Journal of Ecology

Journal of Ecology 2017, **105**, 1657–1667 doi: 10.1111/1365-2745.12795

Dissecting the contributions of dispersal and host properties to the local abundance of a tropical mistletoe

Marcos A. Caraballo-Ortiz*[,1], Aarón González-Castro[1,2], Suann Yang[3], Claude W. dePamphilis[1] and Tomás A. Carlo[1,4]

[1]Biology Department, The Pennsylvania State University, University Park, PA 16802, USA; [2]Island Ecology and Evolution Research Group (IPNA-CSIC), Calle Astrofísico Francisco Sánchez 3, E38206 La Laguna, Tenerife, Canary Islands, Spain; [3]Biology Department, State University of New York Geneseo, 1 College Circle, Geneseo, NY 14454, USA; and [4]Ecology Intercollege Graduate Degree Program, The Pennsylvania State University, University Park, PA 16802, USA

Summary

1. The interplay between dispersal and adaptation to local environments ultimately determines the distribution of plant species, but their relative contribution remains little understood. Tropical mistletoes provide the opportunity to dissect these contributions of dispersal and adaptation, because as hemiparasitic plants, they are typically adapted to grow on a handful of species within diverse tropical communities and are non-randomly dispersed by mutualistic frugivorous birds.

2. Here we hypothesized that the primary determinant of the abundance of a tropical mistletoe (*Dendropemon caribaeus*, Loranthaceae) in Puerto Rico will be the compatibility between the mistletoe and plant species in a community. Alternatively, the mistletoe's abundance could be primarily shaped by other factors such as the availability of potential host plants, or factors that determine how mistletoe seeds are dispersed by avian frugivores. We conducted surveys and experiments to assess the capacity of this mistletoe to grow on trees available in the local community, and measured the monthly phenology and seed dispersal patterns of the mistletoe and other bird-dispersed plants in the community over a period of 4 years. A path model was used to evaluate how the abundance of the mistletoe was shaped by host abundance, fruiting phenology, bird dispersal and compatibilities with host plants.

3. Our analyses show that the compatibility between mistletoe and host tree species, measured by mistletoe survival and growth rate, was the most important factor for mistletoe abundance. The next most important factor was the phenological characteristics of the hosts; this outcome likely arose because frugivory and seed dispersal services for mistletoes and hosts are performed by the same birds.

4. *Synthesis.* Mistletoes often parasitize only a subset of the suitable plant species that are available in a given community. Our results indicate that such patterns are not only determined by host quality and abundance but also by the phenological patterns of trees that influence the probabilities of mistletoe seeds being deposited on them by shared avian seed dispersers.

Key-words: *Dendropemon*, dispersal, dispersal limitation, frugivory networks, Loranthaceae, parasitic plants, phenology, PLS-PM, Puerto Rico, recruitment limitation

Introduction

The interplay between seed dispersal patterns and adaptation to local environments largely determines the distribution of plant species (Venable & Brown 1988; Engelbrecht *et al.* 2007), but we still know little about how both processes interact to shape distributions in heterogeneous environments. As obligate hemiparasites, tropical mistletoes provide good study systems to dissect the influences of dispersal and adaptation on plant distributions (Watson 2001; Aukema 2003). This is because mistletoes are typically adapted to grow on a handful of species in a given community (Norton & Carpenter 1998), while being subject to directed and other non-random spatial seed dispersal patterns by frugivorous birds (Aukema 2004; Carlo & Aukema 2005).

*Correspondence author. E-mails: mac587@psu.edu; marcoscaraballo@gmail.com

© 2017 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Like other plants, most mistletoes species produce fleshy fruits that are eaten exclusively by birds (Calder 1983). However, mistletoes are unique in having seeds coated in viscin – a sticky fibre – that glues seeds to branches of woody plants after birds defecate or regurgitate them (Aukema 2003; Guerra & Pizo 2014). Thus, birds determine the plants where mistletoe seeds are deposited, but the subsequent establishment of the seed depends on whether or not the plant that has been reached is a suitable host (Norton & Carpenter 1998; Watson & Rawsthorne 2013). For example, the successful establishment and growth of mistletoe seedlings on hosts requires physical and physiological compatibilities (Clay, Dement & Rejmanek 1985; Yan 1993a; Rödl & Ward 2002; Fadini, Mellado & Ghizoni 2014). These compatibilities – hereafter referred to as 'plant suitability' – include bark type, thickness of stems, successful haustorial penetration through the bark layers and xylem, and molecular and/or genetic factors, all of which have to be overcome by mistletoes in order to access their host's xylem to acquire water and mineral nutrients.

The likelihood of mistletoe seeds reaching different suitable plants can be affected by the relative abundance (Yan 1993a; Norton & Carpenter 1998; Fadini 2011) and attractiveness to seed-dispersing birds of potential hosts (Aukema 2003; Fadini, Gonçalves & Reis 2010; Watson & Rawsthorne 2013). For instance, frugivorous birds that disperse mistletoe seeds can be especially attracted to plants that bear fruits they also feed on, making dispersal of mistletoe seeds to such plants much more frequent (Carlo & Aukema 2005; Carlo & Tewksbury 2014). Consequently, the relative abundance and temporal availability of the fruit resources produced by potential host plants in the community that overlap with the mistletoe's fruiting periods could further affect mistletoe patterns of seed dispersal (González-Castro *et al.* 2012; Yang, Albert & Carlo 2013). Still, how the abundance of mistletoes is shaped by the joint contribution of bird behaviour and host properties and abundance remains little understood.

Here we evaluate the relative contribution of bird dispersal, the length and intensity of plant fruiting, and the abundance and suitability of plants in shaping the local abundance of the mistletoe *Dendropemon caribaeus* Krug & Urban (Loranthaceae) in Puerto Rico. We hypothesized that the abundance of mistletoes would be primarily shaped by the abundance and suitability of plant species in the environment. Alternatively, deviations from this expectation would be driven by factors that involve interactions between bird behaviour and temporal patterns of fruit production by plants in the community.

Materials and methods

STUDY SYSTEM

Dendropemon caribaeus is native to the eastern Caribbean from Puerto Rico to Barbados (Kuijt 2011). In Puerto Rico, *D. caribaeus* is distributed at low elevations from sea level to over 500 m in dry and mesic environments (Caraballo-Ortiz & Carlo 2013). Like other mistletoes, *D. caribaeus* is a hemiparasitic aerial shrub that is completely dependent on hosts for recruitment. Ripe fruits (length = 8·0 mm ± 0·05 SE, width = 4·1 mm ± 0·03 SE, weight = 89·8 mg ± 1·56 SE, $N = 87$) are dull black and contains viscin concentrated as a disc at their distal end (Kuijt 2011). *Dendropemon caribaeus* has been recorded to parasitize over 40 species of tree representing all major lineages of flowering plants and one gymnosperm (Kuijt 2011). In the northern coast of Puerto Rico, *D. caribaeus* is commonly found parasitizing the native tree *Citharexylum spinosum* L. (Verbenaceae). Other hosts we have recorded in northern Puerto Rico include *Albizia lebbeck* (L.) Willd. (Fabaceae), *Casuarina equisetifolia* L. (Casuarinaceae), *Cestrum diurnum* L. (Solanaceae), *Cestrum laurifolium* L'Hér., *Citrus sinensis* (L.) Osbeck (Rutaceae), *Citrus aurantifolia* (Christm.) Swingle, *Eugenia biflora* (L.) DC. (Myrtaceae), *Goetzea elegans* Wydl. (Solanaceae), *Persea americana* Mill. (Lauraceae), *Pisonia subcordata* Sw. (Nyctaginaceae), *Terminalia catappa* L. (Combretaceae) and *Thespesia populnea* (L.) Sol. Ex Correa (Malvaceae). A comprehensive list of hosts for *D. caribaeus* is provided by Kuijt (2011). Voucher specimens of *D. caribaeus* collected at the study site (Caraballo 3225 and 3226) were deposited at the Pennsylvania State University Herbarium (PAC).

