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Is facilitation a promising strategy for cloud forest restoration?

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ABSTRACT

The loss of primary cloud forest within the original range of this ecosystem is one of the highest worldwide. Facilitation is a process in the plant community dynamics that is potentially useful for the restoration of degraded ecosystems. Secondary cloud forest tree species possess attributes that make them suitable to be used as facilitator species for the establishment of tree species typical of intermediate and late successional stages. In this study we examined the facilitator potential of two early successional species, *Alnus acuminata* and *Trema micrantha*, both of which grow rapidly and are capable of gradually modifying physical micro-environmental conditions of open sites where forest was cleared. The aim was to assess the effects of these two species on the survival and growth of two intermediate successional species, *Juglans pyriformis* and *Quercus insignis*, and one late successional species, *Oreomunnea mexicana*. Open sites were used as control. Survivorship of the three target species was significantly higher under the canopies of *A. acuminata* and *T. micrantha* compared to open sites. Almost all annual growth rates (cover, diameter and height) were not different in both experiments (under the canopy of *A. acuminata* and *T. micrantha*), regarding treatment (under canopy vs. open areas) and species (target species). However, results for target species survival strongly suggest that plantations of early successional species can facilitate the establishment of intermediate and late successional trees, and thus represent a promising strategy for cloud forest restoration.

1. Introduction

Cloud forest or tropical montane forest, widely known in Mexico as *bosque mesófilo de montaña* (mesophyllous montane forest *sensu* Rzedowski 1978), is considered a unique ecosystem because of the enormous diversity that it hosts, including a large number of endemic species (Cayuela et al., 2006; González-Espinosa et al. 2011). Cloud forest is recognized as the most threatened vegetation type among Mexican forests (CONABIO, 2010). Globally, cloud forest loss presently amounts to 165,000 km^2 (44% of the original cover) and recent estimates of its deforestation rates suggest that they are among the highest for tropical forests (Bruijnzeel et al., 2010). Given the degradation faced by this ecosystem, the search for novel strategies that may assist in its restoration is urgent (Bubb et al., 2004; González-Espinosa et al., 2012).

Within the context of degraded ecosystem restoration, the facilitation process has been the focus of numerous studies, most of them conducted in extreme or highly limiting environments (e.g. deserts and glaciers), where sapling establishment of many species is entirely restricted to a few benign microenvironments (under the protection of rocks, grasses or shrubs) (Gómez-Aparicio, 2009; Mendoza-Hernández et al., 2013; Padilla and Pugnaire, 2006). The idea that facilitation ameliorates extreme environments and reduces stressful conditions for young plants has become a paradigm in ecology (Gómez-Aparicio et al., 2004; Kawai and Tokeshi, 2007; Stachowicz, 2001). Conversely, the view that this positive interaction may also play a key role in mild environments, such as those typical of humid regions as suggested by Holmgren and Scheffer (2010), is less accepted due to their relatively stable and benign environments. To date, very few studies have documented the existence of facilitation in tropical forests (e.g. Biaou et al., 2011; Scowcroft and Yeh, 2013; Vieira et al., 1994), but some experiments based on *framework species methods* (Elliott et al., 2003; Lamb 2011) and the nucleation strategy (Zahawi et al. 2012) also provide evidence for the facilitation process in tropical lowland forests. However, we are still lacking sufficient experimental evidence for the existence of facilitation in cloud forests.

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The large influence of facilitation on the organization and dynamics of many plant communities has been demonstrated (Callaway, 2007; Kikvidze et al., 2005; Pugnaire 2010), and its prevalence may be relatively higher in tropical environments than previously thought. The underlying reason may be that late successional species of tropical humid ecosystems have evolved in this environmental context and are therefore finely adapted to a stable microclimate (Holmgren and Scheffer, 2010). Therefore, they have a low tolerance to desiccation and are more sensitive to the stress imposed by the unfavorable, harsh environments typical of open sites (Holmgren et al., 2012).

Early successional cloud forests species may play a facilitator role for the establishment of intermediate and late successional species in this ecosystem, and this possibility may have important consequences in advancing forest restoration strategies (Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006; Sánchez-Velásquez et al., 2004). Two examples of the array of cloud forest early successional, potentially facilitator species are *Alnus acuminata* (Betulaceae) and *Trema micrantha* (Cannabaceae). These two species thrive in open areas created by human or natural disturbances, and both possess remarkable ecological attributes, among which fast-growth rates and a high contribution to the accumulation of soil organic matter are noteworthy (Murcia, 1997; Vázquez-Yanes, 1998; Velázquez and Gómez-Sal, 2009). The ecological behavior of these species strongly contrasts with that of many intermediate and late successional species, which face considerable difficulties to establish in strongly altered environments (Ramírez-Marcial et al., 2001). Sapling establishment of late successional species in open areas is often limited by the high radiation, water stress, low germination rates and intense herbivory occurring in these areas (Holl et al., 2000; Ramírez-Bamonde et al., 2005). However, some of these adverse conditions may be transformed to more benign environments by early successional species (Holmgren and Scheffer, 2010). If we were able to provide evidence that facilitation is not exclusive to extreme environments, then this ecological interaction could be used as a model strategy for cloud forest restoration. Thus, the goal of this research was to assess the performance of two cloud forest early successional species, namely *A. acuminata* and *T. micrantha*, as facilitator species for the establishment of two intermediate successional species, namely *Juglans pyriformis* and *Quercus insignis*, and one late successional species, namely *Oreomunnea mexicana*. We did this by experimentally comparing survival and growth rates of *J. pyriformis*, *Q. insignis* and *O. mexicana* saplings planted under the canopies of *A. acuminata* and *T. micrantha*, using open sites as controls.

