Why mistletoes are more aggregated in disturbed forests? The role of differential host mortality

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A B S T R A C T

Mistletoes rely on biotic seed dispersal to ensure their recruitment on appropriate host plants, as their seeds must be deposited on safe sites to allow attachment. As most host-parasite systems, mistletoe's spatial distribution depends on the spatial arrangement of the hosts and on the seed disperser's behavior. We used the mistletoe *Tristerix corymbosus*, which is solely dispersed by the arboreal marsupial *Dromiciops gliroides*, and it is capable to parasitize a wide range of hosts. We previously found *T. corymbosus* mistletoes to be more abundant and densely aggregated in disturbed habitats, compared to neighboring native forests, at similar levels of disperser abundance and host availability. To explain this pattern, we tested two non-mutually exclusive hypotheses: (1) the larger resource availability in disturbed habitats modify the disperser behavior reducing its home range, and (2) plant species in disturbed habitats are better hosts and offer higher survival probabilities. We sampled 300 mistletoes (98 at the native forest and 202 at the disturbed habitat), which were followed from November 2011 to March 2015 for estimating survival rates and conducting point-pattern analyses. Besides, we tracked ten *Dromiciops gliroides* individuals using VHF telemetry at both habitats to estimate the home range areas in the two habitats. Mistletoes were aggregated in both habitat types, being stronger at the disturbed habitat with dense plant clumps. Besides, no differences were found on home range of individual *D. gliroides* between habitats despite structural and resource availability differences. However, mistletoe survival significantly differed between habitats, as mistletoes had a survival probability of 82.87% at the disturbed habitat, whereas survival probability at the non-disturbed habitat was 53.33%. The most common host species at the non-disturbed habitat is *Pluchea absinthioides*, a seasonal shrub where mistletoes had a survival probability of 29%. At the disturbed habitat, however, the most common hosts are the shade-intolerant shrubs *Aristotelia chilensis* and *Rhaphithamnus spinosus*, which had very low mortality rates. The aggregation pattern found at the disturbed habitat is likely to emerge from differential host mortality rather than behavioral changes on the seed disperser vector.

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1. Introduction

Mistletoes are a diverse group of parasitic plants that constitute a keystone resource of forests worldwide (Watson, 2001). Due to their parasitic life form, mistletoes rely on biotic pollination and seed dispersal to ensure their recruitment on host plants (Tesitel, 2016), resulting in complex plant-animal and plant-plant interactions (e.g., Candia et al., 2014; Mellado and Zamora, 2016). This is particularly relevant for seed dispersal, as mistletoe seeds must be deposited in adequate places (e.g., thick branches) of the host plant to allow their germination and attachment to the phloematic vessels (i.e., safe sites; Reid, 1989). Due to the close relationship with the host, mistletoe spatial arrangement depends on host distribution, susceptibility, and quality, as well as on the movement patterns of the seed dispersers associated (Aukema, 2004; García et al., 2009; Lemaitre et al., 2012; Medel et al., 2004). Therefore, mistletoes present a clumped distribution in the nature, as most host-parasite systems (Medel et al., 2004).

Mistletoe spatial distribution could be altered by factors affecting recruitment and seed disperser vector's behavior, such as habitat structure, resource offer and landscape heterogeneity (García et al., 2011; Salazar and Fontúrbel, 2016; Sasal and Morales, 2013). Landscape modification due to human actions (e.g., habitat fragmentation, selective logging, or the replacement of native vegetation with exotic species) may increase mistletoe abundance, as

less complex habitats are likely to favor their occurrence by the increase in sunlight exposure, interaction rates with mutualists (pollinators, seed dispersers), and the presence of generalist species (Bowen et al., 2009; Fontúrbel et al., 2015; Watson and Rawsthorne, 2013, but also see Rodríguez-Cabal et al., 2007). Also, less complex habitats may present a large offer of fleshy fruits, as they may favor many shade-intolerant plant species (Dalling and Hubbell, 2002), which usually have large fruit displays (Valladares and Niinemets, 2008). As resource offer change, disperser behavior is expected to change accordingly, particularly when resource offer increase, seed disperser vectors are expected to reduce their movement distances, producing denser mistletoe aggregations (Morales et al., 2012). Further, habitat disturbance may alter local mistletoe recruitment and survival due to changes in host plant composition, as potential host species differ in terms of mistletoe compatibility (Roxburgh and Nicolson, 2005) and of adult mistletoe survival probabilities (Roxburgh and Nicolson, 2008).

Along a habitat disturbance gradient, in a first assessment we found that mistletoes were more abundant and densely aggregated at disturbed habitats (Fontúrbel et al., 2015), but why is this happening? To answer this question, we tested two non-mutually exclusive hypotheses: (1) mistletoes are more aggregated at the disturbed habitat because an increased resource offer produces behavioral changes on the disperser (D. gliroides) reducing its home range areas, and (2) mistletoes are more aggregated at the disturbed habitat because host species at those habitats are more resistant and thus mistletoes have higher survival probabilities.

