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Reaching the canopy on the ground: incidence of infection and host-use by mistletoes (Loranthaceae and Viscaceae) on trees felled for timber in Amazonian rainforests

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Abstract There is a profound absence of knowledge of infestation prevalence and host-use by mistletoes of mature South American tropical rainforests. In this study, we fill this gap using information gathered from felled trees at a logging concession area in Amazonian Brazil. We sampled individuals of 18 tree species, which occurred in two forest physiognomies; open forest with canopy interrupted by palm trees and closed, denser forest, with emergent trees. We hypothesized that infection incidence would be higher in open than in closed forest, irrespective of the mistletoe species involved. In addition, we expected that mistletoe parasitism would be higher on host species that were more abundant, taller, deciduous, and had less dense wood. We sampled 870 individual trees in both sites combined. All but one host species was infected by at least one species of mistletoe. We found 13 mistletoe species/morphospecies, Loranthaceae (7) and Viscaceae (6), parasitizing very different hosts. Mistletoe infection incidence was higher in the closed forest (10.3%) than in the open forest (5.4%). In the closed forest, host height influenced incidence positively, while deciduousness had a negative influence. Our results show that mistletoes are common in the canopy of pristine tropical forests and, contrary to expectations, that infection incidence was higher in the closed forest. The positive relation between infection incidence and host height in this forest type suggests that emergent trees have higher chances of being infected than individuals of correspondent species in the lower forest layers.

Keywords Hemiparasite · Host–parasite interaction · Mistletoe assembly · Reduced Impact Logging

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Introduction

Until the early 1980s, the tropical rainforest canopy was little studied by biologists and ecologists. This has changed radically in the last 35 years (Lowman and

Rinker 2004; Nadkarni et al. 2011), with the development of methods and techniques that allowed various degrees of canopy access (including dirigibles, platforms, and cranes), the use of simple, but effective, technologies, such as the use of insecticidal fogging to collect invertebrates (Adis et al. 1998), and the widespread use of rope-based climbing techniques (Lowman 2004). However, even after such qualitative and quantitative progress, groups of organisms of great importance in canopy ecology are still poorly studied. This is the case with mistletoes, aerial hemiparastic plants of the order Santalales, with some 1600 species worldwide (Nickrent 2011).

Mistletoes differ from other canopy-dwelling plants, such as bromeliads and orchids, in that they actively parasitize the tree on which they grow. They remove water, minerals and, in some cases, photoassimilates from hosts, causing damage when in overabundance (Ehleringer et al. 1985). The effect of this parasitism is to reduce growth and accumulated biomass of the host, which may result in host death (Reid et al. 1994). Despite this, mistletoes are considered key species in forest and woodlands worldwide because they provide food and shelter for many animal species (Watson 2001), as well as a depository of leaf-litter nutrients for the entire ecosystem (March and Watson 2010).

As much as there has been a long tradition of mistletoe studies in the temperate forests, woodlands, desert, semi-desert, and tropical savannas (Watson 2001), there has also been a history of regret concerning the lack of knowledge of the diversity, infection incidence, and structure of mistletoe–host interactions in the mature tropical rainforests (Watson 2004). Epiphytes and vines, for example, are much better studied than mistletoes (Benzing 1990; Lowman and Wittman 1996). In Brazil, where there are about 200 mistletoe species (Arruda et al. 2012), ecological studies are still limited and highly concentrated in open vegetation types (Arruda et al. 2006; Fadini and Lima 2012; Scalon et al. 2013; Teodoro et al. 2013). There is not a single study that documented host-use nor the proportion of trees infected by mistletoes (incidence of infection) in Brazilian rainforests, and this lack of information is widespread in mature tropical rainforests in general (Hawksworth 1983). Given the importance of these forests for carbon sequestration (Pan et al. 2011), and the role of mistletoes as tree-debilitating parasites (Mathiasen et al. 2008), understanding how host characteristics and ecological factors determine host-use and mistletoe infection incidence on host trees, could help predict the wide-scale consequences of mistletoe parasitism on tree growth and survivorship.

Despite the fact the tropical forests appear homogenous when looked at from above, variation in soil characteristics and drainage, climate, and various others ecological and evolutionary determinants shape their floristics, structure (biomass), and physiognomy (Castilho et al. 2006; Stropp et al. 2009). Although mistletoes are generally considered to be less affected than their hosts by variations in physical characteristics of the environment (Ehleringer and Marshall 1995), canopy structure (which affects light exposure) could be an important ecological determinant of mistletoes abundance and incidence at local and regional scales. Because mistletoes require full light for germination, establishment, and reproduction (Scharpf 1972), forest physiognomies with open canopies should provide them with more suitable conditions. Additionally, at the host scale, several characteristics such as abundance, height, wood density, and deciduousness could influence host-use by mistletoes (Dzerefos et al. 2003; Roxburgh and Nicolson 2005). Therefore, identifying how forest conditions and host characteristics interact to determine infection incidence and host-use by mistletoes is also key for predicting their occurrence, as well as planning their management and conservation in both pristine and managed tropical rainforests.

