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Host specificity and experimental assessment of the early establishment of the mistletoe *Phoradendron crassifolium* (Pohl ex DC.) Eichler (Santalaceae) in a fragment of Atlantic Forest in southeast Brazil

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ABSTRACT

Mistletoe establishment relies heavily on a seed reaching a proper host plant. Small frugivorous birds usually disperse large numbers of mistletoe seeds. However, in the field, mistletoes are absent from some potential available hosts. We investigated whether the mistletoe *Phoradendron crassifolium* has some preferences for specific host trees in a fragment of Atlantic Forest in southeast Brazil. We surveyed 397 tree individuals of 50 species within 25 families. Seven of those species (14%) bore *P. crassifolium* infections. Although prevalence at the individual level was low (11.6%), there were marked deviations in infection levels among species and families. Most (87%) of the infections (40 of 46) occurred in species belonging to the families Anacardiaceae (*Lithraea molleoides* and *Tapirira guianensis*) and Siparunaceae (*Siparuna guianensis*), which nevertheless accounted for only 26% of the potential individual hosts (103 of 397). We also performed an experiment simulating bird behavior. We inoculated 480 mistletoe seeds to the bark of four potential hosts in field, following the fate of the seeds for five months. No differences in host preference were observed. The low specificity detected at the local level was confirmed by a survey of exsiccata collected over the geographical distribution of the mistletoe, suggesting that *P. crassifolium* prevalence is more dependent on dispersal limitation than on mistletoe-host compatibility.

Key words: host compatibility, prevalence, seed dispersal, seed predation

Introduction

Mistletoes are parasitic plants that belong to the order Santalales, which comprises 12 families, of which 10 occur in Brazil: Aptandraceae, Coulaceae, Erythropalaceae, Loranthaceae, Olacaceae, Opiliaceae, Santalaceae, Schoepfiaceae, Strombosiaceae and Ximeniaceae (Arruda *et al.* 2012; Stevens 2012). These plants grow on twigs and branches of host plants (usually trees) using a specialized system of roots, called haustoria, that penetrate into the vascular tissue of the host and extract essential minerals and water (Kuijt 2003). Mistletoes may alter host growth, reproduction and physiology, decreasing its fitness (Mourão *et al.* 2009; Bell & Adams 2011). Thin twigs (< 1 cm in diameter) often die when infected by mistletoes (Sargent 1995), as can highly infected hosts (Teodoro *et al.* 2013).

The successful establishment of a mistletoe on a host depends on a sequence of stages, from seed dispersal (usually by birds) to seed adhesion to the host bark, survival to seed predators, germination, growth of haustoria and development (Reid 1989). Failure at any of these stages reduces the chances for these parasitic plants to complete their life cycles. Many host traits, such as bark thickness, rugosity, xylem resistance and twig size, influence seed adhesion probability and the ability of the mistletoe to penetrate the host tissue and establish a connection to the host vessels, which is essential to the survival of the parasite (Fadini & Lima 2012). Therefore, seed delivery to suitable hosts is a critical stage in mistletoe biology (Reid 1989). The spatial pattern of seed dispersal of mistletoes depends on the dispersal vectors, usually small frugivorous birds, including *Euphonia* tanagers and tyrant flycatchers, such as *Elaenia* spp. (Restrepo 1987; Cazetta & Galetti 2007; Guerra & Pizo 2014). The seed rain of mistletoes is tied to the post-feeding behavior and plant visiting frequency of their dispersal counterparts (López de Buen & Ornelas 1999; Roxburgh

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& Nicolson 2005). Some mistletoes are considered generalists and show low host specificity, being able to parasitize several species of host plants, whereas others are considered specialists and infect one or a few common hosts (Norton & Carpenter 1998; Fadini 2011). However, even generalist mistletoes may show preferences for certain hosts (Sargent 1995; Cazetta & Galetti 2007; Arruda *et al.* 2012). Empirical data indicate that mistletoes are much more dependent on the bird seed dispersers than vice versa (Guerra & Pizo 2014). Despite the relative high richness of mistletoe species in Brazil, there are still many gaps in our knowledge of their basic biology, which constrain our ability to model their spatial distribution, biogeography and response to disturbances (Arruda *et al.* 2012).