Frugivory and seed dispersal of *D. caribaeus* is performed by a variety of land birds, but most notably by *Mimus polyglottos* L. (Northern Mockingbird) and *Tyrannus dominicensis* Gmel. (Grey Kingbird). For example, Carlo & Morales (2016) reported that in 2013, out of 652 frugivory records in the Finca Montaña, 33 were on *D. caribaeus*. Of those 33 records, 17 were by *M. polyglottos* and 14 by *T. dominicensis*.

The study was conducted at Finca Montaña, municipality of Aguadilla, northwestern Puerto Rico (18°27′54″ N, 67°06′32″ W, 105 m a.s.l.). The study site is administered by the College of Agriculture of the University of Puerto Rico at Mayagüez and consists of 240 ha of managed cattle pastures and 190 ha of secondary forest >50 years old (Martinuzzi *et al.* 2013). Vegetation at the site is subtropical moist karstic forest (Aukema, Carlo & Collazo 2007) with an annual average rainfall of 100–125 cm per year (Daly, Helmer & Quiñones 2003). See Carlo & Morales (2016) for further details on the study site.

MISTLETOE ABUNDANCE AND PATTERNS OF HOST USE

To study the local abundance and demographic structure of *D. caribaeus* mistletoes, we examined all potential hosts (trees and shrubs) and counted all individuals of *D. caribaeus* along a 2-km transect (see Fig. S1 in Appendix S1, Supporting Information). The transect traversed forest edges, hedges and open areas with scattered trees where *D. caribaeus* is naturally found. We also examined forest interior areas, sampling along eleven 100 × 2 m vegetation transects (described in next section) for mistletoes, with special attention to emergent canopy trees (Lira, Caires & Fadini 2017). For each potential host, we recorded species and height, and carefully examined its branches with binoculars to detect as many *D. caribaeus* as possible. During our survey, we dedicated more time and attention to examine trees with considerable size and multiple branches, as mistletoe detection has been shown to be more difficult in large trees (Fadini & Cintra 2015). To calculate the percentage of potential missing observations, we selected 10 random trees and re-checked them for mistletoes using two observers. We classified individuals of *D. caribaeus* into four size classes (based on the length of the longest branch) to gain insights into mistletoe performance on different host species: (i) <30 cm (non-reproductive); (ii) 30–60 cm; (iii) 60–90 cm; and

(iv) >90 cm. All classifications were performed by the same observer (C. Venable). We estimated fecundity within each class size by averaging the number of reproductive structures (all flowers and fruits). Although plants of *D. caribaeus* of different ages can have similar heights, careful observation of their main stem and the number of epicortical roots can provide a hint of their ages. Young *D. caribaeus* (1–2 years old) tend to have a smooth bark with few (<5) epicortical roots not too distant (<12 cm) from the main stem. This contrasts with older mistletoes (>2 years old), whose bark is fissured and have numerous (>10) and long (>12 cm) epicortical roots (often with clonal shoots in older plants; Edouard 1991). We used contingency table analyses and chi-squared tests (Bonferroni corrected) to compare plant use in the community (under the null hypothesis of use i.e. proportional to plant species abundance). Statistical analyses were conducted using the software JMP Pro (version 12.1.0; SAS Institute 2015).

FRUITING PHENOLOGY AND THE BIRD-GENERATED SEED RAIN

From September 2010 to August 2014, we tallied ripe fruits once a month on 205 tagged individuals for the 25 ornithochorous (bird-dispersed) and phylogenetically diverse woody plant species detected during the mistletoe survey (Table S1 in Appendix S2). Four to eleven individuals (median = 8 individuals) were tagged for each of the 25 ornithochorous species, which included 22 trees and 3 shrubs. We used the density of reproductive individuals for the 25 ornithochorous species reported in Carlo & Morales (2016) from 20 vegetation plots/transects haphazardly located on the study landscape as part of their forest-regeneration study: six 100 × 100 m plots in open areas, eleven 100 × 2 m transects in forest patches and three along vegetated fence lines in open areas (Fig. S1 in Appendix S1). For each species, we calculated the mean number of fruits per plant per month over 38 months and then multiplied the mean by the density of reproductive plants in the study area (total plants in sample/total area sampled) and then by the mean number of seeds per fruit to obtain a seed density (seeds per ha) estimate for a given month.

The bird-generated seed rain was measured during the same period using a set of 10 seed traps placed under 3-m tall perches (Fig. S1 in Appendix S1) that were placed in open areas of the Finca Montaña as part of a forest-regeneration study (Fig. S1 in Appendix S1; see Carlo & Morales (2016) for further details). The first set of perches was deployed from September 2010 to August 2012 and yielded seed rain for 20 months (Carlo & Morales 2016). The second set of seed perches was deployed in February 2013 and collected seeds until August 2014 for 18 additional months of seed rain and phenology data. The content of the seed traps was collected at least once per month and seeds were tallied and identified to species level. Bird species activity (perching frequency and time) was monitored on these perches using video cameras (Samsung SMX F-40, Samsung Electronics Co. Ltd., Suwon, South Korea) mounted on tripods for ~300 min (i.e. until each camera battery ran out of power, average = 299·8 min ± 11·9 SE) once per week starting in September 2010 to July 2011. A total of 41 432 min of video was obtained, with each perch receiving equal sampling effort. A second set of seed rain samples was obtained from September 2013 to September 2015 (of the 10 previous sampling site, 7 were new, see Fig. S1 in Appendix S1). During a subset of months of this second sampling period (September 2013–January 2014), we recorded the bird activity on perches 2–3 times per week and obtained 54 352 min of video recording. We visually inspected the footages and obtained the cumulative time (in seconds) for each species on a perch, and examined its correlation with the seed rain of *D. caribaeus*.

Previous observational work in the study site that included sampling in forested areas shows that the *Dendropemon* mistletoes in Puerto Rico are most frequently dispersed by *T. dominicensis* and *M. polyglottos* (Carlo & Morales 2016). However, the perches certainly do exclude other species that are uncommon in pastures and/or that do not like to perch on those structures. The common tanager *Spindalis portoricensis* Bryant (Puerto Rican Spindalis) feeds on *Dendropemon* but it does not disperse the seeds and it drops the seeds as it 'mashes' the seeds (Carlo 1999). *Pyrrhulagra portoricensis* Daudin (Puerto Rican Bullfinch) feeds on the fruits, but it is a seed predator for *Dendropemon* (Carlo 1999; Carlo, Collazo & Groom 2003). *Euphonia musica* Gmelin (Antillean Euphonia) do not feed on lipid-rich fruits of Loranthaceae and to our knowledge have never been recorded feeding on *Dendropemon* (Carlo 1999; Carlo, Collazo & Groom 2003). *Turdus plumbeus* Linnaeus (Red-legged Thrush) and other thrushes and thrashers are certainly species that could very well be effective dispersers, but are of much lesser abundance. Other insectivore–frugivores such as vireos, other tyrant flycatchers and many Neotropical migrants could also be occasional dispersers. Still, our data and observations show that the perches capture the most important components of *Dendropemon* dispersal in the site.

Using the fruiting phenology and seed rain data, we calculated the following parameters for each of the 25 ornithochorous plant species. The 'Fruiting Intensity' was the cumulative number of monthly ripe fruit counts per ha for each of the 25 species. The 'Fruiting Length' was the number of months in which the species had ripe fruit. The 'Seed Rain Length' was the cumulative number of months for which seeds were detected in the seed traps under bird perches. The 'Seed Rain Correlation' was the pairwise correlation value (r) for the number of *D. caribaeus* seeds arriving on traps with the seeds from the 25 potential host species arriving on the traps. Pairwise correlations considered only the months for which there was availability of both mistletoe and a given plant species. Statistical analyses were conducted using the software JMP Pro (version 12.1.0; SAS Institute 2015).

ASSESSING DISPERSAL VS. ESTABLISHMENT LIMITATION WITH PATH MODELLING

To examine the relative contribution of dispersal and plant quality on the establishment and abundance of mistletoes, we conducted a partial least square path modeling (PLS-PM) using the statistical software R (Sanchez 2013; R Core Team 2015). Partial least square path modeling is a statistical data analysis that quantifies the relationship among manifest (measured) and latent (hypothetical) variables without distributional assumptions (Tenenhaus *et al.* 2005; Sanchez 2013). Path coefficients represent the strength and direction of direct effects, which are linear relationships between variables and are represented by arrows and numbers in the directed model.

