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Especificidade por hospedeiro, abundância e prevalência de ervas-de-passarinho (*Psittacanthus* – Loranthaceae) em uma savana amazônica afetada por queimadas

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Manaus, Amazonas

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Sinopse: Foi avaliada a especificidade por hospedeiros, a abundância e a prevalência de infecção de três espécies de ervas-de-passarinho simpátricas do gênero *Psittacanthus* em uma savana sob frequente efeito de queimadas na Amazônia Brasileira. As ervas-de-passarinho foram amostradas repetidamente em seus hospedeiros, a fim de entender como estas espécies estão distribuídas entre diferentes hospedeiros e habitats, dando luz aos processos causadores desses padrões.

Palavras-chave: compatibilidade erva-de-passarinho/hospedeiro; dinâmica de populações; dispersão de sementes; distúrbio; falsas-ausências; ocupação; persistência.

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RESUMO

Ervas-de-passarinho são plantas hemiparasitas fotossintetizantes comumente associadas a árvores e arbustos de savanas, apresentando vários graus de especialização por hospedeiros. A distribuição das ervas-de-passarinho pode depender do seu grau de especialização, da eficiência da dispersão de sementes para hospedeiros compatíveis, e das influências diretas e indiretas de fatores locais (i.e. queimadas) sobre suas populações. O principal objetivo deste estudo foi entender quais fatores determinam a distribuição das ervas-de-passarinho em diferentes escalas espaciais, variando desde a escala dentro de hospedeiros, entre hospedeiros distintos, e entre sítios de savana distintos. Os fatores que explicam a distribuição podem variar desde fatores históricos, assim como fatores ecológicos, e fatores ambientais, dependendo da escala espacial avaliada. Adicionalmente, para subsidiar estudos de monitoramento em larga escala para as ervas-de-passarinho, foi investigado se amostragens únicas aos hospedeiros poderiam subestimar a presença de sementes e infecções pré-estabelecidas de ervas-de-passarinho. Três espécies de ervas-de-passarinho do gênero *Psittacanthus* (Loranthaceae) foram consideradas, todas elas em uma mancha de savana isolada da Amazônia, próxima a Alter do Chão, Pará, Brasil. No primeiro capítulo, foi encontrada uma baixa sobreposição entre as espécies de árvores utilizadas como hospedeiras pelas três espécies de ervas-de-passarinho, em uma área que não foi queimada por aproximadamente 10 anos. A compatibilidade entre as ervas-de-passarinho e hospedeiros, ao invés da deposição de sementes, foi o principal fator relacionado ao padrão de uso de espécies de árvores pelas ervas-de-passarinho. No segundo capítulo, foi conduzido um estudo ao longo de três anos consecutivos para investigar a distribuição em pequena escala espacial de *Psittacanthus plagiophyllus*, a erva-de-passarinho mais comum deste estudo. A dispersão de sementes realizada pela ave *Elaenia cristata* (Tyrannidae) foi mais importante que características do hospedeiro (tamanho da árvore, presença de infecções) para determinar a agregação das ervas-de-passarinho entre hospedeiros de uma mesma espécie. No terceiro capítulo, mostrou-se que amostragens repetidas conduzidas no mesmo hospedeiro podem melhorar a detecção de sementes em até 50%. Além disso, amostragens únicas não foram completamente eficientes para detectar infecções previamente estabelecidas. No último capítulo, a informação acumulada do capítulo 1, referente aos hospedeiros utilizados pelas ervas-de-passarinho, foi utilizada junto com observações simultâneas para amostrar todos os indivíduos das espécies hospedeiras das ervas-de-passarinho em 35 parcelas de savana, sob diferentes históricos de fogo, numa área de 100 km^2. Além disso, 19 sítios de estudo foram

amostrados para determinar o efeito do fogo sobre a dinâmica de recolonização de *P. plagiophyllus*. A tolerância ao fogo e recolonizações bem sucedidas são provavelmente os principais fatores determinando a distribuição destas espécies na savana. *Psittacanthus plagiophyllus* foi a única espécie significativamente afetada pela frequência de fogo. Entretanto, esta espécie foi amplamente distribuída e obteve a maior prevalência entre todas as ervas-de-passarinho. *Psittacanthus collum-cygni* foi mais abundante bem perto das bordas das florestas do que cerca de 100 m longe delas. *Psittacanthus biternatus*, a espécie mais generalista e resistente ao fogo, obteve uma prevalência muito baixa, o que pode estar relacionado à baixa taxa reprodutiva da espécie e, portanto, deve possuir uma baixa habilidade de recolonizar após o fogo. Finalmente, *P. plagiophyllus* foi capaz de colonizar áreas um ano após queimadas de baixa intensidade, mas menos apta a colonizar áreas com alta intensidade de fogo.

ABSTRACT

Mistletoes are photosynthetic hemi-parasitic plants commonly associated to savanna trees and shrubs, showing various degrees of host specialization. I predict that the distribution of mistletoes may depend on their specialization in relation to potential hosts, of seed dispersal efficiency to the right and compatible hosts, and on directly/indirectly influences of local natural environmental factors (i.e. fire events). The aim of this study was to understand how the distribution of different mistletoes is determined by intrinsic and extrinsic factors at different spatial scales. The factors that explain their distribution may be historical, as well as ecological, or environmental, depending on the scale there are evaluated. Additionally, to subsidy large scale monitoring studies on mistletoes; I investigated whether single surveys could underestimate the presence of mistletoe seeds and of infections on their host trees. Three sympatric mistletoe species of the genus *Psittacanthus* (Loranthaceae) were considered, all of them from an isolated Amazonian savanna, near Alter do Chão, Pará, Brazil. In the first chapter, I found a low overlap among trees used as hosts by the three mistletoe species in an area that has been unburned for about 10 years. Mistletoe-host compatibility, instead of seed dispersal, was the main factors responsible for this pattern observed. In the second chapter, I conducted a three-year study to investigate the distribution of *P. plagiophyllus* at small spatial scale, the most common mistletoe species. Seed dispersal performed by *Elaenia cristata* (Tyrannidae, Aves) was more important than host tree conditions (tree size, presence of infections) to determine mistletoe aggregation among host trees of the same species. In the third chapter, I showed that repeated surveys conducted to the same host trees could improve the detection of mistletoe seeds by 50%. Furthermore, single surveys were not efficient to detect perfectly previous established infections. In the last chapter, the information gathered from chapter 1 was used together with simultaneous observers to survey all host trees for mistletoes in 35 savanna plots, under different fire histories, within an area of 100 km^2. Furthermore, 19 study sites were used to determine the effect of fire on the post-recolonization dynamics of *P. plagiophyllus*. High tolerance to fire and successful colonization after fire events were probably the main factors determining the distribution of these species in the savanna. *Psittacanthus plagiophyllus* was the only species affected by fire frequency. However, this species was widely distributed and had the higher prevalence among all mistletoes. *Psittacanthus collum-cygni* was more abundant very close to forest edges than in a hundred meters farther away in continuous savanna. *Psittacanthus biternatus*, the most generalist and fire resistant species, had a very low prevalence, which

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INTRODUÇÃO GERAL

Muitos organismos não ocupam todos os locais aparentemente disponíveis a eles, o que pode ocorrer devido a duas causas principais: (1) baixa qualidade dos locais (microsítios), e (2) reduzida capacidade de colonizar os microsítios; enquanto poucos locais possuem muitos, a maioria possui pouco ou nenhum indivíduo. Para as plantas, estes dois fenômenos recebem o nome de (1) limitação de microsítios e (2) limitação de sementes e, como consequência imediata, suas populações crescem menos do que esperado em condições ideais de recrutamento (Crawley 1990,Eriksson & Ehrlén 1992).

Enquanto a limitação de microsítios pode ocorrer devido aos efeitos de distúrbios ambientais e de predadores de sementes, por exemplo, (Crawley 1990,Crawley 2000); a limitação de sementes pode ocorrer devido à baixa abundância de sementes ou à dispersão ineficiente das mesmas (Muller-Landau *et al.* 2002). Apesar da visão simplista destes mecanismos, a constatação de que a importância deles pode variar conforme a escala espacial avaliada (veja Levin 1992), e a dificuldade em definir a adequabilidade dos microsítios por um critério objetivo, tornam o tema 'limitação de recrutamento' apenas parcialmente resolvido em ecologia de populações de plantas.

Alguns estudos têm tentado determinar os papéis da limitação de microsítios e da limitação de sementes através da realização de experimentos aliados às observações de sistemas naturais. Em um estudo sobre a determinação dos padrões de distribuição de várias espécies de plantas herbáceas dentro e entre manchas de Floresta na Suécia, Ehrlén e Eriksson (2000) introduziram sementes em microsítios previamente ocupados e não ocupados pelas espécies, e acompanharam a chegada natural de sementes a sítios com características abióticas definidas subjetivamente. Após terem registrado a existência de recrutamento nos microsítios não ocupados e uma baixa proporção de microsítios previamente ocupados recebendo sementes naturalmente, eles chegaram à conclusão de que estas espécies são limitadas em pequena escala espacial pela quantidade de sementes e pelos predadores de sementes e, em larga escala espacial, pela dispersão das sementes disponíveis; resultado semelhante ao obtido por Clark *et al.* (1999) em florestas dos Apalaches, e por Svenning e Wright (2005) no Panamá.

Na busca por modelos de estudo, as ervas-de-passarinho são um grupo de plantas muito promissor para entender como mecanismos que estão ligados à limitação de sementes ou à limitação de microsítios atuam para determinar a distribuição de espécies em diferentes escalas espaciais. Isto ocorre devido ao fato de que as ervas-de-passarinho: apresentam microsítios objetivamente definidos dentro de uma assembléia de possíveis hospedeiros; oferecem facilidade para a realização de experimentos controlados; e possuem uma dinâmica populacional relativamente rápida, o que permite obter respostas em curto prazo determinadas por alterações de seu ambiente. O estudo de Aukema (2001) foi o primeiro a utilizar as ervas-de-passarinho com o objetivo de entender como a distribuição espacial de *Phoradendron californicum* (Viscaceae) é determinada pela dispersão de sementes realizada pelo seu dispersor, integrando as escalas espaciais desde 'dentro de hospedeiros' até 'paisagem'.

Ervas-de-passarinho são hemiparasitas arbustivos aéreos e fotossintetizantes da ordem Santalales, que parasitam galhos de árvores e arbustos, obtendo água, minerais e alguns nutrientes, através de um sistema de fixação e sucção denominado haustório (Nickrent 2002). Elas recebem este nome porque são frequentemente dispersas por aves, que removem o exocarpo do fruto e depositam as sementes, envoltas por um visco, nos galhos de seus potenciais hospedeiros através de regurgitação, defecação ou limpando o bico (Aukema 2003).

As ervas-de-passarinho frequentemente não parasitam todos os potenciais hospedeiros disponíveis a elas, podendo variar de muito especialistas a muito generalistas. Isto depende de fatores como a abundância relativa dos hospedeiros, da deposição de sementes efetuadas pelas aves, e da compatibilidade entre elas e seus hospedeiros (Norton & Carpenter 1998). O padrão mais comum encontrado entre as especialistas é de um hospedeiro frequentemente parasitado, enquanto outros atuam apenas como hospedeiros periféricos. Entre as generalistas, muitas espécies de plantas são incluídas como hospedeiras, apesar de ainda mostrarem preferências por algumas espécies em relação a outras (Norton & Carpenter 1998).

As ervas-de-passarinho frequentemente possuem distribuição agregada entre indivíduos de uma mesma espécie, o que pode estar relacionado ao comportamento dos dispersores de sementes, à baixa disponibilidade de sementes, ou às diferenças na adequabilidade dos hospedeiros ao seu desenvolvimento (Roxburgh & Nicolson

2008b). Vários estudos envolvendo experimentos e/ou observações de campo tentaram entender a relação entre ervas-de-passarinho, dispersores e hospedeiros nesta escala espacial (Hoffmann *et al.* 1986,Monteiro *et al.* 1992,López de Buen & Ornelas 1999,Aukema & Martinez del Rio 2002b,López de Buen & Ornelas 2002,Arruda *et al.* 2006). Entretanto, poucos estudos fizeram comparações entre diferentes espécies de hospedeiros (Yan 1993a,Roxburgh & Nicolson 2005a), e apenas um estudo fez comparação entre ervas-de-passarinho congêneres (Yan & Reid 1995). Estudos comparativos entre congêneres são importantes para entender como as interações entre hospedeiros, ervas-de-passarinho e o ambiente, podem variar em resposta a fatores ecológicos, dando menos peso aos fatores evolutivos (Westoby *et al.* 1995).

Entender quais as espécies de hospedeiros são preferidas pelas ervas-de-passarinho também deveria ser um pré-requisito para estudos de monitoramento em larga escala espacial, o que proporciona uma redução do tempo gasto, retirando da amostragem as espécies de árvores ou arbustos que são hospedeiros pouco utilizados ou que não são hospedeiros de fato. Também pode ser essencial incluir um componente de incerteza em programas de monitoramento em larga escala, com o objetivo de reduzir a probabilidade de ocorrer falsos-zeros nas árvores amostradas (Mackenzie *et al.* 2002,Mackenzie & Royle 2005). Por exemplo, múltiplas amostragens na mesma unidade amostral têm sido usadas com sucesso para aumentar o poder de detectar animais (Martin *et al.* 2005) e plantas (Kéry & Gregg 2003) inconspícuos, e melhorar a previsão da estimativa de alguns processos ecológicos como a extinção (Kéry *et al.* 2006,Ferraz *et al.* 2007). Em amostragens onde apenas a presença da erva-de-passarinho em seu hospedeiro é avaliada, esta metodologia de múltiplas amostragens pode ser utilizada com sucesso.

Apesar dos avanços realizados por pesquisadores no campo da ecologia de ervas-de-passarinho em países como a Austrália, Estados Unidos e Canadá (Kuijt 1969,Calder & Bernhardt 1983); este é um campo pouco explorado no Brasil (Arruda *et al.* 2008). O Cerrado alberga cerca de 40% das 180 espécies de ervas-de-passarinho das famílias Loranthaceae e Viscaceae que ocorrem no Brasil (as famílias com maior número de espécies), e concentra a maioria dos estudos com este grupo de plantas (Monteiro *et al.* 1992,Guerra & Marini 2002,Arruda *et al.* 2006,Mourão *et al.* 2006). De acordo com Barboza (2000), *Psittacanthus* é o segundo gênero com maior número de espécies neste bioma (10 espécies), ficando atrás apenas de *Struthanthus* (16

espécies). *Psittacanthus* é frequentemente um táxon com espécies generalistas, infectando muitas espécies de árvores e arbustos em florestas e savanas tropicais, desde o México (Collazo & Geils 2002,López de Buen & Ornelas 2002), até grande parte da região Neotropical (Monteiro *et al.* 1992,Uchôa & Caires 2000).

Psittacanthus é representado por três espécies simpátricas em uma savana Amazônica isolada em Alter do Chão, Pará, Brasil: *Psittacanthus biternatus* Blume, *P. collum-cygni* Eichler, e *P. plagiophyllus* Eichler. As savannas desta região são fisionomicamente similares ao Cerrado, mas com baixa diversidade florística (Miranda 1993,Ratter *et al.* 2003), com queimadas frequentes e de pequena escala (algumas dezenas de hectares), e com tempo de retorno entre dois a três anos (Albertina P. Lima, comunicação pessoal). Entretanto, apesar do papel em potencial das ervas-de-passarinho como plantas-chave fornecendo alimento e locais de nidificação para aves em algumas partes do mundo (Watson 2001,Cooney 2006), ainda não se entende claramente como o regime de fogo influencia diretamente suas populações, além de quais fatores influenciam na sua recolonização após o fogo.

O objetivo do primeiro capítulo deste estudo foi entender qual o papel de diferentes fatores como determinantes das interações entre ervas-de-passarinho do gênero *Psittacanthus* e seus hospedeiros dentro da mesma assembléia de potenciais hospedeiros em Alter do Chão (entre espécies), de modo a responder as seguintes questões: as espécies de ervas-de-passarinho sobrepõem-se na ocupação dos hospedeiros? Quais os mecanismos responsáveis por semelhanças ou diferenças entre os hospedeiros utilizados por elas? (1) Há dispersão de sementes diferenciada para os hospedeiros em potencial? (2) Ou mecanismos de compatibilidade que determinam o reconhecimento entre ervas-de-passarinho e hospedeiros? Os resultados deste primeiro capítulo também fornecerão subsídios para o estudo destas três espécies em larga escala espacial do quarto capítulo. No segundo capítulo, foi estudada a frugivoria, a deposição de sementes e a influência do tamanho do hospedeiro e da presença prévia de infestações sobre a distribuição de *P. plagiophyllys* em uma escala espacial de alguns hectares (entre hospedeiros). O estudo da deposição de sementes foi conduzido durante três anos consecutivos nos mesmos hospedeiros, o que permitiu fazer inferências mais efetivas sobre o papel dos dispersores determinando o padrão de distribuição desta erva-de-passarinho. No terceiro capítulo, *P. plagiophyllus* foi utilizada como um modelo de estudo para investigar como a detecção das sementes e

das infecções desta erva-de-passarinho poderia ser afetada se apenas estudos com uma única visita aos hospedeiros fosse efetuada. No capítulo quatro foi estudado como a abundância e a prevalência das três ervas-de-passarinho (*P. biternatus*, *P. collum-cygni e P. plagiophyllus*) variam de acordo com diferentes regimes de fogo em vários sítios de 3.75 hectares regularmente espalhados ao longo de toda a savana com cerca de 10000 hectares. Também foi conduzido um experimento de fogo controlado e um estudo em curto prazo da dinâmica de ocupação e colonização dos hospedeiros de *P. plagiophyllus* para entender como o fogo influencia em suas populações em um curto espaço de tempo.

OBJETIVOS ESPECÍFICOS

1. Determinar os padrões de uso de hospedeiro para três espécies de ervas-de-passarinho do gênero *Psittacanthus* em uma savana próxima a Alter do Chão, Pará, e entender como a dispersão de sementes e a compatibilidade com o hospedeiro afetam esses padrões;
2. Avaliar como a dispersão de sementes e a suscetibilidade do hospedeiro afetam a distribuição de *P. plagiophyllus* em uma pequena escala espacial (4.5 hectares);
3. Avaliar como a probabilidade de detectar sementes e infecções de ervas-de-passarinho é afetada por características do hospedeiro. O objetivo foi determinar se os hospedeiros devem ser amostrados mais de uma vez para a presença de sementes ou infecções de ervas-de-passarinho para evitar cometer falsos-zeros e melhorar as estimativas de ocupação em estudos de larga escala espacial;
4. Determinar se a abundância e a prevalência de diferentes espécies de *Psittacanthus* são igualmente afetadas pelo histórico de queimadas. Adicionalmente, avaliar se a dinâmica de ocupação por infecções e sementes de *P. plagiophyllus* é afetada diretamente pelas queimadas.

CAPÍTULO 1 – Este manuscrito será submetido ao periódico "Functional Ecology"

Very low host overlap among three congeneric and sympatric mistletoes in an Amazonian savanna: influence of seed rain and mistletoe-tree compatibility

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Running head: Host specificity of mistletoes in Amazonia

Summary

1. Two main hypotheses predominating the literature on mistletoe-host specificity: (1) mistletoes are only likely to specialize on trees in which they are frequently deposited; and (2) mistletoe-tree compatibility is responsible for distinguishing hosts from non-hosts and, eventually, modifying tree selection and seed deposition patterns made by seed dispersers.
2. I explored these hypotheses by studying the seed deposition patterns, and mistletoe-tree compatibility in one population of three congeneric and sympatric mistletoe species of the genus *Psittacanthus (P. biternatus* Blume, *P. collum-cygni* Eichler, *and P. plagiophyllus* Eichler – Loranthaceae).
3. I recorded the presence or absence of these mistletoe species infecting a total of 15 tree species in a savanna patch in Amazonia. Among the five tree species that I found infected, I also recorded if they had at least one mistletoe seed attached to their branches. Finally, I planted seeds of all mistletoe species on the same individual trees of various hosts and non-host species and recorded seed survivorship and seedling establishment within 7 (*P. plagiophyllus*) to 12 months (*P. biternatus* and *P. collum-cygni*) after planting.
4. There was a low overlap among trees used as hosts by the three *Psittacanthus* species. The most specialized mistletoe species occurred in different host trees with low relative abundance (*Psittacanthus collum-cygni* in *Vatairea macrocarpa* (Benth.) Ducke, and *P. plagiophyllus* in *Anacardium occidentale* L.). Mistletoe-tree compatibility, not seed rain, was the factor most likely to explain patterns of host use by *Psittacanthus* species in this study site.
5. These findings contradict the common prediction that as tree species become rare, they are unable to support specialized parasites. Furthermore, this is the

first study suggesting the existence of a mechanism of chemical recognition required by mistletoes (*P. plagiophyllus*) to initiate seed germination on its host trees (*A. occidentale*).

Key-words: host-tree specificity; Loranthaceae; *Psittacanthus*; relative host abundance; resource-fragmentation hypothesis; seed germination; seedling establishment.

Introduction

The most accepted hypothesis to explain the large proportion of generalist parasites in some communities of potential hosts predicts that higher resource (host) subdivision precludes parasite specialization (Janzen 1981). Likewise, for mistletoes, the choice of a subset of tree species (both trees or shrubs) to be parasitized suggest that they are only likely to develop specificity on plants in which they are frequently deposited (Norton & Carpenter 1998). The tree specificity by mistletoes may be developed, among others, under two ecological conditions: (1) when mistletoe seed dispersal is a random process and seeds arrive in trees in proportion to their relative abundance; (2) when mistletoe seed dispersal is not a random process and seed deposition are disproportionate, concentrating on a few tree species. The second hypothesis predicts that mistletoe-host tree compatibility may either contribute or modify the seed rain patterns made by seed dispersers and, actually, distinguishing hosts from non-host trees.

Several studies have supported the notion that high relative abundance of the potential host-trees (in fact any available tree) is essential for the development of mistletoe-tree specificity (Norton & Carpenter 1998, and references therein). For instance, a great majority of specialist mistletoes are parasites of very common trees, a pattern found among mistletoes in the *Eucalyptus* forests of Australia (Barlow & Wiens 1977), and in the *Nothofagus* forests of New Zealand (Norton & de Lange 1999). Local specialization (i.e. the choice of mistletoes for a subset of potential hosts) on a single tree species, on the contrary, is unusual in mistletoes, which lead Norton & Carpenter (1998) to propose a continuum between highly specialist and highly generalist species. However, Norton & Carpenter (1998) go on to suggest that the most common pattern is that specialist mistletoes infect a single common tree

species while retaining the ability to infect a number of other species, with generalists infecting a wide range of trees, still showing some preferences.

Although the high specialization in some mistletoe species may be only the result of frequent encounters between mistletoe seeds and the commonest trees, a few other studies have argued that non-random perch preferences of seed dispersers (i.e. birds) are also important for shaping the patterns of mistletoe infection prevalence (proportion of infected) among different trees, and ultimately, determining mistletoe-tree specificity (Monteiro *et al*. 1992). The decisions taken by birds may either result in a pattern that indeed concentrates mistletoe seeds on the most abundant and tallest trees (López de Buen & Ornelas 1999), or even on the less abundant ones (Aukema & Martinez del Rio 2002a,Roxburgh & Nicolson 2005a).

A different perspective is offered in studies that focus on mistletoe-tree compatibility (May 1971,Yan & Reid 1995). Mistletoe-tree compatibility is a result of the genetically (and, perhaps, environmentally) determined biochemical, mechanical, and physiological processes in the parasite and tree including mistletoe infectivity (such as the production of enzymes) and tree susceptibility (such as bark and xylem resistance) (Yan 1993a). It has been experimentally tested and compared with bird perch preferences or with natural seed rain to evaluate their relative roles in mistletoe-tree specificity; but usually, this is only conducted for host species. For example, López de Buen & Ornelas (1999, 2002) showed that the main seed disperser of *Psittacanthus schiedeanus* in Mexico prefers to perch, and probably deposits more seeds, on the most common and compatible host tree for this species, while Aukema & Martinez del Rio (2002a) showed that some host trees which received mistletoe seeds disproportionately were only slightly infected with *Phoradendron californicum* (Loranthaceae) in Arizona, suggesting that mistletoe-host compatibility may be a key

process in this case. Thus, mistletoe-tree (i.e. host) compatibility is a trait that may counteract (or amplify) the effects of seed rain on the observed distribution of mistletoe and the putative identification of specialists and generalists by their association with tree species. In fact, tree compatibility (and tree choice) may be the best definition for host specificity as it is a property of the individual not the population (Bernays 1998).

Few studies have disentangled the roles of tree species abundance, seed dispersal, and mistletoe-tree compatibility in determining the patterns of mistletoe infection prevalence among different tree species, and among different mistletoes. For example, it has been showed for two non-congener mistletoes in *Acacia* savannas of Africa, that although there was some host overlap between mistletoes, they presented different degrees of tree specificity, and bird behavior were more important than mistletoe-tree compatibility in determining the patterns of prevalence among hosts (Roxburgh & Nicolson 2005a).