The objective of this study was to investigate host specificity of the mistletoe *Phoradendron crassifolium* (Pohl ex DC.) Eichler (Santalaceae) in a remnant of Atlantic Forest in southeast Brazil. To this end, we searched for mistletoes on potential host plants and tested whether mistletoe prevalence follows the abundance of potential host trees. We also employed an experimental approach simulating bird behavior to investigate how mistletoe establishment may vary among potential local hosts.

Methods

Study site and species

This study was carried out in a small (ca. 1 ha) remnant of secondary, seasonal tropical Atlantic Forest in Sorocaba, located in the state of São Paulo, in southeast Brazil (47°31'S; 23°35'W). In the region, the mean annual rainfall is 1311 mm and the mean annual temperature is 22°C (CEPAGRI 2013). The remnant studied is within a matrix of pasturelands and other small forest remnants (1-4 ha). For cattle farming, the pasturelands were planted with African grasses, such as *Urochloa decumbens* (Stapf) R.D. Webster, which replaced the original *cerrado* (savanna) vegetation. Typical *cerrado* trees, including *Qualea grandiflora* Mart., *Caryocar brasiliense* Cambess., *Annona* spp. and *Duguetia furfuracea* (A.St.-Hil.) Saff., are found at the study site, where the most species-rich tree families are Fabaceae, Myrtaceae and Lauraceae. The following are most abundant tree species at the study site (Correia *et al.*, unpublished data): *Tapirira guianensis* Aubl., *Schinus terebinthifolius* Raddi and *Lithraea molleoides* (Vell.) Engl. (Anacardiaceae); *Gochnatia polymorpha* (Less.) Cabrera (Asteraceae); *Copaifera langsdorffii* Desf. (Fabaceae), *Pera glabrata* (Schott) Poepp. ex Baill. (Euphorbiaceae); and *Casearia sylvestris* Sw. (Salicaceae). Within the remnant studied, vines are abundant and there is a history of selective logging.

Phoradendron crassifolium (Pohl ex DC.) Eichler (Santalaceae) is the most locally abundant mistletoe, followed by *Tripodanthus acutifolius* (Ruiz & Pav.) Tiegh. (Loranthaceae). According to Kuijt (2003), the species is distributed throughout the Lesser Antilles, Central America and South America, except Chile, Argentina and Uruguay, at elevations ranging from sea level to 2000 m. The species is a monoecious, aerial hemiparasitic shrub, characterized by opposite, coriaceous and glabrous leaves, and bears spike inflorescences, forming globose and single-seeded berries (3 mm in diameter) that are yellowish-orange when ripe (Kuijt 2003; Moreira & Rizzini 1997). The species is easily recognizable by the pronounced parallel nervures on its leaves (Moreira & Rizzini 1997), and its fleshy fruits are locally consumed by birds such as *Euphonia chlorotica* (Linnaeus, 1766) (A.V. Christianini pers. obs.). Ripe fruits are produced mainly from January to March, when seeds of *Phoradendron* with viscid threads are found attached to the bark of trees.

Host availability and prevalence of infection

Potential host trees for *Phoradendron crassifolium* were surveyed in a 2 × 500 m plot established within the remnant studied. All trees with a diameter at breast height (DBH) ≥ 4.8 cm in the plot were sampled. Each tree was identified to species level, measured (for DBH), and carefully inspected for 5 min by a trained observer searching for established mistletoes with the aid of binoculars. We arbitrarily considered a mistletoe as established when it was at least 10 cm long or had five or more leaves. We thus intended to reduce the risk of false-absences of mistletoe infections, but our data on infection levels may have been slightly underestimated due to unnoticed occurrences in large and tall trees. A status of mistletoe presence or absence was assigned to each individual host, and deviations from expectancy based on host abundance were tested with G-tests. Because the abundance was low for most potential host species, we grouped the plant records by family for statistical tests.

