

# Competition and facilitation determine dwarf mistletoe infection dynamics

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## Summary

**1.** Interspecific interactions have a fundamental role in plant population dynamics, as they may set the conditions for species coexistence. Parasitic plants, like dwarf mistletoes, offer the opportunity to study competition for resources that are different from those consumed by most plants, allowing for a better understanding of the interaction.

**2.** We explored how interspecific interactions between two dwarf mistletoe species (*Arceuthobium*), co-infecting the same host species (even sharing the same individual tree of *Pinus hartwegii*) affect their infection dynamics at two different stages of population development (colonization of new hosts and subsequent growth), and if heterogeneity in resource availability (host density and size structure) affects these interactions. For that purpose, we integrated these processes into a spatially explicit model of density-dependent population growth.

**3.** We found that self-regulation (density-dependence) was strong for both species; however, the intensity and sign of interspecific interactions changed depending on host size and demographic process. Population growth in *Arceuthobium globosum* was reduced by competition, except for smaller hosts where *A. globosum* growth was facilitated by *Arceuthobium vaginatum*. *Arceuthobium vaginatum* was facilitated by *A. globosum* regardless of host size. Colonization of new hosts by *A. globosum* was enhanced by previous infection by the other species, showing intraguild facilitation.

**4.** Demographic importance of interactions depended on stand structure: in homogeneous, low-density forests, facilitation predominates, increasing the population sizes of both species, whereas the opposite occurs in heterogeneous and dense forests. Both species achieved stable coexistence, fulfilling the invasibility criterion because each mistletoe species can invade a forest that is already infected by the other species.

**5. Synthesis.** Despite the fundamentally different mechanisms underlying the interactions between mistletoes compared with non-parasitic plants, our results reveal that their behaviour at the population level is similar. Stabilizing mechanisms, like strong self-limiting population growth, allow dwarf mistletoe coexistence. Interactions shift as populations develop, and they depend largely on environmental factors such as forest structure. Intraguild mutualism is shown as a relevant process for colonization of new spaces, highlighting the complexity of competitive/facilitative interactions between parasitic plants, a formerly unexplored subject. Interactions can only be fully understood when integrating all their components at the population level. Analysing these interactions may contribute to the understanding of plant–plant interactions in general, and convey interesting implications for forest management.

**Key-words:** coexistence, interaction shift, interspecific interactions, intraguild facilitation, intraspecific competition, invasibility criterion, parasitic plants, plant–plant interactions, plant population dynamics

## Introduction

Interspecific interactions structure biological communities and shape different demographic processes within populations (Callaway & Walker 1997). Presently, a vast literature

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supports the idea that competition and facilitation are mechanisms that act in a combined and complex manner, favouring or hindering species coexistence, and thus affecting species richness (Bruno, Stachowicz & Bertness 2003; Brooker *et al.* 2008; Martorell & Freckleton 2014). Depending on the type and strength of interactions, stable or unstable coexistence may occur; both equalizing and stabilizing mechanisms drive this coexistence (Chesson 2000). Equalizing mechanisms minimize the magnitude of fitness differences, delaying local extinction but not preventing it. In contrast, stabilizing mechanisms occur when intraspecific competition is larger than the interspecific competition, indefinitely precluding the extinction of competing species (Chesson 2000; Adler, Hille Ris Lambers & Levine 2007). Under stable coexistence, population sizes are strongly bounded (Chesson 2000). If competition is mainly intraspecific, and species become rare due to external factors such as disturbances, competition is reduced and populations grow back to their previous numbers (Turelli 1978; Chesson 2000). This is better explained by the invasibility criterion: if competing species are able to invade (i.e. increase from low density) in the presence of the rest of the community, stable coexistence occurs (Turelli 1978; Chesson 2000). Stabilization mechanisms may arise in different ways, such as differences in the ecological requirements of the coexisting species (i.e. coexisting species do not have a complete niche overlap) or from specialist natural enemies (Chesson 2000). In such cases, species are strongly self-limited, keeping them from depleting resources and driving their competitors to extinction.

Taking space into account is important when analysing competition. Species segregation in space can act as a stabilizing mechanism too, because it ameliorates interspecific competition (Stoll & Prati 2001). Heterogeneity in resource distribution may enhance intra- and interspecific competition if the resources – and the competitors – are concentrated in specific areas, creating hot spots of interaction in nutrient-rich patches (Casper, Cahill & Jackson 2000; Hutchings, John & Wijesinghe 2003; Snyder & Chesson 2004). Since most of resources are heterogeneously distributed in nature, this can have significant ecological implications, even altering the outcome of interactions between species (Hutchings, John & Wijesinghe 2003).

Facilitative interactions may also promote species coexistence, if one species modifies the local environment benefiting neighbouring species with its presence (Callaway & Walker 1997). Moreover, competitive and facilitative mechanisms can operate simultaneously within the same species mixture (Callaway & Walker 1997), and interaction shifts can occur depending on factors like life stage, plant density, indirect interactions and abiotic environment (Callaway & Walker 1997; Martorell & Freckleton 2014).

The attempts to understand plant–plant interactions and their mechanisms of coexistence are numerous. Parasitic plants may provide new insights into these interactions because the resources they depend on are very different from those used by other plants, being even considered as plants with heterotrophic nutrition. At the same time, parasitic plants

share some basic attributes with autotrophic plants such as lack of mobility and modular growth. Although intuitively it is believed that two parasites tapping the same vascular system must be experiencing exploitative competition for the host's resources, the subject has not been explored formally. Few studies have analysed parasite–parasite interactions from an infection dynamics viewpoint (Scharpf & Parmeter 1982; Donohue 1995), and most of these studies are restricted to invertebrate parasites of animals (Hatcher & Dunn 2011). As it happens with non-parasitic organisms, these studies have shown evidence for stabilizing mechanisms: coexistence requires some degree of niche differentiation among competitors (Holt & Dobson 2006), or else one will exclude the others.