Sampling mistletoe infections from the ground is not easy because plants can be overlooked, even on small trees (Fadini and Cintra 2015). Yet, in mature tropical rainforests, trees can reach 60 m in height, which makes canopy visualization so much more difficult, that censuses are likely to be unproductive (or at least very inaccurate). Rope-based tree-climbing techniques can help, but the sampling scale is very limited given the logistical difficulties, and although detecting mistletoes with airborne imaging spectroscopy and LiDAR has been done (Barbosa et al. 2016), it is not yet possible to identify species with this method. Therefore, alternative methods are required to access the canopy and quantify parasitism by different mistletoe species.

In the Amazon, Reduced Impact Logging (RIL) is the extraction mode of choice in National Forests and therefore, has the potential to affect the more than 50 million hectares of land (Veríssimo et al. 2002). This management system offers an unprecedented opportunity to study mistletoes and other aspects of canopy ecology, by providing a representative number of tree canopies that can be accessed on the ground. Here, we studied mistletoes on felled trees in forests being exploited under the RIL system. Although we did not access the arboreal community in its entirety, we were able to assess the main differences in interactions between mistletoe and their hosts in two distinct forest types, one with an open canopy and another with a dense canopy, and consider the effects of abundance, height, density of wood, and deciduousness of hosts. Our questions were (1) what is the incidence of mistletoe infection for each host species and for the host community in general? (2) Is the incidence of infection higher in open forest than in dense forest? (3) Is the overall incidence of infection (regardless of mistletoe species) higher for those host species that are more abundant, have lower density wood, and are deciduous? And, (4) to what degree are the mistletoes host-specialized?

Methods

Study site and host species sampled

The study was conducted at two sampling sites near Km 67 and Km 83 of the BR-163 (Santarém–Cuiabá) highway, both located in the Tapajós National Forest (Flona Tapajós). Each of the areas are explored under an RIL system being conducted by the Flona Tapajós Joint Cooperative (Coomflona), located and operating between 2° 45′–4° 10′S and 54° 45′–55° 30′W, in the municipality of Belterra, Pará state, Amazonian Brazil. The reduced impact forest management system is so-named because it extracts on average 10–14 m^3/ha (about 3–4 trees/ha: compared to 30–40 m^3/ha for conventional logging), precisely determines the direction of harvested tree fall, and plans log-dragging trails to minimize collateral impact (Sabogal et al. 2000).

The Flona Tapajós comprises 527,319 ha of lowland rainforest with a variety of vegetation types (Espírito-Santo et al. 2005). The climate is *Ami*, according to the Köppen system. Average annual rainfall is around 1820 mm, with the rainiest months occurring from January to May. Average air temperature is 25 °C and relative humidity averages 90%. Deep soils with low cation exchange capacity predominate.

Espírito-Santo et al. (2005) characterized the Km 67 region as dense tropical forest with emergent trees on high plateau sedimentary areas and open rainforest with palms elsewhere. The area around Km 83 was characterized as dense tropical forest with emergent trees on high plateau sedimentary areas. At the Km 67 site, we conducted our study in the open rainforest with palms (called ‘open forest’ in this study), while at Km 83, we studied the dense tropical forest with emergent trees (called ‘dense forest’ from hereon). The species richness of trees in each area is around 200 species (Espírito-Santo et al. 2005).

The two study areas are each some 1000 ha in extent. We collected the data at the dense forest site in 2012, and at the open forest site in 2013. Both studies were conducted between August and December: the time when timber trees are harvested. The species authorized for harvest in the dense forest in 2012 were *Apuleia molaris* Spruce ex Benth., *Astronium lecointei* Ducke, *Couratari stellata* A. C. Smith, *Diplotropis purpurea* (Rich.) Amshoff, *Erisma uncinatum* Warm., *Handroanthus serratifolius* (Vahl) S.O. Grose, *Hymenaea courbaril* L., *Hymenaea parvifolia* Huber, *Hymenolobium petraeum* Ducke, *Lecythis lurida* (Miers) S.A. Mori, *Lecythis pisonis* Cambess., *Manilkara huberi* (Ducke) Chevalier, *Mezilaurus itauba* (Meisn.) Taub. ex Mez, *Parkia multijuga* Benth., *Pseudopiptadenia suaveolens* (Miq.) J.W. Grimes, *Sextonia rubra* (Mez) van der Werff, *Stryphnodendron pulcherrimum* L., *Trattinnickia burserifolia* Mart., and *Vochysia maxima* Ducke. In the open forest, the only species not authorized for harvest in 2013 was *S. rubra*. We sampled all selected species in both years. When an identification was in doubt, we sent herbarium exsicates to a botanical expert who, when necessary, changed the name(s) previously listed in the inventory conducted by Coomflona parabotanists.