In the path model, manifest variables can be considered either formative or reflective, depending if they construct (formative) or are caused by (reflective) the latent variables (Sanchez 2013). In our study, we assigned eight manifest variables for the outer model and four latent variables for the inner model. The first latent variable was 'Phenology', which had two manifest variables: 'Intensity of Fruiting' and 'Length of Fruiting'. The second latent variable was 'Frugivory', which was formed by 'Correlation of Seed Rain' and 'Length of Seed Rain'. The third latent variable, 'Local Abundance of *Dendropemon*', was formed by 'Abundance of Plants' and 'Size of *Dendropemon*'. The fourth latent variable 'Suitability of Plants', was reflected by two manifest variables: 'Fecundity of *Dendropemon*' [average fecundity

(flowers and fruits) of *D. caribaeus* in each host] and 'Establishment of *Dendropemon*' (the number of all individuals of *D. caribaeus* observed growing in each plant species in the field). There is an inner, unidirectional relationship in the model from the latent variables 'Phenology' to 'Frugivory'. We conducted the analysis using the 25 local tree species with fleshy fruits dispersed by *M. polyglottos* and *T. dominicensis* and considered as potential hosts for *D. caribaeus* (Table S1 in Appendix S2).

PLANT SPECIES SUITABILITY EXPERIMENT

In order to evaluate mistletoe–plant compatibility (i.e. plant suitability) and to quantify establishment and growth rates of mistletoe among experimental plants (Yan 1993b; Roxburgh & Nicolson 2008; Messias *et al.* 2014; Okubamichael, Griffiths & Ward 2014; Luo *et al.* 2016), we planted seeds of *D. caribaeus* on branches of selected tree species. We selected 11 locally common and phylogenetically disparate tree species that share avian frugivores with *D. caribaeus* at the study site (see Carlo & Morales 2016): *Casearia guianensis* (Aubl.) Urb. (Salicaceae), *C. spinosum*, *Clusia rosea* Jacq. (Clusiaceae), *Coccoloba diversifolia* Jacq. (Polygonaceae), *Cupania americana* L. (Sapindaceae), *Eugenia monticola* (Sw.) DC. (Myrtaceae), *Guapira fragrans* (Dum. Cours.) Little (Nyctaginaceae), *Krugiodendron ferreum* (Vahl) Urb. (Rhamnaceae), *Nectandra coriacea* (Sw.) Griseb. (Lauraceae), *Sideroxylon salicifolium* (L.) Lam. (Sapotaceae) and *Zanthoxylum martinicense* (Lam.) DC. (Rutaceae). For each of these species, we used five replicate individuals (total: 55 trees). On each tree, we planted 25 *D. caribaeus* seeds. Seeds were collected from local *D. caribaeus* individuals growing on *C. spinosum* (the most commonly used host). All seeds were planted along a single healthy branch ~1·0 cm (diameter) with a seed-to-seed distance of 2·5–3·0 cm. The fruit coat was carefully peeled off to expose the seed and viscin aril, and seeds were attached to branches by connecting the viscin aril to the branch surface using fingers (Honaas *et al.* 2015). Seeds that detached or disappeared from branches within the first 2 weeks of the experiment were replaced by new ones. Although re-planting mistletoe seeds may over-estimate the success of haustorial connections (as our experiment was not suited to test the effects of tree bark properties on survival), we decided to re-plant because our intention was to examine the survival and performance of mistletoes post-haustorial connection, and was important to maintain a sufficient sample size to conduct appropriate analyses on seedling performance on trees. As a control, we planted 30 *D. caribaeus* seeds on five dead branches (1 cm diameter) still attached to a *C. spinosum* tree. In total, we planted 1435 *D. caribaeus* seeds on 56 experimental plant species representing 11 species and a negative control. Mistletoe establishment was determined by their survival to first year after planting, while size to first year was recorded by measuring seedlings from base to apical meristem. The proportion of established seeds was compared among plant species using a generalized linear model with a binomial error family, while data on mistletoe size were analysed using a nonparametric Kruskal–Wallis test due to non-normality of the size data. Statistical analyses were conducted in JMP Pro (version 12.1.0; SAS Institute 2015).

Results

MISTLETOE ABUNDANCE AND PATTERNS OF HOST USE

The 2-km transect survey of plants yielded 494 trees from 50 species (Fig. S2 in Appendix S3). *Dendropemon caribaeus* was found on 73 individual trees of seven woody species, showing a non-random pattern of host use (Fig. S2 in Appendix S3). The vast majority of *D. caribaeus* (95·5%) were found on *C. spinosum*. The other six hosts, *Ardisia obovata* Desv. ex Ham. (Primulaceae), *C. diurnum*, *Randia aculeata* L. (Rubiaceae), *Tetrazygia elaeagnoides* (Sw.) DC. (Melastomataceae), *Trichilia hirta* L. (Meliaceae) and *Vachellia farnesiana* (L.) Wight & Arn., collectively accounted for a slim 4·5% of the mistletoe counts despite most of them being fairly abundant (Fig. S2 in Appendix S3). Most *D. caribaeus* were observed on *C. spinosum* along fences (54%) and open pastures (42%), with few (4%) detected along forest edges. No *D. caribaeus* were found in forest interior areas (far from edges) sampled along vegetation transects. *Citharexylum spinosum* trees with *D. caribaeus* were about 2-m taller (8·11 m ± 0·06 SE) on average than non-parasitized individuals (5·53 m ± 0·34 SE). Overall, *C. spinosum* had more of the larger and more fecund *D. caribaeus* than the other two most commonly used host trees (Fig. 1). Size differences also

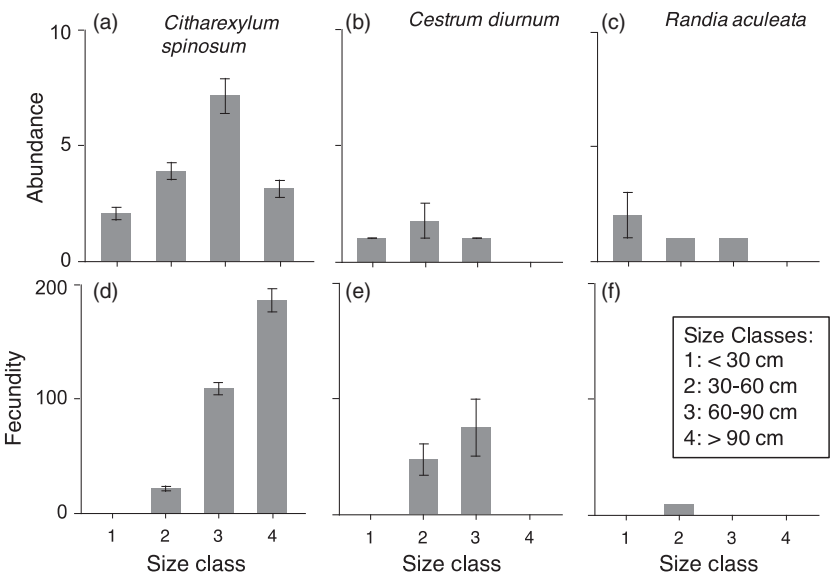


Fig. 1. Average abundance (a–c) and fecundity (d–f) of *Dendropemon caribaeus* by size class at Finca Montaña in Aguadilla, Puerto Rico. Most *D. caribaeus* growing on *Citharexylum spinosum* (a, d) were large and prolific, while other hosts such as *Cestrum diurnum* (b, e) and *Randia aculeata* (c, f) mostly supported small- to medium-sized mistletoes with few flowers and fruits, suggesting that host identity can influence mistletoe size and fecundity. Bars are 1 SE of the mean.

© 2017 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,

translated into large variations in average fecundity among mistletoes growing on the three hosts (Fig. 1). *Dendropemon caribaeus* individuals from the largest size category (>90 cm) on *C. spinosum* had between two to four times more reproductive structures (flowers and fruits) than mistletoes growing on *C. diurnum* and *R. aculeata* plants from all categories combined (Fig. 1). We observed that, on all host species, individuals of *D. caribaeus* showed characteristics of both young and old plants, regardless of host size (Fig. S3 in Appendix S4). Thus, host size does not appear to be playing a large role in the survival of *D. caribaeus*.