Parasitic plants such as dwarf mistletoes, offer the opportunity to test the effect of interspecific interactions on infection dynamics and the mechanisms of coexistence of sympatric plants with heterotrophic nutrition. Because dwarf mistletoes take most of their photosynthates from the vascular system of the host (over 70%; Hull & Leonard 1964), we can assume that competition is mainly for host resources (i.e. photosynthates, water and mineral nutrients) rather than for light. Dwarf mistletoes are common components of temperate forests and they are widespread on commercially valuable conifers (Mathiasen *et al.* 2008). For this reason, dwarf mistletoes have been a frequent subject of research, with an emphasis on their effects on the host (e.g. decreased growth and fecundity Mathiasen *et al.* 2008), changes in water use efficiency and decreased photosynthetic capacity (Meinzer, Woodruff & Shaw 2004). Studies on coexisting parasitic plants (either root or shoot parasites) are limited to the description of their distribution patterns (Watson, Roshier & Wiegand 2007; Fadini & Lima 2012; Queijeiro-Bolaños, Cano-Santana & García-Guzmán 2014), host preferences (Bolin, Maass & Musselman 2011; Li *et al.* 2012; Arruda *et al.* 2013) and their role on interaction networks (Genini *et al.* 2012); but an analysis of their interactions and coexistence mechanisms is still lacking.

Due to the host dependency of parasitic plants, stand structure (host spatial distribution, density, age and size structures) might be an important factor influencing vertical and horizontal spread and intensity of the mistletoe infection because of limited seed dispersal (Robinson & Geils 2006). This limitation may be important in dwarf mistletoes because they undergo predominantly ballistic dispersal, with vertebrates dispersing seeds rarely compared with other mistletoe species (Hudler, Oshima & Hawksworth 1979; Hawksworth & Wiens 1996). In general, mistletoe infection is clumped on a few trees while the rest have little infection (Aukema 2003; Shaw *et al.* 2005); that is, a high host density is associated with a low proportion of infected trees, but not necessarily with the number of parasites per host (Donohue 1995). Trees with larger crowns represent a better seed source, as it improves the dispersion area and also the light incidence on mistletoe shoots; thus, maintaining larger mistletoe populations (Arriaga, Franco & Sarukhán 1988; Shaw *et al.* 2005).

In this study, we explore interspecific interactions between two dwarf mistletoe species, *Arceuthobium globosum* and

*Arceuthobium vaginatum*, co-infecting the same host species, *Pinus hartwegii*, and their respective infection dynamics. We analyse how such dynamics depend on the intra- and inter-specific interactions within infected trees and on the colonization of new hosts, and test whether stable coexistence is expected based on the invasibility criterion, that is, the capability of mistletoe populations to recover when their density is low and the other species is at its equilibrium (Turelli 1978). The invasibility criterion is especially relevant for management, as it allows us to assess whether parasites can invade a forest that is already infected by other mistletoe species. Additionally, we analyse how spatial heterogeneity in resource availability (i.e. host density and size structure) correlates with the interactions among parasites.

## Materials and methods

### STUDY AREA AND SPECIES

The study site is the Papayo and Zoquiapan subregion within the Iztaccíhuatl Popocatepétl National Park (19°18'08.4" N, 98°42'10.7" W), Central Mexico, which is a 4-ha open *P. hartwegii* forest. The climate is temperate subhumid with rains concentrated from June to September; the average annual rainfall is 941 mm, and the mean annual temperature is 9.7 °C (Arriaga *et al.* 2002). The site is at 3420 m a.s.l., with negligible slope. Other tree species, such as *Alnus jorullensis* and *Abies religiosa*, also occur at low frequency.

In this area, two dwarf mistletoe species coexist parasitizing *P. hartwegii*: *Arceuthobium globosum* Hawksworth and Wiens subsp. *grandicaule* Hawksworth and Wiens and *A. vaginatum* (Willdenow) Presl subsp. *vaginatum*. The two species closely resemble each other in that both have scale-like leaves, with flowers, fruits and leaves the same colour as the shoots. *Arceuthobium globosum* is yellow-green shrub of 18–70-cm height, whereas *A. vaginatum* is a dark brown or blackish shrub 20–55 cm in height. Both are widely distributed in Mexico and are considered to cause important damage on pine forests (Hawksworth & Wiens 1996). In Mexico they have been reported to parasitize 13 and 14 pine species, respectively, seven of which they share. At our study site they parasitize *P. hartwegii*, even sharing the same individual tree. They have a ballistic dispersal mechanism in which their seeds are explosively discharged, reaching a maximum distance of 14 m (Robinson & Geils 2006). Colonization of new hosts is favoured by large tree-crowns with larger seed-catching areas (Arriaga, Franco & Sarukhán 1988). Unlike other dwarf mistletoes, these two species develop over the whole host, including the tree trunk (Quejjeiro-Bolaños, Cano-Santana & Castellanos-Vargas 2011).

### FIELD SURVEY

Interactions and their effects on populations can be estimated from repeat-survey abundance data if we have a long observational period and a large amount of individuals (Freckleton & Watkinson 2001). To produce such data, in November 2008 we marked all the *P. hartwegii* individuals taller than 1.5 m ( $N = 276$ ), in an area of 11 000 m<sup>2</sup> within the Papayo subregion. These pines were either not infected ( $N = 95$ ), infected with *A. globosum* ( $N = 98$ ), with *A. vaginatum* ( $N = 27$ ) or with both species ( $N = 56$ ). We assessed the dwarf mistletoe infection on each tree every 6 months for 3 years using a Modified Dwarf Mistletoe Rating system (MDMR; Quejjeiro-Bolaños & Cano-Santana 2016) based on Hawksworth

(1977). The conventional DMR is not recommended for small trees or for trees with irregular branching and long poles (Hawksworth 1977). Moreover, it does not consider stem infection, which is very common on our study species, and it does not distinguish light from severe infections. Because we required a more precise measure of the infection to be able to detect changes through time, in our rating system the tree was divided into thirds, and each third was qualitatively rated. We used the following values for each third of the tree: 0, no infection; 1, a sprout or branch hypertrophy; 2, less than 20% of branches infected; 3, 21–30% of branches infected; 4, 31–50% of branches infected; 5, 51–70% of branches infected; and 6, more than 71% of branches infected. Afterwards, the thirds ratings were added, giving an index ranging from zero to 18. Additionally, we measured the stem diameter at breast height (dbh) for each pine tree and the distance between all trees.

