



**Patrícia Alves Ferreira**

**Influência da perda de habitat sobre a  
diversidade de abelhas e as redes de interação  
planta-abelha em paisagens fragmentadas na  
Bahia**

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**Bahia**

Tese apresentada ao Instituto de Biologia da  
Universidade Federal da Bahia, para a  
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Orientadora: Profa.Dra. Blandina Felipe Viana.

Co-orientador: Prof.Dr. Danilo Boscolo.

**Salvador**

**2013**

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*“Saber reconhecer o valor da natureza e de todo o ambiente na qual se encontra, é uma dádiva à espécie humana. Faltam-nos expressões suficientemente adequadas para descrevermo-nos. Das mais nobres virtudes da natureza, do mais simples gesto, da mais sábia realidade baseada na ciência, encontra-se o verdadeiro sentido de toda a existência, reconhecendo, assim, que com pequenos gestos vêm, também, grandes mudanças.”*

Jacqueline Ferreira

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## Resumo

1 Questões sobre como as modificações do habitat afetam a biodiversidade foram  
2 investigadas no projeto "Biogeografia, fragmentação florestal e limiares de extinção: um  
3 estudo *multi-táxon* na Mata Atlântica da Bahia, Brasil". Como parte desse projeto, na  
4 presente tese, verificamos como a redução de habitat afeta a diversidade de abelhas  
5 visitantes florais e a estrutura das redes planta-polinizador. A polinização é um dos principais  
6 processos ecológicos e é ameaçado pelo desmatamento e intensificação da agricultura.  
7 Entretanto, ainda há poucas evidências empíricas que analisaram esses efeitos. Este  
8 trabalho foi dividido em três capítulos. No primeiro capítulo, revisamos a literatura sobre os  
9 efeitos das alterações da paisagem natural e da intensificação da agricultura nas plantas, nos  
10 visitantes florais e nas redes de interação planta-polinizador. Vimos que as modificações nas  
11 paisagens diminuem a diversidade e disponibilidade de polinizadores, afetam a polinização  
12 cruzada e a reprodução sexual de plantas. Estes efeitos ocorrem, sobretudo, devido ao  
13 isolamento de habitats e a redução dos recursos florais e áreas para nidificação.  
14 Aproximadamente 50% dos 155 trabalhos analisados mostraram efeitos negativos da  
15 intensificação da agricultura sobre os polinizadores e o processo de polinização, como  
16 resultado da conversão de áreas naturais para usos agrícolas. Encontramos um trabalho que  
17 discutiu esses efeitos para redes de interação planta-polinizador. Vimos assim, que há uma  
18 lacuna no conhecimento sobre os efeitos das modificações das paisagens nas redes de  
19 interação planta-polinizador. No segundo capítulo, avaliamos como a perda de habitat afeta a  
20 diversidade de polinizadores no sub-bosque da Floresta Atlântica na Bahia. As abelhas são  
21 os principais polinizadores de angiospermas no mundo e são sensíveis as modificações do  
22 habitat natural. Nossos resultados mostram que as paisagens com maior proporção de  
23 floresta são importantes para as abelhas, mesmo quando a floresta é altamente  
24 fragmentada. No terceiro capítulo, questionamos como a perda de habitat afeta a estrutura  
25 das redes de interação planta-polinizador no sub-bosque de Floresta Atlântica na Bahia.  
26 Observamos que, nas paisagens com menos floresta, as redes são menores, têm menos  
27 espécies e são mais conectadas e aninhadas, *i.e.* apresentam mais interações entre  
28 espécies generalistas em um núcleo coeso, e há poucas espécies especialistas interagindo  
29 com generalistas nestas redes. Acreditamos que, devido a degradação ambiental, as  
30 espécies de visitantes florais generalistas são as mais capazes de permanecer nas  
31 paisagens mantendo as redes e também as populações vegetais. Concluindo, estudos sobre  
32 redes de interação na perspectiva da paisagem e em florestas tropicais podem fornecer  
33 informações para a conservação de plantas, polinizadores e da polinização. Habitats  
34 florestais são importantes para a manutenção da diversidade de abelhas, das redes planta-  
35 abelha, e dos serviços de polinização.

36

37 **Palavras-chave:** Abelhas, Polinizadores, Plantas, Redes de Interação, Paisagem,  
38 Sub-Bosque, Floresta Tropical, Bahia, Brasil.

## Abstract

1            Questions about how landscape changes affect biodiversity were investigated in the  
2 project "Biogeography, forest fragmentation and extinction thresholds: a multi-taxon study in  
3 the Atlantic Rainforest of Bahia, Brazil." As part of this project, in this thesis we examine how  
4 habitat reduction affects the diversity of flower visiting bees and the structure of plant-  
5 pollinator networks. Pollination is a major ecological process and is threatened by  
6 deforestation and agricultural intensification. However, there is a lack of empirical evidence  
7 that analyzed these effects. This work encompasses three chapters. In the first chapter we  
8 review the literature on the effects of natural landscape changes and agricultural  
9 intensification on plants, pollinators and plant-pollinator networks. We have seen that changes  
10 in landscapes decrease the diversity and availability of pollinators, affect cross-pollination and  
11 sexual reproduction of plants. These effects occur, mainly, because habitat isolation and  
12 reduction of floral resources and nesting areas. Approximately 50% of the 155 analyzed  
13 studies showed negative effects of agricultural intensification, with conversion of natural areas  
14 into agricultural uses. We found one study that discussed these effects for plant-pollinator  
15 networks. So, there is a gap in knowledge about the effects of changes in landscapes on  
16 plant-pollinator networks. In the second chapter we evaluate how habitat loss affects  
17 pollinator diversity in the understory of the Atlantic Forest in Bahia. Bees are the main  
18 pollinators of flowering plants in the world and are sensitive to changes in the natural habitat.  
19 Our results show that landscapes with a higher proportion of forest are important to bees,  
20 even when the forest is highly fragmented. In the third chapter we question how habitat loss  
21 affects the structure of plant-pollinator networks in the understory of the Atlantic Rainforest in  
22 Bahia. We observed that in less forested landscapes networks are smaller, have fewer  
23 species and are more connected and nested, *i.e.* have more generalist species interacting  
24 with each other in a cohesive core, and there are few specialist species interacting with  
25 generalists in these networks. We believe that, due to environmental degradation, generalist  
26 flower visitor species are better able to remain in the landscapes, maintaining the networks  
27 and also the plant populations. In conclusion, studies on interaction networks from the  
28 perspective of the landscape and tropical forests can provide important insights for the  
29 conservation of plants, pollinators and pollination. Forest habitats are important for  
30 maintaining the diversity of bees, plant-bee networks, and pollination services.

31

32            **Keywords:** Bees, Pollinator, Plant, Networks, Habitat Changes, Landscape,  
33 Understory, Atlantic Rainforest, Bahia, Brazil.

## Apresentação

*"The loss and fragmentation of natural habitats by human activities are the main driving forces behind current biodiversity loss. Animal-mediated pollination is a key process for the sexual reproduction of most extant flowering plants, and the one most consistently studied in the context of habitat fragmentation."*

Aguilar et al. 2006

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1           As modificações do habitat põe em risco a biodiversidade. A partir de certos  
2 valores de redução de hábitat a perda de biodiversidade pode ser abrupta. Contudo  
3 são escassas as informações para quais comunidades essa perda abrupta de  
4 biodiversidade é observada, ou quais são os valores críticos de perda de hábitat, ou  
5 ainda como podem ser mitigados esses efeitos. Estas e outras questões estão  
6 sendo investigadas por pesquisadores e estudantes do Instituto de Biologia da  
7 Universidade Federal da Bahia vinculados ao projeto "Biogeografia, fragmentação  
8 florestal e limiaries de extinção: um estudo *multi-táxon* na Mata Atlântica da Bahia".  
9 Os estudos desenvolvidos incluem desde a comparação da biodiversidade entre  
10 localidades que possuem diferentes quantidades de floresta e diferentes históricos  
11 biogeográficos até o desenvolvimento de modelos computacionais que simulam a  
12 resposta dessas comunidades à perda de hábitat. Uma das metas do projeto é  
13 contribuir para a produção de conhecimento científico que possa colaborar com a  
14 gestão da biodiversidade; principalmente no estado da Bahia.

15           A presente tese faz parte desse projeto, e procura verificar os efeitos da  
16 redução do habitat na diversidade de abelhas visitantes florais e na estrutura das

1 redes de interação mutualísticas entre plantas e polinizadores. A polinização é um  
2 dos principais processos ecológicos em ambientes terrestres. Uma das principais  
3 ameaças a esse processo é a perda de habitat provocada pelo desmatamento e  
4 intensificação da agricultura. As mudanças da paisagem, assim como a quantidade  
5 e qualidade do hábitat e a configuração das paisagens podem modificar a  
6 diversidade, o comportamento dos polinizadores e conseqüentemente a reprodução  
7 sexual das plantas em sistemas naturais e agrícolas. Entretanto poucos trabalhos  
8 empíricos analisam as interações planta-polinizador e as respostas das  
9 comunidades às mudanças na paisagem.

10 Mais recentemente foram desenvolvidos modelos teóricos para acessar os  
11 efeitos das mudanças na paisagem sobre o mutualismo planta-polinizador. Esses  
12 modelos preveem que as comunidades de polinizadores e de plantas são afetadas  
13 através da desestabilização da estrutura das redes de interação planta-polinizador.  
14 Os modelos mostram também que, as comunidades persistem a vários níveis de  
15 extinção, mas que há um limiar, ou seja, um valor crítico no qual as comunidades  
16 colapsam e que os animais são mais rapidamente afetados que as plantas.  
17 Entretanto, ainda há poucas evidências empíricas que suportem essas previsões.

18 Este trabalho foi dividido em três capítulos, que serão submetidos  
19 individualmente a periódicos científicos especializados para a divulgação dos  
20 principais resultados. O primeiro capítulo da tese apresenta uma revisão da literatura  
21 especializada na qual fizemos um levantamento sobre o conhecimento empírico e  
22 teórico acerca dos efeitos das alterações na paisagem, como a perda e a  
23 fragmentação de habitats nas interações planta-polinizador. Além disso, neste  
24 capítulo questionamos o que se sabe sobre os efeitos das modificações na  
25 paisagem nas redes de interação planta-polinizador, e como a intensificação da  
26 agricultura convencional afeta as interações planta-polinizador. Vimos que as  
27 modificações nas paisagens naturais afetam a polinização cruzada e a reprodução  
28 sexual de plantas. Porém, há uma lacuna no conhecimento sobre os efeitos das

1 modificações nas paisagens naturais nas redes planta-polinizador. Abordagens  
2 integradas podem ser úteis para a conservação dessas interações e dos serviços de  
3 polinização em ecossistemas naturais e agrícolas. Esse capítulo foi publicado no  
4 periódico *Ecological Indicators* e está disponível *online* desde setembro de 2012.

5 No segundo capítulo, avaliamos como a perda de habitat afeta a diversidade  
6 de abelhas visitantes florais no sub-bosque da Floresta Atlântica remanescente na  
7 Bahia. As abelhas são os principais polinizadores de angiospermas no mundo. Por  
8 isso esses animais têm elevada importância ecológica e econômica. As abelhas são  
9 sensíveis às modificações do habitat natural, pois dependem desse para o uso de  
10 recursos alimentares e locais de nidificação. Neste capítulo levantamos três  
11 hipóteses: 1) Há maior diversidade de abelhas em paisagens com maior cobertura  
12 florestal; 2) Áreas com maior abundância de flores apresentam maior diversidade de  
13 abelhas; e 3) A perda do habitat natural afeta diferentemente os grupos funcionais  
14 de abelhas caracterizados pelos tipos de ninhos e de socialidade.

15 Finalmente, no terceiro capítulo, discutimos sobre como a perda de habitat  
16 afeta a estrutura das redes de interação planta-polinizador no sub-bosque de  
17 Floresta Atlântica na Bahia. Mais especificamente, caracterizamos e determinamos o  
18 padrão estrutural dessas redes, e hipotetizamos que a perda de habitat influencia  
19 negativamente o tamanho das redes (número total de espécies animais e plantas), a  
20 conectância e o aninhamento das redes.

21 Os métodos comuns aos capítulos 2 e 3 serão descritos nas seções "Área  
22 de Estudo" e "Coleta de Dados" nas páginas 20-27.

# *Introdução Geral*

## 1. Introdução Geral

1 A perda de habitats naturais modifica a disponibilidade de recursos, o  
2 tamanho das populações e aumenta as probabilidades de extinção de espécies  
3 (Fahrig 2003). As alterações na paisagem são as maiores ameaças à  
4 biodiversidade, pois modificam a estrutura das comunidades, isolam populações,  
5 podem modificar os processos ecológicos, afetando negativamente a sobrevivência  
6 das espécies e interações entre espécies (Steffan-Dewenter & Tscharntke 2002,  
7 Steffan-Dewenter et al 2002, Tscharntke et al. 2002, Fahrig 2003, Bascompte  
8 2009a). As interações entre espécies podem ser bons modelos para investigar a  
9 qualidade dos ambientes modificados, uma vez que sua conservação pode ser mais  
10 importante para a manutenção da biodiversidade e de serviços ecológicos do que a  
11 preservação de espécies isoladas em ambientes fragmentados (Steffan-Dewenter &  
12 Tscharntke 1999, Diaz & Cabido 2001, Forup & Memmott 2005).

13 A redução da quantidade de habitat pode modificar o comportamento de  
14 forrageio dos insetos visitantes florais, limitando ou impedindo a movimentação  
15 desses entre as manchas de habitat remanescentes (Brosi et al. 2007). Esses  
16 processos também modificam os padrões de transferência de pólen (Memmott et al.  
17 2004, Fortuna & Bascompte 2006), restringindo a quantidade de pólen compatível  
18 depositado sobre os estigmas e afetando negativamente a reprodução sexual de  
19 plantas polinizadas por animais (Nazareno & Carvalho 2009). O isolamento espacial  
20 de manchas de habitat limita o número de polinizadores disponíveis, reduzindo o  
21 sucesso reprodutivo das plantas, aumentando a depressão endogâmica e a erosão  
22 genética de populações isoladas (Aizen & Feinsinger 1994a, 1994b, Steffan-  
23 Dewenter & Tscharntke 1999).

24 A polinização por animais é um processo ecológico chave nos ecossistemas  
25 terrestres que garante o sucesso reprodutivo das plantas e, indiretamente, mantém  
26 outras espécies animais que dependem dessas plantas (Kearns et al. 1998, Fortuna  
27 & Bascompte 2006). Em florestas tropicais, onde a diversidade vegetal é

1 extremamente elevada, a polinização por animais, principalmente abelhas, é muito  
2 importante para a manutenção das comunidades vegetais (Bawa 1990, Tabarelli et  
3 al. 2008). Por exemplo, nas florestas tropicais da América Central, Amazônia e da  
4 costa atlântica brasileira, os animais são responsáveis pela reprodução da maioria  
5 das espécies vegetais (Bawa 1990, Ramalho & Batista 2005). Os animais visitantes  
6 florais parecem ser mais sensíveis e respondem mais rapidamente às mudanças no  
7 habitat do que as plantas (Aizen & Feinsinger 1994b, Steffan-Dewenter & Tscharrntke  
8 1999, Taki & Kevan 2007). As relações mutualistas entre plantas e animais são  
9 importantes para a manutenção da biodiversidade, principalmente em ambientes  
10 tropicais (Bascompte 2007).

11 A demanda por serviços de polinização aumenta, ao mesmo tempo em que a  
12 diversidade de polinizadores diminui nas regiões temperadas e tropicais. De todas  
13 as culturas ao redor do mundo, quase 5% (regiões temperadas) e 8% (regiões  
14 tropicais) são dependentes de polinização animal (Aizen et al. 2009). As abelhas  
15 apresentam grande importância ecológica e econômica (Brosi et al. 2007, Winfree et  
16 al. 2009, 2011), e são afetadas pela perda de suas fontes de alimento e locais de  
17 nidificação, devido à perda e fragmentação dos habitats naturais (Kearns et al. 1998,  
18 Potts et al. 2010). Nos trópicos, pouco se sabe sobre a diversidade das  
19 comunidades de abelhas em paisagens alteradas. Além disso, muitos estudos  
20 utilizam a comparação entre fragmentos de diferentes tamanhos em uma mesma  
21 paisagem e poucos estudos utilizam diferentes paisagens como unidades amostrais  
22 para avaliar como a estrutura da paisagem afeta abelhas e outros animais  
23 polinizadores (Viana et al. 2012).

24 Redes de interações bióticas desempenham um papel importante na  
25 organização e persistência da biodiversidade e podem afetar a resistência dos  
26 ecossistemas às alterações da paisagem (Fortuna & Bascompte 2006; Bascompte  
27 2009a). Como essas mudanças afetam muitas espécies ao mesmo tempo, essas  
28 abordagens permitem análises de várias espécies e suas interações



1 simultaneamente (Tylianakis et al. 2008). Por isso, as redes de interações são  
2 descritores úteis de sistemas ecológicos e fornecem um quadro conceitual para  
3 avaliar as consequências das perturbações nas comunidades ecológicas face às  
4 mudanças ambientais (Bascompte 2009a).

5 Estudos de conservação geralmente visam a preservação da diversidade de  
6 espécies. Contudo, a extinção de espécies como um resultado de alterações  
7 ambientais tais como a perda de habitat, pode levar à perda das interações entre  
8 espécies, quando um dos parceiros desaparece. Assim, a perda da interação  
9 propriamente dita entre as espécies pode também conduzir à extinção de um ou  
10 ambos os parceiros. Portanto, não considerar as redes ecológicas dentro das quais  
11 uma espécie ameaçada está incorporada pode levar a medidas de gestão  
12 contraproducentes (Tylianakis et al. 2010). Estudos sobre redes ecológicas  
13 permitem uma melhor avaliação dos efeitos de mudanças de habitat sobre a perda  
14 de biodiversidade e podem fornecer suporte para a conservação das espécies e dos  
15 ambientes (Forup & Memmott 2005, Sabatino et al. 2010).

16 Redes mutualistas têm distribuição heterogênea das interações, são  
17 aninhadas e podem ser compartimentalizadas. As redes aninhadas têm um núcleo  
18 coeso de interações assimétricas, onde as espécies generalistas interagem umas  
19 com outras e espécies especialistas interagem com o subgrupo de espécies  
20 generalistas, criando um centro denso de interações entre espécies. Por exemplo,  
21 plantas raras dependem, em grande parte, de polinizadores generalistas que, por  
22 sua vez, dependem de plantas generalistas, mais comuns nas comunidades  
23 (Bascompte et al. 2003, Bascompte 2009b). Essas características proporcionam  
24 estabilidade ao sistema e respostas alternativas das espécies de plantas e animais  
25 às mudanças ambientais (Bascompte et al. 2003, Jordano et al. 2007).

26 A arquitetura e a estrutura das redes mutualísticas podem fornecer  
27 informações importantes que ajudam a compreender como as espécies respondem  
28 às mudanças ambientais (Tylianakis et al. 2008, Bascompte 2010). Adicionalmente,

1 através da compreensão da estrutura de redes ecológicas, é possível avaliar como  
2 estas redes são capazes de resistir à extinção de espécies em cenários que  
3 sofreram ou estão sofrendo perda de habitat, ou outras influências antropogênicas.  
4 Modelos sugerem que extinções aleatórias não são capazes de afetar a estrutura da  
5 rede, entretanto, quando as espécies generalistas, que interagem com muitas outras  
6 espécies nas redes, são extintas, as redes tendem a entrar em colapso muito  
7 rapidamente (Bascompte 2009a).

8 Poucos estudos analisaram as interações entre plantas e visitantes florais a  
9 partir da perspectiva das redes tróficas em ambientes tropicais brasileiros (Pigozzo &  
10 Viana 2010). Além disso, poucos estudos empíricos testaram os efeitos de  
11 mudanças na paisagem nas redes de interações planta-polinizador (Aizen &  
12 Feinsinger 1994b, Steffan-Dewenter & Tscharntke 1999, Memmott et al. 2004,  
13 Fortuna & Bascompte 2006, Ferreira et al. 2013), em comunidades naturais (Diaz &  
14 Cabido 2001), na escala da paisagem (Lennartsson 2002) e na Floresta Atlântica  
15 brasileira (Ramalho & Batista 2005).

16 A Floresta Atlântica brasileira é um ambiente extremamente diverso contendo  
17 cerca de 1-8% do total de espécies do mundo e apresentando altas taxas de  
18 endemismo de espécies. Este bioma tem sido historicamente submetido à  
19 degradação e restam apenas 12% de sua extensão original distribuídos em  
20 manchas remanescentes, muitas, menores do que 50 ha. Contudo esse importante  
21 ambiente foi pouco estudado (Ribeiro et al. 2009). Os pequenos fragmentos  
22 remanescentes da Floresta Atlântica brasileira podem não incluir toda a diversidade  
23 de plantas e da fauna associada. No entanto, a conservação de habitats florestais é  
24 importante para a manutenção das interações entre as espécies e da biodiversidade.  
25 Por isso, florestas tropicais devem ser mantidas e protegidas (Lopes et al. 2009).

## 1.1. Objetivos

1            Nesse contexto, a presente tese teve por objetivo (1) examinar o que há de  
2 conhecimento disponível sobre a influência da perda de habitat nos polinizadores,  
3 plantas e redes de interação planta-polinizador; (2) verificar a influência da perda de  
4 habitat em paisagens florestais fragmentadas na Bahia, Nordeste brasileiro sobre a  
5 riqueza e abundância de abelhas visitantes florais; e (3) sobre a estrutura das redes  
6 de interação entre plantas e abelhas. Neste estudo, concentramo-nos na  
7 comunidade vegetal do sub-bosque da Floresta Atlântica brasileira, um ambiente  
8 tropical pouco estudado, extremamente biodiverso e altamente ameaçado (Ribeiro et  
9 al. 2009, Lopes et al. 2009).

10            Inicialmente, para o primeiro capítulo, fizemos um levantamento da literatura  
11 especializada disponível e questionamos quais os efeitos das alterações na  
12 paisagem nas interações plantas-visitantes florais e como intensificação da  
13 agricultura afeta essas interações. Objetivamos entender se há informações  
14 suficientes para a criação de paisagens amigáveis às interações planta-polinizador  
15 com efeitos positivos para a conservação e manejo de plantas, polinizadores e  
16 serviços de polinização em habitats naturais, alterados e agrícolas, assim como  
17 sugerido por Viana et al. (2012).

18            Avaliamos, no segundo capítulo, como a perda de habitat afeta a diversidade  
19 de polinizadores no sub-bosque da Floresta Atlântica na Bahia. Apesar de nossos  
20 procedimentos de amostragem incluírem todos os insetos visitantes florais, focamos  
21 esse estudo particularmente nas abelhas, o principal grupo de polinizadores de  
22 angiospermas (Roubik 1995, Ramalho & Batista 2005), e o grupo mais abundante  
23 em nossas amostras para todos os locais de estudo (70% de todos os visitantes  
24 florais coletados). A diversidade de abelhas está positivamente associada com a  
25 diversidade de plantas nos habitats (Ramalho & Batista 2005, Grundel et al. 2010).  
26 As abelhas dependem do habitat natural para o uso de recursos alimentares e locais  
27 de nidificação (Brosi et al. 2007, Kremen et al. 2007, Ricketts et al. 2008). Sendo

1 assim, hipotetizamos que há maior diversidade das comunidades de abelhas em  
2 paisagens onde há maior cobertura florestal no nível da paisagem e no nível dos  
3 fragmentos. Esperávamos, também, encontrar maior diversidade de abelhas em  
4 áreas com maior abundância de flores. Investigamos, ainda, como a perda de  
5 habitat natural afeta os grupos funcionais de abelhas caracterizados por tipos de  
6 ninhos e socialidade.

7 Finalmente, no terceiro capítulo, objetivamos entender como a perda de  
8 habitat afeta redes de interação planta-abelha no sub-bosque de Floresta Atlântica  
9 na Bahia. Mais especificamente, pretendemos caracterizar redes de interação  
10 planta-abelha e determinar o padrão estrutural dessas redes. Esperávamos que a  
11 redução da cobertura habitat afetasse a estrutura e topologia das redes de interação  
12 planta-abelhas (Guimarães et al. 2007). Assim, a nossa hipótese é que a perda de  
13 habitat influencia negativamente o tamanho das redes planta-abelhas, reduzindo o  
14 número de espécies de abelhas e plantas por rede, e influenciando positivamente a  
15 conectância e o aninhamento das redes.

