, tree 3: $p = 0.005$, Fig. 1 b).

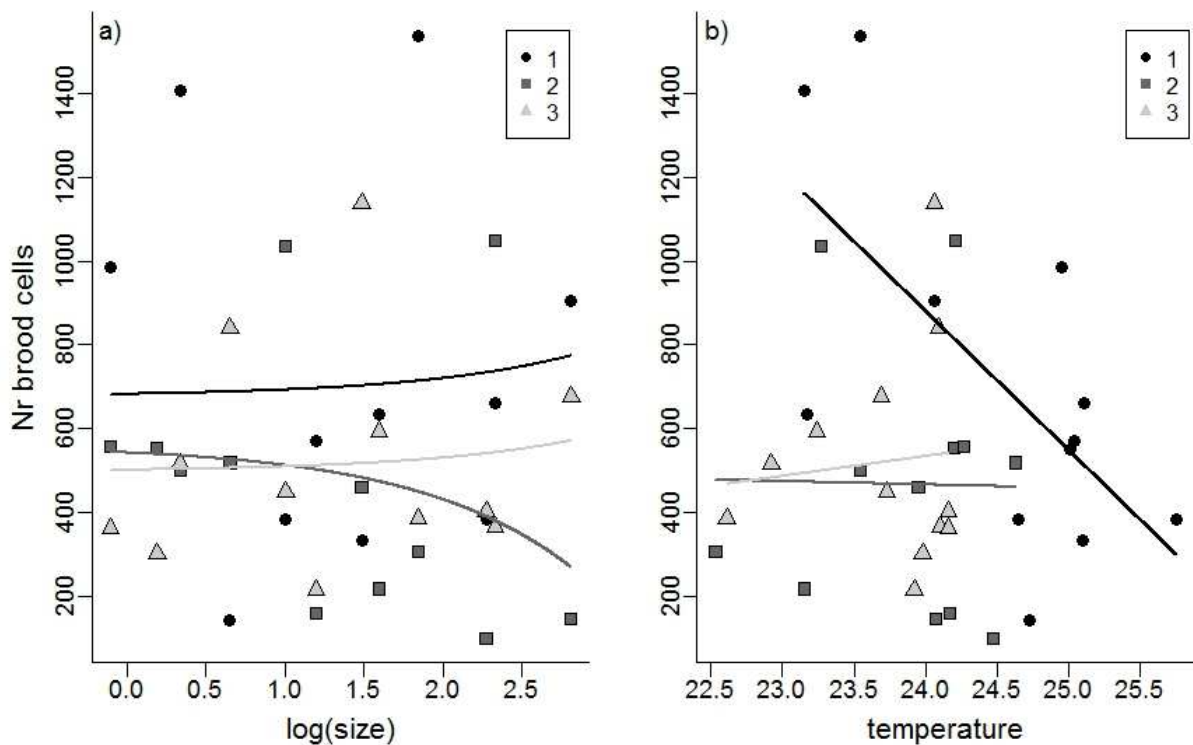


Fig. 1 Effects of **a)** the interaction between size and location respectively **b)** temperature and location on the abundance of trap-nesting hymenopterans (location: tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center).

Tab. 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. Results of final models are shown.

	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
	tree2*size*temperature	3.113	0.001854 **
	tree3*size*temperature	0.508	0.61126

4. Fragment size, tree location and temperature effects on mortality rates

Fragment size alone had no influence on mortality rate (Table 2). But interestingly larger fragments had higher mortality rates inside the forest (tree 2: $p = 0.00317$, tree 3: $p = 0.00868$, Fig. 2 a)) 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. 2 b).

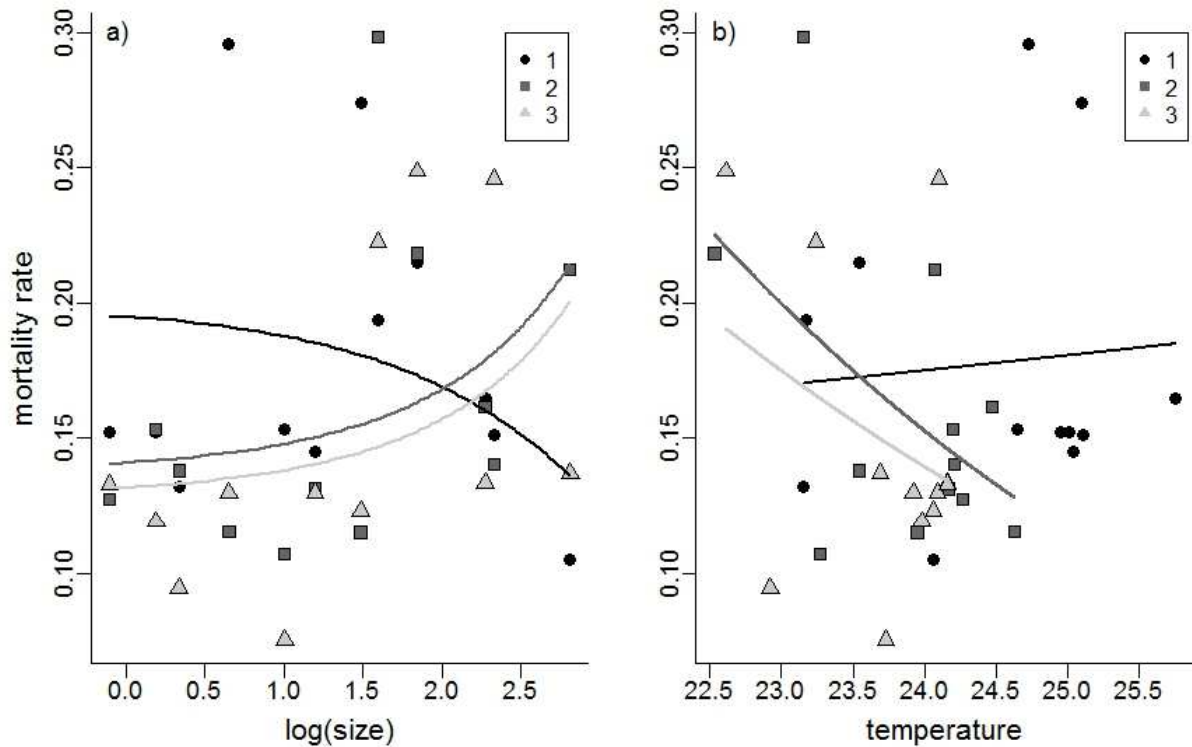


Fig. 2 Effects of **a)** the interaction between size and location respectively **b)** temperature and location on the mortality rate of trap-nesting hymenopterans (location: tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center).

5. 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 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 lead to lower parasitism at intermediate trees. (Fig. 3).

We additionally found interactive effects of size, location and temperature on parasitism rates (Fig.4). Temperature is not influencing the response of the parasitism rates to size at the edge and the forest center, but 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 or middle range, but increased strongly with higher temperatures.

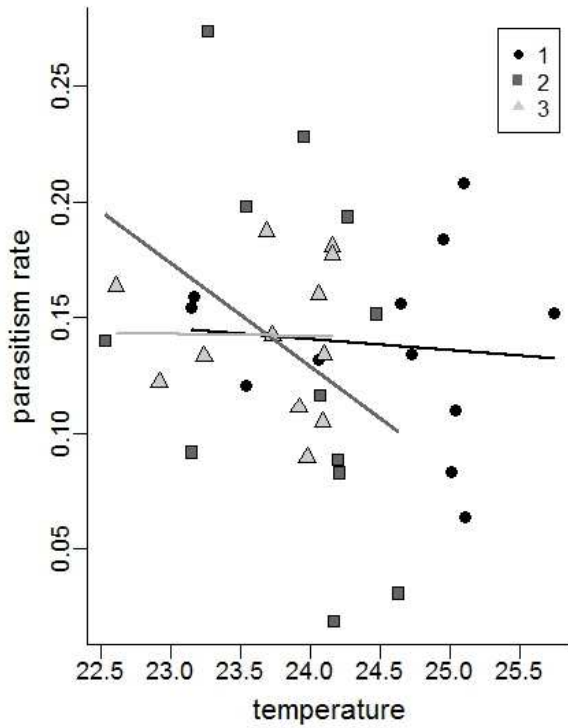


Fig. 3 Effects of temperature and location on the parasitism rate of trap-nesting hymenopterans (location: tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center).

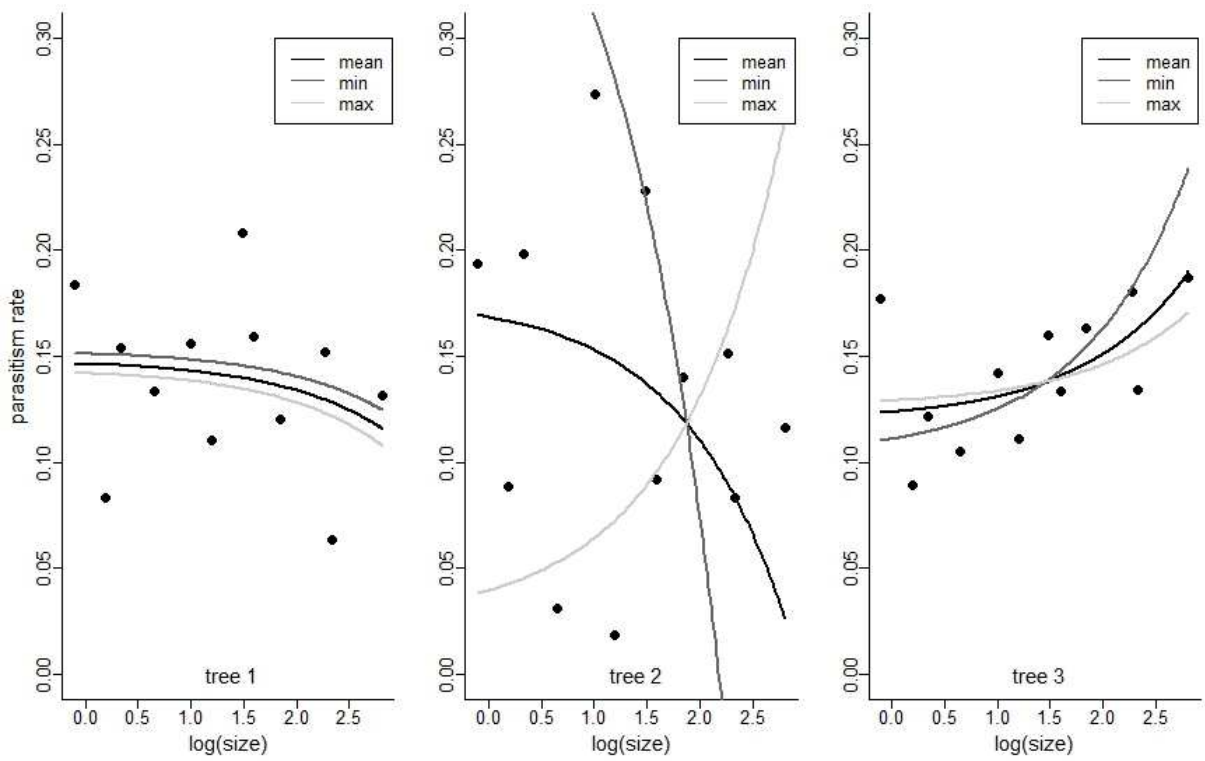


Fig. 4 Size effects on the parasitism rate for three different temperatures (mean, minimal and maximal temperature at the forest border (tree 1) at intermediate distance (tree 2) in the forest center (tree 3)).

Discussion

1. Bees, wasps and natural enemies

In this study the abundance and diversity of wasps in small secondary forest remnants was much higher when compared to bees. Former studies in the Central Amazon and Northern Brazil (Morato and Campos 2000; Batista Matos et al. 2013) also found a higher abundance of wasp 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 were found more often found in small forest remnants and cleared areas (Morato and Campos 2000).

2. 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. But other factors also characterize edge and center locations, such as light conditions, humidity, wind speed and interactions with other organisms (Ewers et al. 2007; Ewers et al. 2009). Forest borders frequently have reduced humidity, increased light and greater temperature variability (Saunders et al. 1991; Laurance and Williamson 2001; Hunter 2002). But since temperature explained much of the variety in the models, we decided to include this important factor.

3. Fragment size, tree location and temperature effects on abundances

Size did not have a significant influence on the hymenopteran abundance. Some studies demonstrate that habitat loss leads to a loss in 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 (Offerman et al. 1995; Gascon et al. 1999), 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 (ap. 50%) of wasps are of 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 of the genus *Centris* (see Table 1). With a

higher percentage of habitat generalists species interactions may already have changed and could have led to a lack of pollination and higher herbivory rates through changes in the relative abundance of predation and parasitism in food webs (Klein et al. 2006). Further studies, which investigate the threshold of minimal habitat for containing a rich hymenopteran fauna are needed.

The abundance of bees and wasps was higher at the edge compared to the forest interior, because they get access to complementary resources like 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 theory 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 low ability of thermoregulation (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 get harmed by habitat loss and fragmentation, but also by rising temperatures.

The influence of rising temperatures depended on the tree location. At the edge, where we found the highest abundance, rising temperatures had a highly negative impact on bees and wasps. Higher mean temperatures are correlated to higher fluctuations of temperatures at sites with direct sun exposure, with temperature extremes above 40 degrees and more intensive radiation (Murcia 1995). More thermo-sensitive bee and wasps species presumably cannot compensate further such steep temperature fluctuations (Fye 1972). However higher temperatures inside the forest led to a higher 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 for wasps it is known, that they respond highly to relative humidity, which is connected 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 which extent even hymenopterans adapted to disturbed conditions can compensate for projected climate warming (Buckley et al. 2013).

4. 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, typically found in the center of larger fragments. They therefore respond with higher mortality rates, for example because of mold infestation (personal observation) and because hymenopterans are known to be sensitive to light and humidity due to their low ability for thermoregulation (Loyola and Martins 2006).

5. Fragment size, tree location and temperature effects on parasitism rates

Higher trophic levels, like parasitoids, experience fragmentation more severe than their hosts (Nouhuys 2005; Pimm and Lawton 1977; Ries and Sisk 2004; Tscharrntke et al. 2005) and interactions may be more susceptible due to their sensitivity, for example to 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 rate rises at the forest border. But curiously, parasitism rates were highest at the intermediate trees and highly variable when comparing the range of rates to edge and center. So the question is why parasitoids cannot exploit the greater host abundance at the edge? Probably their high trophic position and their high specialization, e.g. their narrower niche, are the reason for their vulnerability and higher habitat requirements (Holt et al. 1999). This could be one reason for the edge preference of hosts as they find a lower risk of being parasitized. Little is known about parasitoids in general and less 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 that parasitoids prefer the conditions in the forest center. The only reasonable explanation for a higher parasitism rate at intermediate distances could be that parasitoids try to follow the host abundance to the forest border, but are not able to survive the climatic conditions there. The best compromise between climatic conditions and host abundance would then be the intermediate distance.

This is further confirmed by our finding that at this intermediate location a rise in temperature did significantly lower the parasitism rate, presumably since parasitoids respond negatively to higher temperatures (Thomson et al. 2001). This pattern depended however on fragment size, as the parasitism rate was lower at the intermediate trees in larger fragments compared to smaller ones. It was expected, that the parasitism rate drops in smaller instead of larger fragments (Valladares et al. 2006). But this decrease takes only place at the intermediate location, 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 a variety of studies (Nouhuys 2005; Pimm and Lawton 1977; Tscharrntke et al. 2005). But apparently in our size range, this is no longer true, perhaps because most of the higher specialized parasitoids have already gone extinct. Since the results of our study are unable to document this possibility, this would be an interesting topic for future studies, because 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 alone 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.

Supplementary

Tab. 3 Interactive effects of fragment size, tree location (tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center) and temperature on the abundance, mortality and parasitism rates of bees vs. wasps.

	Bees			Wasps		
	Explanatory variables	z-value	p-value	Explanatory variables	z-value	p-value
Abundance	size	-3.197	0.00139 **	size	1.366	0.172067
	tree 2	-0.8	0.42388	tree 2	-2.048	0.040555 *
	tree 3	-0.674	0.50052	tree 3	-2.637	0.008353 **
	temperature	-1.99	0.04657 *	temperature	-3.691	0.000224 ***
	size*tree 2	1.999	0.04564 *	size*tree 2	-5.409	6.32e-08 ***
	size*tree 3	2.184	0.02896 *	size*tree 3	-0.499	0.618084
	size*temperature	3.196	0.00139 **	tree 2*temperature	2.046	0.040786 *
			tree 3*temperature	2.559	0.010495 *	
Mortality rate	size	1.63	0.103	tree 2	-1.978	0.0479 *
				tree 3	-1.582	0.1136
Parasitism rate	temperature	-1.566	0.117	temperature	-1.588	0.112

III Vertical diversity patterns and biotic interactions of trap-nesting bees along a fragmentation gradient of small secondary rainforest remnants

This chapter has been submitted to *Apidologie* as: Stangler ES, Hanson P, Steffan-Dewenter I: Vertical diversity patterns and biotic interactions of trap-nesting bees along a fragmentation gradient of small secondary rainforest remnants.