### INFECTION DYNAMICS MODELLING

Dwarf mistletoe infection dynamics involves two main population processes: spread into uninfected hosts, which we will refer to as colonization, and changes in the amount of mistletoe (including possible disappearance) within infected hosts, which we will call infection growth (Shaw *et al.* 2005). Dwarf mistletoes form clumps making it very difficult to discern between individuals, so we used the MDMR ratings as a measure of abundance in a host. Thus, infection dynamics in this paper does not have the meaning of changes in the number of individuals through time, although it is a related concept.

We set a discrete-time model for population dynamics that allowed us to estimate the intensity of the interactions and to project their effects to the whole population. For both species we modelled separately infection growth and colonization of uninfected trees. The models that describe these processes were chosen after a thorough procedure in which different functions were tested considering different factors (presence/absence of interspecific competition, effect/no effect of tree-size, effect of distance to and MDMR of neighbouring infected trees), and obtaining the ones with the lowest Akaike Information Criterion. Here, we report only the selected models, while the selection procedure is detailed in Appendix S1, Supporting Information.

The growth models tested had all the same structure: they were the sum of the dynamics within a tree (e.g. changes in size or death of already established mistletoes plus recruitment from seeds produced within a host) plus a term including the effects of seeds that arrive to the tree from neighbouring, infected trees. The within-host component of the model was chosen from discrete-time growth models that have proved useful for plants (Gompertz, Hassell and Ricker models; Dennis *et al.* 2006; Freckleton & Watkinson 2001). The component related to immigrating seeds was either zero (no effect of seed rain in colonized trees), a constant (as it would be expected if all seeds were produced out of the stand) or a term that depended on mistletoe. In the latter case, different options in which the distance to other infected trees or their size were or were not considered (see Appendix S1 for details).

The growth models were fitted using only data from trees that were already colonized by the focal species at time  $t$ . For both mistletoes, the selected function to model the mean MDMR at time  $t + 1$  in a host tree  $i$  was a modification of the Gompertz growth equation (Dennis *et al.* 2006),

$$N_{i,t+1} = N_{i,t} \cdot \exp(r + (\alpha - 1) \cdot \ln N_{i,t} + \beta \cdot \ln S_{i,t}) + \gamma \cdot M_{i,t}, \quad \text{eqn 1}$$

where  $N_{i,t}$  is the MDMR of the focal species in the  $i$ -th tree at time  $t$ ,  $S_{i,t}$  is the MDMR of the associate species in the  $i$ -th tree at time  $t$ ,  $\gamma$  is a conversion parameter,  $r$  is the intrinsic rate of increase in MDMR

of the focal species, and  $\alpha$  and  $\beta$  represent the intraspecific and interspecific interaction parameters respectively. In *A. globosum*, we found that a linear dependency of  $r$ ,  $\alpha$  and  $\beta$  to the size (dbh) of the  $i$ -th host  $D_i$  described better the data than assuming them constant (for instance,  $r = r_0 + r_1 D_i$ , where  $r_0$  and  $r_1$  are parameters). The converse occurred in *A. vaginatum* where the parameters were constant for all trees irrespective of their size. It must be noted that the distribution of  $N_{i,t}$  was best described in *A. globosum* by a negative binomial distribution (thus requiring an additional parameter to describe the variance around the mean) and in *A. vaginatum* by a binomial distribution. Finally, immigration  $M_{i,t}$  is a measure of the potential influx of seeds into the  $i$ -th tree at time  $t + 1$  from neighbouring hosts, and was found (see Table S1.1) to be best modelled as:

$$M_{i,t} = \sum_{j \neq i} N_{j,t} \cdot D_j / d_{ij} \quad \text{eqn 2}$$

where  $N_{j,t}$  is the MDMR of the neighbouring tree  $j$  at time  $t$ ,  $D_j$  is the dbh of the  $j$ -th tree and  $d_{ij}$  is the distance between trees  $i$  and  $j$ .

The functions that described the colonization of previously uninfected trees were different from those not only used for infection growth but also had two components: one related to the influx of seeds from the neighbourhood and another reflecting the status of the tree that received such seeds. We will refer to the first as colonization potential. This can be envisaged as a number of seeds that arrive to the site where a host is found, and can thus potentially colonize it. Only a fraction (hereafter named colonization restriction) of these seeds is actually intercepted by the host itself and become established. This colonization restriction is likely to depend on host size (Arriaga, Franco & Sarukhán 1988) and on the presence and MDMR of the associated species (Queijeiro-Bolaños, Cano-Santana & García-Guzmán 2014). In contrast, colonization potential may depend on the MDMR of the focal species in neighbouring trees and the distance to them, as stated earlier.

To model colonization we used only data of trees with no infection at time  $t$  ( $N_{i,t} = 0$ ), and modelled their MDMR at first infection time ( $t + 1$ ). We tested the same functions described above for immigrating individuals in the growth function. Because the infection of a previously uncolonized tree depends entirely on the propagules provided by the mistletoes existing in neighbouring trees, colonization of the  $i$ -th tree,  $c_{i,t}$ , due to dispersion from its vicinity was best described by (see Appendix S1, Table S1.2):

$$c_{i,t} = \delta \cdot \sum_{j \neq i} N_{j,t} / d_{ij}, \quad \text{eqn 3}$$

where  $\delta$  is a conversion parameter. Note that this is basically equivalent to eqn 2 without the size of the neighbouring trees. Colonization may be restricted by the size of the host and the pre-existing infection of the associated species. The restriction may range from non-existent (in which case 100% of the colonization potential is achieved) to complete (i.e. the MDMR of the focal species may remain as zero despite seed arrival). Hence, the restriction ( $h_i$ ) was modelled as a logistic function, which is bounded between zero and one. The selected model (Appendix S1, Table S1.2) was:

$$h_{i,t} = \exp(\varepsilon + \zeta \cdot S_{i,t}) / (1 + \exp(\varepsilon + \zeta \cdot S_{i,t})), \quad \text{eqn 4}$$

where  $\zeta$  is the interspecific interaction intensity during colonization. In the case of *A. globosum*,  $\varepsilon$  depended linearly on  $D_i$ . In both species, the MDMR at time  $t + 1$  of previously uncolonized trees was found to follow a negative binomial distribution with mean (Table S1.2):

$$\mu = c_{i,t} \cdot h_{i,t}. \quad \text{eqn 5}$$

The models' parameters were estimated through maximum likelihood using the observed changes in MDMR in infected trees every

semester as input data (Freckleton & Watkinson 2001). We used the dream package (Guillaume & Andrews 2012) to explore the likelihood function over a space of possible parameter values and find a set of parameter values close to the global maximum of this function. Once this set was found, we used the optim function in R (R Development Core Team 2012) to find the actual set of values at the global maximum. Appendix S1 describes the use of these algorithms in full detail and Appendix S2 presents the associated R code used to fit the models.