2. Materials and methods

2.1. Study site and species

This study has been conducted at the Valdivian Coastal Reserve (39°57′S 73°34′W), a private protected area established by the NGO The Nature Conservancy (TNC) that currently protects 50,530 ha of austral temperate rainforests (Delgado, 2010). The northern part of this Reserve presents a habitat mosaic composed by native forest stands and transformed stands composed by abandoned *Eucalyptus globulus* plantations with native understory vegetation regenerated in-between, which is structurally simpler than the native forest (Fontúrbel et al., 2015); those plantations were never managed or harvested. For comparative purposes, we will consider the native habitat as the non-disturbed situation and the transformed habitat as the disturbed situation.

We focused this study on the hemiparasitic mistletoe *Tristerix corymbosus* (Loranthaceae), which flowers during the winter providing food for the pollinator hummingbird *Sephanoides sephanoides* during the scarcity period, and provide sugar-rich fruits during the summer, which are consumed by four bird species and one small mammal (Aizen, 2003). However, below 37°S, this mistletoe is solely dispersed by the arboreal marsupial *Dromiciops gliroides* (Microbiotheriidae) as result of a color polymorphism that causes ripe fruits to remain green, not detectable for birds (Amico et al., 2011). As most parasitic plants, *T. corymbosus* presents a spatially clumped distribution, as result of host distribution and susceptibility, habitat structure, and disperser behavior (Aukema, 2004; Medel et al., 2004; Salazar and Fontúrbel, 2016; Sasal and Morales, 2013). However, at this study site *T. corymbosus* is more abundant and clumped at the disturbed habitat, compared to the native forest, where shade-intolerant fleshy-fruited plants are more abundant and diverse (Fontúrbel et al., 2015).

Previous studies in this site showed that *D. gliroides* abundances are similar between non-disturbed and disturbed habitats, as well as the availability of potential host species. (Fontúrbel et al., 2014,

2015; Salazar and Fontúrbel, 2016). *Tristerix corymbosus* is able to parasitize a wide range of species (Amico et al., 2007) with similar infection probabilities, for this reason we consider infection probabilities to be similar between habitats but with a different host community composition. Non-disturbed habitat is dominated by *Nothofagus dombeyi*, *N. pumilio* and *Eucryphia cordifolia* (all susceptible to mistletoe infection), whereas the exotic *E. globulus* (non-susceptible to infection) is the only canopy species at the disturbed habitat, allowing more sunlight exposure and therefore a large variety of shade-intolerant plants to thrive. Understory vegetation at the non-disturbed is sparse and dominated by *Pluchea absinthioides*, *Laurelia philippiana*, *Drimys winteri*, *Saxegothaea conspicua*, *Caldcluvia paniculata*, and *Mitraria coccinea* (all susceptible to mistletoe infection), with sparse clumps of the native bamboo *Chusquea quila* (not susceptible) and a few *Lapageria rosea* vines (susceptible). At the disturbed habitat, there is abundant understory vegetation dominated by *Aristotelia chilensis*, *Rhaphithamnus spinosus*, *Ugni molinae*, *Luma apiculata*, *Amomyrtus luma*, *Amomyrtus meli*, and *Fuchsia magellanica* (all shade-intolerant fleshy-fruited species, susceptible to mistletoe infection), thick *C. quila* clumps, and abundant *L. rosea* vines climbing on the *E. globulus* stems. The availability of ripe fleshy fruits during the austral summer (corresponding to the fruiting peak in February) were of 35 ± 9 fruits per plant at the non-disturbed habitat and 451 ± 98 fruits per plant at the disturbed habitat (Fontúrbel et al., 2015). Besides *T. corymbosus*, *D. gliroides* consumes fleshy fruits of many other plant species, showing no marked preferences over the species present at the non-disturbed or the disturbed habitats (Amico et al., 2009).

2.2. Plant mapping and following

Starting on August 2011, we georeferenced (using a Garmin Map 62s device, with ≤3 m error) and tagged every mistletoe found at the study area, reaching 300 mistletoe plants (Fig. 1) parasitizing 217 different hosts belonging to 24 species (Table S1, available online as Supplementary Material), which corresponded to all mistletoes found at the sampling area during the study. After August 2011, we performed eight additional mistletoe assessments to determine if the previously marked plants were still alive and if there were new plants, those assessments were conducted in November 2011, March 2012, November 2012, January 2013, February 2013, March 2013, February 2014 and March 2015. With such information we build a survival matrix for the entire observation period (Table S2). Sample effort was similar between non-disturbed and disturbed habitats (120 h of active search per habitat type), and covered 1401 and 1375 ha respectively.

2.3. Spatial aggregation assessment

We used a point-pattern analysis to quantify the extent of mistletoe spatial aggregation at the non-disturbed and disturbed habitats. We used a heterogeneous Poisson null model with a non-parametric kernel estimator, based on the assumption that mistletoes are non-randomly distributed in space (Medel et al., 2004). The heterogeneous null model (999 simulations) redistributes individuals locally within a 30-m radius, determined by mean disperser's activity (Fontúrbel et al., 2010; Salazar and Fontúrbel, 2016). We used two summary statistics to quantify the spatial point aggregation patterns: (1) the pair correlation function $g(r)$, which describes the expected density of mistletoes at distance r from the focal individual, and (2) the L-function, which is the variance-stabilized form of the K-function (Wiegand and Moloney, 2014). To improve the pair correlation function $g(r)$ visualization, we standardized raw $g(r)$ values by dividing them by the expected $g(r)$ value and then applying a logarithmic transformation. By doing this, the expected results under the null model