Running title: Fragmentation effects on bees

Key words: fragmentation effects, parasitism rate, mortality rate, secondary forest fragments, vertical stratification

Abstract

Secondary rainforest remnants might contribute to biodiversity conservation and preservation of healthy interspecific interactions with ongoing fragmentation. We studied the vertical distribution of trap-nesting bees along a fragmentation gradient of secondary forest remnants in Costa Rica. No size effects on abundance, diversity and parasitism- and mortality rates were found. Bees were more abundant in the canopy and the understory compared to an intermediate height and bee diversity was higher in the canopy. Edge effects did not affect abundance, but bee diversity since most species preferred the forest interior. The cuckoo bees *Aglaomelissa duckei* and *Coelioxys* sp. 1 only partly followed their hosts' patterns, two *Centris* species. Edge effects affected the bee community, so that increasing edge habitat will influence the conservation value of secondary forest fragments.

Introduction

Global environmental change threatens biodiversity, species persistence and distributions as well as antagonistic and mutualistic interactions (Barlow et al. 2007). In the tropics ongoing deforestation results in a mosaic of forest fragments distributed between pastures and plantations (Vitousek et al. 1997; Tilman et al. 2001). Habitat fragmentation is a major threat to biodiversity (Davies et al. 2000; Fahrig 2003) as it leads to declines in species richness and populations (Donovan and Flather 2002), loss of genetic diversity (Gibbs 2001) and to disruption of trophic interactions, e.g. predation and parasitism. On the other hand, secondary forest fragments can be valuable for biodiversity (Turner and Corlett 1996), since their coverage is expanding while that of continuous primary forest habitat is limited, and they enhance landscape connectivity (Barlow et al. 2007).

In tropical rainforests arthropods have been shown to be equally or more diverse in the canopy than in the understory (Erwin 1982; Stork and Grimbacher 2006), but canopy diversity, especially their community patterns, are understudied (Kays and Allen 2001; Ulyshen et al. 2010). Some studies have found vertical stratification of bees with respect to flight height and floral resource use (Frankie and Coville 1979; Roubik et al. 1982; Bawa 1990; Ramalho 2004; Ulyshen et al. 2010), whereas others have not (Roubik 1993). Many trap-nesting bees in tropical rainforests prefer the canopy, at least in primary forest and large fragments (Morato and Campos 2000; Thiele 2003). However, studies along a fragmentation gradient of small secondary forest remnants are lacking.

Most studies investigating whole communities of trap-nesting bees with large sample sizes in tropical countries have been done in agro-ecosystems or along land-use gradients (Klein et al. 2002; Tylianakis et al. 2005; Klein et al. 2006), but few studies have investigated the trap nesting bee communities in tropical forests (Morato and Campos 2000; Morato 2001; Thiele 2003; Loyola and Martins 2006; Loyola and Martins 2011). None of the studies investigated a fragmentation gradient of secondary forest remnants, which is important due to their potential for conservation and maintenance of ecosystem services for agricultural areas (Klein et al. 2003; Brosi et al. 2007a).

Bees are the most important group of pollinators (Didham et al. 1996), especially for native plants in tropical forests, where animal-mediated pollination is more frequent than in temperate regions (Bawa 1990; Ollerton et al. 2011). Trap-nesting bees inhabiting native forest are considered sensitive to habitat fragmentation (Morato and Campos 2000) since they depend on nesting sites (Potts et al. 2005), materials for nest construction (Taki et al. 2008) and food resources (Tschamtker et al. 1998). There is less knowledge of species interactions

(Godfray et al. 1999) especially in the canopy. Trap nests are well suited for gaining information on biodiversity, abundance and community parameters such as mortality and parasitism rates (Tschardt et al. 1998). Higher trophic levels are more affected by habitat modification (Valladares et al. 2006; Fenoglio et al. 2012) because their interactions are more sensitive to phenology, behavior, physiology and abundances of multiple species (Suttle et al. 2007; Tylianakis et al. 2007).

This study investigated the vertical distribution of bee communities, single species patterns and community parameters along a fragmentation gradient of small secondary forests in the Sarapiquí region in Costa Rica. We hypothesized that larger fragments would sustain a more species rich and abundant bee community, with higher parasitism - and lower mortality rates. We expected a higher abundance and species diversity in the canopy and at the forest edge, although individual species may respond differently. We assumed that mortality rates would be lower in the forest center compared to the edge and that the rate would not respond to different heights, because this would be species dependent. Concerning the parasitism rate of *Centris* species and their cuckoo bees, we expected, that cleptoparasites would be more affected by fragmentation.

Material and Methods

Study region and study sites

This study was conducted in lowland rainforest fragments in the Sarapiquí region in northeastern Costa Rica during a one year period, between February 2011 and February 2012. Twelve differently sized secondary forest fragments (0.9 – 16.62 ha) with no recent management activities with at least 2 km distance between each and a similar amount of forest (ap. 30%) in a 2 km circle were selected. The surrounding landscape consisted of forest remnants, pastures for cattle and farmland producing pineapple, ornamental plants and banana.

Study design

In each of the 12 fragments three trees were selected along a transect line, one tree in the forest center, one in an intermediate distance and the last one at the forest edge. At each tree three packages of three trap nests were placed at three heights (2 m, 10 m, 20 m), amounting to 27 trap nests per fragment. Trap nests consisted of a PVC tube filled with different diameters of about 120 reed internodes (*Phragmites australis*) cut to 20 cm length (Tschardt et al. 1998).

During regular inspections (1 - 2 months) completed nests, recognized by closures of soil or plant materials (Krombein 1967), were collected and replaced by empty internodes of similar diameters. In the lab nests were opened and identified to morpho-species; living, dead and parasitized cells were counted in order to calculate number of brood cells and the mortality- and parasitism rates. The nests were then placed in pieces of transparent plastic tube and closed with cotton at both ends. After emergence, adults were killed for later identification to species or morpho-species level.

Statistics

The Shannon-Index and the ICE estimator were calculated with the Software Estimate S (Vs. Win 910, 2014).

For the variables (1) number of brood cells, (2) parasitism rate, (3) mortality rate, (4) raw species richness, (5) mean ICE and (6) Shannon-Index we calculated linear mixed effects models containing all interactions of size, location and height with the statistical program R (R Development Core Team VS R 3.0.3). The number of brood cells was analyzed with a poisson model, whereas the mortality- and parasitism rates were analyzed with a binomial model and the species diversity measures with a gaussian model (Crawley 2002). To account for the nested design the random term “fragment” was included. Where necessary an overdispersion correction term was included in the final models.

Size effects on the variables (1) species richness per fragment, (2) percentage of *Centris* cells of all brood cells and (3) percentage parasitism per fragment were analyzed with linear models. The same procedure was chosen to analyze the preferences of individual species with sufficient sample size with respect to size, location and height. The best models were chosen according to the lowest AIC (Burnham and Anderson 2002).

Results

We found a total of 2340 brood cells of 16 different bee species, comprising ten non-parasitic and six parasitic bee species. Fragment size alone had no impact on the response variables (Tab I, Tab II). Location (tree 1 at the forest edge, tree 2 at an intermediate distance, tree 3 at the forest center) and height (2, 10 and 20 m) had significant effects on the response variables.

Tab. 1 Effects of fragment size, tree location and height on bee abundance, parasitism- and mortality rates
 (*: $p < 0.05$, **: $p < 0.01$; ***: $p < 0.001$)

response variable	explanatory variable	z-value	p-value
abundance	size	\	\
	height 10	-4.019	5.86e-05 ***
	height 20	-1.109	0.2673
	tree 2	\	\
	tree 3	\	\
	height 10*size	0.907	0.3643
	height 20*size	-1.944	0.0519
parasitism rate	size	\	\
	height 10	-1.923	0.0545
	height 20	-1.957	0.0503
	tree 2	-0.896	0.3702
	tree 3	1.192	0.2331
mortality rate	size	1.81	0.0703
	height 10	-1.854	0.0637
	height 20	-2.499	0.0124 *
	tree 2	\	\
	tree 3	\	\

Tab. 2 Effects of fragment size, tree location and height on species richness, ICE and Shannon diversity index (*: $p < 0.05$, **: $p < 0.01$; ***: $p < 0.001$)

response variable	explanatory variable	t-value	p-value
Species richness	size		
	height 10	-4.752	3.08e-06 ***
	height 20	-3.643	0.000315 ***
	tree 2	0.079	0.936923
	tree 3	2.218	0.027299 *
ICE	size	-0.37	0.718802
	height 10	10.433	< 2e-16 ***
	height 20	13.494	< 2e-16 ***
	tree 2	5.41	1.29e-07 ***
	tree 3	8.989	< 2e-16 ***
	height 10 * size	-2.354	0.019240 *
	height 20 * size	-4.153	4.28e-05 ***
	height 10 * tree 2	-3.194	0.001551 **
	height 20 * tree 2	-3.656	0.000302 ***
	height 10 * tree 3	-5.259	2.76e-07 ***
	height 20 * tree 3	-5.908	9.40e-09 ***
	size * tree 2	-1.232	0.218835
	size * tree 3	-2.18	0.030071 *
	Shannon Index	size	-1.451
height 10		12.075	< 2e-16 ***
height 20		19.559	< 2e-16 ***
tree 2		2.489	0.013344 *
tree 3		7.044	1.24e-11 ***
height 10 * size		-2.326	0.020697 *
height 20 * size		-4.307	2.23e-05 ***

1. Fragment size effects on species diversity, percentage of *Centris* and parasitism rate

Fragment size did not influence species diversity calculated per fragment (species richness: $p = 0.112$; ICE: $p = 0.256$; Shannon: $p = 0.09$). The percentage of the most abundant genus and the parasitism rates calculated per fragment did not respond to fragment size (% *Centris*: $p = 0.25037$; parasitism rate: $p = 0.835090$).

2. Vertical distribution of bee abundance and diversity patterns

Bee abundance was significantly lower at 10 m compared to other heights ($p < 0.001$, Fig. 1).

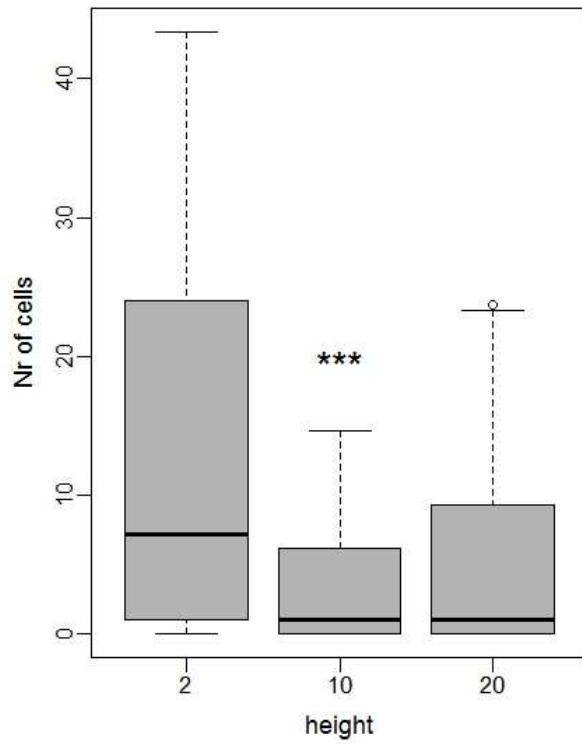


Fig. 1 Vertical distribution of bee abundance (***: $p < 0.001$, height in m)

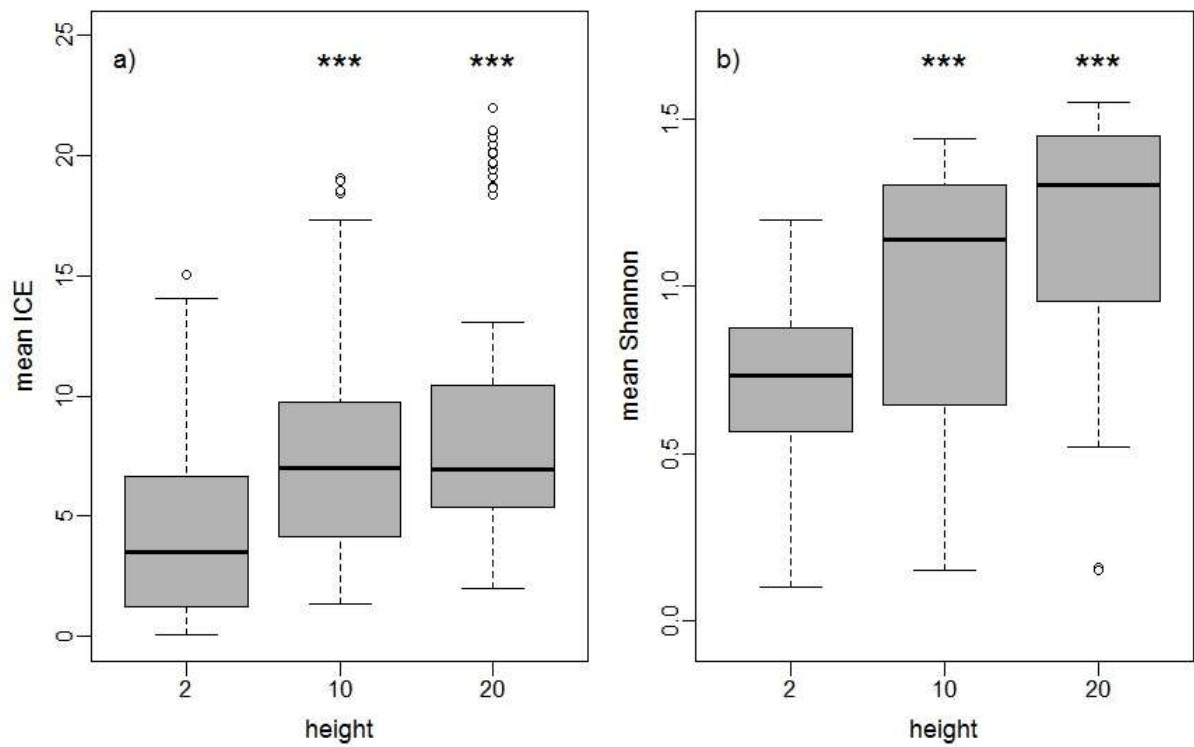


Fig. 2 Vertical distribution of species diversity with **a)** the estimator ICE and **b)** Shannon diversity index (***: $p < 0.001$, height in m)

Species richness was lower at 10 and 20 m height ($p < 0.001$, Tab. II), whereas ICE and Shannon index indicated a higher species diversity at 10 and 20 m (ICE: $p < 0.001$, Shannon: $p < 0.001$, Fig.2). We found a significantly lower species diversity at 10 and 20 m in larger compared to smaller fragments (ICE: 10 m: $p < 0.05$, 20 m: $p < 0.001$; Shannon: 10 m: $p < 0.05$, 20 m: $p < 0.001$). With ICE, diversity was estimated to be lower at heights of 10 m and 20 m on both inner trees (see Tab. II, $p < 0.01$ for 10 m at the intermediate distance, $p < 0.001$ for 20 m at the intermediate tree and 10 and 20 m height for the inner tree).