FRUITING PHENOLOGY AND THE BIRD-GENERATED SEED RAIN

Dendropemon caribaeus had ripe fruits in 37 out of the 38 sampled months (Figs 2 and 3a), showing a nearly continuous fruiting capacity only exceeded by *C. diurnum*, which had ripe fruits in all months (Fig. 3a). Many plant species were not always represented in the seed rain at times when they were available as shown by the discrepancies in the number of months between the fruiting length (Fig. 3a) and the seed rain length (Fig. 3b). The dispersal of *D. caribaeus* seeds showed positive significant correlations with five tree species (*Calyptranthes pallens* Griseb., *C. diurnum*, *C. laurifolium*, *C. spinosum* and *C. rosea*) (Fig. 3c); three of these species are known hosts of *D. caribaeus* at the study site (*C. diurnum*, *C. laurifolium* and *C. spinosum*).

The fruiting intensity values (cumulative number of fruits in 38 months) differed markedly between species (Fig. 3d). Under perches we collected a total of 2638 seeds from the 26 ornithochorous plant species (including *D. caribaeus*, Fig. 3e). The five species most consumed by birds at the study site during the 4-year study period were *Z. martinicense* (17%), *C. diurnum* (14%), *S. salicifolium* (9%), *D. caribaeus* (9%) and *C. spinosum* (8%) (Fig. 3e). The temporal seed rain pattern of *D. caribaeus* at perches followed its monthly phenology (Fig. 2), with seeds dispersed during 32 months, second only to *C. diurnum* (Fig. 3b). Most of the seed rain at the study site was composed of seeds from *Z. martinicense* and *C. diurnum* with 17% and 14%, respectively (Fig. 3e), while the rest of the species comprised less than 9% of the seed rain (median seed intensity = 72, SE = 22·95). With 235 dispersed seeds, *D. caribaeus* comprised 9% of the seed rain (Fig. 3e).

We observed a total of 12 bird species using the perches in 95 784 min of video footage. Most of these species were granivores that normally do not disperse seeds in a viable state (see Carlo & Morales 2016). Despite multiple bird species using the perches, the two main seed dispersers of *D. caribaeus* and its host trees dominated the perching time: *M. polyglottos* (42·2% of perching time) and *T. dominicensis* (46·8% of perching time). The individual perching time of *T. dominicensis* was strongly positively correlated with the number of *D. caribaeus* arriving under perches ($r^2 = 0{\cdot}34$, $F_{1,18} = 7{\cdot}02$, $P = 0{\cdot}0067$), while the perching time of *M. polyglottos* was not ($r^2 = 0{\cdot}002$, $F_{1,18} = 0{\cdot}06$, $P = 0{\cdot}8203$).

ASSESSING DISPERSAL VS. ESTABLISHMENT LIMITATION WITH PATH MODELLING

Results of the path model show that factors describing 'Suitability of Plants' are more influential than factors related to 'Phenology' and 'Frugivory' explaining the 'Local Abundance of *Dendropemon*' at the study site (Fig. 4). The 'Phenology' of trees in the community was the second most important variable explaining 'Local Abundance of *Dendropemon*', followed by bird 'Frugivory'. 'Phenology' showed a strong inner relationship to 'Frugivory', while from

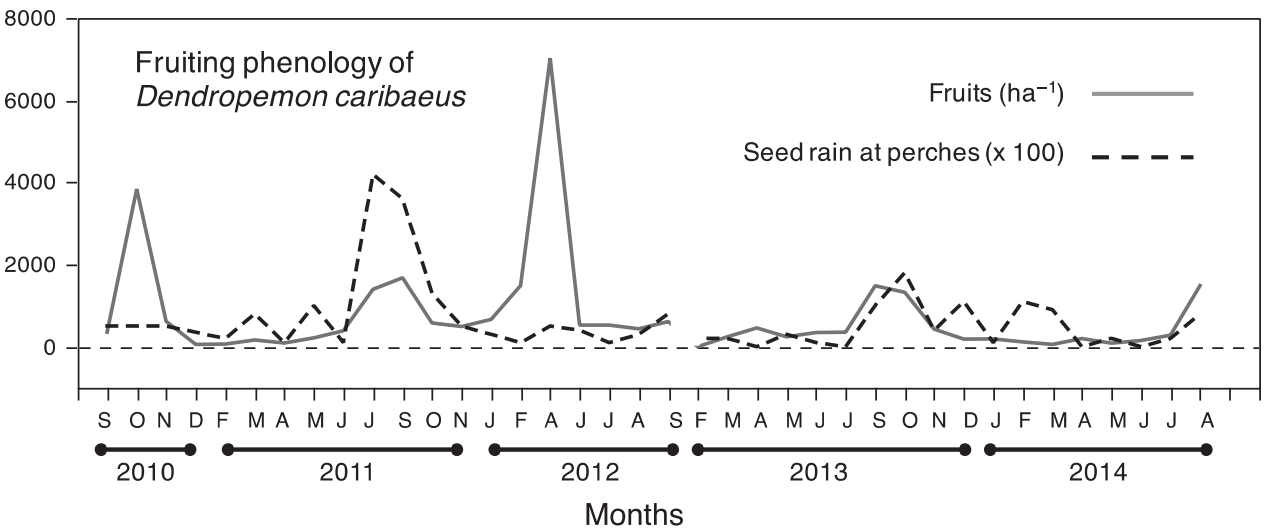


Fig. 2. Fruiting phenology of the mistletoe *Dendropemon caribaeus* at Finca Montaña in Aguadilla, Puerto Rico from 2010 to 2014. Estimated Fruits of *D. caribaeus* at the study site were estimated using visual counts (for 'Fruits') on tagged sample plants. The seed rain ('Seed rain at perches', original values multiplied by 100 for visualization purposes) was measured in seed traps under perches placed in open areas of the study site. Months with data are shown with their first letter in chronological order.