Field work

The study searched the canopy of cut trees for mistletoes 1 day after tree harvesting. The delay was a safety measure, to reduce the danger from falling branches still attached to standing trees. We selected host individuals for sampling by analyzing the extraction-plan map, so preventing over-concentration on a small number of host species, as well as to increase the spatial variation of the sampling area.

For each tree inspected, we recorded: total height (measured with a 50 m tape measure); geographical coordinates (using a GPS); tree species; and the presence/absence of mistletoe. We collected specimens of each mistletoe species found and made herbarium exsicates for subsequent identification. Fertile specimens in good condition were incorporated into the herbarium of the National Institute for Amazon Research (INPA), Manaus. In addition to the data collected in the field, we obtained information on the degree of deciduousness (evergreen and deciduous) of host species, by consulting information in Lorenzi (2009, 2014a, b). For those species where such information was lacking, we used knowledge available from experienced parabotanists.

Wood density data for each host species were obtained from the supplementary material in Chave et al. (2006). These stemwood-derived density data were used to refer to the density of wood of the finer branches (to which mistletoes, in fact, adhere), because studies indicate a positive and significant correlation between these two measures (Swenson and Enquist 2008). To obtain the abundance of host species, we used forest inventory data (where trees above 35 cm of DBH were inventoried), kindly provided by Coomflona.

Statistical analyzes

All descriptive data are presented as mean ± standard deviation. To analyze incidence, we grouped all mistletoe species due to the small number of individuals infected by each species in each area. Species were separated only to describe the interactions between an individual mistletoe species and their host(s). We compared the proportion of infected individuals between sites using a paired t test. To analyze the effect of deciduousness ($0 =$ perennial, $1 =$ deciduous or semi-deciduous) on the proportion of infected individuals, we used a generalized linear model (GLM), with binomial error distribution, and several covariates (sample size, average height, and density of wood). In the case of overdispersion, we correct the standard errors using a quasipoisson GLM (Zuur et al. 2009). We conducted a separate analysis for each study area because the characteristics of species involved (i.e., abundance, height, and sample size) varied between the two sampling sites. Initially, we made models including all predictor variables, but remove the less important variables until a suitable minimal model was achieved (Crawley 2007). We used the software R (R Development Core Team 2012) for all analyzes.

Results

Description of the characteristics of tree communities

We sampled a total of 870 trees: 483 in 2012 in the dense forest and 387 in 2013 in the open forest. We removed *Ocotea* sp. from the analysis because it was not possible to verify whether all the individuals belonged to the same species, and *Handroanthus serratifolius* because there were only four sampled individuals in the two study areas. There was a strong positive correlation between the abundance of each species and the proportion of individuals sampled in each area (dense forest: $r = 0.86$, $P < 0.001$; open forest: $r = 0.64$, $P = 0.004$), showing that the effort was proportional to abundance. There was also a strong positive correlation between the abundance of species in the two study areas ($r = 0.77$, $P < 0.001$), showing that a species common in one area also occurred frequently in the other.

The least abundant tree species in the dense forest was *S. pulcherrimum*, and the most abundant was *L. lurida*. In the open forest, the least abundant species was *D. purpurea*, while the most abundant was *C. stellata* (Table 1). Individual trees were on average 1.8 m lower in height in dense forest than in open forest (paired t test: $t = -2.35$, $P = 0.03$). There was a significant difference in height of the hosts in both the dense ($F = 6.34$, $P < 0.001$) and open forest ($F = 12.02$, $P < 0.001$). In both cases, *H. courbaril* was the tallest species. The species with the densest wood was *M. huberi*, while *P. multijuga* wood had the lowest density (Table 1). Half of the 18 species were perennial with the other half consisting of deciduous or semi-deciduous species.