## DEMOGRAPHIC IMPORTANCE OF INTERACTIONS

To estimate the demographic importance of interactions, that is, their effect on the population sizes of both mistletoe species (Martorell & Freckleton 2014), we performed spatially explicit simulations of the infection dynamics of each species growing alone and in a mixture. In each simulation, we started with a forest with 270 hosts (similar to the number of individuals sampled), a random subset of which were infected. Using eqns (1) and (5) and negative binomial random number generators (except for *A. vaginatum* growth, for which we used binomial), we proceeded to simulate the changes in MDMR in each host over time (see Appendix S1). The model was iterated 3000 times. The population size  $N$  was estimated as the sum of the MDMR in all trees in the forest averaged over the last 2500 iterations. The first 500 were dropped as they reflected only transient dynamics. The demographic importance of the interactions was calculated as a log-response ratio (Goldberg & Scheiner 2001):

$$I = \ln(N_c / N_a), \quad \text{eqn 6}$$

where  $N_c$  is the population size of the focal species in coexistence with the second, and  $N_a$  is the population size in the absence of the associated species. Positive  $I$  values indicate that the population size increases in the presence of the associated species, that is, the net effect of the interaction is facilitative; in contrast, competition predominates if  $I$  is negative.

The demographic importance of the interaction may depend on the attributes of the forest such as density and size structure (Fichtner *et al.* 2012). Thus, we performed simulations changing the stand density, the mean dbh of hosts, and the heterogeneity of dbh values in the stand. We used the densities 0.01, 0.02, 0.05, 0.1 and 0.2 ind m<sup>-2</sup> (the observed density was 0.02). A dbh value was assigned to each tree in the artificial forest using a truncated log-normal distribution (to avoid extremely large, unrealistic dbh values) with means 0.1, 0.15, 0.25 and 0.4 m (which are within the observed dbh range in the study site) and standard deviations 0 (homogeneous forest), 0.05, 0.10, 0.15 and 0.20 m (highly heterogeneous forest; see details in Appendix S1).

To assess if coexistence is stable through the invasibility criterion, that is, if the presence of one mistletoe species does not preclude infection by the other, we performed a second set of simulations. We generated an artificial forest with 270 trees, setting the density and dbh of the hosts to the values observed in our forest (see Appendix S1 for a full description of this procedure). We infected some trees with one of the mistletoe species, and iterated the model until it attained its equilibrium population size. We then introduced the other species by infecting different numbers (1, 2, 3, 5, 10, 25, 50, 75 and 100 trees) of randomly selected trees with an initial MDMR of one. The model was then iterated 100 times, and we recorded whether the new species was still present. If so, it was considered that the invasion was successful. This procedure was repeated 500 times. Another set of identical simulations was performed, except

that the invader mistletoe was introduced into a forest where the associated species was absent. Appendix S2 presents the associated R code used to perform the simulations.

## Results

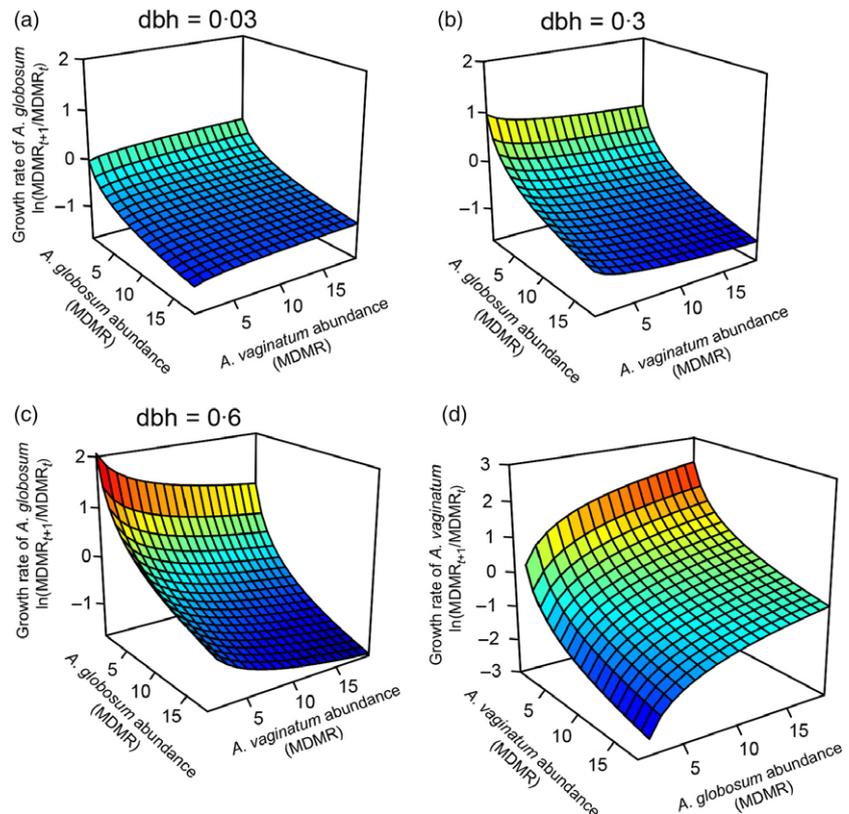
The function that best described dwarf mistletoe growth dynamics was the Gompertz model (eqn 1) with negative binomial distribution for *A. globosum* ( $R^2 = 0.44$ ) and binomial for *A. vaginatum* ( $R^2 = 0.36$ ), where both intra- and interspecific interactions affect these dynamics. The growth rate of both mistletoe species was larger in trees with several large, heavily infected trees in its vicinity, that is, with high immigration rates (eqn 2).