In this study, I set out to distinguish the hosts from non-host trees of three congeneric mistletoe species (*Psittacanthus biternatus Blume*, *P. collum-cygni* Eichler, and *P. plagiophyllus* Eichler – Loranthaceae) while controlling for patterns of seed rain. I investigated three of the potential processes that determine the observed association between mistletoes and tree species: seed deposition, seed survivorship and seedling establishment. My main questions were: (i) Do mistletoes overlap their tree species used as hosts? (ii) What are the roles of seed deposition and mistletoe-tree compatibility in determining associations between mistletoes and tree species? I expanded the predictions of Norton & Carpenter (1998) by considering all trees as potential hosts, and therefore, I used ‘mistletoe-host compatibility’ in place of ‘mistletoe-tree compatibility’, and ‘mistletoe-tree specificity’, in place of ‘mistletoe-

host specificity'. I predicted that (1) mistletoe species would specialize on the most common trees; further, I predicted that (2) mistletoes would infect the closely related trees; and (3) mistletoes would more frequently infect the tallest tree species because these trees are perch sites for birds. I explored these predictions by surveying for mistletoe infections on various species of trees in an isolated patch of savanna in the central Amazon. For the plant species recorded as hosts, I also recorded the presence of different mistletoe seeds on the same trees within a sampling plot which is unburned for the past 10 years. Finally, I planted seeds of all mistletoes on the same individual trees in nine different species of both host and non-hosts and recorded survivorship and seedling establishment within 7 to 12 months.

Methods

STUDY SITE

I conducted this study in a patch of savanna (1 km x 1 km) on the right margin of the Tapajos River, near Alter do Chão, Santarém, Pará, Brazil (S 2º 31', W 59º 00'). The region is dominated by a grassy savanna intermingled with small forest fragments, and it is periodically burned due to anthropogenic fires (at intervals of 1-3 years). The study site is an exception to this common fire regime, being unburned for the last 10 years (Albertina Lima, pers. comm.). It presents large clumps of fire sensitive shrubs and at least 22 tree species (30% of the woody species) such as *Byrsonima* spp. (Malpighiaceae) and *Salvertia convallariaeodora* (Vochysiaceae) (Sanaiotti & Magnusson 1995). Canopy is descontinuous, and the average tree height is 3.17 m (Miranda 1993). Most of the rainfall is between December and April. Mean annual rainfall is 2192 mm, and mean annual temperature is 27.5 ºC.

STUDY SPECIES

I studied three congener and sympatric loranthaceous mistletoe which occur in this savanna patch and could be easily identified from a distance because of very distinctive foliage: *Psittacanthus biternatus* Blume, *P. collum-cygni* Eichler, and *P. plagiophyllus* Eichler. These species are distributed through Central and Northern of Brazil, and Northern of South America, either in savannas or in river banks (Barboza 2000). Furthermore, they were all recorded in the vicinity of Santarem 150 year ago (Eichler 1868). They are woody, aerial hemi parasitic shrubs, possessing a single and large haustorium deeply encrusted on their hosts branches, which provide them all water, minerals, and some nutrients (Marshall & Ehleringer 1990). Mature fruits are black berries whose seeds are mostly dispersed by tyrant flycatchers through regurgitation. Fruits of *P. biternatus* are 10 mm wide (± 1.1 mm) and are produced in small quantities between February to August (peak in June), during the rainy season. *Psittacanthus collum-cygni* produce fruits between February to June (peak in May), fruits are 12 mm wide (± 1.3 mm) and individual plants produce comparatively more fruits than *P. biternatus*. *Psittacanthus plagiophyllus* produce fruits of 10.3 mm wide (± 0.66 mm) between June to October (dry season, peak in the first week of August), and individuals produced as many fruits as *P. collum-cygni*. All mistletoe seeds are easily distinguishable from each other because of the number, shape, size and aspect of their cotyledons.

MISTLETOE INFECTION AND SEED RAIN PATTERNS

From middle August to November of 2006, I quantified the general pattern of parasitism among available tree species (dataset 1) using a table of random digits to select 16 sampling points within the study site. Points were at least 50 m apart, and all

trees ≥ 2 m of height were counted in a circle of 10 m radius. For each tree I recorded: species, height, DSH (diameter at soil height), presence/absence of mistletoe infections, and mistletoe species, if present. To increase the sample size, I also used a second dataset (dataset 2) in which I searched actively for all host trees infected by the three mistletoes found in dataset 1 in a 4.5 ha plot (150 m x 300 m) on the central part of the study site. In this second dataset I recorded the presence of mistletoe seeds as well as the number of mistletoe infections on the host trees. Furthermore, to minimize the potential effects of false-absences (sensu Martin *et al.* 2005; R.F.F., unpublished manuscript), two observers performed the sampling simultaneously. I searched for mistletoes from the ground using binoculars when the tree was large, while the second observer climbed on the tree using an aluminium ladder. In the calculation of mistletoe infection prevalence, I only considered the hosts actually infected by each one of the mistletoe species.

SEED SURVIVORSHIP AND SEEDLING ESTABLISHMENT

From the end of March to mid May 2007, individuals of nine experimental tree species were inoculated simultaneously with seeds of *P. biternatus* and *P. collum-cygni* (Table 1). Due to logistical problems, seeds of *P. plagiophyllus* were inoculated on the same trees one and a half year later. I chose two groups of experimental trees, those I previously knew to be infected by at least one mistletoe species (for which I slightly increased sample size), and those with a high relative abundance in my study site but without previous information on parasitism (6 to 10 individuals per host species, mean = 7.1 ± 1.4). Experimental trees were not parasitized, had at least 2 m of height, and appeared healthy on the beginning of the experiment. Individuals were

georreferenced, marked with aluminium tags, and located at least 50 m from each other to minimize pseudoreplication.

I collected fruits from mistletoes on different trees outside the plot and placed them into two separated paper bags to be inoculated one day after. Three branches were marked with numbered aluminium tags and measured with a calliper (precision = 0.1 mm). I chose the mistletoe species to be inoculated on each branch at random, and inoculated seeds of *P. biternatus* and *P. collum-cygni* in two of them. I returned 18 months after (September 2008) to conduct the same experiment with *P. plagiophyllus* on the remaining branch. Earlier inoculation does not seem to trigger an immune response, and therefore, influence the establishment of *P. plagiophyllus*. I removed the pericarp of five fruits by hand and arranged seeds linearly 2 cm apart onto the tagged horizontal branches. I took care to remove most of the viscin above the seeds to minimize fungal attack, while allowing a sufficient quantity for them to remain firmly attached on tree branches. The proportion of established seedlings (those presenting elongated leaves), and seeds that stayed alive (established seedlings + germinated seeds) were counted in the 12^{th} month for *P. biternatus* and *P. collum-cygni*, and in the 7^{th} month for *P. plagiophyllus*. I arcsine-square root transformed proportions prior to analysis. All results are presented with their means ± SE.

Results

TREE ABUNDANCE, HEIGHT, AND PATTERNS OF INFECTION

I recorded 553 individuals of 15 tree species in the dataset 1 (Table 2). Only four species (1.4% of trees) presented mistletoe infections, but other 13 species were infrequently infected outside plots in this same study area (Appendix 1). *Psittacanthus bitternatus* infected mainly the commonest tree species (*Byrsonima crassifolia*, 23%

of individuals), its congeneric (*B. coccolobifolia*, 5.2%), and *Pouteria ramiflora* (8.5%), while *P. plagiophyllus* infected uniquely one of the less abundant species, the cashew tree (*Anacardium occidentale*, 1%). Other common trees such as *S. convallariodora* and *Qualea grandiflora* were not infected by mistletoes. Although I did not find *P. collum-cygni* infections in any tree species, it was found parasitizing *Vatairea macrocarpa* (8.5%) outside sampling plots, and I included this host in the dataset 2. Furthermore, on the comparisons involving the dataset 2, I considered these five tree species as potential hosts for the analyses of seed rain (see next item).

Tree height differed among species (Anova on log transformed height: $F_{14, 538} = 4.56$, $P < 0.001$; Fig. 1). The taller trees were *Sclerolobium paniculatum* (5 m ± 2.1, N = 27) and *S. convallariodora* (4.9 m ± 2.4, N = 70), while the shorter trees were *Simarouba amara* (3 m ± 0.5, N = 8), *B. crassifolia* (3.2 m ± 1, N = 127), and *B. coccolobifolia* (3.2 m ± 1.3, N = 29). Furthermore, host trees were on average 0.6 m smaller, not taller, than non-host trees, rendering the test non-significant ($t = 4.05$, $P > 0.05$).

Byrsonima crassifolia had the highest relative abundance in the dataset 2 (1475/4102 = 36%), followed by *V. macrocarpa* (1212, 30%), *P. ramiflora* (825, 20%), *B. coccolobifolia* (468, 11%), and *A. occidentale* (122, 3%). While *B. crassifolia* was the most abundant species it had the lowest mistletoe infection prevalence (6 hosts infected, 0.4%), followed by *P. ramiflora* (14, 1.7%), *B. coccolobifolia* (15, 3.2%), *V. macrocarpa* (55, 4.5%), and *A. occidentale* (48, 39%). Additionally, *B. coccolobifolia* and *P. ramiflora* had much more infected individuals than expected from their relative abundance ($\chi^2 = 6.64$, df = 2, $P < 0.05$), while *B. crassifolia* was less infected than expected (Fig 2).

The number of mistletoe infections per infected host differed significantly among host species (Anova on log-transformed data: $F_{4, 133} = 5.5$, $P < 0.001$). Due to the non-significant differences between *Byrsonima* spp. and *P. ramiflora*, I pooled the data for analysis. The comparisons were made among mistletoe species instead of hosts. Intensity of infection among mistletoes was significantly different (Anova on log-transformed data: $F_{2, 135} = 10.8$, $P < 0.001$). *Psittacanthus plagiophyllus* had on average 3.2 times more infections than *P. biternatus* (5.5 vs. 1.7), and two times more infections than *P. collum-cygni* (5.5 vs. 2.7) (Tukey HSD test: $P < 0.001$). *Psittacanthus biternatus* and *P. collum-cygni* did not differ significantly.

SEED RAIN PATTERNS

About 19.5% of trees in the dataset 2 (801 individuals) received at least one seed of any one mistletoe species. Of these, a large proportion of trees received mistletoe seeds of *P. plagiophyllus* (67.7% of 801, 542 trees), and of *P. collum-cygni* (30.7%, 246 trees), while seeds of *P. biternatus* were found in only 13 trees (1.6%). Seeds of *P. biternatus* arrived at 0.4% of its host individuals (*B. coccolobifolia*, *B. crassifolia* and *P. ramiflora* pooled); *P. collum-cygni* in 3.4% of *V. macrocarpa*; and *P. plagiophyllus* in 24.6% of *A. occidentale*.

Sixty-seven individuals (8.3% of 801) had seeds of both *P. collum-cygni* and *P. plagiophyllus*; five individuals (0.6%) of *P. biternatus* and *P. plagiophyllus*; 2 individuals (0.25%) of *P. biternatus* and *P. collum-cygni*, and only one individual (0.1%) had all three mistletoe seeds. Therefore, patterns of seed deposition among mistletoe species were not spatially correlated, since there was low overlap among individual trees receiving more than one mistletoe species. On the other hand, a similar proportion of each tree species received seeds of both *P. collum-cygni* and *P.*

plagiophyllus (Monte Carlo test: r = 0.85, P = 0.03, after 100 randomizations), but not of *P. plagiophyllus* and *P. biternatus* (r = 0.15, P = 0.46), or *P. collum-cygni* and *P. biternatus* (r = 0.55, P = 0.15).

Seed deposition was not proportional to relative tree abundance in *P. plagiophyllus* (χ^2 = 89.9, df = 4, P < 0.001); or in *P. collum-cygni* (χ^2 = 33.4, df = 4, P < 0.001). The statistical result for *P. biternatus* is not included, due to the low expected frequencies. The frequency of *V. macrocarpa* with mistletoe seeds was always lower than expected from its abundance for all mistletoe species. Furthermore, a higher proportion of *B. crassifolia* received seeds than expected from its abundance for all mistletoes but *P. plagiophyllus* (Fig. 3).

SEED SURVIVORSHIP AND SEEDLING ESTABLISHMENT

Survivorship of seeds of *P. biternatus* and *P. collum-cygni* was widespread but markedly different across the nine tree species after one year (Anova on proportion of surviving seeds: $F_{8, 119}$ = 3.14, P = 0.003). Although the proportion of surviving seeds was on average 1.8 times higher on *P. collum-cygni* that on *P. biternatus* (0.26 ± 0.37 vs. 0.14 ± 0.25, $F_{1, 119}$ = 5.76, P = 0.02), differences between the two mistletoes depend greatly on the tree species considered (tree x mistletoe interaction: $F_{8, 119}$ = 4.64, P < 0.001). *Psittacanthus collum-cygni* performed better than *P. biternatus* on four tree species, while *P. biternatus* did it on five species (Fig. 4). Additionally, there was a negative but not significant correlation between the proportion of seed survivorship of *P. collum-cygni* and *P. biternatus* (Spearman rho = - 0.57, P = 0.1).

Seedling establishment, on the other hand, was limited to three species for *P. biternatus* and to one species for *P. collum-cygni* (Fig. 5). At least 6.3% of seeds of *P. biternatus* established in the first year, and 6.7% of *P. collum-cygni*. The total

percentage of seedling establishment was 49% for *P. collum-cygni* in *Vatairea macrocarpa*; and for *P. biternatus* was 32%, 2%, and 10% for *Byrsonima coccolobifolia*, *B. crassifolia* and *Pouteria ramiflora*, respectively. This result was not related to differences in branch diameter (branch diameter x tree interaction: $F = 0.9$, $P = 0.38$). Furthermore, because *B. coccolobifolia*, *B. crassifolia* and *P. ramiflora* had the same number of experimental individuals (10), I compared the relative performance of *P. biternatus* on them, and found a higher establishment in *B. coccolobifolia* (32%) than in *B. crassifolia* (2%) or *P. ramiflora* (10%).

Although I did not compare *P. plagiophyllus* with *P. biternatus* and *P. collum-cygni* due to differences in environmental conditions during the time of seed exposure, *P. plagiophyllus* appeared to be highly specialized on *A. occidentale* after seven months (Fig. 5). Only 6.3 % of 270 seeds (17 seeds) survived in this period, 14 in *A. occidentale* (14/30 = 47%) and 3 (3/30 = 10%) in *V. macrocarpa*. However, mistletoe seeds did not germinate or establish in *V. macrocarpa*, while 78% of surviving individuals had primordial leaves at the end of the 7^{th} month in *A. occidentale*.

Discussion

There was a low overlap among trees used as hosts by three *Psittacanthus* species occurring in an Amazonian savanna patch. While *P. biternatus* was a generalist, parasitizing some of the most common tree species, *P. collum-cygni* occurred mainly in tree species of the nitrogen-fixing family Fabaceae (especially *Vatairea macrocarpa*), and *P. plagiophyllus* occurred only in one of the less abundant species, the cashew tree *Anacardium occidentale*. This contradicts the current ideas suggesting that when tree species have low relative abundance, they are unable to support

specialized parasites (Janzen 1981,Norton & Carpenter 1998). Furthermore, this study highlights the importance of species-specific mistletoe-tree compatibility as an important determinant on host use and the patterns of infection prevalence in mistletoes.

INFECTION PATTERNS: TREE ABUNDANCE AND HEIGHT

Mistletoe infection prevalence was only partially related to relative tree abundance in one of the three mistletoe species. As predicted, *P. biternatus* infected the commonest tree species, *B. crassifolia*, and its congener, *B. coccolobifolia* (together performing 28.2% of tree individuals). On the other hand, mistletoes did not infect the 2nd and 3rd most common trees (*S. convallariodora* and *Q. grandiflora*, Vochysiaceae; 23.8% of individuals) on the sampling plots. This is interesting because members of this family are the main host trees for another *Psittacanthus* species (*P. robustus*) in Central Brazilian Cerrado, and there, their relative abundance seems to influence mistletoe specificity (Monteiro *et al.* 1992) . The other tree species infected by *P. biternatus* was *Pouteria ramiflora*. Despite being the 4th most common tree in this study site, this species corresponds to only 8.5% of tree individuals. In sum, I have not found evidence to support the hypothesis that tree abundance is the main factor leading to infection patterns.

In their study of the plant infected by *Struthanthus polyanthus* (Loranthaceae), Arruda *et al*. (2006) suggests other factors, in addition to abundance, were also responsible for patterns of infection observed such as the rough bark of the species, and the incapacity to accumulate silica on its tissues, that act as a physical barrier to mistletoe haustorium penetration on trees. A crucial next step in this research would

be to investigate the role of these tree traits explaining patterns of mistletoe infection and mistletoe-tree association.

Although *P. biternatus* was the most generalist mistletoe species, it was not totally unspecific with respect to host trees, being more prevalent than expected in *B. coccolobifolia* and in *P. ramiflora*, the two least common hosts. This is evidence that other factors, in addition to host abundance are necessary to explain mistletoe infection prevalence for this species. A similar pattern has been shown for other mistletoe species, where this is probably related to disproportionate seed rain on some host trees (López de Buen & Ornelas 1999,Aukema & Martinez del Rio 2002a) and/or to mistletoe-host compatibility (López de Buen & Ornelas 2002).

Another common predicted pattern in mistletoes is the size-occupancy relationship wherein larger trees are disproportionately infected (Overton 1994). Roxburgh & Nicolson (2005a) had extrapolated this to between tree species and found a significant effect of tree height on mistletoe prevalence for one of the two mistletoe species they studied. The results presented in this study allowed me to ask whether species with taller trees were more likely to be infected, possibly because they are the preferred post-foraging perches for seed dispersers. However, I found that the tallest trees in the study site (*Salvertia convallariaeodora* and *Sclerolobium paniculatum*) were not infected by mistletoes. Preliminary observations suggest that, at least for *P. plagiophyllus* and *P. collum-cygni*, the Plain-crested Elaenia (*E. cristata*), a small omnivorous tyrant flycatcher, is its main seed disperser (R.F.F. *et al.*, unpublished manuscript). This species prefer to perch on taller than average trees in Brazilian Amazonian savannas, but not the tallest (Cintra 1997), which could partially explain the absence of mistletoe infections on these trees. However, the complete absence of infection suggests that other factors were likely to influence the interaction host-

parasite (see the item *Mistletoe-host compatibility*). Furthermore, the existence of a positive relationship between tree size and the probability of receiving mistletoe seeds in this study (data not shown, chapter 2) indicate that the intraspecific size-occupancy relationship is still likely to play an important role in this study system, affecting two of the three mistletoe species, *P. collum-cygni* and *P. plagiophyllus*. Therefore, the effect of tree size on the deposition of mistletoe seeds should be considered in studies of mistletoe infection and abundance.

SEED RAIN PATTERNS

Few tree individuals shared seeds of different mistletoe species, but the proportion of each tree individual of each species receiving seeds was highly correlated between *P. collum-cygni* and *P. plagiophyllus*. Despite the low number of seeds of *P. biternatus*, these results suggest that seed dropping locations of seed dispersers after consuming mistletoe fruits of different species were not correlated, indicating absence of spatial autocorrelation or that they were not grouped by spatial proximity, which may arising from distinct positions of mistletoe species within the sampling plot. On the other hand, there was a high correlation between the proportion of host trees receiving seeds of either *P. collum-cygni* or *P. plagiophyllus*. As these two mistletoe species do not overlap their fruiting periods, they could be dispersed by the same birds. Furthermore, because they parasitize different tree species, seed dispersers should play a small role in determining their tree specificity. A similar approach has been suggested for two Australian mistletoes (Yan 1993a), but the present study is the first to provide an empirical evidence of this mechanism (or the lack of it).

A disproportionate seed rain on tree species occurred for all mistletoes. This provides indirect evidence that birds visit some tree species more often than expected

from their abundance. Several other studies have made observations of bird dispersers visiting some host trees more frequently than others (López de Buen & Ornelas 1999,Roxburgh & Nicolson 2005a). In this study, I also considered other non-host trees mainly in trying to explain specialization, but I was also able to comment on the prevalence for one species. Only *P. biternatus* had a disproportionate seed rain onto one of its host trees. Nevertheless, seed rain does not fully predict the current patterns of mistletoe infection prevalence, and therefore, mistletoe-tree compatibility may be a major factor influencing infection (e.g. López de Buen & Ornelas, 2002). For *P. collum-cygni*, I found a higher proportion of *B. crassifolia* receiving mistletoe seeds than expected, but its unique host *V. macrocarpa* had a lower proportion of individuals receiving seeds than predicted. Finally, a much greater than expected proportion of *P. plagiophyllus* seeds was found on *A.occidentale* and *P. ramiflora*. However, this result disappeared when I removed the infected trees of its own host species (*A. occidentale*) from the analysis. In summary, except for *P. biternatus*, seed rain patterns were not related to trees selected as hosts by mistletoe species, being more common on non-host than on host trees. I believe these patterns may be well understood if we take an approach that considers the positions of mistletoe infections, the relative abundance of tree species, and the movement of bird dispersers within the subplots. Ideally, there should be a combination of post-foraging observations of potential bird dispersers and a survey of mistletoe seeds for all tree species available (e.g. Medel *et al.* 2004; Roxburgh & Nicolson 2005).

MISTLETOE-HOST COMPATIBILITY

Seedling establishment of mistletoes on different tree species provided unequivocal evidence that mistletoe-tree compatibility is the main factor driving the observed

pattern of mistletoe specialization in *Psittacanthus* species. Additionally, the patterns of mistletoe infection prevalence on *P. biternatus* nicely match the results of the field experiment (Fig. 2), suggesting that the action of frugivorous birds is not required to explain the patterns I found. The seed inoculation experiment revealed that: mistletoe seedlings could survive for one year or more without establishing on non-host trees (Lamont 1983); congener mistletoe species living in sympatry may require very different host stimuli and/or resources to establish on unrelated host species (Yan & Reid 1995); and some mistletoe species (*P. plagiophyllus*) may not even be able to germinate on the wrong tree species.

Several studies have found that mistletoes soon germinate after being released from the exocarp (Lamont 1983,Yan 1993a, and references therein). In this study, *P. biternatus* germinated a few hours after being released, while *P. collum-cygni* germinated in a few months (not shown). Nevertheless, mistletoe seedlings are often short-lived, frequently dying within one year or less (Yan & Reid 1995,Roxburgh & Nicolson 2005a). A large proportion of seedlings of *P. collum-cygni* survived within 1 year after experimental seed inoculation in some non-host trees (e.g. 67% in *A. occidentale*, and 54% in *B. crassifolia*) (see López de Buen & Ornelas 2002 for a similar pattern on host trees). In the same way, most mistletoe seedlings of *P. biternatus* had also survived on potential host trees in this period. Nonetheless, these seedlings all died by two years after inoculation (R.F.F., personal observation); some of them had, though, produced fissures on the bark of hosts and non-host trees species during the cotyledon phase. This suggests that most seeds do not recognize the host but simply germinate and then suffer delayed mortality because of host incompatibility that occurs at the stage in which the haustorium penetrates the host

bark (Yan 1993b); or that mistletoes may not establish successfully unless specific host attractive physiological conditions are met.

Unlike seed germination, successful seedling establishment frequently depend on the tree species in which the mistletoe seed is deposited (Hoffmann *et al*. 1986,Yan 1993b). Calder (1983) suggested that mistletoe penetration on the host tissues depend primarily on host resistance, and on the mistletoe infectivity. Therefore, trees with thicker barks may resist mistletoe penetration, while a mistletoe that penetrates should also produce sufficient enzymes to invade the xylem (Yan 1993b). In this study, all mistletoes were unable to establish in four out of the nine host species; three have thick barks (*H. sucuuba*, *Q. grandiflora*, and *S. convallariodora*), and one have an exfoliating bark (*L. pacari*). However, it is unlikely that bark resistance was the main barrier to mistletoe penetration, perhaps because the branch thickness selected for experiments were too thin to prevent the haustorium development (Sargent 1995). Among the five tree species selected as hosts by mistletoe species, three also have thick barks (*P. ramiflora*, *A. occidentale*, *B. coccolobifolia*), and therefore, I believe it is more likely that a specific chemical recognition between mistletoe and host is required to allow haustorium penetration into the xylem, instead of a simple bark physical barrier (but see Yan 1993b for a different conclusion). Furthermore, the presence of silicon and the association with ants in some host species such as *L. pacari* and *Q. grandiflora* should also be evaluated as potential factors precluding the penetration of mistletoe haustorium on host tissues.

The strongest evidence suggesting that mistletoes require specific stimuli to grow on a subset of tree species is exemplified by the relationship between *P. plagiophyllus* and *A. occidentale*. Seeds or seedlings of *Psittacanthus plagiophyllus* was not observed in different host trees, neither in sampling plots nor outside them.

Likewise, none of the 240 seeds inoculated on non-host trees germinated (presented cotyledon expansion). There are no studies documenting this pattern for mistletoes that I am aware of.

CONCLUDING REMARKS

This short-term study helped to identify the main host trees used by *Psittacanthus* species in a small savanna patch in Alter do Chão. It is intriguing how closely related mistletoe species parasitize very different host species living in sympatry. However, this study provided only a snapshot of many potentially labile mistletoe-tree associations occurring in the isolated savanna patches of the Amazonia. For example, *P. plagiophyllus* was also found in *A. occidentale* in three other localities of the Pará state, while in Suriname it was found on *Pouroma* sp. (Cecropiaceae) (MOBOT herbarium). Therefore, this large web of savanna patches that probably had been isolated since the Holocene (Prance 1996) provides the raw material for the coevolution between seed vectors, mistletoes and host trees under different ecological and evolutionary pressures. Unfortunately, even a simple database listing the interactions between mistletoes and their host plants is completely lacking in Brazilian herbaria, making difficult to test the generalities of these associations.