16

## 17 **1.2. Área de Estudo**

18 Este estudo foi realizado no sub-bosque da Floresta Atlântica na Bahia,  
19 região Nordeste do Brasil, um ambiente extremamente diverso, pouco conhecido e  
20 que abriga espécies ameaçadas de extinção (Ribeiro et al. 2009). Clima dessa região  
21 é classificado com tropical úmido (*Af* - Köppen-Geiger) com temperatura média entre  
22 24°C e 27°C, pluviosidade total anual superior a 2000 mm de precipitação e  
23 precipitação média mensal superior a 60 mm em todos os meses do ano (Peel et al.  
24 2007). Sete paisagens quadradas de 36km<sup>2</sup> (6 x 6 km, totalizando 3600ha) foram  
25 amostradas em um gradiente de paisagens variando de 15 a 55% de cobertura de  
26 florestal. Amostramos a Floresta Atlântica em estágios de regeneração variando de  
27 médio a avançado e altitude variando entre 23m e 416m (ver Tabela 0). O tamanho  
28 das paisagens (36km<sup>2</sup>) foi determinado arbitrariamente, pois esta escala pode

- 1 permitir a observação de processos como a movimentação local de populações, por
- 2 exemplo. Áreas desmatadas compostas de pastagem e/ou plantio de vegetação
- 3 herbáceas/arbustivas foram consideradas matriz de não-habitat (Figura 1).

Tabela 0: Localização das sete paisagens de 36km<sup>2</sup> (3600ha) amostradas ao longo de um gradiente de cobertura florestal de 15% a 55%, de Floresta Atlântica na Bahia, Brasil.

| Localização<br>(cidades abrangidas) | Cobertura<br>Florestal (%) | Altitude | Estádio<br>Successional | Tipo de<br>Floresta | Dossel<br>(m) | Coordenadas<br>Geográficas |
|-------------------------------------|----------------------------|----------|-------------------------|---------------------|---------------|----------------------------|
| Pres. Tancredo<br>Neves             | 15                         | 181      | Médio                   | Ombrófila           | 8-11          | 13°23'28"S<br>39°19'06"W   |
| Valença/Pres. T.<br>Neves           | 25                         | 144      | Médio                   | Ombrófila           | 10-13         | 13°20'32"S<br>39°11'43"W   |
| Amargosa/Ubaíra                     | 30                         | 416      | Avançado                | Ombrófila           | 12-15         | 13°07'19"S<br>39°39'34"W   |
| Taperoá/Nilo<br>Peçanha/Ituberá     | 35                         | 31       | Avançado                | Ombrófila           | 11-14         | 13°38'58"S<br>39°12'37"W   |
| Wenceslau<br>Guimarães              | 40                         | 249      | Médio/Avançado          | Ombrófila           | 11-14         | 13°33'14"S<br>39°42'07"W   |
| Camamu                              | 45                         | 23       | Médio/Avançado          | Ombrófila           | 11-14         | 14°00'51"S<br>39°10'56"W   |
| Jaguaripe                           | 55                         | 47       | Médio                   | Ombrófila           | 10-13         | 13°11'44"S<br>39°01'26"W   |



**Figura 1: Exemplos de áreas de matriz de não habitat compostas de plantio de culturas herbácea/arbustivas e/ou pastagens em paisagens de 36km<sup>2</sup> (3600ha) amostradas ao longo de um gradiente de cobertura florestal de 15% a 55%, na Floresta Atlântica da Bahia, Nordeste do Brasil.**

1 Com base no Atlas de Remanescentes Florestais da Mata Atlântica  
2 ([www.sosma.org.br](http://www.sosma.org.br) e [www.inpe.br](http://www.inpe.br)), selecionamos as sete paisagens de 36km<sup>2</sup>  
3 assumindo o intervalo entre 15, 25, 30, 35, 40, 45 e 55%, até  $\pm 2\%$  (Fig. 2A).  
4 Utilizamos imagens de satélite com projeção cartográfica LAT/LONG e datum  
5 WGS84 (World Geodetic System 1984 - 24S), como resultado do mapeamento feito  
6 pelo SOS Mata Atlântica. Nós transformamos essas imagens em arquivos raster  
7 (Geo-TIFF) com pixels de 20m de lado (extensão de 300x300 pixels) no software  
8 ArcGIS 9.3. Os arquivos Geo-TIFF foram analisados por meio de métricas de classe  
9 no software FRAGSTATS 4.1. Devido à presença de manchas de floresta  
10 extremamente pequenas nas paisagens, decidimos usar as métricas ponderadas  
11 pela área dos fragmentos (McGarigal & Marks 1995). Estabelecemos três critérios  
12 para controlar a variabilidade ambiental entre as paisagens. Primeiro cada paisagem  
13 de 36km<sup>2</sup> deveria estar inserida em uma paisagem mais ampla (18km de lado,  
14 totalizando uma área de 324km<sup>2</sup>) com percentual de cobertura florestal semelhante  
15 entre as escalas. Segundo, ambas as paisagens de 36km<sup>2</sup> e 324km<sup>2</sup> deveriam  
16 apresentar valores semelhantes para o índice de maior fragmento (*Large patch*  
17 *index - LPI*), que determina o percentual ocupado pela maior área de floresta na  
18 paisagem (McGarigal & Marks 1995). Este critério visou evitar a influência de  
19 fragmentos florestais que pudessem servir como áreas fonte nas proximidades das  
20 paisagens amostradas, que poderiam confundir os resultados (Fig. 2B). Terceiro,  
21 pelo menos 80% da matriz de ambas as paisagens deveria consistir de áreas de  
22 não-habitat compostas por áreas não florestadas de pastagem e/ou vegetação  
23 herbácea/arbustiva. Dessa forma, evitamos que diferentes matrizes tivessem  
24 influência na resposta das espécies, por exemplo, matrizes de áreas urbanas que  
25 poderiam servir como barreira à dispersão e movimentação de espécies, ou matrizes  
26 arbóreas que poderiam servir como áreas fonte de espécies (Swift & Hannon 2010).



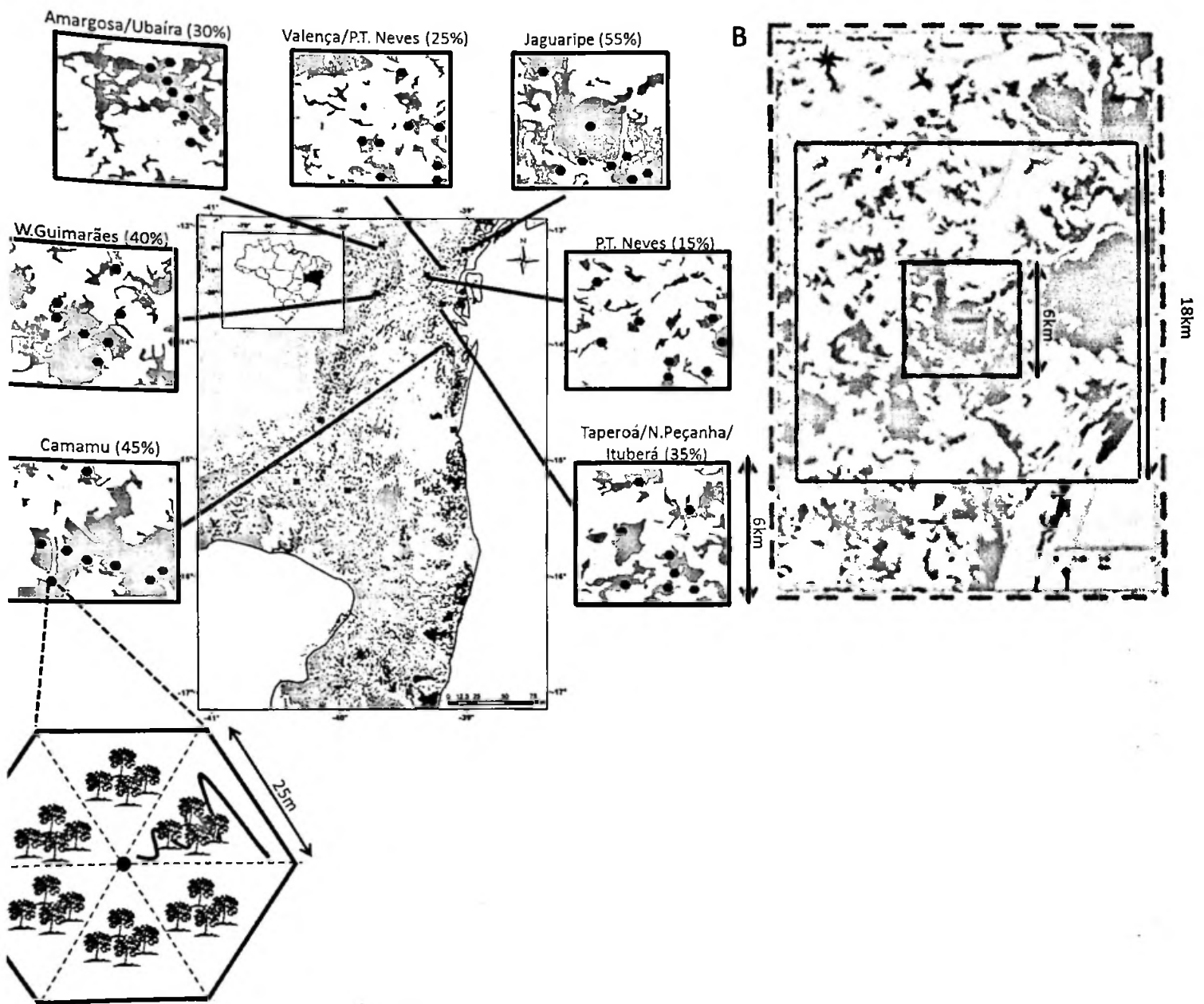


Figura 2: A) Paisagens  $36\text{km}^2$  ( $3600\text{ha}$ ) amostradas, com respectivos percentuais de cobertura florestal ao longo de um gradiente de cobertura florestal de 5% a 60%, na Floresta Atlântica da Bahia Nordeste do Brasil. As paisagens foram selecionadas a partir do Atlas de Remanescentes Florestais da Mata Atlântica em estágios de regeneração de médio a avançado ([www.sosma.org.br](http://www.sosma.org.br) e [www.inpe.br](http://www.inpe.br)). C) Parcelas hexagonais de 25m de lado ( $0.06\text{ha}$ ). Em detalhe, a linha interna representa o caminho padronizado para amostragem de visitantes florais a partir do centro para as bordas de hexágonos. B) Paisagem  $36\text{km}^2$  ( $6 \times 6\text{km}$ ), cinza = floresta, branco = matriz não-florestal. Cada paisagem foi inserida numa área de  $324\text{km}^2$  ( $18 \times 18\text{km}$ ), com valor de percentagem de cobertura florestal semelhante à percentagem da paisagem com  $36\text{km}^2$ .

### 1.3. Coleta dos dados

1 Os dados foram coletados em 2011, em dois períodos (de janeiro a abril e de  
2 agosto a novembro), para evitar o período mais chuvoso do ano e variações  
3 sazonais. Em cada uma das nove paisagens, foram selecionadas através de sorteio  
4 oito parcelas hexagonais regulares com 25m de lado (0.16ha), totalizando 63  
5 parcelas e 11.5ha amostrados. As parcelas foram estabelecidas dentro dos  
6 fragmentos florestais, distando, pelo menos, 50m de todas as bordas (Fig. 2C), a  
7 uma distância de pelo menos 600m entre si para garantir a independência de dados  
8 (Taki & Kevan 2007). As unidades amostrais (parcelas hexagonais) apresentaram  
9 altura do dossel superior a oito metros. Em cada parcela, medimos a riqueza e  
10 abundância das espécies de abelhas, bem como a abundância de plantas com flores  
11 no sub-bosque. Abelhas visitantes florais foram coletadas em cada parcela durante  
12 um dia por parcela, totalizando oito dias por paisagem, em dias quentes e sem  
13 chuva (20-31°C), das 6:00-17:00h, totalizando 96 horas de amostragem por  
14 paisagem. Em cada parcela, nos orientamos por um caminho padronizado do centro  
15 para as bordas dos hexágonos, e fizemos observações de 15 minutos em todas as  
16 plantas com flores em alturas até dois metros acima do solo. Durante essas  
17 observações, as abelhas visitantes florais dessas plantas foram coletadas com redes  
18 entomológicas. Se abelhas visitantes florais escapassem antes de serem coletadas,  
19 nós registrávamos o morfotipo da abelha e o horário de visita. Quando possível os  
20 morfotipos foram identificados em gênero ou espécie.

21 Nós coletamos ramos floridos de todas as espécies de plantas encontradas  
22 no hexágono para identificação. A fim de estimar a abundância de flores por  
23 espécies por hexágono, contamos o número de flores por ramo de um indivíduo de  
24 cada espécie de planta com flor. Multiplicamos esse valor para todos os ramos da  
25 planta e para o número de indivíduos dessa espécie no hexágono.

26 Abelhas e plantas foram identificadas por especialistas no nível taxonômico  
27 mais específico possível, de acordo com a classificação proposta por Michener

- 1 (2000) e APG III (Bremer et al. 2009), respectivamente. As abelhas foram fixadas e
- 2 depositadas no Museu de Zoologia - UFBA (Universidade Federal da Bahia). As
- 3 plantas foram depositadas no Herbário Alexandre Leal Costa (ALCB) - UFBA.

# *Capítulo I*

*What do we know about the effects of  
landscape changes on plant-pollinator  
interaction networks?*



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## What do we know about the effects of landscape changes on plant–pollinator interaction networks?

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### ABSTRACT

Biotic interactions play an important role on the organization and persistence of biodiversity. Unnatural modifications of landscape structure such as habitat loss and fragmentation can isolate populations and disrupt biological communities, affecting species survival and altering the complex set of relationships between plants and pollinators. Plant–pollinator interaction networks have characteristics such as asymmetry and nestedness that may influence the stability and robustness of networks to landscape changes. Species in mutualistic networks might respond to landscape modifications with a sudden collapse at critical habitat destruction thresholds. In this work we review general trends in the scientific literature related to the effects of landscape changes on plant–pollinator networks. For this, a survey in Scopus and Web of Knowledge databases was conducted in May 2011 using all seven possible combinations of the terms “pollinat\*” with the terms “landscape”, “habitat loss” and “network”. We found 155 papers and 92% of those showed significant effects of landscape changes on pollinator diversity and plant reproductive success. Approximately 50% of all analyzed papers showed effects of agriculture intensification as a result of increases in the conversion of natural areas into agricultural crops on plant–pollinator interactions. Landscape modifications affected cross-pollination and the sexual reproduction of plants largely because of reduced diversity and availability of pollinators due to increased habitat isolation and reduction of floral resources and nesting areas in the remaining available habitat. An integrated approach concerning the effects of modified landscapes on natural ecosystems regarding how these variations can affect the stability and robustness of pollination networks can be extremely useful for conservation of plant–pollinators interactions, with positive overall consequences for conservation of plant, pollinators and pollination services in natural and agricultural ecosystems.

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### 1. Introduction

Biodiversity is more than a collection of species. Networks of biotic interactions involving predation, parasitism and pollination play an important role on the organization and persistence of biodiversity (Fortuna and Bascompte, 2006; Bascompte, 2009). In addition, biotic interactions may affect the resilience of ecosystems to landscape modifications (Montoya, 2008). Because of that, studies including information on ecological networks often allow a better assessment of the possible effects of habitat changes on biodiversity loss (Forup and Memmott, 2005; Montoya, 2008;

Sabatino et al., 2010). These studies have great potential to assist in the conservation of biodiversity (Jongman, 2004).

Plant–pollinator networks consist of a special type of ecological network with specific characteristics, such as asymmetry of interactions, with specialist species frequently interacting with generalists and nestedness (Bascompte, 2009). These networks structural attributes may influence the stability and robustness of interactions and network responses to changes (Bascompte et al., 2003). Nestedness and asymmetry generate cohesive network cores which may help withstand species loss, since the most linked species play a central role in the network stability (Bascompte et al., 2003; Bascompte, 2009). For that reason plant–pollinator networks could be more resistant to negative effects of landscape changes (Ramos-Jiliberto et al., 2009; Olesen and Jordano, 2002; Memmott et al., 2004, 2005; Petanidou et al., 2008; Vilà et al., 2009). Species in mutualistic networks might also respond to landscape modifications with a sudden collapse at critical habitat destruction thresholds (Fortuna and Bascompte, 2006). Kaiser-Bunbury et al. (2010) showed that there must be a strong impact

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on networks stability when more than half of the most connected species is lost and most network cores can no longer be supported. At these critical values the extinction of pollinators may abruptly increase, leading to the disruption and collapse of plant–pollinator interactions (Viana et al., 2012).

Landscape changes caused by habitat loss and fragmentation have become a central issue in conservation biology (Haila, 2002; Fischer and Lindenmayer, 2007). Decreasing habitat availability at the landscape level can isolate populations and disrupt the structure of biological communities, directly affecting species survival and interactions. These processes can alter the complex set of relationships between plants and pollinators (Fortuna and Bascompte, 2006), promoting higher rates of plant self-fertilization and consequent inbreeding depression due to reduced success of animal driven cross-pollination (Lennartsson, 2002). This can lead to important changes in both presence and relative abundance of different reproductive traits of plant species, resulting in reduced functional diversity of plant communities in natural areas (Girão et al., 2007).

In this paper we aimed to search for general trends in the scientific literature dealing with the effects of landscape changes, including habitat loss and fragmentation on plant–pollinator interactions. We asked what is known about the effects of landscape changes on plant–pollinator interaction networks and inquired how agriculture intensification with increased conversion of natural areas into crops can affect plant–pollinator interactions. Overall, we want to understand if there is enough knowledge available to efficiently design plant–pollinator friendly landscapes with positive effects for the conservation and management of plants, pollinators and pollination services in changed habitats.

## 2. Procedures

We conducted a survey of the scientific literature in May 2011 using all seven possible combinations of the terms “pollinat\*”, “landscape”, “habitat loss” and “network” in the Web of Science and Scopus databases. From the search results we selected all articles which dealt with the effects of landscape modifications on pollinators, plants and/or pollination. We did not include in the analysis papers that exclusively evaluated the responses of plant–pollinator networks without any explicit mention to the effects of landscape change. We performed exploratory analyses to identify general patterns in the scientific literature regarding the effects of habitat modification on plant–pollinator interactions. In cases where the same study measured more than one variable, we considered all response variables separately.

Many studies analyzed in the present review used some terms without an explicit or specific definition, what could make proper interpretations difficult. Definition of concepts and their standardization is also an important step when surveying scientific knowledge for environmental management purposes as attributing the effect of a certain term to a similar but essentially different factor can make it difficult to understand the available information and may lead to wrong conclusions. Therefore, to avoid the drawbacks derived from conceptual problems, we standardized all technical terminology related to landscape ecology in accordance with Metzger (2001) and Fahrig (2003), as suggested by Viana et al. (2012), and normalized papers analyzed according to the categories previously defined (Table 1).

## 3. Overview

We found 155 papers that evaluated directly or indirectly, explicitly or implicitly, the effects of landscape modifications on plant–pollinator interactions. Overall, 92% (143 papers) showed

significant effects of landscape changes on the diversity, frequency and movement patterns of pollinators and/or on the diversity, reproductive systems, reproductive success and productivity of plants. Most effects were relative to changes of the spatial distribution of landscape elements (65%). About one quarter of the analyzed papers reported effects of landscape composition, specially the proportion of land covered by different types of environments (Supplementary material 1).

One of the most frequently observed patterns was that pollinators diversity is affected by habitat loss and fragmentation (Liow et al., 2001; Darvill et al., 2006; Nates-parra et al., 2008; Winfree et al., 2009; Quintero et al., 2010), mostly due to increased isolation of habitat patches (Greenleaf and Kremen, 2006; Brosi et al., 2007; Zurbuchen et al., 2010) and also because of reduced landscape complexity caused by environmental simplification (Steffan-Dewenter et al., 2001; Bartomeus et al., 2010; Hoehn et al., 2010; Holzschuh et al., 2010). From the pollinators point of view, loss of landscape complexity usually lead to the reduction of floral resources and nesting areas in the remaining available habitat patches, impairing population survival and reducing their overall diversity (Potts et al., 2003; Klein et al., 2004; Brosi et al., 2008; Jha and Vandermeer, 2009; Goulson et al., 2010). Reduced diversity was observed mainly for bees (Ahrne et al., 2009; Jauker et al., 2009; Hoehn et al., 2010; Quintero et al., 2010), the worldwide most important pollinators (Roubik, 1995), but also for other pollinator groups such as birds (Breitbach et al., 2010) and bats (Quesada et al., 2003, 2004; MacSwiney et al., 2007; Willig et al., 2007).

Landscape modifications also affected cross-pollination and the sexual reproduction of plants largely due to reduced diversity and availability of pollinators (Parra-Tabla et al., 2000; Dick et al., 2003; Aguilar et al., 2006). Reduced plant population density and number of pollen donors available in landscapes may also cause disruption of pollination processes (Fuchs et al., 2003; Uchiyama et al., 2009), which changes the selection pressures of floral traits, modifying the set of reproductive strategies of whole plant communities (Lopes et al., 2009). Plant population density changes may have deep effects on the amount (Fuchs et al., 2003) and quality of plant progeny (Cascante et al., 2002; Lennartsson, 2002; Lowe et al., 2005; Eckert et al., 2009).

We also found that 77 studies (approximately 50% of all 155 analyzed papers) showed effects of landscape changes caused by agriculture intensification on plant–pollinator interactions as a result of increased conversion of natural areas to agricultural crops (Kremen et al., 2007; Steffan-Dewenter and Westphal, 2008). Approximately 75% of these studies advocated that landscape changes affects the diversity, movement and frequency of pollinators, and 36% the diversity, reproductive systems, reproductive success, resources and productivity of plants.

Nevertheless we found only one paper explicitly assessing the effects of landscape changes from the perspective of complex networks of plant–pollinator interactions. Hagen and Kraemer (2010) observed significant structural differences of plants and floral visitors networks in structurally diverse landscape mosaic within forest, forest edge and farmlands in Kenya.

Overall, in our review we noted that most available studies focused mainly on the effects of landscape modifications on pollinator diversity and/or plant reproductive success. Nevertheless, there are some studies which indicate that nested and asymmetric mutualistic networks tend to be reasonably robust and resilient to most landscape changes (Olesen and Jordano, 2002; Memmott et al., 2004, 2005; Petanidou et al., 2008; Ramos-Jiliberto et al., 2009; Vilà et al., 2009). Theoretical, empirical or manipulative studies about mutualistic networks answers to landscape changes could reveal important information for the maintenance of these networks, and specifically of plant–pollinator interaction networks under modified environments.

**Table 1**  
List of categories used for organizing and analyzing the selected papers found in May 2011 using all seven possible combinations of the terms “pollinat” with the terms “landscape”, “habitat loss” and “network” on Web of Science and Scopus.

| Variables           | Categories  | Descriptions   |
|---------------------|---|--|
| Year                |   |  |
| Authors             |   |  |
| Journal             |   |  |
| Study location      |   |  |
| Climatic region     | Tropical<br>Subtropical<br>Temperate  |  |
| Ecosystem           | Agriculture<br>Forest<br>Savanna<br>Desert<br>Agro-forestry<br>Urban                          |  |
| Matrix              | Agriculture<br>Natural<br>Savanna<br>Forest<br>Agro-forestry<br>Urban<br>Mix                  |  |
| Landscape           | Agriculture<br>Natural<br>Savanna<br>Agro-forestry<br>Mix<br>Urban                            |  |
| Study type          | Empirical<br>Revision<br>Meta-analyze<br>Modeling<br>Theoretical                              |  |
| Methods             | Descriptive<br>Observational<br>Experimental<br>Literature survey<br>Modeling<br>Meta-analyze |  |
| Objectives          | Descriptive<br>Establish relations<br>Explicative<br>Modeling<br>Review                       |  |
| Approach level      | Landscape<br>Patches<br>Buffer  |  |
| Sample unity        | Individuals<br>Population<br>Community  |  |
| Study object        | Plant<br>Pollinator<br>Interaction  |  |
| Dependent variables | Plants diversity  | Plants richness and abundances   |
|                     | Plants reproductive systems   | Plants reproductive traits as self compatibility<br>Fruit and seed set |
|                     | Plants reproductive success   |  |
|                     | Plants productivity<br>Floral resources   | Crops production<br>Nectar and pollen available in the system          |
|                     | Pollinators diversity<br>Pollinator's visits frequency<br>Pollinators movements               | Pollinators richness and abundances                                    |

Table 1 (Continued)

| Variables              | Categories   | Descriptions   |
|------------------------|--|--|
| Independent variables  | Patches area<br>Patches isolation<br>Landscape composition         | How landscape elements are spatially distributed<br>Which are the landscape elements available |
|                        | Landscape configuration  |  |
|                        | Matrix<br>Edge<br>Floral resources                                 |  |
| Variables relationship | Positive<br>Negative<br>Unrelated<br>Differences<br>No differences |  |

We found several indications that landscape modifications affect plant–pollinator interactions by reducing the abundance and diversity of pollinators (Steffan-Dewenter and Tschardt, 1999; Kremen et al., 2002; Chacoff and Aizen, 2006; Fujimori et al., 2006), which leads to lower seed production (Brudvig et al., 2009; Nazareno and Carvalho, 2009; Lander et al., 2010; Vesik et al., 2010). Deforestation can also affect plant reproductive processes by changing the foraging behavior of pollinators and consequently the quality of plant gene flow (Ghazoul and McLeish, 2001). In general the diversity of floral visitors and the frequency of observed visits decreased with increasing the distance to natural habitats (Chacoff and Aizen, 2006). The richness and abundance of flying floral visitors, for example, dropped more than 80% over a distance of 500 m from natural habitat in tropical and subtropical agro-forestry systems (Carvalho et al., 2010). Additionally, bees usual foraging distances, which depend on maximum efficiency foraging strategies, are smaller than their maximum measured flight distance, indicating that nearby areas can function as key habitat structures to preserve bee populations (Zurbuchen et al., 2010).