Both species displayed strong intraspecific competition (see the slope, that is, the decrease in growth rate per MDMR unit in Fig. 1). It became more intense with host size for *A. globosum* (Fig. 1a–c), but did not depend on the tree's dbh for *A. vaginatum* (Fig. 1d). Likewise, interspecific interactions for *A. globosum* depended largely on the host size, where an interaction shift occurred between small and larger trees: in small trees (dbh = 0.03 m, Fig. 1a) the growth rate of *A. globosum* increased with *A. vaginatum* abundance, indicating a greater probability of intensification of *A. globosum* under the presence of the second species. In contrast, in larger trees (dbh = 0.3 and 0.6; Fig. 1b and c), a transition towards competition occurred. It is important to note that even on the largest trees interspecific competition was milder than the intraspecific interaction (as shown by the steeper slope over the conspecific density axis compared with the heterospecific

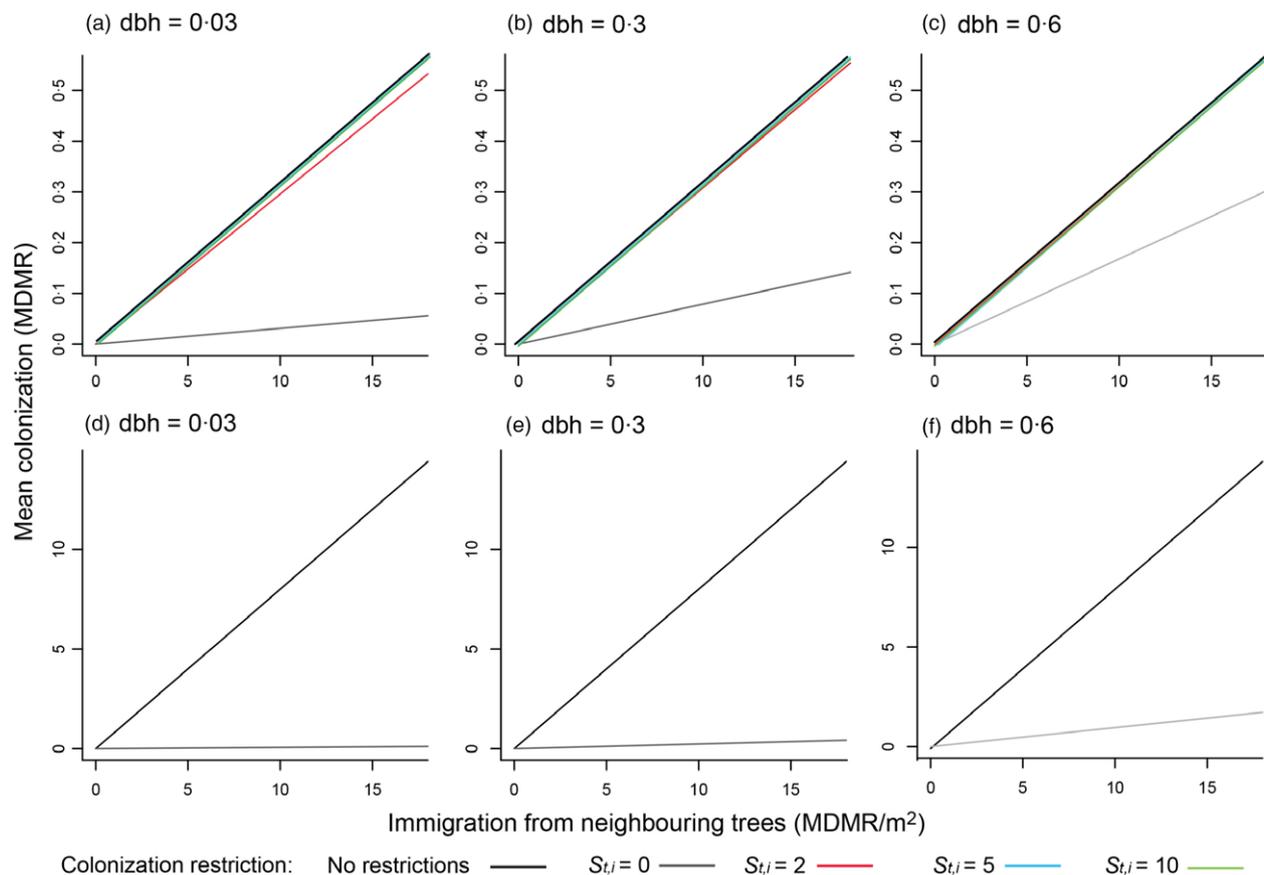
axis; Fig. 1c). Tree size did not affect interspecific interactions for *A. vaginatum*, where this species was always strongly facilitated by *A. globosum* (Fig. 1d).

For both species, colonization (eqn 5) depended on the distance to infected neighbouring trees and their MDMR, indicating that greater densities of heavily infected hosts in the vicinity resulted in greater chances that a healthy host became infected (Fig. 2). Host size imposed an important restriction in colonization for both species, where mean number of colonists was severely reduced when the restriction was introduced (Fig. 2,  $S_t = 0$ ). However, the restriction for *A. globosum* was less severe in medium and large size trees (Fig. 2b and c), and in the presence of *A. vaginatum* the mean number of colonists increased, even matching the colonization without restriction in trees that were already infected by the second species ( $R^2 = 0.103$ , Fig. 2a–c). In contrast, the presence of the associated species had no effect on *A. vaginatum* colonization ( $R^2 = 0.062$ ; Fig. 1d–f).

Once the growth and colonization models were combined to estimate the overall demographic importance of interactions, contrasting effects on the interspecific interactions experienced by both species became apparent. The sign and magnitude of the demographic importance depended on host's dbh, density and stand heterogeneity. This was very evident for *A. globosum* (Fig. 3, left column), where positive interactions were of great importance on homogeneous stands, composed of small trees (mean dbh < 0.25 m): whereas this species was unable to persist in low-density stands ( $\leq 0.05$  ind  $m^{-2}$ ) with homogeneous, small-sized trees (mean dbh  $\leq 0.15$  m and standard deviation = 0 or 0.05 m; Fig. 3a, c



**Fig. 1.** Growth rate of the two dwarf mistletoes species as a function of their own abundance and the abundance of the second species. Abundance is reported following the Modified Dwarf Mistletoe Rating (MDMR) system, which in this study ranges from 0 to 18. Host diameter at breast height (dbh) was only important for *Arceuthobium globosum*, where (a) dbh = 0.03, (b) dbh = 0.3 and (c) dbh = 0.6, but not for *A. vaginatum* (d). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**Fig. 2.** Colonization of *Arceuthobium globosum* (a, b and c) and *A. vaginatum* (d, e and f) as a function of the mean colonization (x-axis; following eqn 3) and the host mean dbh. The lines within each plot represent differences in the colonization restriction: no restriction, host size restriction (where  $S_{t,t} = 0$ ) and size restriction plus presence of the other species ( $S_{t,t} \neq 0$ ).  $S_{t,t}$  refers to the associated species MDMR at the  $i$ -th tree at time unit  $t$ . [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

and e), with slightly higher densities (Fig. 3g and i), *A. globosum* was able to persist only if *A. vaginatum* was also present. This facilitative effect vanished as tree size increased. On larger trees (mean dbh  $\geq 0.25$  m), regardless of stand density, interactions were mainly competitive, and its importance increased with forest heterogeneity.