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Table 1. Number of individuals of nine tree species in which mistletoe seeds were experimentally inoculated in Alter do Chão, Pará, Brazil.

Host species	**Mistletoe species**		
	P. biternatus	*P. collum-cygni*	*P. plagiophyllus*
Anacardium occidentale	6	6	6
Byrsonima coccolobifolia	10	8	6
B. crassifolia	10	7	6
Hymatanthus sucuuba	7	7	6
Lafoensia pacari	7	7	6
Pouteria ramiflora	10	8	6
Qualea grandiflora	7	7	6
Salvertia convallariaeodora	7	7	6
Vatairea macrocarpa	7	10	6
Number of seeds→	355	335	270

Table 2. Tree abundance and prevalence of three mistletoe species of *Psittacanthus* (Loranthaceae) in a savanna patch near Alter do Chão, Pará, Brazil. Host trees with at least one infected individual are in bold.

Tree species	**Family**	**Total abundance**	**Average abundance** (± SD)	**Number of plots**	*Psittacanthus biternatus* Prevalence (%)	*Psittacanthus collum-cygni* Prevalence (%)	*Psittacanthus plagiophyllus* Prevalence (%)
Anacardium occidentale*	Anacardiaceae	6	0.38 ± 0.7	4	-	-	3 (50)
Xylopia aromatica	Annonaceae	33	2.06 ± 2.3	12	-	-	-
*Hymatanthus sucuuba**	Apocynaceae	43	2.7 ± 2.3	14	-	-	-
Tabebuia ochracea	Bignoniaceae	6	0.38 ± 0.7	4	-	-	-
Bowdichia virgilioides	Fabaceae	10	0.63 ± 0.8	7	-	-	-
*Vatairea macrocarpa**	Fabaceae	47	2.94 ± 2.1	14	-	-	-
Sclerolobium paniculatum	Fabaceae	27	1.7 ± 3.1	8	-	-	-
*Lafoensia pacari**	Lythraceae	35	2.2 ± 1.4	15	-	-	-
Byrsonima coccolobifolia*	Malpighiaceae	29	1.8 ± 1.3	13	3 (10)	-	-
Byrsonima crassifolia*	Malpighiaceae	127	7.9 ± 5.8	16	1 (0.8)	-	-

Tree species	Family	Total abundance	Average abundance (± SD)	Number of plots	*Psittacanthus biternatus* Prevalence (%)	*Psittacanthus collum-cygni* Prevalence (%)	*Psittacanthus plagiophyllus* Prevalence (%)
Roupala montana	Proteaceae	3	0.2 ± 0.8	1	-	-	-
Pouteria ramiflora*	Sapotaceae	47	2.9 ± 3.5	13	1 (2)	-	-
Simarouba amara	Simaroubaceae	8	0.5 ± 0.9	5	-	-	-
*Qualea grandiflora**	Vochysiaceae	62	3.9 ± 2.4	16	-	-	-
*Salvertia convallariaeodora**	Vochysiaceae	70	4.4 ± 3.6	15	-	-	-
Total		553		16			

*Species inoculated with mistletoe seeds.

Figure legends

Fig. 1. Mean height of host (black) and non-host (white) tree species of three mistletoe species of the genus *Psittacanthus* near Alter do Chão, Pará, Brazil. *Ao = Anacardium occidentale, Bv = Bowdichia virgilioides, Bco = Byrsonima coccolobifolia, Bcr = B. crassifolia, Hs = Hymatanthus sucuuba, Lp = Lafoensia pacari, Pr = Pouteria ramiflora, Qg = Qualea grandiflora, Rm = Roupala montana, Sc = Salvertia convallariaeodora, Sa = Simarouba amara, To = Tabebuia ochraceae, Sp = Sclerolobium paniculatum, Vm = Vatairea macrocarpa, Xy = Xylopia aromatica.*

Fig. 2. Observed and expected number of hosts infected with *Psittacanthus biternatus* in a 4.5 ha savanna plot, Alter do Chão, Pará, Brazil. *Bco = Byrsonima coccolobifolia*, *Bcr = B. crassifolia*, *Pr = Pouteria ramiflora*.

Fig. 3. Observed and expected number of hosts with seeds of *P. biternatus*, *P. collum-cygni* and *P. plagiophyllus* in a 4.5 ha savanna plot, Alter do Chão, Pará, Brazil.

Fig. 4. Average proportion (± SE) of mistletoe seeds surviving in the 12th month in nine tree species near Alter do Chão, Pará, Brazil, monitored from March 2007 to March 2008.

Fig. 5. Average proportion (± SE) of mistletoes seedlings established in the 12th month (to *P. biternatus* and *P. collum-cygni*), and in the 7th month (to *P. plagiophyllus*), in nine tree species near Alter do Chão, Pará, Brazil, monitored from

March 2007 to March 2008 (*P. biternatus* and *P. collum-cygni*), and from September 2008 to April 2009 (*P. plagiophyllus*).

Fig. 1.

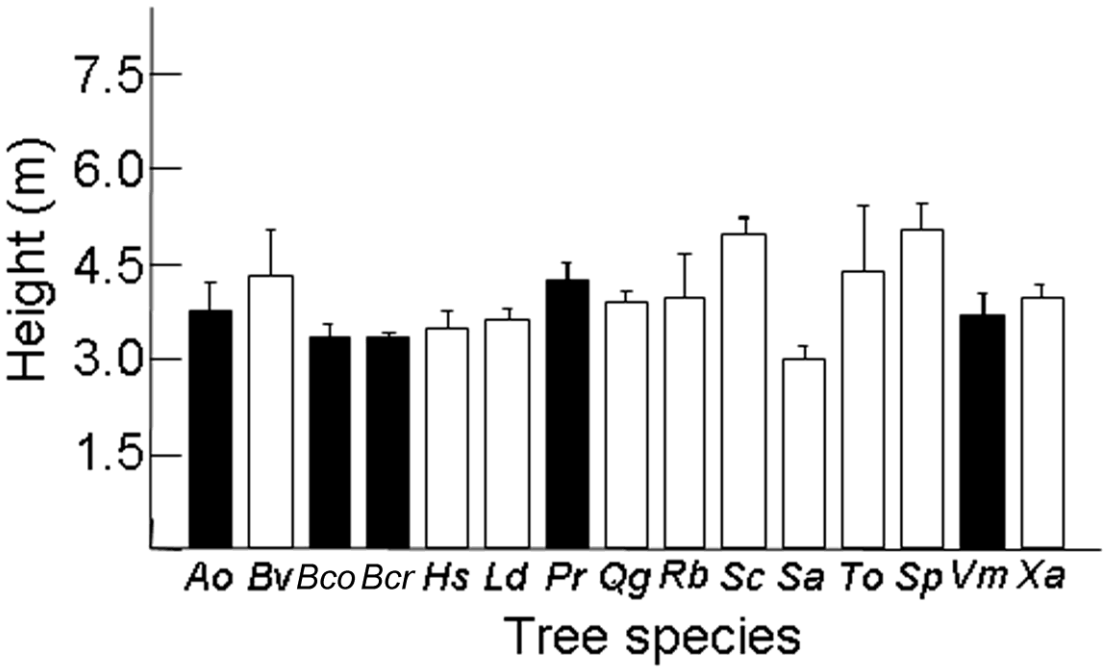

Height (m)
7.5
6.0
4.5
3.0
1.5
Ao
Bv
Bco
Bcr
Hs
Ld
Pr
Qg
Rb
Sc
Sa
To
Sp
Vm
Xa
Tree species

Fig. 2.

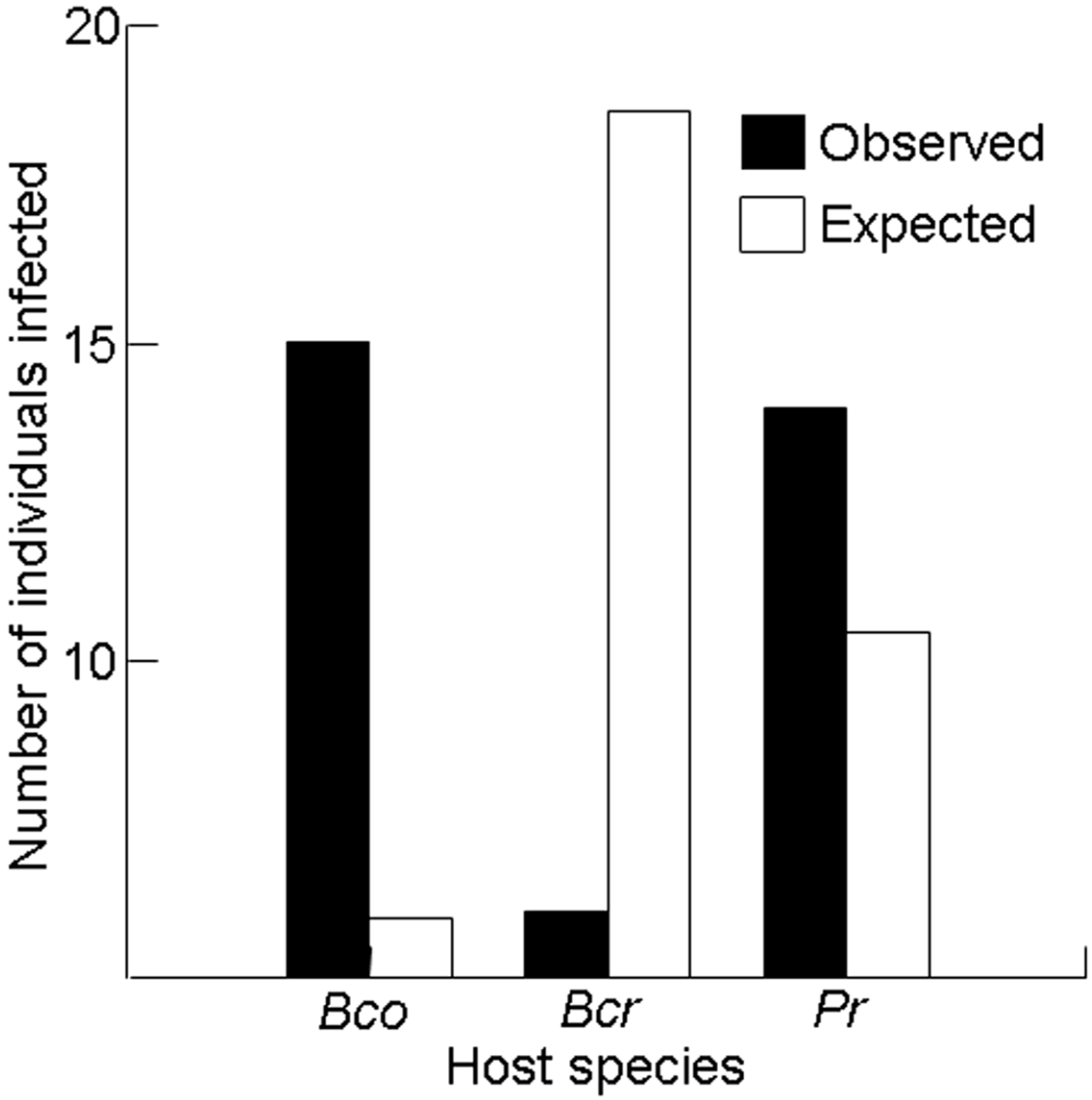

20
15
10
Number of individuals infected
Observed
Expected
Bco
Bcr
Pr
Host species

Fig. 3.

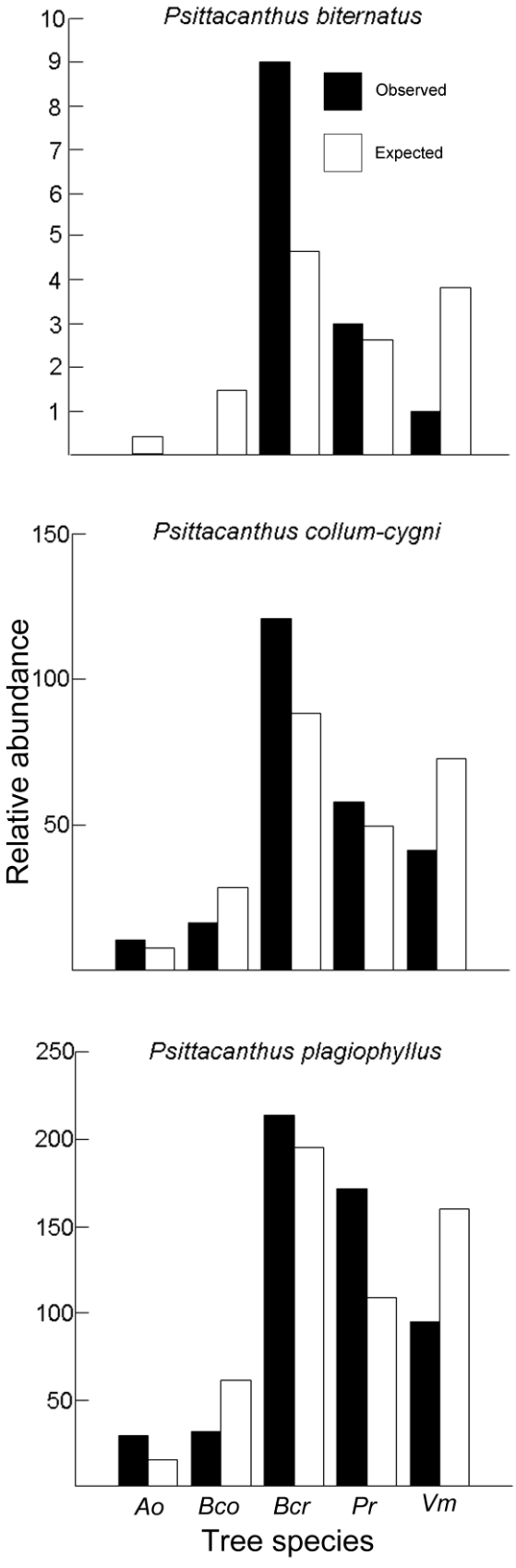

Psittacanthus biternatus
Observed
Expected
Psittacanthus collum-cygni
Relative abundance
Psittacanthus plagiophyllus
Ao
Bco
Bcr
Pr
Vm
Tree species

Fig. 4.

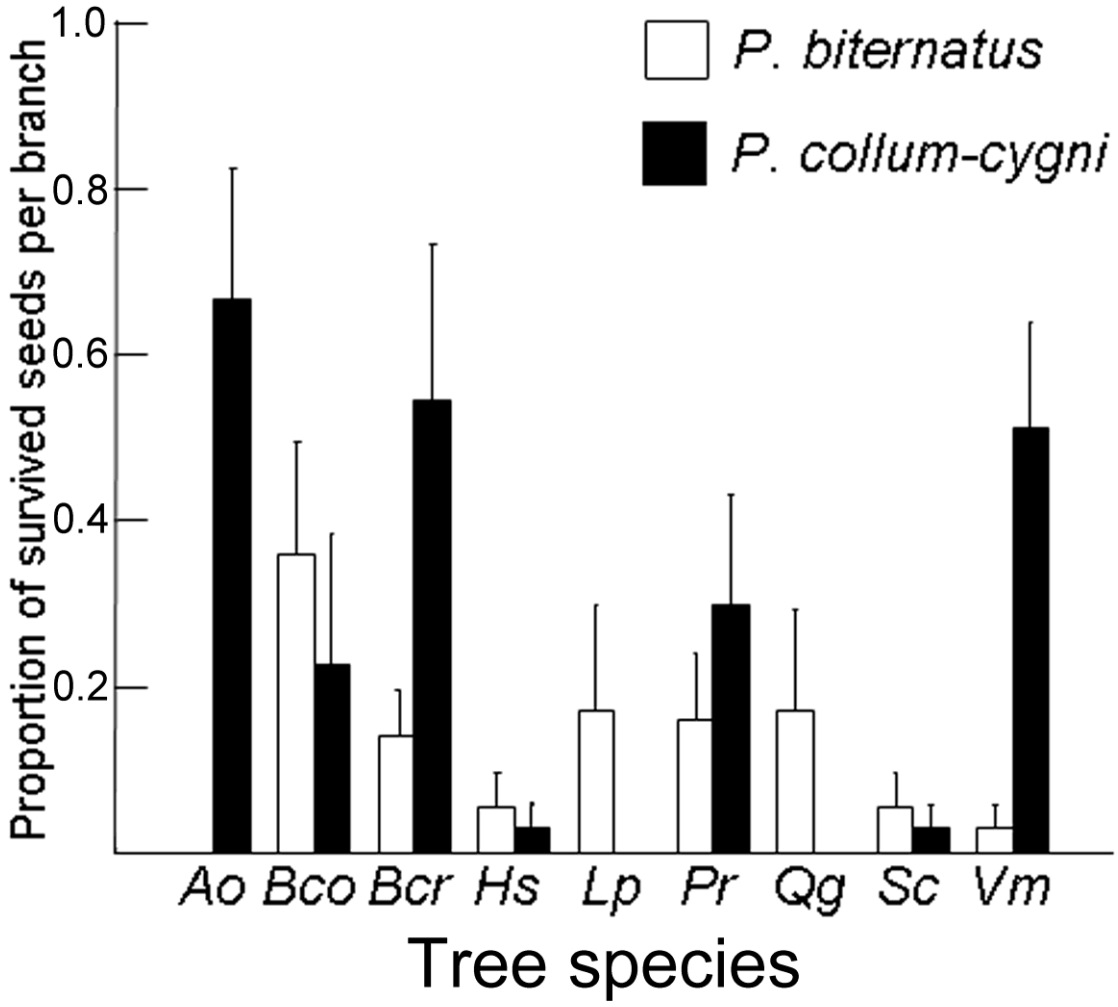
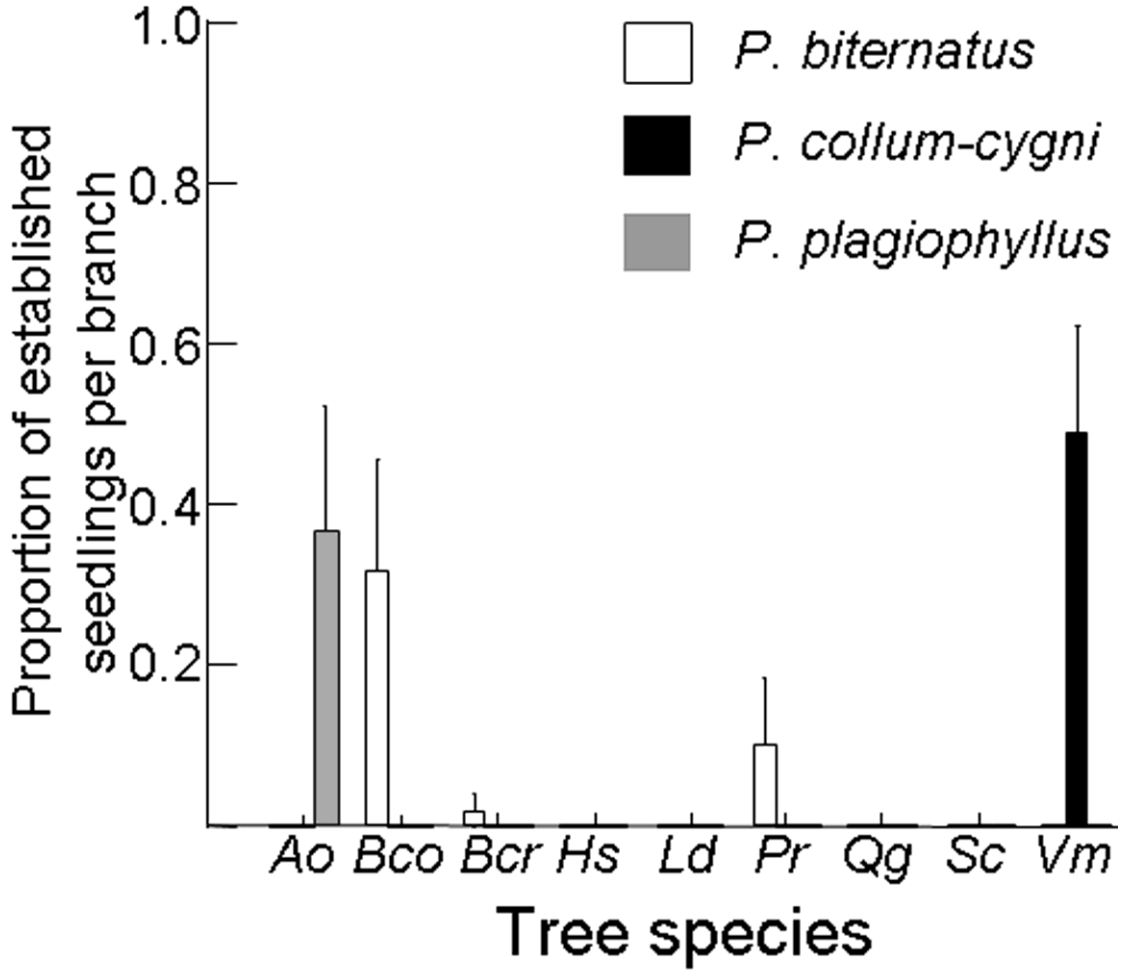

P. biternatus
P. collum-cygni
Proportion of survived seeds per branch
1.0
0.8
0.6
0.4
0.2
Ao
Bco
Bcr
Hs
Lp
Pr
Qg
Sc
Vm
Tree species

Fig. 5.


1.0
0.8
0.6
0.4
0.2
Proportion of established seedlings per branch
P. biternatus
P. collum-cygni
P. plagiophyllus
Ao
Bco
Bcr
Hs
Ld
Pr
Qg
Sc
Vm
Tree species

Appendix 1. List of host species infected by three sympatric *Psittacanthus* species in the savanna of Alter do Chão, Pará, Brazil.

Host species	Host Family	Habit	Mistletoe species		
			Psittacanthus bitternatus	*Psittacanthus collum-cygni*	*Psittacanthus plagiophyllus*
Anacardium occidentale	Anacardiaceae	T	X		X
Himatanthus sucuuba	Apocynaceae	T	X	X	
Hirtella racemosa	Chrysobalanaceae	S	X		
Erythroxylum suberosum	Erythroxylaceae	S	X		
Bowdichia virgilioides	Fabaceae	T		X	
Copaifera martii	Fabaceae	S	X*		
Sclerolobium paniculatum	Fabaceae	T		X*	
Vatairea macrocarpa	Fabaceae	T		X	
Casearia sylvestris	Flacourtiaceae	S	X	X*	
Byrsonima coccolobifolia	Malpighiaceae	T	X		

Host species	Host Family	Habit	Mistletoe species		
			Psittacanthus bitternatus	*Psittacanthus collum-cygni*	*Psittacanthus plagiophyllus*
Byrsonima crassifolia	Malpighiaceae	T	X		
Miconia fallax	Melastomataceae	S	X		
Myrcia obtusa	Myrtaceae	S	X		
Myrcia sylvatica	Myrtaceae	S	X		
Eugenia biflora	Myrtaceae	S	X		
Roupala brasiliensis	Proteaceae	T	X		
Pouteria ramiflora	Sapotaceae	T	X		
Qualea grandiflora	Vochysiaceae	T	X	X*	

*Non-reproductive individuals found only once

T = Tree; S=Shrub.

CAPÍTULO 2 – Manuscrito aceito para publicação no periódico "Australian Journal of Botany"

Consistency in seed deposition patterns and the distribution of mistletoes among its host trees in an Amazonian savanna

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Running title: Mistletoe distribution in an Amazonian savanna

Abstract

This paper describes the spatial distribution of the mistletoe *Psittacanthus plagiophyllus* Eichl. on its host, the cashew tree *Anacardium occidentale* L. in a Brazilian Amazonian savanna. Our aim was to understand the roles of bird seed dispersers and host quality in determining the mistletoe distribution among its host trees. In 2006, we marked 118 cashew trees in a 4.5 ha plot and counted the number of mistletoes and the presence of seeds attached to host branches in 2006, 2007 and 2008. On average 36% of hosts were infected each year. The infection load and the probability of being infected increased significantly with host crown diameter. On average 25% of hosts received at least one mistletoe seed in each year, being taller and previously infected hosts more prone to receive seeds in all three years. *Elaenia cristata* was the main seed disperser, visiting *P. plagiophyllus* 48 times in 35 hours of focal records. Additionally, in a field experiment, we used the presence of infection and host size as surrogates for host quality and tested their effect on mistletoe survivorship. After nine months, 16.5% of seeds survived and 14% had established, but neither host conditions nor host size influenced seed survivorship. Therefore, we suggest that mistletoe distribution is a consequence of a consistent dispersal of seeds onto larger and previously parasitized hosts across years.

Key-words: *Anacardium occidentale*, *Elaenia cristata, Psittacanthus plagiophyllus,* host suitability, parasitism.

Introduction

Mistletoes are plant parasites commonly aggregated within a few individuals in a population of its host trees (Aukema 2003). Three main kinds of hypotheses have been postulated to explain this pattern. First, because taller hosts are frequently the old ones, most infections accumulate in their crowns, and aggregation is acquired through time (Overton 1994). Second, as birds usually perch and deposit mistletoe seeds preferentially on the taller hosts, they accumulate mistletoes in their crowns (Reid and Stafford Smith 2000; Aukema and Martinez Del Rio 2002). A third nonexclusive hypothesis predicts that if host trees vary in quality and influence mistletoe survivorship, establishment or development, host quality could also influence mistletoe distribution (Watson 2009).