Seed inoculation experiment

We selected four common local tree species as potential hosts for the experiments: *Tapirira guianensis* Aubl. and *Lithraea molleoides* (Vell.) Engl. (both Anacardiaceae); *Siparuna guianensis* Aubl. (Siparunaceae); and *Tabernaemontana catharinensis* A.DC. (Apocynaceae). The first three species were observed bearing mistletoes in the study site. Four individuals of each species were randomly selected for the experiments. Each tree was 4-15 m from the nearest congeneric experimental tree. On each tree, we randomly selected 30 twigs of 1.0-1.5 cm in diameter on which to inoculate seeds. We collected ripe fruits directly from five individuals of *Phoradendron crassifolium* found on several hosts for the experiments. The pericarp of the fruits was removed by hand and the content was rubbed in the hand to produce viscid threads that aid seed adhesion to the bark of trees simulating bird behavior (see Sargent 1995). Before we performed the experiment, we tested the germinability of a sample of 30 seeds in the laboratory, and we confirmed that seed germination was high (93%; P. A. Messias pers. obs.). On the same day, we inoculated potential host trees by transferring a seed with the viscid thread to the bark of a selected twig. Each twig was individually marked to facilitate further monitoring. A total of 480 seeds were inoculated in the field (one seed per twig, 30 twigs on each of four experimental plants within four host species). Each seed was followed weekly for 157 days (ca. five months). At each time point, the fate of the seed was recorded as alive (whole, intact and bright green, or with protrusion of a radicle) or dead (ascribed to seeds that had disappeared, showed signs of predation or had withered). Mistletoe seed survival was compared between potential host species by means of survival analysis using Peto and Peto log-rank tests (Pyke & Thompson 1986). Survival analysis takes into account the total time elapsed from the beginning of observations until the death of each individual or the end of observations, in the case of individuals that remained alive until the end of study. It is a more powerful method of comparison than traditional goodness-of-fit tests applied to the proportion of individuals surviving to the end of observations. This survival analysis therefore enabled us to compare the survival curves among the host species used in the inoculation experiments. A significant difference would indicate that mistletoe survival (life-span) differed between the host species under comparisons (Pyke & Thompson 1986).

Results

Host availability and prevalence of infection

We sampled a total of 397 potential host individuals of 50 species among 25 families (Tab. 1). Although the prevalence was 11.6%, there were marked deviations in infection levels among host species and families (Tab. 1, Fig. 1). Of the 46 individuals infected, 40 (87%) were of species belonging to the families Anacardiaceae (*Lithraea molleoides* and *Tapirira guianensis*) or Siparunaceae (*Siparuna guianensis*), those two families nevertheless accounting for only 103 (26%) of the 397 potential individual hosts. Therefore, the great number of records of mistletoe establishment on Anacardiaceae and Siparunaceae was not driven by host abundance when compared against the expectancy of mistletoes records in all other families (G=88.55; df=1; p<0.001). Of the 50 potential host tree species, seven (14%) hosted mistletoes (Fig. 1). There was a low prevalence of *Phoradendron crassifolium* on some common host trees (such as in *Pera glabrata* (Schott) Poepp. ex Baill.) and a very high prevalence on others. However, it is not possible to draw general conclusions at the specific level because some species with mistletoes, such as *Sebastiania commersoniana* (Baill.) L.B. Sm. & Downs, *Ocotea velloziana* (Meisn.) Mez., and *Chrysophyllum marginatum* (Hook. & Arn.) Radlk., showed low abundance (Tab. 1).

Seed inoculation experiment

Final seed survival was lowest (26.7%) in *Tabernaemontana catharinensis*, whereas it was highest in *Lithraea molleoides* and *Siparuna guianensis* (35% in both) and intermediate (31.7%) in *Tapirira guianensis*. However, as it is shown in Fig. 2, there were no significant differences among the survivorship curves of the different species ($\chi^2 \leq 1.8$; $p \geq 0.10$ for all).