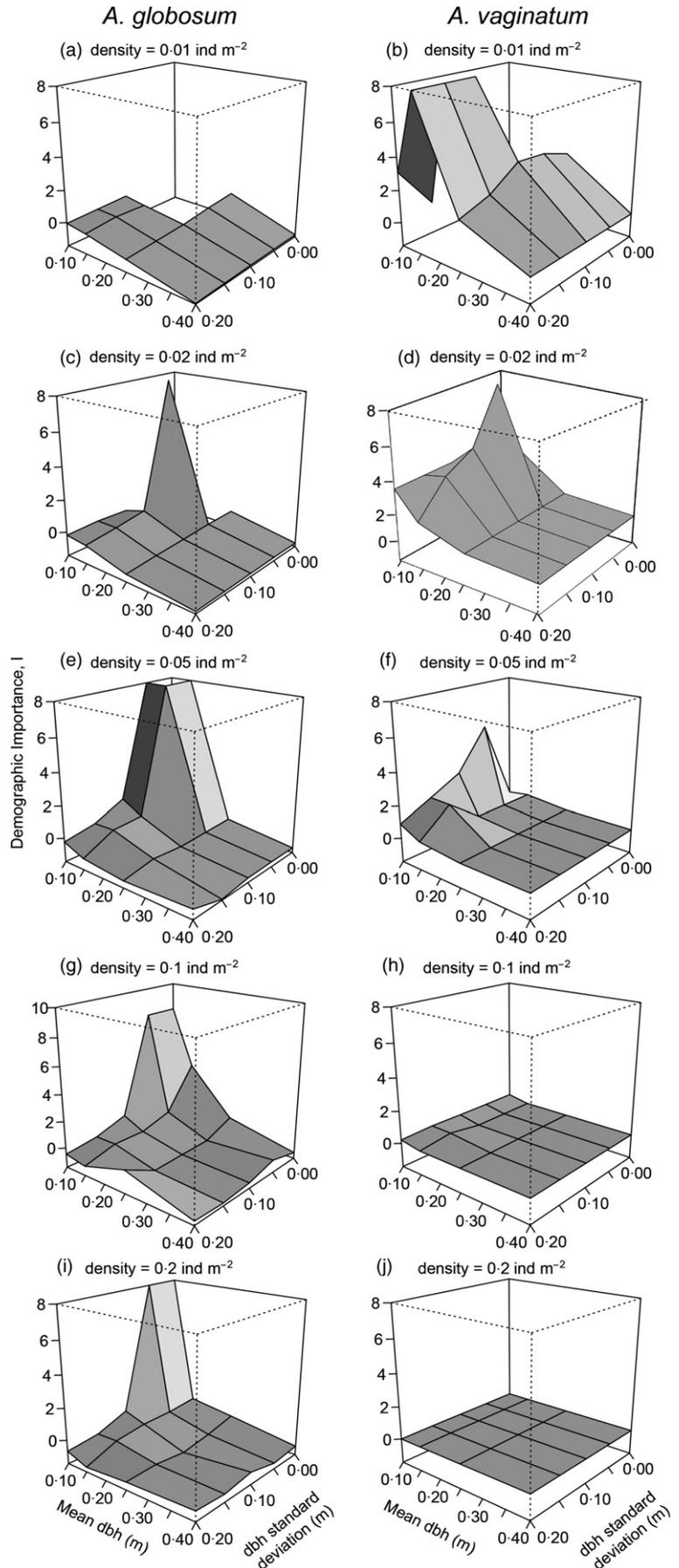
For *A. vaginatum*, a trend is observed in relation to forest density (Fig. 3 right column), where interactions became less important as stand density and mean size increased. Like *A. globosum*, this species cannot persist in low-density stands ( $\leq 0.02$  ind  $m^{-2}$ ) with homogeneous, small-sized trees (mean db  $\leq 0.15$  m and standard deviation = 0 or 0.05 m). But, for the rest of the combinations on the low-density forests ( $\leq 0.02$  ind  $m^{-2}$ ; Fig. 3b and d) the effects of *A. globosum* were positive. Such facilitative effect was particularly important in stands with a mean dbh of 0.15 m and relatively low densities. Under such conditions, *A. vaginatum* may not even persist in the absence of *A. globosum* depending on stand heterogeneity (Fig. 3b and d).

Both mistletoe species were capable of invading stands even when only one tree was initially infected, regardless of whether the other species was already present or not. Stand infection probability for both species increased rapidly with the number of trees initially infected. In *A. globosum*, the

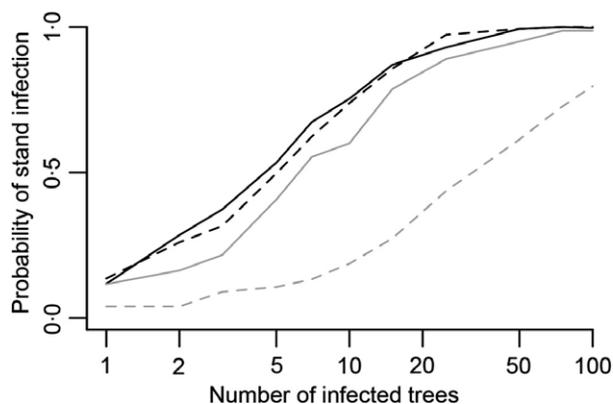
probability of successful invasion was not strongly affected by *A. vaginatum* (Fig. 4), where there seems to be no difference between the probabilities of infection under these two conditions. On the other hand, *A. vaginatum* showed a greater probability of invading a plot if the associated species was already present (Fig. 4).