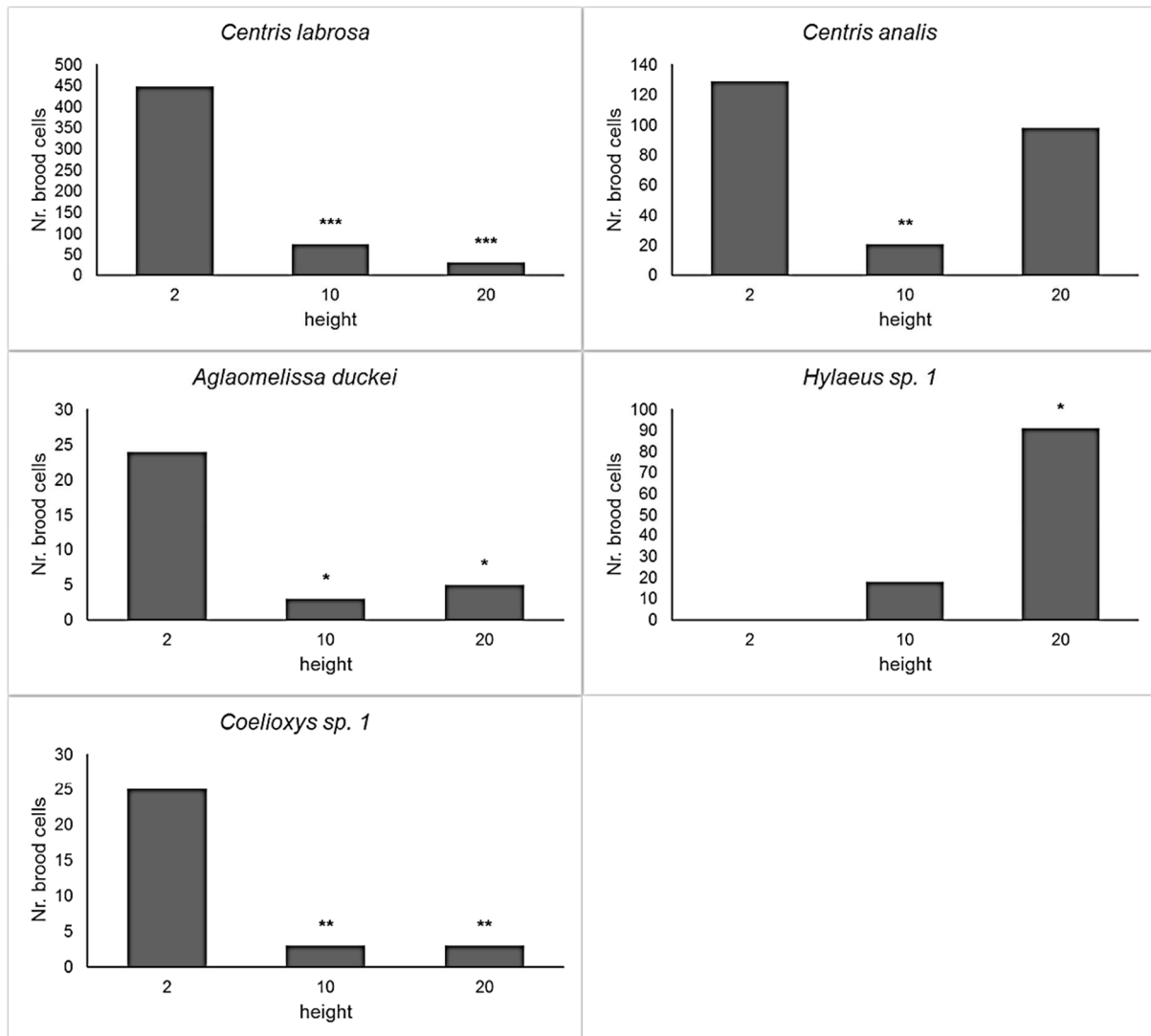


Fig. 3 Vertical distribution of the abundance of individual species (***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, height in m).

Overall species diversity was higher in the canopy, but individual species responded differently (Fig. 3). *C. labrosa* preferred the forest understory at 2 m for nesting ($p < 0.001$), and *C. analis* followed the general abundance pattern, preferring 2 or 20 m ($p < 0.01$). The

two parasitic species *Aglaomelissa duckei* and *Coelioxys sp. 1* followed the patterns of their hosts *C. labrosa* and *C. analis* and preferred to attack nests at 2 m (*A. duckei*: $p < 0.05$, *C. sp.1*: $p < 0.01$). In contrast *Hylaeus sp. 1* was a canopy nester ($p < 0.05$) and did not construct a single nest at 2 m, which was also the case for *Anthodioctes gualanense* ($p = 0.0552$). Worth noting is *Duckeanthidium thielei*, which was found for the second time in Costa Rica, near the original locality La Selva, in the canopy of a 1.2 ha forest fragment. This species was described in 2002 (Michener 2002) and is only known from these two localities.

3. Edge effects on bee abundance and diversity patterns

The different tree locations did not affect overall bee abundance (Tab. I), but species diversity was higher in the forest center compared to the forest edge. All three diversity variables (raw species diversity, ICE and Shannon index) responded positively to the forest center (species richness: $p < 0.05$, ICE: $p < 0.001$, Shannon: $p < 0.001$; Fig.4). ICE and Shannon estimated species diversity to be higher at the intermediate tree (ICE: $p < 0.001$, Shannon: $p < 0.05$). However larger fragment sizes resulted in a lower ICE at the forest center ($p < 0.05$, Tab. I).

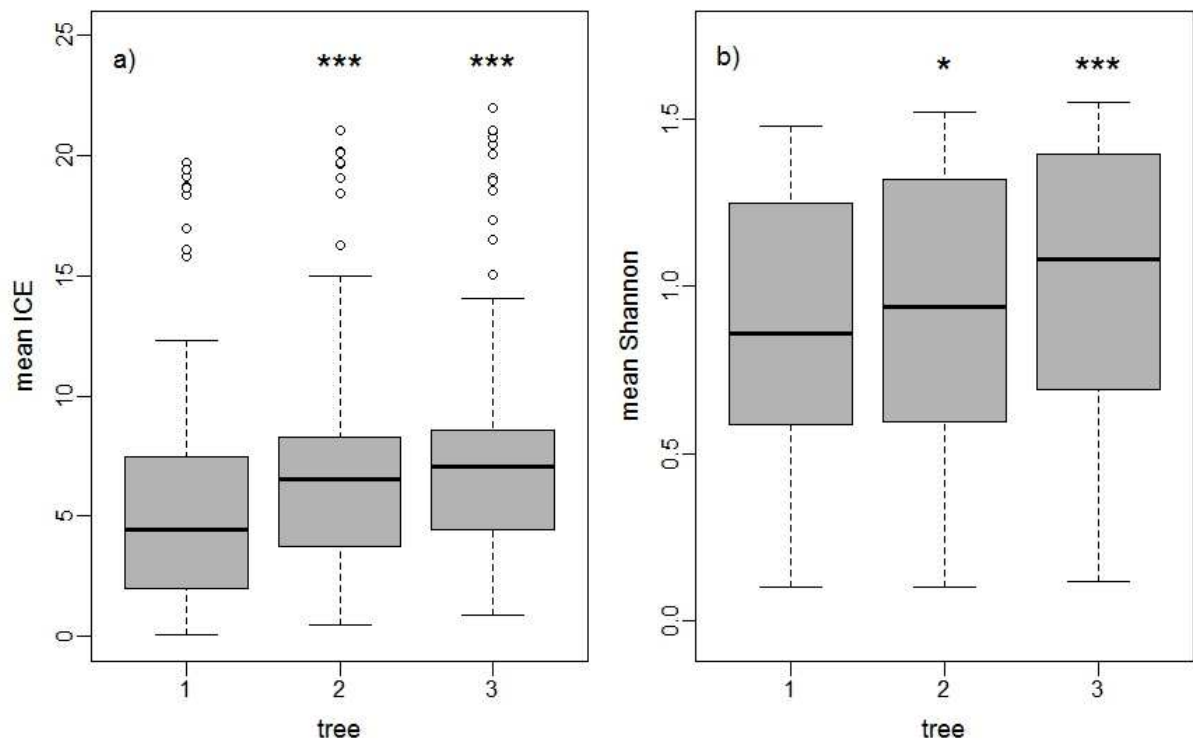


Fig. 4 Edge effects on species diversity with **a)** the estimator ICE and **b)** Shannon diversity index (***: $p < 0.001$, *: $p < 0.05$; tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center)

Most species preferred forest conditions, but individual species responded differently. We found, that *Megachile* sp. 2 ($p < 0.05$), *Hylaeus* sp. 1 ($p < 0.05$), *Centris labrosa* ($p < 0.05$) and their cleptoparasites *Aglaomelissa duckei* ($p < 0.01$) and *Coelioxys* sp.1 ($p < 0.05$) preferred the forest interior for nesting (Fig. 5), whereas *C. analis* ($p < 0.05$) and *Tetrapedia maura* ($p < 0.01$) preferred edge conditions.

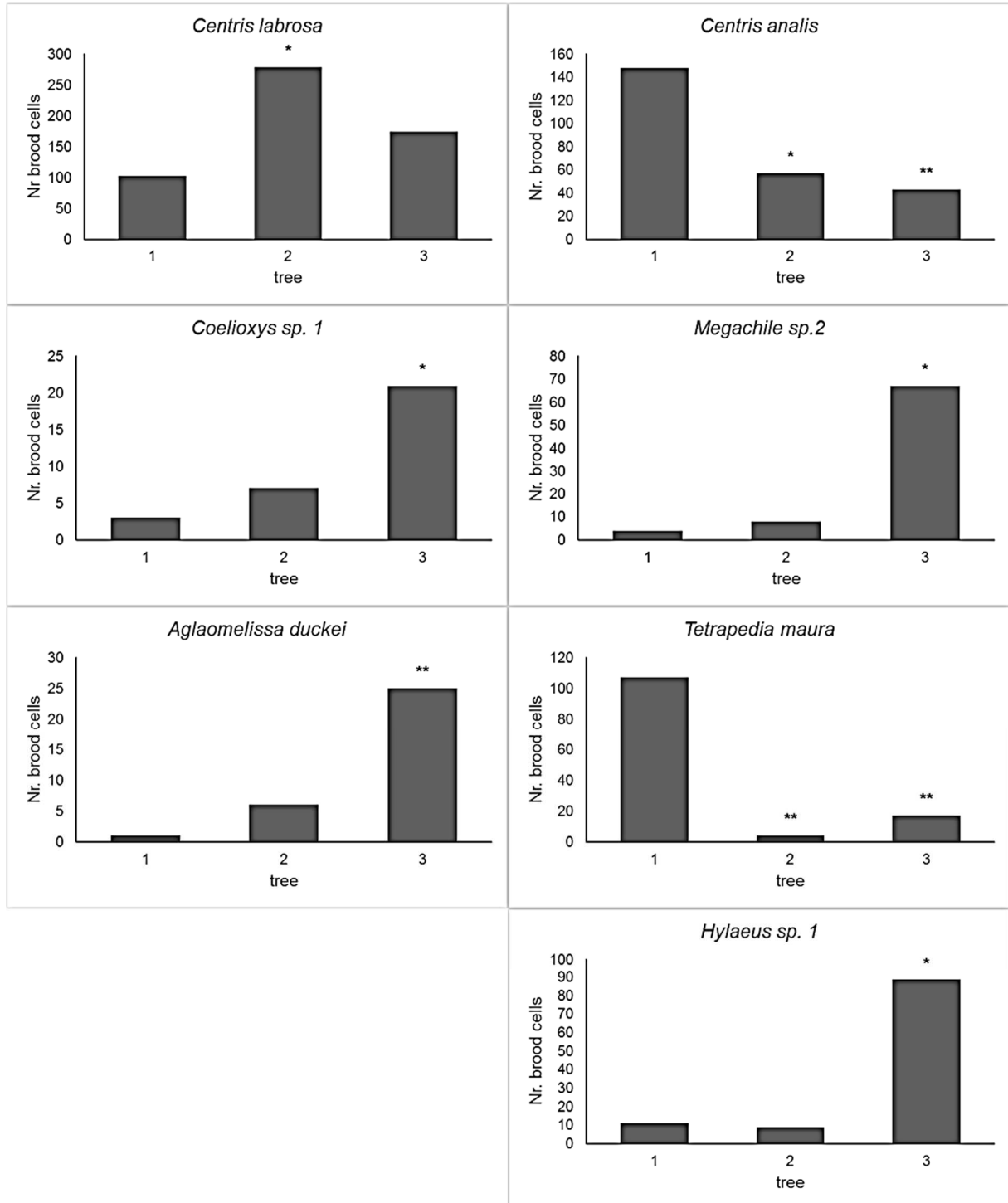


Fig. 5 Edge effects on the abundance of individual species (***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$; tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center)

4. Effects of fragment size, tree location and height on the mortality and parasitism rate

Mortality rates did not change significantly with fragment size, but tended to increase in larger fragments ($p = 0.0703$). However height significantly affected mortality rates, being highest in the understory and lowering with height, slightly non-significant for 10 m ($p = 0.0637$), but significant for 20 m ($p = 0.0124$, Fig. 6).

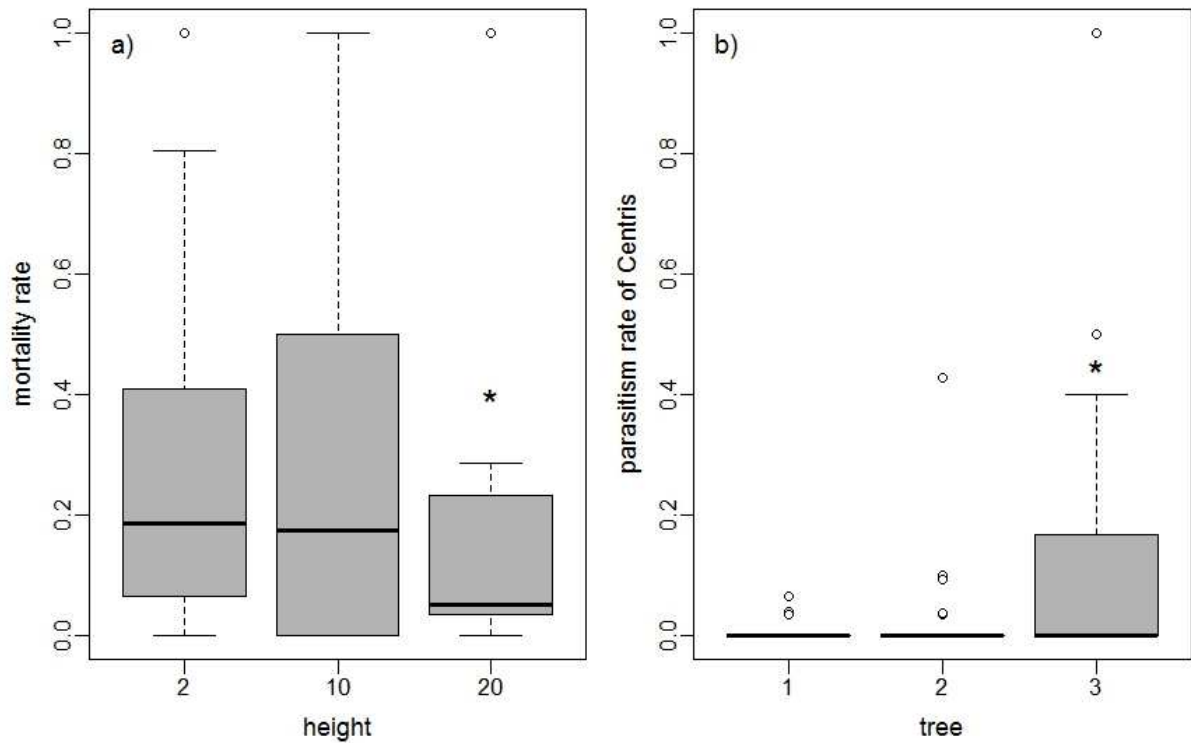


Fig. 6 a) Mortality rate in relation to different heights (2, 10 20 m),
 b) Parasitism rate of *Centris* and their cuckoo bees in relation to different locations in the forest (tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center; *: $p < 0.05$)

Parasitism rates were not significantly related to fragment size and location, but tended to be lower at 10 and 20 m height (Tab. I). As shown in Fig. 6 b), the parasitism rates of the cuckoo bees *Aglaomelissa duckei* and *Coelioxys* sp. 1 on both *Centris* species was higher in the forest center than at the edge ($p < 0.05$).

Discussion

1. Fragment size effects on species diversity, percentage of *Centris* and parasitism rate

Contrary to our expectations fragment size did not influence bee diversity. Previous studies in tropical systems relating bee diversity to size have revealed variable results, some showing an increase in diversity with size (Chacoff and Aizen 2005; Brosi 2009; Meneses Calvillo et al. 2010) and others finding no relationships between fragment size and diversity (Brosi et al. 2007b; Gazola and Garófalo 2009). This variability could be due to many factors, since little is known about nesting behavior of bees in tropical forests. Presence or absence of specific tree species, occurrence of natural nesting sites and food availability (Tscharrntke et al. 1998; Viana et al. 2001; Morato and Martins 2006) among other factors can affect bee species diversity unrelated to fragment size. However, our small-sized fragments appear to offer nesting opportunities and food resources for bees as we found similar species numbers as Morato and Campos (2001) in large Amazonian fragments. Possibly size would have had a significant impact if we had included larger fragments, since the latter contain more tall dead trees with nesting sites for bees (Didham and Lawton 1999; Thiele 2003; Morato and Martins 2006).

In small fragments there is often a dominance of few abundant species (Laurance et al. 2002; Zhu et al. 2004), but the amount of *Centris* was not influenced by size since all our fragments were relatively small and *Centris* bees seem to be generally abundant in Neotropical habitats (Buschini 2006; Morato and Campos 2000; Thiele 2003; Viana et al. 2001).

We expected that antagonists suffer more from habitat fragmentation (Valladares et al. 2006; Fenoglio et al. 2012), but parasitism rates did not respond to fragment size. Fragments in our size range seem to provide sufficient hosts, but further research is needed to see whether a size effect would occur when larger fragments or primary forest are included.

2. Vertical distribution of bee abundance and diversity patterns

The higher bee abundances in the understory can be explained through the abundant *C. labrosa* and their cleptoparasites *Aglaomelissa duckei* and *Coelioxys sp.1*. There were less abundant species like *Hylaeus sp. 1* and *Anthodiocetes gualanense* that preferred the canopy, and *C. analis* was abundant in the understory and the canopy. However none of the species preferred the intermediate height of 10 m. The reasons for strata preference could be microclimate and natural nesting availabilities (Morato 2001; Thiele 2003). Natural cavities are possibly more abundant in the canopy due to sunlight exposure whereas higher humidity in the understory leads to higher activity of fungi (Morato and Martins 2006). Moreover

solitary bee species are often philopatric (Morato and Martins 2006), i.e. that they search for nesting sites where they emerged.