The positive relationship of age and prevalence, age and number of parasites, or age and probability of being infected, is a common pattern in many host-parasite systems (Anderson and Gordon 1982, Pacala and Dobson 1988). In most cases, because the majority of the host population is composed of young individuals, they just had not enough time to be infected by parasites. By far, this is the simplest way to explain mistletoe aggregation without requiring any biological mechanism, and therefore, a variety of ecological studies have been conducted to explore alternative mechanistic and ecological hypotheses.

Bird perch preferences after consuming mistletoe seeds is the most supported mechanism that could lead to mistletoe aggregation in taller trees (Martinez Del Rio *et al*. 1995, 1996; Medel *et al.* 2004). Birds such as tyrant flycatchers and tanagers, which are among the main seed dispersers of mistletoes (Restrepo *et al.* 2002), perch frequently on taller host trees to localize other mistletoe infections from a distance, or to defend their territories, being more likely to deposit mistletoe seeds on these hosts. Furthermore, birds may also visit previously infected hosts disproportionately, dispersing mistletoe seeds within

the same infected host tree, or bringing seeds from other source trees (Aukema and Martinez Del Rio 2002).

Another factor that could lead to differential mistletoe exploration of host trees is host quality. Although differences among hosts have been postulated as an important cause of parasite distribution (Anderson and Gordon 1982), only recently Watson (2009) proposed an unified hypothesis for parasitic plants. The 'host-quality hypothesis' (Watson 2009) propose that gradual variation in the quality of host trees is an important prerequisite for the nonrandom distribution of these plants. As host quality may be related to soil properties, the position of hosts along the water gradient, for example, should also influence plant parasites. Other characteristics of host trees may also influence parasitic plants such as host size and infection status (Overton 1994; Roxburgh and Nicolson 2008). Taller host trees should be less water stressed than smaller host trees, while the presence of parasites in a host tree could indicate it is more likely to develop a new mistletoe infection than a non-infected tree. Therefore, we expected that both taller and infected host trees are better microsites for mistletoes than smaller and non-infected trees.

In this study, our aim was to describe the pattern of distribution of the mistletoe *Psittacanthus plagiophyllus* Eich. on its host trees and to relate this pattern with seed deposition on the same host trees in a savanna plot in the Amazon. We tested two main predictions frequently encountered in mistletoe-host literature: 1) mistletoe prevalence and intensity should be positively related to host size; 2) the chance of receiving mistletoe seeds is higher on larger and previously infected host trees. The novelty provided in this study is that we measured seed deposition on the same host trees along three consecutive years. Because bird movements and seed deposition could be highly variable between fruiting seasons, one-year studies could be insufficient to relate seed rain and the patterns of mistletoe distribution Therefore, we can understand if mistletoe-host relationships are maintained

through time, and if hosts receiving mistletoe seeds in the first year are more likely to receive mistletoe seeds in the following years. Finally, 3) we also conducted a seed inoculation experiment to test if host quality (given by host size and infection status) would influence seed survivorship and establishment, independently of seed deposition.

Materials and Methods

Study site and species

We studied the distribution of the mistletoe *Psittacanthus plagiophyllus* Eichl. (Loranthaceae) on its host trees in a 4.5 ha plot (150 m x 300 m) in Alter do Chão (S 2º 31', W 59º 00'), Pará, Brazil. The region is dominated by savanna, with sparse trees such as *Byrsonima* spp., *Salvertia convallariaeodora*, *Qualea grandiflora* and other few species (Miranda 1993). Tree crown is discontinuous and average tree height is only 3.17 m (Miranda 1993). The study site also has large clumps of shrubs, composed mainly of species of the Myrtaceae and Melastomataceae families (Sanaiotti & Magnusson 1995). The area has two clear climatic seasons, with a dry season from July to November. Most of the rainfall is between December and April (Sanaiotti & Magnusson 1995), and the annual average is 2192 mm (Miranda 1993).

Psittacanthus plagiophyllus occurs in savannas of Central, North and Northeast of Brazil and in the North of South America, and produces fruits from mid June to early October. Mature fruits are black, elliptical (length = 10.3 mm ± 0.68, width = 7.76 mm ± 0.66, N = 40), with a sticky viscin adhered to the seed. Fruits are mainly consumed by a resident bird, the Plain-crested Elaenia (*Elaenia cristata*, R. Fernandes, pers.obs.), which regurgitates seeds intact. Seeds deposited on the right host do not germinate as soon as they are released from the epicarp, which is not common in mistletoes. An exhaustive sampling of tree species at a spatial scale of 10 km x 10 km and a seed inoculation experiment (R. Fadini,

unpublished data) indicate that *P. plagiophyllus* is locally specialized on the cashew tree (*Anacardium occidentale*, Anacardiaceae), which is an economically important indigenous species used as food resource and as medicine by local people.

Patterns of mistletoe seed rain and established infections

We marked all cashew trees (≥1 m of height) with numbered aluminum tags from August to September 2006 in a 4.5 ha plot. For each tree, we recorded: tree height (m), crown diameter (m), number of mistletoes alive and dead, and the presence/absence of mistletoe seeds attached to host branches. At the end of two other mistletoe fruiting periods in late September 2007 and 2008, we once again recorded the number of mistletoes in each host tree, and also the number of mistletoe seeds attached to branches after careful inspection. Both alive and dead seeds dispersed in the current fruiting season were considered in the surveys. Recent dispersed seeds were easily separated from old ones because the former had a sticky viscin still attached to the base. Because seeds are small and the majority of host trees frequently receive a small quantity of them (Martinez Del Rio *et al.* 1995a), all observations were conducted by two observers simultaneously to improve detection probability, while one observer climbed on the taller trees, the other searched for seeds or infections from the ground. There are other two species of *Psittacanthus* in the area, but their seeds were easily distinguished from each other because of distinct number of cotyledons and of seed size.

Frugivory and seed dispersal

In order to describe the frugivory and seed dispersal of *P. plagiophyllus*, we marked eight fruiting mistletoes plants at the study site in June 2007 spaced one from the others by at least 50 m. These observations would help us to relate bird behavior with seed rain patterns found

in the field. We recorded bird dispersers visiting marked plants during 1 h observation sessions between 6 and 9 AM, from July to September. For each individual bird we recorded: bird species, number of fruits taken per visit, time spent on the host tree, whether the bird regurgitated a seed or not, and behavior after a feeding bout according to the following categories: (1) rest on the host tree, (2) rest on the mistletoe branch or (3) flight to another tree.

Host tree quality: effect of host tree size and infection status

We performed an experiment to test if host size (large *vs.* small) and host infection status (infected *vs.* uninfected) would affect mistletoe seed survivorship and seedling establishment, and therefore contribute to shape mistletoe distribution. Using the host trees within the experimental plot, we separated them in categories according to size and infection conditions. We used the ad-in Pop tools Supplement (Hood 2005) to randomly select 36 individuals in a combination of *size* and *infection conditions* (nine individuals in each of the four experimental treatments). Tree crown diameter of small hosts ranged from 0.6 to 1.7 m (1.3 m ± 0.42) while that of the large hosts ranged from 3 to 8 m (5.2 m ± 1.7). We collected fruits from several mistletoes outside the plot, removed their epicarp, and inoculated five seeds onto one horizontal branch of each experimental host one day after collecting them. Seeds were firmly attached to the branches and arranged linearly 2 cm apart. Branches were tagged and measured with a caliper (precision = 0.1 mm), and the numbers of seeds that had remained green or had established (presented hypocotyls elongation) were counted in the third, sixth and ninth months after inoculation. The number of sprouting leaves and the size of the largest leaf were measured in the ninth month.

Data analyses

We used linear and logistic regression to questions related to intensity and occupancy of mistletoe infections or seeds, respectively. General Linear Mixed Models (GLMMs) were used to understand the variation in seed occupancy of host trees in response to host size and the presence of adult mistletoe infections. We used GLMM because it is useful to dealing with longitudinal designs, in which repeated observations are conducted within the same subject (Hedeker 2005). In ordinary GLM's, the linear predictor include only fixed effects and take the form:

$$\eta = x_i\beta$$

In a GLMM, a random effect 'v_i' is added to account for the correlation in the data:

$$\eta = x_i\beta + v_i$$

First, we tested two complete models presenting all fixed effects (host size, presence of adult mistletoe infection, time, and interactions) but with the random term taking one of two forms: i) subjects (individual hosts) varying in their intercepts, and ii) subjects varying in their intercepts and time trends. After that, we compared both models using the function 'anova' in R software (R Development Core Team 2009), and adopted the first one for simplicity. Finally, we compared two models using the same random effect varying in intercept ($1 \mid \text{subject}$), but removing time interactions that were not significant in the first model. We used a similar procedure to test if probability of receiving mistletoe seeds in 2007 and 2008 were higher in host trees that received at least one seed in 2006. All analyses were conducted in the R package 'lme4' (Bates and Maechler 2009).

We used an univariate repeated measures ANCOVA to analyze seed survivorship in the third, sixth, and ninth months (proportion of seeds remaining since the beginning of the experiment) (modified from von Ende 1993). We first tested for interactions of the covariate *host branch diameter* with the two predictor variables, and removed them if no significant

relationships were found. Host status (infected, uninfected) and host size (large, small) were the predictor variables. The proportion of surviving seeds (that remained green + established) was arcsine square-root transformed before analyses (Zar 1996). Results were expressed as means ± SD. Finally, we used a chi-square statistic to test for differences in the frequency of post-foraging movements of birds, using three categories to describe these movements (staying in the mistletoe, resting in the host tree, or flying to other tree).

Results

Patterns of distribution of mistletoe infections and seeds

A similar percentage of host trees were infected across years (Table 1), and the majority of mistletoe infections were aggregated in a few host trees (Fig. 1A). Infected hosts were 1.7 times taller (4.6 m vs. 2.6 m) and their crowns were 2.9 times larger than of non-infected hosts (4.3 m vs. 1.5 m). Because host height and crown diameter were highly correlated (Pearson's correlation, $r = 0.77$, $p < 0.001$, $N = 118$), all analyses were performed with host crown diameter only. The number of mistletoe infections increased with increasing tree crown diameter (linear regression for infected hosts in a log-scale: $r^2 = 0.36$, $F = 23.37$, $p < 0.001$) (Fig. 1B), likewise, the chance of an individual being infected increased with tree crown diameter (logistic regression: $\chi^2 = 51.96$, $p < 0.001$, $N = 118$) (Fig. 1C).

As for mistletoe infections, seed deposition was also highly aggregated among host trees in 2007 and 2008 (Fig 2), but showing a large variation in the quantity of mistletoe seeds found between years (Table 1). The mixed model analyses showed that the effect of host size and of the presence of infections did not vary significantly over time. However, after removing the interactions with time from the model, the chance of receiving mistletoe seeds increased significantly with increasing host size and the presence of infection (Table 2). Further, the chance of receiving mistletoe seeds in 2007 and 2008 was 7 times higher for host

trees that received at least one mistletoe seed in 2006, showing that seed rain was very consistent across years ($\beta = 1.94$, $z = 3.85$, $p = 0.001$).

Frugivory and seed dispersal

We recorded 50 bird visits in 35 h of observation. Only one species performed the majority of the visits, the Plain-crested Elaenia (*Elaenia cristata*, N = 48 visits), and therefore, we had used only data from its visits in the analysis. The other visitor was the Great Kiskadee (*Pitangus sulphuratus*, N = 2 visits). Birds visited plants in 21 observation periods (one observation period = 1 h), generally singly. The rate of visits was low (2.38 visits.h^{-1} ± 1.83) and visits were of short duration (57.3 seconds ± 44.5). Birds removed fruits in 26 visits and fruit consumption rate was low (1 fruit.$visit^{-1}$ ± 0.64). They deposit seeds by regurgitation onto plant branches, but we observed this in only two events when one and three seeds were regurgitated. Bird behavior was recorded in 25 visits. After fruit consumption, birds stayed at mistletoes (10 visits) or rested at hosts (10 visits) more frequently than they flew to other trees (5 visits), but these frequencies were not different from a null expectation ($\chi^2 = 2$, df = 2, $p = 0.37$).

Host tree quality

Branch diameter of bigger hosts was, on average, 1.9 mm larger than that of smaller hosts (df = 34, $t = 1.99$, $p = 0.06$). However, using branch diameter as a covariate controlled for this smaller and biologically non-meaningful difference. Seed survivorship (those that remained green + established) reduced significantly from 31% in the third month, to 18% in the sixth, and 16.5% in the ninth (df = 2, $F = 9.66$, $p < 0.001$, Fig. 3). However, host status (df = 1, $F = 0.6$, $p = 0.44$) and host size (df = 1, $F = 2.7$, $p = 0.1$) did not influenced significantly seed survivorship, nor they were affected by time interaction (RMA: time x host status: $F = 0.67$, p

= 0.5; time x host size: F = 1.67, p = 0.2). Seedling establishment varied from 10% in the third month, to 14% in the sixth and ninth months. There was no significant difference in establishment of seeds planted on hosts of distinct categories at the ninth month (χ^2 = 1.1, df = 1, p > 0.05).

Discussion

In this three-year study, we showed that the aggregated distribution of mistletoes within a few host trees is likely to be a result of seed dispersal in taller and previously infected host trees, rather than differential seed survivorship and establishment of seedlings among host trees. Comparing seed deposition in taller and smaller hosts within the same time interval, ours results suggest that host size, and not age, is the main factor leading to mistletoe aggregation in taller than average host trees. Roxburgh and Nicolson (2008a) conducted one year field observations of bird dispersers and a seed inoculation experiment to understand the higher prevalence of mistletoes in taller trees. They controlled the effect of host age in analyses using the residuals of regression of host size and host trunk diameter, instead of host size purely. They showed that mistletoes are more prevalent on taller trees not only due to higher seed deposition, but also due to higher survivorship of established mistletoes on these trees in comparison with smaller host trees. Although we did not showed this in our study, *ad libitum* observations suggest that smaller hosts supporting massive mistletoe infections may die sooner than taller host trees.

Several studies have tried to understand the mechanisms leading to nonrandom distribution of mistletoes, many of which had highlighted the role of bird dispersers as the main agents of mistletoe distribution (Martinez Del Rio *et al.* 1995a). Cintra (1997) showed that *Elaenia cristata* prefers to perch in taller trees at various sites in Amazonian savannas, which could direct seeds to taller hosts. *Elaenia* seems to consume mistletoe fruits

preferentially in periods of high productivity, probably being attracted to previously infected hosts and leading to reinfection. Lopez de Buen and Ornelas (1999) showed that longer visits performed by birds to infected host trees might suggest reinfestation. However, because visits of *Elaenia* were frequently short, it is likely that previously infected hosts receive seeds from external rather than from internal sources.

Interestingly, not only the importance of factors predicting seed arrival in host trees remains similar across years, but also the spatial location of seeds. Hampe *et al*. (2008) showed that seed rain could be highly consistent to very unpredictable across years for three species of plants in various study sites. In their study, predictability helps to identify the potential 'hotspots' for plant regeneration, and their characterization should be particularly important for planning plant management and conservation. In this study, ours results suggest that mistletoe spreading is very limited and that birds present a long-term memory to locate fruiting trees and deposit mistletoe seeds in the same host trees. Therefore, knowing that seed deposition is temporally consistent may help to control pest-mistletoes or to improve host quality (water and nutrient availability) to preserve highly threatened species (Norton & Reid 1997).

Our arbitrary categories of host quality did not produce any evidence of influencing mistletoe survivorship and establishment. Overton (1994) found a similar result for *Phrygilanthus sonorae* planted in infected and non-infected host trees in Mexico. Although Roxburgh and Nicolson (2008) found a similar result for *Phragmanthera dschallensis* growing in small and large *Acacia sieberana* trees in Zambia, mistletoes survived better on larger hosts over a 3-year study. According to Norton *et al*. (1997), larger hosts are more buffered against water scarcity than smaller hosts because the former have deeper roots than the latter, and may acquire water from profound soils. Additionally, when infections grow in smaller hosts, they may interfere with host acquisition of water and minerals, causing host

death within a few years (R. Fadini, pers. obs.). Therefore, it is premature to conclude that host characteristics do not influence mistletoe distribution. Further, regions presenting gradients of productivity or humidity may offer a new perspective to understand the influence of host quality on mistletoe distribution in a landscape scale (Lei 1999,Watson 2009). Experimental modification of host quality have a great potential to be studied, but it is still underexplored in tropical systems (see Bickford *et al.* 2005a for an example with temperate forests).

Our study strongly supports the hypothesis that birds play a crucial role in determining mistletoe distribution in host stands without evident environmental gradients. They will not only disperse mistletoe seeds disproportionately in some host trees within a single year, as it is commonly showed, but also across several fruiting seasons in the same host trees. Future studies should help to link seed dispersal to population dynamics and genetic structure of mistletoes, combining techniques to reveal the origin of dispersed seeds and of established infections.

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Table 1. Comparison of the percentage and the number of mistletoe infections and seeds along three consecutive years in an Amazonian savanna plot, Alter do Chão, Brazil.

Year	% infected	Total number of infections	% of hosts with seeds	Total number of seeds
2006	37	261	23.7	-
2007	37	227	25.4	65
2008	34.5	150	25.6	161

Table 2. Comparison of two GLMM's in which the subjects of the random term were allowed to vary in their intercepts. (See text for details).

Source	Model 1			Model 2		
	Estimate	**SE**	**P**	**Estimate**	**SE**	**P**
Time	-0.90	0.59	0.12	0.06	0.19	0.76
Host size	0.25	0.34	0.46	0.55	0.19	0.003
Infection	1.37	1.50	0.36	2.83	1.13	0.012
Time x size	0.16	0.14	0.26	-	-	-
Time x infection	0.72	0.45	0.11	-	-	-
Size x infection	-0.18	0.27	0.51	-0.20	0.26	0.43

Figure legends

Fig. 1. A) Distribution pattern of *Psittacanthus plagiophyllus* infections on host trees of *Anacardium occidentale* in a savanna plot at Alter do Chão, Pará, Brazil. **B)** Size-intensity relationship among tree crown diameter and number of mistletoe infections. **C)** Size-occupancy relationship among tree crown diameter and the proportion of hosts infected.

Fig. 2. Histogram of the number of mistletoe seeds per host tree along two consecutive years in a savanna plot, Alter do Chão, Brazil.

Fig. 3. Mean percentage (±SD) of *Psittacanthus plagiophyllus* seeds that survived (remain green + established) at the third, sixth, and ninth months after seed inoculation onto *Anacardium occidentale* hosts in a savanna plot near Alter do Chão, Pará, Brazil. The number of seeds inoculated per branch was five. Sample size was N = 9 hosts per experimental treatment, except for the *large-uninfected* category, which had 8 replicates due to a host death.

Fig. 1.

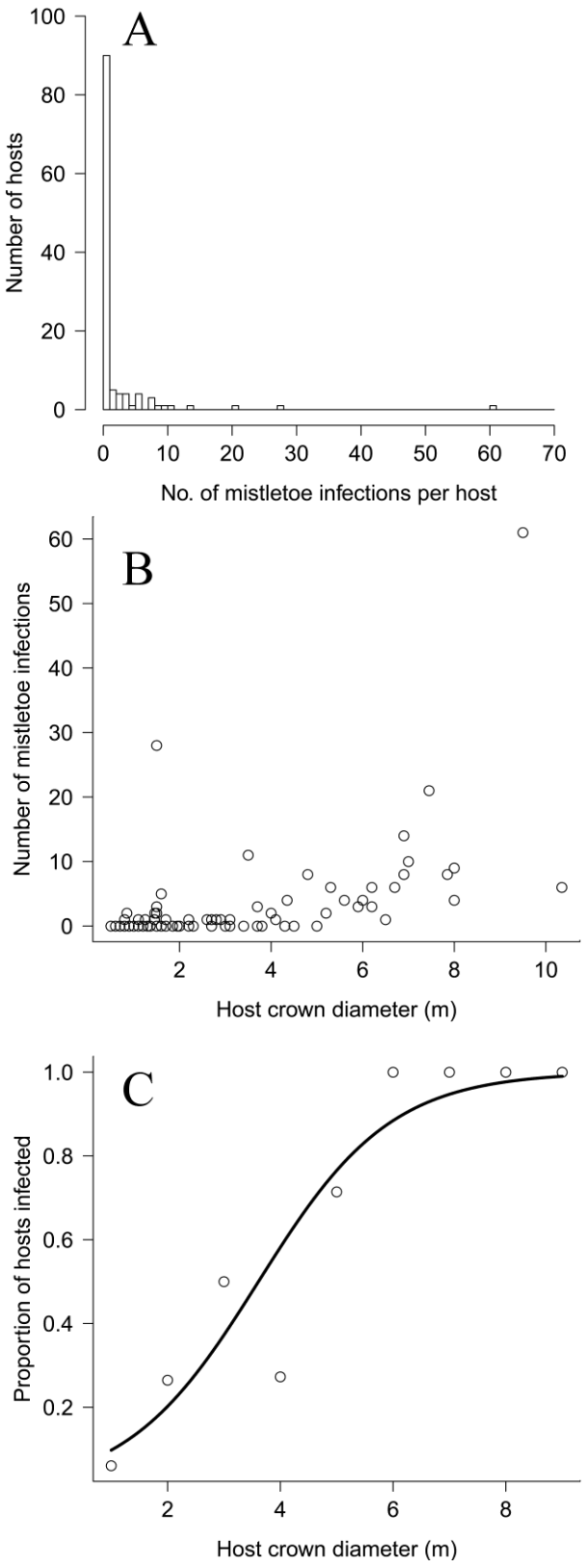

A
Number of hosts
No. of mistletoe infections per host
B
Number of mistletoe infections
Host crown diameter (m)
C
Proportion of hosts infected
Host crown diameter (m)

Fig. 2.

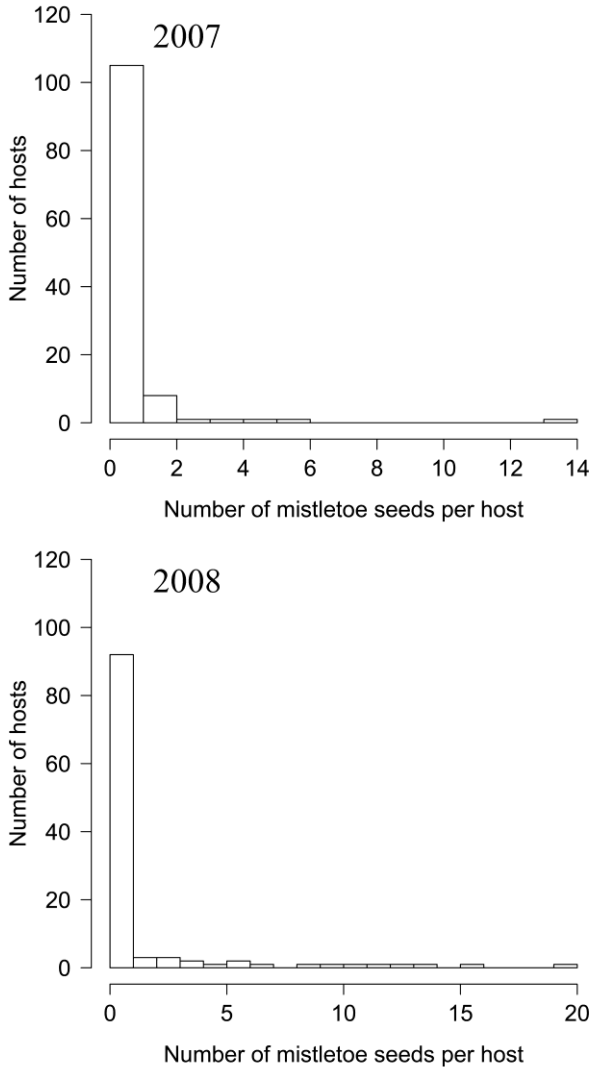
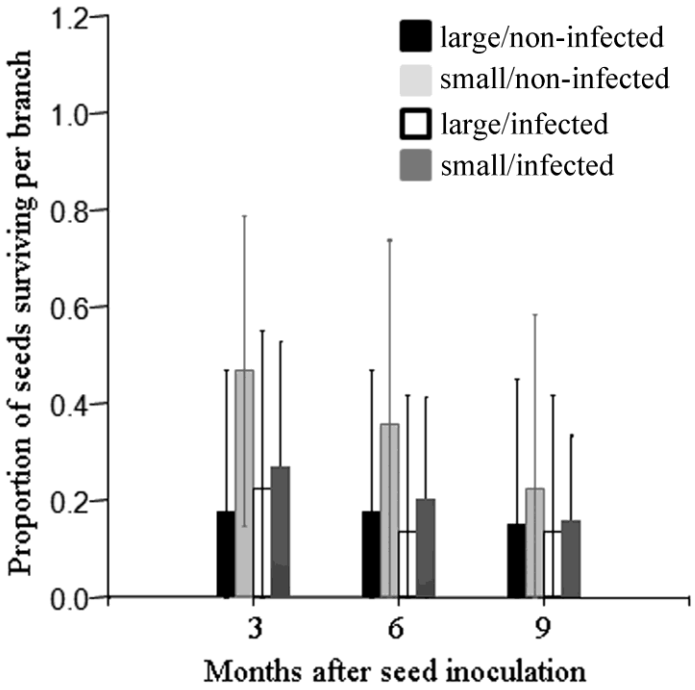

2007
Number of hosts
120
100
80
60
40
20
0
0
2
4
6
8
10
12
14
Number of mistletoe seeds per host
2008
Number of hosts
120
100
80
60
40
20
0
0
5
10
15
20
Number of mistletoe seeds per host

Fig. 3.