## Discussion

Numerous studies have tested the role of intra- and interspecific interactions on plant population dynamics; nevertheless, very few of these have focused on parasitic plants (see Hautier *et al.* 2010 for an example including density dependence on *Rhinanthus alectorolophus*). Despite the large difference in the resource supply of non-parasitic plants and dwarf mistletoes, their population dynamics shared some characteristics with non-parasitic plants, such as: (i) population dynamics is driven by interactions, both intra- and interspecific (Volkov *et al.* 2009; Martorell & Freckleton 2014); (ii) resource availability and heterogeneity have an important influence on strength and sign of the interactions (Casper, Cahill & Jackson 2000; Hutchings, John & Wijesinghe 2003); (iii) coexistence is promoted by stabilizing mechanisms related to the self-regulation of each species that arises from intraspecific



**Fig. 3.** Demographic importance ( $I$ , following eqn 6) of the interactions between the two mistletoe species in forests with different forest densities and tree sizes. Effects on *Arceuthobium globosum* are shown on the left column and on *A. vaginatum* on the right one. Missing portions of the surface in the plots correspond to mean and variance combinations in which the species cannot persist in the forest. Interaction values  $>8$  represent the cases where a species cannot persist in the absence of the other (and thus rather correspond to  $+\infty$ ), and are added to aid visualization. dbh = diameter at breast height of the host tree.



**Fig. 4.** Probability of stand infection (y-axis) depending on the number of initial trees infected (x-axis) with a MDMR = 1. The lines within the plot correspond to the two species (black: *Arceuthobium mglobosum* and grey: *A. vaginatum*) with two different conditions: no previous mistletoe infection (dashed lines) or previously infected by the second species (continuous line).

competition (Adler, Hille Ris Lambers & Levine 2007; Johnson *et al.* 2012; Martorell & Freckleton 2014); (iv) facilitation is important for species establishment (Callaway & Walker 1997); and (v) interaction shifts occur depending on the demographic process (Martorell & Freckleton 2014). However, it is important to highlight the particularities that this parasitic system provides.

#### INTRA- AND INTERSPECIFIC EFFECTS

We found compelling evidence not only for interspecific competition but also for intraguild mutualism among mistletoes. Intraguild mutualism takes place among species that consume the same resource and thus compete, but yet may have positive effects on each other, such as improved access to resources or inhibition of a third competitor (Crowley & Cox 2011), which eventually can be translated into population growth. Recent evidence shows that intraguild mutualism may be much more common in nature than previously thought (Crowley & Cox 2011). The mechanisms for the competitive effect that mistletoes have on each other, that is, resource consumption, are straightforward to envisage, but it is less clear why facilitation occurs. Three hypotheses can be advanced in this respect:

**1** In parasitic species, a species may facilitate infection of a second one by weakening the host and reducing its resistance (Tkacz & Schmitz 1986; Nebeker *et al.* 1995). This would be a case of by-product facilitation between parasites because consumption by one predator modifies the prey's conditions, benefiting the second predator (Crowley & Cox 2011).

**2** It is known that photosynthates produced by mistletoes may provide some resources to their host (Hawksworth & Wiens 1996); needleless pines survive longer when they are infected than the uninfected ones as a result of a possible translocation of photosynthates from mistletoe to the host (Weir 1916; Rediske & Shea 1961). Thus, the availability of nutrients may be changed by the presence of one parasitic

plant. The latter may benefit nutrient uptake by a second species, especially on small-sized trees that may have less resources. Facilitation was found to take place especially on smaller trees, regardless of the mistletoe species or the process (colonization or growth) analysed; however, physiological relationships within this context need further research.

**3** Birds can incidentally transport dwarf mistletoe seeds on their feathers, and often prefer to use infected trees for nesting or feeding, thus enhancing colonization of new trees or intensification on already infected ones (Hudler, Oshima & Hawksworth 1979; Aukema 2003). The latter would be relevant if birds promote a directed dispersal by moving seeds specifically towards previously colonized trees by either species. Our models include a term for immigration, but it is purely phenomenological and does not depict any specific dispersal mechanism, and thus sheds no light on how animal vectors may affect mistletoe spread.

As expected from coexistence theory, stabilizing mechanisms seem to be involved in the coexistence of the mistletoe species. This is the case when populations undergo strong self-regulation (Chesson 2000). It was evident that intraspecific competition was intense for both species, thus, self-limiting population growth and precluding competitive exclusion (Chesson 2000). In contrast, interspecific competition was milder than the intraspecific one (in the case of *A. globosum*) or even undetectable (we found only evidence of facilitation in *A. vaginatum*). Niche differences, which can arise from differences in resource uptake or specialized predation (Levine & Hille Ris Lambers 2009), cause species to limit their own population more than they limit their competitors, resulting in a negative frequency-dependent growth (Levine, Adler & Hille Ris Lambers 2008). There is some evidence that hints at niche differences in our dwarf mistletoes, which have a differential distribution over the host stem, with *A. vaginatum* located more frequently in the lower parts of the tree (Quejido-Bolaños, Cano-Santana & Castellanos-Vargas 2011). Although stabilizing mechanisms have been discussed in different studies dealing with 'ordinary' competition (see for example Chesson 2000; Adler, Hille Ris Lambers & Levine 2007; Levine, Adler & Hille Ris Lambers 2008; Levine & Hille Ris Lambers 2009), our results show that positive interactions may enhance stability when intraguild facilitation occurs. In this sense, the fact that the probability of stand invasion by *A. vaginatum* (and to a lesser degree *A. globosum*) increases with the presence of the other mistletoe species shows that the facilitation makes an important contribution to stable coexistence.

#### DEMOGRAPHIC IMPORTANCE

Resource availability and spatial arrangement, in this case represented by host size, density and stand heterogeneity, have been recognized as important factors influencing the outcome of interactions on population dynamics of two or more competing species (Casper, Cahill & Jackson 2000; Hutchings, John & Wijesinghe 2003). Our results suggest that this

is also the case in mistletoes. The importance and sign of interactions depended on stand structure. Under some conditions, the negative component of the intraguild mutualism interaction predominated, while facilitation prevailed in others.