Trees with limited distribution and reduced genetic variation were more likely to go extinct in the face of landscape changes (Hamrick, 2004). Seed production may be affected by reduced amount of pollen transfer between flowers (Schmucki and Blois, 2009), but plants which can produce fruits by self-fertilization are usually favored in landscapes where plant individuals are isolated and pollinators and pollen flow is reduced or improbable (Pinto-Torres and Koptur, 2009). Composition of plant communities in landscapes, which have experienced severe fragmentation can be modified in favor of species pollinated and dispersed mainly by passive processes such as wind pollination and with detriment of species that are pollinated and dispersed by animals (Regal, 1982; Ghazoul and Shaanker, 2004).

A stochastic individual-based simulation model developed by Keitt (2009) suggests that as landscapes are changed and native habitat is removed, plant–pollinator systems tend to be altered and even small disturbances may cause plant–pollinator interactions collapse within the remaining habitat patches in fragmented landscapes. Keitt (2009) suggested that extinction thresholds for plant–pollinator interaction systems may occur at about 50–60% of habitat loss, when pollinators and plants generalist species start to disappear from communities. But not only habitat loss can cause the disruption of pollination interaction networks. According to the model developed by Kaiser-Bunbury et al. (2010), there must be a strong impact on networks stability when more than half of the most connected species is lost, which causes a sudden and rapid collapse of the total strength of the networks. These

complementary results indicate that there is a pungent need to set which are the critical values of habitat loss that can increase pollinators' extinction up to the point where natural plant–pollinator interaction networks may collapse (Viana et al., 2012). However, strictly defined values may not really exist, with each case being unique. Also, empirical field studies concerning ecological networks often lack replication and these different responses associated with plants and pollinators make their results difficult to be understood (Dupont et al., 2009). In addition, both sides of the mutualistic interaction must be assessed in order to properly predict pollinators' extinction chances and plant reproductive vulnerability to landscape changes (Ashworth et al., 2004).

Moreover, studies about habitat fragmentation which focused solely on the differences of biodiversity patterns of non-fragmented versus fragmented landscapes are generally inadequate to represent the gradual effects of habitat changes. Nevertheless, this approach is still the more frequently used in empirical fragmentation studies (Ewers and Didham, 2006). On the other hand, simulations based on real landscapes and species with distinct life histories have been useful to increase our comprehension about the relationships between landscape dynamics and biodiversity (Burel et al., 1998). Approaches that take into account continuous measures of landscape changes along gradients of habitat degradation could be more thoroughly used to evaluate the effects of gradual habitat modifications on plant–pollinator interactions.

Agriculture intensification and conversion of natural to urban environments also changes natural habitats features, affecting plant and pollinators diversity (Ahrne et al., 2009; Frankie et al., 2009; Bommarco et al., 2011), pollinators community composition (Carre et al., 2009), pollinators floral visits behavior (Ricketts et al., 2008) and may influence plant reproductive success (Priess et al., 2007; Kim et al., 2006). Additionally, conventional agricultural management which uses large crop areas, insecticides, herbicides and exotic pollinators may also negatively influence local plant–pollinator interaction networks because of environmental simplification and resources reduction for pollinators, consequently lessening the availability of pollinators for plants (Klein et al., 2007; Jha and Vandermeer, 2010). These changes may have important implications for pollination processes, with important effects even for crop production (Richards, 2001), as pollinators are important for more than 75% of the world's most important agricultural plants species (Klein et al., 2007).

The value of ecosystem services promoted by standing forest patches for agriculture and other human-made systems is still little known. Ricketts et al. (2004), however, estimated that the actual costs of reduced pollination services are probably higher than previously expected. Spatially explicit land use change simulations clearly indicate that most of the ecological and economic values of natural habitats can potentially be saved over the coming decades if the remaining patches are preserved within agricultural landscapes (Priess et al., 2007). An approach which integrates agricultural areas, natural habitats and planned urban ecosystems may improve pollination services efficiency in these ecosystems. The maintenance of natural habitats surrounding agricultural areas may improve pollination services in the crops while the conservation of native pollinators may also be important for pollination of wild plants species. (Goulson et al., 2008; Hannon and Sisk, 2009; Hennig and Ghazoul, 2011).

Alternative management practices, such as organic farming (Andersson et al., 2012), and urban gardens (Ahrne et al., 2009) had positive effects on pollinator diversity at different landscape scales (Gabriel et al., 2010; Jha and Vandermeer, 2010; Van Rossum, 2010). However, Winfree et al. (2008) pointed out that the heterogeneity of habitats surrounding crops could be more important than the farm management system for maintaining the diversity of native bees. For example, the resource mass production offered

by some crops can also promote the maintenance of pollinating bee species (Walther–Hellwig and Frankl, 2000). The proximity of natural areas to crops can facilitate pollination due to the higher diversity of pollinators in natural habitats, where they can find proper nesting sites and appropriate supplementary resources in times of scarcity (Ricketts, 2004; Klein, 2009; Lonsdorf et al., 2009; Tschardt et al., 2011), allowing high seed-set and more stable reproductive success of both native and cultivated plants (Dick et al., 2003; Greenleaf and Kremen, 2006). Landscape heterogeneity and connectivity can also increase pollinator diversity and plant reproductive success (Van Rossum, 2010). Proximity of natural habitats, green areas in urban landscapes, proper environmental management and pollinator-friendly landscape arrangements can promote the conservation of pollination services in natural, urban and agricultural systems (Marshall and Moonen, 2002; Zhang et al., 2007; Klein et al., 2008; Ricketts et al., 2008; Brudvig et al., 2009; Keitt, 2009; Brittain et al., 2010; Jha and Vandermeer, 2010; Van Rossum, 2010; Hennig and Ghazoul, 2011; Viana et al., 2012).

#### 4. Conclusions

Deforestation can affect the reproductive processes of plants by causing changes in the abundance and foraging behavior of pollinators and, consequently, the quality and quantity of plant gene flow (Ghazoul and McLeish, 2001). The maintenance of heterogeneous landscapes can increase local and regional biodiversity and possibly maintain ecosystem services (Morreale and Sullivan, 2010). The consolidation of knowledge concerning ecological processes such as pollination at the landscape level are of extreme importance for the management of natural areas with the aim of conserving ecosystem services (Tschardt et al., 2004; Nazareno and Carvalho, 2009; Olschewski et al., 2010). Overall, the papers we analyzed showed that it is possible to consider the creation of landscape designs which could maintain pollinators diversity (Priess et al., 2007; Goulson et al., 2008; Hannon and Sisk, 2009; Jauker et al., 2009; Hennig and Ghazoul, 2011), as well as plants and pollination services. However, we found only one paper (Hagen and Kraemer, 2010) which empirically analyzed the effects of landscape changes on plant–pollinator networks. Remaining papers studied the effects of landscape changes on pollinator diversity and/or the reproductive success of plants without directly assessing its consequences to the stability of pollination networks. This indicates that there still exist a profound need to increase scientific efforts on the study of landscape changes consequences on plant–pollinators networks structures and stability. An integrated approach concerning the study of the effects of modified landscapes on natural ecosystems and how these variations can affect the stability and robustness of pollination networks may be extremely useful for conservation of plant–pollinators interactions, with positive overall consequences for conservation of plant, pollinators and pollination services in natural and agricultural ecosystems. We believe that studies of interaction networks on landscapes perspective may provide important information and understanding of the best strategies for plant, pollinators and pollination conservation.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2012.07.025>.

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## *Capítulo II*

*Effects of habitat loss on bees in the  
Brazilian Atlantic Rainforest*

# Effects of habitat loss on bees in the Brazilian Atlantic Rainforest

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## Abstract

1 Anthropogenic habitat loss and fragmentation tend to isolate pollinator  
2 populations negatively affecting sexual reproduction of animal-pollinated plants. We  
3 evaluated how habitat loss affects pollinator diversity in the understory of Atlantic  
4 Rainforest fragments in Northeastern Brazil. We focused on bees, the main group of  
5 pollinators for angiosperms and the most frequent group sampled in our study area  
6 (70% of all flower visitors). We assessed how forest cover at regional (landscape)  
7 and local scales affected bee diversity (richness, abundance and composition). We  
8 also examined how habitat loss affected trait groups of bees characterized by nesting  
9 types and levels of sociality. Our results showed that bee community diversity was  
10 positively influenced by forest cover at both regional and local scales; landscapes  
11 with greater forest cover had more diverse communities. These results suggest that  
12 landscapes where Atlantic Rainforest is abundant are important for bees, even when  
13 the forest is highly fragmented. Nevertheless, higher fragmentation could lead to  
14 higher spatial homogenization (or lower diversity) of bee communities. Our results  
15 also showed that the effect of deforestation on bees depends on their traits, social  
16 bees that nest above ground (e.g. in trees or dead wood) are positively influenced by  
17 forest cover; while solitary bees that nest in the ground benefited from some levels of  
18 deforestation, making use of open areas within large forested areas. However, this  
19 group were composed mostly generalist species. This result highlights the  
20 importance of considering species traits when evaluating impacts of deforestation.

21 **Keywords:** Bees, Forest Understory, Atlantic Rainforest, Landscape  
22 changes, Bahia, Brazil.

## 1. Introduction

1           Pollination is a key ecological process that ensures the reproductive success  
2 of plants and has indirect positive effects for other species that also depend on these  
3 plants (Kearns et al. 1998; Fenster et al. 2004; Fortuna and Bascompte 2006). Most  
4 plant species are pollinated by insects. When habitat is lost and fragmented the  
5 structure of biological communities may be disrupted, directly affecting ecological  
6 processes related to species survival and interactions (Tscharntke et al. 2002).  
7 These disturbances may modify the behavior of pollinators and the composition  
8 (Brosi 2009) of their communities (Brosi et al. 2007, 2008, 2009), potentially  
9 modifying species interactions and pollen transfer patterns (Fortuna and Bascompte  
10 2006), limiting the amount of compatible pollen deposited on stigmas, thereby  
11 negatively affecting sexual reproduction of animal pollinated plants (Nazareno and  
12 Carvalho 2009; Lander et al. 2010; Veski et al. 2010).

13           In tropical rainforests, where plant diversity is extremely high, pollination by  
14 animals, mostly bees, is very important for the maintenance of plant communities  
15 (Bawa 1990; Tabarelli et al. 2008). In the rainforests of Central America, the Amazon  
16 and the Brazilian Atlantic coast forests, these animals are responsible for the  
17 reproduction of most plant species (Bawa 1990; Ramalho 2004; Ramalho and Batista  
18 2005). Among the tropical forests, due to its geographical and altitudinal range, the  
19 Brazilian Atlantic Rainforest is an extremely biodiverse environment containing about  
20 1–8% of the world's total species and a high endemism rate. This still poorly studied  
21 biome has been historically submitted to degradation and only about 12% of its  
22 original extension remains, with most patches being very isolated and smaller than  
23 50ha (Ribeiro et al. 2009). Hence, in the Brazilian Atlantic Rainforest most forest  
24 patches may not include all possible diversity of plants and its attendant mutualists.  
25 However, remnant tropical forest habitats provide several important ecosystem  
26 services and species interactions must be maintained if their protection is aimed for  
27 (Lopes et al. 2009).

1           Despite the well-established knowledge on the ecological and economic  
2 importance of bees (Brosi et al 2007; Winfree et al 2009, 2011), little is known of the  
3 effects of habitat loss on their food and nesting sources (Kearns et al. 1998; Ghazoul  
4 2005, Steffan-Dewenter et al. 2005; Frankie et al. 2009; Potts et al. 2010). Even less  
5 information is available on the drivers of bee community change (richness and  
6 abundance) in tropical landscapes. Additionally, most studies compare patches  
7 within a landscape to assess how landscape structure affects pollinators and few  
8 studies use whole landscapes as sampling units (Viana et al. 2012; Ferreira et al.  
9 2013).

10           In this study we evaluated how habitat loss affects pollinators diversity in the  
11 understory of fragmented Atlantic Rainforest in Bahia, Northeast Brazil. Although our  
12 sample procedures included all floral visitor insects, we particularly focused this study  
13 on bees, the main group of pollinators for angiosperms (Roubik 1995; Ramalho and  
14 Batista 2005), and the most abundant group in our study sites (70% of all flower  
15 visitors). Given the high dependency of bees on natural habitat for food resources  
16 and nesting sites (Brosi et al. 2007; Kremen et al. 2007; Ricketts et al. 2008) and that  
17 bee diversity is expected to be positively associated with plant diversity (Ramalho  
18 and Batista 2005; Grundel et al. 2010), we hypothesized that bee communities would  
19 be more diverse in landscapes where forest cover was higher at regional and local  
20 scales. Additionally, we expected that forest cover affected distinct bee trait groups  
21 defined by nest types and sociality.

22

23

## 24           **2. Materials and methods**

25           Study area and Methods were the same for Chapters 2 and 3 and are  
26 described in "Area de Estudo" and "Coleta de Dados" sections in page 20-27.

## 2.1. Landscape Analysis

1 Forest cover data was analyzed in two different spatial scales: regional scale,  
2 landscapes, and local scale. In this way we could access the effects of variations in  
3 forest cover on bee diversity at different complementary spatial scales. We calculated  
4 the percentage of forest cover at the regional scale considering all area of the 36km<sup>2</sup>  
5 (3600ha) landscapes, and at local scale through concentric circular areas (buffers)  
6 with 300m radius (28.2ha), centered at the hexagonal plot center. This radius was  
7 based on the mean foraging range for solitary bees described by Gathmann and  
8 Tscharntke (2002). We used the Atlas of Forest Remnants of the Atlantic Forest  
9 (SOSMA, 2008) and Quantum GIS 1.8.0 software to calculate forest cover (%) at  
10 both scales.

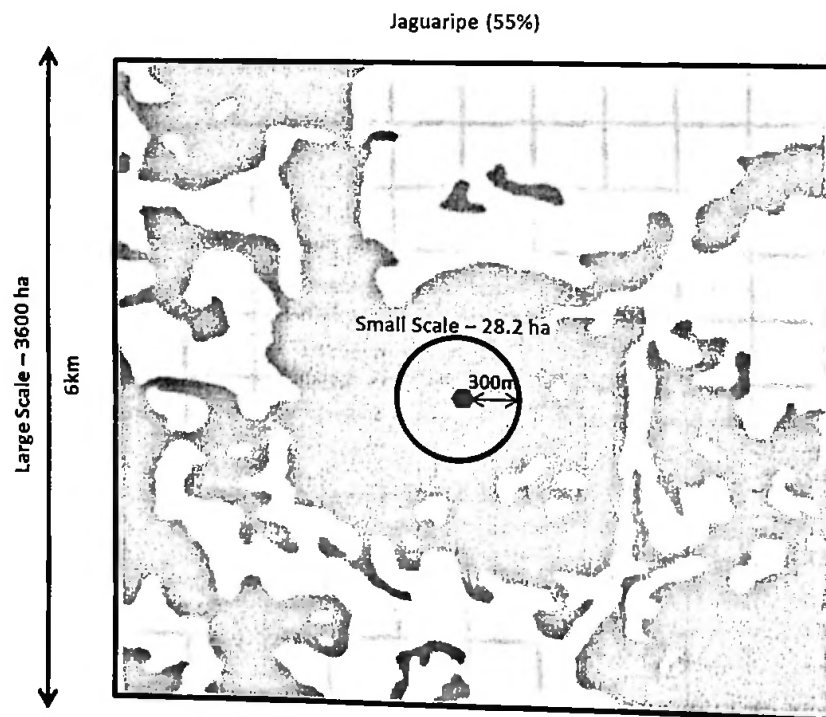


Figure 3: We calculated percentage of forest cover at landscape scale (large scale) with square areas of 36km<sup>2</sup> (3600ha) and at local scale (small scale) with concentric circular areas of 300m (28.2ha) radius with hexagonal plots in the center.



## 2.2 Data Analyses

1           We calculated the Similarity in bee community structure among landscapes  
2 based on Bray-Curtis distances and tested for significant differences with different  
3 levels of forest cover by doing Analysis of Similarities (ANOSIM) test (Quinn and  
4 Keough 2002) in R 2.15.1 (R Development Core Team 2009).

5           Considering that the influence of landscape context on the biological  
6 populations tends to have high complexity, with several factors acting together, we  
7 choose a models selection approach. We used as selection criterion the maximum  
8 likelihood between models created in search of that model which best describe our  
9 dataset. For each selected response variable in this study, we ordered models using  
10 the lowest values of Akaike information criterion with a second-order correction for  
11 small sample sizes (AICc). The probability of a model being the one that best  
12 explains the data set was evaluated by the Akaike weight of evidence (w). We built  
13 simple generalized linear mixed models (GLMM) (Burnham and Anderson 2002) with  
14 one explanatory variable, and also additive and interactive models of the same kind  
15 with two or more explanatory variables.

16           To assess how forest cover affected bee composition we performed a  
17 Principal Coordinates Analysis (PCoA, Multidimensional scaling, MDS) with bray-  
18 curtis dissimilarities matrices. To assess how forest cover affected bee diversity  
19 (species richness and abundance) we used Generalized Linear Mixed Models  
20 (GLMM) assuming Poisson error distribution of data. A model selection procedure  
21 was carried out (in R package lme4) using forest cover at regional and local scales  
22 as fixed explanatory variables. All possible combinations of explanatory variables and  
23 their interactions were considered. The most parsimonious model was selected as  
24 that with the lowest AICc (Burnham and Anderson 2002).

25           To evaluate whether habitat loss affected bees differently depending on their  
26 traits, we grouped bees according to the type of nest (above ground, which includes  
27 bees that nest in the air, on trees and dead wood, for instance; and below ground,

1 including bees that nest on the ground) and social structure (social species, for bees  
2 species that exhibits any level of sociality; and solitary species). From a biological  
3 point of view, most social bees that nest in the air tend to be generalists which are  
4 able to use all the available resources in the environment. Along with it, species that  
5 nest above the ground, in trees, logs sheets, etc. are dependent on forest. These  
6 characteristics may influence the resistance of those species to habitat modifications  
7 (Williams et al. 2010). Information on traits was compiled from the primary literature,  
8 from Moure's Bee Catalogue (Moure et al. 2012) and Bees of the World (Michener  
9 2000). If published data were unavailable, we relied on a consensus of experts  
10 opinions. Whenever information about sociality and nest type for a given species was  
11 not available we used available knowledge on closely related species or genus of  
12 bees.

13 In order to assess the importance of traits in the response of bees to  
14 changes in forest cover we performed model selection with Generalized Linear Mixed  
15 Models, with Poisson error distribution. We considered the fixed explanatory  
16 variables forest cover at both scales, sociality and nest type. The best model was the  
17 one with the lowest value of AIC, Akaike information criterion (Burnham and  
18 Anderson 2002).

19 To handle overdispersion in GLMM with Poisson distribution, it was added a  
20 random factor (plot identity) which estimated an intercept for each plot for all  
21 performed models (Crawley 2007). All analyses were performed using the software R  
22 2.15.1 (R Development Core Team 2009).

23

### 24 **3. Results**

25 Bees represented 70% of the flower visitors we found. We sampled a total of  
26 492 bees from 59 species (see Supplementary Material 2). A new species of the  
27 genus *Chilicola* was recorded for the first time in Bahia (Oliveira et al. 2011). Bee  
28 communities varied among landscapes and their composition, number of different

1 species per landscape was positively influenced by forest cover (ANOSIM: R=  
 2 0.4004; P < 0.001). Landscapes with lower forest cover had more similar bee  
 3 communities among their constituent patches (beta diversity) than landscapes with  
 4 higher forest cover, which support more diverse bee communities.

5 Forest cover significantly affected bee diversity (composition, richness and  
 6 abundance). PCoA results evidenced difference in bee community composition along  
 7 forest cover sampled gradient (Table 2). The best model according to AICc showed  
 8 that bee richness increased significantly with forest cover at the Regional scale, and  
 9 tending to increase (but not significantly) with forest cover at the local scale.  
 10 However, the interaction between Regional and Local scales values of forest cover  
 11 had a negative and not significantly effect on bee richness (Table 3, Figure 2). Bee  
 12 abundance also significantly increased with forest cover at both scales. However, the  
 13 positive effect of forest cover at local scale was significantly more accentuated when  
 14 forest cover at regional scale was high (i.e. there was a significant interaction  
 15 between forest cover at local and regional scales). The greater the quantity of forest  
 16 in both scales greater bee abundance values (Table 3, Figure 2).

Table 2: Results of Principal Coordinates Analysis (PCoA, Multidimensional scaling, MDS) with Bray-curtis dissimilarities matrix. Bee communities' composition varies among sampled sites. Multidimensional scaling axis (MDS1 to MDS4).

|                       | MDS1   | MDS2    | MDS3    | MDS4    |
|-----------------------|--------|---------|---------|---------|
| Site                  | 30.540 | -14.672 | -5.619  | -4.613  |
| Abundance             | 28.180 | 13.655  | 1.094   | 4.169   |
| Richness              | 13.000 | 0.375   | 4.546   | 6.811   |
|                       | MDS1   | MDS2    | MDS3    | MDS4    |
| Eigenvalue            | 0.105  | 0.01604 | 0.00589 | 0.00333 |
| Proportion Explained  | 0.8061 | 0.12313 | 0.04523 | 0.02558 |
| Cumulative Proportion | 0.8061 | 0.92919 | 0.97442 | 1       |

Table 3: Results of three best models for bee richness and abundance, from generalized linear mixed models, with *Poisson* error distribution ordered by AICc (corrected for small sample *Akaike* information criterion) and the probability of a model being the one that best explains the data set was evaluated by the *Akaike* weight of evidence (w). Models explanatory variables: regional scale (forest cover at landscape scale - Rs); local scale (forest cover at plot scale - Ls) and period (P).

| Response Variables (Y)  | Intercept | Rs     | Ls     | P      | Rs x Ls | P*Ls   | AICc  | w      |
|---|-----------|--------|--------|--------|---------|--------|-------|--------|
| <b>RICHNESS</b>   |           |        |        |        |         |        |       |        |
| Model1 = Rs + Ls + (Rs * Ls) (best model)   |           | 0.0190 | ns     | -      | ns      | -      | 76.1  | 0.185  |
| Model2 = Rs + Ls  |           | 0.0550 | ns     | -      | -       | -      | 76.4  | 0.152  |
| Model3 = null   |           | -      | -      | -      | -       | -      | 76.8  | 0.125  |
| Best model Estimates  | 0.2294    | 0.0364 | 0.0081 | -      | -0.0004 | -      |       |        |
| Best model Std. Error   | 0.5356    | 0.0155 | 0.0096 | -      | 0.0003  | -      |       |        |
| Bee Richness = $e^{(0.2294 + 0.0081 \times Ls + 0.0364 \times Rs - 0.0004 \times Ls \times Rs)}$  |           |        |        |        |         |        |       |        |
| <b>ABUNDANCE</b>  |           |        |        |        |         |        |       |        |
| Model1= Rs + Ls + P + (Rs * Ls) + (P * Ls) (best model)   |           | <0.001 | 0.008  | ns     | < 0.001 | 0.0472 | 115.5 | -0.007 |
| Model2 = Rs + Ls + (Rs * Ls)  |           | 0.0491 | 0.0095 | -      | ns      | -      | 116.5 | -0.004 |
| Model3 = Rs + Ls + P + (Rs * Ls)  |           | 0.0422 | 0.0194 | ns     | 0.01938 | -      | 117.4 | -0.003 |
| Best model Estimates  | 1.2260    | 0.0440 | 0.0039 | -      | -0.0005 | <0.001 |       |        |
|   |           |        |        | 0.0043 |         |        |       |        |
| Best model Std. Error   | 0.5129    | 0.0152 | 0.0102 | 0.0019 | 0.0003  | <0.001 |       |        |
| Bee Abundance = $e^{(1.2260 + 0.0039 \times Ls + 0.0440 \times Rs - 0.0005 \times Ls \times Rs)}$ |           |        |        |        |         |        |       |        |

P-value obtained from a likelihood ratio test in which deviances with and without that term in the model were compared. 'ns',  $P > 0.05$ . '-' Indicated variable not included in the model. Number of observations was 55 in seven sampled landscapes (random variable).