1.2
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of seeds surviving per branch
large/non-infected
small/non-infected
large/infected
small/infected
3
6
9
Months after seed inoculation

CAPÍTULO 3 – Este manuscrito foi submetido para o periódico “Botany”, previamente conhecido como “Canadian Journal of Botany”

Detectability should be taken into account when conducting presence-absence surveys of mistletoe seeds and infections in a Brazilian Amazonian savanna

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Abstract

The presence or absence of an organism in a given habitat patch is a kind of dataset commonly used in epidemiology or metapopulation studies. Similarly, a key component of research into mistletoe population ecology and host plant interactions is the presence-absence of mistletoe seeds or infections on host trees recorded on single survey studies. However, the failure to detect mistletoe seeds or infections is still a drawback. I tried to fix this by conducting repeated surveys on the same host plants (*Anacardium occidentale* L.) for a mistletoe species (*Psittacanthus plagiophyllus* Eich.) in Amazonia, and constructing detection-non-detection histories for each host tree using multiple observers. Therefore, it was evaluated how detectability would be affected by host characteristics such as size, proximity to other infected hosts and the presence of infections. The detection of mistletoe seeds decreased 50% from smallest to tallest host trees, and 21% from non-isolated to isolated individuals. The presence of infections had a negligible effect on the detectability of seeds. Although there was weak evidence that host characteristics would affect the detectability of mistletoe infections, I still suggest that we should adopt this method to survey other mistletoe plants and epiphytes worldwide.

Keywords: *Anacardium occidentale*; detection probability; false-absences; hemiparasite; long-distance seed dispersal; *Psittacanthus plagiophyllus*.

Introduction

Presence and absence data may provide useful information for understanding the distribution and dynamics of plants such as mistletoes (Overton 1994) and epiphytes (Tremblay et al. 2006), that comprise about 25,000 vascular species worldwide, many of which occur in the Neotropics (Benzing 1990). Although collecting presence-absence data is less time consuming than on abundance within host trees, the detection of seeds or established plants on host branches may be not an easy task; moreover, detectability is completely neglected in all ecological studies of mistletoes of which I am aware (for example, Martinez del Rio *et al.* 1995b,López de Buen & Ornelas 2001,Aukema & Martinez del Rio 2002d,Medel *et al.* 2004). The large size of some host trees, the small size of some plant life stages, plant dormancy, and the complex structure of tree canopy may reduce the detectability of mistletoes and other epiphytes in presence-absence surveys. Therefore, it is probably crucial to account for detectability in surveys of mistletoes and epiphytes in general. For instance, the failure to detect existing individuals may overestimate extinction rates (Kéry 2004), and reduce the chances of estimating long-distance seed dispersal events (Cain et al. 2000), which are particularly important for persistence of plants with metapopulation structure such as mistletoes (Overton 1994) and epiphytes (Tremblay et al. 2006).

The failure to detect an existing individual in a sampling station is known as a false-absence or false-zero (Martin et al. 2005). It is possible to deal with false-absences by conducting repeated surveys on the same site with a short interval between surveys (Mackenzie et al. 2006). Furthermore, it is possible to calculate the influence of ecological covariates such as host size and neighborhood characteristics on either occupancy or detectability simultaneously (Mackenzie et al. 2002).

I searched hosts for the mistletoe *Psittacanthus plagiopyllus* Eichler (Loranthaceae) and used a multiple-observer approach to test for the effect of some covariates on the detectability of mistletoe seeds and established plants. I tested three predictions related to detectability: (1) detectability of mistletoe seeds as well as of mistletoe infections is negatively affected by host size, due to difficulty to find mistletoe seeds and infections on larger hosts; (2) detectability of mistletoe seeds and infections is positively affected by proximity to infected neighbors, due to higher seed deposition on the neighbors of infected hosts, and the consequent accumulation of mistletoe infections; (3) previously infected hosts attract bird seed dispersers more often than non-infected hosts (Medel *et al.* 2004,Roxburgh & Nicolson 2005b), which in turn deposit seeds disproportionately on them. Therefore, detectability of mistletoe seeds is higher on previously parasitized hosts.

Methods

This study was conducted in a fire-prone Amazonian savanna near Santarém, Pará, Brazil (S 2º 31', W 59º 00') (Santos et al. 2008). Fruits of *P. plagiophyllus* are dispersed from mid June to late September. Mature fruits are black, elliptical (length = 11.25 mm ± 0.56, width = 8.86 mm ± 0.38, N = 80) and have a natural sticky viscin adhered to the seed. Regurgitated seeds are light green and are visible from a distance when in contrast with tree branches. The mistletoe *P. plagiophyllus* grows uniquely on native populations of the cashew tree (*Anacardium occidentale*, Anacardiaceae), which is a medium sized tree (height = 4.8 ± 1.4 m, N = 557) with nearly horizontal branches and wide crowns (crown diameter = 4.4 ± 2.3 m, N = 557).

I randomly chose 24 to 28 cashew trees (hosts) in each of five host populations with high mistletoe prevalence to conduct a multiple-observer sampling design between 5 and 24 August 2008, when the majority of seeds had already been dispersed (R. Fadini, pers. obs.).

Hosts were chosen using a random digit table to sort angles between 0 and 259 degrees. Therefore, I walked 50 m in the direction which was drawn and marked the nearest host tree with an aluminum tag. Hosts were georreferenced and separated from each other by at least 50 m. I conducted a new draw if points were less than this minimum distance. For three populations (80 hosts), two observers, one at a time, climbed on the host trees and searched independently for mistletoe seeds and infections. Shorter hosts were accessed with an aluminum ladder because of branch fragility. While one observer was searching for seeds, the others looked away. There was no communication between the observers during and after the searching period, which lasted 3 min. Therefore, the first observer annotated in a spreadsheet the 'detection' or 'non-detection' of mistletoe seeds or infections right after he had climbed down from the host tree. The second observer did the same. For the remaining two host populations (50 hosts), there were three observers instead of two. Only I sampled all populations.

I chose three site (host) covariates to account for variation in mistletoe detectability: (1) "host size" (crown diameter in meters); (2) presence/absence of infected hosts within 50 m of focal hosts (hereafter "presence of infected neighbors"); (3) presence/absence of previous infections on the focal host (hereafter "presence of infection"). This last covariate was only recorded for seeds because it intuitively only affects the detectability of seeds and not of infections. Furthermore, and very relevant, because host size is frequently correlated with the abundance of mistletoe seeds and infections (Aukema & Martinez del Rio 2002d, but see Roxburgh & Nicolson 2008b), it is a good covariate for mistletoe detectability. Other characteristics such as date since seed deposition and the season in which seeds were surveyed were not taken into account, but it should not influence detectability because seeds remain green during all the season.

I constructed six *a priori* models for seed deposition and four for mistletoe infections dataset. Each host tree that was searched for seeds or mistletoes infections had its own detection/non-detection history composed of a sequence of ones (detection) and zeros (non-detection), corresponding to observations of the same host made by multiple observers. The product of all detection/non-detection histories generated a likelihood model which is maximized to obtain the maximum likelihood estimates of *p* (detectability). All models designed to estimate detection probabilities were constructed with a general model for occupancy (Ψ (size + neighbor + infection)) for seeds, and (Ψ (size + neighbor)) for established infections. Moreover, I also evaluated the efficacy of conducting multiple surveys by measuring the variation in occupancy Ψ (.) given different detection probabilities (*p*). Comparison among models was made using a parsimonious penalized likelihood ranked by AIC values (Burnham & Anderson 2004) provided by the software Presence 2.0 (Hines 2006). Moreover, it was possible to include missing observations and model covariates in detection probability. Results were expressed as means ± SE, except when previously stated.

Results and Discussion

The most parsimonious model for detection probability of seeds included the covariates "host size" and "presence of infected neighbors", accounting for 54% of model weights (Table S1). The presence of infection, on the contrary, was not meaningful. The presence of infected neighbors increased the detectability of seeds by 21%, on average (Fig.1a), while detectability decreased about 50% from smallest to largest hosts (Fig. 1b). However, in the first case the confidence intervals did not overlap, and therefore the results are more robust than in the second case, where they were larger on the extremes. Furthermore, the failure to detect seeds underestimated occupancy by an average of 2.3% with a constant detection

probability, to 9%, when the covariate “presence of infected neighbors” was included (Fig. 2).

Detectability of mistletoe infections was weakly affected by covariates, and the most parsimonious model had a constant detection probability *p* (.) (Table S2). However, detection was not complete. For instance, when mistletoe infections were found on a host tree, at least one of the observers had failed to do so in 26% of times; all were seedlings or small juveniles. In fact, the failure to detect infections underestimated occupancy by 1.6 % when *p* was maintained constant, to 4.4%, with the covariates “size” and “presence of infected neighbors” (not shown).

These results support the first two hypotheses on detectability of *P. plagiophyllus* seeds, given its presence on host trees: (1) detectability decreased with increase of host size; and (2) detectability increased on hosts with infected neighbors. The third hypothesis, on disproportionate seed rain into previously infected hosts, was not supported, suggesting that seed dispersal of this mistletoe species is mainly between, rather than within, host trees. Therefore, the failure to detect mistletoe seeds on large individual hosts may cause a serious underestimation of colonization rates. Moreover, the existence of false zeros on isolated hosts leads to underestimation of long-distance seed dispersal events (Willson 1993,Cain *et al.* 2000) , and to a decreased strength of the rescue effect (Moilanen 2002), which is particularly important for the maintenance of isolated and fire-prone populations such as those of this study.

On the other hand, the results did not show much influence of detectability on the occupancy estimates of established mistletoe infections. However, the relative importance of host size and isolation should increase when life stages being searched are small, as found for the terrestrial orchid *Cleistes bifaria* (Kéry & Gregg 2003). For instance, many small

Neotropical epiphytes (like *Lepanthes* spp., Orchidaceae) are single-surveyed from the forest floor on trees of medium size (*ca.* 15 m) (Tremblay 1997,Merwin *et al.* 2003), and problems related to detection failure are unknown. Unfortunately, presence-absence data may be difficult to obtain for species inhabiting the canopy of tall rainforest trees, where other more complex methods are hence applied, like mobile cranes (Nieder et al. 2000) and climbing techniques (Cardelus 2007). However, these methods are costly and only provide information on very small spatial scales (Wolf et al. 2009), which may be less useful for conservation purposes.

The message of this paper is clear: we should increase sampling effort on larger and isolated hosts to increase detectability of *P. plagiophyllus* seeds. Furthermore, if we have previous knowledge of the occupancy and detectability in our study system, we may allocate effort according to some pre-defined rules (Mackenzie & Royle 2005). Because in my study system detectability was generally medium to high (0.5 to 0.9), and occupancy approached 0.6, the number of surveys on individual hosts should vary from 4 to 2, respectively (Mackenzie & Royle 2005). Moreover, I suggest the adoption of this method to survey epiphytes with similar problems of detectability worldwide (see Merwin *et al.* 2003,Snäll *et al.* 2003). Epiphytes comprise one third to half of all vascular species in some Neotropical forests (Benzing 1990), and despite the large number of threatened epiphytes in this region (*ca.* 340 species) (IUCN 2008), a small effort has been made to conduct good surveys of plants of this group at large spatial scales. For instance, there are no epiphyte surveys in Brazilian Cerrados and other Neotropical savannas, where the techniques I applied here would certainly be efficient, but are still unexplored.

Acknowledgements

This research was supported by CNPq (Edital Universal: project no. 479130/2006-0) and IEB (Programa BECA: fellowship B/2007/01/DEP/07). The idea of this paper arose while I was attending the Workshop "Parameter Estimation and Decision-Making for Conservation and Management of Animal Populations and Communities". I am indebted to the families of Mr. Laudelino Vasconcelos and of Mr. Raimundo Castelo for assistance and friendship. I am grateful to Wellton Sousa, Wanderson and Wellington Ferreira for helping during the fieldwork. Scott C. Stark, Fabrício Baccaro, Renato Cintra, and Pedro Santos gave valuable suggestions on the manuscript. Gonçalo Ferraz and Jim Nichols helped to clarify my ideas. RFF receives a doctoral fellowship from CAPES.

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Table S1 Relative AIC (ΔAIC), model weight (w), -2 Likelihood (-2l) and number of parameters (No. Par) of six *a priori* selected models to predict the detectability (*p*) of seeds of the mistletoe *Psittacanthus plagiophyllus* on its host *Anacardium occidentale*, while maintaining a general model for occupancy Ψ (size + neighbor + infection).

Model	**ΔAIC**	**w**	**-2l**	**No. Par**
p (size + neighbor)	0	0.54	306.6	7
p (size + neighbor + infection)	2	0.20	306.6	8
p (neighbor)	2	0.20	310.6	6
p (size)	4.6	0.05	313.2	6
p (.)	8.6	0.01	319.3	5
p (infection)	10.6	0.00	319.2	6

Table S2 Relative AIC (ΔAIC), model weight (w), -2 Likelihood (-2l) and number of parameters (No. Par) of four models selected *a priori* for predicting detectability (*p*) of infections of the mistletoe *Psittacanthus plagiophyllus* on its host *Anacardium occidentale*, while maintaining a general model for occupancy Ψ (size + neighbor).

Model	**ΔAIC**	**w**	**-2l**	**No. Par**
p (.)	0	0.40	288.4	4
p (size)	0.69	0.28	287.1	5
p (neighbor)	1.7	0.17	288.1	5
p (size + neighbor)	1.97	0.15	286.4	6

Figure legends

Fig. 1 Estimated detection probability of mistletoe seeds of *Psittacanthus plagiophyllus* deposited on the branches of the host *Anacardium occidentale* according to A) host size and B) proximity to infected hosts. In a), the black circles represents estimated means and white circles represent 95% confidence intervals (β coefficient: host size: -0.19 ± 0.1). In b), central square represents means, and lines represent 95% confidence intervals (β coefficient: presence of infected neighbors: 1.12 ± 0.45). Values of β were obtained from a model with both parameters.

Fig. 2 Variation in seed occupancy probability given different models for detection probability. The model for occupancy was maintained constant Ψ (.) for all combinations of detectability.

Fig. 1

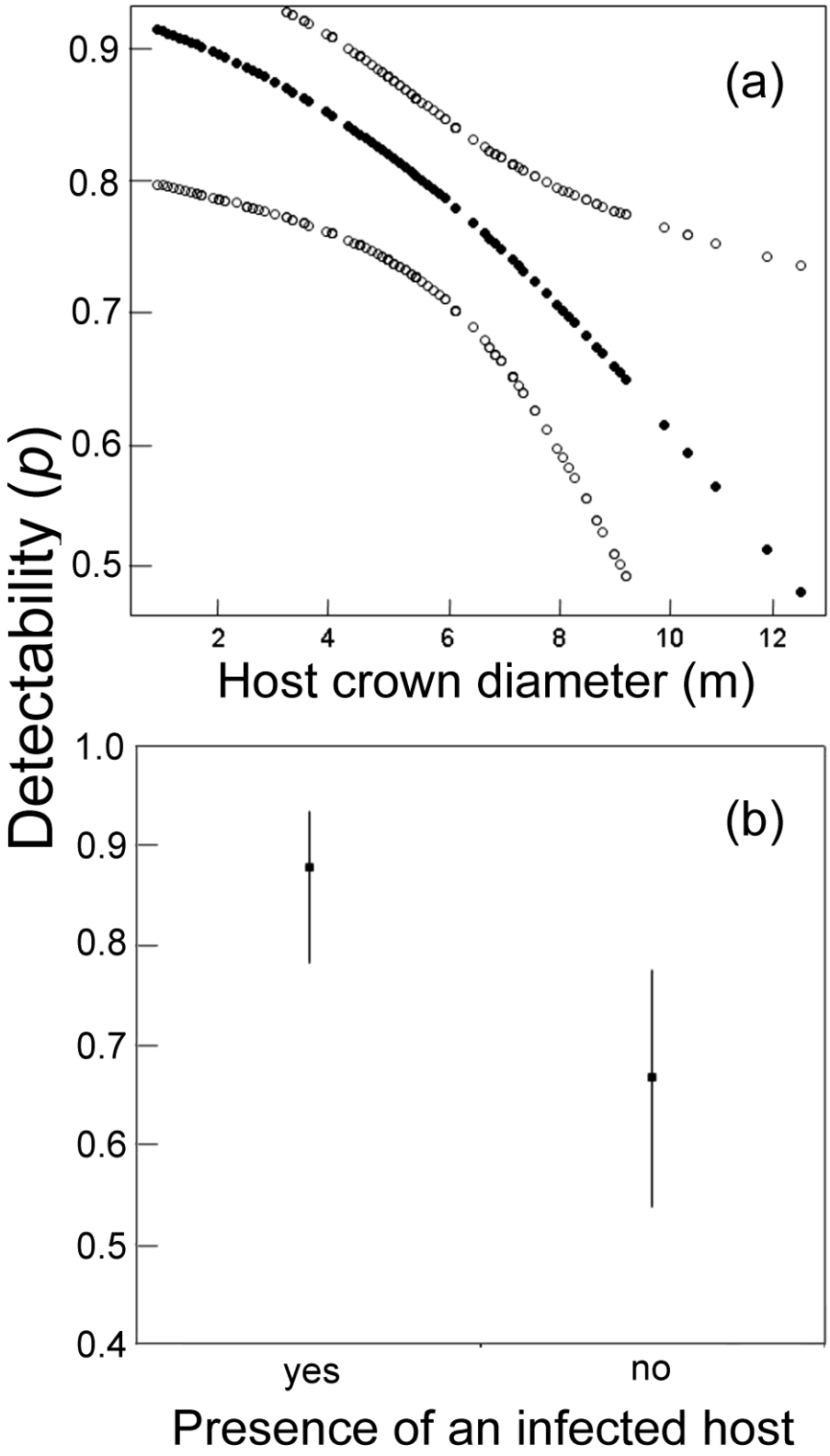
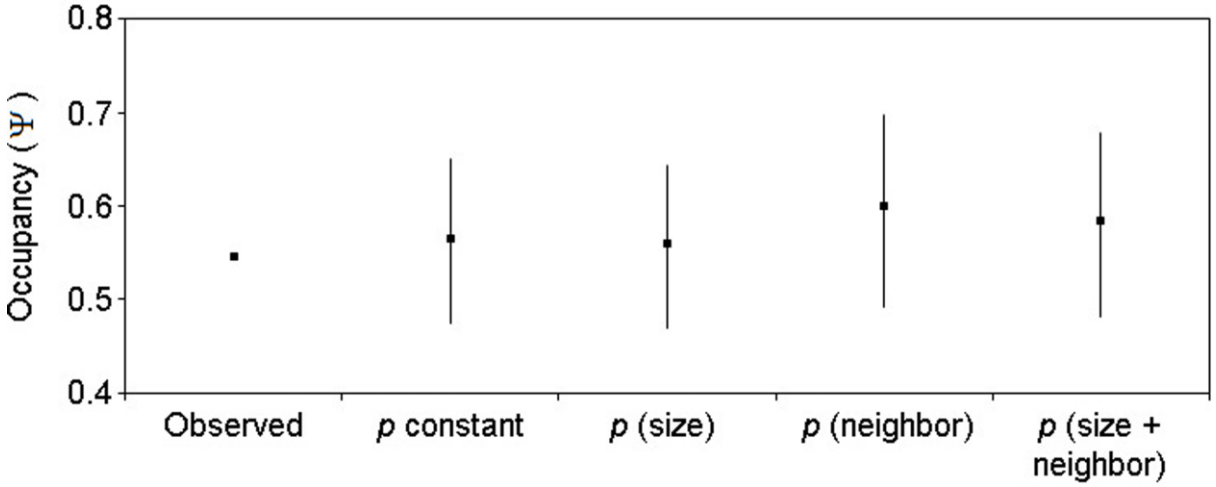

(a)
0.9
0.8
0.7
0.6
0.5
Detectability (p)
2
4
6
8
10
12
Host crown diameter (m)
(b)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
yes
no
Presence of an infected host

Fig. 2


0.8
0.7
0.6
0.5
0.4
Occupancy (Ψ)
Observed
p constant
p (size)
p (neighbor)
p (size + neighbor)

CAPÍTULO 4 – Este manuscrito será submetido para o periódico “Biotropica”

LRH: Fadini, R. F.

RRH: Mistletoes in a fire prone savanna in Brazil

Patterns of abundance and prevalence of mistletoes (*Psittacanthus* spp. – Loranthaceae), and short term dynamics of *P. plagiophyllus* under a frequent fire regime in an Amazonian savanna

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ABSTRACT

Mistletoes are a group of species frequently aggregated in response to biotic and abiotic factors. While at small spatial scales, biotic factors may dominate; at larger spatial scales, abiotic factors should prevail. Fire plays an important role in determining the distribution of plant species in savannas worldwide. In this study, the prevalence of three sympatric mistletoes of the genus *Psittacanthus* (Loranthaceae) was studied in 35 plots of savanna with different fire histories in Alter do Chão, Pará, Brazil. The proportion of hosts infected varied greatly among species: *P. biternatus* (1.5%), *P. collum-cygni* (4.8%) and *P. plagiophyllus* (20%). *Psittacanthus plagiophyllus* was negatively related to the frequency of fire, while the two other species were not. Furthermore, I applied fire to individuals of the three species using a portable propane flamethrower to test for the influence of mistletoe species, plant size and fire intensity (single or double burn) on mistletoe survivorship after one year. *Psittacanthus biternatus* had a higher probability to survive than the other two species, and larger plants were more likely to survive under low intense fires (single burn treatment) and regenerate through sprouting than smaller plants. Finally, I followed mistletoe seed arrival and occupancy of *P. plagiophyllus* in ten populations burning between 2007 and 2008 and in nine populations not burning. Mistletoe populations were not negatively influenced by fires of low intensity, but due to the aggregated distribution of mistletoe infections and seeds among its host trees, large scale and very intense fires may preclude the chances of successful recolonization.

Key words: congener species; colonization dynamics; fire frequency; survivorship; turnover.

INTRODUCTION

FIRE EVENTS ARE IMPORTANT COMPONENTS IN THE LANDSCAPE OF BRAZILIAN SAVANNAS (OR CERRADOS) (Miranda *et al.* 2002). It is known to be an ancient phenomenon in this biome (Desjardins *et al.* 1996,Sanaiotti *et al.* 2002), altering plant populations directly by killing their individuals, or indirectly by affecting conditions and resources. Although plant populations may rapidly return to their pre-fire states, recurrent fires may be a great man-induced environmental problem to most of the fire-sensitive species such as slow-growing trees (Whelan 1995, Hoffmann 1999).

In the Amazonian savannas, fire has been central in determining population dynamics and distribution of various organisms by changing their resources (Faria *et al.* 2004,Layme 2008). In these isolated patches, a few numbers of tree species occur (Miranda 1993,Ratter *et al.* 2003). The most common strategy is to sprout vigorously after fire, during the beginning of rainy period. The direct effects of fire on trees depend on the size of the tree, amount of fuel, wind speed, and season (Whelan 1995). The rate of post-fire regeneration is intrinsically linked to the life history traits of plants, including those resistant to fire passage through sprouting of pre-existing individuals or from seed banks (sprouters); or plants that are only able to recolonize from seeds (obligate seeders) (Whelan 1995).

Most studies on fire ecology in Brazil have been conducted with trees (Hoffmann 1999,Hoffmann *et al.* 2003). In general, mistletoes have been largely ignored, despite the fact that these organisms are an important part of the ecosystem as food sources for pollinators, seed dispersers (Restrepo 1987,Watson 2001), and as nesting sites for birds (Cooney 2006). Past studies have documented effects of fire on the distribution of single mistletoe species growing on commercial pine forests in U.S. (Kipfmueller & Baker 1998,Conklin & Armstrong 2005). There are no studies of which I am aware documenting the role of fires determining the distribution of conspecific mistletoes growing on different host trees.

Mistletoes are hemi parasitic shrubs lacking corky barks, and are highly dependent on their host trees. Most mistletoe species are host generalists, with few host specialists (Norton & Carpenter 1998), and this may affect their reestablishment after fire events. Plants of many mistletoe species often died when their hosts are killed by fire; indeed most mistletoes will also die if they are scorched, even when their host survives. Mistletoes are thought to be obligate seeders but, unlike other obligate seeders they have no seed bank to initiate a new population. Their seeds have to be dispersed on the branch of a suitable host by a bird (Aukema 2003). After fire has killed a population of mistletoes the only source of seed is another population, usually one growing outside the burnt area. It becomes even more drastic when the host is fire sensitive, such as in *Acacia* populations (Reid & Stafford Smith 2000). Then the process of recolonization cannot begin until the hosts have regenerated.