Incidence of infection

In the two areas studied, we found 71 individual trees infected with mistletoes, 10.3% in the dense forest (50 individuals), and 5.4% in the open forest (21 individuals) (Fig. S1). There was a significant difference in

Table 1 Abundance, percentage of sampled individuals, height, percentage of infected, density, and deciduousness for the host species sampled in dense and open forest in the Tapajós National Forest, Pará, Brazil

Host family	Host species	Tree abundance		# Individuals sampled		Height ± SD (m)		Infected (%)		Wood density (g/cm^3)	Deciduousness
		Dense	Open	Dense	Open	Dense	Open	Dense	Open		
Anacardiaceae	*A.lecointei*	910	208	51	19	42.3 ± 4.6	40.7 ± 3.7	3 (5.9)	1 (5.3)	0.77	1
Burseraceae	*T.burserifolia*	137	160	11	11	35.7 ± 3.2	36.8 ± 3.1	1 (9.1)	0	0.46	1
Fabaceae	*H. petraeum*	170	114	11	6	38.5 ± 7.3	41.8 ± 5.5	1 (9.1)	0	0.75	1
Fabaceae	*P. suaveolens*	893	1111	17	17	38.7 ± 5	40.2 ± 4.0	4 (23.5)	1 (5.9)	0.68	0
Fabaceae	*S. pulcherrimum*	109	235	5	5	36 ± 7.1	38 ± 1.6	0	1 (20)	0.47	1
Fabaceae	*P. multijuga*	277	319	15	5	35.8 ± 3.9	39 ± 3.8	8 (53.3)	3 (60)	0.39	0
Fabaceae	*A. moralis*	171	164	9	9	41.3 ± 4.1	43.3 ± 3.1	0	1 (11.1)	0.73	1
Fabaceae	*H. courbaril*	529	523	30	31	45.8 ± 2.3	45.5 ± 4.1	8 (26.7)	3 (9.7)	0.77	1
Fabaceae	*H. parvifolia*	321	361	19	19	37.8 ± 2.7	40 ± 2.7	1 (5.3)	1 (5.3)	0.88	1
Fabaceae	*D. purpurea*	118	75	5	5	36 ± 5.7	40.8 ± 5.8	1 (20)	0	0.76	0
Lauraceae	*M. itauba*	390	317	19	19	35.7 ± 7.4	37 ± 5.6	1 (5.3)	0	0.74	0
Lauraceae	*S. rubra*	1121	–	31	–	33.6 ± 3.4	–	1 (3.2)	–	0.55	0
Lecythidaceae	*L. lurida*	3302	2002	71	71	34.3 ± 4	35.5 ± 3.9	2 (2.8)	4 (5.6)	0.86	0
Lecythidaceae	*L. pisonis*	447	347	7	7	37 ± 4.8	34.1 ± 3.9	0	0	0.86	1
Lecythidaceae	*C. stellata*	1917	2280	47	48	41.6 ± 4.1	43.3 ± 5.3	3 (6.4)	1 (2.1)	0.63	1
Sapotaceae	*M. huberi*	2948	581	70	62	36.6 ± 4.2	39.3 ± 4.1	4 (5.7)	0	0.93	0
Vochysiaceae	*V. maxima*	339	209	39	27	41.4 ± 4.2	41.3 ± 4.8	9 (23.1)	4 (14.8)	0.49	0
Vochysiaceae	*E. uncinatum*	602	1684	26	26	37.2 ± 5.7	36 ± 5.1	3 (11.5)	1 (3.8)	0.51	0

the incidence of infection between the two areas (paired t test: $t = 3.40$, $P = 0.007$) (Fig. 1), with dense forest having a higher proportion of infected hosts. Of the 18 analyzed species, only *L. pisonis* was never found infected. Host species with the largest number of infected individuals (both sites combined) were *V. maxima* (13), *H. courbaril* (11), and *P. multijuga* (11) (Table 1). Of these, the species with the highest infection incidence (both sites combined) were *P. multijuga* (55%, 11/20) and *V. maxima* (19.7%, 13/66) (Table 1). For the dense forest, the species with the highest infection incidence were *P. multijuga* (53.3%) and *H. courbaril* (26.7%) (Table 2). For the open forest, *P. multijuga* had the highest infection incidence (60%), followed by *S. pulcherrimum* (20%) and *V. maxima* (14.8%) (Table 3). Finally, although we did not measure infection severity on many trees because of logistical and security problems, we note that infections caused by viscaceous mistletoes were much more numerous than that caused by loranthaceous, reaching 40–60 infections per host in some mistletoe/host combinations (e.g., *P. obtusissimum* on *P. multijuga* and *P. racemosum* on *P. suaveolens*). This corresponds to 25–50% of crown covered by infections..

Effect of host characteristics on the incidence of infection

For dense forest, our models suggest that the average height of host species and degree of deciduousness influence, respectively, positively and negatively the incidence of mistletoe infection. We made two models, the first with, and the second without, *P. multijuga*—which was an outlier in our first model. After removal of this species, the results had not changed, but model fit improved significantly (Table 4). The negative effect of deciduousness on the prevalence of infection was unexpected. The other host variables did not influence the prevalence of infection in this forest type. For open forest, wood density had a negative effect on infection incidence. However, this effect was caused by a single high leverage point represented by *P. multijuga*. When we removed this point, none of the variables significantly influenced the prevalence of infection (data not shown).