© 2017 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,

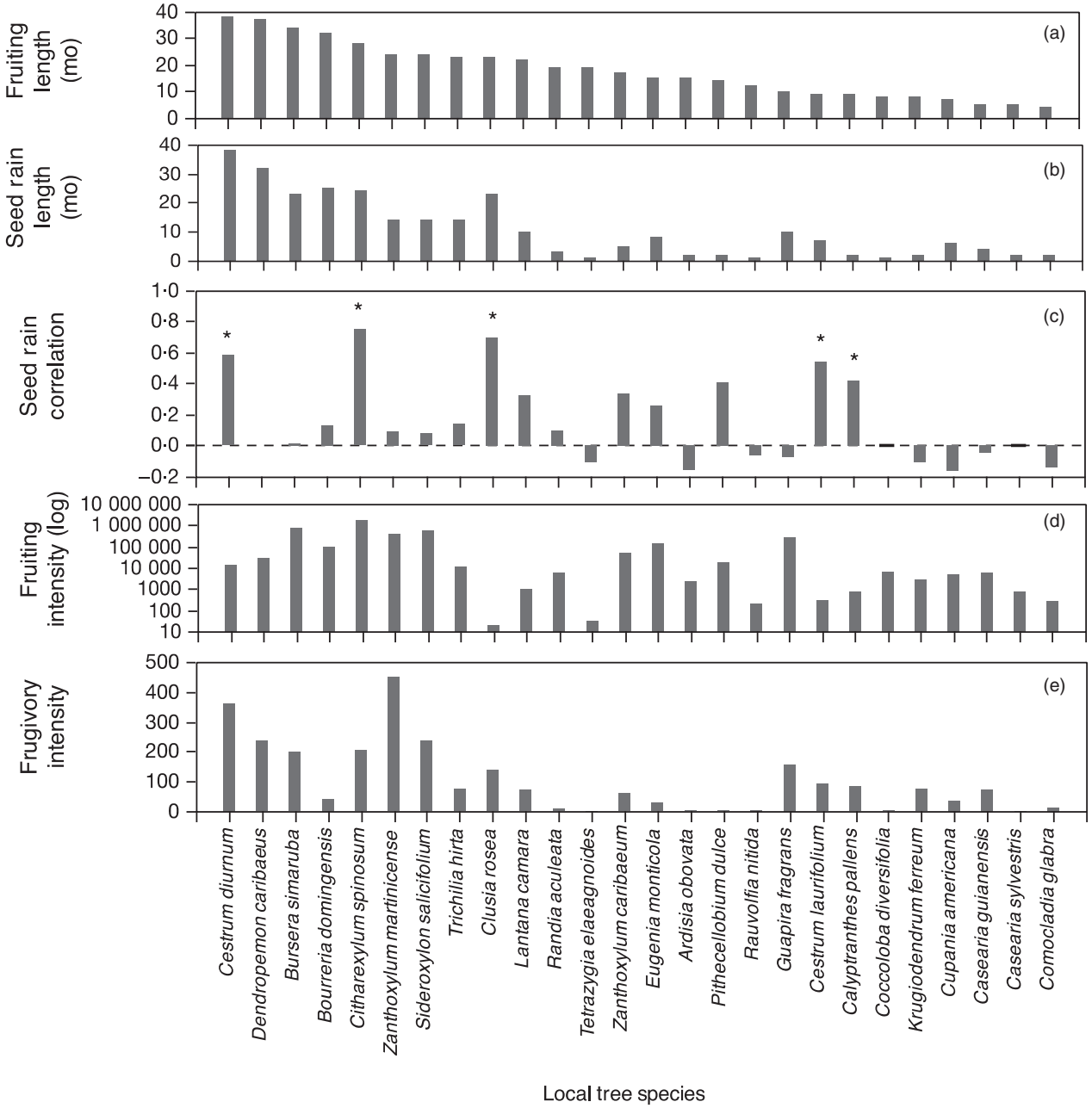


Fig. 3. (a) Fruiting length (in months), (b) seed rain length (in months), (c) seed rain correlation between local tree species and *Dendropemon caribaeus* [asterisks (*) indicates significant pairwise correlations at $\alpha = 0{\cdot}05$], (d) fruiting intensity (number of fruits, log transformed) and (e) frugivory intensity (number of seeds) of bird-dispersed local tree species present at Finca Montaña in Aguadilla, Puerto Rico (total period = 38 months).

the two variables forming 'Phenology', the 'Intensity of Fruits' in the community had a higher path coefficient value than the 'Length of Fruiting' season. In contrast, the variable 'Frugivory' was better explained by the 'Length of Seed Rain' followed by 'Correlation of Seed Rain' (Fig. 4). The two manifest variables 'Abundance of Plants' and 'Size of *Dendropemon*' showed similar path coefficient values forming 'Local Abundance of *Dendropemon*' (Fig. 4). Last, 'Suitability of Plants' was better reflected by 'Fecundity of *Dendropemon*' than by 'Establishment of *Dendropemon*' (Fig. 4).

PLANT SPECIES SUITABILITY EXPERIMENT

Ninety-eight per cent of the mistletoe seeds planted germinated within the first 5 days, and marked differences in the proportion of established mistletoes were evident 1 year after the experimental plantings (GLM $\chi^2 = 95{\cdot}2$, d.f. = 10, $P < 0{\cdot}0001$, Fig. 5a). Seeds planted in control (i.e. dead) branches also germinated but all seedlings died within 2 months. *Eugenia monticola* had the highest per capita seedling establishment at 1 year from planting with 33 mistletoe

© 2017 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,

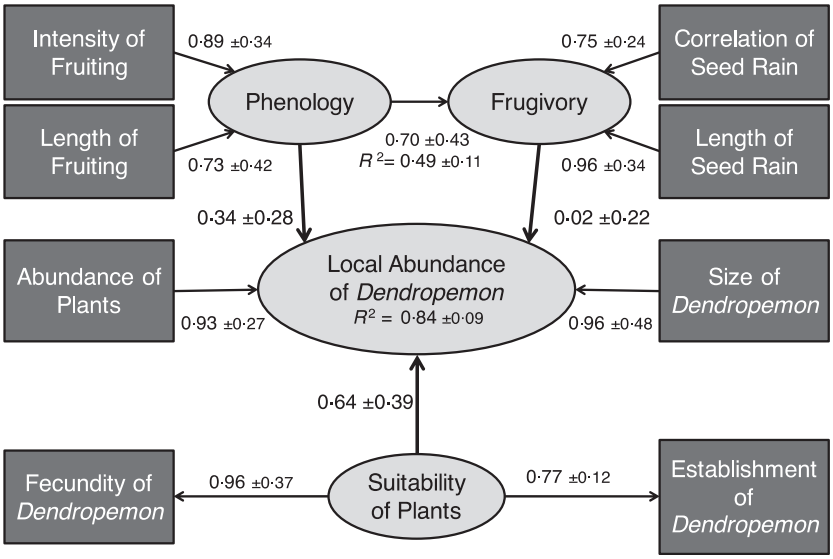


Fig. 4. Directed graph of the partial least squares path model representing the relative contribution of multiple variables to explain the local abundance of *Dendropemon caribaeus* mistletoes at Finca Montaña in Aguadilla, Puerto Rico. Manifest (i.e. measured) variables are shown in rectangles, while latent (i.e. hypothetical) variables are shown in elliptic shapes. Values (±SE) indicate loadings (correlations between latent variables and their manifests), path coefficients (in bold with thicker arrows) and coefficient of determination (R^2). All values were calculated from 1000 bootstrap replicates. The prediction performance and structural quality of the model was verified with the goodness of fit (GoF) statistic, which was 0·71.

plants (26·4%). Establishment on *S. salicifolium*, *Z. martinicense* and *G. fragrans* was 11–14%, while the rest of the species had fewer than 8% (Fig. 5a). None of the mistletoe seedlings planted on two of the experimental plants (*C. americana* and *C. guianensis*) survived the first year (Fig. 5a). Mistletoes showed significant variation in growth rates across tree species (Kruskal–Wallis ANOVA, $\chi^2 = 66{\cdot}35$, d.f. = 8, $P < 0{\cdot}0001$, Fig. 5b). Seedlings growing on six of the experimental plant species (*C. diversifolia*, *C. rosea*, *K. ferreum*, *N. coriacea*, *S. salicifolium* and *Z. martinicense*) remained alive after 1 year, but their growth was overwhelmingly arrested at the cotyledon stage with no production of true leaves despite the presence of an apparent haustorial connection (Figs 5 and S4 in Appendix S5). In contrast, two experimental trees (*E. monticola* and *G. fragrans*) proved to be more suitable than the above-mentioned plants – albeit in varied degree – for *D. caribaeus* growth. For example, 21·2% of 1-year seedlings in *E. monticola* remained arrested at cotyledon stage, while the rest were able to develop leaves, reaching a maximum stem length of 5·5 cm. Similarly, 14·3% of 1-year seedlings on *G. fragrans* were arrested at cotyledon stage, but a few individuals attained considerable growth (>20 cm stem length, Figs 5b,c and S4b in Appendix S5). But the plant species where *D. caribaeus* clearly grew the best was *C. spinosum*, where the average seedlings stem length was an order of magnitude higher than the average length in all other plants (Figs 5b,e and S4a in Appendix S5).

Discussion

Here we show that the interplay between plant suitability and directional seed dispersal patterns governs the local abundance pattern of *D. caribaeus* in our study site. We found that the local abundance of *D. caribaeus* appears primarily shaped by the differential suitability of plants for its establishment and growth, and secondarily by the patterns of fruit production of a subset of hosts that are also bird-dispersed in the local community. While our results are in agreement with previous studies (e.g. Yan 1993a, b; Fadini 2011), they contrast with others that emphasize a larger role of dispersal patterns as compared to plant compatibility in shaping mistletoe abundance (Roxburgh & Nicolson 2005; Glatzel & Geils 2008; Okubamichael, Griffiths & Ward 2014). Our results also point out that dispersal is important, but in ways that reflect the intricacies of plant–frugivore interactions (Fig. 4). For example, plant characteristics such as the quantity and temporal availability of bird-dispersed fruits appear important for mistletoe abundance as they influence frequencies of frugivory and consequently, how strongly directional are the mistletoe seed rain on potential hosts by shared frugivores (Wenny 2001; Yang, Albert & Carlo 2013; Carlo & Tewksbury 2014; González-Castro *et al.* 2015).