Species richness declined with height, which was opposite to the trends of the ICE and the Shannon-Index. The latter two variables are more reliable, because counted species richness does not reflect differences in abundance and is therefore misleading. We conclude that species diversity of trap-nesting bees was higher at the canopy level. The abundant species in the understory can be considered rainforest specialists, e.g. *C. labrosa* (Thiele 2003), whereas the majority of bees preferred the sunny dry conditions in the canopy. Moreover bee pollination is especially predominant in the canopy of tropical lowland forest (Bawa et al. 1985), so nesting closer to their food resources might be more attractive. Our results suggest that the canopy preference could be also due to the lower mortality rate and the lower risk of being parasitized. Both studies investigating the vertical distribution of trap nesting bee communities in tropical rainforest found a canopy preference of bees in primary forest and large fragments (Morato 2001; Thiele 2003), like we did in small secondary forest remnants. Therefore it is important monitor bees and other insects at the canopy level.

Species diversity at 10 and 20 m was lower in larger compared to smaller fragments and at the inner tree at 10 and 20 m, which can be explained through our study design. 10 and 20 m have different microclimatic conditions depending on forest structure since canopy height is lower in smaller fragments and at the edge (Didham and Lawton 1999). The trap nests at 20 m at the edge and in smaller fragments were more sun exposed than those in larger fragments or in the forest center, where there are taller trees, resulting in more humid conditions, which affects nesting success. Bees also find a more natural nesting sites in larger fragments and the forest center, resulting in a lower species diversity in the trap nests (Viana et al. 2001).

3. Edge effects on bee abundance and diversity patterns

Bee abundance did not vary from edge to center due to different preferences of individual species. *C. labrosa*, *Megachile sp. 2*, *Coelioxys sp. 1*, *Aglaomelissa duckei* and *Hylaeus sp. 1* preferred the forest interior, whereas *Tetrapedia maura* and *C. analis* preferred the forest edge. As a result, we found a similar number of brood cells at the different locations. So single species responses can be more informative than combined abundance and richness data in tropical forest remnants (Nemésio and Silveira 2006) and species-based analyses can help to understand contradictory responses to habitat fragmentation in the tropics.

Species diversity was higher in the forest center and most bees preferred forest conditions, probably due to the more stable microclimate, since temperature increases from the center to the edge in Amazonia and the evaporation rate follows the same pattern (Didham and Lawton

1999). Bee diversity was shown to be higher in continuous forest and natural gaps in the Amazon and bees are highly sensitive to fragmentation (Morato and Campos 2000). With ongoing deforestation and fragmentation and the resulting increase of edge conditions, natural bee communities could become more threatened in future, which could lead to pollination deficits of natural plant communities (Didham et al. 1996; Liow et al. 2001).

The lower ICE estimates at the inner trees in larger fragments could be due to more available natural nesting cavities because of taller and more dead trees in larger fragments since this can affect nesting success in trap nests (Viana et al. 2001).

Most species preferred the forest center, but a few species preferred edge conditions, e.g. *C. analis*, which has a broad geographical range from Brazil to Mexico (Moure 1960) and *T. maura*. These two species seem to be better adapted to steeper temperature and humidity fluctuations and will probably profit from ongoing fragmentation and increased edge conditions. Morato and Campos (2000) also found that despite an overall preference for continuous forest and natural gaps, some species preferred disturbed habitats and deforested areas. With respect to the effects on pollination, the question is whether the decline in most pollinators due to fragmentation can be compensated by the disturbance-adapted species. This depends on the degree of specialization in pollination, which is highly variable in the tropics (Bawa 1990). Because most species preferred the forest interior, small forest fragments can help to sustain bee communities and to stabilize pollination services, which has been shown for stingless bees (Brosi et al. 2007b). However further fragmentation leading to an even greater increase in edge conditions will negatively affect trap-nesting bees.

4. Effects of fragment size, location and height on the mortality and parasitism rate

Mortality rates tended to increase in larger fragments, which is probably due to higher humidity, that results in a higher fungal infestation rate of nests (personal observation). However larger fragments contain more tall trees (Didham and Lawton 1999), providing natural nesting opportunities for the majority of bees (Morato and Martins 2006), so that larger fragments may be more suitable for some of the scarcer species. Tree location did not affect mortality rates, because of the preferences of individual species. Species probably prefer certain locations due to their advantage in survival, which is dependent on individual species traits (Nemésio and Silveira 2006).

The most interesting pattern was the significantly lower mortality in the canopy. Since the mortality rate was separated from the parasitism rate, the latter can be excluded as explanation. Most bee species prefer the canopy (Morato 2001; Thiele 2003), probably because it provides better conditions for survival as shown in our data. It is possible, that the

drier sunnier conditions in the canopy helps to reduce infestations by fungi. It is also probably easier for bees to find nectar and pollen resources in the canopy (Bawa 1990), although this explanation has been questioned by some authors (e.g. Roubik, 1993).

The overall parasitism rate was not related to fragment size or tree location, but did show the tendency of being higher in the understory, which is probably due to the dominance of *Centris* and their related cleptoparasites. The higher parasitism rate of the two cuckoo bees *Aglaomelissa duckei* and *Coelioxys sp. 1* on *C. labrosa* and *C. analis* in the forest center was interesting, because it did not follow the patterns of host abundance. *C. labrosa* preferred the intermediate distance between edge and forest center and *C. analis* even the forest edge. So the two parasite species seem to prefer the forest center for other reasons, for example the higher humidity and more stable temperature conditions (Didham and Lawton 1999) as long as they find enough hosts. This agrees with the hypothesis, that higher trophic levels are more susceptible to habitat fragmentation (Nouhuys 2005; Valladares et al. 2006). We conclude that ongoing fragmentation and deforestation will affect diversity and trophic interactions of bee communities, with currently unknown long-term consequences for the survival of forest specialists and plant-pollinator interactions.

IV Fragmentation effects on the trap-nesting community from the understory to the canopy with special emphasis on higher trophic levels

This chapter is in preparation for publication as: Stangler ES, Hanson P, Steffan-Dewenter I; Fragmentation effects on the trap-nesting community from the understory to the canopy with special emphasis on higher trophic levels.

Running title: Fragmentation effects on different trophic levels

Key words: area effects, edge effects, vertical stratification, natural enemies, trophic interactions, secondary forest remnants

Abstract

The effects of habitat fragmentation on host and especially antagonist communities from the understory to the canopy are still poorly understood in tropical forests. With ongoing deforestation, small secondary forest fragments might contribute to the conservation of biodiversity, trophic interactions and ecosystem services. This study investigated fragmentation effects on the trap-nesting communities with special emphasis on the antagonists from the understory to the canopy as well as the relation between host and antagonists in secondary forest fragments in the northeastern lowlands of Costa Rica.

We demonstrate the importance of monitoring biodiversity, community compositions and trophic interactions from the understory to the canopy. Fragment size affected antagonists more than their hosts, showing higher trophic levels to be more sensitive to habitat area. However, edge conditions strongly affected both host and antagonist richness, as well as their community composition, so that ongoing fragmentation and increased edge habitat will favor a few abundant disturbance-adapted species over the rare and more diverse forest-adapted species. We also observed a positive-density dependent parasitism rate, as well as an increase of the parasitism rate not only with antagonist abundance but also diversity.

Small secondary forest fragments can contribute to the conservation of biodiversity and trophic interactions, but an increase of edge habitat will have highly negative consequences on above-ground nesting Hymenoptera, which in turn will affect important interactions such as pollination, predation and parasitism.

Introduction

Global environmental changes threaten species survival, alter species abundances and species interactions (Barlow et al. 2007). Habitat fragmentation consisting of habitat loss and spatial configuration of habitat, is considered a major threat to biodiversity (Fahrig 2003). Fragmentation can cause lower biodiversity, declines of populations and resulting loss of genetic diversity, as well as the disruption of trophic interactions such as predation and parasitism (Gibbs 2001; Laurance et al. 2002; Steffan-Dewenter 2003; Klein et al. 2006). In the tropics, where deforestation of rainforests has led to forest fragments becoming embedded in a matrix of pastures and plantations (Vitousek et al. 1997; Tilman et al. 2001), a range of studies investigating fragmentation has been conducted (e.g. Brosi et al. 2007b; Brosi 2009; Meneses Calvillo et al. 2010), but the effects of fragmentation can be highly eclectic (Laurance et al. 2002). Generally intact primary forest contains more species per unit area than fragments (Laurance et al. 2002; Barlow et al. 2007), but as deforestation rapidly goes on (Barraclough 2013), it is important to evaluate secondary forest fragments as a one possible resource for biodiversity conservation (Barlow et al. 2007).

Studies investigating the arthropod communities in tropical forests are lacking and would be highly valuable for understanding the mechanisms of maintaining the enormous diversity (Godfray et al. 1999). This diversity is partly due to vertical stratification since most insect communities in tropical forests prefer distinct strata (Basset et al. 2003; Vance et al. 2007; Paniagua et al. 2009), many of them being more diverse in the canopy (Morato 2001; Stork and Grimbacher 2006). However most studies investigating fragmentation did not include the vertical distribution of arthropod communities, which is often due to difficulties in sampling in all strata equally or in sampling the canopy (Basset et al. 2003). In particular, the effects of fragmentation on higher trophic levels with a high degree of specialization are not well studied throughout their entire vertical distribution. This, however, is of great interest as they are at a high risk of extinction (La Salle 1993; Shaw and Hochberg 2001).

Trap-nesting bees, wasps and their natural enemies have been used as bio-indicators in a range of studies to evaluate the quality of habitat and land use (Tylianakis et al. 2005; Loyola and Martins 2006; Steckel et al. 2014) due to their sensitivity to environmental alterations. Trap nests are a valuable system not only to monitor biodiversity, but also community compositions and trophic interactions such as pollination, predation and parasitism (Tscharrntke et al. 1998). Their inhabitants, bees and wasps are essential components of terrestrial systems in the tropics (Loyola and Martins 2009) since bees are considered the most important pollinator group (Didham et al. 1996; Kremen et al. 2007) and wasps are

known to be important predators and parasitoids in natural and agricultural habitats (Penagos and Williams 1995; Klein et al. 2004). The trap-nesting host community has been shown to be sensitive to fragmentation in native Neotropical forests (Morato and Campos 2000) as they depend on nesting sites (Potts et al. 2005), materials for nest constructions (Taki et al. 2008) and pollen or arthropod food resources (Tscharrntke et al. 1998).

With respect to the antagonist community, tropical studies have been conducted along a land-use gradient (Tylianakis et al. 2006; Tylianakis et al. 2007) or on the antagonist community of plant gillers (Paniagua et al. 2009), but studies on the antagonistic community of trap-nesting Hymenoptera of secondary forest fragments are missing and few data exist on specific groups of predators and parasitoids in tropical canopies (Godfray et al. 1999). Such studies are greatly needed, because higher trophic levels are assumed to be more vulnerable to environmental changes (Holt et al. 1999; Rand et al. 2012) and they may act as keystone species in ecosystems (La Salle 1993). Natural enemies play an important role as they can regulate population dynamics from the top by positive density dependent parasitism or predation (Hassel and Wilson 1997; Berryman and Turchin 2001), but knowledge of ecological interactions between hosts and natural enemies are especially scarce (Paniagua et al. 2009). Those interactions could be disrupted by increasing destruction of habitat, for example deforestation and fragmentation (Tscharrntke and Brandl 2004; Tylianakis et al. 2006). Coexistence mechanisms could be affected because parasite loads seem to correlate positively with host abundance (Durrer and Schmid-Hempel 1995), so that common species are expected to be affected most by natural enemies (Steffan-Dewenter and Schiele 2008). Moreover, Tylianakis et al. (2006) showed, that the parasitism rate correlated positively with parasitoid diversity, which was higher in more modified habitats.

There is a lack of studies in the tropics investigating the effects of fragmentation on the community composition of trap-nest inhabitants and even more importantly, their antagonist community in small secondary forest fragments. We assessed the abundance, the diversity and the trophic interactions of trap-nesting Hymenoptera along a fragmentation gradient of 12 differently sized forests at three different locations from the forest edge to the forest centre and at three different heights in a tropical lowland forest in Costa Rica. This was done to answer the following questions:

- 1) Does the abundance, diversity and community composition of hosts or antagonists differ between the three different heights?
- 2) Does fragmentation – fragment sizes and edge effects (= tree locations) affect the abundance, diversity and community composition of host and antagonists?

- 3) Are the effects stronger for the higher trophic level?
- 4) How is the parasitism rate affected by host and antagonist abundance and diversity?
- 5) What is the conservation value of secondary forest fragments for above-ground nesting Hymenoptera, especially for the antagonists?

Material and Methods

Study region and study sites

Twelve secondary rainforest fragments were selected in the Sarapiquí region near La Virgen in northeastern Costa Rica. Field work was performed during a one-year period from February 2011 to February 2012. The landscape in Sarapiquí consists of forest remnants, pastures for cattle and farmland producing pineapple, ornamental plants and banana. According to the Holdridge life zone system, Sarapiquí belongs to the “tropical moist forest” (Holdridge 1967). All study sites were separated by a distance of at least 2 km and contained approx. 30 % forest cover in a 2 km circle.

Study design and sampling

At each of the twelve study sites three trees were selected on a transect line, one tree in the forest center, one in an intermediate distance and the last one at the forest edge. 27 trap nests were installed at each forest fragment with 9 trap nests per tree. Three trap nests were joined to a package, which was installed at three heights (2 m, 10 m and 20 m).

Every trap nest consisted of a plastic tube filled with approx. 120 reed internodes (*Phragmites australis*) cut to 20 cm with different diameters (Tscharrntke et al. 1998). When nest building was completed, e.g. when internodes were closed by soil or plant materials (Krombein 1967), nests were collected during regular inspections (1 - 2 months intervalls). In the lab, nests were opened and identified to morpho-species. We counted the living and parasitized cells in order to calculate the parasitism rates. The nests were then stored in pieces of transparent plastic tubes and closed with cotton at both ends. After emergence, adults were killed for later identification. Most hymenopterans were identified to genus level and in part to morpho-species or species level (with the exception of some Chalcidoidea and Ichneumonoidea).

Statistics

Based on abundance and species diversity data with the taxonomic levels that were available (at least genus level) we calculated different diversity measures and community similarity indices using the Software Estimate S (Vs. Win 9.10, 2014). Because measures of diversity

and community similarity were correlated and revealed the same results in the analyses, we selected the Shannon-Wiener-Index, one of the most widely used diversity indices (De' Ath 2012), and the Chao's abundance-based Jaccard Index (CJEA, since it was shown to be better suited for assemblages with numerous rare species (Chao et al. 2005) for hosts and antagonists.

Linear mixed effects models were calculated for every response variable, 1) the abundance (number of brood cells) 2) counted species richness 3) Shannon-Index 4) the parasitism rate 5) Chao's abundance-based Jaccard Index (= CJEA) of hosts and antagonists using R (R Development Core Team VS R 3.0.3). In all models fragment size, tree location and height, as well as the random term "fragment" were included. In the abundance models for the antagonists and the models for the parasitism rate we also included the abundance of the host or the diversity of the host. To test for a potential different sensitivity of host vs. antagonists, we additionally calculated all models including the two-factored trophic level antagonists vs. hosts. The number of brood cells and the counted species richness were analysed using a Poisson distribution for count data (Crawley 2002), whereas we used a Gaussian distribution for the diversity measures and a binomial model for the parasitism rate. An overdispersion correction term was included in the final models where necessary and models were selected according to the lowest AIC.

Results

The community consisted of 38 hymenopteran genera comprising seven nonparasitic and two parasitic bee genera and 15 nonparasitic and 14 parasitic wasp genera. We also found antagonists from four families of Coleoptera, four families of Diptera as well as Acari and Lepidoptera (see Tab. 1).

Vertical distribution of species richness and community composition

The counted species richness did not differ between the tree heights, but the Shannon-Index differed between strata (Tab. 3). Host diversity was higher at 10 and 20 m compared to 2 m height ($p < 0.001$, Fig. 1). The antagonists followed the patterns of their host with a higher diversity at 10 and 20 m ($p < 0.001$, Fig. 1). Moreover antagonists showed a significantly steeper diversity increase at 10 and 20 m than hosts (Shannon: 10 m * hosts $p < 0.001$, 20m * hosts $p < 0.001$).