Discussion

Our observations and experiments suggest that *Phoradendron crassifolium* is able to colonize at least seven species among six families of available host plants at the study site, although there was a marked preference for Anacardiaceae (*Lithraea molleoides* and *Tapirira guianensis*) and Siparunaceae (*Siparuna guianensis*). The three most frequently infected host trees are typical of the initial stages of secondary forest succession. These plants have traits of short-lived pioneer plants, with rapid growth and soft wood (Muller-Landau 2004). Soft wood may facilitate the establishment of a connection between the developing haustoria and host, increasing mistletoe survival probabilities (Dzerefos *et al.* 2003). However, not all pioneer plants showed high infestation levels, as evidenced by the case of *Schinus terebinthifolius* (Anacardiaceae). In the Amazon forest, differences in wood density among tree species have been shown to be unrelated to the likelihood of infection by several Loranthaceae and Viscaceae mistletoes (Pereira 2014). Preferences may also be driven by other host traits, such as bark thickness and xylem resistance, and by the behavior of seed-dispersing frugivorous birds, such as seed treatment (seed manipulation in the bill, bill wiping on twigs and gut passage time) and the frequency of seed deposition, the number of seeds deposited, or a combination of the two (Reid 1989; López de Buen & Ornelas 1999; Arruda *et al.* 2006; Fadini 2011; Guerra & Pizo 2014). In addition, mistletoe survival probability may be affected by potential differences among host plants in terms of the risk of post-dispersal seed predation (Fadini *et al.* 2014).

The results of our seed inoculation experiment indicated that *Phoradendron crassifolium* is able to survive attached to the bark of several potential hosts, including species commonly infected by *P. crassifolium*, such as *Tapirira guianensis*, *Lithraea molleoides* and *Siparuna guianensis*. However, the mistletoe was also able to survive the seed stage on *Tabernaemontana catharinensis*, a species never recorded as infected at our study site. Although the time frame of our observations did not allow us to follow the fate of seeds until mistletoe establishment and growth, this result suggests that *P. crassifolium* can successfully colonize alternative hosts such as *T. catharinensis*. The absence of *P. crassifolium* on certain plant hosts at our study site is therefore probably due to dispersal limitation (see Reid 1989), although our

Table 1. Potential and infected hosts of *Phoradendrum crassifolium* (Pohl ex DC.) Eichler (Santalaceae) sampled in an Atlantic forest remnant of southeast Brazil. The total number of plants sampled per species and the proportion infected by the parasite (prevalence) is indicated. Codes following species names indicate rank abundance.

Family	Species (code)	Individuals sampled	Number infected (%)
Anacardiaceae	*Lithrea molleoides* (Vell.) Engl. (6)	28	11 (39.3)
	Mangifera indica L.* (28)	1	0
	Schinus terebinthifolius Raddi (10)	11	0
	Tapirira guianensis Aubl. (3)	34	17 (50.0)
Apocynaceae	*Tabernaemontana catharinensis* A.DC. (2)	35	0
Araliaceae	*Dendropanax cuneatus* (DC.) Decne. & Planch. (14)	5	0
	Schefflera vinosa (Cham. & Schltdl.) Frodin & Fiaschi (29)	1	0
Arecaceae	*Syagrus romanzoffiana* (Cham.) Glassman (30)	1	0
Asteraceae	*Baccharis dracunculifolia* DC. (31)	1	0
	Moquiniastrum polymorphum (Less.) G.Sancho (4)	34	0
Bignoniaceae	*Handroanthus chrysotrichus* (Mart. ex DC.) Mattos (32)	1	0
Burseraceae	*Protium heptaphyllum* (Aubl.) Marchand (33)	1	0
Cannabaceae	*Celtis brasiliensis* (Gardner) Planch. (8)	19	0
	Celtis iguanaea (Jacq.) Sarg. (22)	2	0
Euphorbiaceae	*Sebastiania brasiliensis* Spreng. (34)	1	0
	Sebastiania commersoniana (Baill.) L.B. Sm. & Downs (23)	2	2 (100.0)
Fabaceae	*Leptolobium elegans* Vogel (19)	3	0
	Copaifera langsdorffii Desf. (15)	5	0
	Acosmium dasycarpum Vogel (18)	4	0
	Machaerium villosum Vogel (35)	1	0
Lacistemataceae	*Lacistema hasslerianum* Chodat (20)	3	0
Lamiaceae	*Aegiphila integrifolia* (Jacq.) B.D. Jacks. (36)	1	0
	Aegiphila verticillata Vell. (16)	5	0
Lauraceae	*Lauraceae* sp.1 (37)	1	0
	Lauraceae sp.2 (38)	1	0
	Nectandra grandiflora Nees & Mart. (39)	1	0
	Nectandra lanceolata Nees & Mart. (40)	1	0
	Ocotea pulchella (Nees & Mart.) Mez (41)	1	0
	Ocotea velloziana (Meisn.) Mez (42)	1	1 (100.0)
	Persea willdenovii Kosterm. (13)	8	0
Malvaceae	*Luehea speciosa* Willd. (43)	1	0
Meliaceae	*Trichilia pallida* Sw. (44)	1	0
Moraceae	*Ficus enormis* (Mart. ex Miq.) Mart. (24)	2	0
Myrtaceae	*Eugenia paracatuana* O.Berg (17)	5	0
	Eugenia pluriflora DC. (7)	22	0
	Myrcia sp.1 (25)	2	0
	Myrcia sp.2 (45)	1	0
	Myrcia tomentosa (Aubl.) DC. (46)	1	0
	Myrciaria floribunda (H. West ex Willd.) O.Berg (47)	1	0
	Psidium guajava L.* (48)	1	0
Peraceae	*Pera glabrata* (Schott) Poepp. ex Baill. (1)	74	2 (2.7)
Rutaceae	*Zanthoxylum rhoifolium* Lam. (49)	1	0
	Zanthoxylum riedelianum Engl. (11)	10	0
Salicaceae	*Casearia decandra* Jacq. (12)	9	0
	Casearia sylvestris Sw. (9)	16	0
Sapindaceae	*Dodonaea viscosa* Jacq. (50)	1	0
Sapotaceae	*Chrysophyllum marginatum* (Hook. & Arn.) Radlk. (26)	2	1 (50.0)
Siparunaceae	*Siparuna guianensis* Aubl. (5)	29	12 (41.4)
Styracaceae	*Styrax pohlii* A.DC. (21)	3	0
Vochysiaceae	*Qualea grandiflora* Mart. (27)	2	0
	TOTAL	397	46 (11.6)