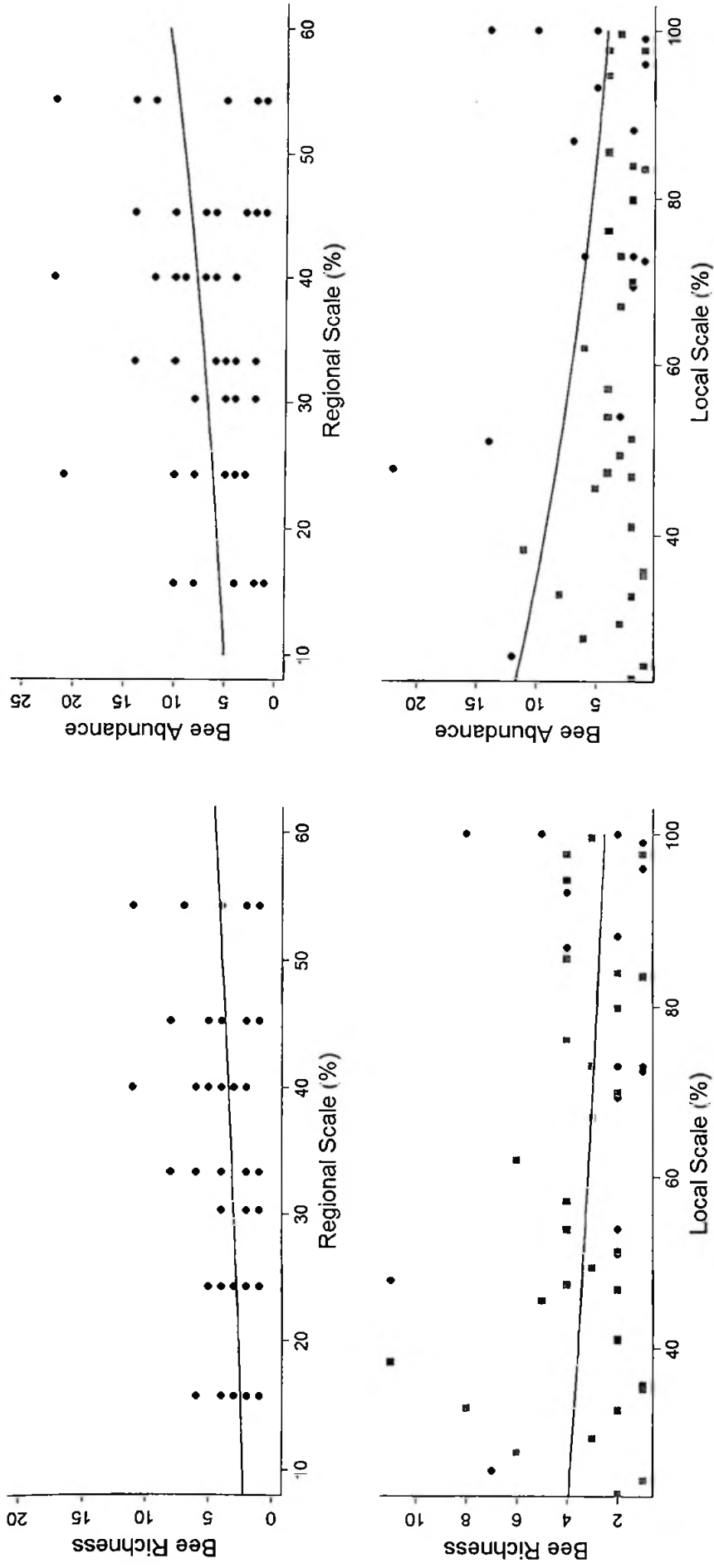


Figure 2: Positive effects of forest cover at Regional scale on bee richness and abundance, sampled in seven fragmented landscapes on the Atlantic Rainforest in Bahia Northeastern Brazil from January–November 2011. Results of the best model (Generalized Linear Mixed Models - GLMM), with Poisson error distribution selected by corrected for small sample Akaike information criterion (AICc). Line represents the best model predicted values for bee richness and abundance at regional scale, considering the constant average value (57.16%) of forest cover at local scale. Negative effects of forest cover at local scale on bee richness and abundance. Gray squares represent plots in landscapes with less than 40% forest cover. Black circles represent plots in landscapes with more than 40% forest cover. Line represents the best model predicted values for bee richness and abundance at local scale, considering the constant average value (35.12%) of forest cover at regional scale.

1           The majority of the sampled bee species (43 out of 59, 73%) exhibited some  
2 level of sociality and 16 species (27%) were considered solitary. We sampled 34  
3 species of bees (58%) that nest above ground and 25 species (42%) that nest below  
4 ground. Among all social bees, 28 species (47%) nest above ground, while 15 social  
5 species nest below ground (25%). Six solitary bee species (10%) nest above ground  
6 and 10 solitary species (17%) make their nests below ground. The effect of forest  
7 cover (regional and local scales) on bee abundance depended on bee sociality and  
8 type of nest. Forest cover at regional scale positively affected the abundance of  
9 social bees that nest above ground, but at local scale had a negative effect on the  
10 abundance of social bees that nest above ground. Forest cover at both scales had a  
11 negative effect on the abundance of solitary bees that nest above ground (Figure 3,  
12 Table 4).

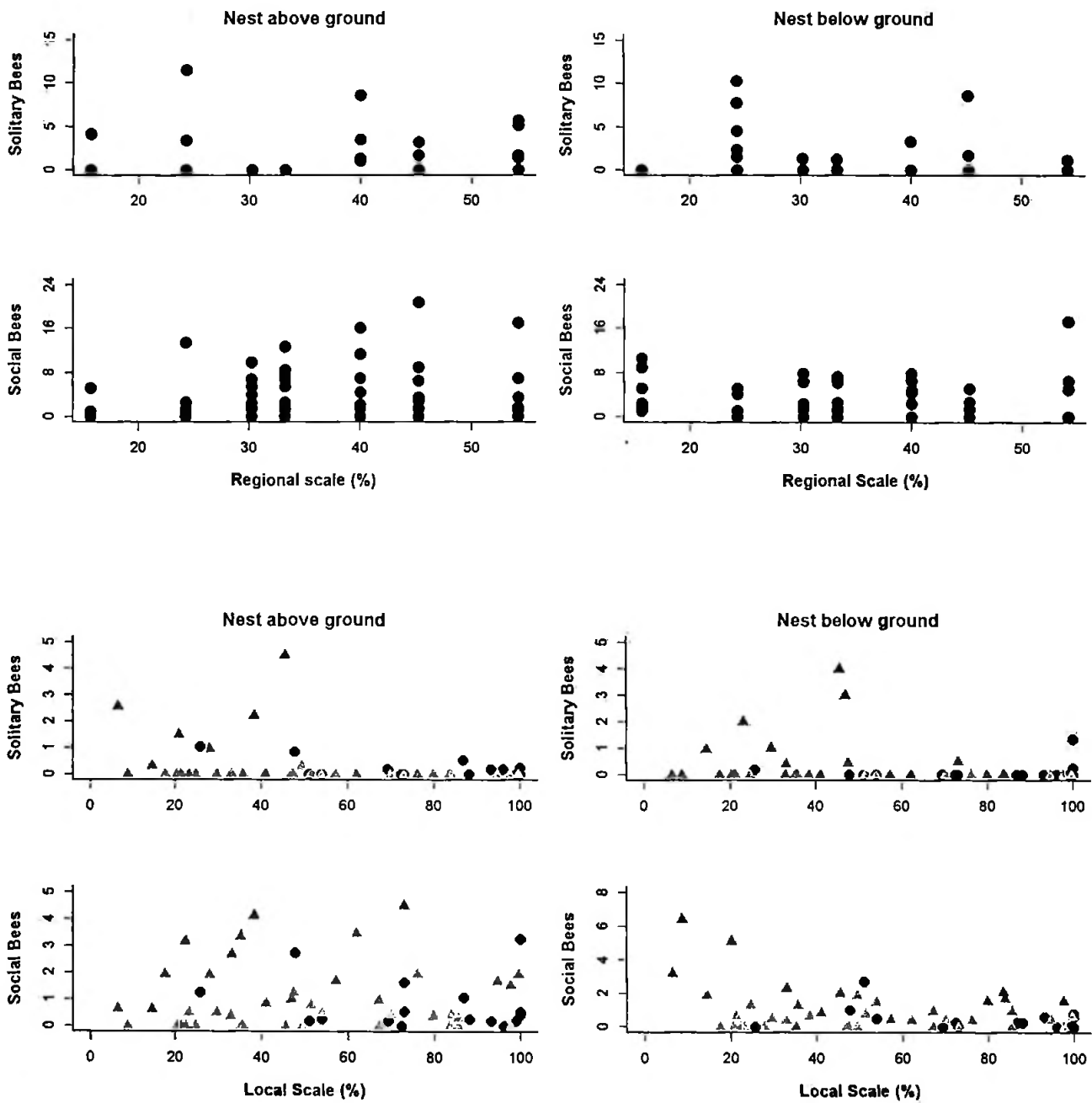


Figure 3: Effects of forest cover at regional and local scales on the abundance of social or solitary bees that nest above or below ground, sampled in seven fragmented landscapes on the Atlantic Rainforest in Bahia Northeastern Brazil from January-November 2011. Results of Generalized linear mixed models (GLMM), with *Poisson* error distribution selected by *Akaike* information criterion (AIC). Gray triangles represent plots in landscapes with less than 40% forest cover and black circles represent plots in landscapes with more than 40% forest cover.

Table 4: Results of bee abundance in functional groups characterized by sociality (social or solitary) and nesting types (above or below ground). Comparison of the three best models obtained for each response variable. Generalized linear mixed models, with Poisson error distribution ordered by AIC (Akaike information criterion). Explanatory variables in the models are forest cover at regional scale (Rs) and at local scale (Ls), Sociality (Social vs. Solitary), Nesting (above ground vs below ground).

| Response Variables (Y) | Intercept | Rs     | Ls      | Sociality | Nesting | Rs*Social | Rs*Nest | Ls*Social | Ls*Nest | Social*Nest | Rs*Social*Nest | Ls*Social*Nest | AIC          |
|------------------------|-----------|--------|---------|-----------|---------|-----------|---------|-----------|---------|-------------|----------------|----------------|--------------|
| <b>ABUNDANCE</b>       |           |        |         |           |         |           |         |           |         |             |                |                |              |
| Model1 (best model)    |           | 0.001  | < 0.001 | < 0.001   | < 0.001 | ns        | < 0.001 | < 0.001   | 0.0367  | 0.003       | 0.001          | < 0.001        | 632.2        |
| Model2                 |           | 0.005  | < 0.001 | < 0.001   | 0.0001  | ns        | 0.003   | -         | -       | 0.011       | 0.048          | -              | 641.1        |
| Model3                 |           | 0.004  | < 0.001 | < 0.001   | 0.0002  | -         | -       | 0.002     | ns      | 0.009       | -              | -              | 0.0142 643.7 |
| Best model Estimates   | 0.2808    | 0.0289 | -0.0055 | -0.5783   | 0.933   | 0.019     | -0.0317 | -0.0269   | -0.0018 | -0.0964     | -0.0325        | -              | 0.0266       |
| Std. Error             | 0.2798    | 0.0075 | 0.0031  | 0.5558    | 0.4012  | 0.0149    | 0.0115  | 0.0074    | 0.0047  | 0.7936      | 0.0242         | -              | 0.0109       |

P-value obtained from a likelihood ratio test in which deviances with and without that term in the model were compared. 'ns', P > 0.05. '-', indicated variable not included in the model. Number of observations was 219 for four functional group in seven sampled landscapes (random variable).



#### 4. Discussion

1 Bees are considered the main pollinators of angiosperms, particularly in  
2 tropical forests (Roubik 1989). However, little information is available on pollinator  
3 abundance and diversity in tropical forest understory. Modern man driven landscape  
4 changes are an ongoing process, particularly within tropical environments (Hagen  
5 and Kraemer 2010, Melo et al. 2013). Here we showed that, in agreement to  
6 previous studies (e.g. Brosi et al. 2008), natural habitat availability at regional scale  
7 positively affects bee communities.

8 Bee communities were more diverse and spatially heterogeneous in  
9 landscapes with higher proportions of Atlantic Rainforest. As changes in natural bee  
10 communities can directly affect their interactions with plants (Winfree et al. 2009), the  
11 loss of bee diversity may have important ecological (78% of angiosperms depends  
12 on insects for pollination, Ollerton et al. 2011) and economic (e.g. crop pollination,  
13 see Garibaldi et al. 2013) impacts.

14 Around the world, natural habitat loss tends to encompass more generalist  
15 species in bee communities (Taki and Kevan 2007). Our results also suggest that  
16 generalist bee species are more persistent on occupy small forest patches (Table 4,  
17 Figure 4). This result may be due to edge effects, generalist bees possibly taking  
18 advantage of the higher flower abundance caused by the invasion by plant species in  
19 smaller and more irregular patches, which tend to have higher proportions of edge  
20 environments (Tabarelli et al. 2008; Lopes and Buzato 2007, Lopes et al. 2009).  
21 Some social generalist bee species (e.g. *Trigona braueri*) forage with large numbers  
22 of individuals, are able to explore a wide variety of floral resources, and are capable  
23 of forage in open areas and edges of patches. Additionally, some of these social  
24 species that nest below ground do not depend on forest because they need open soil  
25 to nest (Cane et al. 2006).

26 Bees are dependent on flowers throughout their life cycle and their existence  
27 is closely related to the presence and abundance of flowers (Potts et al. 2006;

1 Grundel et al. 2010). The availability of floral resources in remaining forests or its  
2 surroundings may be one of the most limiting factors for the maintenance of these  
3 floral visitor species (Ghazoul 2002; Potts et al. 2003; Ramalho 2004). Hegland and  
4 Boeke (2006), for instance, showed that the density of flowers were a better predictor  
5 of the presence of bees than plants species richness. Therefore, in landscapes with  
6 high deforestation, even the smallest forest patches are important. These areas  
7 might sustain generalist bee species, such as *Trigona* sp., which are important for  
8 maintaining pollination for native plant species and crops (Ricketts 2004; Ricketts et  
9 al. 2008; Taki et al. 2010).

10 Diversity of bees is also related to availability of nesting sites (Gathmann and  
11 Tscharntke 2002), since bees nest in different environments (soil, tree hollows, under  
12 fallen logs, etc. Michener 2000). As suggested by our results, the abundance of  
13 social above ground nesting bees was positively influenced by forest cover at  
14 regional scale and solitary bees that nest above ground were negatively affected by  
15 forest cover at both scales. Appropriate sites of natural forest available for bees to  
16 nests may be important as indicators on the risk of decline for bee species that  
17 depend on forest to nest (Cane et al. 2006; Osborne et al. 2008; Williams et al.  
18 2010). The observed importance of forest to social bees that nest above ground  
19 maybe due to enhanced nesting opportunities available within the forest patches. For  
20 social bees that live in groups with many individuals the presence of forested habitat  
21 is important for enabling supply the need of these bees for nesting and food  
22 resources within forests. Therefore, the resources present in the forest are important  
23 for maintaining the social bee species that nest above ground. Solitary bees, and  
24 bees that live in small groups and nesting below ground in open areas with exposed  
25 soil, are less affected by the reduction of forest habitat. However, these are also the  
26 most common species foraging in small forest fragments and edges of the fragments.  
27 Therefore, despite this difference forest resources may also be important for solitary  
28 bees nesting below ground.

#### 4.1. Implications for conservation and ecosystem services

1           Our results show that even though overall bee communities are positively  
2 influenced by forest cover at the regional scale, this effect will vary depending on bee  
3 functional groups. Forest resources are important for maintaining social bee species  
4 that nest above ground. While forest fragmentation, i.e. the transformation of  
5 continuous habitat into smaller patches of habitat fragments, may favor generalist  
6 solitary bee species (Pardini et al. 2009) an increase in the presence of generalist  
7 species may not represent a benefit for the pollination of more pollinator-specialized  
8 native plants of the Atlantic Rainforest. Moreover, bee species with different traits  
9 may have different functions (e.g. pollinating different species, Fontaine et al. 2006,  
10 Hoehn et al. 2008). Therefore, to ensure the reproductive success of a vast number  
11 of plant species, it is important to conserve trait diversity of bee communities.

12           Knowledge consolidation concerning ecological processes such as pollination  
13 at the landscape level is of extreme importance for the management of natural areas  
14 with the aim of conserving ecosystem functioning and services (Tscharntke and  
15 Brandl 2004; Nazareno and Carvalho 2009; Olschewski et al. 2010; Viana et al.  
16 2012). Here we showed that in Atlantic Rainforest, natural habitat loss negatively  
17 affected bees, reducing richness and homogenizing bee communities. Such changes  
18 in pollinator communities of tropical forest landscapes are likely to be important for  
19 the reproduction of understory plants, affecting the quality and quantity of plant gene  
20 flow (Ghazoul and McLeish 2001) and also for pollination services in surrounding  
21 agricultural fields (Ricketts 2004; Klein et al. 2007; Morreale and Sullivan 2010). As  
22 we show that fragmentation has a negative impact for most groups of bees,  
23 management strategies that increase the area available for bee populations through  
24 the restoration of connectivity between habitats may be important for the  
25 maintenance and conservation of species, ecological functioning and ecological  
26 services (Ramalho and Batista 2005).

27

## 4.2. Conclusions

1           Our results showed that forest cover at both regional and local scales had a  
2 positive effect on bee communities (richness, abundance and composition). We also  
3 found that social bees that nest above ground are positively influenced by forest  
4 cover at regional scale while solitary bees that nest above ground were negatively  
5 influenced by forest cover at both scales. This result highlights the importance of  
6 forest to bees that nest above the ground (Williams et al. 2010). Further studies are  
7 also needed to better understand the gaps in the knowledge of critical values of  
8 habitat loss that may increase pollinator extinction rates (Viana et al. 2012), in order  
9 to evaluate the best strategies for pollinator management and conservation. We also  
10 suggest a more integrated approach for land use planning in tropical ecosystems,  
11 with more pollinator friendly agricultural practices, especially for bees (Melo et al.  
12 2013).

13

14

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## *Capítulo III*

*Forest fragmentation effects on plant-  
pollinator interaction networks in  
Northeastern Brazil*

# **Forest fragmentation effects on plant-pollinator interaction networks in Northeastern Brazil**

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## Abstract

1           Mutualistic interactions between plants and pollinators or plants and seed  
2 dispersers play an important role on the organization and persistence of biodiversity.  
3 The structure of the network of such interactions affects the resilience of ecosystems.  
4 The conservation of these interactions may be more important for maintaining  
5 biodiversity and ecological services than the preservation of isolated species in  
6 fragmented environments. In this study we investigate if there are effects of habitat  
7 loss and landscape changes on the structure of plant-pollinator networks in  
8 understory of Brazilian Atlantic Rainforest. Here we explore in more depth the role of  
9 landscape configuration, the quantity and spatial pattern of remnant forest patches,  
10 on the structure of plant-pollinator interaction networks. Our results indicate that  
11 habitat loss affects the structure of plant-bee networks in fragmented Atlantic  
12 Rainforest in Northeast Brazil. Network traits such as the number of bee species and  
13 network size were positively influenced by the amount of available forest in the  
14 landscape. Conversely, network connectance declined with increasing forest cover.  
15 Nestedness declined with mean patch area and increased with mean shape index  
16 (more irregular patch shapes). We consider that the reduction of habitat may have  
17 determined the loss of species and the reduction of network sizes. In those simplified  
18 networks, the increased connectance could mean that the remaining generalist plant  
19 and bee species tend to interact with each other in a more widespread way, and  
20 many of the possible interactions in the network are actually performed. Similarly, the  
21 positive effect of patch shape in network nestedness could also be an indication that  
22 more irregular shapes of forest patches might lead to higher frequency of interactions  
23 among generalist species, due to edge effects. This generalist species generate a  
24 cohesive interaction core in these networks. In summary, the reduction of forest  
25 habitat may simplified network structure by reducing number of species, network  
26 size, and increasing the tendency of interactions to occur in a more cohesive core of  
27 generalist species. Overall, the nested organization indicates that generalist bee  
28 species and plants are the ones that potentially drive and keep the entire interaction  
29 web in fragmented landscapes in Bahia. Our results add a new perspective to studies  
30 of plant-pollinator networks in fragmented landscapes. Interaction networks can also  
31 be indicators of effects of changes in natural habitat. We saw here that the network  
32 structure vary with the quality of the habitat and this variation can have important  
33 effects on pollinator and plant communities in these environments.

34           **Keywords:** Bees, plants, interaction networks, mutualistic web, fragmented  
35 landscapes, Brazilian Atlantic Rainforest.

## 1. Introduction

1           Mutualistic interactions between plants and pollinators or plants and seed  
2 dispersers play an important role on the organization and persistence of biodiversity  
3 and may affect the resilience of ecosystems (Fortuna & Bascompte 2006, Bascompte  
4 2007, Bascompte 2009a). Species interactions are good models for investigate the  
5 quality of modified environments. The conservation of these interactions could be  
6 more important for maintaining biodiversity and ecological services than preservation  
7 of species isolated in fragmented environments (Steffan-Dewenter & Tscharntke  
8 1999, Diaz & Cabido 2001, Forup & Memmott 2005).

9           Habitats loss and fragmentation of natural habitats are the greatest current  
10 threats to biodiversity, disrupting community structure and consequently the  
11 interactions between species (Steffan-Dewenter & Tscharntke 2002, Steffan-  
12 Dewenter et al. 2002, Fahrig 2003, Bascompte 2009a). Such changes can increase  
13 local species extinction and reduce landscapes functional connectivity (Lennartsson  
14 2002). Additionally, cascading effects, e.g. secondary extinctions, may be more  
15 important than the initial species extinction for the ecosystems (Steffan-Dewenter &  
16 Tscharntke 1999). Habitat loss changes abundance and richness of pollinators by  
17 altering resources availability. Likewise, spatial isolation of habitat patches negatively  
18 affect plant pollinator interactions by limiting the number of available pollinators,  
19 reducing plant reproductive success and consequently increase inbreeding  
20 depression and genetic erosion of plants populations (Steffan-Dewenter &  
21 Tscharntke 1999).

22           The study of interaction networks structure may provide important information  
23 that helps to understand species and ecosystem responses to environmental  
24 changes (Tylianakis et al. 2008, Bascompte 2009a, Bascompte 2010). Those studies  
25 allow a better assessment of the effects of habitat changes on biodiversity loss and  
26 may provide support to conservation of biodiversity and environments (Forup &  
27 Memmott 2005, Sabatino et al. 2010, Ferreira et al. 2013). Theoretical models

1 suggests that random extinctions may not affect the whole network structure, but when  
2 well-connected generalist species are extinct, networks tend to collapse very rapidly.  
3 It is predicted a structural threshold beyond that these networks collapse with  
4 secondary species extinctions (Bascompte 2009a, Kaiser-Bunbury et al. 2010).