Tab. 1 Mean and range of abundances and numbers of fragments inhabited of all genera found

genus	trophic level	Mean abundance	Range abundance	Nr of fragments inhabited
Anthophoridae				
<i>Centris</i>	h	134.83	2 - 229	12
<i>Aglaomelissa</i>	a	2.83	0 - 11	7
Megachilidae				
<i>Megachile</i>	h	38.83	0 - 142	11
<i>Duckeanthidium</i>	h	0.33	0 - 4	1
<i>Anthodioctes</i>	h	4.50	0 - 31	2
<i>Coelioxys</i>	a	2.92	0 - 10	8
Colletidae				
<i>Hylaeus</i>	h	9.17	0 - 59	6
Apidae				
<i>Tetrapedia</i>	h	10.83	0 - 37	7
Spheciform wasps				
<i>Ampulex</i>	h	1.33	0 - 7	6
<i>Liris</i>	h	10.67	0 - 62	5
<i>Nitela</i>	h	1.92	0 - 10	5
<i>Penepodium</i>	h	0.08	0 - 1	1
<i>Pison</i>	h	26.58	0 - 123	10
<i>Podium</i>	h	153.58	32 - 342	12
<i>Trigonopsis</i>	h	0.42	0 - 3	3
<i>Trypoxylon</i>	h	1139.50	538 - 1668	12
Pompilidae				
<i>Ageniella</i>	h	0.17	0 - 2	1
<i>Auplopus</i>	h	122.92	8 - 380	12
<i>Dipogon</i>	h	0.58	0 - 4	2
<i>Priocnemella</i>	h	9.33	0 - 55	10
Eumeninae				
<i>Montezumia</i>	h	1.33	0 - 14	2
<i>Pachodynerus</i>	h	16.25	0 - 110	6
<i>Zethus</i>	h	11.08	0 - 48	9
Chalcidoidea				
<i>Brachymeria</i>	a	0.17	0 - 1	2
<i>Leucospis</i>	a	3.58	0 - 17	7
<i>Melittobia</i>	a	18.33	1 - 80	12
Perilampidae	a	0.08	0 - 1	1

Fragmentation effects on different trophic levels

genus	trophic level	Mean abundance	Range abundance	Nr of fragments inhabited
Chrysididae				
<i>Caenochrysis</i>	a	18.42	2 - 36	12
<i>Chrysis</i>	a	0.75	0 - 7	2
<i>Exochrysis</i>	a	6.33	0 - 28	10
<i>Ipsiura</i>	a	0.67	0 - 3	4
<i>Neochrysis</i>	a	1.42	0 - 6	3
<i>Pleurochrysis</i>	a	0.92	0 - 4	5
Ichneumonidae				
Ichneumonidae	a	2.33	0 - 6	11
Mutillidae				
Sphaerophthalmina	a	3.33	0 - 22	5
Coleoptera				
<i>Tetraonyx</i>	a	2.17	0 - 9	7
Dermestidae	a	1.33	0 - 8	4
Nitidulidae	a	0.08	0 - 1	1
Diptera				
<i>Anthrax</i>	a	2.33	0 - 9	5
Dolichopodidae	a	101.08	11 - 257	12
Sarcophagidae	a	4.08	0-15	10
Arachnida				
Acari	a	4.00	0-10	10
Lepidoptera				
Lepidoptera	a	2.08	0-11	4

Host abundance and antagonist abundance did not differ between the different strata since height was not selected in the final models.

Community composition of hosts and antagonist were significantly different at the different heights (Chao's abundance-based Jaccard Index = CJEA 10 m and 20 m: $p < 0.001$ both for hosts and antagonists, Fig. 2). Some families showed a higher percentage at some strata, for example Anthophoridae preferred 2 m height, whereas Eumeninae were more often found at 10 or 20 m height. The majority of the host community always consisted of spheciform wasps, especially of the genus *Trypoxylon*. We found high percentages of two groups of antagonists, Diptera, which showed higher presence at 2 m and Chrysididae, which showed higher presence at 10 and 20 m height.

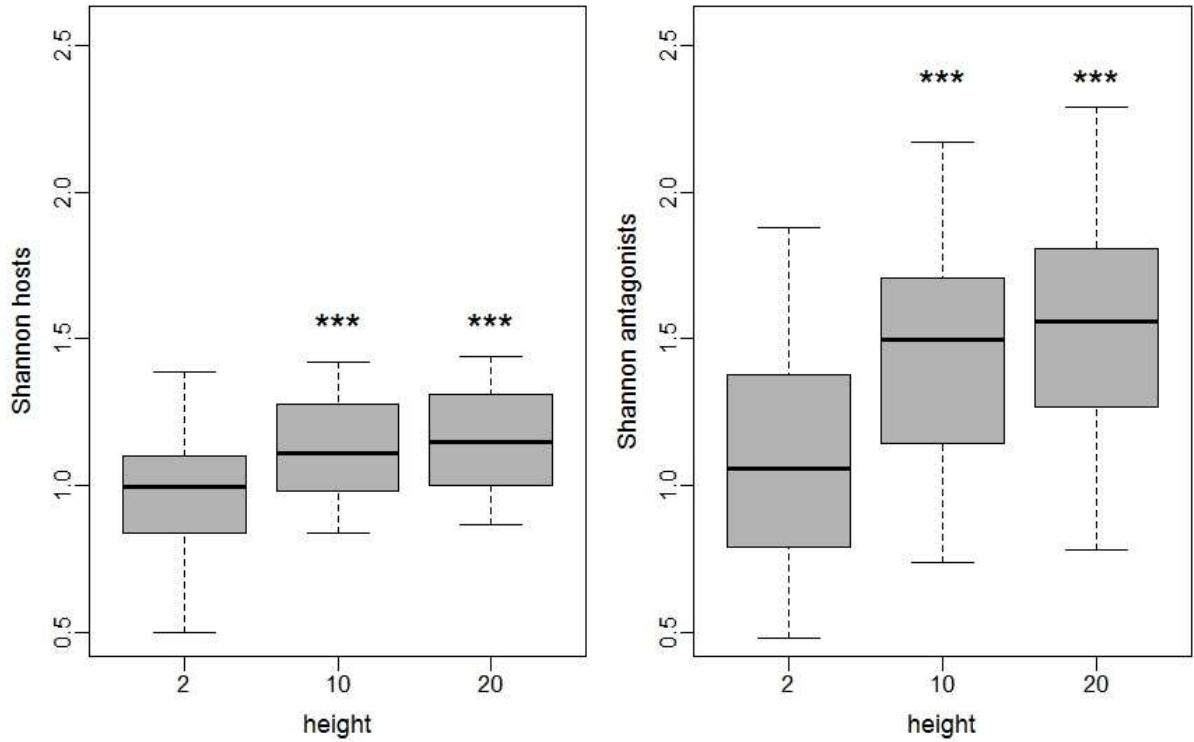


Fig. 1 The Shannon-Index for hosts (at the left side) and for antagonists (at the right side) in relation to the height (2, 10 or 20 m; ***: $p < 0.001$).

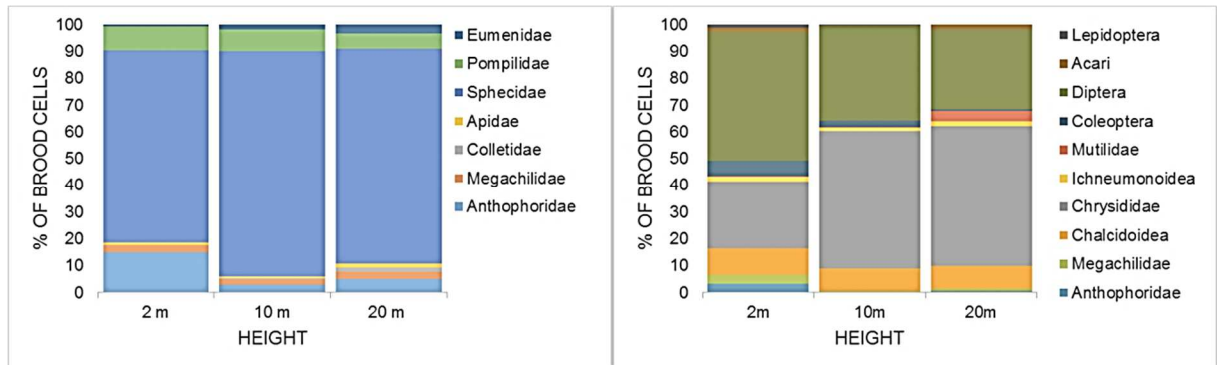


Fig. 2 The community composition for hosts (at the left side) and for antagonists (at the right side) in relation to height (2, 10 or 20 m).

Fragmentation effects on different trophic levels

Tab. 2 Results of generalized linear mixed effects models relating the response variables 1) abundances 2) counted species richness and 3) parasitism rates to the explanatory variables fragment size, tree location (tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center) and height. Results of final models are shown.

response variable	explanatory variables	z-value	p-value
abundance hosts	size	/	/
	tree 2	-3.621	<0.001
	tree 3	-0.981	0.3268
	height	/	/
abundance antagonists	abundance hosts	17.515	<0.001
	tree 2	-1.018	0.3085
	tree 3	2.07	0.0384
abundance with trophic level	host	23.345	<0.001
	tree 2	-4.856	<0.001
	tree 3	-1.069	0.285
counted species richness with trophic level	size	1.394	0.1635
	hosts	4.666	<0.001
	tree 2	-5.205	<0.001
	tree 3	-0.342	0.7324
	size*host	-2.088	0.0368
	host*tree 2	3.977	<0.001
	host*tree 3	1.991	0.0465
parasitism rate per genus	abundance host per fragment	4.892	<0.001
	size	1.52	0.128
parasitism rate with Shannon	Shannon antagonists	3.464	<0.001
	antagonist abundance	12.769	<0.001

Tab. 3 Results of generalized linear mixed effects models relating the response variables 1) counted species richness 2) Shannon-Indices and 3) abundance-based Jaccard Indices to the explanatory variables fragment size, tree location (tree 1 at the forest border, tree 2 at intermediate distance and tree 3 in the forest center) and height. Results of final models are shown.

response variable	explanatory variables	t-value	p-value
counted species richness hosts	size	/	/
	tree 2	-0.68	0.4968
	tree 3	3.872	<0.001
	height	/	/
counted species richness antagonists	counted species richness hosts	6.394	<0.001
	size	/	/
	tree 2	-4.599	<0.001
	tree 3	-1.553	0.12
Shannon hosts	height	/	/
	size	-1.869	0.0911
	tree 2	7.013	<0.001
	tree 3	9.189	<0.001
Shannon antagonists	height 10	13.705	<0.001
	height 20	16.404	<0.001
	Shannon hosts	10.542	<0.001
	size	2.704	0.0219
	tree 2	3.648	<0.001
Shannon with trophic level	tree 3	6.073	<0.001
	height 10	10.246	<0.001
	height 20	12.449	<0.001
	size	3.276	0.0079
	hosts	7.136	<0.001
	tree 2	5.18	<0.001
	tree 3	7.874	<0.001
	height 10	13.504	<0.001
	height 20	17.098	<0.001
	size*hosts	-17.434	<0.001
	hosts*tree 2	-1.685	0.0924
hosts*tree 3	-2.977	0.0030	
hosts * height 10	-5.684	<0.001	
hosts * height 20	-7.465	<0.001	
Chao's abundance-based Jaccard Index	size	1.516	0.161
Chao's abundance-based Jaccard Index	tree 2	-30.43	<0.001
	tree 3	-13.21	<0.001
Chao's abundance-based Jaccard Index	height 10	12.9	<0.001
	height 20	23.15	<0.001
Chao's abundance-based Jaccard Index	size	-1.206	0.256
Chao's abundance-based Jaccard Index	tree 2	4.357	<0.001
	tree 3	5.388	<0.001
Chao's abundance-based Jaccard Index	height 10	4.024	<0.001
	height 20	-6.325	<0.001

Effects of fragment size on species richness and community composition

Diversity of hosts (both counted species richness and Shannon-Index) did not respond to fragment size (Fig. 3, Tab. 1). The diversity measures of the antagonists differed in their response to fragment size. Counted species richness did not respond to fragment size, whereas the Shannon-Index measured antagonist diversity higher in larger fragments ($p < 0.05$, see Fig. 3).

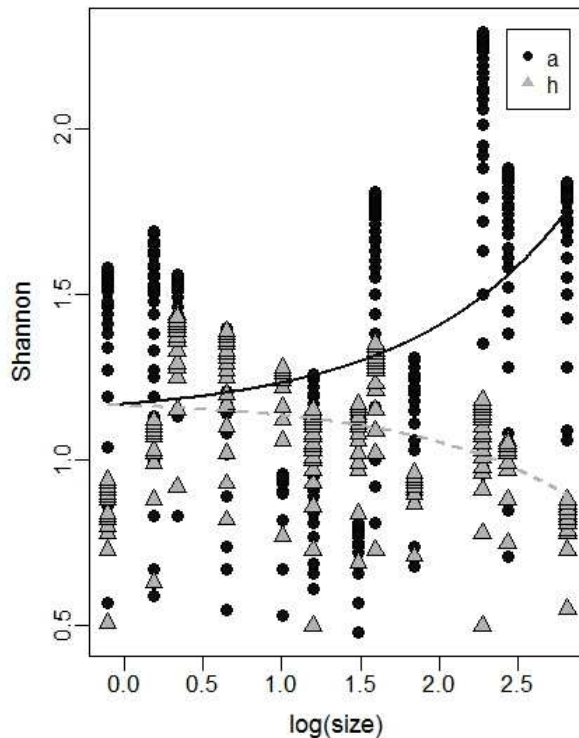


Fig. 3 The Shannon-Index of antagonists (a: black circles) and hosts (h: grey triangles) in relation to fragment size.

Responses of host vs. antagonist diversity (with both measures) to fragment size significantly differed since antagonist diversity responded more positively to larger fragment sizes (counted species richness: $p < 0.05$, Shannon: $p < 0.001$). Abundances of hosts and antagonists did not respond to fragment size (Tab. 2).

The community compositions of hosts and antagonists (Chao's abundance-based Jaccard Index = CJEA) did not differ with fragment size (CJEA: $p = 0.161$ for hosts and CJEA: $p = 0.256$ for antagonists).

Effects of tree location on species richness and community composition

The counted species numbers of hosts were higher at the tree in the forest centre (Tab. 3) and the Shannon-Index at the inner trees was higher compared to the forest edge ($p < 0.001$, Fig.

4). The antagonists showed significantly fewer species numbers at the intermediate trees (Tab. 3) and they followed the patterns of their hosts with a higher diversity at the inner trees ($p < 0.001$) with the Shannon-Index (Fig. 4). Host and antagonist diversity showed a significantly different response to tree location. Antagonists reacted more positively to the conditions inside the forest when comparing the slopes of the Shannon-Index, but comparing the slopes of the analyses with species numbers, we found that host and not antagonists reacted more positively to the conditions inside the forest (counted species richness: tree 2*hosts: $p < 0.01$; tree 3*hosts: $p < 0.001$ / Shannon: tree 2*hosts: $p = 0.092$; tree 3*hosts: $p < 0.01$).

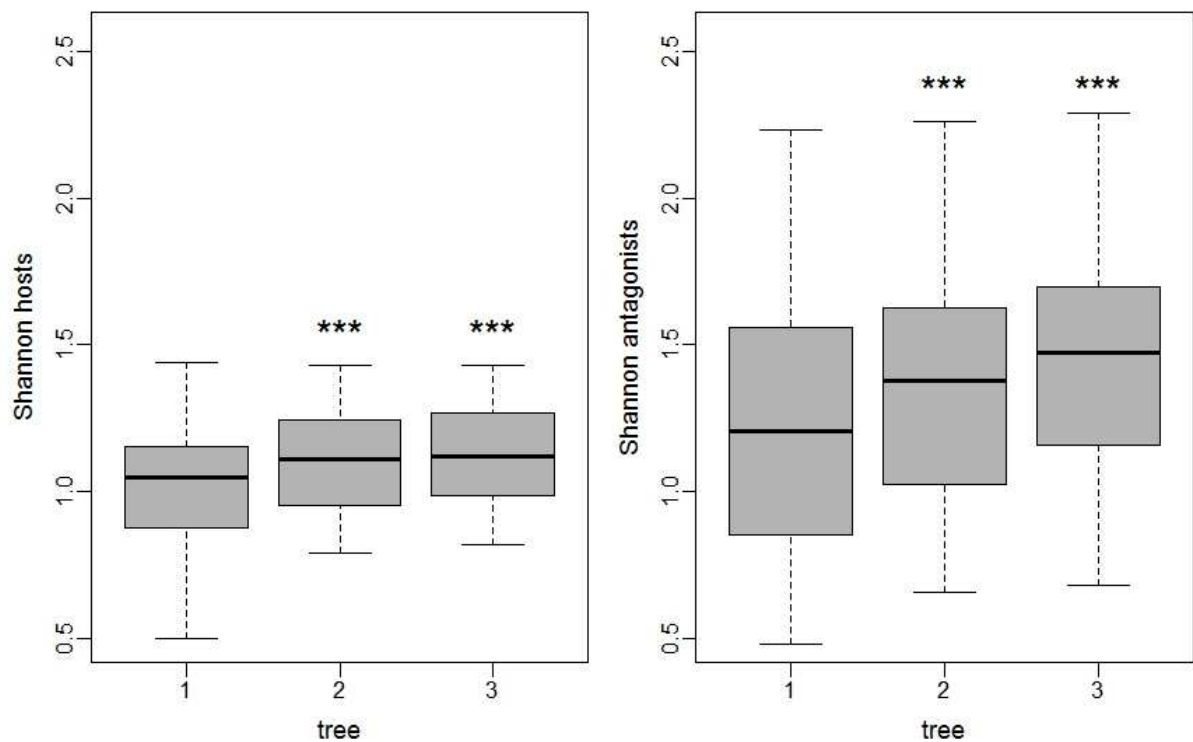


Fig. 4 The Shannon-Index for hosts (at the left side) and for antagonists (at the right side) in relation to tree location (tree 1 at the forest edge, tree 2 at an intermediate distance and tree 3 at the forest center; ***: $p < 0.001$).