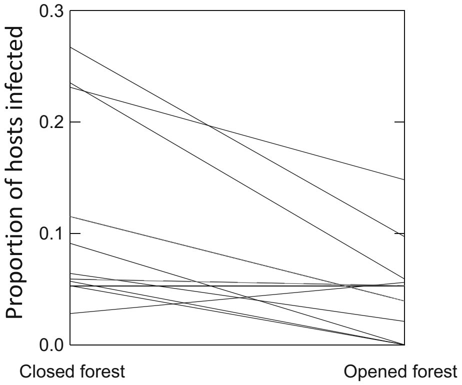

Fig. 1 Proportion of infected hosts in the dense forest (tropical forest dense emerging trees) and open forest (open tropical forest with pams), Belterra municipality, Pará state, Brazil. *Lines* connect the same host species on both sites

Mistletoe species

One of the authors (C. S. Caires) identified 11 of the 13 found morphospecies to specific level. Difficulties with precise identification for some specimens lay in their being of sterile material. These specimens were morphotyped. We found the following species and morphospecies for Loranthaceae: *Oryctanthus alveolatus* (Kunth) Kuijt, *Oryctanthus florulentus* (Rich.) Tiegh, *Passovia* sp., *Passovia pedunculata* (Jacq.) Kuijt, *Psittacanthus carnosus* Kuijt, *Psittacanthus eucalyptifolius* (Kunth) G. Don., *Struthanthus phillyreoides* (Kunth) Blume, and *Passovia/Struthanthus* group. For the Viscaceae, we found the following species: *Dendrophthora warmingii* (Eichler) Kuijt, *Phoradendron mucronatum* (DC.) Krug & Urb., *Phoradendron obtusissimum* (Miq.) Eichler, *Phoradendron racemosum* (Aubl.) Krug & Urb., *Phoradendron inaequidentatum* Rusby, and *Phoradendron* sp.

Passovia and *Struthanthus* were the genera most commonly found in dense forest and together infected eight species of trees (Table 2). In the open forest, *Passovia* was also the most opportunistic genus, infecting four species (Table 3). At both study sites, the species *D. warmingii (*Eichler) Kuijt and *P. obtusissimum* parasitized only *V. maxima* and *P. multijuga*, respectively (Tables 2, 3). On average, each loranthaceous mistletoe parasitized three times more host species than did viscaceous ones (3.37 ± 1.5 vs. 1.1 ± 0.31). The identity of parasitized host species was very different for the two families (Tables 2, 3; Fig. S2), with only the Viscaceae parasitizing Fabaceae and Vochysiaceae. In

Table 2 Number of infected individuals, number of samples and species identity of mistletoe species, and host in the dense forest (tropical dense forest with emergent trees)

Host species	Mistletoe species								
	Denwar	*Oryalv*	*Pas/Str*	*Phomuc*	*Phoobt*	*Phorac*	*Psieuc*	*Psicar*	*Struphy*
Hympet	0	1/11	0	0	0	0	0	0	0
Trabur	0	0	1/11	0	0	0	0	0	0
Vocmax	8/39	0	1/39	0	0	0	0	0	0
Strpul	0	0	0	0	0	0	0	0	0
Psesua	0	0	0	1/17	0	1/17	0	0	2/17
Parmul	0	0	0	0	8/15	0	0	0	0
Apumor	0	0	0	0	0	0	0	0	0
Mezita	0	1/19	0	0	0	0	0	0	0
Leclur	0	0	1/71	0	0	0	0	0	1/71
Hymcou	0	0	0	0	0	0	0	8/30	0
Hympar	0	0	0	0	0	0	0	1/19	0
Sexrub	0	0	0	0	0	0	0	1/31	0
Manhub	0	0	3/70	0	0	0	0	0	1/70
Astlec	0	0	2/51	0	0	0	1/51	0	0
Eriunc	0	2/26	0	0	0	0	0	1/26	0
Lecpis	0	0	0	0	0	0	0	0	0
Dippur	0	0	1/5	0	0	0	0	0	0
Couste	0	0	0	0	0	0	0	0	3/47