5         However, few empirical studies have analyzed the structure of mutualistic  
6 interaction networks and tested the effects of landscape changes on plant-pollinator  
7 interactions (e.g. Aizen & Feinsinger 1994, Steffan-Dewenter & Tschamntke 1999,  
8 Memmott et al. 2004, Fortuna & Bascompte 2006, Ferreira et al. 2013), at the  
9 landscape scale (Lennartsson 2002) and from the perspective of trophic networks in  
10 tropical fragmented Brazilian environments (Pigozzo & Viana 2010). We practically  
11 do not know how fragmentation affects or has affected the dynamics of local  
12 interactions between flowers and pollinators in the Atlantic Forest. It is important to  
13 know these effects because there is an urgent need for information that allows better  
14 strategies on the conservation and maintenance of plants and pollinators in the  
15 Brazilian Atlantic Rainforest fragmented landscapes (Ramalho & Batista 2005).

16         In this study we investigate if there are structural changes in plant-pollinator  
17 interaction networks due to habitat loss and landscape modifications in understory of  
18 Northeast Brazilian Atlantic Rainforest remnants in fragmented landscapes. More  
19 specifically, we intended to characterize plant-pollinator interaction networks and to  
20 determine the structural pattern of these networks. We expect that habitat loss and  
21 landscape configuration affect size, number of species, connectance and nestedness  
22 of networks.

23

## 24         **2. Materials and methods**

25         Study area and Methods were the same for Chapters 2 and 3 and are  
26 described in "Area de Estudo" and "Coleta de Dados" sections in page 20-27.

## 2.1. Data Analyses

1 For each landscape, it were assessed eight indexes that describe structure of  
2 networks: 1. Network size - sum of the total number of bees and plants species per  
3 network; 2. Number of bee species per network; 3. Number of plants species per  
4 network; 4. Network connectance - ratio between the number of observed  
5 interactions and the total number of possible interactions, measures the percentage  
6 of interactions that occur in real (Biesmeijer et al. 2005); 5. Number of compartments  
7 - tendency of a network to become organized in "compartments" characterized by a  
8 group of species interacting more strongly among themselves than with other species  
9 in the web; 6. Nestedness - specialist species interact with specific subsets of  
10 generalist species, that interacts among themselves; 7. Interaction evenness; and 8.  
11 Interaction strength asymmetry - some species interact strongly with another that  
12 tends to depend less on the first one (Bascompte & Jordano 2007). We select those  
13 metrics because they were considered more sensitive to changes in landscapes  
14 (Biesmeijer et al. 2005, Tylianakys et al. 2007, Bascompte 2010). All metrics were  
15 calculated using bipartite package from R (R Development Core Team 2009) and we  
16 used these metrics as response variables.

17 To check the effects of landscape composition and configuration in the  
18 structure of sampled networks we used six landscape class metrics: 1. Percentage of  
19 landscape forest cover (PLAND); 2. Core area percentage of landscape (CPLAND) -  
20 (percentage of landscape comprised of forest core areas, considering edge depth as  
21 50m; 3. Number of Patches (NP) - number of forest patches in the landscape; 4.  
22 Mean Patch Area (AREA\_MN) - area of all forest patches in each landscape; 5.  
23 Mean of Shape Index (SHAPE\_AM) - forest patches perimeter (m) divided by the  
24 square root of forest patch area ( $m^2$ ), adjusted by a constant; and 6. Landscape  
25 proximity index (PROX\_AM) - size and proximity of all forest patches whose edges  
26 are within 600m of search radius (Metzger 2003). We used 600m to ensure sampling  
27 independency (Taki & Kevan 2007). PLAND and CPLAND measured the amount of

1 available forest habitat, yet, CPLAND measured area in forest patch interior  
2 disregarding the forest edges. Due to the presence of very small patches within the  
3 landscapes we used patches metrics weighted by the mean area of the patches. Due  
4 to the presence of extremely small forest patches in the landscape, we decided to  
5 use the metrics weighted by the area of the fragments. All landscape metrics were  
6 calculated on Fragstats 4.1 (McGarigal & Marks 1995). We used these metrics as  
7 explanatory variables.

8         Considering that the influence of landscape context on the biological  
9 populations tends to have high complexity, with several factors acting together, we  
10 choose an approach of models selection. We used as selection criterion the  
11 maximum likelihood between models created in search of that model which best  
12 describe our dataset. For each selected response variable in this study, we ordered  
13 models using the lowest values of AICc (*Akaike* information criterion with a second-  
14 order correction for small sample sizes). The probability of a model being the one  
15 that best explains the data set was evaluated by the weight of evidence Akaike (*w*).  
16 We build simple models with one explanatory variable, and additive and interactive  
17 models with two or more explanatory variables. The model coefficients were  
18 calculated from the class of generalized linear models (GLM) (Burnham & Anderson  
19 2002)

20         To understand how landscape explanatory affected network structure, we  
21 applied a model selection procedure. To check if any explanatory and response  
22 variables were correlated with each other we used *Pearson's* product-moment  
23 correlation tests. We did not use correlated explanatory variables in the same  
24 additive model. We used Generalized Linear Models - GLM, with *Poisson* error  
25 distribution for count data and *Gaussian* error distribution for normal distributed data,  
26 in R package *nlme*. All possible combinations of explanatory variables and their  
27 interactions were considered. The most parsimonious model was selected as that  
28 with the lowest AICc, *Akaike* information criterion corrected for small samples



1 (Burnham & Anderson 2002). All analyses were performed using the software R,  
2 package (R Development Core Team 2009).

3

### 4 **3. Results**

5 We sampled 75 plant and 63 floral visitor bee species in understory of  
6 Brazilian Atlantic Rainforest fragmented landscapes (Figure 7). The list of plants and  
7 their bee floral visitors sampled in each landscape is available in Supplementary  
8 Material 3. Our results show that species numbers (network size and bee richness)  
9 and connectance were influenced by habitat quantity (forest cover) while nestedness  
10 was influenced by indicators of habitat quality (mean patch area and mean patch  
11 shape). Plant-bee interaction networks, in fragmented landscapes of Atlantic  
12 Rainforest in Bahia, Brazil are heterogeneous, nested, with asymmetric interactions  
13 (see Table 5). The graphs of the relationship between each network metric with  
14 forest cover (disregarding the edge areas of 50m depth - CPLAND) in sampled  
15 landscapes are presented in Supplementary Material 4. We observe that there were  
16 positive correlations between the number of bees and the size of the network, and  
17 between the number of bees and interactions asymmetry strength. We also observed  
18 negative correlations between size of networks and connectance and number of  
19 bees and networks connectance (Table 6).

20 As we expected there was a positive correlation between the metrics  
21 regarding percentage of forest (PLAND and CPLAND), and also between percentage  
22 of forest (PLAND + CPLAND) and mean patch area (AREA\_MN). We observed  
23 negative correlations between the percentage of forest (PLAND + CPLAND) and  
24 patch area (AREA\_MN) with the number of patches in the landscape (NP). We also  
25 observed a significant negative correlation between shape index (SHAPE\_MN) and  
26 number of patches in the landscape (NP; Table 7).

27 Networks size and number of bee species in the networks were positively  
28 influenced by the percentage of forest in the landscapes. Network connectance

1 index, *i.e.* the ratio between the number of observed interactions and the number of  
2 possible interactions in the networks, was negatively influenced by the percentage of  
3 forests in the landscapes. Despite nestedness was not influenced by forest cover. It  
4 declined with forest mean patch area in the landscapes and increased with  
5 landscape mean shape index (Table 8, Figure 8).

6 We did not observe significant effects of explanatory variables on network  
7 number of plant species, number of compartments, interactions strength asymmetry  
8 and interaction evenness. For these metrics the best models selected (with lower  
9 *AICc*) were the null models.

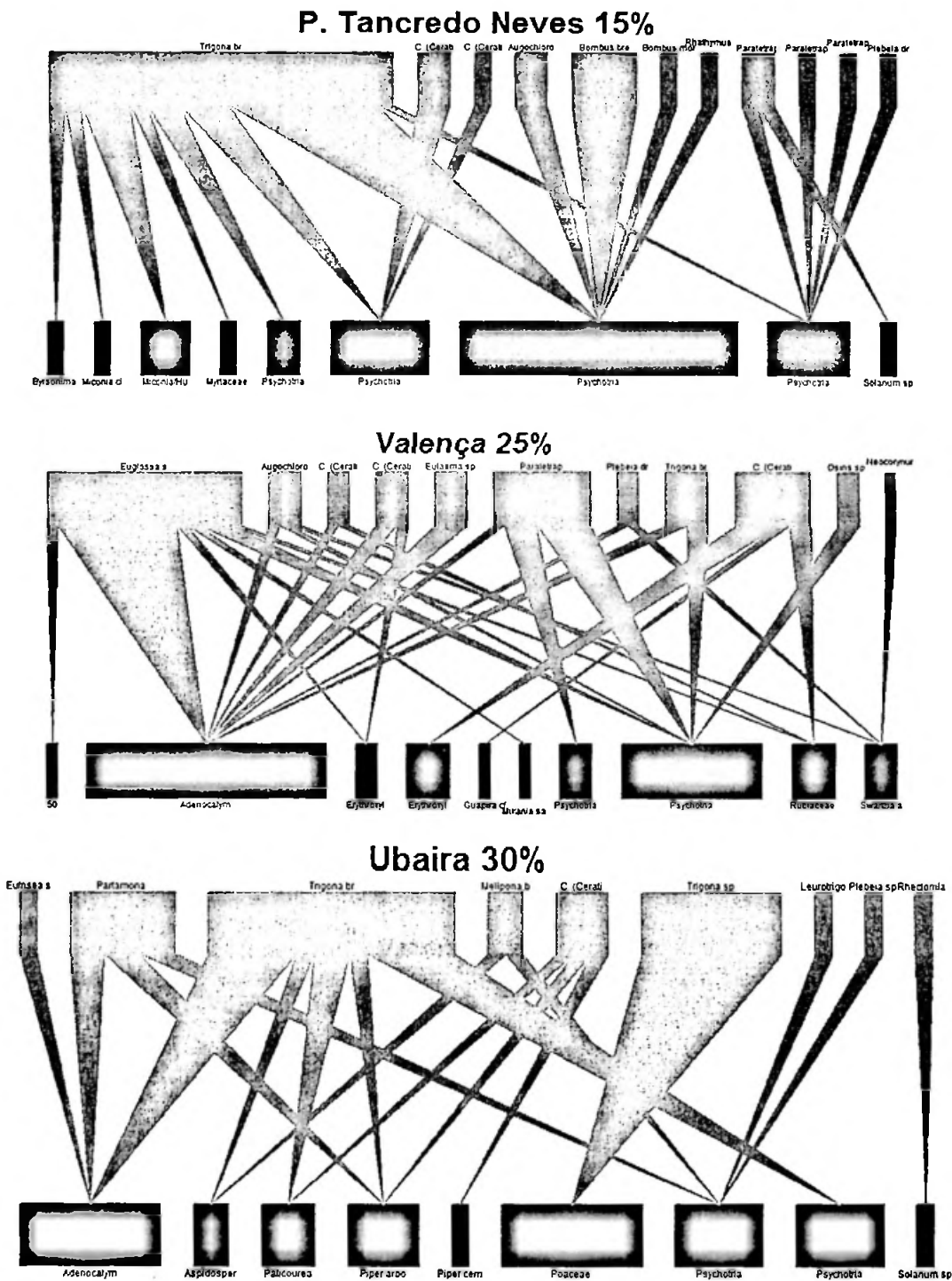
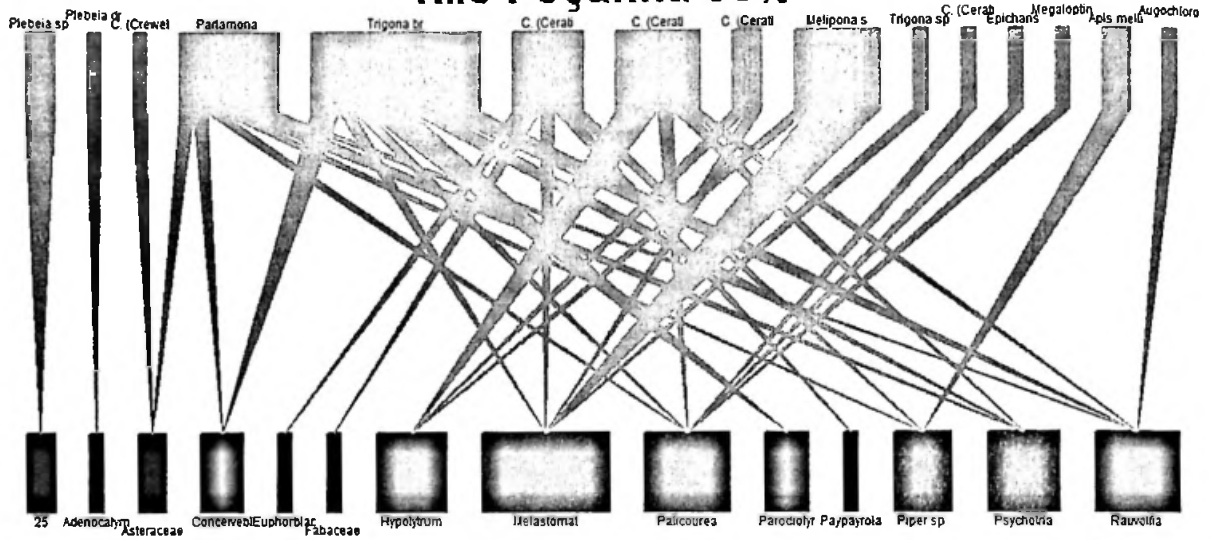
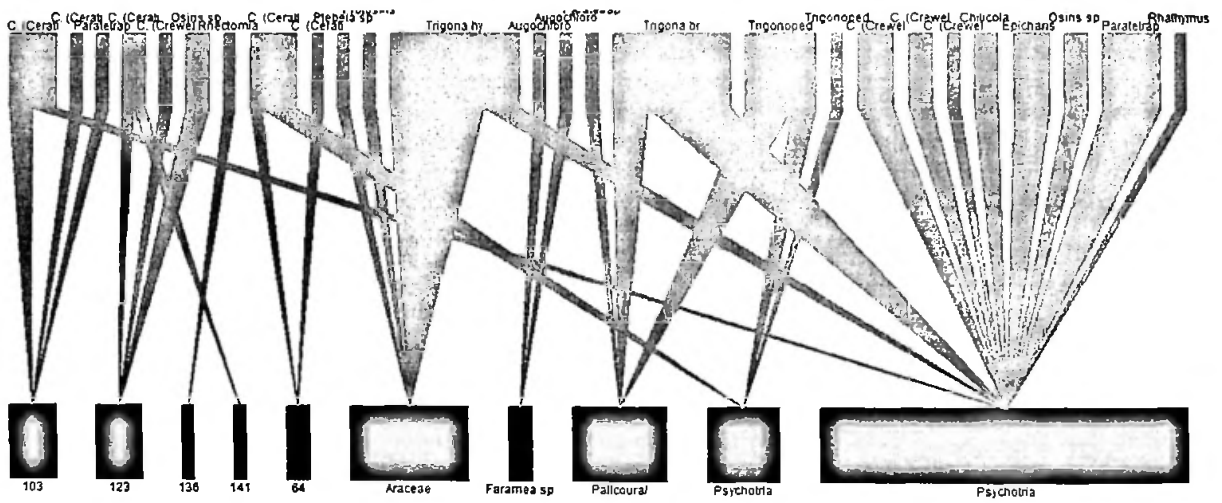


Figure 7: Plant-bee networks plots for each of the seven sampled landscapes on the Atlantic Rainforest in Bahia Northeastern Brazil from January to November of 2011. Plant (below) and bees (above) are represented by rectangles. The widths of the rectangles are proportional to the species abundance at landscape and the size of the triangles connecting the rectangles represents the frequency of interactions at landscape.

### Nilo Peçanha 35%



### Wenceslau Guimarães 40%



### Camamu 45%

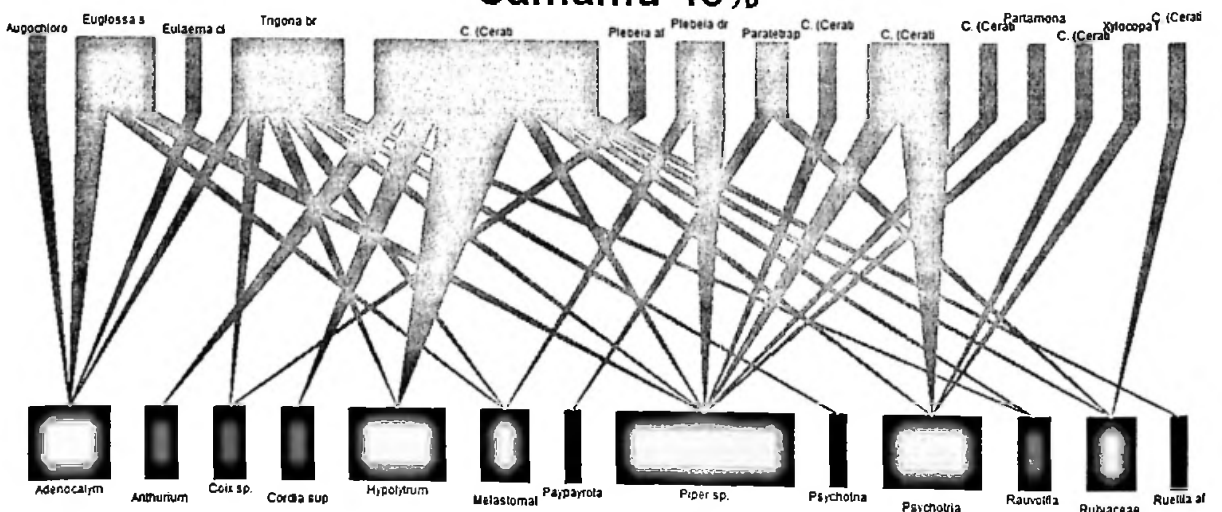


Figure 7: Continuation.

## Jaguaripe 55%

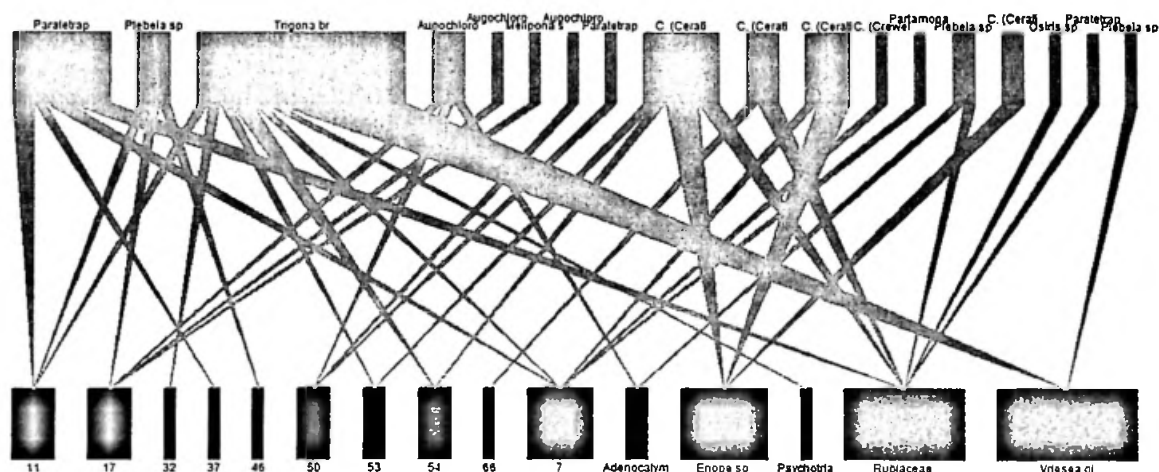


Figure 7: Continuation. Plant-bee networks plots for each of the seven sampled landscapes on the Atlantic Rainforest in Bahia Northeastern Brazil from January to November of 2011. Plant (below) and bees (above) are represented by rectangles. The widths of the rectangles are proportional to the species abundance at landscape and the size of the triangles connecting the rectangles represents the frequency of interactions at landscape. List of plant and bee species per landscape are provided in Supplementary Material 3.

Table 5: Results of analyses in R package bipartite of plant-bee network sampled in seven landscapes of 36km<sup>2</sup> (3600ha) along a gradient of forest cover from 15% to 55%, on the Atlantic Rain Forest in Bahia Northeastern Brazil.

| Local                   | Network Size | N of Bees | N of Plants | Connectance | Nestedness | Compartments | Interaction Strength Asymetry | Interaction Evenness |
|-------------------------|--------------|-----------|-------------|-------------|------------|--------------|-------------------------------|----------------------|
| P. Tancredo Neves 15%   | 20           | 11        | 9           | 0.19        | 16.7       | 1            | 0.02                          | 0.90                 |
| Valença 25%             | 21           | 11        | 10          | 0.24        | 20.3       | 1            | 0.08                          | 0.90                 |
| Ubaira 30%              | 18           | 9         | 9           | 0.22        | 28.1       | 3            | -0.14                         | 0.89                 |
| Nilo Peçanha 35%        | 29           | 15        | 14          | 0.16        | 16.1       | 3            | -0.04                         | 0.96                 |
| Wenceslau Guimarães 40% | 36           | 26        | 10          | 0.12        | 23.2       | 4            | 0.38                          | 0.93                 |
| Camamu 45%              | 28           | 15        | 13          | 0.17        | 13.1       | 1            | -0.11                         | 0.96                 |
| Jaguaripe 55%           | 33           | 18        | 15          | 0.14        | 17.3       | 1            | 0.05                          | 0.91                 |
| Mean                    | 26.4         | 15        | 11.4        | 0.18        | 19.3       | 2            | 0.03                          | 0.92                 |

Table 6: *Pearson's* correlations between all plant-bee network metrics sampled in seven landscapes of 36km<sup>2</sup> (3600ha) along a gradient of forest cover from 15% to 55%, on the Atlantic Rainforest in Bahia Northeastern Brazil. Significant correlations ( $p < 0.01$ ) are in boldface letters.

| Network Metrics               | N of Bees | N of Plants | Total Size  | Connectance  | Interaction Strength Asymetry | Compartments | Nestedness | Interaction Evenness |
|-------------------------------|-----------|-------------|-------------|--------------|-------------------------------|--------------|------------|----------------------|
| N of Bees                     | 1         | ns          | <b>0.94</b> | <b>-0.89</b> | <b>0.80</b>                   | ns           | ns         | ns                   |
| N of Plants                   |           | 1           | ns          | ns           | ns                            | ns           | ns         | ns                   |
| Total Size                    |           |             | 1           | <b>-0.94</b> | ns                            | ns           | ns         | ns                   |
| Connectance                   |           |             |             | 1            | ns                            | ns           | ns         | ns                   |
| Interaction Strength Asymetry |           |             |             |              | 1                             | ns           | ns         | ns                   |
| Compartments                  |           |             |             |              |                               | 1            | ns         | ns                   |
| Nestedness                    |           |             |             |              |                               |              | 1          | ns                   |
| Interaction Evenness          |           |             |             |              |                               |              |            | 1                    |

'ns',  $P > 0.05$ .

Table 7: *Pearson's* correlations between all landscape metrics of seven landscapes of 36km<sup>2</sup> (3600ha) along a gradient of forest cover from 15% to 55%, on the Atlantic Rainforest in Bahia Northeastern Brazil. Significant correlations ( $p < 0.01$ ) are in boldface letters.

| Landscape Metrics | PLAND | CPLAND      | NP           | AREA_AM      | SHAPE_AM     | PROX_AM |
|-------------------|-------|-------------|--------------|--------------|--------------|---------|
| PLAND             | 1     | <b>0.99</b> | <b>-0.83</b> | <b>0.83</b>  | ns           | ns      |
| CPLAND            |       | 1           | <b>-0.82</b> | <b>0.86</b>  | ns           | ns      |
| NP                |       |             | 1            | <b>-0.83</b> | <b>-0.78</b> | ns      |
| AREA_AM           |       |             |              | 1            | ns           | ns      |
| SHAPE_AM          |       |             |              |              | 1            | ns      |
| PROX_AM           |       |             |              |              |              | 1       |

'ns',  $P > 0.05$ .