PLANT SPECIES SUITABILITY EXPERIMENT: MISTLETOE SURVIVAL

Our results show that even for mistletoes like *D. caribaeus* that can be labelled as a 'host generalist', judging by the tens of host species on which it has been recorded (Kuijt 2011), local population abundance is still influenced primarily by fine-scale variability in its compatibility with host plants. For example, our planting experiments showed gradients in the capacity of *D. caribaeus* to survive the first year on different tree species in the community, ranging from about ~25% survival rate on *E. monticola* and *G. fragrans*, to zero in *C. americana* and *C. guianensis* (Fig. 5a). In some plant species, recruitment appears driven by compatibility following the formation of a haustorial connection, while in others it appears limited by purely mechanical factors. For example, poor compatibility is clear for *D. caribaeus* planted on trees like *C. diversifolia*, *N. coriacea* and *S. salicifolium* because seedlings survive to 1 year at relatively high rates, but their growth remains arrested at the cotyledon stage (Figs 5c,d and S4 in Appendix S5). In these cases, we observed a clear

© 2017 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,

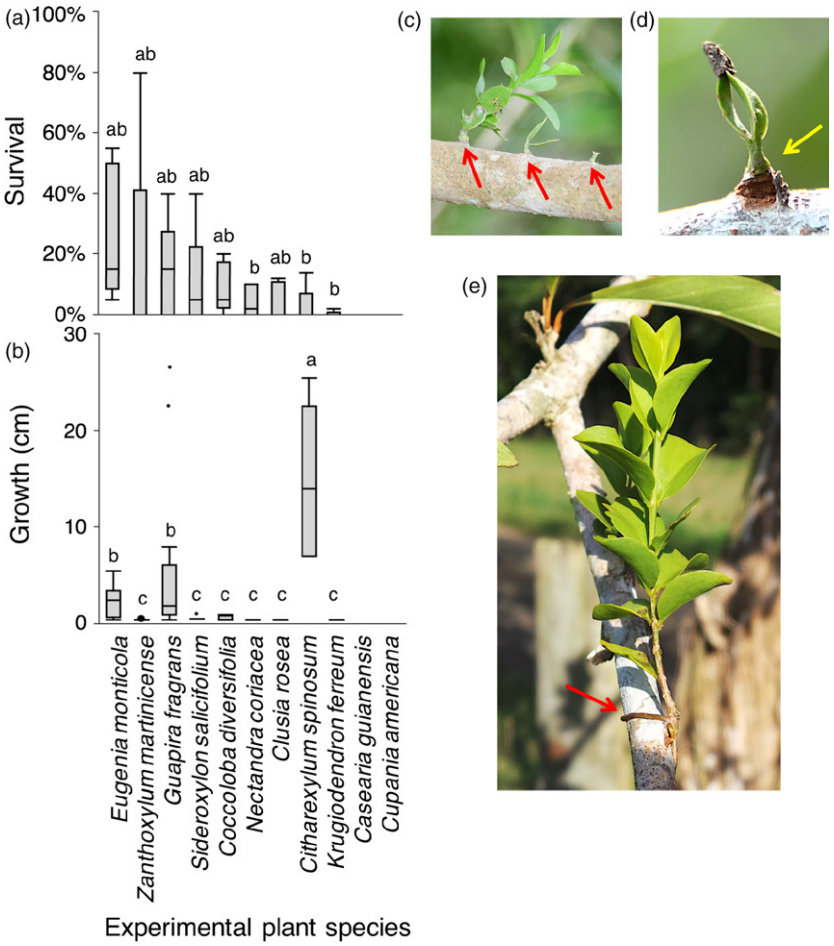


Fig. 5. Survival (a) and growth (b) of the mistletoe *Dendropemon caribaeus* at 1 year after planting on experimental plants at Finca Montaña in Aguadilla, Puerto Rico. Mistletoes can survive in many plants, but not all plants are suitable for optimal growth. For example, mistletoes planted on *Zanthoxylum martinicense* showed a high survival percentage during the first year, but none of them were able to grow beyond cotyledon stage. Mistletoes growing on some plants such as *Eugenia monticola* (c) showed variability in growth rates, ranging from plants arrested at the cotyledon stage to seedlings with normal development (arrows indicate mistletoe seedlings). Other seedlings such as the ones planted in *Coccoloba diversifolia* (d) remained arrested at the cotyledon stage and developed a swelling at the connecting point with the host (arrow indicates base of mistletoe). In contrast, few of the seeds planted in *Citharexylum spinosum* were able to survive, but these few survivors achieved the highest growth rates and were vigorous (e), which is reflected in the development of epicortical haustorial roots (indicated with arrow). Boxplots show standard error bars and different letters indicate significant differences from pairwise contrasts. Photo credits: T.A.C. (c, d); M.A.C.O. (e).

swelling of the region where the haustorial disc of *D. caribaeus* met tree branches (Figs 5d and S4 in Appendix S5), as is typical when mistletoes establish on hosts (Kuijt 1969). This suggests that *D. caribaeus* is able to establish functional haustorial connections in this type of host, at least to tap enough water to keep them alive in the arrested growth stage for an extended period. Otherwise, seedlings would have died within 2 months after planting, like those of the negative control treatment (i.e. those planted on dead branches).

Our planting experiment also showed that factors unrelated to compatibility at molecular levels (e.g. mechanical) can further influence mistletoe establishment. This is shown by the remarkably low seed per capita establishment rate of *D. caribaeus* on *C. spinosum*. *Citharexylum spinosum* was by far the most important host for *D. caribaeus* in our study site (Fig. S2 in Appendix S3) and it also was the host where the largest and more fecund mistletoe individuals were naturally found (Fig. 1). How can low recruitment rates be explained in *C. spinosum*? One possibility is that selection has shaped the inverse relationship between establishment – controlled by dispersal frequency – and growth as is common in host–parasite systems: increased growth capacity on the mistletoe side can select for plant species that are more tolerant to infection (Råberg, Graham & Read 2009).

We have noted that both very young (<1·0 cm in diameter) and older twigs (>1·5 cm in diameter) of *C. spinosum* prevent the establishment of *Dendropemon* (M.A. Caraballo-Ortiz, unpublished data). Compared to other plants, it seems that there is a narrower range of twig surface suitable for establishment of *D. caribaeus* on *C. spinosum*, which could explain the inverse relationship we found between mistletoe establishment and growth rates (Fig. 5). The long and overlapping fruiting season recorded for *D. caribaeus* and *C. spinosum* (Fig. 3a) combined with the high correlation of the seed rain between both species (Fig. 3c) suggest that there is plenty of opportunity for *D. caribaeus* seeds to reach suitable sites on *C. spinosum*. Thus, limited recruitment sites keep the number of mistletoes on *C. spinosum* proportionally low relative to the high propagule pressure generated by birds. In fact, we expect that all potential host species offer limited recruitment sites to *D. caribaeus* given that many above-ground host surfaces are inadequate for establishment, which is why host phenology appears as an important driver of mistletoe abundance in our path model analysis (Fig. 4).

PLANT SPECIES SUITABILITY EXPERIMENT: MISTLETOE GROWTH

The spectrum of compatibility between mistletoe and hosts is also illustrated in the diversity of growth rates exhibited by *D. caribaeus* across the experimental plant species that we tested. *Dendropemon caribaeus* grew quickly on its principal

host *C. spinosum* (Fig. 5e and S4 in Appendix S5), contrasting with the complete lack of establishment in some trees (e.g. *C. guianensis*, Fig. 5a). Perhaps, more intriguing is the variation we found in the growth of *D. caribaeus* established on *E. monticola* and *G. fragrans*. These two species of trees were – in addition to *C. spinosum* (the 'positive' control) – the only experimental plants where *D. caribaeus* grew beyond the cotyledon stage. In *C. spinosum*, the length of 1-year-old *D. caribaeus* ranged between 8 and 26 cm in length, while those growing on *E. monticola* and *G. fragrans* showed a broader range of developmental stages after 1 year, from plants arrested at the cotyledon stage to individuals equalling the largest of individuals on *C. spinosum* treatments (see outlier points, Fig. 5b).