2. Methods

2.1. Study region

This study was conducted between July 2009 and July 2012 in the mountains of central Veracruz State, Mexico. In this region native cloud forest occurs between 1000 and 2100 m a.s.l. Although it rains all year, the climate is temperate humid and three seasons can be readily distinguished: a cold, humid season from November to March, a dry, warm short season in April and May, and a warm, rainy season from June through October. Average annual precipitation ranges between 1500 and 1700 mm, and mean annual temperature is 16 °C (we recorded a mean of 18.2 °C in the two study years). Historically the region has undergone an intense process of land use/land cover change, which has transformed the original forest-dominated landscape into a complex mosaic of pastures, agricultural fields, secondary vegetation, and some patches of relatively well-preserved cloud forest (Williams-Linera et al., 2002).

Two independent experiments were conducted in areas where *Alnus acuminata* and *Trema micrantha* occur. The selection of the two early successional species was mainly based on their ease of propagation and fast growth (Russo, 1990; Vázquez-Yanes, 1998). All sites were covered by second-growth vegetation (8–10 years after abandonment), with a prevalence of *Pteridium aquilinum*, a highly competitive fern species capable of arresting the successional process during long periods of time (e.g. Marrs et al., 2000; Royo and Carson, 2006).

2.2. Experimental design

The two independent experimental plantations for the two early successional species were established in two phases. Phase I consisted in the planting of *Alnus acuminata* (the basis for experiment 1) (1430–1730 m a.s.l.; 19°12–18′N, 96°55–59′W) or the planting of *Trema micrantha* (the basis for experiment 2) (1100–1425 m a.s.l.; 19°10–26′N, 96°57–59′W), each in two different plots (a total of four plots 35 × 35 m each). In Phase II, which started one year later, saplings of the three target species were transplanted under the canopies of the potential facilitator species and in open sites. Experiment 1 consisted in planting *J. pyriformis, Q. insignis*, and *O. mexicana* saplings under the canopy of *A. acuminata* and in two open plots; experiment 2 was the same, except that in this case the facilitator species was *T. micrantha*. Seeds were collected from mature and healthy trees (at least ten) in forests of the same region; they were placed in plastic bags (15 × 25 cm filled with forest soil) in a rustic nursery where they stayed until the saplings were transported into the field; in the nursery, the seedlings were watered whenever necessary.

Prior to the start of Phase I (July 2009), the pre-existing cover of *Pteridium aquilinum* was removed with machete. We then planted *A. acuminata* and *T. micrantha* saplings according to the following procedure: we planted in total 560 *A. acuminata* saplings (280 in each plot), and 560 *T. micrantha* saplings (280 in each plot). Saplings were planted with an inter-plant distance of 2 m; the few plants that died in the first month were replaced. Means (±1SD) for height, diameter at the base and cover were 64 ± 26 cm, 6.9 ± 3.8 mm and 38.1 ± 16.3 cm^2 for *A. acuminata*, and 25 ± 7.6 cm, 5.1 ± 1.8 mm, and 17.9 ± 10.5 cm^2 for *T. micrantha*. In attempting to maximize plant survivorship of the two potentially facilitator species, we conducted maintenance actions, particularly manual control with *machete* of *Pteridium aquilinum*, three times during the first year and twice during the second one. Irrigation was not needed in the plantations and there were no problems with insect pest either in the plantations or the nursery.

2.3. Establishment of Junglans pyriformis, Quercus insignis, and Oreomunnea mexicana plantations

Seeds of the target species were collected from parental mature and healthy trees (at least ten) in forests of the same region. The seeds were placed in plastic bags (15 × 25 cm filled with forest soil) in the nursery and the seedlings were also watered whenever necessary. In July and August 2010 we randomly planted saplings of *J. pyriformis* (6 months old), *Q. insignis* (6 months old), and *O. mexicana* (20 months old) under the canopies of the putative facilitator species and in open sites. In central Veracruz, saplings of *O. mexicana* grow very slowly, whilst mature trees of this species have a large proportion of non-viable seeds (30%) and are scarce in forests (per. obs.), thus the seeds of *O. mexicana* were placed in plastic bags one year before the field experiments started. Saplings of all three target species were planted 1 m apart from the base of facilitator species individuals and with no less than 2 m between saplings. For each experiment (i.e., for *A. acuminata*