*Exotic species

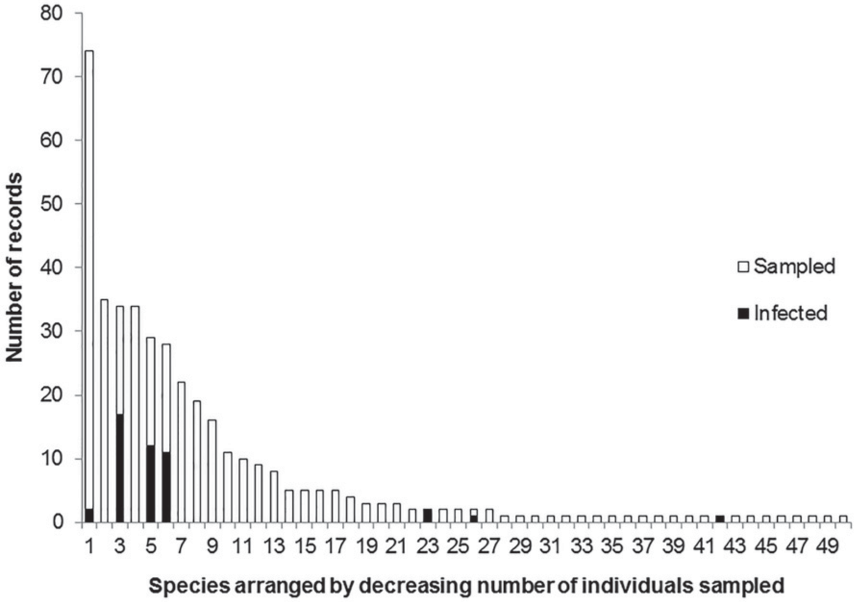

Figure 1. Rank-abundance patterns of infections by the mistletoe *Phoradendron crassifolium* among potential host plants in a fragment of Atlantic Forest in southeast Brazil. Of the 397 individual plants sampled, 46 were infected, representing seven of the 50 potential host species (see Tab. 1 for details on species sampled and sample sizes). Note the right-skewed distribution of infections, the majority of potential hosts showing no record of infection.