FRUITING PHENOLOGY AND THE BIRD-GENERATED SEED RAIN

The finding that some seedlings of *D. caribaeus* were able to grow experimentally on *E. monticola* and *G. fragrans* provides important additional insights on the causes of heterogeneities in the abundance of mistletoes on available plants. For example, *E. monticola* – one of the most common trees of lowlands in Puerto Rico and the most common tree in forest fragments and fence lines in the study site – has never been documented as a host of *D. caribaeus* in Puerto Rico or elsewhere in the Caribbean. The second species, *G. fragrans*, appears to be a rare host for *D. caribaeus* and has been documented only once (a historical herbarium record from Puerto Rico) in spite of being one of the most common trees in Puerto Rico. On the other hand, *C. diurnum* – also a common species at edges and fences in lowlands – was found to be a host of *D. caribaeus* at the study site (Fig. 1b). *Cestrum diurnum* has extended phenology patterns (the longest in the community, see Fig. 3a,b) and is one of the top three most consumed fruits by *M. polyglottos* and *T. dominicensis* in the site and elsewhere (Carlo & Morales 2008, 2016). Unlike *C. diurnum*, *E. monticola* and *G. fragrans* have short and more unpredictable fruiting episodes, and thus, are not as important for the shared avian vectors. In turn, trees with extended fruiting seasons and highly preferred by birds such as *C. rosea* (Carlo, Collazo & Groom 2003; Carlo & Morales 2016) were not detected hosting *D. caribaeus* despite the fact that the seed rain of *C. rosea* and *D. caribaeus* were strongly positively correlated (Fig. 3c). Furthermore, our planting experiments showed that seedlings of *D. caribaeus* do not grow beyond the cotyledon stage in *C. rosea*. Altogether, these results show that plant phenology is playing an important role in restricting mistletoe seed rain towards the trees that birds use the most, irrespective of whether they are suitable hosts (e.g. *C. spinosum*, *C. diurnum*) or not (e.g. *C. rosea*), while decreasing the chances of seeds reaching some suitable hosts (e.g. *E. monticola*, *G. fragrans*).

SEED DISPERSAL AND BIRD BEHAVIOUR

The intensity, timing and spatial patterning of fleshy fruit production on the landscape are important factors shaping plant–frugivore interaction networks (Morales *et al.* 2012; Yang, Albert & Carlo 2013). Consequently, the attractiveness of fleshy fruit crops to the frugivorous birds that disperse the seeds of *D. caribaeus* could influence plant use by mistletoes. For example, in the same study site, Carlo & Morales (2016) reported that generalist frugivores such as *M. polyglottos*, *S. portoricensis* and *T. dominicensis* were feeding on the fruits of *D. caribaeus*. However, only *M. polyglottos* and *T. dominicensis* ingested the fruits whole and defecated the seeds in a viable state, while *S. portoricensis* 'mashed' the fruits and dropped seeds without dispersing them. Furthermore, only the perching activity of one of these species, *T. dominicensis*, was correlated with seed arrival under perches. Thus, differences in visitation rates to potential host trees that bear fruit create heterogeneity in the abundance of *D. caribaeus* among suitable host species because differences in visitation translate into differences in propagule pressure (Aukema 2004; Carlo & Aukema 2005).

INSIGHTS ON MISTLETOE–HOST RELATIONSHIPS

The variability we found in the establishment and performance of *D. caribaeus* is ecologically and evolutionary significant, as it likely shows the raw material that allows mistletoes to adapt to the diverse tree assemblages they face on tropical Caribbean Islands and other diverse environments. It appears that *D. caribaeus* is not specialized on particular plant lineages as it was able to grow well on three distantly related angiosperms in the experiment (*C. spinosum*, an Asterid; *G. fragrans* in Caryophyllales; *E. monticola*, a Rosid; see Fig. S5 in Appendix S6) in addition to parasitizing hosts from many orders of Angiosperms and a Gymnosperms in Puerto Rico and elsewhere (Kuijt 2011). Plant defences or physiological or molecular incompatibilities are candidate causes for the low survival and arrested growth seen in *D. caribaeus* on some of the trees used for the plant suitability experiment. For example, the bark layer and/or the xylem of some plants can impede the establishment or arrest the growth of mistletoes (Tainter & French 1971; Roth 1974; Hoffmann *et al.* 1986; Yan 1993a). It is still unclear why established mistletoes do not perform well on some plants, but possible explanations include the inability of the mistletoe's haustoria to produce the necessary enzymes to penetrate into xylem tissues, and the lack of sufficient cytokinins from hosts to stimulate mistletoe growth (Kuijt 1969; Yan 1993a).

In conclusion, our results underscore the importance of the interplay between host plant qualities and avian seed dispersal in shaping the local abundance of mistletoes. Differences in fruiting phenology of suitable hosts underlie part of the variation in patterns of mistletoe occurrence across plants in the community. This results in the establishment of *D. caribaeus* seedlings on more host species than what would be naturally observed in the field, showing that the behaviour of birds strongly limits the recruitment of *D. caribaeus*. It is also ecologically significant that the variation in the capacity of *D. caribaeus* to establish and survive on hosts is observed both within and across species of host. Such variability in

© 2017 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,

establishment and performance remains little understood and deserves attention by future studies to elucidate its role in the evolutionary ecology of plant hemiparasites, especially to determine if the mechanisms that control mistletoe establishment on hosts are molecular, allelic or epigenetic in nature.

Authors' contributions

M.A.C.O. and T.A.C. conceived the ideas and designed the study; M.A.C.O., T.A.C., A.G.C. and S.Y. collected and analysed the data; M.A.C.O. and T.A.C. wrote first draft of manuscript and all authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank Y. Gavilán, W. Hernández Aguiar and C. Venable for assistance in the field, and L. Añeses, A. Casas, A. Rodríguez, D. Cianzio and the personnel of Finca Montaña (University of Puerto Rico-Mayagüez) for providing access to the study site and assistance. We also thank J. Ross, D. Watson and two anonymous reviewers for their valuable comments to improve the manuscript. Gastón Sanchez provided assistance with the PLS-PM analysis. This research was supported by NSF grants DEB-1028174 and DEB-1145994 to T.A.C., the Alfred P. Sloan Foundation to M.A.C.O. and the Biology Department at the Pennsylvania State University. None of the authors have a conflict of interest to declare.

Data accessibility

All data used for this study are presented in the paper.

References

Aukema, J.E. (2003) Vectors, viscin, and Viscaceae: mistletoes as parasites, mutualists, and resources. *Frontiers in Ecology and the Environment*, **1**, 212–219.

Aukema, J.E. (2004) Distribution and dispersal of desert mistletoe is scale-dependent, hierarchically nested. *Ecography*, **27**, 137–144.

Aukema, J.E., Carlo, T.A. & Collazo, J.A. (2007) Landscape assessment of tree communities in the northern karst region of Puerto Rico. *Plant Ecology*, **189**, 101–115.

Calder, D.M. (1983) Mistletoes in focus: an introduction. *The Biology of Mistletoes* (eds D.M. Calder & P. Bernhardt), pp. 1–18. Academic Press, Sydney, NSW, Australia.

Caraballo-Ortiz, M.A. & Carlo, T.A. (2013) Resurrection of *Dendropemon sintenisii* (Loranthaceae): an endemic mistletoe from Puerto Rico. *Phytotaxa*, **82**, 1–6.

Carlo, T.A. (1999) *Diet, fruit preference and seed dispersal capabilities of fruit eating birds in north central Puerto Rico*. MS thesis, North Carolina State University, Raleigh, NC.

Carlo, T.A. & Aukema, J.E. (2005) Female-directed dispersal and facilitation between a tropical mistletoe and a dioecious host. *Ecology*, **86**, 3245–3251.

Carlo, T.A., Collazo, J.A. & Groom, M.J. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia*, **134**, 119–131.

Carlo, T.A. & Morales, J.M. (2008) Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density, and landscape aggregation. *Journal of Ecology*, **96**, 609–618.

Carlo, T.A. & Morales, J.M. (2016) Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. *Ecology*, **97**, 1819–1831.

Carlo, T.A. & Tewksbury, J.J. (2014) Directness and tempo of avian seed dispersal increases emergence of wild chiltepins in desert grasslands. *Journal of Ecology*, **102**, 248–255.

Clay, K., Dement, D. & Rejmanek, M. (1985) Experimental evidence for host races in mistletoe (*Phoradendron tomentosum*). *American Journal of Botany*, **72**, 1225–1231.