Abundance was affected by tree location. Hosts were most abundant at the edge and least abundant at intermediate locations ($p > 0.001$). The antagonists followed the hosts' patterns. They were most abundant at the edge, tended to be less abundant at the intermediate location and were significantly more frequent at the forest centre ($p > 0.05$). The responses of the abundance of the two trophic levels did not differ significantly (Tab. 2).

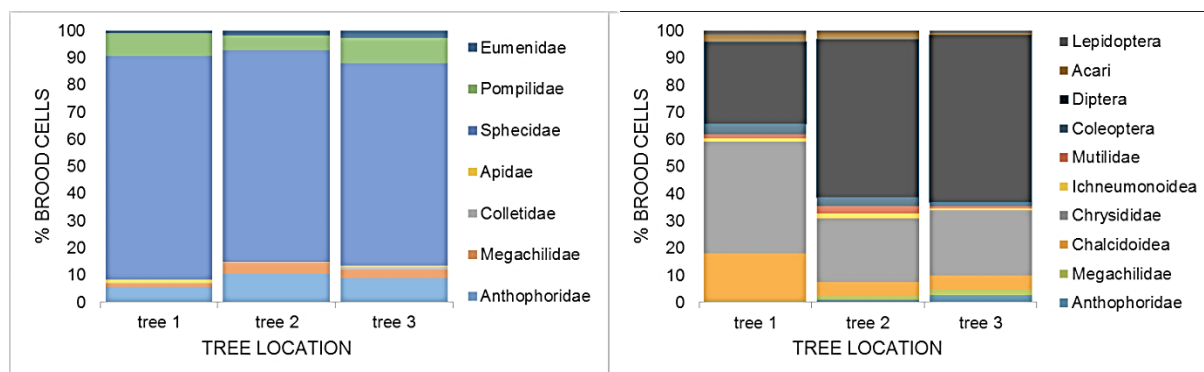


Fig. 5 The community composition for hosts (left side) and for antagonists (right side) in relation to tree location (tree 1 at the forest edge, tree 2 at an intermediate distance and tree 3 at the forest center).

Host and antagonist community compositions differed from edge to center. The inner trees showed a significantly different community composition for hosts and antagonists compared to the edge tree (CJEA: tree 2 and tree 3 $p < 0.001$, Fig. 5). Apidae were only found at edge trees, whereas Colletidae were only present at the inner trees and the Eumeninae were found with higher percentages inside the forest. Antagonist community composition clearly differed due to Diptera and Chrysididae. Flies were found more often inside the forest, whereas Chrysididae parasitized a higher percentage of cells at the edge.

The parasitism rate and its relation to host and antagonist richness

We found that abundant genera suffer a greater parasitism rate than rare genera ($p < 0.001$, Fig. 6). The parasitism rate rose both with antagonist abundance ($p < 0.001$), but also with antagonist diversity ($p < 0.001$). We found a positive density-dependent response of the antagonists since the antagonist abundance was significantly higher with more abundant hosts ($p < 0.001$). We also found a higher antagonist diversity with a higher host diversity ($p < 0.001$, Fig. 6).

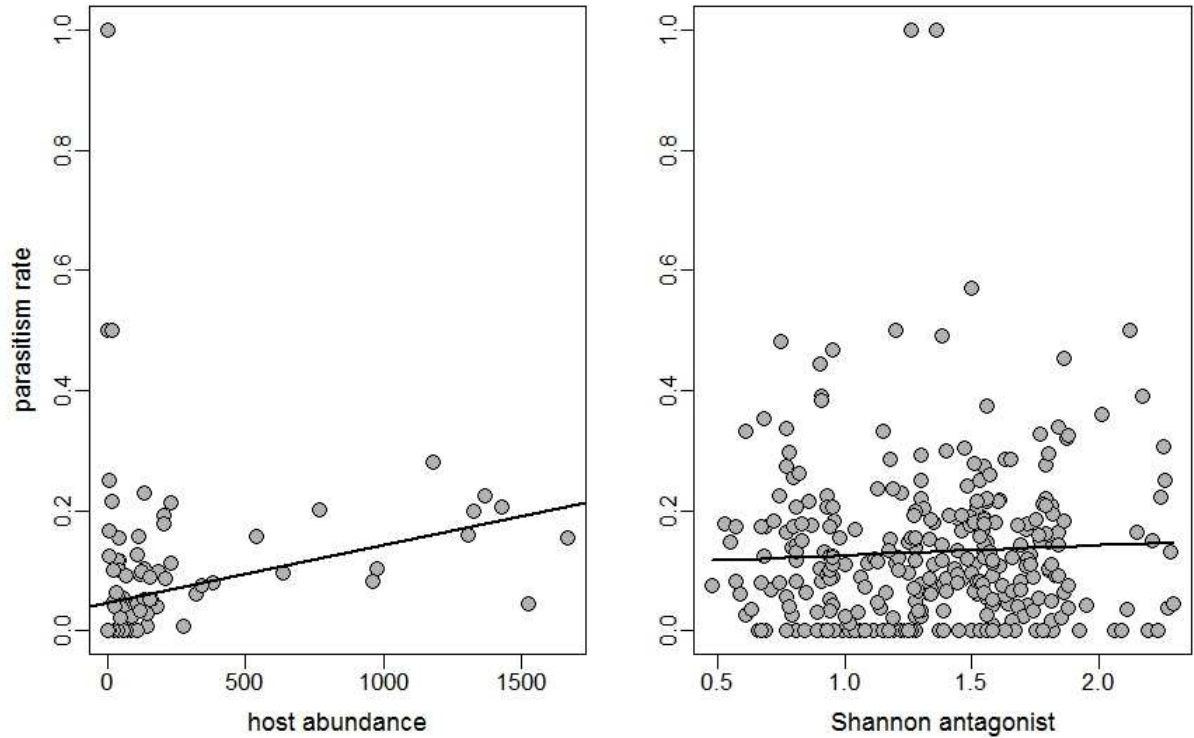


Fig. 6 The parasitism rate in relation to the abundance of genera (at the left side, each point represents the parasitism rate of one genus per fragment.) and in relation to the Shannon diversity of antagonists.

Discussion

We found a similar number hymenopteran host genera as in other studies from Neotropical forests (Morato and Campos 2000; Thiele 2003; Batista Matos et al. 2013). However, we found a greater number of antagonist groups (31 groups) compared to the only nine antagonist species found along a land-use gradient in Ecuador (Tylianakis et al. 2006)

Vertical distribution of richness and community composition

Species diversity of hosts and antagonists was higher at 10 and 20 m when calculated with the Shannon-Index (and also the ICE, data not shown), but counted species richness did not differ between the strata. We trust more in the analyses with the Shannon-Index compared to the ones conducted with species counts, since the latter is problematic with a high number of rare species (Pianka 1966). With both variables antagonists showed a steeper diversity increase with height than their hosts. A higher species diversity at the canopy level has been shown in previous studies of Neotropical bees and wasps (Morato 2001; Thiele 2003). This is, however, the first study showing vertical stratification for the antagonists of the trap-nesting

community in the tropics. Previous studies of antagonist communities revealed preferences for either the canopy or the understory (Moran and Southwood 1982; Schowalter 1989; Winchester and Ring 1996; Vance et al. 2007). Rainforests are structurally stratified (Richards 1983) due to microclimatic conditions and resource availability. The canopy, the site of the majority of primary productivity (Ozanne et al. 2003) seem to offer more favourable conditions for the majority of the trap-nesting Hymenoptera. The canopy has shady and less humid conditions (e.g. Blanc 1990; Parker 1995; Barker 1996) and a higher availability of resources (flowers for bees; prey for wasps due to a higher leaf biomass for herbivores; nesting materials) (Hallé 1998; Gibbons and Lindenmeyer 1996). This leads to niche division of host communities and of the antagonist community due to their reliance on their hosts (e.g. Steckel et al. 2014), resulting in different community compositions of both hosts and antagonists at different strata.

We did not find differences between the responses of host and antagonist abundances to the three heights. Previous studies found ambiguous responses of hymenopteran abundances to strata with higher abundances in the understorey, in the canopy or with no differences (Basset 2001; de Dijin 2003; Vance et al. 2007). We probably did not find differences in the abundance of hosts and antagonists due to species-specific preferences of trap-nesting bees and wasps (Morato 2001; Thiele 2003), which is confirmed by our result of different community compositions between the three heights.

Our results emphasize the importance of including different strata when monitoring in tropical rainforests since there is still a lack of studies in forest canopies (Thiele 2003; Ulyshen et al. 2010).

Effects of fragment size on species richness and community composition

Host diversity did not respond to fragment size, which contradicts the expectation of a positive relation between diversity and habitat area (e.g. as in Steffan-Dewenter 2003; Meneses Calvillo et al. 2010). However the effects of forest fragmentation can be highly variable (Laurance et al. 2002); for example Brosi et al. (2007b) did not find a relationship between fragment size and species richness. We conclude that such small secondary forest fragments seem to provide equal resources for the trap-nesting host community, which is further shown by our result that community composition was not altered with fragment size.

The situation was different with the antagonists since we found a more species-rich community in larger fragments, which is in accordance to the hypothesis of a higher sensitivity of antagonists to fragmentation (Holt et al. 1999; Brückmann et al. 2010; Rand et al. 2012). This has been shown for tropical cuckoo bees (Meneses Calvillo et al. 2010), in

temperate regions (Steffan-Dewenter 2003), and in theory (Cronin 2004). The community similarity of antagonists however did not differ significantly with fragment size. Fragments in that size range sustain similar communities of hosts and antagonists, which could be due to an already degraded community (Laurance and Bierregaard 1997; Gascon et al. 1999). Further studies are needed to confirm this by including larger fragments or by the comparison with primary forests, but it is highly probable that community structure would change between primary and secondary forests (Barlow et al. 2007)

Independent of the trophic level abundances did not respond to fragment size. We expected higher abundances in larger fragments, but abundance responses to habitat area are often highly variable (Connor et al. 2000).

Effects of tree location on richness and community composition

Tree location had more pronounced effects than fragment size since species diversity of hosts and also of antagonists was higher inside the forest, whereas the abundances showed the opposite patterns. Community composition also changed significantly. The results partly differed between the Shannon-Index and the species numbers, but the Shannon-Index is more reliable especially in datasets including rare species (Pianka 1966). At the edge, which is characterized by reduced humidity and greater temperature variability (Saunders et al. 1991; Laurance and Williamson 2001; Hunter 2002), but lacks the structural richness of the forest canopy, we probably find abundant disturbance-adapted species. These species might profit from complementary resources, such as food and nesting materials in adjacent habitats (Ries and Sisk 2004), which could explain the high abundance at the edge habitat. Under the forest canopy with a cooler and moister environment (Fetcher et al. 1985) a more species rich, but less abundant forest-adapted host community can be found (Laurance et al. 2002). The antagonists however were more abundant and diverse in the forest centre, confirming the higher sensitivity of higher trophic levels to environmental changes (Holt et al. 1999; Kruess and Tschardtke 2000; Kondoh 2003). Increasing edge habitat will affect species diversity and species interactions negatively, so that ecological mechanisms, (for example, control by natural enemies) could be changed (Valladares et al. 2006; Fagan et al. 1999; Laurance et al. 2000).

The parasitism rate and its relation to host and antagonist richness

We found that abundant genera suffer from a higher parasitism rate which confirms the expectation that common species are most affected by antagonists, because parasite loads correlate positively with host abundance (Durrer and Schmid-Hempel 1995). This positive

density-dependent parasitism can regulate population dynamics (Hassel and Wilson 1997; Berryman and Turchin 2001) and could be one mechanism for maintaining high tropical biodiversity (Godfray et al. 1999) since this top-down control of more competitive and abundant species can facilitate coexistence with less abundant genera. We did not find an influence of fragment size on this positive density-dependent parasitism, so our results did not show that environmental changes may affect species interactions and ecosystem functioning (Tscharrntke and Brandl 2004; Valladares et al. 2006; Tylianakis et al. 2006). However, these results might be different if we had included larger forest fragments.

The finding that higher antagonist richness was related to higher host richness confirms that the most important resource for antagonists are their hosts (Steffan-Dewenter 2003; Steckel et al. 2014). Maintaining the biodiversity of hosts is therefore crucial for maintaining ecosystem functions such predation and parasitism.

We found a higher parasitism rate with increasing antagonist abundance, but interestingly also with higher antagonist diversity, which is in accordance with a study from Ecuador (Tylianakis et al. 2006). This result can indirectly be a cause for concern since antagonist diversity depends on fragment size, suggesting that species interactions are affected by habitat loss (Valladares et al. 2006). Even abundant antagonists probably cannot compensate for the role of rarer, more specialist species.

Conclusions

We demonstrate that monitoring biodiversity at different strata is crucial for recording biodiversity and trophic interactions in tropical forests. Fragment size of small secondary forest fragments did not affect host communities, i.e. abundance and diversity, but antagonist diversity did increase with larger fragments. An increase of edge habitat will strongly affect hosts and antagonists and has already altered community composition of both host and antagonists. Parasitism was shown to regulate host populations and to depend on both host and antagonist abundance and diversity. We cannot provide a threshold size for secondary forest fragments for biodiversity conservation of the trap-nesting community, but increasing edge conditions will negatively affect bees, wasps and their antagonists, especially forest-adapted species, which in turn will affect ecosystem functions like pollination, predation and parasitism. Further studies are much needed to investigate the differences along a fragmentation gradient including larger fragments, and from secondary forests to primary forests.

V General Discussion

Increasing deforestation in tropical regions, the terrestrial biodiversity hotspots (Myers et al. 2000), threaten biodiversity and trophic interactions (Turner 1996; Davies et al. 2000; Laurance et al. 2002; Fahrig 2003; Klein et al. 2006). In this study we evaluated the fragmentation effects along the vertical distribution of the trap-nesting community in secondary forest fragments. The first chapter concentrates on the possible interactive effects of microclimate and fragmentation on the abundance, mortality and parasitism rates (Chapter II). The second and third chapter evaluated the effects of fragmentation on the vertical distribution of bee biodiversity and species-specific patterns (Chapter III) respectively on hosts and antagonist communities (Chapter IV).

Vertical gradients of biodiversity

Our results highlight the need to monitor biodiversity, community structure and trophic interactions not only in the understory, but despite of the associated difficulties also in the canopy (Chapter III; Chapter IV) since there is still a lack of studies in forest canopies (Thiele 2003; Ulyshen et al. 2010; Basset et al. 2013). The diversity of hosts and antagonists was higher in the canopy, whereas species numbers did not demonstrate stratification or the pattern was opposite for bees (Chapter III; Chapter IV). The Shannon-Index and the ICE estimator better reflect biodiversity patterns, because species numbers do not include abundances, which is especially problematic for data-sets with a high amount of rare species (Pianka 1966). Higher strata seem to harbor a more diverse but less abundant community. The abundances of hosts and antagonists did not differ between heights (Chapter IV), but bee abundances were higher in the understory (Chapter III), which is probably due to the dominance of the *Centris* species and their related antagonists. Former studies found ambiguous responses of hymenopteran abundances to strata with higher abundances in the understory, in the canopy or with no differences (Basset 2001; de Dijin 2003; Vance et al. 2007). This shows the value of species-based analyses since single species responses can be more informative than combined abundance and diversity data (Nemésio and Silveira 2006). The biodiversity patterns found are further confirmed by the results of chapter IV since communities of hosts and antagonist differ between the three heights, which was more pronounced for the antagonist community.

The explanation for the stratification of the trap-nesting community in secondary rainforest fragments lies in the structural stratification of rainforests in microclimatic conditions and resource availability, which results in a variety of different niches (Basset et al. 2003). The

canopy is the site of the majority of primary productivity (Ozanne et al. 2003) and is characterized by lighter and less humid conditions (e.g. Blanc 1990; Parker 1995; Barker 1996) and a higher availability of resources (flowers for bees; prey for wasps due to a higher leaf biomass for herbivores; nesting materials; Hallé 1998; Gibbons and Lindenmeyer et al. 1996). The understory in contrast offers darker and more humid conditions leading to higher activity of fungi. Since we found a lower mortality rate in the canopy (presumably due to drier sunnier conditions in the canopy and resulting less infestations by fungi; Chapter III), this could be the reason for the canopy preference of the majority of trap-nesting bees. For other arthropod taxa vertical stratification with equal or higher diversity in the canopy has been demonstrated before (e.g. Erwin 1982; Stork and Grimbacher 2006) as well as for trap-nesting bees and wasps in primary forest, both fragments and continuous (Chapter III; Chapter IV; Morato 2001; Thiele 2003).