Several factors may influence the reestablishment of mistletoes after fire, including the resistance to fire events, and degree of aggregation. Mistletoes are frequently spatially aggregated within and between host trees, between host species, and up to several kilometers (Aukema 2004). All these characteristics would reduce the chances of rapid population increase of mistletoes due to very short spatial interactions. Because birds are their main seed dispersers, factors affecting bird behavior would ultimately determine mistletoe recovery after fire. For example, birds may perch preferentially on taller than average hosts and on previously infected trees, leading to more seed concentration on plants with these characteristics than would be expected by chance (Aukema & Martinez del Rio 2002b). Additionally, host trees close to previously infected ones may be more likely to receive mistletoe seeds than hosts far away from infections (but see Overton 1996).

Despite the small scale colonization dynamics of mistletoes, some studies had described them as plants possessing metapopulation dynamics (Overton 1994,Aukema & Martinez del Rio 2002c,but see Freckleton & Watkinson 2002). This is important because

although local populations may constantly become extinct and recolonize afterwards, the regional distribution of species is frequently more constant (Eriksson 1996). However, when mistletoes occur within a landscape forming a mosaic of 'good' and 'bad' patches in response to disturbance events, differences in species distribution may arise as a response to source-sink dynamics (Pulliam 1988). Therefore, populations on 'bad' patches are only likely to survive through continuous input of individuals from 'good' patches.

Here I studied the variation in the abundance and prevalence of three sympatric mistletoes of the genus *Psittacanthus* (Loranthaceae) in relation to fire frequency. I asked three main questions: (1) Are mistletoe species equally abundant and prevalent? (2) Are congener mistletoe species equally likely to respond to fire frequency? (3) How mistletoes would respond to fires in a short time interval? I explored these questions studying 35 plots spread in a 10,000 ha savanna patch and monitored for fire in the last 10 years. I also conducted surveys in the edges of forest fragments and in the nearest savannas to explore the alternative hypothesis that mistletoes have been pushed to forest edges in response to fires, or that forest edges are indeed the true 'sources' for some species inhabiting the patches of savanna. Additionally, I conducted a controlled fire experiment to understand how mistletoes survive in different proportions after burning with distinct fire intensities. Finally, I surveyed 19 populations of one of the three mistletoe species (*P. plagiophyllus*) to understand how they have changed between years in response to fires. I also investigated how the chances of hosts being occupied or receiving mistletoe seeds are affected by local characteristics (host size, presence of infections, and proximity to infected neighbors).

METHODS

STUDY SITE

I conducted this study in a large (10 km x 10 km) area of savanna on the right margin of the Tapajós River, near Alter do Chão, Santarém, Pará, Brazil (S 2º 31', W 59º 00') (Figure 1). The soil is sandy (92-94%) and poor in nutrients (Sanaiotti & Magnusson 1995). The majority of sites are clay poor, as were all my study sites. The region is dominated by a grassy savanna intermingled with small forest fragments (0.5 to 360 ha), and it is burned due to anthropogenic fires every 2-3 years. In the savanna two species of grasses predominate (*Trachypogon plumosus* and *Paspalum carinatum*), and a dozen species of sparse and small to medium trees, such as *Salvertia convallariaeodora*, *Byrsonima crassifolia*, *Lafoensia pacari*, and patches of shrubby vegetation composed mainly of Melastomataceae and Myrtaceae (Sanaiotti & Magnusson 1995). The region has two clear climatic seasons, with a dry season between June to November. Mean annual rainfall is 2192 mm, and mean annual temperature is 27.5 ºC.

MISTLETOE SPECIES

The three species of Loranthaceous mistletoe species co-occur in the savanna of Alter do Chão: *Psittacanthus biternatus* Blume, *P. collum-cygni* Eichler, and *P. plagiophyllus* Eichler. Due to their distinct morphologies, they are easily identified in the field. These species are distributed through Central, North and Northeast of Brazil, and North of South America, either in savannas, gallery forests, or along river banks. They are shrubby, aerial hemi parasitic mistletoes, with a single and large haustorium deeply encrusted on their hosts branches. While *P. biternatus* is a generalist species, parasitizing mostly three host species (*Byrsonima coccolobifolia*, *B. crassifolia*, and *Pouteria ramiflora*); *P. collum-cygni* and *P. plagiophyllus* are specialists, parasitizing *Vatairea macrocarpa* and *Anacardium occidentale*, respectively. Fruits are berries whose seeds are mostly dispersed by tyrant flycatchers, but occasionally cotingas and tanagers, which disperse seeds through regurgitation. Fruits of *P.*

biternatus are produced between February and August, during the rainy season; *P. collum-cygni* produces fruits between February to June, and *P. plagiophyllus* produces fruits between June and October (Rúbia Reis, pers. comm.).

MISTLETOES ABUNDANCE, PREVALENCE, AND INTENSITY

I counted the number of live and dead mistletoes and of potential host trees (chapter 1) (≥ 2 m of height) in 35 sampling plots (150 m x 250 m) spread on an area of 10 x 10 km (Fig. 1), from the end of January through the end of March 2008. In each plot, two well-trained observers searched simultaneously for mistletoes in four sub-plots of 250 m (10 m of each side, covering 2 hectares per plot). I determined the abundance index of infection as the total number of host trees infected per plot, the prevalence of infection for each mistletoe species as the proportion of its hosts infected per plot, and the intensity of infection as the number of mistletoes per infected host.

PREDICTOR VARIABLES RELATED TO MISTLETOE ABUNDANCE AND PREVALENCE

I investigated the influence of two variables (number of fire events, and number of hosts) on the abundance and prevalence of mistletoes of the four *Psittacanthus* spp. species in the 35 sampling plots. Number of fires and fire extension has been documented for each sampling plot since 1997 (except 1998) (Albertina P. Lima, unpubl. data). Presence or absence of scorched vegetation was noted along the four sub-plots within each plot after the end of dry and the beginning of the next rainy season. I transformed these data in 'proportion of area burned.plot^{-1}.year^{-1}'. In more than 80% of times the plots were searched, they had either burned almost completely (100% of foliage scorch) or didn't burn (0%). Regardless of the proportion burned, I also counted the number of fire events on each sampling plot since 1997, and found a significant correlation with the average proportion of area burned ($r = 0.85$, $P <$

0.001), and also a strong negative correlation between the number of fire events and time since last fire ($r = -0.66$, $P < 0.001$). Therefore, I used the number of fire events in analyses instead of the proportion of area burned or time since last fire because I believe it is more biologically meaningful for these plants. Number of hosts was counted in the 35 plots as previously stated. I constructed two general linear models (GLMs) (two for each mistletoe species) with different response variables (number of infected hosts and prevalence of infected hosts). I conducted three separated analyses for each one of the host trees of *P. biternatus*, but also one with the host species pooled. Due to the low occurrence of *P. collum-cygni*, I used the presence of the species in sampling plots as a response variable in a logistic regression, instead of abundance or prevalence.

THE RELATIVE EFFECT OF FIRE ON DIFFERENT MISTLETOE SPECIES

I evaluated the survivorship of mistletoes subjected to two fire treatments in an experimental study. From beginning to mid of April 2008, I georreferenced and marked with aluminium tags135 mistletoes (45 of each species) in a site of 1 km x 1 km near to the village. Seventy-fire percent of mistletoes were marked on separate hosts, and 25% were clustered on larger hosts. I recorded the following attributes for each host: mistletoe species, mistletoe height, mistletoe crown diameter, haustorium diameter, host species, host height and diameter of the infected branch.

Mistletoes were visually grouped into three size classes according to haustorium diameter (15 small, average = 3 cm; 15 medium, average = 4.6 cm; 15 large, average = 7.5 cm for each species). Therefore, I chose at random five individuals of each size class and applied one of two experimental treatments: single burn, double burn, and control (no treatment). Fire treatments were applied with a portable propane flamethrower always maintained the valve on the same position for all applications (*ca.* 500 ºC). In the ‘single

burn' treatment, the flame was directed once across the whole mistletoe canopy from bottom to top and from side to side in order to scorch all foliage and haustorium. Duration of burning was recorded with a stop watch. In the 'double burn' treatment, when a single burn was complete, burning was repeated in the same way as the 'single burn' application a few minutes after the first application (Kelly *et al.* 1997). I recorded mistletoe survivorship (0 = resprouting or 1 = non-resprouting) one year after burning (April 2009). I used GLM to evaluate the survivorship of mistletoe species one year after fire application, using fire treatment and species as factors, and the haustorium diameter as a covariate for plant size.

MISTLETOES IN THE FOREST EDGE VS. SAVANNA

At the end of April 2008, I haphazardly chose 13 points distributed 20 to 30 m from the forest edges with the aid of a map. Sampling points were as spread as possible, taken into account the access facilities (Figure 1). For each point, I randomly selected the side to be sampled and traced a transect line of 150 m x 20 m on that way, which I called the 'forest edge' transect. At the end of each edge transect, I used a compass to trace another line transect parallel to this first one, but 100 m apart, which I called the 'savanna' transect. I sampled the main host species of *Psittacanthus* spp. along these 26 line transects (13 edge *vs.* 13 savanna). For each host species I recorded: species, tree diameter at soil height (DSH), infection (0 or 1), mistletoe species, and the number of mistletoes per host.

I compared the average diameter at soil height, and the average number of host trees between savanna and forest edge using a paired t-test. Likewise, I compared the proportion of hosts infected for each mistletoe species, and pooled the data for the three host trees of *P. biternatus*. The observed 't' value was compared with a randomized distribution (expected 't') of the same data using a Monte Carlo procedure (Manly 2007) to run 1000 simulations in PopTools (Hood 2005). The number of times the estimated values were equal or larger than

the observed statistic; or equal or smaller than its symmetrical value (a two-tailed test), was used to obtain the P-values related to the null distribution. Further, because the samples were taken quite randomly, the p-values may provide a generalization of the results (Manly 2007).

SHORT-TERM POPULATION DYNAMICS OF *PSITTACANTHUS PLAGIOPHYLLUS*

In July 2007, I selected 19 sampling plots spread on the 10 km x 10 km to survey *P. plagiophyllus* on its host trees (i.e. cashew trees, *Anacardium occidentale*). Plots were selected according to their fire histories (see above) while allowing a large coverage of the sampling region: 9 with a low frequency of fires in the last ten years (≤ 5 times), and 10 with a high frequency on the same period (> 5 times). At the middle of each sampling plot, I started to select randomly 22 to 30 host trees (average = 29.4, N = 556) spread within an area of radius of 250 m from the initial point. I selected hosts using a random digit table to sort angles between 0 and 259 degrees. Therefore, I walked 50 m in the direction which was drawn and marked the nearest host tree with an aluminium tag. Hosts were georreferenced and separated from each other by at least 50 m. I conducted a new draw if points were located less than this minimum distance or more than 250 m from the central point. For each host tree, I recorded the following attributes (focal attributes): UTM coordinates, host height, height of the tallest tree within 10 m of the focal host, abundance of neighbor trees (r = 10 m), presence of neighbor infected hosts (r = 50 m), presence of mistletoe infections in the focal host, and presence of mistletoe seeds. Two observers conducted the surveys simultaneously to reduce the chance of false zeros (chapter 3). Surveys were conducted in August and November of 2007, and on the same months in 2008. I checked for the presence of recent fires while performing the surveys.

I used paired t-tests and GLMs to evaluate the response of mistletoes to fire, and the factors affecting their occurrence and colonization of host trees, respectively. Burned and

unburned sites were analyzed separately. In the burned sites, I hypothesized that fire would reduce the proportion of hosts infected between years; likewise, the proportion of hosts receiving mistletoe seeds would also decrease. For these sites, I used a one tailed paired t-test (2008 – 2007) and Monte Carlo with 1000 randomizations to obtain the p-values. I used a two-tailed hypothesis in unburned sites to test for differences between years. I used GLMs to test for effects of each focal attribute on mistletoe occurrence and colonization using host trees as sampling units, which is more meaningful in a parasite transmission sense (McCallum *et al.* 2001). I pooled the data from both years because separate analyses (one for each year) provided qualitatively similar results. Only 6 hosts (1%) died in this period, and I conducted the analysis only for the survivors. All analysis other than randomization tests were run in SYSTAT 8.0 (Wilkinson 1998).

RESULTS

MISTLETOE PREVALENCE AND INTENSITY

I searched for mistletoes on 13,274 individuals of the five tree species cited above (Table 1). Other trees parasitized by mistletoes while I was conducting the surveys were: 1) *P. biternatus* (*Myrcia obtusa*, Myrtaceae (1 record); *Miconia* sp., Melastomataceae (1 record); *Roupala brasiliensis*, Proteaceae (2 records); and *Qualea grandiflora*, Vochysiaceae (1 record); 2) *P.collum-cygni (Bowdichia virgilioides*, Fabaceae (1 record). *P. plagiophyllus*, on the other hand, was never found in other host besides of *A. occidentale*. Overall prevalence was higher for *P. plagiophyllus*, *P. collum-cygni*, and *P. biternatus*, respectively (Table 1). *Psittacanthus biternatus* was more prevalent on *P. ramiflora* than on any other host. The prevalence was not correlated among mistletoe species (Spearman rho: *P. biternatus* vs. *P. collum-cygni* = 0.21; *P. biternatus* vs. *P. plagiophyllus* = 0.38; *P. plagiophyllus* vs. *P. collum-cygni* = 0.32, N = 35, P > 0.05 for all correlations). *Psittacanthus biternatus* and *P.*

plagiophyllus occurred in 71% (25) and 60% (21) of plots, respectively, while *P. collum-cygni* occurred in 26% (9), being all highly aggregated (Figure 2). The intensity of infection differed among mistletoes species (Anova: $F_{2, 387} = 9.4$, $P < 0.001$), being higher for *P. plagiophyllus* than for any other mistletoe (Table 1). Moreover, for *P. biternatus* parasitizing different hosts, the intensity of infection was similar among *B. crassifolia*, *B. coccolobifolia* and *P. ramiflora* (Table 1, $P > 0.05$ for all correlations).

FACTORS RELATED TO MISTLETOE ABUNDANCE AND PREVALENCE

Mistletoe abundance was significantly related to the number of fires and host trees in only one of the two mistletoes (*P. plagiophyllus*: $F_{2, 32} = 17.7$, $P < 0.001$, $R^2 = 0.5$) (Table 2, Figure 3). The removal of an outlier and a point with large leverage gave qualitatively the same results, and I maintained them for analysis. The whole model was also significant for *P. plagiophyllus* prevalence ($F_{2, 32} = 9.6$, $P = 0.001$, $R^2 = 0.34$), but it was only significantly related to the number of fires, and not to the number of host trees (Table 2, Figure 3). On the other hand, abundance or prevalence of *P. biternatus* was neither significantly related to number of fires nor the number of host trees (Table 2). Results were also not significant for each host tree analyzed separately (*B. coccolobifolia*, *B. crassifolia*, and *P. ramiflora*, not shown). Finally, the occurrence of *P. collum-cygni* was neither related to the number of fires (coefficient = -0.01 (0.35 SE), $p = 0.97$) nor to the number of host trees (coefficient = 0.03 (0.02), $p=0.2$) (*P. collum-cygni*: Macfaden's $rho^2 = 0.16$, $p = 0.08$).

FIRE EXPERIMENT

Plant survivorship differed significantly among mistletoe species (Table 3). Fifth-three percent of *P. biternatus*, 38% of *P. collum-cygni*, and 29% of *P. plagiophyllus* survived at the 12th month. Both *P. collum-cygni* and *P. plagiophyllus* had, approximately, one fifth of the

probability that *P. biternatus* had to survive. Mistletoes submitted to fire treatment survived less than controls for all species (Table 3). Forty percent of *P. biternatus* individuals submitted to fire survived, 20% of *P. collum-cygni*, and only 6.67% of *P. plagiophyllus*. Furthermore, survivorship of single burned mistletoes was significantly higher for individuals with larger haustorium diameters, but not for double burned ones (Table 3). Survivorship of all mistletoes, on the other hand, was not significantly affected by haustorium diameter.

FOREST EDGE VS. SAVANNA

The host tree diameter at soil height (DSH) was, on average, very similar between forest edges and savanna transects for all hosts species but *P. ramiflora* (Figure 4a). However, the results were not significant for this species as well (after 1000 randomizations). The abundance of host trees was also similar among all hosts but *V. macrocarpa*, which had, on average, 8 individuals more per transect in forest edges than in savanna (Figure 4b). Finally, the proportion of host trees infected with *P. biternatus* and *P. collum-cygni* was significantly higher in forest edges than in savanna transects. *P. plagiophyllus*, on the other hand, was similarly infected in both habitats (Figure 5).

MISTLETOE DYNAMICS

The proportion of hosts receiving seeds in 2007 varied between 0 and 73% (average = 23.5%), while in 2008 varied between 0 and 87% (average = 30%). Fifteen and sixteen percent of the non-infected hosts received seeds in 2007 and 2008, respectively, versus 73.6% and 79% of the infected ones. The proportion of infected hosts varied between 0 and 43% in 2007 (average = 13%), and between 0 and 57% (average = 22.7%) in 2008. The proportion of hosts receiving seeds increased between 2007 and 2008, on average, 6.5% per site, while the proportion of hosts infected increased 9.2% per site. Nine sites (47%) were burned between

surveys (Figure 6). For these sites, the proportion of hosts receiving seeds increased 6%, on average, but this difference was not statistically significant (P = 0.14). Likewise, the proportion of infected hosts also increased slightly (3.6% per site), but not significant (P = 0.23). On the remaining ten non-burned sites, the proportion of hosts receiving seeds decreased 7% per site (P = 0.08), while the proportion of hosts infected increased 16% per site (P = 0.002). A comparison made between non-burned and burned sites in 2007 showed that this significant result was not an effect of a higher proportion of non-infected hosts receiving seeds in the former than in the latter (P = 0.21).

The odds ratio of the GLM model indicated that hosts with infected neighbors within 50 m from them had 4.05 times higher probabilities of receive mistletoe seeds than hosts that did not have infected neighbors. Additionally, host trees previously infected by mistletoes increased their probabilities of receiving mistletoe seeds by 13.6 times when compared to non-infected hosts. Host height, on the other hand, only slightly affected the probability of hosts receiving seeds (Table 4). The GLM model for established mistletoes indicated that the probability of mistletoe infection occurrence increased 1.57 times with increasing host heights; while the presence of infected neighbors increased the probability of mistletoe infection in 8.41 times when compared to hosts with non-infected neighbors (Table 4).

DISCUSSION

PATTERNS

VARIATION IN MISTLETOE ABUNDANCE AND PREVALENCE

I found that the distribution of all mistletoe species was highly aggregated, while most plots have very few mistletoes, a few plots harbored most of the infections. This pattern has been frequently documented for mistletoes within individual host trees or within neighborhoods of infected trees, where bird dispersers create a positive feedback in seed deposition (Aukema

2003). On the other hand, the mechanisms leading to aggregation of mistletoes at large spatial scales have been relatively less studied, and comparative studies of different mistletoe species are even rarer (e.g. Dzerefos *et al.* 2003). Mistletoes may be aggregated at larger spatial scales due to a combination of intrinsic and extrinsic processes. For example, Martinez del Rio *et al.* (1996) suggested that the distribution of the mistletoe *Tristeris aphyllus* at large spatial scales could be explained by the behavior of bird dispersers which concentrates their activities in areas of high mistletoe prevalence, creating a positive feedback on seed deposition; while Aukema (2004) suggested that *Phoradendron californicum* were aggregated at larger spatial scales in response to host distribution or to physiological intolerance to freezing at higher altitudes. In this study, I found that one of the three mistletoes was highly negatively related to fire frequency, as is common for *Arceuthobium* species in lodgepole forests in the U.S (Kipfmueller & Baker 1998); while two other species were not related to fire frequency at all. Thus, I suggest that even closely related mistletoe species may be aggregated for very different reasons, and respond to disturbance events in very different ways.

Abundance of infected, but not prevalence, was also positively related to total host abundance in *Psittacanthus plagiophyllus*. This is particularly important for mistletoes to overcome fire events, rather than to indicate successful transmission dynamics. For example, as plants, mistletoes would spread their risk of extinction (sensu Den Boer 1968) in having various hosts infected within a population; while as parasites, they should parasitize many of the hosts available (frequency-dependent transmission, Martinez del Rio *et al.* 1996), independent of how many hosts there are. The other manner to spread the risk of extinction is harboring a higher number of infections per individual up to a point that mistletoes begin to cause harm to their hosts , and therefore, the benefits of having more chance to overcome fire events may be lost because they make hosts (and themselves) more susceptible to be killed.

Thus, the large crowns of taller *A. occidentale* individuals may have a decisive role in avoiding local mistletoe extinction, by permitting the establishment of various infections on its branches.

THE ROLE OF FOREST EDGES

An intriguing component of this study was the difference in prevalence between forest edge and savanna for two of the three species studied; *P. biternatus* and *P. collum-cygni*. Mistletoes may concentrate in forest edges for various reasons. For example, Bickford *et al.* (2005b) studied the mistletoe *Arceuthobium vaginatum* growing in *Pinus* forest at the U.S. They showed that forest thinning affected mistletoe performance by altering indirectly the physiological state of their hosts. Likewise, Norton & Smith (1999) suggested that roads in the arid central Australia can exert high influence on mistletoes through facilitating water infiltration and benefiting host trees closer to them. In my study, total water and nutrient availability could be higher in forest edge than in savanna. However, the net uptake of these resources could be lower when accounting for higher competition in this habitat, as in Bickford *et al.* (2005b). Thus, tests including the various life stages of mistletoe plants and controlled experiments should be performed in forest edges and savannas to understand better this pattern.

Forest edges may also be zones with higher movement rates of birds searching for food. If birds concentrate in forest edges (Marina Anciães, pers. comm.), higher rates of mistletoe seed dispersal closer to them should be expected, or birds may just follow the distribution of mistletoes and increase seed dispersal on previously infected edges. Lamont & Southall (1982,cited in Norton & Stafford Smith 1999) suggested that the higher movement of bird dispersers along roads in Australia may be the cause of higher mistletoe prevalence in these sites when compared to an adjacent reserve. Cintra (1997) did not record *Elaenia*

cristata, one of the main bird dispersers of *Psittacanthus*, in forest edges in Amazonian savannas. However, he did record *Pitangus sulphuratus*, another potential seed disperser, and I recorded a forest species (White-tailed Cotinga, *Xypholena lamellipennis*) dispersing seeds of *P. biternatus* in forest edge. Seed dispersal and abundance of bird dispersers should be evaluated in forest edges and savannas to test this hypothesis.

Alternatively, mistletoes may have been pushed to forest edges in response to savanna fires, and forest edges are only 'pseudo-sources' for *P. biternatus* and *P. collum-cygni*. It may be that forest edges are not physiologically the best environments for mistletoe species, neither for their hosts. Regardless of the mechanism, they have few opportunities to persist in savannas due to frequent fires, and use forest edges in an opportunistic way.

PROCESSES

EFFECTS OF FIRES ON MISTLETOES

Although all mistletoe species was severely affected by experimental fire treatments, *P. biternatus* was much more likely to resprout than *P. collum* or *P. plagiophyllus*. Furthermore, mistletoe size was effective in reduce the probability of plant death in single burn treatment, but not in double burn, suggesting that intense fires may counteract the protective effect of bark thickness of larger plants. A similar study was conducted by Kelly *et al.* (1997) with *Amyema miquelii* and *A. pendula* in Australia. They found that burning was effective in killing 53% to 60% of mistletoes two years after burning, and that increasing mistletoe size also increased probability of sprouting in 1.01 times.

The probability of sprouting after fire may not only depend on plant characteristics and fire intensity, but also on post fire conditions experienced by scorched plants, such as air humidity and water availability (Whelan 1995). Furthermore, plants may be affected in different ways if presenting distinct phenologies during fires. For example, when a fire occurs

in the rainy season, as in this experiment, plants may be more likely to regenerate due to the high availability of water; while a fire occurring during the reproductive events, as here for all species, all the chances of increasing population sizes may be wasted. In this study savanna, fires generally occur in October, in the peak of the dry season, just after the fruiting period of *P. plagiophyllus* and prior to flowering in *P. biternatus* and *P. collum-cygni* (Rúbia P. F. Reis, pers. comm.). Thus, timing of fire can differentially determine the success of mistletoe species. A fire just prior to seed dispersal or during the flowering, such as to *P. biternatus* and *P. collum-cygni* during the dry season, may kill seeds before any reach the right host trees; while for *P. plagiophyllus*, a fire just after seed dispersal may only kill seeds that have passed to various other ecological filters.

Fires may not only affect mistletoes directly, but also indirectly by killing their host trees and modifying other resources such as light availability, abundance of herbivores, and abundance of bird dispersers. For example, dense vegetation may shade mistletoe seeds deposited by birds and inhibit mistletoe development due to insufficient light (Dzerefos *et al.* 2003). Therefore, fires could increase light availability by removing host leaves and the herbaceous layer that covers the white sand soil, leading to increased germination of mistletoe seeds. In fact, I conducted an experiment to test this prediction and found that seed survived 2.3 times more on burned areas than on unburned areas after three months, but both treatment and control areas burned after this. Mistletoes that survive post-fire may also be benefited by an increase in the density of bird dispersers. For example, Cintra & Sanaiotti (2005) showed that *E. cristata* nearly doubled its density in a 2000 ha area two months after fire, that would probably increase seed dispersal of fruiting individuals. In sum, controlled fire applied directly to mistletoes affected survivorship negativelly, but less intense fires may increase mistletoe establishment and dispersal in larger areas, which deserve more merit in future studies. We must also consider that the controlled conditions of fire application may

provide unrealist results, and that long-term monitoring of marked populations of mistletoes should be further considered.