Denwar, D. warmingii; Oryalv, O. alveolatus; Pas/Str, Passovia/Struthanthus; Phomuc, P. mucronatum; Phoobt, P. obtusissimum; Phorac, P. racemosum; Psieuc, P. eucalyptifolius; Psicar, P. carnosus; Struphy, S. phillyreoides; Hympet, H. petraeum; Trabur, T. burserifolia; Vocmax, V. maxima; Strpul, S. pulcherrimum; Psesua, P. suaveolens; Parmul, P. multijuga; Apumor, A. moralis; Mezita, M. itauba; Leclur, L. lurida; Hymcou, H. courbaril; Hympar, H. parvifolia; Sexrub, S. rubra; Manhub, M. huberi; Astlec, A. lecointei; Eriunc, E. uncinatum; Lecpis, L. pisonis; Dippur, D. purpurea; Couste, C. stellata

addition, about half of the species occurred in both areas, with viscaceous mistletoes occurring on the same host species in both areas (except *Phoradendron racemosum*). This pattern was not observed for Loranthaceae, suggesting that representatives of the first family have more specific relationships with their hosts (regardless of the context and physiognomy) than the second.

Discussion

This study is the first conducted in rainforest where it has been possible to determine the incidence of infestation and the patterns of host-use for mistletoes in assemblages of tall mature trees of commercial value, or of any mature South American tropical forest in general. Prior to this, a number of studies had been conducted in arid or semi-arid scrublands (Aukema and Martínez del Rio 2002), savannas (Dzerefos et al. 2003), temperate forests and woodlands (Daugherty and Mathiasen 2003), tropical forests with low floristic diversity (Rist et al. 2011), or forest fragments (de Buen et al. 2002). In the current study, access to the canopy of trees felled during a low-impact logging operation, enabled sampling effort on a scale never before achieved in the rainforest (870 trees, 18 host species, and covering an area of some 15 km^2), allowing us to make estimates of (1) the diversity of parasitized commercial species (almost 100% of the species), (2) the diversity of species of mistletoes in a tropical rainforest canopy (at least 11 species), (3) the prevalence of infection (8.1% of trees infected), (4) the differences in infection incidence depending on host species, the species of mistletoes, and the physiognomy of vegetation, (5) the determinants of infestation, and (6) the host usage patterns to several species of loranthaceous and viscaceous mistletoes.

Table 3 Number of infected individuals, number of samples and species identity of mistletoe species, and host in the dense forest (open tropical forest with palms)

Host species	Mistletoe species										
	Denwar	*Oryalv*	*Oryflo*	*Pas* sp.	*Pasped*	*Pas/Str*	*Phorac*	*Phoina*	*Phomuc*	*Phoobt*	*Pho* sp.
Hympet	0	0	0	0	0	0	0	0	0	0	0
Trabur	0	0	0	0	0	0	0	0	0	0	0
Vocmax	3/27	1/27	0	0	0	0	0	0	0	0	1/27
Strpul	0	0	0	0	0	0	1/5	0	0	0	0
Psesua	0	0	0	0	0	0	0	0	1/17	0	0
Parmul	0	0	0	0	0	0	0	0	0	3/5	0
Apumor	0	0	0	0	0	0	0	0	0	0	0
Hanser	0	0	0	0	0	0	0	0	0	0	0
Mezita	0	0	0	0	0	0	0	0	0	0	0
Leclur	0	1/71	0	3/71	0	0	0	0	0	0	0
Hymcou	0	0	0	1/31	0	1/31	0	1/31	0	0	0
Hympar	0	1/19	0	0	0	0	0	0	0	0	0
Manhub	0	0	0	0	0	0	0	0	0	0	0
Astlec	0	0	0	0	1/19	0	0	0	0	0	0
Eriunc	0	0	0	0	0	0	0	1/26	0	0	0
Lecpis	0	0	0	0	0	0	0	0	0	0	0
Dippur	0	0	0	0	0	0	0	0	0	0	0
Couste	0	0	0	0	1/48	0	0	0	0	0	0

Host names in Table 1

Denwar, D. warmingii; Oryalv, O. alveolatus; Oryflo, O. florulentus; Pas sp., *Passovia* sp.; *Pasped, P. pedunculata; Pas/Str, Passovia/Struthanthus; Phorac, P. racemosum; Phoina, P. inaequidentatum; Phomuc, P. mucronatum; Phoobt, P. obtusissimum, Pho* sp., *Phoradendron* sp.