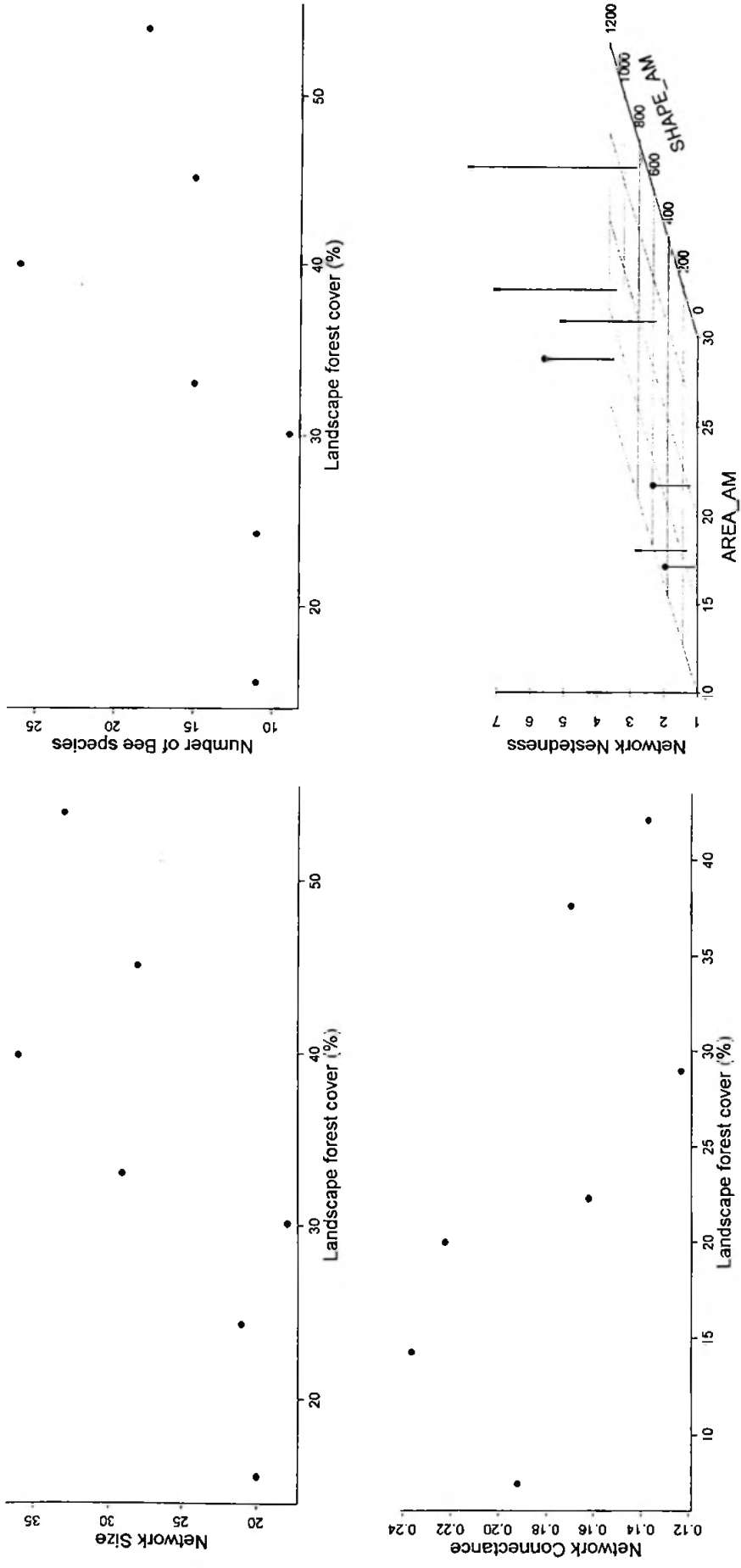


Figure 8: Results of best significant models of landscape explanatory variables effects on network structure, in seven fragmented landscapes on the Atlantic Rainforest in Bahia Northeastern Brazil from January to November of 2011. Networks size and number of bee species in the networks were positively influenced by the percentage of forest in the landscapes. Network connectedness was negatively influenced by the percentage of forests in the landscapes. Nestedness declined with forest mean patch area (AREA\_AM) and increased with landscape mean shape index (SHAPE\_AM).

Table 8 Results of network models: comparison of the three best models obtained for each response variable, from generalized linear models, with Poisson and Gaussian error distribution ordered by AICc (corrected for small sample Akaike information criterion). Explanatory variables in the models, Percentage of Landscape (PLAND), Core Area Percentage of Landscape (CPLAND), Number of Patches (NP), Patch Area (AREA\_AM), Shape Index (SHAPE\_AM) and Proximity Index (PROX\_AM).

| Response Variables (Y)        | Intercept | PLAND   | CPLAND | AREA_AM | SHAPE_AM | PROX_AM | NP | AICc  | W      |
|-------------------------------|-----------|---------|--------|---------|----------|---------|----|-------|--------|
| <b>Network Size</b>           |           |         |        |         |          |         |    |       |        |
| Model1 (best model)           | -         | 0.0128  | -      | -       | -        | -       | -  | 47.3  | 0.3463 |
| Model2                        | -         | -       | 0.016  | -       | -        | -       | -  | 47.7  | 0.2821 |
| Model3                        | -         | -       | -      | -       | -        | -       | -  | 49.3  | 0.1256 |
| Best model Estimates          | 2.7271    | 0.0153  | -      | -       | -        | -       | -  | -     | -      |
| Best model Std. Error         | 0.2383    | 0.0062  | -      | -       | -        | -       | -  | -     | -      |
| <b>Number of Bees Species</b> |           |         |        |         |          |         |    |       |        |
| Model1 (best model)           | -         | 0.0342  | -      | -       | -        | -       | -  | 46.3  | 0.2537 |
| Model2                        | -         | -       | -      | -       | -        | -       | -  | 46.6  | 0.2166 |
| Model3                        | -         | -       | 0.0431 | -       | -        | -       | -  | 46.7  | 0.2069 |
| Best model Estimates          | 2.086     | 0.017   | -      | -       | -        | -       | -  | -     | -      |
| Best model Std. Error         | 0.319     | 0.008   | -      | -       | -        | -       | -  | -     | -      |
| <b>Network Connectance</b>    |           |         |        |         |          |         |    |       |        |
| Model1 (best model)           | -         | 0.0929  | -      | -       | -        | -       | -  | -20.9 | 0.2353 |
| Model2                        | -         | -       | -      | -       | -        | -       | -  | -20.8 | 0.2193 |
| Model3                        | -         | -       | 0.1017 | -       | -        | -       | -  | -20.7 | 0.2107 |
| Best model Estimates          | 0.2537    | -0.0022 | -      | -       | -        | -       | -  | -     | -      |
| Best model Std. Error         | 0.0390    | 0.0011  | -      | -       | -        | -       | -  | -     | -      |
| <b>Network Nestedness</b>     |           |         |        |         |          |         |    |       |        |
| Model1 (best model)           | -         | -       | -      | 0.0297  | 0.009    | -       | -  | 44.3  | 0.4379 |
| Model2                        | -         | -       | -      | -       | -        | -       | -  | 46.3  | 0.1577 |
| Model3                        | -         | -       | -      | -       | ns       | -       | -  | 46.5  | 0.1436 |
| Best model Estimates          | 9.5499    | 0.0362  | -      | -0.0095 | 4.3714   | -       | -  | -     | -      |



| Response Variables (Y)                        | Intercept | PLAND  | CPLAND | AREA AM | SHAPE AM | PROX AM | NP | AICc  | W      |
|---|-----------|--------|--------|---------|----------|---------|----|-------|--------|
| Best model Std. Error                         | 0.5685    | 0.0173 | -      | 0.0029  | 0.9211   | -       | -  | -     | -      |
| <b>Number of Plant species</b>                |           |        |        |         |          |         |    |       |        |
| Model1 (null best model)                      | -         | -      | -      | -       | -        | -       | -  | 35.9  | 0.4231 |
| Model2  | ns        | -      | -      | -       | -        | -       | -  | 38.3  | 0.1308 |
| Model3  | -         | ns     | -      | -       | -        | -       | -  | 38.3  | 0.1282 |
| Best model Estimates                          | 2.4361    | -      | -      | -       | -        | -       | -  | -     | -      |
| Best model Std. Error                         | 0.1118    | -      | -      | -       | -        | -       | -  | -     | -      |
| <b>Network Compartments</b>                   |           |        |        |         |          |         |    |       |        |
| Model1 (null best model)                      | -         | -      | -      | -       | -        | -       | -  | 24.9  | 0.5039 |
| Model2  | -         | -      | -      | -       | -        | -       | ns | 28.2  | 0.0995 |
| Model3  | -         | -      | -      | -       | -        | ns      | -  | 28.2  | 0.0949 |
| Best model Estimates                          | 0.6931    | -      | -      | -       | -        | -       | -  | -     | -      |
| Best model Std. Error                         | 0.2673    | -      | -      | -       | -        | -       | -  | -     | -      |
| <b>Network Interaction Strength Asymmetry</b> |           |        |        |         |          |         |    |       |        |
| Model1 (null best model)                      | -         | -      | -      | -       | -        | -       | -  | -0.8  | 0.5580 |
| Model2  | -         | -      | -      | ns      | -        | -       | -  | 3.1   | 0.0805 |
| Model3  | -         | -      | -      | -       | ns       | -       | -  | 3.3   | 0.0733 |
| Best model Estimates                          | 0.0339    | -      | -      | -       | -        | -       | -  | -     | -      |
| Best model Std. Error                         | 0.0662    | -      | -      | -       | -        | -       | -  | -     | -      |
| <b>Network Interaction Evenness</b>           |           |        |        |         |          |         |    |       |        |
| Model1 (null best model)                      | -         | -      | -      | -       | -        | -       | -  | -25.5 | 0.3937 |
| Model2  | -         | -      | ns     | -       | -        | -       | -  | -23.2 | 0.1259 |
| Model3  | ns        | -      | -      | -       | -        | -       | -  | -22.8 | 0.1056 |
| Best model Estimates                          | 0.9215    | -      | -      | -       | -        | -       | -  | -     | -      |
| Best model Std. Error                         | 0.0114    | -      | -      | -       | -        | -       | -  | -     | -      |

P-value obtained from a likelihood ratio test in which deviances with and without that term in the model were compared. 'ns', P > 0.05. '-' Indicated variable not included in the model. Number of observations was 51 in seven landscapes. AIC weighted (W) values presented.

#### 4. Discussion

1           We observed through our results that there is an effect of habitat loss and  
2 landscapes configuration in the structure of plant-bee interaction networks in  
3 fragmented Atlantic Rainforest in Bahia, Brazil. Species richness (network size and  
4 bee richness) and connectance were mostly influenced by habitat quantity (forest  
5 cover) while nestedness was influenced by indicators of habitat quality (mean patch  
6 area and shape). It is known that modifications in the structure of pollination networks  
7 may cause major consequences for plant population performance and local  
8 persistence (Gómez et al. 2011). Therefore, in sampled landscapes habitat loss may  
9 affect plant and bee diversity and ecological processes associated to these species,  
10 as pollination, through network structure changes.

11           Mutualistic interactions such as pollination and seed dispersal are known to  
12 form heterogeneous, nested networks built on weak and asymmetric links among  
13 animal and plant species. We observed in landscapes with less forest cover that few  
14 nodes (or species) are much more connected than would be expected by chance.  
15 Asymmetric interactions and nested organization make networks more robust to the  
16 extinction of species with few links (Memmott et al. 2004, Vázquez & Aizen 2004).  
17 Nestedness and asymmetry introduces functional redundancy and the possibility for  
18 alternative routes for system persistence if some of the interactions disappear  
19 (Bascompte & Jordano 2007). Asymmetry means that specialists tend to interact with  
20 the most generalist species (Vázquez & Aizen 2004, Bascompte & Jordano 2007).  
21 Thus, asymmetry provides pathways for the persistence of specialists (Bascompte et  
22 al. 2003). Yet, networks that are robust to random loss of nodes may be very fragile  
23 to the extinction of the most generalist species. Network robustness is measured as  
24 the fraction of the species that must become extinct to result in network species loss  
25 (Albert et al. 2000). Our results show that changes in forest habitat quantity and  
26 quality negatively affect the robustness of the networks, through the loss of species.  
27 These results show that species may have been lost due to habitat loss, but

1 nestedness and connectance kept networks structure and species could be  
2 supported by this structure in these landscapes.

3 Network structure characteristics tend to be simplified according to habitat  
4 loss and natural landscape modification. Habitat loss have influenced loss of species  
5 and increased the tendency to structure simplification in these networks. As species  
6 were lost, the number of bee species and size of the network decreased and  
7 interactions tended to form more cohesive network cores in these landscapes. The  
8 suppression of links between highly connected nodes may reflect both differences in  
9 networks structure (species loss and more connected core of interactions) and in  
10 their response to different perturbations (Melián & Bascompte 2002).

11 Anthropogenic landscape changes that promote species extinction might  
12 induce a sudden collapse of pollination networks, by affecting the most connected  
13 species in the networks (Kaiser-Bunbury et al. 2010). In our study we saw that  
14 habitat loss reduced number of species, but the network structure was maintained in  
15 plant-bee webs. As also shown by Fortuna & Bascompte (2006), real networks start  
16 to lose species sooner than simulated networks, but the community structure as a  
17 whole persists for higher values of habitat loss. For instance, due to asymmetry both  
18 specialist and generalist plant species regarding pollination exhibit similar  
19 susceptibility to habitat loss. Specialist plants that depend on a single pollinator tend  
20 to interact with the most generalist animal species (Ashworth et al. 2004), and  
21 therefore more resistant to secondary extinctions.

22 Our results showed a negative correlation between the number of bees and  
23 networks connectance and size of networks and connectance. These results show  
24 that when there is fewer species in more connected networks those species tend to  
25 be more connected among themselves, since many of the possible connections are  
26 actually established. We observed that landscapes with lower proportion of remaining  
27 habitat supported networks that fulfill a higher proportion of the possible interactions.  
28 This means that the core of the interaction within networks tends to be more

1 connected. This may be a result of the reduction of specialist species that interact  
2 weakly with fewer species in networks (Bascompte et al. 2003). These networks  
3 have less species, most of them highly connected generalist and the resulting  
4 networks tend to be more nested. Consequently, even in highly fragmented  
5 landscapes the structure of networks is maintained, and species are protected from  
6 secondary extinctions and failure of ecological process in the communities.

7         Gómez et al. (2011) suggest that nested and highly connected local pollinator  
8 assemblages might result in highly robust structured networks. As we saw in our  
9 results, the increased connectance of the networks in landscapes with less remaining  
10 forest could mean that networks have become more simplified and the generalist  
11 species are relatively more abundant and play a more important role in the network.  
12 Our results suggest that network connectance could be an indicator of plant-bee  
13 network integrity were, within a certain range, more connected networks may be the  
14 most simplified ones, as a result of landscape changes.

15         The recognition of generalist and specialist species must be valuable for  
16 better understanding our results. Common and generalist species seem to interact  
17 unconstrained, while rare and specialized species are constrained in their low  
18 encounter rate due to its lower abundance (Olesen et al. 2011). The reduction of the  
19 diversity of bees observed in landscapes with lower forest cover (see chapter 2) may  
20 lead to greater frequency of interactions among generalist species remaining in these  
21 landscapes. Our result shows that network cores with more interactions among  
22 generalist species and few specialist interactions tend to be more common in  
23 landscapes with less habitat remaining.

24         The positive effect of patch shape in network nestedness could also be an  
25 indication that more irregular shape of forest patches might lead to higher frequency  
26 of interactions among generalist species remaining in networks. Irregular shapes can  
27 increase edge effects and invasion of more generalist species that use resources  
28 inside and/or outside forested areas. Additionally, we calculated that approximately

1 10% of all sampled area is composed of edges in the landscapes. Empirical evidence  
2 showed that increasing of edge density in agricultural lands, not by habitat  
3 fragmentation but through preservation and restoration of natural habitats, may favor  
4 the maintenance of diverse and abundant insect pollinators (Chacoff & Aizen 2006).

5 Our results show that network connectance and nestedness reveal that an  
6 interaction core provided by generalist species is kept in the networks in situations of  
7 high reduction of forest area and increased edge effects. In landscapes with less  
8 forested habitat the most sensitive species may disappear and the resilient species  
9 (which are usually the most generalist species) tends to be kept in these landscapes  
10 and interactions tend to be more frequently performed among this generalist species.  
11 Those results highlight the importance of maintaining forested areas for conservation  
12 of ecological processes such as pollination, at the landscape scale for the  
13 conservation of mutualistic networks (Fortuna & Bascompte 2006).

14

#### 15 **4.1. Conclusions**

16 We have made the first attempt to empirically characterize the structure of  
17 plant-bee interaction networks in fragmented landscapes in Atlantic Rainforest in  
18 Bahia, Northeast Brazil. This is an important step for understanding the organizing  
19 patterns of such important associations and to produce knowledge to its conservation  
20 and management.

21 In summary, some studies have predicted that environmental changes that  
22 lead to species extinction in the networks could reduce networks size and the  
23 number of weak interactions of specialist species, keeping only the core of the  
24 generalist species interaction in the networks (Bascompte et al. 2003, Memmott et al.  
25 2004, Fortuna & Bascompte 2006). Our data show that generalist species, even after  
26 species extinction, may sustain networks core of cohesive interactions, protecting the  
27 network as a whole. We observed that networks are smaller, with less species, the  
28 interactions happened among generalists species in a cohesive core, and there were

1 few specialist species interacting with generalist species in these networks in  
2 landscapes with less forest habitat remaining. We believe that, due to the high  
3 degree of environmental degradation of these landscapes, generalist species are  
4 able to manage to stay in these landscapes and keep networks core of interactions  
5 and structure.

6 Our results showed empirical evidence that networks tend to simplify its  
7 structure when species are lost. Networks in landscapes with less forest may have  
8 already gone through this process. Overall, the nested and asymmetric organization  
9 indicates that generalist species of bees and plants are the ones that potentially are  
10 able to keep the entire web of interactions in fragmented landscapes in Bahia. Our  
11 findings add a new perspective to studies of plant-pollinator networks in fragmented  
12 landscapes. Interaction networks can also be indicators of effects of changes in  
13 natural habitat. We saw here that the network structure vary with the quality of the  
14 habitat and this variation can have important effects on pollinators and plant  
15 communities in these environments.

16

## 17 **5. Acknowledgements**

18 We want to thank the financial research support by INOMEP-PRONEX-  
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## *Considerações Finais*

## Considerações Finais

1 A consolidação do conhecimento sobre os processos ecológicos como a  
2 polinização no nível da paisagem é de extrema importância para a gestão de áreas  
3 naturais e manutenção dos serviços ecossistêmicos (Tscharntke & Brandl 2004,  
4 Nazareno & Carvalho 2009, Viana et al. 2012). Abordagens integradas entre o  
5 estudo dos efeitos de paisagens naturais modificadas sobre os ecossistemas  
6 naturais e como estas variações afetam a estabilidade das comunidades (Viana et  
7 al. 2012) e a estrutura das redes de interação planta-polinizador (Memmott et al.  
8 2004, Fortuna & Bascompte 2006) são úteis para a conservação dessas interações,  
9 bem como para a conservação de plantas, polinizadores e serviços de polinização  
10 em ecossistemas naturais e agrícolas.

11 A conservação destas interações pode ser mais importante para a  
12 manutenção da biodiversidade, do que a preservação de espécies isoladas (Steffan-  
13 Dewenter & Tscharntke 1999, Diaz & Cabido 2001, Forup & Memmott 2005). Através  
14 da investigação dos efeitos da perda de habitat, nas comunidades de abelhas  
15 visitantes florais e nas interação planta-abelha avaliamos a qualidade desses  
16 ambientes modificados, em paisagens florestais fragmentadas na Bahia, nordeste do  
17 Brasil. Percebemos através da revisão da literatura que há lacunas no conhecimento  
18 sobre valores críticos de perda de habitat que podem aumentar as taxas de extinção  
19 de polinizadores e sobre os efeitos das mudanças das paisagens naturais na  
20 estrutura das redes de interação planta-polinizador.

21 As abelhas são importantes para a manutenção de plantas nativas (Winfree  
22 et al 2009, 2011) e também importantes agentes polinizadores de culturas agrícolas  
23 essenciais para a vida humana (Klein et al. 2007, Brosi et al. 2008). Vimos através  
24 dos nossos resultados que a perda de habitat afeta negativamente a diversidade de  
25 abelhas. Além disso, a presença de floresta é importante para as abelhas sociais  
26 que nidificam acima do solo.

1 Vimos também que a quantidade e qualidade de floresta nas paisagens  
2 amostradas influenciou as variáveis estruturais das redes planta-abelha,  
3 principalmente o tamanho (numero total de espécies), o numero de espécies de  
4 abelhas, a conectância e o aninhamento das redes. O tamanho e o número de  
5 espécies foram positivamente influenciados pela quantidade de habitat. Enquanto a  
6 conectância foi inversamente relacionada à quantidade de floresta. O aninhamento  
7 foi negativamente influenciado pela área média dos fragmentos e positivamente  
8 influenciado pelo índice de forma médio dos fragmentos nas paisagens.

9 As alterações ambientais que levam a extinção espécies nas redes  
10 mutualísticas podem reduzir o tamanho e o número de interações entre espécies  
11 especialistas. No entanto, estas redes, mesmo após a extinção de espécies tendem  
12 a manter um núcleo coeso de interações entre espécies generalistas, protegendo a  
13 rede como um todo (Bascompte et al. 2003). Nas paisagens com menor proporção  
14 de florestas, observamos que as redes de interação planta-abelha são menores  
15 (com menos espécies). Nessas redes as interações ocorrem principalmente entre as  
16 espécies generalistas em um núcleo coeso, e há poucas espécies especialistas  
17 interagindo com espécies generalistas. Acreditamos que, devido ao elevado grau de  
18 degradação ambiental dessas paisagens as espécies generalistas são as mais  
19 capazes de se manter e compor o núcleo de interações das redes planta-polinizador.

20 Nós acreditamos que os estudos de redes de interação na perspectiva de  
21 paisagens em florestas tropicais e no sub-bosque podem fornecer informações  
22 importantes e permitem a compreensão das melhores estratégias para conservação  
23 de plantas, polinizadores e dos serviços de polinização. Sugerimos para a  
24 conservação das redes de interação abelhas e plantas em paisagens fragmentadas  
25 na Bahia a manutenção de paisagens com habitats florestais disponíveis. Esses  
26 habitats são importantes para a manutenção da diversidade de abelhas e da  
27 estrutura de suas redes de interação com as espécies vegetais.