Canopy research is inevitable for biodiversity monitoring (Ozanne et al. 2003) and it is highly important to evaluate if stratification could change between continuous forest and fragments, as indicated by the study of Morato (2001) in the comparison between large fragments and continuous forest respectively with primary and secondary fragments.

Effects of fragment size

Habitat loss can lead to loss of biodiversity (Debinski and Holt 2000; Hooper et al. 2012), which can affect ecosystem functions and services (Balvanera et al. 2006; Perrings et al. 2011).

Fragment size did not influence host and antagonist abundances (Chapter II; Chapter III; Chapter IV) and in general patterns for abundance-area relationships are variable (Connor et al. 2000). Diversity of hosts did not respond to fragment size (Chapter III; Chapter IV), which contradicts the expectation of a positive relation between diversity and habitat area (e.g. as in Steffan-Dewenter 2003; Meneses Calvillo et al. 2010), while other studies also could not find a relationship between fragment size and species richness (Bruna et al. 2005; Brosi et al. 2007b). The diversity of natural enemies, however, increased in larger fragments (Chapter IV), which is in accordance with the hypothesis of a higher sensitivity of antagonists to fragmentation (Holt et al. 1999; Brückmann et al. 2010; Rand et al. 2012). Community compositions of host and antagonists did not change within our range of fragment sizes (Chapter IV). This could be due to an already degraded community (Laurance and Bierregaard 1997; Gascon et al. 1999). Due to the weak effects of fragment sizes on biodiversity and abundance patterns, parasitism and mortality rates were also not significantly affected (Chapter II; Chapter III).

Possibly size would have had an higher impact if we had included larger fragments, but further studies are needed to compare secondary with primary forests since it is highly probable that community structure would change between primary and secondary forests (Barlow et al. 2007; Gibson et al. 2011).

Edge effects

Edge effects are known to be dominant drivers of fragmentation dynamics in tropical rainforests (Laurance et al. 2011a) and the trap-nesting community was much more affected by tree location (i.e. edge effects) than by fragment size. Tree location affected host abundance, which was generally higher at the edge (Chapter II; Chapter IV), except for bees alone (Chapter III). Diversity in contrast was higher in the forest center for hosts and antagonists (Chapter III; Chapter IV). Tree location also did change community compositions and trophic interactions. The parasitism rates were higher at the intermediate distances and the mortality rates rose inside the forest (Chapter II). Only for bees alone parasitism rates were not influenced by tree location (Chapter III).

The patterns can be explained through a gradient from edge to center both of temperature and humidity (Didham and Lawton 1999), with lower humidity and greater temperature variability at forest borders (Saunders et al. 1991; Laurance and Williamson 2001; Hunter 2002) to moister and cooler conditions in the forest center (Fetcher et al. 1985). The borders share the drier conditions with the forest canopy, but lack their structural variability and are therefore inhabited by few abundant disturbance-adapted species (Laurance et al. 2002) whereas inside the forest a species-richer but less abundant forest-adapted community was found (Chapter IV). The edge community can profit from complementary resources, for example food resources or nesting materials from the surrounding matrix (Ries and Sisk 2004), whereas the high structural variety inside the forest offers a diversity of niches for many more specialized species (Ghazoul and Sheil 2010). The significant change of the community composition and the more sensitive reaction of the antagonists (Chapter IV) results in changes in trophic interactions so that despite of a positive-density dependent parasitism (Chapter IV) natural enemies are not able to fully exploit the high host abundance at the edge, probably because they are less adaptable to steeper temperature and humidity fluctuations (Chapter II; Hance et al. 2007). The higher mortality rates inside the forest (Chapter II) probably resulted from higher fungal activity (personal observation). This could be the reason why the majority of species preferred the canopy and only rainforest specialist,

such as *Centris labrosa* preferred the understory. At least for bees the mortality rate was significantly lower in the canopy but it did not depend on tree location (Chapter III).

To conclude, increasing edge conditions will greatly harm bees and wasps and to a greater amount their natural enemies, resulting in disturbance of trophic interactions and degraded communities with unknown consequences for ecosystem functioning.

Interactions of fragmentation and microclimate

Microclimate is known to affect arthropods (Dial et al. 2006; Rico-Gray et al. 2011). As part of microclimate, mean temperature did affect the responses of hymenopteran abundance, the parasitism and mortality rates (Chapter II). Higher temperatures, especially at the forest borders, resulted in lower abundances (Chapter II), which proves an interaction between fragmentation and microclimatic conditions. This gives cause for concern, because a continued temperature rise will negatively influence above ground-nesting bees and wasps in high temperature tropical lowland habitats. It is even more worrying, since even the abundant and disturbance adapted hymenopterans at the border were negatively affected by higher temperatures and thus could have problems to adapt to projected climate warming (Buckley et al. 2013). This could affect adjacent agro-ecosystems by loss of pollination and pest control services.

The conservation value of small secondary forest fragments

Small secondary forest fragments sustain a trap-nesting community (Chapter II; Chapter III; Chapter IV) but comparisons with larger fragments or with primary forests are lacking or are not comparable due to different study designs (as for (Thiele 2003)). A more pronounced area effect was expected, but only antagonist diversity responded to fragment size (Chapter IV). This dissertation could show that especially the interior of small secondary forest fragments can contribute to biodiversity conservation. There is however no doubt of the importance of continuous primary forest for biodiversity conservation (Gibson et al. 2011) and comparisons of the community compositions of primary forests vs. secondary ones were always significantly different (Barlow et al. 2007). Since edge effects were dominant drivers of the patterns found (Chapter II; Chapter III; Chapter IV), an increase of edge habitat will negatively affect above-ground nesting solitary bees, wasps and especially their natural enemies and probably already has affected the communities in the small fragments. With ongoing deforestation secondary forest fragments can be utile for trap-nesting Hymenoptera, however, for conservation a landscape-wide plan with key areas of undisturbed forests,

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.

Conclusions

We could demonstrate the necessity of including vertical stratification of biodiversity and trophic interactions in tropical forests and also of the value of species-specific response to fragmentation. Fragment size nearly had no influence on the trap-nesting community, with exception of the antagonist diversity. Therefore it will be important to investigate the threshold size to sustain a diverse trap-nesting community. There is however no doubt, that an increase of edge habitat will negatively influence biodiversity, which was more pronounced for higher trophic levels. It is therefore probable, that fragmentation and the resulting increase of edge habitat already has changed trap-nesting communities and their trophic interactions in the studied forest fragments. Since community compositions changed from edge to center, an increase of edge habitat will threaten specialized forest-adapted species more, whereas disturbance-adapted generalist will profit. Moreover we could show interactive effects of microclimate and fragmentation, so that climate change additionally could harm biodiversity and trophic interactions. Key ecosystem functions such as pollination, predation and parasitism could be affected with still unknown consequences. Further studies are highly needed to investigate the differences along a fragmentation gradient including larger fragments and the comparison between secondary and primary forests as well as the interactions of various global change drivers.

References

- Balvanera, P., Pfisterer, A.B., Buchmann, N., et al. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156.
- Barker, M.G. (1996) Vertical profiles in a Brunei rainforest: I. Microclimate associated with a canopy tree. *J. Trop. For. Sci* 8, 505–519.
- Barlow, J., Gardner, T.A., Araujo, I.S., et al. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proc. Natl. Acad. Sci. USA* 104, 18555–18560.
- Barracough, S. (2013) *Agricultural expansion and tropical deforestation: international trade, poverty and land use*. Routledge.
- Basset, Y. (2001) Invertebrates in the canopy of tropical rain forests: How much do we really know? *Plant Ecol.* 153, 87–107.
- Basset, Y., Hammond, P.M, Barrios, H., Holloway, J.D, et al. (2003) *Vertical stratification of arthropod assemblages. Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. Cambridge University Press
- Basset, Y., Cizek, L., Cu, P., et al. (2013) Arthropod diversity in a tropical forest. *Science* 338, 1481–1484.
- Batista Matos, M.C., Sousa-Souto, L., Almeida, R.S., Teodoro, A.V. (2013) Contrasting patterns of species richness and composition of solitary wasps and bees (Insecta: Hymenoptera) according to land-use. *Biotropica* 45, 73–79.
- Bawa, K.S., Bullock, S.H., Perry, D.R., Coville, R.E., Grayum, M.H. (1985) Reproductive biology of tropical lowland rainforest trees. II. Pollination systems. *Amer. J. Bot.* 72, 346–356.
- Bawa, K.S. (1990) Plant-pollinator interactions in tropical rainforests. *Annu. Rev. Ecol. Syst.* 21, 399–422.
- Berkum, F.H. van (1988) Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *Am. Nat.* 132, 327–343.
- Berryman, A., Turchin, P. (2001) Identifying the density-dependent structure underlying ecological time series. *Oikos* 92, 265–270.

- Blanc, P. (1990) Bioclimatologie compare de la canopée et du sous-bois. Biologie d'une canopée de forêt équatoriale. Rapport de mission radeau des Cimes octobre-novembre 1989, Petit Saut – Guyane Française. Montpellier/Paris: Montpellier II et CNRS-Paris VI.
- Brosi, B.J., Daily, G.C., Ehrlich, P.R. (2007a) Bee community shifts with landscape context in a tropical countryside. *Ecol. Appl.* 17, 418–430.
- Brosi, B.J., Daily, G.C., Shih, T.M., et al. (2007b) The effects of forest fragmentation on bee communities in tropical countryside. *J. Appl. Ecol.* 45, 773–783.
- Brosi, B.J. (2009) The effects of forest fragmentation on euglossine bee communities (Hymenoptera: Apidae: Euglossini). *Biol. Conserv.* 142, 414–423.
- Brückmann, S.V., Krauss, J., van Achterberg, C., Steffan-Dewenter, I. (2010) The impact of habitat fragmentation on trophic interactions of the monophagous butterfly *Polyommatus coridon*. *J. Insect. Conserv.* 15, 707–714.
- Bruna, E.M., Vasconcelos, H.L., Heredia, S. (2005) The effect of habitat fragmentation on communities of mutualists: Amazonian ants and their host plants. *Biol. Conserv.* 124, 209–216.
- Buckley, L.B., Tewksbury, J.J., Deutsch, C.A. (2013) Can terrestrial ectotherms escape the heat of climate change by moving ? *Proc. R. Soc. B* 280, 1–6.
- Burnham, K.P., Anderson, D.R. (2002) Model selection and multimodel inference: A practical information – theoretic approach, second edition. Springer Verlag.
- Buschini, M.L.T. (2006) Species diversity and community structure in trap-nesting bees in Southern Brazil. *Apidologie* 37, 58–66.
- Chacoff, N.P., Aizen, M.A. (2005) Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *J. Appl. Ecol.* 43, 18–27.
- Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.-J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* 8, 148–159.
- Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs: High diversity of trees and corals is maintained. *Science* 199, 1302–1310.
- Connor, E.F., Courtney, A.C., Yoder, J.M. (2000) Individuals-area relationships: The relationship between animal population density and area. *Ecology* 81, 734–748.

- Cornell, H.V., Hawkins, B.A. (1993) Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. *Am. Nat.* 141(6), 847–865.
- Crawley, M.J. (2002) *Statistics: An introduction using R*. John Wiley & Sons, Ltd.
- Cronin, J.T. (2004) Host-parasitoid extinction and colonization in a fragmented prairie landscape. *Oecologia* 139, 503–514.
- Davies, K.F., Margules, C.R., Lawrence, J.F. (2000) Which traits of species predict population declines in experimental forest fragments? *Ecology* 81, 1450–1461.
- de Dijin, B.P.D. (2003) Vertical stratification of flying insects in a Surinam lowland rainforest. *Arthropods Trop. For. Spat. Dyn. Resour. use canopy*.
- De´ Ath, G. (2012) The multinomial diversity model : linking Shannon diversity to multiple predictors. *Ecology* 93, 2286–2296.
- Debinski, D.M., Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conserv. Biol.* 14, 342–355.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., et al. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS* 105, 6668–6672.
- Dial, R.J., Ellwood, M.D., Turner, E.C., Foster, W.A. (2006) Arthropod abundance, canopy structure and microclimate in a Bornean lowland tropical rainforest. *Biotropica* 38, 643–652.
- Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J. (1996) Insects in fragmented forests: a functional approach. *Trends Ecol. Evol.* 11, 255–260.
- Didham, R.K., Lawton, J.H. (1999) Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31, 17–30.
- Donovan, T.M., Flather, C.H. (2002) Relationships among North American songbird trends, habitat fragmentation and landscape occupancy. *Ecol. Appl.* 12, 364–374.
- Durrer, S., Schmid-Hempel, P. (1995) Parasites and the regional distribution of bumblebee species. *Ecography* 18, 114–122.
- Erwin, T.L. (1982) Tropical forests : their richness in Coleoptera and other arthropod species. *Coleopt. Bull.* 36, 74–75.
- Ewers, R.M., Didham, R.K.(2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev. Camb. Philos. Soc.* 81, 117–142.

- Ewers, R.M., Thorpe, S., Didham, R.K. (2007) Synergistic interactions between edge and area effects in a heavily fragmented landscape. *Ecology* 88, 96–106.
- Ewers, R.M., Scharlemann, J.P.W., Balmford, A., Green, R.E. (2009) Do increases in agricultural yield spare land for nature? *Global Change Biology*, 15(7), 1716–1726.
- Fagan, W.F., Cantrell, R.S., Cosner, C. (1999) How habitat edges change species interactions. *Am. Nat.* 153, 165–182.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34, 487–515.
- Fenoglio, M.S., Srivastava, D., Valladares, G., Cagnolo, L., Salvio, A. (2012) Forest fragmentation reduces parasitism via species loss at multiple trophic levels. *Ecology* 93, 2407–2420.
- Fetcher, N., Oberbauer, S.F., Strain, B.R. (1985) Vegetation effects on microclimate in lowland tropical forest in Costa Rica. *Int. J. Biometeor.* 29, 145–155.
- Frankie, G.W., Coville, R. (1979) An experimental study on the foraging behaviour of selected solitary bee species in the Costa Rican dry forest (Hymenoptera: Apoidea). *J. Kans. Entomol. Soc.* 52, 591–602.
- Frankie, G.W., Vinson, S.B., Newstrom, L.E., Barthell, J.F. (1988) Nest site and habitat preferences of *Centris* bees in the Costa Rican dry forest. *Biotropica* 20(4), 301–310.
- Fye, R.E. (1972) The effect of forest disturbances on populations of wasps and bees in Northwestern Ontario (Hymenoptera: Aculeata). *Can. Entomol.* 104, 1623–1633.
- Gascon, C., Lovejoy, T.E., Bierregard, R.O., Malcolm, J.R., et al. (1999) Matrix habitat and species richness in tropical forest remnants. *Biol. Conserv.* 91, 223–229.
- Gazola, A.L., Garófalo, C.A. (2009) Trap-nesting bees (Hymenoptera: Apoidea) in forest fragments of the State of São Paulo, Brazil. *Genet. Mol. Res.* 8, 607–622.
- Ghazoul, J., Sheil, D. (2010) *Tropical rainforest ecology, diversity and conservation*. Oxford Biology.
- Gibbs, J.P. (2001) Demography versus habitat fragmentation as determinants of genetic variation in wild populations. *Biol. Conserv.* 100, 15–20.
- Gibbons, P., Lindenmayer, D.B. (1996) Issues associated with the retention of hollow-bearing trees within eucalypt forests managed for wood production. *For. Ecol. Manage* 83, 245–279.

- Gibson, L., Lee, T.M., Koh, L.P., et al. (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381.
- Gibson, L., Lynam, A.J., Bradshaw, C.J.A., et al. (2013) Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science* 341, 1508–1510.
- Godfray, H.C., Lewis, T., Memmott, J. (1999) Studying insect diversity in the tropics. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 354, 1811–1824.
- González-Varo, J.P., Biesmeijer, J.C., Bommarco, R., et al. (2013) Combined effects of global change pressures on animal-mediated pollination. *Trends Ecol. Evol.* 28, 524–530.
- Hallé, F.(1998) Distribution vertical des métabolites secondaires en forêt équatoriale – une hypothèse. *Biologie d’une canopée de forêt équatoriale – III. Rapport de la mission d’exploration scientifique de la canopée de Guyane, octobre – décembre 1996*, Paris: Pro Natura International, Opération Canopée.
- Hance, T., van Baaren, J., Vernon, P., Boivin, G. (2007) Impact of extreme temperatures on parasitoids in a climate change perspective. *Annu .Rev. Entomol.* 52, 107–126.
- Hanski, I., Zurita, G.A., Bellocq, M.I., Rybicki, J. (2013) Species-fragmented area relationship. *Proc. Natl. Acad. Sci. USA* 110, 12715–12720.
- Hassel, M.P., Wilson, H.B. (1997) The dynamics of spatially distributed host-parasitoid systems. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press.
- Hill, J.K., Hughes, C.L., Dytham, C., Searle, J.B. (2006) Genetic diversity in butterflies: Interactive effects of habitat fragmentation and climate-driven range expansion. *Biol. Lett.* 2, 152–154.
- Holdridge, L.R. (1967) *Life zone ecology*. Tropical Science Center. San Jose, Costa Rica.
- Holt, R.D., Lawton, J.H., Polis, G.A., Martinez, N.D.(1999) Trophic rank and the species-area relationship. *Ecology* 80(5), 1495–1504.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., et al. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–108.
- Huggett, A.J. (2005) The concept and utility of “ecological thresholds” in biodiversity conservation. *Biol. Conserv.* 124, 301–310.