Daly, C., Helmer, E.H. & Quiñones, M. (2003) Mapping the climate of Puerto Rico, Vieques and Culebra. *International Journal of Climatology*, **23**, 1359–1381.

Edouard, J.A. (1991) La multiplication végétative du *Dendropemon caribaeus* Krug & Urban (Loranthaceae) observé à la Martinique. *Bulletin de la Société Botanique de France: Lettres Botaniques*, **138**, 79–84.

Engelbrecht, B.M., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. & Hubbell, S.P. (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–82.

Fadini, R.F. (2011) Non-overlap of hosts used by three congeneric and sympatric loranthaceous mistletoe species in an Amazonian savanna: host generalization to extreme specialization. *Acta Botanica Brasilica*, **25**, 337–345.

Fadini, R.F. & Cintra, R. (2015) Modeling occupancy of hosts by mistletoe seeds after accounting for imperfect detectability. *PLoS ONE*, **10**, e0127004.

Fadini, R.F., Gonçalves, D.C.M. & Reis, R.P.F. (2010) Consistency in seed-deposition patterns and the distribution of mistletoes among its host trees in an Amazonian savanna. *Australian Journal of Botany*, **57**, 640–646.

Fadini, R.F., Mellado, A. & Ghizoni, L.P. (2014) A host creates an enemy-free space for mistletoes by reducing seed predation caused by a woodboring beetle: a hypothesis. *Biotropica*, **46**, 260–263.

Glatzel, G. & Geils, B.W. (2008) Mistletoe ecophysiology: host-parasite interactions. *Botany-Botanique*, **87**, 10–15.

González-Castro, A., Yang, S., Nogales, M. & Carlo, T.A. (2012) What determines the temporal changes of species degree and strength in an oceanic island plant-disperser network? *PLoS ONE*, **7**, e41385.

González-Castro, A., Yang, S., Nogales, M. & Carlo, T.A. (2015) Relative importance of phenotypic trait matching and species' abundances in determining plant-avian seed dispersal interactions in a small insular community. *AoB Plants*, **7**, plv017.

Guerra, T.J. & Pizo, M.A. (2014) Asymmetrical dependence between a Neotropical mistletoe and its avian seed disperser. *Biotropica*, **46**, 285–293.

Hoffmann, A.J., Fuentes, E.R., Cortés, I., Liberona, F. & Costa, V. (1986) *Tristerix tetrandrus* (Loranthaceae) and its host-plants in the Chilean matorral: patterns and mechanisms. *Oecologia*, **69**, 202–206.

Honaas, L., Caraballo-Ortiz, M.A., McNeil, J. & dePamphilis, C.W. (2015) Cultivation of parasitic flower plants for research and teaching. *AERGC Newsletter (Association of Education and Research Greenhouse Curators)*, **27**, 4–8.

Kuijt, J. (1969) *The Biology of Parasitic Flowering Plants*. University of California Press, Berkeley, CA, USA.

Kuijt, J. (2011) Monograph of *Dendropemon* (Loranthaceae). *Systematic Botany Monographs*, **92**, 1–110.

Lira, J., Caires, C.S. & Fadini, R.F. (2017) 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. *Plant Ecology*, **218**, 251–263.

Luo, Y., Sui, Y., Gan, J. & Zhang, L. (2016) Host compatibility interacts with seed dispersal to determine small-scale distribution of a mistletoe in Xishuangbanna, Southwest China. *Journal of Plant Ecology*, **9**, 77–86.

Martinuzzi, S., Lugo, A.E., Brandeis, T.J. & Helmer, E.H. (2013) Case study: geographic distribution and level of novelty of Puerto Rican forests. *Novel Ecosystems: Intervening in the New Ecological World Order* (eds R.J. Hobbs, E.S. Higgs & C.M. Hall), pp. 81–87. Wiley & Sons, Hoboken, NJ, USA.

Messias, P.A., Vidal, J.D.D. Jr, Koch, I. & Christianini, A.V. (2014) 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. *Acta Botanica Brasilica*, **28**, 577–582.

Morales, J.M., Rivarola, M.D., Amico, G. & Carlo, T.A. (2012) Neighborhood effects on seed dispersal by frugivores: testing theory with a mistletoe–marsupial system in Patagonia. *Ecology*, **93**, 741–748.

Norton, D.A. & Carpenter, M.A. (1998) Mistletoes as parasites: host specificity and speciation. *Trends in Ecology & Evolution*, **13**, 101–105.

Okubamichael, D.Y., Griffiths, M.E. & Ward, D. (2014) Reciprocal transplant experiment suggests host specificity of the mistletoe *Agelanthus natalitius* in South Africa. *Journal of Tropical Ecology*, **30**, 153–163.

R Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Råberg, L., Graham, A.L. & Read, A.F. (2009) Decomposing health: tolerance and resistance to parasites in animals. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **364**, 37–49.

Rödl, T. & Ward, D. (2002) Host recognition in a desert mistletoe: early stages of development are influenced by substrate and host origin. *Functional Ecology*, **16**, 128–134.

Roth, L.F. (1974) Juvenile susceptibility of ponderosa to dwarf mistletoe. *Phytopathology*, **64**, 689–691.

Roxburgh, L. & Nicolson, S.W. (2005) Patterns of host use in two African mistletoes: the importance of mistletoe–host compatibility and avian disperser behaviour. *Functional Ecology*, **19**, 865–873.
Roxburgh, L. & Nicolson, S.W. (2008) Differential dispersal and survival of an African mistletoe: does host size matter? *Plant Ecology*, **195**, 21–31.
Sanchez, G. (2013) *PLS Path Modeling with R*. Trowchez Editions, Berkeley, CA, USA.
SAS Institute (2015) *JMP Pro, Version 12.1.0*. SAS Institute, Cary, NC, USA.
Tainter, F.H. & French, D.W. (1971) The role of wound periderm in the resistance of eastern larch and jack pine to dwarf mistletoe. *Canadian Journal of Botany*, **49**, 501–504.
Tenenhaus, M., Vinzi, V.E., Chatelin, Y.M. & Lauro, C. (2005) PLS path modeling. *Computational Statistics & Data Analysis*, **48**, 159–205.
Venable, D.L. & Brown, J.S. (1988) The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *The American Naturalist*, **131**, 360–384.
Watson, D.M. (2001) Mistletoe–a keystone resource in forests and woodlands worldwide. *Annual Review of Ecology and Systematics*, **32**, 219–249.
Watson, D.M. & Rawsthorne, J. (2013) Mistletoe specialist frugivores: latterday 'Johnny Appleseeds' or self-serving market gardeners? *Oecologia*, **172**, 925–932.
Wenny, D.G. (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research*, **3**, 37–50.
Yan, Z. (1993a) Resistance to haustorial development of two mistletoes, *Amyema preissii* (Miq.) Tieghem and *Lysiana exocarpi* (Behr.) Tieghem ssp. *exocarpi* (Loranthaceae), on host and nonhost species. *International Journal of Plant Sciences*, **154**, 386–394.
Yan, Z. (1993b) Germination and seedling development of two mistletoes, *Amyema preissii* and *Lysiana exocarpi*: host specificity and mistletoe-host compatibility. *Australian Journal of Ecology*, **18**, 419–429.
Yang, S., Albert, R. & Carlo, T.A. (2013) Transience and constancy of interactions in a plant-frugivore network. *Ecosphere*, **4**, 1–25.

Received 18 September 2016; accepted 4 April 2017

Handling Editor: Andrew MacDougall

Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Map of the study site.

Appendix S2. Potential hosts for *Dendropemon caribaeus* at the study site.

Appendix S3. Frequency of natural occurrence of *Dendropemon caribaeus* mistletoes at the study site.

Appendix S4. Height distribution for the three main hosts of *Dendropemon caribaeus* at the study site.

Appendix S5. Growth of *Dendropemon caribaeus* mistletoes on plants at 1 year after planting.

Appendix S6. Phylogenetic tree of angiosperms illustrating the position of plants used in the suitability experiment, the local tree species recorded during the mistletoe abundance survey at the study site in Puerto Rico, and known hosts of *Dendropemon caribaeus* reported in the literature.

© 2017 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.,