experimental approach do not allow us to exclude the influence of other factors such as bark thickness, twig angle and physiological compatibility of hosts (Arruda *et al.* 2012). Fleshy fruited plants whose fruiting season overlaps with that of mistletoes have an increased probability of contact with mistletoe seeds (López de Buen & Ornelas 1999). All hosts tested in the seed inoculation experiment produce seeds dispersed by birds. *Tapirira guianensis*, *L. molleoides*, *S. guianensis* and *T. catharinensis* have at least a partial fruiting phenology overlap with *P. crassifolium* at the study site (P. A. Messias, pers. obs.), although traits other than plant phenology may also influence the infection patterns. Such traits include spatially contagious seed dispersal, in which the frugivorous birds are attracted to and deposit seed in the surroundings of previously infected hosts, thus increasing infestation levels at small spatial scales (Watson & Rawsthorne 2013).

The *Phoradendron crassifolium* preferences for hosts are not driven by host abundance alone, given that many locally abundant potential host plants show low or no levels of infestations (Tab. 1). For instance, although the most abundant potential host in our sample, *Pera glabrata*, accounts for almost 20% of the available hosts, only 4% of *P. glabrata* individuals were infected. At a local scale, this result contrasts with the expectation raised by Norton & Carpenter (1998) that mistletoes would specialize in the most abundant hosts. However, a survey of records of hosts of *P. crassifolium* in exsiccata from herbaria indicated that over the geographical range of the mistletoe at least 59 species are used as hosts by *P. crassifolium* (P. Messias and J. D. Vidal Jr., pers. obs.), suggesting that this mistletoe is indeed a generalist able to successfully colonize various hosts. Therefore, mistletoe specialization decreases with increasing spatial scales (Arruda *et al.* 2012; but see Grenfell & Burns 2009). A survey of 1657 mistletoe records deposited in the *species*Link database revealed the occurrence of *P. crassifolium* in 52 genera and 32 families (CRIA 2013). Another survey, carried out via the Global Biodiversity Information Facility (GBIF 2013), revealed only four entries with host information, in a total of 1325 sheets. We are not able to determine whether there is some regional pattern of preferences for certain host trees, because most exsiccata of *P. crassifolium* do not provide information on host identity. Unfortunately, as highlighted by Arruda *et al.* (2012), most

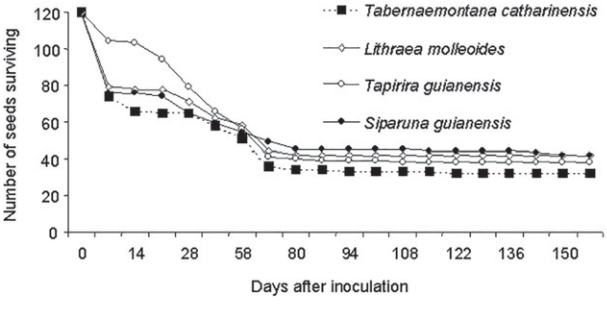

Figure 2. Survival of seeds of *Phoradendron crassifolium* manually inoculated onto the bark of four host plants in southeast Brazil: *Tabernaemontana catharinensis* A.DC. (dashed line, filled squares); *Lithraea molleoides* (Vell.) Engl. (unbroken line, open diamonds); *Tapirira guianensis* Aubl. (unbroken line, open circles); *Siparuna guianensis* Aubl. (unbroken line, filled circles).

records in herbaria in Brazil do not include information about the host plant, constraining the understanding of host preference over the range of the mistletoe. Studies analyzing the factors influencing host preference at different scales are worthwhile (Rist *et al.* 2011). Studies combining information from field and herbaria specimens may help bridge this gap. However, even studies carried out at local scales may increase our knowledge on mistletoe biology. At our local scale, *Phoradendron crassifolium* had a marked preference for a small number of host trees in Anacardiaceae and Siparunaceae, but was able to successfully colonize several other tree species. The results from our experimental approach indicate that the absence of *P. crassifolium* on some hosts, such as *Tabernaemontana catharinensis*, are probably due to seed dispersal limitation, and not host-plant incompatibility at early developmental stages.

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