Regardless of the type of vegetation evaluated, the vast majority of studies assessing infection incidence and host-use by mistletoes are species specific, for the hosts, the mistletoes, or both (Blick et al. 2013). For natural forest environments, in particular, information on the patterns of infection at the community level is even scarcer and, when available, has come from locales that are more accessible, and/or where observation is easier, such as tracks, roads, open fields, or forest edges (Genini et al. 2012). Many species of mistletoes increase in abundance and prevalence on the edges of forest fragments (de Buen et al. 2002), in the vicinity of roads (Norton and Smith 1999), or on isolated trees (Norton and Reid 1997). The consequence of sampling being conditional on ease of access and observation is that the patterns of abundance and prevalence of infection in general may be overestimated, while the diversity of species of mistletoes may be underestimated. Because our study was conducted in a tree community that was mature, and normally lacked access, it is also the first to offer an attempt to determine how common parasitism by mistletoes is in intact tropical rainforests. We show that, with the exception of one species, all studied trees were infected by at least one species of mistletoe. Our sample of hosts, although concentrated on commercial species, suggests that mistletoes are ubiquitous in the rainforest canopy and that they can occur on species of several botanical families with different ecological characteristics.

Patterns of infestation

Mistletoes, as a group of heliophyte species that transpire much more than their hosts (Luttge et al. 1998), should favor more open places, such as forest edges and clearings (de Buen et al. 2002), as well as forests with more open canopies, where there is less

Table 4 Results of two generalized linear models (maximum and minimum adequate ones) showing the effects of several covariates on mistletoe infection prevalence in the dense forest (tropical dense forest with emergent trees)

Model	Model term	Maximum model			Minimum adequate model		
		Coeff.	*p*	Odds ratio	Coeff.	*p*	Odds ratio
With *Parkia*	Intercept	−8.97	**0.01**	–	−9.37	**0.003**	–
	Sample size	−0.03	0.13	–	−0.03	**0.017**	0.97
	Abundance	0.0004	0.49	–	–	–	–
	Host height	0.24	**0.01**	1.28	0.22	**0.004**	1.25
	Wood density	−2.05	0.23	–	–	–	–
	Deciduousness	−1.35	**0.03**	0.25	−1.54	**0.005**	0.21
Without *Parkia*	Intercept	−1.26	**0.0001**	–	−11.6	**<0.001**	–
	Sample size	−0.002	0.07	–	−0.02	**0.01**	0.98
	Abundance	0.0002	0.53	–	–	–	–
	Host height	0.29	**0.0002**	1.34	0.27	**<0.001**	1.3
	Wood density	0.098	0.93	–	–	–	–
	Deciduousness	−1.56	**0.001**	0.21	−1.43	**<0.001**	2.37

Significant results (<0.05) are showed in bold

overlap of individual canopies. Therefore, when comparing the prevalence of infection among forests with different vegetation types, with host species controlled for, we expected infection to be higher in the more open forest. However, we found exactly the opposite. On a smaller scale, but also in relation to the availability of light, deciduous or semi-deciduous hosts were parasitized less than perennial hosts in the dense forest, again contradicting our predictions. In one hand, this could indicate that light is less important than other features in the forest canopy in determining parasitism by mistletoes; that birds, in this second case, avoid perching on deciduous trees because of a higher chance of predation or even that mistletoes in a deciduous crown would be more likely to be eaten. On the other hand, the positive relationship between host height and the overall incidence of infection in the densest forest casts doubt on our first conclusion.

A relation between host height to mistletoe infection has been shown in several population-level studies (Aukema and Martinez del Rio 2002; de Buen et al. 2002), and here we show this occurs for the mistletoe assemblage as a whole. A high incidence of light is crucial for successful germination, establishment, and growth of mistletoes (Norton et al. 1997), so greater infestation prevalence on species of trees that are taller than average may be because these offer better conditions for the development of these plants. In the open forest, although the canopy is more discontinuous, with the interior probably receiving a higher incidence of light, the vertical canopy profile is more homogeneous, with “depressions” being formed in areas where palms predominate. With this in consideration, it is likely that the size of the tree is not relevant in determining which hosts are more infected in this forest type, since the canopies of all trees would be subject to similar lighting conditions. Additionally, it is likely that differential infection of the tallest trees is linked not only to the greater availability of light, but also to the behavior of seed dispersers. Mistletoes are largely bird-dispersed species and studies show that seed dispersers prefer perching and foraging on higher host plants than average, which makes it more likely that such trees will receive mistletoe seeds and so become infected (Medel et al. 2004; Roxburgh and Nicolson 2005). In any case, the presence of emergent trees may be the key to explaining the higher levels of mistletoe infestation in the sampled dense forest. In consequence, we would expect a higher prevalence and more extensive level of infestation in Amazonian forest types with emergent trees.