Heterogeneous environments, where resource quality is variable – in this case uneven sized stands –, may enhance interspecific competition and intraspecific aggregation (Casper, Cahill & Jackson 2000). Dwarf mistletoes have short-distance dispersal mechanisms, with seed dispersal up to 14 m (Robinson & Geils 2006), and in many cases limited to the same source tree. This would cause intraspecific aggregation and augment intraspecific competition. Large trees also represent nutrient-rich patches that concentrate a greater amount of competing individuals (Casper, Cahill & Jackson 2000; Hutchings, John & Wijesinghe 2003). It has been reported that in uneven-aged forests, dwarf mistletoes clump on larger trees, creating interactions ‘hot spots’ (Smith 1977; Shaw *et al.* 2005). Stands with small trees and low heterogeneity would lack such clumping. This could ameliorate the negative component of the mistletoe–mistletoe interactions, and may contribute to explain why facilitation predominates under such conditions.

Facilitation is very important in forests with low heterogeneity, especially those composed of small trees and low densities. It is known that low-density, open stands favour mistletoe spread, as light incidence improves fruiting and seeding (Shaw *et al.* 2005). At high densities, we would expect competition to predominate as the resource becomes depleted, as Fig. 3 shows, so the positive components of the interaction are likely to become more important at low densities. This may prevent either species from becoming extinct when it is at low density, fulfilling the invasibility criterion (Turelli 1978). The fact that the probability of invasion at very low densities of the focal mistletoe species was always increased when the associated species was present (even if the associated species may have a negative effect on the population size of the focal one when both are at equilibrium densities) illustrates how a stabilizing effect may arise from intraguild facilitation.

Our simulations provide some interesting insights on the role of dispersal and facilitation on mistletoe dynamics. At low densities, especially when trees are small, both species always become extinct. This may occur if the colonization of new trees fails to counterbalance the stochastic extinction events from individual hosts. This may happen because of two different processes: (i) When density is low, the pines are far away to each other, making colonization events unlikely; (ii) In the growth models for both species, large trees in the neighbourhood of a given tree increase its MDMR. Pines with low MDMR are more likely to lose their parasites due to chance reductions in infection intensity. If the density of the stand or the sizes of the trees are slightly larger to that where both species go extinct, then one of the mistletoes can persist in the system. It is interesting that in those cases the presence of the other parasitic species is promoted. Such strong dependence on a facilitator under conditions that can be deemed as

‘extreme’ for the facilitated species have been already reported for other plant species that are near the limits of their environmental tolerance (Liancourt, Callaway & Michalet 2005; Brooker *et al.* 2008).

As it happens, in most studies where interactions are estimated from time-series data, the amount of variation explained by our fitted models was relatively small, especially for the colonization models. This suggests that there are other ecological factors, not accounted for in this study that could be significant for the infection dynamics of dwarf mistletoes. Natural enemies, such as birds, mammals and insects, have been registered using different parts of mistletoes (shoots, fruits or seeds) (Hawksworth & Wiens 1996; Watson 2001). For mistletoe’s Mexican taxa, the information about associated animals is scarce; in a study done in the same area and mistletoe species, the interaction with vertebrates seems weak, however, arthropods from 15 different orders were recorded (Chávez-Salcedo 2013). The evidence for herbivory in that study was negligible, perhaps due to the small size of these arthropods, so it is believed that its effect on mistletoes is minor. Nonetheless, such natural enemies, if they are species-specific, could explain the strong density dependence observed in the mistletoes (Chesson 2000), and thus may offer an alternative explanation to competition. Field and experimental studies are necessary to understand the role of these natural enemies on population dynamics.

Other factors that we did not measure may have considerable effects on the predictive power of our model, such as fires, which did not occur during our study. Nevertheless, on the same time period, fires were observed at nearby areas, after which incidence (percentage of infected trees) increased or decreased (Queijeiro-Bolaños & Cano-Santana 2015). Thus, such events may lead to different dynamics in the long run than those simulated in the present study.

#### IMPLICATIONS FOR MANAGEMENT

The key role of mistletoes in biological communities has been poorly acknowledged (Watson 2001). These taxa have long been seen as harmful parasites, so control methods have emerged frequently in literature, including biological, chemical and genetic resistance methods (Hawksworth & Wiens 1996; Geils & Hawksworth 2002; Shaw, Oester & Filip 2009). The most used one is silvicultural control, which usually involves making modifications to the stands, such as reducing tree density, removal of the infected overstorey or ensuring an even age composition (Hawksworth & Wiens 1996; Shaw, Oester & Filip 2009). If we consider management through stand structure modification, ignoring facilitation in low-density homogeneous stands, we may inadvertently promote facilitation processes between mistletoes species.

As may be expected in intraguild facilitation, we also found evidence for competition. Under certain conditions, competition between predators may reduce the effects that they have on prey compared to the case where only one predator is present, although the opposite may also happen (Sih, Englund &

Wooster 1998). However, competition between mistletoes probably arises because they deplete resources (tree sap), which would have a negative impact on the host that also depends on them.

Our results also suggest that modifying the stand structure can be used to control mistletoe populations, but only for a short time. Reducing the stand's density by felling the largest trees may result in a sparse forest of small pines where none of the mistletoe species can persist. However, as trees grow, the eventual colonization of the stand by one of the species may rapidly make it suitable for the other. Only a strict and rapid eradication of any invading mistletoe species would prevent this from happening.

In conclusion, interactions between dwarf mistletoes present an overlooked and underestimated research opportunity, where negative interactions resemble below-ground competition of non-parasitic plants, involving resources such as water, mineral nutrients and space (Casper, Cahill & Jackson 2000), but where competition for light is negligible. These species also display facilitation, as it happens in many other plants. It is interesting to note that, despite the peculiarities of the mistletoe resource-acquisition strategies, our results coincide with what theory states for non-parasitic plants in terms of population dynamics. It remains an interesting question how these processes function with coexisting parasitic species, where, from our results, interactions shifts and invasibility are perceived as emerging research subjects on parasitic plants with important implications for forest management and conservation.

## Authors' contributions

M.Q.-B., C.M. and Z.C.-S. conceived the ideas and designed methodology; M.Q.-B. collected the data; M.Q.-B., C.M. and E.G. analysed the data. All authors contributed critically to the drafts and gave final approval for publication.

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## Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.tm5sv> (Queijeiro-Bolaños et al. 2016).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Modelling and simulation procedures.

**Appendix S2.** R code for the modelling and simulation procedures.