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## Material Suplementar

Supplementary material 1 (Chapter 1): Papers found in May 2011 using all seven possible combinations of the terms "pollinat\*" with the terms "landscape", "habitat loss" and "network" in the titles, abstract and keywords in Scopus and with the filter 'topic' in Web of Science.

| Autors                    | Year | Journal   | Study Location | Climatic region | Dependent variables         | Independent variables   | Variables relationship |
|---------------------------|------|---|----------------|-----------------|-----------------------------|-------------------------|------------------------|
| Aguilar, R et al          | 2006 | Ecology Letters 9: 968–980  | Do not apply   | Do not apply    | Plants reproductive success | Landscape configuration | Negative               |
| Aguirre, A et al          | 2011 | Journal of Tropical Ecology 27: 25 –33  | Mexico         | Tropical        | Pollinators diversity       | Landscape resources     | Positive               |
| Ahme, K et al             | 2009 | Plos One 4: 1-9   | Switzerland    | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Aizen, MA & Feinsinger, P | 1994 | Ecological Applications 4: 378-392  | Argentina      | Tropical        | Visits frequency            | Landscape composition   | Negative               |
| Aizen, MA & Rovere, AE    | 2010 | Oikos 119: 696–706  | Argentina      | Tropical        | Plants reproductive success | Landscape resources     | Different              |
| Altermatt, F & Ebert, D   | 2010 | Ecology 91: 2975–2982   | Baltic Sea     | Temperate       | Another                     | Landscape resources     | Positive               |
| Anitha, K et al           | 2010 | Ecological Complexity 7: 217–224  | India          | Tropical        | Plants diversity            | Landscape configuration | Negative               |
| Archer, S & Pyke, DA      | 1991 | Journal of range management 44: 558-565   | Do not apply   | Do not apply    | Plants reproductive success | Landscape resources     | Positive               |
| Artz, DR & Waddington, KD | 2006 | Journal of Ecology, 94: 597-608   | USA            | Temperate       | Pollinators diversity       | Patches area            | Positive               |
| Bartomeus, I et al        | 2010 | Journal of Ecology 98: 440–450  | Germany        | Temperate       | Pollinators diversity       | Landscape resources     | No related             |
| Bernard, E & Fenton, MB   | 2003 | Biotropica 35: 262-277  | Brazil         | Tropical        | Pollinators movements       | Landscape configuration | No related             |
| Biswas, SR & Mallik, AU   | 2010 | Ecology 91: 28–35   | Canada         | Temperate       | Plants reproductive systems | Landscape configuration | Negative               |
| Bommarco, R et al         | 2011 | Proceedings of the royal society b-biological sciences 15. doi:10.1098/rspb.2011.0647 | Switzerland    | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Born, C et al             | 2008 | Molecular Ecology 17: 2041–2050   | Africa         | Tropical        | Plants diversity            | Landscape configuration | Negative               |
| Breitbach, N et al        | 2010 | Oecologia 162: 965–976  | Germany        | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Brittain, C et al         | 2010 | Biological Conservation 143: 1860–1867  | Italy          | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Brosi, JB et al           | 2007 | Ecological Applications 17: 418–430   | Costa Rica     | Tropical        | Pollinators diversity       | Patches area            | Positive               |
| Brosi, BJ et al           | 2008 | Journal of Applied Ecology 45:773-783   | Costa Rica     | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Brosi, Bj et al           | 2009 | Forest Ecology and Management 258: 1846–1855  | Costa Rica     | Tropical        | Pollinators diversity       | Patches area            | No related             |
| Bruvig, LA et al          | 2009 | PNAS 106: 9328–9332   | USA            | Temperate       | Plants productivity         | Patches isolation       | Negative               |
| Bruna, EM et al           | 2005 | Biological Conservation 124: 209–216  | Brazil         | Tropical        | Another                     | Landscape configuration | Positive               |
| Byrne, M et al            | 2008 | Conservation Genetics 9: 97–105   | Australia      | Tropical        | Plants reproductive success | Landscape configuration | Negative               |
| Cane, JH & Tepedino, VJ   | 2001 | Conservation Ecology 5: 1-6   | Do not apply   | Do not apply    | Do not apply                | Do not apply            | Do not apply           |

| Autors                   | Year | Journal  | Study Location        | Climatic region | Dependent variables         | Independent variables   | Variables relationship |
|--------------------------|------|--|-----------------------|-----------------|-----------------------------|-------------------------|------------------------|
| Carre, G et al           | 2009 | Agriculture, Ecosystems and Environment 133: 40–47   | UK                    | Temperate       | Pollinators diversity       | Landscape composition   | Positive               |
| Carvalho, LG et al       | 2010 | Journal of Applied Ecology 47: 810–820               | Africa                | Tropical        | Pollinators diversity       | Landscape configuration | Positive               |
| Carvell, C et al         | 2007 | Journal of Applied Ecology 44: 29–40                 | England               | Temperate       | Floral resources            | Landscape configuration | Positive               |
| Cascante, A et al        | 2002 | Conservation Biology 16: 137–147                     | Costa Rica            | Tropical        | Plants reproductive success | Landscape configuration | Negative               |
| Chacoff, NP & Aizen, MA  | 2006 | Journal of Applied Ecology 43: 18–27                 | Argentina             | Tropical        | Pollinators diversity       | Patches isolation       | Negative               |
| Corlett, RT              | 2001 | Journal of Tropical Ecology 17: 155–161              | China                 | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Craft, KJ & Ashley, MV   | 2007 | Forest Ecology and Management 239: 13–20             | USA                   | Temperate       | Plants reproductive success | Landscape configuration | Negative               |
| Cruz-Neto, O et al       | 2011 | Biodiversity Conservation 20: 751–765                | Brazil                | Tropical        | Pollinators diversity       | Landscape resources     | Positive               |
| Cussans, J et al         | 2010 | Plos One 5: e11753                                   | UK                    | Temperate       | Plants reproductive success | Landscape composition   | Negative               |
| Darvill, B et al         | 2006 | Molecular Ecology 15: 601–611                        | UK                    | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Dauber, J et al          | 2010 | Journal of Ecology 98: 188–196                       | Europe                | Temperate       | Plants reproductive success | Patches area            | Negative               |
| Dick, CW et al           | 2003 | Molecular Ecology 12: 753–764                        | Brazil                | Tropical        | Pollinators movements       | Landscape configuration | Negative               |
| Didham, RK et al         | 1996 | Tree 2: 255–260                                      | Do not apply          | Do not apply    | Pollinators diversity       | Landscape configuration | Negative               |
| Eckert, CG et al         | 2009 | Trends in Ecology and Evolution 25: 35–43            | Do not apply          | Do not apply    | Plants reproductive success | Landscape configuration | Negative               |
| Ewers, RM & Didham, RK   | 2006 | Biological Review 81: 117–142                        | Do not apply          | Do not apply    | Pollinators diversity       | Landscape configuration | Negative               |
| Farwig, N et al          | 2009 | Landscape Ecology 24: 919–927                        | Switzerland           | Temperate       | Pollinators diversity       | Landscape composition   | No related             |
| Frankie, GW et al        | 2009 | Journal of the Kansas entomological society 82: 1–20 | Costa Rica            | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Fuchs, EJ et al          | 2003 | Conservation Biology 17: 149–157                     | Costa Rica            | Tropical        | Another                     | Patches isolation       | Negative               |
| Fujimori, N et al        | 2006 | Journal of Plant Research 119: 195–203               | Japan                 | Temperate       | Pollinators diversity       | Patches isolation       | Negative               |
| Gabriel, D et al         | 2010 | Ecology Letters 13: 858–865                          | UK                    | Temperate       | Pollinators diversity       | Another                 | Negative               |
| Ghazou, J                | 2004 | Biotropica 36: 156–164                               | Thailand              | Tropical        | Plants reproductive success | Landscape configuration | Negative               |
| Ghazou, J & Shaanker, RU | 2004 | Biotropica 36: 180–183                               | Do not apply          | Do not apply    | Pollinators diversity       | Landscape configuration | Negative               |
| Ghazou, J & Shaanker, RU | 2004 | Biotropica 36: 128–130                               | Do not apply          | Do not apply    | Plants reproductive success | Landscape configuration | Negative               |
| Ghazou, J & McLeish, M   | 2001 | Plant Ecology 153: 335–345                           | Thailand / Costa Rica | Tropical        | Plants reproductive success | Landscape configuration | Negative               |
| Goldman, RL et al        | 2007 | Ecological Economics 64: 333–343                     | Do not apply          | Do not apply    | Another                     | Landscape composition   | Different              |
| González-Varo, JP et al  | 2009 | Biological Conservation 142: 1058–1065               | Spain                 | Temperate       | Plants reproductive success | Landscape configuration | Negative               |

| Autors                    | Year | Journal  | Study Location | Climatic region | Dependent variables         | Independent variables   | Variables relationship |
|---------------------------|------|--|----------------|-----------------|-----------------------------|-------------------------|------------------------|
| Gorresen, PM & Willig, MR | 2004 | Journal of Mammalogy 85: 688–697                                     | Paraguay       | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Goulson, D et al          | 2008 | Journal of Applied Ecology 47: 1207–1215                             | Do not apply   | Do not apply    | Pollinators diversity       | Landscape configuration | Negative               |
| Goulson, D et al          | 2010 | Annual Review of Entomology 53: 191–208                              | UK             | Temperate       | Another                     | Landscape configuration | No related             |
| Goverde, M et al          | 2002 | Biological Conservation 104: 293–299                                 | Switzerland    | Temperate       | Visits frequency            | Patches area            | Positive               |
| Greenleaf, SS & Kremen, C | 2006 | PNAS 103: 13890–13895  | USA            | Temperate       | Plants reproductive success | Another                 | Positive               |
| Grundel, R et al          | 2010 | Ecological Applications 20: 1678–1692                                | USA            | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Hagen, M & Kraemer, M     | 2010 | Biological Conservation 143: 1654–1663                               | Kenya          | Tropical        | Plants diversity            | Landscape configuration | Different              |
| Hamrick, JL               | 2004 | Forest Ecology and Management 197: 323–335                           | Do not apply   | Do not apply    | Plants diversity            | Another                 | Different              |
| Hannon, LE & Sisk, TD     | 2009 | Biological Conservation 142: 2140–2154                               | USA            | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Hendrix, SD et al         | 2010 | Biodiversity Conservation 19: 1699–1709                              | USA            | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Hennig, EI & Ghazoul, J   | 2011 | Perspectives in Plant Ecology, Evolution and Systematics 13: 137–150 | Switzerland    | Temperate       | Visits frequency            | composition             | Negative               |
| Hoehn, P et al            | 2010 | Biodiversity Conservation 19: 2189–2200                              | Indonesia      | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Holzschuh, A et al        | 2010 | Journal of Animal Ecology 79: 491–500                                | Germany        | Temperate       | Pollinators diversity       | Landscape resources     | Positive               |
| Honnay, O et al           | 2005 | New Phytologist 166: 723–736   | Do not apply   | Do not apply    | Plants diversity            | Landscape composition   | Different              |
| Jauker, F et al           | 2009 | Landscape Ecology 24: 547–555  | Germany        | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Jha, S & Dick, CW         | 2008 | Current Biology 18: 1126–1128  | Mexico         | Tropical        | Plants diversity            | Landscape configuration | Positive               |
| Jha, S & Dick, CW         | 2010 | PNAS 107: 13760–13764  | Mexico         | Tropical        | Pollinators diversity       | Landscape configuration | Positive               |
| Jha, S & Vandermeer, JH   | 2010 | Biological Conservation 143: 1423–1431                               | Mexico         | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Jha, S & Vandermeer, JH   | 2009 | Journal of Tropical Ecology 25:13–22.                                | Mexico         | Tropical        | Visits frequency            | Landscape composition   | Positive               |
| Jules, ES & Priya, S      | 2003 | Journal of Vegetation Science 14: 459–464                            | Do not apply   | Do not apply    | Pollinators diversity       | Landscape configuration | Negative               |
| Kamm, U et al             | 2010 | Landscape Ecology 25: 903–911  | Switzerland    | Temperate       | Pollinators movements       | Matrix                  | Different              |
| Keitt, TH                 | 2009 | Ecological Applications 19: 1561–1573                                | Do not apply   | Do not apply    | Plants reproductive success | Landscape composition   | Positive               |
| Kim, J et al              | 2006 | Journal of the Kansas Entomological Society 79: 309–320              | USA            | Temperate       | Another                     | Landscape configuration | Negative               |
| Klein, A et al            | 2003 | Ecology 89: 935–943  | Indonesia      | Tropical        | Plants reproductive success | Landscape configuration | Negative               |
| Klein, A et al            | 2007 | Proceedings the Royal of Society Biological Sciences 270: 955–961    | Do not apply   | Do not apply    | Plants productivity         | Landscape configuration | Negative               |

| Autors                      | Year | Journal   | Study Location       | Climatic region | Dependent variables         | Independent variables   | Variables relationship |
|-----------------------------|------|---|----------------------|-----------------|-----------------------------|-------------------------|------------------------|
| Klein, AM                   | 2009 | Proceedings the Royal of Society Biological Sciences 274: 303–313 | Indonesia            | Tropical        | Pollinators diversity       | Landscape resources     | Positive               |
| Klein, AM et al             | 2008 | Forest Ecology and Management 258: 1838–1845                      | Do not apply         | Do not apply    | Plants reproductive success | Landscape configuration | Negative               |
| Klein, AM et al             | 2002 | Journal of Animal Ecology 73: 517–525                             | Indonesia            | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Klein, AM et al             | 2004 | Conservation Biology 16: 1003-1014                                | Indonesia            | Tropical        | Pollinators movements       | Landscape configuration | Negative               |
| Krauss, J et al             | 2009 | Journal of Applied Ecology 46: 194–202                            | Germany              | Temperate       | Pollinators diversity       | Patches area            | Positive               |
| Kremen, C et al             | 2007 | PNAS 99: 16812–16816  | Do not apply         | Do not apply    | Plants reproductive success | Landscape configuration | Negative               |
| Kremen, C et al             | 2002 | Ecology Letters 10: 299–314                                       | USA                  | Temperate       | Pollinators diversity       | Patches isolation       | Negative               |
| Kreyer, D et al             | 2004 | Biological Conservation 116: 111–118                              | Germany              | Temperate       | Pollinators movements       | Landscape configuration | No Different           |
| Laborde, J et al            | 2008 | Ecoscience 15: 6-16   | Mexico               | Tropical        | Plants reproductive success | Landscape configuration | Negative               |
| Lacerda, AEB & Kanashiro, M | 2008 | Biotropica 40: 462–470  | Brazil               | Tropical        | Plants diversity            | Patches isolation       | Negative               |
| Lander, TA et al            | 2010 | Biological Conservation 143: 2583–2590                            | Chile                | Tropical        | Plants reproductive success | Patches isolation       | Negative               |
| Lennartsson, T              | 2002 | Ecology 83: 3060–3072   | Switzerland          | Temperate       | Plants reproductive success | Landscape configuration | Negative               |
| Liow, LH et al              | 2001 | Journal of Applied Ecology 38: 180-192                            | Singapore / Malaysia | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Lonsdorf, E et al           | 2009 | Annals of Botany 103: 1589–1600                                   | Do not apply         | Do not apply    | Pollinators diversity       | Landscape configuration | Negative               |
| Lopes, AV et al             | 2009 | Biological Conservation 142: 1154–1165                            | Brazil               | Tropical        | Plants reproductive systems | Landscape configuration | Negative               |
| Lowe, AJ et al              | 2005 | Heredity 95: 255–273  | Do not apply         | Do not apply    | Another                     | Landscape configuration | Negative               |
| MacSwiney, MC et al         | 2007 | Biological Conservation 136: 499 – 509                            | Mexico               | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Marshall, EJP & Moonen, AC  | 2002 | Agriculture, Ecosystems and Environment 89: 5–21                  | Do not apply         | Do not apply    | Plants productivity         | Edge                    | Positive               |
| Meyer, JY                   | 1998 | Biotropica 30: 609-624  | Tahiti               | Tropical        | Plants reproductive systems | Another                 | Different              |
| Mimura, M et al             | 2009 | Molecular Ecology 18: 4180–4192                                   | Australia            | Tropical        | Plants reproductive systems | Landscape configuration | Negative               |
| Morreale, SJ & Sullivan, KL | 2010 | Revista de Biologia Tropical 56: 1295-1308                        | Do not apply         | Do not apply    | Do not apply                | Do not apply            | Do not apply           |
| Murua, M et al              | 2010 | Acta Oecologica 36: 191-196                                       | Chile                | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Nates-Parra, G et al        | 2008 | Conservation Genetics 10: 1789–1793                               | Colombia             | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Nayak, KG & Davidar, P      | 2010 | Ecological Complexity 7: 314–319                                  | India                | Tropical        | Plants reproductive success | Another                 | Different              |
| Nazareno, AG & Carvalho, D  | 2009 | Journal of Applied Ecology 36: 519-533                            | Brazil               | Tropical        | Plants reproductive success | Patches isolation       | Negative               |

| Authors                   | Year | Journal  | Study Location | Climatic region | Dependent variables         | Independent variables   | Variables relationship |
|---------------------------|------|--|----------------|-----------------|-----------------------------|-------------------------|------------------------|
| Olschewski, R et al       | 2010 | Biological Conservation 142: 888–898                                 | Ecuador        | Tropical        | Another                     | Landscape configuration | Negative               |
| Osborne, JL et al         | 1999 | Biological Conservation 94: 335–340                                  | UK             | Temperate       | Pollinators movements       | Landscape configuration | Negative               |
| Ottewell, KM et al        | 2009 | Perspectives in Plant Ecology, Evolution and Systematics 11: 157–189 | Australia      | Subtropical     | Plants reproductive success | Patches isolation       | No related             |
| Parra-Tabla, V et al      | 2000 | Revista de Biología Tropical 56: 1295–1308                           | Mexico         | Tropical        | Plants reproductive success | Landscape configuration | Negative               |
| Pautasso, M               | 2009 | Acta Oecologica 36: 191–196  | Do not apply   | Do not apply    | Plants diversity            | Landscape configuration | Negative               |
| Pejchar, L et al          | 2008 | Biological Conservation 141: 536–544                                 | Costa Rica     | Tropical        | Another                     | Landscape configuration | Negative               |
| Philpott, SM et al        | 2009 | Ecological Applications 19: 1858–1867                                | Do not apply   | Do not apply    | Another                     | Landscape configuration | Positive               |
| Pinto-Torres, & Koptur, S | 2009 | Annals of Botany 104: 1301–1311                                      | USA            | Tropical        | Plants reproductive systems | Landscape composition   | Negative               |
| Potts, SG et al           | 2003 | Ecology 84: 2628–2642  | Israel         | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Potts, SG et al           | 2010 | Trends in Ecology and Evolution 25: 345–353                          | Do not apply   | Do not apply    | Pollinators diversity       | Landscape configuration | Negative               |
| Priess, JA et al          | 2007 | Ecological Applications 17: 407–417                                  | Indonesia      | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Prober, SM & Smith, FP    | 2009 | Agriculture, Ecosystems and Environment 132: 173–191                 | Do not apply   | Do not apply    | Do not apply                | Do not apply            | Do not apply           |
| Quesada, M et al          | 2003 | Oecologia 135:400–407  | Mexico         | Tropical        | Plants reproductive success | Landscape configuration | Negative               |
| Quesada, M et al          | 2004 | Biotropica 36: 131–138   | Mexico e       | Tropical        | Plants reproductive success | Patches isolation       | Negative               |
| Quesada, M et al          | 2009 | Forest Ecology and Management 258: 1014–1024                         | Costa Rica     | Do not apply    | Do not apply                | Do not apply            | Do not apply           |
| Quintero, C et al         | 2010 | Biodiversity Conservation 19: 257–274                                | Argentina      | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Quintero, I & Roslin, T   | 2005 | Ecology 86: 3303–3311  | Brazil         | Tropical        | Another                     | Landscape configuration | Negative               |
| Ramos-Jiliberto, R et al  | 2009 | Oecologia 160: 697–706   | Chile          | Temperate       | Plants diversity            | Landscape configuration | Negative               |
| Regal, PG                 | 1982 | Annual Review of Ecology, Evolution and Systematics 13: 497–524      | Do not apply   | Do not apply    | Plants reproductive systems | Another                 | Different              |
| Renner, SS & Feil, JP     | 1993 | American journal of botany 80: 1100–1107                             | Do not apply   | Do not apply    | Pollinators diversity       | Landscape resources     | Positive               |
| Richards, AJ              | 2001 | Annals of Botany 88: 165–172   | Do not apply   | Do not apply    | Pollinators diversity       | Another                 | Negative               |
| Ricketts, TH              | 2004 | Conservation Biology 18: 1262–1271                                   | Costa Rica     | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Ricketts, TH et al        | 2004 | PNAS 101: 12579–12582  | Costa Rica     | Tropical        | Pollinators diversity       | Landscape configuration | Negative               |
| Ricketts, TH et al        | 2008 | Ecology Letters 11: 499–515  | Do not apply   | Do not apply    | Plants reproductive success | Patches isolation       | No related             |

| Autors                              | Year | Journal   | Study Location | Climatic region | Dependent variables         | Independent variables   | Variables relationship |
|-------------------------------------|------|---|----------------|-----------------|-----------------------------|-------------------------|------------------------|
| Rooney, TP et al                    | 2004 | Conservation Biology 18: 787-798  | USA            | Temperate       | Plants diversity            | Landscape configuration | Negative               |
| Roubik, DW                          | 2001 | Conservation Ecology 5: 1-14  | Panama         | Tropical        | Pollinators diversity       | Another                 | No related             |
| Rusterholz, HP & Baur, B            | 2010 | Oecologia 163: 141-152  | Switzerland    | Temperate       | Plants diversity            | Landscape configuration | No related             |
| Sande, SO et al                     | 2009 | Biological Conservation 142: 2703-2709                                  | Kenya          | Tropical        | Another                     | Patches isolation       | Negative               |
| Schmucki, R & Blois, S              | 2009 | Oecologia 160:721-733   | Canada         | Temperate       | Pollinators diversity       | Patches area            | Negative               |
| Slagle, MW & Hendrix, SD            | 2009 | Oecologia 161:813-823   | USA            | Temperate       | Plants reproductive success | Patches area            | Negative               |
| Sobek, S et al                      | 2009 | Forest Ecology and Management 258: 609-615                              | Germany        | Temperate       | Pollinators diversity       | Landscape resources     | Positive               |
| Sodhi, NS et al                     | 2004 | Annual Review of Ecology, Evolution and Systematics 35: 323-345         | Do not apply   | Do not apply    | Pollinators diversity       | Landscape configuration | Negative               |
| Steffan-Dewenter, I & Tscharntke, T | 1999 | Oecologia 121: 432-440  | Germany        | Temperate       | Pollinators diversity       | Patches isolation       | Negative               |
| Steffan-Dewenter, I et al           | 2001 | Proceedings Biological sciences The Royal Society 268 (1477), 1685-1690 | Germany        | Temperate       | Pollinators diversity       | Landscape configuration | Negative               |
| Taki, H et al                       | 2010 | Basic and Applied Ecology 11: 594-602                                   | Japan          | Temperate       | Pollinators movements       | Landscape configuration | Negative               |
| Tscharntke, T & Brandl, R           | 2004 | Annual Review of Entomology 49: 405-430                                 | Do not apply   | Do not apply    | Pollinators diversity       | Landscape configuration | Positive               |
| Tscharntke, T et al                 | 2011 | Journal of Applied Ecology 48 (3), 619-629                              | Do not apply   | Do not apply    | Plants productivity         | Another                 | Positive               |
| Tscheulin, T et al                  | 2011 | Bulletin of Entomological Research 1-8                                  | Greece         | Temperate       | Pollinators diversity       | Landscape composition   | Positive               |
| Uchiyama, K et al                   | 2009 | Conservation Genetics 10, 1265-1275                                     | Japan          | Temperate       | Plants reproductive success | Landscape resources     | Positive               |
| Uriarte, M et al                    | 2011 | Ecology 92: 924-937   | Brazil         | Tropical        | Floral resources            | Landscape composition   | Negative               |
| Uriarte, M et al                    | 2010 | Ecology 91: 1317-1328   | Brazil         | Tropical        | Plants reproductive success | Landscape configuration | Negative               |
| Van Geert, A et al                  | 2010 | Journal of Ecology 98 (1), 178-187                                      | Belgium        | Temperate       | Pollinators movements       | Landscape composition   | Positive               |
| Van Rossum, F                       | 2010 | Perspectives in Plant Ecology, Evolution and Systematics 12 (1), 21-29. | Belgium        | Temperate       | Plants reproductive success | Landscape configuration | Negative               |
| Veddeler, D et al                   | 2010 | Oecologia 162: 755-762  | Ecuador        | Tropical        | Pollinators diversity       | Landscape resources     | Negative               |
| Vermaat, JE et al                   | 2004 | Journal of Sea Research 52: 321- 328                                    | Filipinas      | Tropical        | Plants reproductive success | Landscape resources     | Negative               |
| Vesk, PA et al                      | 2010 | Austral Ecology 35: 60-71   | Australia      | Tropical        | Plants reproductive success | configuration           | Negative               |
| Vieira, FA & Carvalho, D            | 2008 | Biodiversity and Conservation 17 (10), 2305-2321                        | Brazil         | Tropical        | Plants diversity            | Patches isolation       | Positive               |
| Walther-Hellwig, K & Frankl, R      | 2000 | Journal of Applied Entomology 124 (7-8), 299-306                        | Germany        | Temperate       | Pollinators movements       | Landscape configuration | Positive               |
| Ward, M et al                       | 2005 | Heredity 95: 246-254  | Do not apply   | Do not apply    | Plants reproductive systems | Landscape resources     | Negative               |
| Williams, NM &                      | 2007 | Ecological Applications 17 (3), 910-921                                 | USA            | Temperate       | Another                     | Landscape configuration | Negative               |

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| Autors             | Year | Journal                                  | Study Location | Climatic region | Dependent variables   | Independent variables                   | Variables relationship |
|--------------------|------|--|----------------|-----------------|-----------------------|---|------------------------|
| Willig, MR et al   | 2007 | Biotropica 39 (6) 737-746                | Peru           | Tropical        | Pollinators diversity | Landscape configuration<br>Patches area | Negative               |
| Winfree, R et al   | 2007 | Conservation Biology 21: 213-223         | USA            | Temperate       | Pollinators diversity | Patches area                            | Negative               |
| Winfree, R et al   | 2008 | Journal of Applied Ecology 45: 793-802   | USA            | Temperate       | Pollinators diversity | Landscape composition                   | No related             |
| Winfree, R et al   | 2009 | Ecology 90: 2068-2076                    | Do not apply   | Do not apply    | Pollinators diversity | Landscape configuration                 | Negative               |
| Zhang, W et al     | 2007 | Ecological Economics 64 (2), 253-260     | Do not apply   | Do not apply    | Plants productivity   | Floral resources                        | Positive               |
| Zurbuchen, A et al | 2010 | Biological Conservation 143 (3), 669-676 | Switzerland    | Temperate       | Pollinators movements | Patches isolation                       | Negative               |