SHORT-TERM POPULATION DYNAMICS OF *P. PLAGIOPHYLLUS* AND ITS RESPONSE TO FIRE

The short term response of mistletoes to fire was nicely illustrated to *P. plagiophyllus.* This species was highly negatively affected by both fire treatments in the fire experiment. Even larger individuals just slightly resisted to single or double burns. Field observations confirmed that intense fires may be locally catastrophic for this species. This occurred in site 26 in which fire reached the top of trees, killing all mistletoes of the 8 infected hosts in that site, and reducing to zero the percentage of trees receiving mistletoe seeds in the following year (Fig. 6). Therefore, when high intensity fires occur, mistletoes must recolonize from nearby unburned sites.

Unlike other epiphytes that have air-born dispersed propagules (Benzing 1990), mistletoes rely on birds to disperse their seeds. The problem is that mistletoe seed dispersal is commonly very limited to the neighborhood of infected trees, and long-distance seed dispersal events are less common (Ward & Paton 2007). Here I showed that hosts with infected neighbors within 50 m from them, had 4 times higher probabilities to receive mistletoe seeds than hosts that did not have infected neighbors. This would probably make recolonization events much slow, and sites with fire return intervals of two to three years or less may avoid the establishment of new mistletoe plants by killing their seeds. Unexpectedly, the other attribute frequently related to higher probabilities of mistletoe colonization in other studies (i.e. host height) (Martinez del Rio *et al.* 1995b,Aukema & Martinez del Rio 2002b) did not increase the probability of hosts receiving mistletoe seeds more than expected by chance alone.

When fires are less intense or patchy, flame height frequently average 1.5 m in the savannas of Alter do Chão (Sanaiotti & Magnusson 1995). Although it may kill many seeds through heating, and smoking (Shaw *et al.* 2004), previously established mistletoes may still survive. In this study, all but one fire event was of low intensity, only scorching tree crowns partially. This may explain why burned populations had little variation in the proportion of hosts infected when both years were compared. However, when burned and non-burned populations were compared, mistletoes in the former increased 4.4 times less than in the latter, even though a similar proportion of non-infected trees received seeds in both areas. This suggests that fire failed to kill mistletoes, but not recently dispersed seeds. Finally, the appearance of a positive and significant relationship between host size and the probability of being infected suggest that mistletoes could be protected from fire on taller trees, and this pattern may not be only a result of birds depositing mistletoe seeds on taller than average hosts, as previously mentioned.

Although I conducted all the analyses considering hosts as static habitats, some studies have revealed that the dynamics of hosts may also have profound impacts on epiphytes populations. For example, Snäll *et al.* (2005) showed that high rates of host destruction by fire in the past may have determined the low occupancy of the epiphytic lichen *Lobaria pulmonaria* in Finland; while longer fire return intervals would limit host regeneration due to competition with other trees. Therefore, I believe that in predicting long term maintenance of mistletoes in this Amazonian savanna, host population dynamics should also be included.

CONCLUDING REMARKS

Many plant populations may be maintained regionally through endogenous processes such as birth and death rates, and therefore, small scale dynamics determine regional distribution of

plants (Ehrlén & Eriksson 2003). However, when disturbance is an important local phenomenon and kill most or all individuals, regional maintenance of species cannot be understood without consideration of colonization and extinction processes (Quintana-Ascencio & Menges 1996); even when events of long-distance seed dispersal are rare (> 50 m in this study) (> 100 m in Cain *et al.* 2000). Furthermore, mistletoe population dynamics should not be evaluated at a unique spatial scale; while all species may have patchy dynamics in small spatial scales, they may have source-sink or true metapopulations dynamics at larger ones.

In conclusion, in this study I showed that congener mistletoes may respond differently to fire events in a Brazilian Amazonian savanna; while one species was negatively related to the frequency of fire events, two other species were not related to fire frequency at all. Furthermore, different distribution patterns of mistletoe prevalence between forest edge and savanna may indicate that some of the species have been pushed to forest edges in response to fires; or that they use the savanna only as sinks for their individuals. A fire experiment showed that some mistletoe species and larger plants were more likely to survive low intense fires (single burn treatment) and regenerate through sprouting than others; while intense fires may be locally catastrophic at least to *P. plagiophyllus*, which may depend on the proximity to other fruiting mistletoes to have higher chances to recolonize. Mistletoes may have a key role in this landscape, and very short fire return intervals caused by hunters, cattle ranchers, and traditional farmers, may preclude the reestablishment of their populations.

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TABLE 1. Average abundance (± SD), mistletoe infection prevalence, and intensity of infection (total no. of infections and mean per infected host ± SD) in 35 study plots of an isolated Amazonian savanna near Alter do Chão Pará, Brazil. *Anacardium occidentale* is parasitized by *P. plagiophyllus*; *Byrsonima crassifolia*, *B. coccolobifolia* and *Pouteria ramiflora* by *P. biternatus*; and *Vatairea macrocarpa* by *P. collum-cygni*. Intensities of infection with different superscript letters are significantly different (pairwise t-test, $P < 0.05$ after Bonferroni).

Host	**Average abundance.ha^{-1}**	**Prevalence (%)**	**Intensity of infection**
Anacardium occidentale L.	6.3 ± 3.23	167/828 (20.1)	729 (4.3 ± 7.2)[a]
Byrsonima crassifolia (L.) Kunth	51.5 ± 17	36/6849 (0.5)	168 (2.4 ± 2.9)
Byrsonima coccolobifolia Kunth	22.5 ± 10.5	70/3008 (2.3)	74 (2 ± 3.3)
Pouteria ramiflora (Mart.) Radlk.	12.1 ± 7.3	66/1531 (4.3)	206 (3.1 ± 3.4)
Byrcra + Byrcoc + Pouram	86.8 ± 28.3	172/11388 (1.5)	448 (2.6 ± 3.2)[b]
Vatairea macrocarpa (Benth.) Ducke	8.3 ± 7.9	51/1058 (4.8)	91 (1.6 ± 1.4)[b]

TABLE 2. Results of the GLM relating the abundance and prevalence of *Psittacanthus* species (*P. biternatus* and *P. plagiophyllus*) to two predictive variables (number of hosts and number of fire events) in 35 study sites in an isolated Amazonian savanna near Alter do Chão, Pará, Brazil. SE is between parentheses. A similar analysis with *P. collum-cygni* is not presented due to few data (see text). Collinearity was checked before analysis using the variance inflation factor (VIF).

	Number of hosts infected		**Proportion of hosts infected**	
Species/Variables	Coefficient	P	Coefficient	P
Psittacanthus biternatus[a]				
Number of hosts	0 (0.01)	0.9	0	0.65
Number of fire events	-1.2 (0.7)	0.09	-0.009 (0.007)	0.17
Psittacanthus plagiophyllus				
Number of hosts	0.27 (0.06)	<0.001	0.002 (0.002)	0.35
Number of fire events	-1.15 (0.39)	0.007	-0.05 (0.01)	0.001

TABLE 3. Model parameters for GLMs of mistletoe species, fire treatment, and haustorium diameter on mistletoe survivorship, one year after the experimental fire application in a savanna patch near Alter do Chão, Pará, Brazil. Values of odds ratio are interpreted as how many times a unit change in the value of a given variable increase the odds of a positive response, while the other variables are held fixed.

Source	**df**	**Estimate**	**SE**	**Z value**	**P**	**Odds ratio**
Mistletoe species						
P. biternatus	0	-	-	-	-	-
P. collum-cygni	1	-1.53	0.62	-2.47	0.01	0.22
P. plagiophyllus	1	-1.79	0.62	-2.9	0.004	0.17
Treatment						
Control	0	-	-	-	-	-
Single burn	1	-5.97	1.51	-3.95	< 0.001	0
Double burn	1	-5.26	1.47	-3.57	< 0.001	0.01
Haustorium	1	-0.05	0.16	-0.32	0.75	0.95
Control x Haustorium	0	-	-	-	-	
Single burn x Haustorium	2	0.64	0.24	2.67	0.008	1.9
Double burn x Haustorium	2	0.4	0.24	1.67	0.09	1.49

TABLE 4. Model parameters of focal attributes recorded for 560 host trees in 19 plots of savanna in Alter do Chão, Pará, Brazil. These focal attributes were hypothesized to influence the probability of focal hosts receiving mistletoe seeds or being infected by mistletoe plants.

Source	df	Estimate	SE	Z value	P	Odds ratio
Seeds						
Host height	1	0.15	0.08	1.89	0.06	1.17
Height of the tallest tree	1	-0.06	0.05	-1.1	0.27	0.94
Abundance of neighbors	1	-0.01	0.01	-0.93	0.35	0.99
Infected neighborhood	1	1.4	0.25	5.54	<0.001	4.05
Presence of infection	1	2.61	0.28	9.45	<0.001	13.6
Mistletoe infections						
Host height	1	0.45	0.08	5.66	< 0.001	1.57
Abundance of neighbors	1	0.02	0.01	1.52	0.13	1.02
Infected neighborhood	1	2.13	0.24	8.99	< 0.001	8.41

FIGURE LEGENDS

FIGURE 1. Map of the study site and detail of a sampling plot near Alter do Chão, Pará, Brazil. Areas filled with dark gray are covered with forest, and those in light gray are covered with savanna. Squares represent the 35 sampling plots in savanna. Starts represent 13 line transects on forest edges. Letter 'E' indicates the site where the fire experiment was conducted.

FIGURE 2. Distribution of abundance and prevalence of mistletoes (*Psittacanthus* spp.) in 35 sampling plots of savanna near Alter do Chão, Pará, Brazil.

FIGURE 3. Partial regression results of the relationship between the number of host trees infected by the mistletoe *Psittacanthus plagiophyllus* and the number of fire events (from 1997 to 2007), and: a) the number of hosts infected, and b) the proportion of hosts infected per plot. N = 35.

FIGURE 4. Average difference of: a) the number of individuals of each host species and b) the diameter at soil height (DSH) of host species between forest edges and paired savanna transects (N = 13). Anaocc = *Anacardium occidentale*, Byrcoc = *Byrsonima coccolobifolia*, Byrcra = *Byrsonima crassifolia*, Pouram = *Pouteria ramiflora*, Vatmac = *Vatairea macrocarpa*. * $P < 0.05$.

FIGURE 5. Average difference between the proportion of hosts infected by *Psittacanthus* spp. in forest edges and paired savanna transects. Psibit = *P. biternatus*, Psicol = *P. collum-cygni*, Psipla = *P. plagiophyllus*. * $P < 0.05$. The dotted line indicates the zero value.

FIGURE 6. Variation in the proportion of hosts receiving seeds and being infected by the mistletoe *Psittacanthus plagiophyllus* between 2007 and 2008 in 19 study sites near Alter do

Chão, Pará, Brazil. The solid line indicates the region of no net increase between years. Sites that had burned between surveys are in black, while non-burned sites are in white.

FIGURE 1.

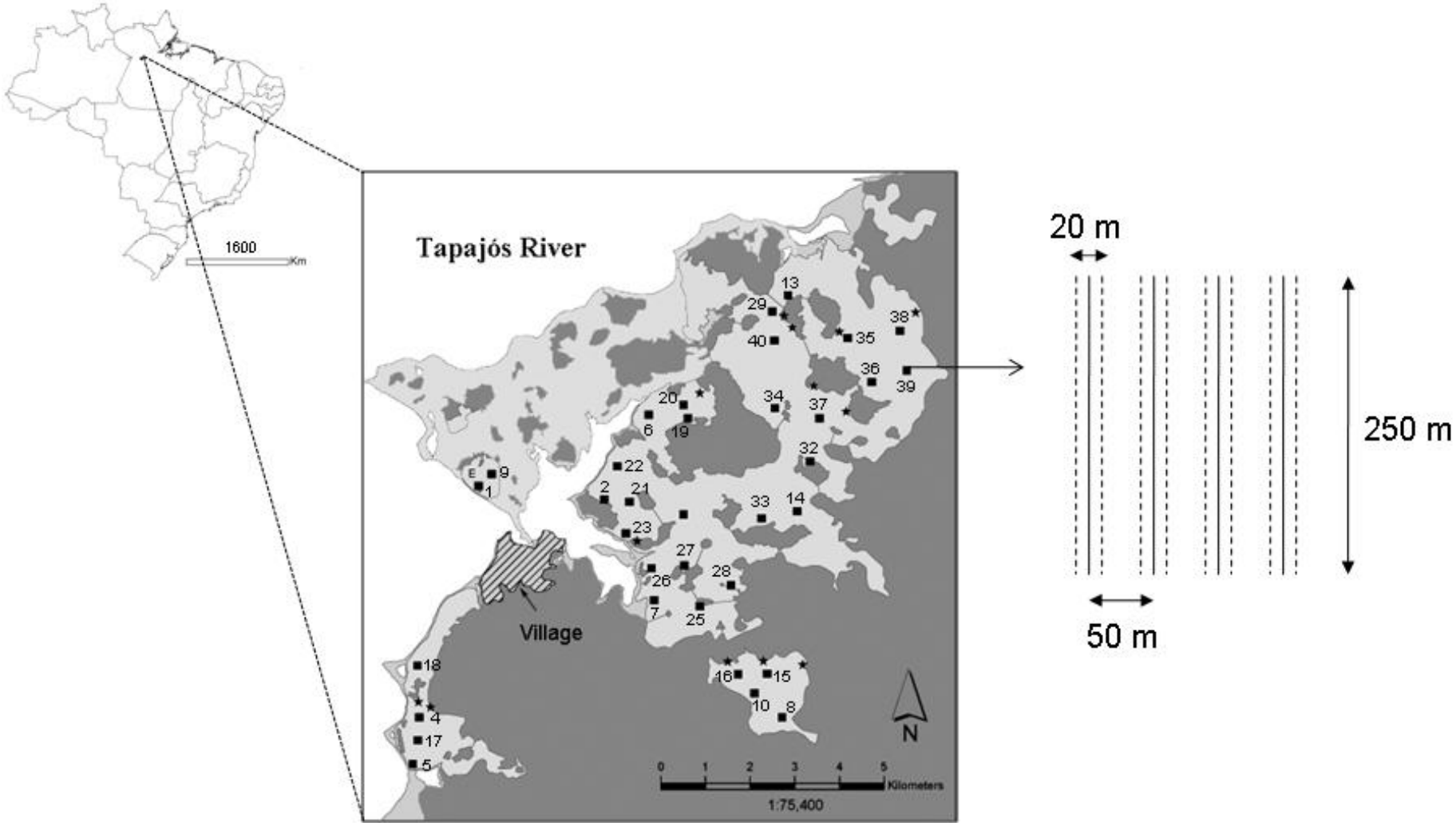

1600
Km
Tapajós River
Village
N
0 1 2 3 4 5
Kilometers
1:75,400
20 m
50 m
250 m

FIGURE 2.

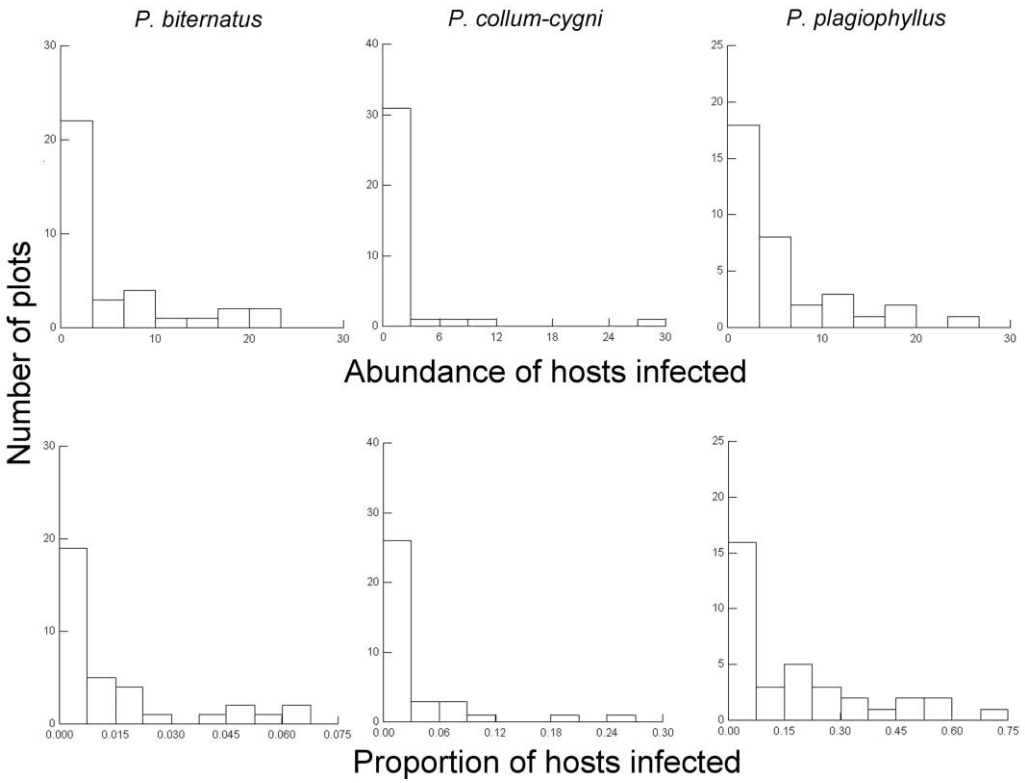

P. biternatus
P. collum-cygni
P. plagiophyllus
Number of plots
Abundance of hosts infected
Proportion of hosts infected

FIGURE 3.

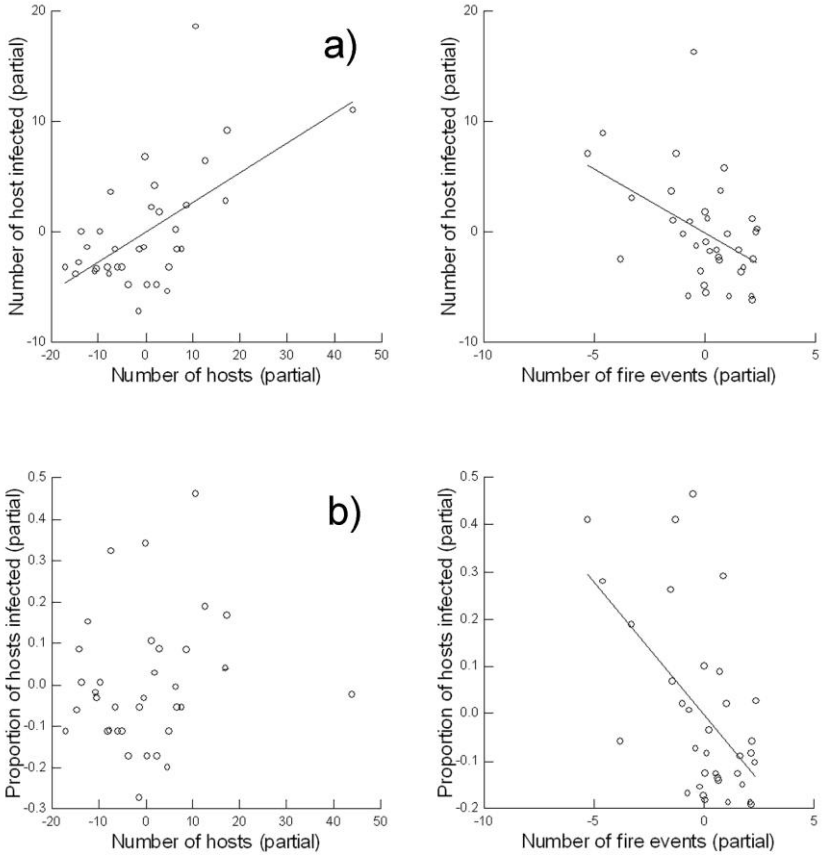

a)
Number of host infected (partial)
Number of hosts (partial)
Number of host infected (partial)
Number of fire events (partial)
b)
Proportion of hosts infected (partial)
Number of hosts (partial)
Proportion of hosts infected (partial)
Number of fire events (partial)

FIGURE 4.

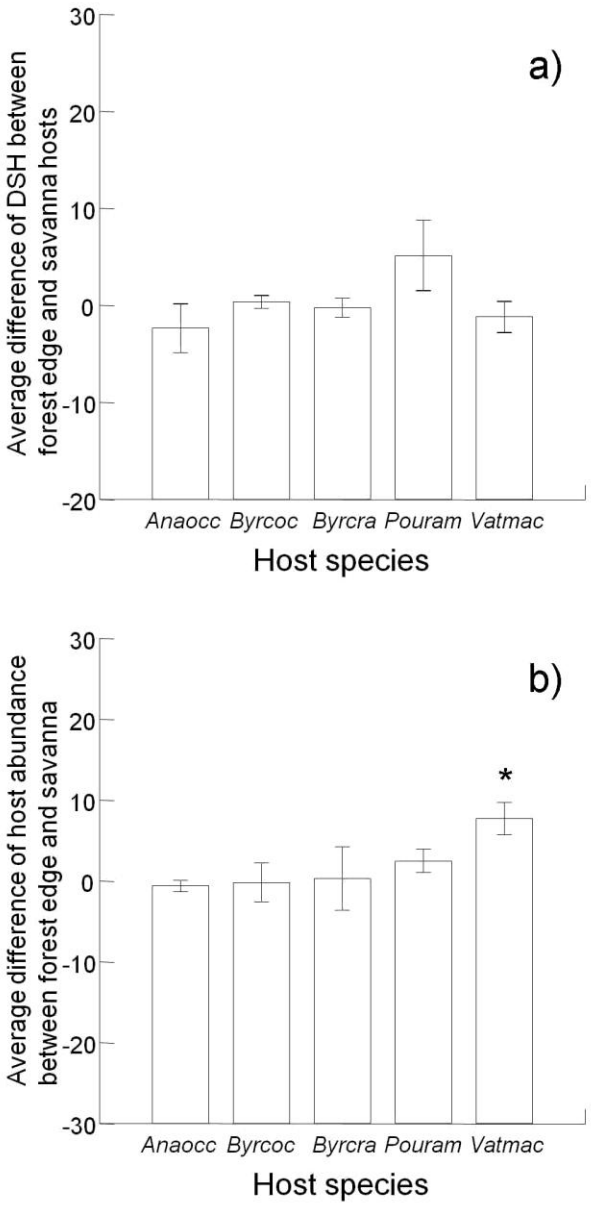

a)
Average difference of DSH between forest edge and savanna hosts
30
20
10
0
-10
-20
Anaocc Byrcoc Byrcra Pouram Vatmac
Host species
b)
Average difference of host abundance between forest edge and savanna
30
20
10
0
-10
-20
-30
*
Anaocc Byrcoc Byrcra Pouram Vatmac
Host species

FIGURE 5.

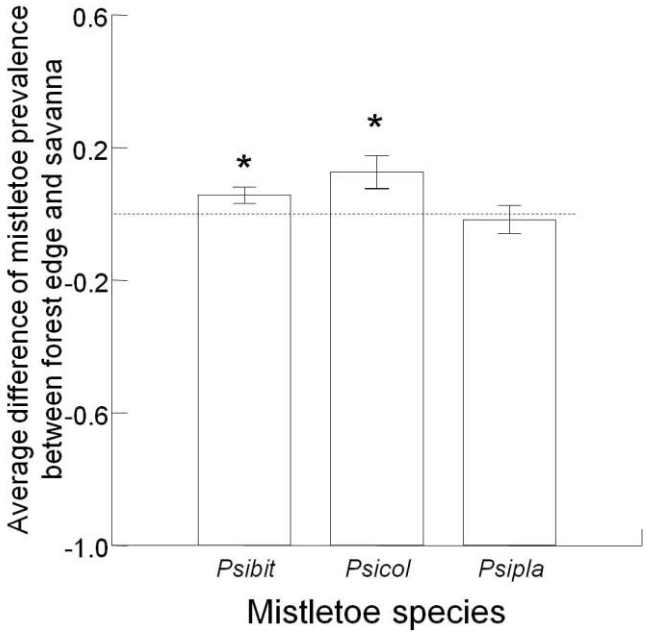
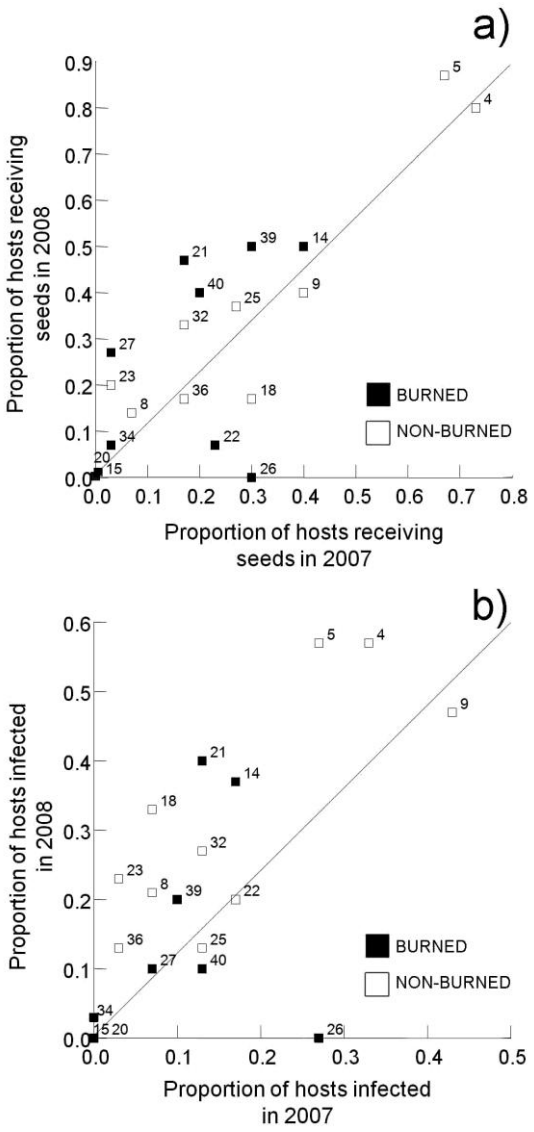

Average difference of mistletoe prevalence between forest edge and savanna
0.6
0.2
-0.2
-0.6
-1.0
*
*
Psibit
Psicol
Psipla
Mistletoe species

FIGURE 6.


a)
Proportion of hosts receiving seeds in 2008
Proportion of hosts receiving seeds in 2007
BURNED
NON-BURNED
b)
Proportion of hosts infected in 2008
Proportion of hosts infected in 2007
BURNED
NON-BURNED

CONCLUSÕES GERAIS

As espécies de *Psittacanthus* estudadas (*P. biternatus*, *P. collum-cygni*, *P. plagiophyllus*) não utilizam todos os ambientes disponíveis à ocupação nas várias escalas espaciais estudadas.