- Hunter, M.D. (2002) Landscape structure, habitat fragmentation, and the ecology of insects. *Agric. For. Entomol.* 4, 159–166.
- Kays, R., Allen, A. (2001) Arboreal tropical forest vertebrates: current knowledge and research trends. *For. Sci.* 69, 109–120.
- Klein, A.-M., Steffan-Dewenter, I., Buchori, D., Tscharntke, T. (2002) Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conserv. Biol.* 16, 1003–1014.
- Klein, A.-M., Steffan-Dewenter, I., Tscharntke, T. (2003) Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *J. Appl. Ecol.* 40, 837–845.
- Klein, A.-M., Steffan-Dewenter, I., Tscharntke, T. (2004) Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. *J. Anim. Ecol.* 73, 517–525.
- Klein, A.-M., Steffan-Dewenter, I., Tscharntke, T. (2006) Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry. *J. Anim. Ecol.* 75, 315–323.
- Kondoh, M. (2003) Foraging adaptation and the relationship between food-web complexity and stability. *Science* 299, 1388–1391
- Kremen, C., Williams, N.M., Aizen, M.A., et al. (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.* 10, 299–314.
- Krombein, K.V. (1967) *Trap-nesting wasps and bees: life histories, nests and associates.* Smithsonian Press
- Kruess, A., Tscharntke, T. (2000) Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* 122, 129–137.
- Kuussaari, M., Bommarco, R., Heikkinen, R.K., et al. (2009) Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* 24, 564–571.
- La Salle, J. (1993) *Parasitic Hymenoptera, biological control and biodiversity.* Hymenopt. Biodivers.
- Laurance, W.F., Bierregaard, R.O. Jr. (1997) *Tropical forest remnants.* University of Chicago Press, Chicago.

- Laurance, W.F. (2000) Do edge effects occur over large spatial scales? *Trends Ecol. Evol.* 15, 134–135.
- Laurance, W.F., Williamson, G.B. (2001) Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conserv. Biol.* 15, 1529–1535.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., et al. (2002) Ecosystem decay of Amazonian forest fragments : a 22-year investigation. *Conserv. Biol.* 16, 605–618.
- Laurance, W.F., Camargo, J.L.C., Luizão, R.C.C., et al. (2011a) The fate of Amazonian forest fragments: A 32-year investigation. *Biol. Conserv.* 144, 56–67.
- Laurance, W.F., Carolina Useche, D., Shoo, L.P., et al. (2011b) Global warming, elevational ranges and the vulnerability of tropical biota. *Biol. Conserv.* 144, 548–557.
- Laurance, W.F., Useche, D.C., Rendeiro, J., et al. (2012) Averting biodiversity collapse in tropical forest protected areas. *Nature* 489, 290–294.
- Lindenmayer, D.B., Luck, G. (2005) Synthesis: Thresholds in conservation and management. *Biol. Conserv.* 124, 351–354.
- Liow, L.E.E.H., Sodhi, N.S., Elmqvist, T. (2001) Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *J. Appl. Ecol.* 38, 180–192.
- Lippok, D., Beck, S.G., Renison, D., et al. (2014) Topography and edge effects are more important than elevation as drivers of vegetation patterns in a Neotropical montane forest. *J. Veg. Sci.* 25, 724–733.
- Loyola, R.D., Martins, R.P. (2006) Trap-nest occupation by solitary wasps and bees (Hymenoptera: Aculeata) in a forest urban remnant. *Neotrop. Entomol.* 35, 41–48.
- Loyola, R.D., Martins, R.P. (2009) On a habitat structure-based approach to evaluating species occurrence: cavity-nesting Hymenoptera in a secondary tropical forest remnant. *J. Insect Conserv.* 13, 125–129.
- Loyola, R.D., Martins, R.P. (2011) Small-scale area effect on species richness and nesting occupancy of cavity-nesting bees and wasps. *Rev. Bras. Entomol.* 55, 69–74.
- Mantyka-Pringle, C.S., Martin, T.G., Rhodes, J.R. (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Glob. Chang. Biol.* 18, 1239–1252.

- Meneses Calvillo, L., Meléndez Ramírez, V., Parra-Tabla, V., Navarro, J. (2010) Bee diversity in a fragmented landscape of the Mexican Neotropic. *J. Insect. Conserv.* 14, 323–334.
- Moran, V., Southwood, T. (1982) The guild composition of arthropod communities in trees. *J. Anim. Ecol.* 51, 289–306.
- Morato, E.F. (2001) Efeitos da fragmentação florestal sobre vespas e abelhas solitárias na Amazônia Central . 11 . Estratificação vertical. *Rev. Bras. Zool.* 18, 737–747.
- Morato, E.F., Campos, L.A. de O (2000) Efeitos da fragmentação florestal sobre vespas e abelhas solitárias em uma área da Amazônia Central. *Rev. Bras. Zool.* 17, 429–444.
- Morato, E.F., Martins, R.P. (2006) An overview of proximate factors affecting the nesting behavior of solitary wasps and bees (Hymenoptera: Aculeata) in preexisting cavities in wood. *Neotrop. Entomol.* 35, 285–298.
- Moure, J.S. (1960) Notes on the types of the neotropical bees described by Fabricius (Hymenoptera: Apoidea). *Stud. Entomol.* 3, 97–160.
- Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.* 10, 58–62.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., et al. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Neame, L.A., Griswold, T., Elle, E. (2013) Pollinator nesting guilds respond differently to urban habitat fragmentation in an oak-savannah ecosystem. *Insect. Conserv. Divers* 6, 57–66.
- Nemésio, A., Silveira, F.A. (2006) Edge effects on the orchid-bee fauna (Hymenoptera: Apidae) at a large remnant of Atlantic rainforest in southeastern Brazil. *Neotrop. Entomol.* 35, 313–323.
- Nordén, J., Penttilä, R., Siitonen, J., et al. (2013) Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *J. Ecol.* 101, 701–712.
- Nouhuys, S. van (2005) Effects of habitat fragmentation at different trophic levels in insect communities. *Ann. Zool. Fennici.* 42, 433–447.
- Ockinger, E., Schweiger, O., Crist, T.O., et al. (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecol. Lett.* 13, 969–979.

- Offerman, H.L., Dale, V.H., Pearson, S.M., Bierregaard, Jr., O'Neill, R.V. (1995) Effects of forest fragmentation on Neotropical fauna: current research and data availability. *Environ. Rev.* 3, 191–211.
- Ollerton, J., Winfree, R., Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos* 120, 321–326.
- Opdam, P., Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biol. Conserv.* 117, 285–297.
- Orme, C.D.L., Davies, R.G., Burgess, M., et al. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436, 1016–1019.
- Ozanne, C.M.P., Anhuf, D., Boulter, S.L., et al. (2003) Biodiversity meets the atmosphere: a global view of forest canopies. *Science* 301, 183–186.
- Paniagua, M.R., Medianero, E., Lewis, O.T. (2009) Structure and vertical stratification of plant galler-parasitoid food webs in two tropical forests. *Ecol. Entomol.* 34, 310–320.
- Parker, G.G. (1995) Structure and microclimate of forest canopies. *Forest canopies*. San Diego: Academic Press, 431–455.
- Penagos, D.I., Williams, T. (1995). Important factors in the biology of heteronomous hyperparasitoids (Hym.: Aphelinidae): agents for the biological control of whiteflies and scale insects. *Acta Zool. Mex.* 66, 31–57.
- Perrings, C., Naeem, S., Ahrestani, F.S., et al. (2011) Ecosystem services, targets, and indicators for the conservation and sustainable use of biodiversity. *Front. Ecol. Environ.* 9, 512–520.
- Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *Am. Nat.* 100, 33 – 46.
- Pimm, S.L., Lawton, J. (1977) The number of trophic levels in ecological communities. *Nature* 268, 329–331.
- Potts, S.G., Vulliamy, B., Roberts, S., et al. (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecol. Entomol.* 30, 78–85.
- Ramalho, M. (2004) Stingless bees and mass flowering trees in the canopy of Atlantic Forest : a tight relationship. *Acta. Bot. Bras.* 18, 37–47.

- Rand, T.A., Tylianakis, J.M., Tscharntke, T. (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* 9, 603–614.
- Rand, T.A., van Veen, F.J.F., Tscharntke, T. (2012) Landscape complexity differentially benefits generalized fourth, over specialized third, trophic level natural enemies. *Ecography* 35, 97–104.
- Richards, P.W. (1983) The three-dimensional structure of tropical rain forest, pages: Tropical rain forest: ecology and management. Oxford Blackwell Scientific
- Rico-Gray, V., Díaz-Castelazo, C., Ramírez-Hernández, A., et al. (2011) Abiotic factors shape temporal variation in the structure of an ant–plant network. *Arthropod Plant Interact.* 6, 289–295.
- Ries, L., Sisk, T. (2004) A predictive model of edge effects. *Ecology* 85, 2917–2926.
- Roubik, D.W., Ackerman, J.D., Copenhaver, C., Smith, B.H. (1982) Stratum, tree and flower selection by tropical bees: Implications for the reproductive biology of outcrossing *Chochlopermum vitifolium* in Panama. *Ecology* 63, 712–720.
- Roubik, D.W. (1993) Tropical pollinators in the canopy and understory: Field data and theory for stratum “preferences.” *J. Insect. Behav.* 6, 659–673.
- Ruibal, R. (1961) Thermal relations of five species of tropical lizards. *Evolution* 15, 98–111.
- Saunders, D.A., Hobbs, R.J., Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: A review. *Conserv. Biol.* 5, 18–32.
- Schowalter, T. (1989) Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. *Can. J. For. Res.* 19, 318–322.
- Shaw, M., Hochberg, M. (2001) The neglect of parasitic Hymenoptera in insect conservation strategies: The British fauna as a prime example. *J. Insect. Conserv.* 5, 253–263.
- Steckel, J., Westphal, C., Peters, M.K., et al. (2014) Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. *Biol. Conserv.* 172, 56–64.
- Steffan-Dewenter, I. (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conserv. Biol.* 17, 1036–1044.

- Steffan-Dewenter, I., Schiele, S. (2008) Do resources or natural enemies drive bee population dynamics in fragmented habitats? *Ecology* 89, 1375–1387.
- Stork, N.E., Grimbacher, P.S. (2006) Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proc. Biol. Sci.* 273, 1969–1975.
- Suttle, K.B., Thomsen, M.A., Power, M.E. (2007) Species interactions reverse grassland responses to changing climate. *Science* 315, 640–642.
- Taki, H., Viana, B.F., Kevan, P.G., et al. (2008) Does forest loss affect the communities of trap-nesting wasps (Hymenoptera: Aculeata) in forests? Landscape vs. local habitat conditions. *J. Insect Conserv.* 12, 15–21.
- Tewksbury, J.J., Huey, R.B., Deutsch, C.A. (2008) Putting the heat on tropical animals. *Science* 320, 1296–1297.
- Thiele, R. (2005) A new species of *Ctenioschelus* Romand from Costa Rican dry forest (Hymenoptera : Apidae : Ericrocidini). *J. Kansas. Entomol. Soc.* 78, 272–276.
- Thiele, R. (2003) Reproduktionsbiologie von Bienen und ihre Beziehungen zu Blütenpflanzen in einem neotropischen Regenwald: Fallstudie La Selva, Costa Rica. 1–147.
- Thomson, L.J., Robinson, M., Hoffmann, A.A. (2001) Field and laboratory evidence for acclimation without costs in an egg parasitoid. *Funct. Ecol.* 15, 217–221.
- Thomson, L.J., Hoffmann, A.A. (2009) Vegetation increases the abundance of natural enemies in vineyards. *Biol. Control* 49(3), 259–269.
- Tilman, D., Fargione, J., Wolff, B., et al. (2001) Forecasting agriculturally driven global environmental change. *Science* 292, 281–284.
- Tscharntke, T., Gathmann, A., Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *J. Appl. Ecol.* 35, 708–719.
- Tscharntke, T., Brandl, R. (2004) Plant-insect interactions in fragmented landscapes. *Annu. Rev. Entomol.* 49, 405–430.
- Tscharntke, T., Klein, A.-M., Kruess, A., et al. (2005) Landscape perspectives on agricultural intensification and biodiversity - “ ecosystem service management. *Ecol. Lett.* 8, 857–874.

- Turner, I.M. (1996) Species loss in fragments of tropical rain forest: a review of the evidence. *J. Appl. Ecol.* 33, 200–209.
- Turner, I.M., Corlett, R.T. (1996) The conservation value of small, isolated fragments of lowland tropical rainforest. *Trends Ecol. Evol.* 11, 330–333.
- Tylianakis, J.M., Klein, A.-M., Tscharntke, T. (2005) Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology* 86, 3296–3302.
- Tylianakis, J.M., Tscharntke, T., Klein, A.-M. (2006) Diversity, ecosystem function, and stability of parasitoid-host interactions across a tropical habitat gradient. *Ecology* 87, 3047–3057.
- Tylianakis, J.M., Tscharntke, T., Lewis, O.T. (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445, 202–205.
- Ulyshen, M.D., Soon, V., Hanula, J.L. (2010) On the vertical distribution of bees in a temperate deciduous forest. *Insect. Conserv. Divers.* 3, 222–228.
- Valladares, G., Salvo, A., Cagnolo, L. (2006) Habitat fragmentation effects on trophic processes of insect-plant food webs. *Conserv. Biol.* 20, 212–217.
- Vance, C.C., Smith, S.M., Malcolm, J.R., et al. (2007) Differences between forest type and vertical strata in the diversity and composition of Hymenopteran families and mymarid genera in Northeastern temperate forests. *Environ. Entomol.* 36, 1073–1083.
- Vaughn, N.R., Asner, G.P., Giardina, C.P. (2014) Centennial impacts of fragmentation on the canopy structure of tropical montane forest. *Ecol. Appl.* 24, 1638–1650.
- Viana, B.F., Silva, F.O., Kleinert, A.M.P. (2001) Diversidade e sazonalidade de abelhas solitárias (Hymenoptera: Apoidea) em dunas litorâneas no Nordeste do Brasil. *Neotrop. Entomol.* 30, 245–251.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science* 277, 494–496.
- Wardhaugh, C.W., Stork, N.E., Edwards, W. (2014) Canopy invertebrate community composition on rainforest trees: Different microhabitats support very different invertebrate communities. *Austral. Ecol.* 39, 367–377.
- Williams, N.M., Crone, E.E., Roulston, T.H., et al. (2010) Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.* 143, 2280–2291.

- Wilson, E.O. (1988) The current state of biological diversity. *Biodiv.* 3, 3 – 18.
- Wimp, G.M., Murphy, S.M., Lewis, D., Ries, L. (2011) Do edge responses cascade up or down a multi-trophic food web? *Ecol. Lett.* 14, 863–870.
- Winchester, N.N., Ring, R.A. (1996) Northern temperate coastal sitka spruce forests with special emphasis on canopies: Studying arthropods in an unexplored frontier. *Northwest Sci.* 70, 94–103.
- Worm, B., Duffy, J.E. (2003) Biodiversity, productivity and stability in real food webs. *Trends Ecol. Evol.* 18, 628–632.
- Zhu, H., Xu, Z.F., Wang, H., Li, B.G. (2004) Tropical rain forest fragmentation and its ecological and species diversity changes in southern Yunnan. *Biodivers. Conserv.* 13, 1355–1372.

Author Contributions

Chapter II

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The work distribution among authors was as follows

ES and ISD designed the study, ES collected data, ES analyzed the data, interpreted the results and wrote the manuscript, PH and ISD proof-read the manuscript.

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Chapter IV

This chapter is yet to be submitted.

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Erklärung

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation mit dem Titel „Effects of habitat fragmentation on trap-nesting bees, wasps and their natural enemies in small secondary rainforest fragments in Costa Rica“ selbständig, am Lehrstuhl für Tierökologie und Tropenbiologie (Zoologie III) der Julius-Maximilians-Universität Würzburg, unter der Anleitung und Betreuung durch Herrn Prof. Dr. Ingolf Steffan-Dewenter angefertigt habe und dabei keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet habe. Ich erkläre außerdem, dass die vorliegende Dissertation weder in gleicher, noch in ähnlicher Form bereits in einem Prüfungsverfahren vorgelegen hat. Des Weiteren habe ich außer den mit dem Zulassungsantrag urkundlich vorgelegten Graden keine weiteren akademischen Grade erworben oder zu erwerben versucht.