Supplementary material 2 (Chapter 2): Bee sampled in seven fragmented landscapes on the Atlantic Rainforest in Bahia Northeast Brazil from January to November of 2011. Information on sociality (in social species, for bees species that exhibits any level of sociality, and solitary species) and nest type (in above ground, e.g. bees that nest on trees or dead wood and below ground).

| Family | Species                           | Nest**       | Sociality** | Local   | N. Individuals |
|--------|-----------------------------------|--------------|-------------|---|----------------|
| Apidæ  | <i>Apis mellifera</i>             | Above Ground | Social      | Nilo Peçanha  | 2              |
|        | <i>Bombus brevivillus</i>         | Below Ground | Social      | P. Tancredo Neves   | 4              |
|        | <i>Bombus morio</i>               | Below Ground | Social      | P. Tancredo Neves   | 1              |
|        | <i>Ceratina (Ceratinula) sp.1</i> | Above Ground | Social      | Camamu, Itamaraju, Jaguaripe, Nilo Peçanha, Valença, Wenceslau Guimarães                    | 46             |
|        | <i>Ceratina (Ceratinula) sp.2</i> | Above Ground | Social      | Camamu, Jaguaripe, Wenceslau Guimarães  | 7              |
|        | <i>Ceratina (Ceratinula) sp.3</i> | Above Ground | Social      | Itamaraju, Nilo Peçanha, Wenceslau Guimarães  | 12             |
|        | <i>Ceratina (Ceratinula) sp.4</i> | Above Ground | Social      | Camamu, Itamaraju, Jaguaripe, Nilo Peçanha, P. Tancredo Neves, Valença, Wenceslau Guimarães | 24             |
|        | <i>Ceratina (Ceratinula) sp.5</i> | Above Ground | Social      | Ubaira, Wenceslau Guimarães   | 5              |
|        | <i>Ceratina (Ceratinula) sp.6</i> | Above Ground | Social      | Camamu, Ilhéus, Jaguaripe, Valença  | 13             |
|        | <i>Ceratina (Ceratinula) sp.8</i> | Above Ground | Social      | Camamu, Nilo Peçanha, P. Tancredo Neves   | 3              |
|        | <i>Ceratina (Ceratinula) sp.9</i> | Above Ground | Social      | Camamu  | 1              |
|        | <i>Ceratina (Crewella) sp.1</i>   | Above Ground | Social      | Jaguaripe, Nilo Peçanha, Wenceslau Guimarães  | 5              |
|        | <i>Ceratina (Crewella) sp.2</i>   | Above Ground | Social      | Wenceslau Guimarães   | 2              |
|        | <i>Ceratina (Crewella) sp.3</i>   | Above Ground | Social      | Wenceslau Guimarães   | 1              |
|        | <i>Ceratina (Crewella) sp.4</i>   | Above Ground | Social      | Wenceslau Guimarães   | 1              |
|        | <i>Epicharis cockerelli</i>       | Below Ground | Solitary    | Wenceslau Guimarães   | 3              |
|        | <i>Epicharis flava</i>            | Below Ground | Solitary    | Ilhéus, Itamaraju, Nilo Peçanha   | 5              |
|        | <i>Eufriesea sp.1</i>             | Below Ground | Solitary    | Ubaira  | 1              |
|        | <i>Euglossa sp.1</i>              | Below Ground | Solitary    | Camamu, Ilhéus, Jaguaripe, Valença  | 37             |
|        | <i>Eulaema athleticana</i>        | Below Ground | Solitary    | Ilhéus  | 1              |
|        | <i>Eulaema cingulata</i>          | Below Ground | Solitary    | Camamu  | 1              |
|        | <i>Leurotrigona muelleri</i>      | Above Ground | Social      | Ubaira  | 1              |
|        | <i>Melipona scutellaris</i>       | Above Ground | Social      | Jaguaripe, Nilo Peçanha   | 7              |
|        | <i>Melipona bicolor</i>           | Above Ground | Social      | Ubaira  | 2              |
|        | <i>Osiris sp.1</i>                | Below Ground | Solitary    | Valença, Wenceslau Guimarães  | 4              |



| Family     | Species                             | Nest**       | Sociality** | Local  | N. Individuals |
|------------|-------------------------------------|--------------|-------------|--|----------------|
|            | <i>Osiris</i> sp.2                  | Below Ground | Solitary    | Itamaraju, Wenceslau Guimarães   | 3              |
|            | <i>Osiris</i> sp.3                  | Below Ground | Solitary    | Jaguaripe  | 1              |
|            | <i>Paratetrapedia</i> sp.1          | Above Ground | Solitary    | Wenceslau Guimarães  | 1              |
|            | <i>Paratetrapedia</i> sp.2          | Above Ground | Solitary    | Camamu, Jaguaripe, Wenceslau Guimarães   | 4              |
|            | <i>Paratetrapedia</i> sp.3          | Above Ground | Solitary    | Jaguaripe, P. Tancredo Neves, Valença  | 20             |
|            | <i>Paratetrapedia</i> sp.4          | Above Ground | Solitary    | Jaguaripe, P. Tancredo Neves, Wenceslau Guimarães                                      | 7              |
|            | <i>Paratetrapedia</i> sp.5          | Above Ground | Solitary    | P. Tancredo Neves  | 1              |
|            | <i>Paratrigona subnuda</i>          | Below Ground | Social      | Ilhéus   | 1              |
|            | <i>Parlaimona</i> sp.1              | Above Ground | Social      | Camamu, Ilhéus, Jaguaripe, Nilo Peçanha, Ubaira  | 17             |
|            | <i>Plebeia</i> aff. <i>droryana</i> | Above Ground | Social      | Camamu   | 1              |
|            | <i>Plebeia droryana</i>             | Above Ground | Social      | Camamu, Ilhéus, Itamaraju, Nilo Peçanha, P. Tancredo Neves, Valença                    | 10             |
|            | <i>Plebeia</i> sp.1                 | Above Ground | Social      | Ilhéus, Itamaraju, Jaguaripe, Nilo Peçanha   | 8              |
|            | <i>Plebeia</i> sp.2                 | Above Ground | Social      | Jaguaripe  | 1              |
|            | <i>Plebeia grapiuna</i>             | Above Ground | Social      | Jaguaripe  | 2              |
|            | <i>Plebeia</i> sp.4                 | Above Ground | Social      | Wenceslau Guimarães  | 1              |
|            | <i>Plebeia</i> sp.5                 | Above Ground | Social      | Ubaira   | 1              |
|            | <i>Protosiris</i> sp.1              | Below Ground | Solitary    | Wenceslau Guimarães  | 1              |
|            | <i>Rhathymus</i> sp.1               | Below Ground | Social      | P. Tancredo Neves, Wenceslau Guimarães   | 2              |
|            | <i>Trigona braueri</i>              | Below Ground | Social      | Camamu, Ilhéus, Itamaraju, Jaguaripe, Nilo Peçanha, P. Tancredo Neves, Ubaira, Valença | 129            |
|            | <i>Trigona hyalinata</i>            | Above Ground | Social      | Wenceslau Guimarães  | 11             |
|            | <i>Trigona spinipes</i>             | Above Ground | Social      | Ilhéus, Nilo Peçanha, Ubaira   | 47             |
|            | <i>Trigonopedia</i> sp.1            | Below Ground | Social      | Wenceslau Guimarães  | 6              |
|            | <i>Trigonopedia</i> sp.2            | Below Ground | Social      | Wenceslau Guimarães  | 1              |
|            | <i>Xylocopa frontalis</i>           | Above Ground | Solitary    | Camamu   | 1              |
| Colletidae | <i>Chilicola kevani*</i>            | Above Ground | Social      | Wenceslau Guimarães  | 2              |
| Halictidae | <i>Augochlorodes</i> sp.1           | Below Ground | Social      | Wenceslau Guimarães  | 1              |

| Family       | Species                    | Nest**       | Sociality** | Local   | N. Individuals |
|--------------|----------------------------|--------------|-------------|---|----------------|
|              | <i>Augochlorodes</i> sp.2  | Below Ground | Social      | Wenceslau Guimarães   | 1              |
|              | <i>Augochloropsis</i> sp.1 | Below Ground | Social      | Camamu, Jaguaripe, Nilo Peçanha, P. Tancredo Neves, Valença | 10             |
|              | <i>Augochloropsis</i> sp.2 | Below Ground | Social      | Itamaraju   | 4              |
|              | <i>Augochloropsis</i> sp.3 | Below Ground | Social      | Jaguaripe   | 1              |
|              | <i>Augochloropsis</i> sp.4 | Below Ground | Social      | Jaguaripe   | 1              |
|              | <i>Megaloptina</i> sp.1    | Below Ground | Social      | Nilo Peçanha  | 1              |
|              | <i>Neocorynura</i> sp.1    | Below Ground | Social      | Itamaraju, Valença  | 3              |
|              | <i>Rhectomia mourei</i>    | Above Ground | Social      | Ubaira, Wenceslau Guimarães                                 | 2              |
| <b>Total</b> |                            |              |             |   | 492            |

\*New species describe (Oliveira et al. 2011).

\*\*Information from Moure's Bee Catalogue (Moure et al. 2012), Bees of the World (Michener 2000) and experts opinions. Whenever information for a given species was not available we used available knowledge on the closely related species or genus of bees.

Supplementary Material 3 (Chapter 3): Lists of plant and bees sampled in seven fragmented landscapes on the Atlantic Forest in Bahia Northeastern Brazil from January to November of 2011.

| Landscape               | Plant                               | Bees                        |                             |
|-------------------------|-------------------------------------|-----------------------------|-----------------------------|
| P. Tancredo Neves (15%) | <i>Byrsonima sericea</i>            | <i>Trigona braueri</i>      |                             |
|                         | <i>Miconia ciliate</i>              | <i>Trigona braueri</i>      |                             |
|                         | <i>Miconia/Huberia</i>              | <i>Trigona braueri</i>      |                             |
|                         | <i>Myrtaceae</i>                    | <i>Trigona braueri</i>      |                             |
|                         | <i>Psychotria carthagenensis</i>    | <i>Trigona braueri</i>      |                             |
|                         | <i>Psychotria hoffmannseggiana</i>  |                             | <i>C. (Ceratinula) sp.4</i> |
|                         |                                     |                             | <i>C. (Ceratinula) sp.8</i> |
|                         |                                     |                             | <i>Trigona braueri</i>      |
|                         | <i>Psychotria schlechtendaliana</i> |                             | <i>Augochloropsis sp.1</i>  |
|                         |                                     |                             | <i>Bombus brevivillus</i>   |
|                         |                                     |                             | <i>Bombus morio</i>         |
|                         |                                     |                             | <i>Rhathymus sp.</i>        |
|                         |                                     |                             | <i>Trigona braueri</i>      |
|                         | <i>Psychotria sp.</i>               |                             | <i>Paratetrapedia sp.3</i>  |
|                         |                                     |                             | <i>Paratetrapedia sp.4</i>  |
|                         |                                     |                             | <i>Paratetrapedia sp.5</i>  |
|                         |                                     |                             | <i>Plebeia droryana</i>     |
|                         |                                     | <i>Trigona braueri</i>      |                             |
| <i>Solanum sp.</i>      |                                     | <i>Rhectomia mourei</i>     |                             |
|                         |                                     |                             |                             |
| Valença (25%)           | 50                                  | <i>Euglossa sp.</i>         |                             |
|                         | <i>Adenocalyma coriaceum</i>        |                             | <i>Augochloropsis sp.1</i>  |
|                         |                                     |                             | <i>C. (Ceratinula) sp.4</i> |
|                         |                                     | <i>C. (Ceratinula) sp.6</i> |                             |
|                         |                                     | <i>Euglossa sp.</i>         |                             |
|                         |                                     | <i>Eulaema sp.</i>          |                             |
|                         |                                     | <i>Paratetrapedia sp.3</i>  |                             |
|                         |                                     | <i>Plebeia droryana</i>     |                             |
|                         |                                     | <i>Trigona braueri</i>      |                             |
|                         | <i>Erythroxylum magnoliifolium</i>  |                             | <i>C. (Ceratinula) sp.6</i> |
|                         |                                     |                             | <i>Euglossa sp.</i>         |
|                         | <i>Erythroxylum sp.</i>             |                             | <i>C. (Ceratinula) sp.1</i> |
|                         |                                     |                             | <i>C. (Ceratinula) sp.1</i> |
|                         | <i>Guapira cf.</i>                  |                             | <i>Euglossa sp.</i>         |
|                         | <i>Mikania salzmannifolia</i>       |                             | <i>Paratetrapedia sp.3</i>  |
|                         | <i>Psychotria hoffmannseggiana</i>  |                             | <i>Augochloropsis sp.1</i>  |
|                         | <i>Psychotria martiana</i>          |                             | <i>Euglossa sp.</i>         |
|                         |                                     | <i>Osiris sp.1</i>          |                             |

| Landscape          | Plant                           | Bees                        |
|--------------------|---------------------------------|-----------------------------|
| Ubaira (30%)       |                                 | <i>Paratetrapedia</i> sp.3  |
|                    |                                 | <i>Trigona braueri</i>      |
|                    | Rubiaceae                       | <i>C. (Ceratinula)</i> sp.1 |
|                    |                                 | <i>C. (Ceratinula)</i> sp.4 |
|                    |                                 | <i>Euglossa</i> sp.         |
|                    | <i>Swartzia apetala</i>         | <i>Augochloropsis</i> sp.1  |
|                    |                                 | <i>Neocorynura</i> sp.1     |
|                    | <i>Solanum</i> sp.              | <i>Paratetrapedia</i> sp.3  |
|                    |                                 | <i>Eufrisea</i> sp1         |
|                    |                                 | <i>Partamona</i> sp.        |
|                    |                                 | <i>Trigona braueri</i>      |
|                    |                                 | <i>Melipona bicolor</i>     |
|                    | <i>Trigona braueri</i>          |                             |
|                    | <i>C. (Ceratinula)</i> sp.5     |                             |
|                    | <i>Trigona braueri</i>          |                             |
|                    | <i>C. (Ceratinula)</i> sp.5     |                             |
|                    | <i>Partamona</i> sp.            |                             |
|                    | <i>Trigona braueri</i>          |                             |
|                    | <i>C. (Ceratinula)</i> sp.5     |                             |
|                    | <i>Trigona spinipes</i>         |                             |
|                    | <i>Leurotrigona muelleri</i>    |                             |
|                    | <i>Melipona bicolor</i>         |                             |
|                    | <i>Partamona</i> sp.            |                             |
|                    | <i>Plebeia</i> sp.5             |                             |
|                    | <i>Trigona braueri</i>          |                             |
|                    | <i>Trigona braueri</i>          |                             |
| Nilo Peçanha (35%) | 25                              | <i>Plebeia</i> sp.1         |
|                    | <i>Adenocalyma coriaceum</i>    | <i>Plebeia droryana</i>     |
|                    | Asteraceae                      | <i>C. (Crewella)</i> sp.1   |
|                    |                                 | <i>Partamona</i> sp.        |
|                    | <i>Conceiveblastrum</i> sp      | <i>Partamona</i> sp.        |
|                    |                                 | <i>Trigona braueri</i>      |
|                    | Euphorbiaceae                   | <i>C. (Ceratinula)</i> sp.4 |
|                    | Fabaceae                        | <i>C. (Ceratinula)</i> sp.4 |
|                    | <i>Hypolytrum schraderianum</i> | <i>C. (Ceratinula)</i> sp.1 |
|                    |                                 | <i>C. (Ceratinula)</i> sp.3 |
|                    |                                 | <i>Melipona scutellaris</i> |
|                    | Melastomataceae                 | <i>C. (Ceratinula)</i> sp.3 |
|                    | <i>C. (Ceratinula)</i> sp.4     |                             |
|                    | <i>Melipona scutellaris</i>     |                             |

| Landscape                 | Plant                              | Bees                        |
|---------------------------|------------------------------------|-----------------------------|
|                           |                                    | <i>Trigona braueri</i>      |
|                           |                                    | <i>Trigona spinipes</i>     |
|                           | <i>Palicourea rigida</i>           | <i>C. (Ceratinula) sp.1</i> |
|                           |                                    | <i>C. (Ceratinula) sp.8</i> |
|                           |                                    | <i>Epicharis flava</i>      |
|                           |                                    | <i>Megaloptina sp.1</i>     |
|                           |                                    | <i>Partamona sp.</i>        |
|                           |                                    | <i>Trigona braueri</i>      |
|                           | <i>Parodiolyra sp.</i>             | <i>Trigona braueri</i>      |
|                           | <i>Paypayrola blanchetiana</i>     | <i>C. (Ceratinula) sp.4</i> |
|                           | <i>Piper sp.</i>                   | <i>Apis mellifera</i>       |
|                           |                                    | <i>C. (Ceratinula) sp.4</i> |
|                           |                                    | <i>Partamona sp.</i>        |
|                           | <i>Psychotria sp.</i>              | <i>C. (Ceratinula) sp.1</i> |
|                           |                                    | <i>Partamona sp.</i>        |
|                           |                                    | <i>Trigona braueri</i>      |
|                           | <i>Rauvolfia grandiflora</i>       | <i>Augochloropsis sp.1</i>  |
|                           |                                    | <i>C. (Ceratinula) sp.1</i> |
|                           |                                    | <i>Partamona sp.</i>        |
|                           |                                    | <i>Plebeia droryana</i>     |
| Wenceslau Guimarães (40%) | 64                                 | <i>C. (Ceratinula) sp.2</i> |
|                           |                                    | <i>C. (Ceratinula) sp.3</i> |
|                           | 103                                | <i>C. (Ceratinula) sp.4</i> |
|                           |                                    | <i>C. (Ceratinula) sp.5</i> |
|                           |                                    | <i>Paratetrapedia sp.1</i>  |
|                           | 123                                | <i>C. (Ceratinula) sp.1</i> |
|                           |                                    | <i>C. (Crewella) sp.4</i>   |
|                           |                                    | <i>Osiris sp.2</i>          |
|                           | 136                                | <i>Rhectomia mourei</i>     |
|                           | 141                                | <i>C. (Ceratinula) sp.1</i> |
|                           | <i>Araceae</i>                     | <i>Plebeia sp.4</i>         |
|                           |                                    | <i>Protosiris sp.</i>       |
|                           |                                    | <i>Trigona hyalinata</i>    |
|                           | <i>Faramea sp.</i>                 | <i>Augochlorodes sp.1</i>   |
|                           |                                    | <i>Augochlorodes sp.2</i>   |
|                           | <i>Palicourea/Psycotria</i>        | <i>Paratetrapedia sp.2</i>  |
|                           |                                    | <i>Trigona braueri</i>      |
|                           |                                    | <i>Trigonopedia sp.1</i>    |
|                           | <i>Psychotria hoffmannseggiana</i> | <i>C. (Ceratinula) sp.2</i> |
|                           |                                    | <i>Trigonopedia sp.1</i>    |
|                           |                                    | <i>Trigonopedia sp.2</i>    |

| Landscape    | Plant                               | Bees   |
|--------------|-------------------------------------|--|
|              | <i>Psychotria schlechtendaliana</i> | <i>C. (Ceratinula) sp.4</i><br><i>C. (Crewella) sp.1</i><br><i>C. (Crewella) sp.2</i><br><i>C. (Crewella) sp.3</i><br><i>Chilicola kevani</i><br><i>Epicharis cockerelli</i><br><i>Osiris sp.1</i><br><i>Paratetrapedia sp.4</i><br><i>Rhathymus sp.</i><br><i>Trigona braueri</i><br><i>Trigona hyalinata</i> |
| Camamu (45%) | <i>Adenocalyma coriaceum</i>        | <i>Augochloropsis sp.1</i><br><i>Euglossa sp1</i><br><i>Eulaema cingulata</i><br><i>Trigona braueri</i>  |
|              | <i>Anthurium affine</i>             | <i>C. (Ceratinula) sp.1</i>  |
|              | <i>Coix sp.</i>                     | <i>Plebeia aff. droryana</i><br><i>Trigona braueri</i>   |
|              | <i>Cordia superba</i>               | <i>C. (Ceratinula) sp.1</i>  |
|              | <i>Hypolytrum schraderianum</i>     | <i>C. (Ceratinula) sp.1</i><br><i>Trigona braueri</i>  |
|              | <i>Melastomataceae</i>              | <i>Euglossa sp1</i><br><i>Plebeia droryana</i><br><i>Trigona braueri</i>   |
|              | <i>Paypayrola blanchetiana</i>      | <i>Paratetrapedia sp.2</i>   |
|              | <i>Piper sp.</i>                    | <i>C. (Ceratinula) sp.1</i><br><i>C. (Ceratinula) sp.4</i><br><i>C. (Ceratinula) sp.6</i><br><i>C. (Ceratinula) sp.8</i><br><i>Euglossa sp1</i><br><i>Partamona sp.</i><br><i>Plebeia droryana</i><br><i>Trigona braueri</i>   |
|              | <i>Psychotria purpurascens</i>      | <i>Trigona braueri</i>   |
|              | <i>Psychotria sp.</i>               | <i>C. (Ceratinula) sp.1</i><br><i>C. (Ceratinula) sp.6</i><br><i>C. (Ceratinula) sp.9</i><br><i>Xylocopa frontalis</i>   |
|              | <i>Rauvolfia grandiflora</i>        | <i>C. (Ceratinula) sp.1</i><br><i>Trigona braueri</i>  |

| Landscape       | Plant                               | Bees   |
|-----------------|-------------------------------------|--|
| Jaguaripe (55%) | <i>Rubiaceae</i>                    | <i>C. (Ceratinula) sp.1</i><br><i>C. (Ceratinula) sp.2</i><br><i>Paratetrapedia sp.2</i>   |
|                 | <i>Stromanthe porteana</i>          | <i>Trigona braueri</i>   |
|                 | 7                                   | <i>C. (Ceratinula) sp.6</i><br><i>C. (Crewella) sp.1</i><br><i>Paratetrapedia sp.3</i><br><i>Partamona sp.</i><br><i>Trigona braueri</i>                               |
|                 | 11                                  | <i>Paratetrapedia sp.3</i><br><i>Plebeia sp.1</i><br><i>Trigona braueri</i>  |
|                 | 17                                  | <i>Augochloropsis sp.1</i><br><i>Augochloropsis sp.3</i><br><i>Melipona scutellaris</i><br><i>Plebeia sp.1</i>   |
|                 | 32                                  | <i>Trigona braueri</i>   |
|                 | 37                                  | <i>Paratetrapedia sp.3</i>   |
|                 | 46                                  | <i>Plebeia sp.1</i>  |
|                 | 50                                  | <i>Augochloropsis sp.1</i><br><i>Augochloropsis sp.4</i><br><i>Paratetrapedia sp.2</i>   |
|                 | 53                                  | <i>C. (Ceratinula) sp.4</i><br><i>Trigona braueri</i>  |
|                 | 54                                  | <i>C. (Ceratinula) sp.4</i><br><i>Trigona braueri</i>  |
|                 | 66                                  | <i>C. (Ceratinula) sp.1</i>  |
|                 | <i>Adenocalyma coriaceum</i>        | <i>Augochloropsis sp.1</i><br><i>Plebeia grapiuna</i>  |
|                 | <i>Eriope sp.</i>                   | <i>C. (Ceratinula) sp.2</i><br><i>C. (Ceratinula) sp.4</i><br><i>C. (Ceratinula) sp.6</i>  |
|                 | <i>Psychotria schlechtendaliana</i> | <i>Trigona braueri</i>   |
|                 | <i>Rubiaceae</i>                    | <i>C. (Ceratinula) sp.1</i><br><i>C. (Ceratinula) sp.4</i><br><i>Osiris sp.</i><br><i>Paratetrapedia sp.3</i><br><i>Paratetrapedia sp.4</i><br><i>Plebeia grapiuna</i> |
|                 | <i>Vriesea gigantean</i>            | <i>Plebeia sp.2</i>  |

Supplementary Material 4 (Chapter 3): Graphs of each network metric in function of forest cover (disregarding the edge areas of 50m depth - CPLAND) in seven fragmented landscapes on the Atlantic Tropical Rainforest in Northeastern Brazil Bahia from January to November of 2011.