We found no relationship between wood density and the prevalence of infection. Mistletoe does not penetrate wood, but wood density affects mistletoes negatively, reducing its proliferation (Kuijt 1969; Dzerefos et al. 2003). Dzerefos et al. (2003) showed that the proportion of infected hosts was negatively correlated with the density of wood in an African savanna, so our result may be an artifact of our combining species in the overall analysis. *Parkia multijuga* and *V. maxima* were species with low density wood and were highly infested by mistletoes, but with a highly specific relationship with representatives of the Viscaceae. While in most species infestations are restricted to smaller diameter branches (Sargent 1995), these two also had infestations on the main trunk and on very thick branches (ca. 20 cm), suggesting that the species' softer wood could be responsible for this unusual pattern of penetration. The species with the highest wood density, *H. courbaril*, also had a high proportion of infected individuals, mainly by *P. carnosus*. Meanwhile, *Passovia* and *Struthanthus* genera infected hosts of different densities of wood. Thus, it is possible that different mistletoes adopt different penetration strategies on the host according to the degree of host defense and haustorial penetration capability, with viscaceous species parasitizing mainly host species with light wood (*P. suaveolens, V. maxima*, and *P. multijuga*), while loranthaceous ones parasitize a variety of species irrespective of their wood density. Other subtleties may have lost in our combined dataset.

Mistletoe-host specificity

Parasitic plants are considered to be generalists when they demonstrate no clear pattern of host preference (Kartoolinejad et al. 2007). Areas with high species richness tend to have more generalist species (Kavanagh and Burns 2012). In our study, members of the genera *Passovia* and *Struthanthus* tended to be more generalist. This result is in agreement with the idea proposed by Norton and Carpenter (1998) that loranthaceous mistletoes show low host specificity in tropical forests (i.e., in New Guinea) because the greater species richness, combined with a greater evenness in the relative abundance of hosts, and low frequency of individuals of each species, reduces the opportunities for species–species specialization. However, in the current study, the genus *Phoradendron* and the species *Dendrophthora warmingii* (both Viscaceae) were quite species specific, a result similar to that found by Genini et al. (2012). The high degree of specialization among Viscaceae compared to Loranthaceae may be due to closer relationship between dispersers and mistletoes in the former than in the latter (Restrepo et al. 2002). In areas with lower host species richness, specialization is favored because of elevated frequency of encounters of mistletoe seeds with the most common hosts, thus the relative abundance of hosts is the key to specialization (Norton and Carpenter 1998; Roxburgh and Nicolson 2005). Our study was conducted in rainforest with high diversity of host species, and species-specialist mistletoes were not associated with the most abundant species, a result similar to that observed by Blick et al. (2013), using data for all known mistletoe–host interactions in the literature. Therefore, the results of the current study contradicts the main idea of Norton and Carpenter (1998), at least for some mistletoe species. The role of the relative host abundance in determining host specificity on tropical rainforest mistletoes have been assumed as true for almost two decades, simply because of lack of information to confront this hypothesis. Now, we have the opportunity to move this on.

A final note on the conservation of mistletoes

Timber extraction can provide increased light, water, and nutrients to the remaining trees (de Buen et al. 2002) and thus, can have a positive effect on mistletoe growth and development. A study conducted by Queijeiro-Bolaños et al. (2011) revealed that the proportion of hosts infected by *Arceuthobium vaginatum* (Viscaceae) increased post-logging due to the higher incidence of light resulting from the timber extraction. Similarly, Bickford et al. (2005) found that the thinning of *Pinus ponderosa* stands stimulated the growth of *A. vaginatum* subsp. *cryptopodum* due to increasing water and nutrient uptake by the hosts resulting from reduced post-thinning competition between them.

According to Bickford et al. (2005), the changes in the capture of host tree resources that follow human activities such as logging have positive effects on parasitic plants, and these can extend or spread throughout the ecosystem. However, such effects may also be negative. In the Amazon, the overexploitation of host trees may result in local extinction of mistletoes species with restricted distributions and/or are dependent on one or a few host species. In our study, we collected a species with restricted distribution, *P. carnosus,* previously known only from a collection made in 1989 in the state of Rondonia, more than 1000 km away. Locally, the species occurred on four host species, but 70% of infected individuals were of the species *H. courbaril*, whose wood is favored for the production of fine furniture, making it one of the ten most exploited trees in the Amazon. While the restricted distribution maybe an artifact of collection (Hopkins 2007), it remains the case that high host-specificity predisposes to a greater chance of local extinction if the most important hosts are preferentially harvested.

Mistletoes may represent key resources for pollinators and seed dispersing birds, as well as for several families of mammals, during periods of food shortage. Therefore, their removal can cause ripple effects across various webs of ecological interaction (Watson 2001). In addition, processes that fragment and degrade forests may disrupt the mutualisms that exist between mistletoes and their seed dispersers, with severe consequences not only for recruitment but also for mistletoe demography (Rodríguez-Cabal et al. 2007). Further research is required the better to understand and measure the consequences, in the short- and medium-term, that forest harvesting activities have on mistletoes and their interactions with their hosts and mutualists.

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