Diferente do que é encontrado em muitos estudos, em que espécies de hemiparasitas aparentadas possuem hospedeiros semelhantes e parasitam as espécies mais comuns, virtualmente não há sobreposição entre os hospedeiros utilizados por *Psittacanthus* spp. A compatibilidade pelo hospedeiro, e não a deposição de sementes diferenciada entre os possíveis hospedeiros é o processo responsável por tal diferenciação.

As espécies de ervas-de-passarinho também são agregadas dentro das espécies de hospedeiros. A deposição de sementes nos hospedeiros maiores e previamente infectados ao longo de vários anos são provavelmente dois dos processos responsáveis por este padrão em *Psittacanthus plagiophyllus*, o que deve acontecer também para as demais espécies. Outro fator que poderia colaborar para a agregação das ervas-de-passarinho, a qualidade do hospedeiro, parece não influenciar sua distribuição nos primeiros estádios de desenvolvimento.

No ínterim entre os estudos de pequena (capítulos 1 e 2) e larga escala (capítulo 4), mostrou-se que amostragens repetidas aos mesmos hospedeiros podem aumentar a detecção das sementes das ervas-de-passarinho em estudos de presença e ausência, o que é comum quando estudamos organismos em larga escala espacial. Existe também um potencial para amostragens repetidas aos mesmos hospedeiros de ervas-de-passarinho já estabelecidas, técnica que poderia ser estendida para epífitas em geral.

Em larga escala espacial, as espécies de *Psittacanthus* estão agregadas em poucos sítios amostrados. Para *P. plagiophyllus*, espécie sensível ao fogo, a agregação parecer ser influenciada pela frequência de queimadas nos últimos dez anos. Para as outras duas espécies (*P. biternatus* e *P. collum-cygni*), apesar do fogo afeta-las diretamente causando sua morte, não houve relação com a frequência de queimadas, o que pode estar relacionado com algum mecanismo que aumenta a prevalência destas espécies nas bordas de floresta ao invés da savana.

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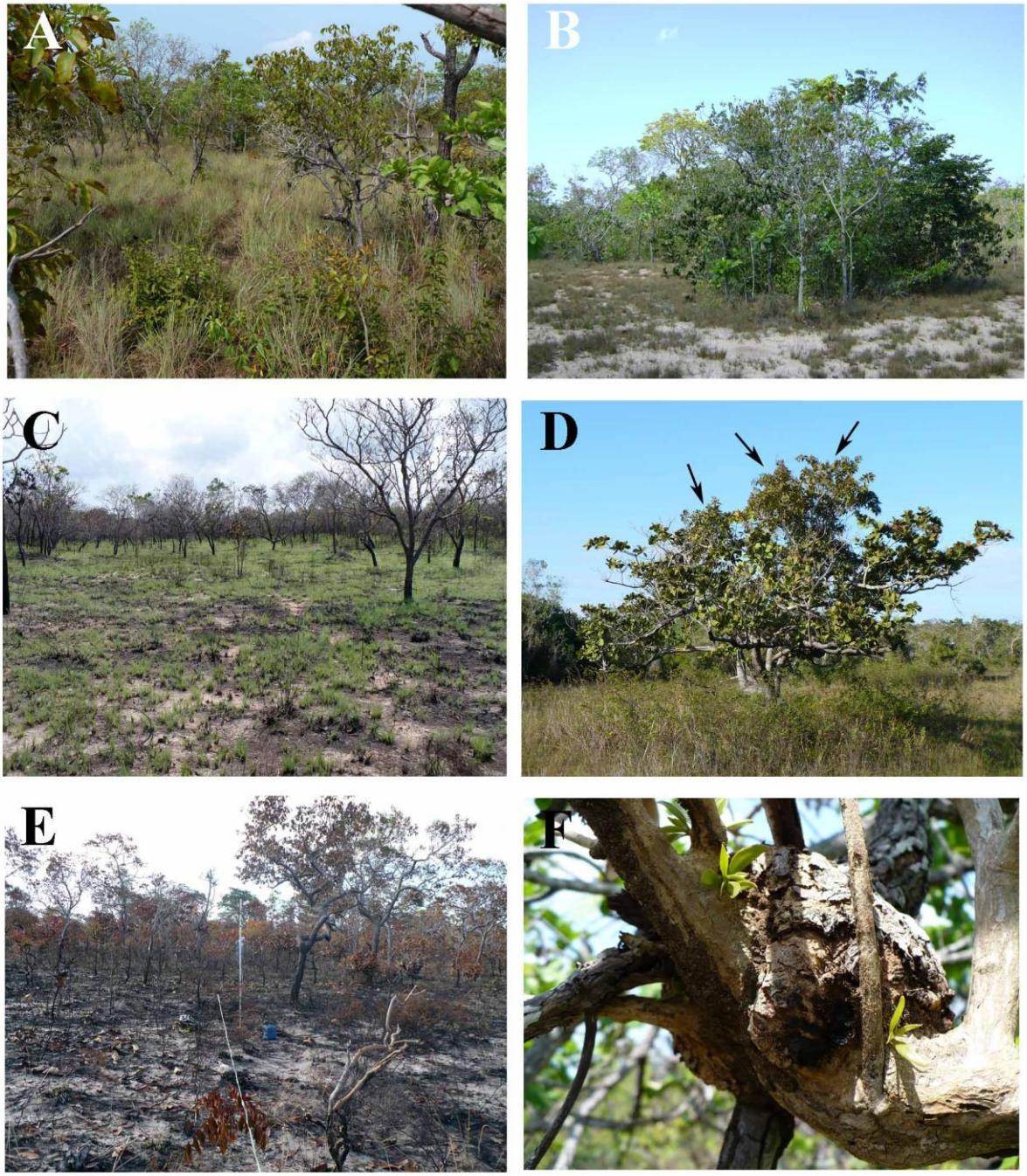
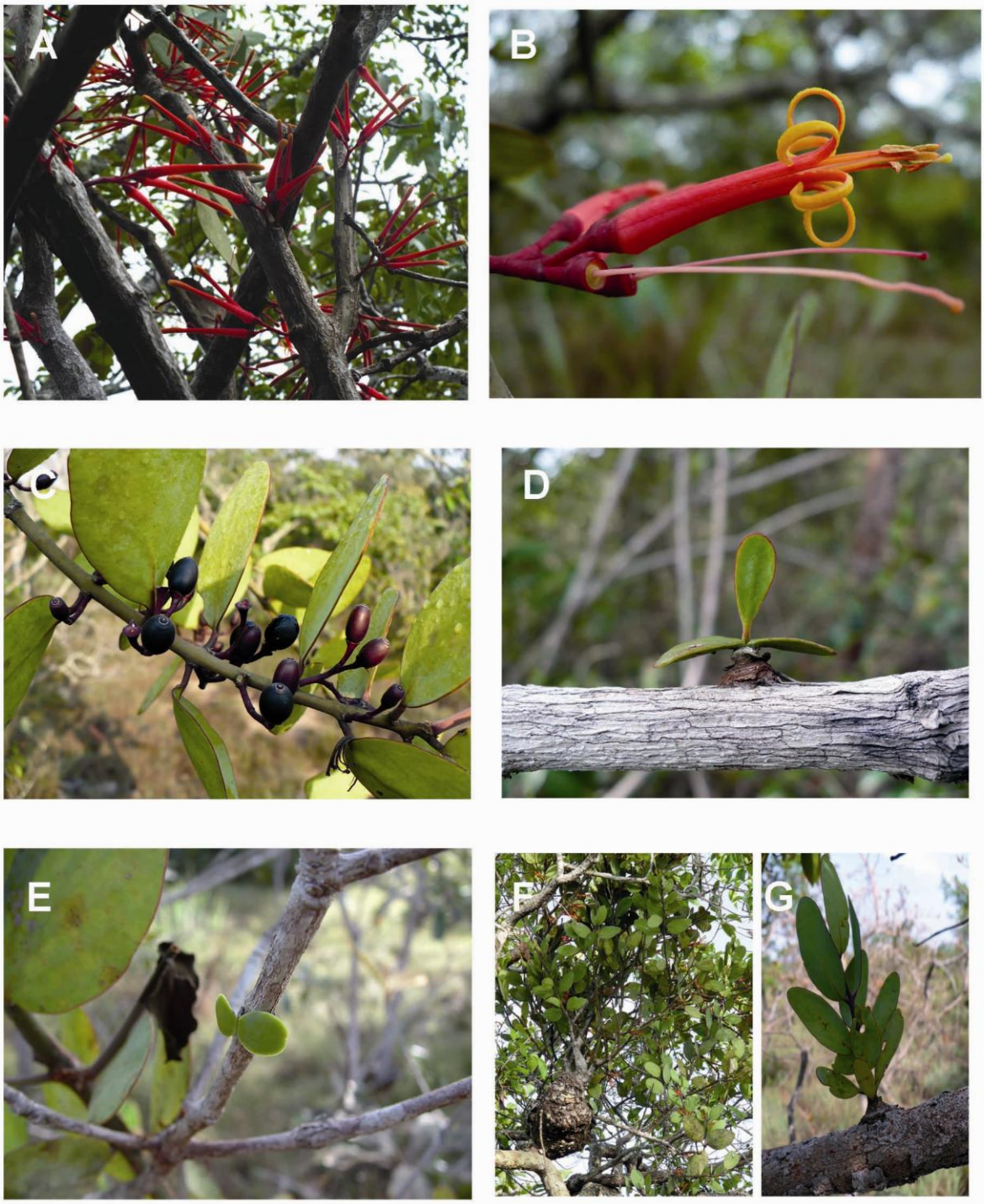
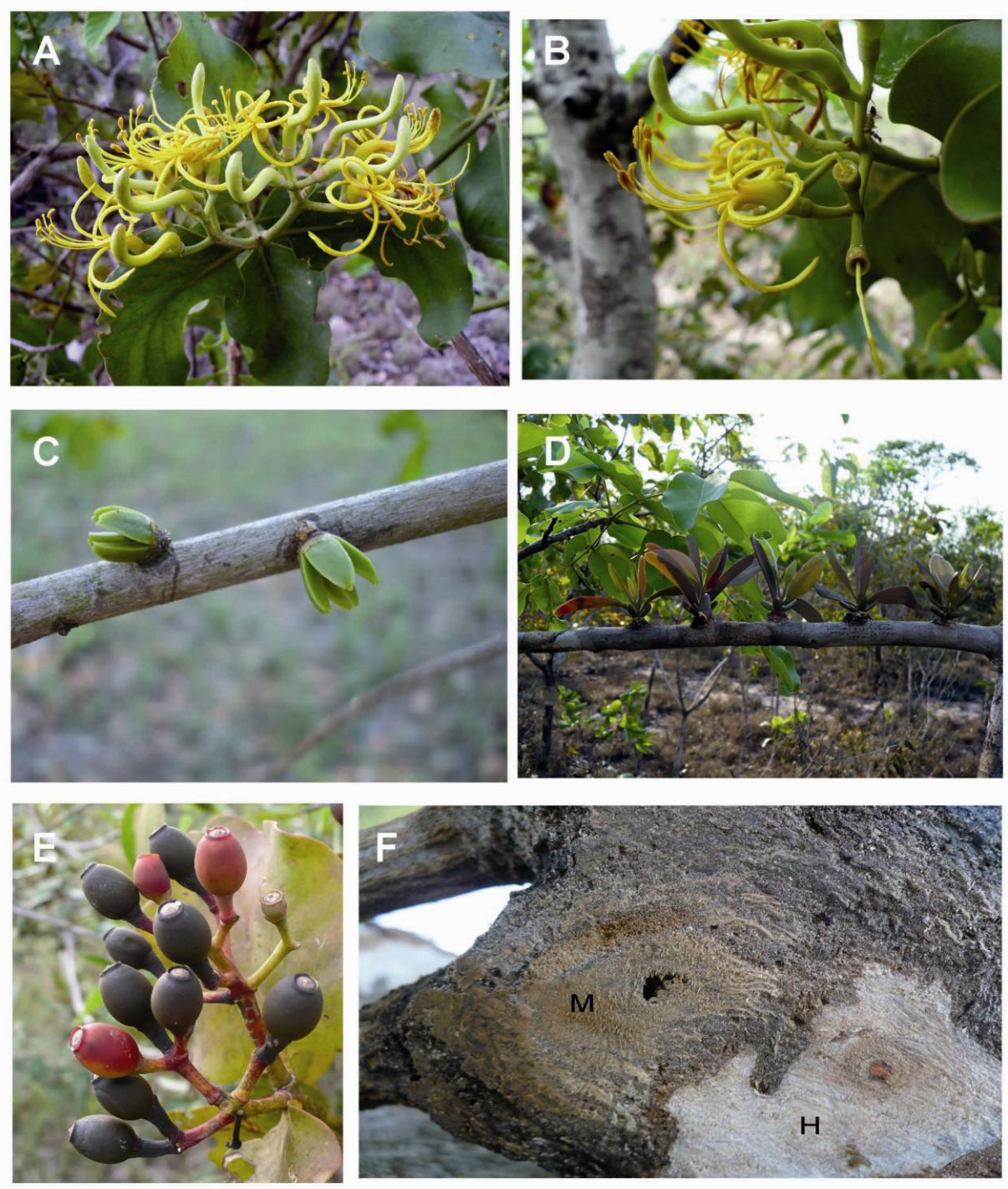
ANEXO A – Pranchas ilustrativas da área de estudo e das espécies estudadas nesta tese.



A)Unburned savanna; B) Shrubby and arboreal vegetation forming patches. Common to savanna plot stu died in chapter 2. C) Burned savanna, a few weeks after burning. D) Infected cashew tree (arrows). E) Recently burned savanna. F) Haustorium resprouting (*P. plagiophyllus*).



Psitacanthus biternatus: A) flowers; B) flower in close-up; C) fruits; D) established seedling; E) germinated seed; F) adult individual; G) sapling.



Psittacanthus collum-cygni: A) Inflorescence; B) flower in close-up; C) germinated seedlings; D) hand inoculated established seedlings; E) fruits; F) haustorium section.

Psittacanthus plagiophyllus: A) Inflorescence; B)left to right: *P. plagiophyllus*, *P. biternatus*, *P. collum-cygni*; C) infrutescence; D) seed attached to a branch; E) established seedling; F) seed showing viscin; G) bird nest on a mistletoe plant.

APÊNDICE 1 - Cópias da ficha de avaliação da aula de qualificação, da parte escrita e da defesa oral da tese de doutorado.

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INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): RODRIGO FERREIRA FADINI
Curso: ECOLOGIA
Nível: Doutorado
Orientador(a): RENATO CINTRA (INPA)

Título:

"ECOLOGIA DA INTERAÇÃO ENTRE A ERVA DE PASSARINHO *Psittacanthus robustus* E SEU HOSPEDEIRO *Anacardium occidentale* NA SAVANA AMAZÔNICA DE ALTER DO CHÃO, PA"

BANCA JULGADORA:

TITULARES:

GONÇALO FERRAZ (INPA/PDBFF)
MÁRIO COHN-HAFT (INPA)
THIAGO JUNQUEIRA IZZO (INPA)
ROGÉRIO GRIBEL (INPA)
WILSON R. SPIRONELLO (INPA)

SUPLENTES:

EDUARDO M. VENTICINQUE (INPA)
WILLIAM E. MAGNUSSON (INPA)

EXAMINADORES	PARECER	ASSINATURA
GONÇALO FERRAZ	(X) Aprovado ( ) Reprovado	
MÁRIO COHN-HAFT	(X) Aprovado ( ) Reprovado	
THIAGO JUNQUEIRA IZZO	(X) Aprovado ( ) Reprovado	
ROGÉRIO GRIBEL	( ) Aprovado ( ) Reprovado	
WILSON R. SPIRONELLO	(X) Aprovado ( ) Reprovado	
EDUARDO M. VENTICINQUE	( ) Aprovado ( ) Reprovado	
WILLIAM E. MAGNUSSON	( ) Aprovado ( ) Reprovado	

Flávia Costa

Manaus(AM), 20 de janeiro de 2006

OBS: A banca sugere que o aluno melhore seu embasamento teórico com mais leitura, para que possa definir uma questão geral e unificadora de seu trabalho. Além disso, faltaram conhecimentos específicos sobre o sistema de estudo, que deverão ser obtidos.

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Referee evaluation sheet for PhD thesis

Title: **Host specificity, abundance, and prevalence of mistletoes (Psittacanthus – Loranthaceae) in a fire-prone Brazilian Amazonian savanna**

Candidate: **RODRIGO FERREIRA FADINI**

Supervisor: **Renato Cintra** Co-supervisor: -----

Examiner: DAVID M WATSON

Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.

	Excellent	Satisfactory	Needs improvement	Not acceptable
Relevance of the study	( )	( )	(X)	( )
Literature review	( )	( )	(X)	( )
Sampling design	( )	( )	(X)	( )
Methods/procedures	( )	( )	(X)	( )
Results	( )	( )	( )	(X)
Discussion/conclusions	( )	( )	( )	(X)
Writing style and composition	( )	( )	(X)	( )
Potential for publication in peer reviewed journals	( )	( )	(X)	( )

FINAL EVALUATION

( ) Approved without changes

( ) Approved with changes (no need for re-evaluation by this reviewer)

(**X**) Potentially acceptable, conditional upon review of a corrected version (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)

( ) Not acceptable (This product is incompatible with the minimum requirements for this academic level)

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Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to Rosirene Farias da Silva rosirenefs@gmail.com and Claudia Keller claudiakeller23@gmail.com or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.

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Instituto Nacional de Pesquisas da Amazônia - INPA
Graduate Program in Ecology

Avaliação de tese de doutorado

Título: **Especificidade por hospedeiro, prevalência e abundância de ervas-de-passarinho (*Psittacanthus* – Loranthaceae) em uma savana amazônica afetada por queimadas**

Aluno: **RODRIGO FERREIRA FADINI**

Orientador: **Renato Cintra**

Avaliador:

Por favor, marque a alternativa que considerar mais apropriada para cada ítem abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(x)	( )	( )	( )
Revisão bibliográfica	(x)	( )	( )	( )
Desenho amostral/experimental	(x)	( )	( )	( )
Metodologia	(x)	( )	( )	( )
Resultados	(x)	( )	( )	( )
Discussão e conclusões	(x)	( )	( )	( )
Formatação e estilo texto	( )	(x)	( )	( )
Potencial para publicação em periódico(s) indexado(s)	( )	(x)	(x)	( )

PARECER FINAL

( ) **Aprovada**

(x) **Aprovada com correções** (indica que as modificações mesmo extensas podem ser incluídas a juízo do orientador)

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Kleber Del Claro

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail a Rosirene Farias da Silva rosirenefs@gmail.com e Claudia Keller claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

Endereço para envio de correspondência:

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Referee evaluation sheet for PhD thesis

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Candidate: **RODRIGO FERREIRA FADINI**

Supervisor: **Renato Cintra** Co-supervisor: -----

Examiner: **LORENA LOPEZ DE BUEN**

Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.

	Excellent	Satisfactory	Needs improvement	Not acceptable
Relevance of the study	(x)	( )	( )	( )
Literature review	( )	( )	(x)	( )
Sampling design	( )	(x)	( )	( )
Methods/procedures	( )	(x)	( )	( )
Results	( )	(x)	( )	( )
Discussion/conclusions	( )	(x)	( )	( )
Writing style and composition	(x)	( )	( )	( )
Potential for publication in peer reviewed journal(s)	(x)	( )	( )	( )

FINAL EVALUATION

( ) Approved without changes

(x) Approved with changes (no need for re-evaluation by this reviewer)

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( ) Not acceptable (This product is incompatible with the minimum requirements for this academic level)

VERACRUZ, VERACRUZ 28 AGOSTO 2009

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Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to Rosirene Farias da Silva rosirenefs@gmail.com and Claudia Keller claudiakeller23@gmail.com or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.

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Avaliação de tese de doutorado

Título: **Especificidade por hospedeiro, prevalência e abundância de ervas-de-passarinho (*Psittacanthus* – Loranthaceae) em uma savana amazônica afetada por queimadas**

Aluno: **RODRIGO FERREIRA FADINI**

Orientador: **Renato Cintra**

Avaliador: **Marco Aurélio Pizo**

Por favor, marque a alternativa que considerar mais apropriada para cada ítem abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(X)	( )	( )	( )
Revisão bibliográfica	( )	(X)	( )	( )
Desenho amostral/experimental	(X)	( )	( )	( )
Metodologia	(X)	( )	( )	( )
Resultados	(X)	( )	( )	( )
Discussão e conclusões	(X)	( )	( )	( )
Formatação e estilo texto	(X)	( )	( )	( )
Potencial para publicação em periódico(s) indexado(s)	(X)	( )	( )	( )

PARECER FINAL

(X) **Aprovada**

( ) **Aprovada com correções** (indica que as modificações mesmo extensas podem ser incluídas a juízo do orientador)

( ) **Necessita revisão** (indica que há necessidade de uma reformulação do trabalho e que o revisor quer avaliar a nova versão do trabalho antes de emitir uma decisão final)

( ) **Reprovada** (indica que o trabalho não tem o nível de qualidade adequado para uma tese)

Marco A. Pizo

Rio Claro - SP — Local
10 de setembro de 2009 — Data
Assinatura

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail a Rosirene Farias da Silva rosirenefs@gmail.com e Claudia Keller claudiakeller23@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

Endereço para envio de correspondência:

Claudia Keller
DCEC/CPEC/INPA
CP 478
69011-970 Manaus AM
Brazil

Instituto Nacional de Pesquisas da Amazônia - INPA
Graduate Program in Ecology

Avaliação de tese de doutorado

Título: **Especificidade por hospedeiro, prevalência e abundância de ervas-de-passarinho (*Psittacanthus* – Loranthaceae) em uma savana amazônica afetada por queimadas**

Aluno: **RODRIGO FERREIRA FADINI**

Orientador: **Renato Cintra**

Avaliador:

Por favor, marque a alternativa que considerar mais apropriada para cada ítem abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	( )	(x)	( )	( )
Revisão bibliográfica	(x)	( )	( )	( )
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Metodologia	(x)	( )	( )	( )
Resultados	(x)	( )	( )	( )
Discussão e conclusões	(x)	( )	( )	( )
Formatação e estilo texto	( )	(x)	( )	( )
Potencial para publicação em periódico(s) indexado(s)	(x)	( )	( )	( )

PARECER FINAL

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( ) **Reprovada** (indica que o trabalho não tem o nível de qualidade adequado para uma tese)

Manaus, 05 de outubro de 2009

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INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

Ministério da Ciência e Tecnologia

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ATA DA DEFESA PÚBLICA DA TESE DE DOUTORADO DE DISCENTE DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

Aos 12 dias do mês de janeiro do ano de 2010, às 09:00 horas, na sala de aula do Programa de Pós-Graduação em Ecologia - PPG-ECO/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: **Dra. Flávia Regina Capellotto Costa**, do Instituto Nacional de Pesquisas da Amazônia, Profa. **Dra. Marina Anciães**, do Instituto Nacional de Pesquisas da Amazônia, **Dr. Antônio Carlos Webber**, da Universidade Federal do Amazonas, tendo como suplentes o Dr. Eduardo Martins Venticinque, da Universidade Federal do Amazonas, e o Dr. Michael John Gilbert Hopkins, do Instituto Nacional de Pesquisas da Amazônia, sob a presidência da primeira, afim de proceder a arguição pública da **TESE DE DOUTORADO** de **RODRIGO FERREIRA FADINI**, intitulada "Especificidade por hospedeiro, abundância e prevalência de ervas-de-passarinho (Psittacanthus – Loranthaceae) em uma savana amazônica afetada por queimadas".

Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☒ APROVADA ☐ REPROVADA

☒ POR UNANIMIDADE ☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Dr(a). Flávia Regina Capellotto Costa _____

Dr(a). Marina Anciães _____

Dr(a). Antonio Carlos Webber _____

Coordenação do PPG-ECO/INPA
CLAUDIA KELLER
Coordenadora do Curso de Pós-graduação em Ecologia-INPA
Portaria

Beatriz Ronchi Teles
Coordenadora de Capacitação - COCP
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