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Effects of environmental filters on early establishment of cloud forest trees along elevation gradients: Implications for assisted migration

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ABSTRACT

Cloud forest tree species are reported to be shifting and retracting their distributional ranges in response to increasing temperatures. However, there is limited information regarding the impact of increasing temperatures on the recruitment of cloud forest trees, a critical phase in population dynamics. Evaluating the establishment of introduced seedlings along an elevation gradient offers an opportunity to assess the influence of environmental change on the early establishment and potential response of cloud forest tree species to assisted migration into higher elevations as a mitigation strategy. We evaluated the early seedling establishment of 3240 seedlings of 12 cloud forest tree species introduced into nine degraded forests subjected to traditional selective logging along an elevation gradient (1250–2517 m a.s.l.) in southern Mexico. We examined (1) how the probability of successful seedling establishment varies along the elevation gradient and (2) how temperature, canopy cover, herbaceous cover and humidity affect seedling survival and growth. Seedling survival, relative growth rates and environmental factors were recorded over a period of two years. Most species displayed high survival (~90%), and survivorship was most strongly related to canopy cover and temperature. Survival probability increased with canopy cover in five species. Seedling survival and growth decreased with increasing temperature in five species, while the opposite trend was found in two species. Growth rates increased with herbaceous cover in seven species. Humidity had no effect on seedling performance. Our experiment shows that most of the study species have a high probability of seedling survival under canopy cover, even outside the limits of their reported elevational ranges. The results indicate that five of the studied cloud forest species may already benefit from assisted migration to cooler climatic conditions at higher elevations. This study supports the design of management guidelines for assisting the migration of cloud forest tree species with narrow distributions, as a climate change mitigation strategy.

1. Introduction

There is increasing concern that many species may not be able to keep pace with projected global warming (Malcolm et al., 2002; Thomas et al., 2004). Possible responses of species to climate change include: (1) individuals displaying phenotypic plasticity or acclimation, (2) species adapting via genetic modification, (3) species shifting their distributions or migrating, or (4) species undergoing local or global extinction (Holt, 1990; Aitken et al., 2008; Feeley et al., 2012). Predicting whether species will be able to acclimate or shift their distributions presents a challenge to forest management given that knowledge of differential responses among species is extremely limited, particularly in the tropics (Feeley et al., 2012; Rehm, 2014). Moreover, existing analyses of range shifts in plants as a result of climate change have found contrasting results, including non-significant and contradictory patterns (Chen et al., 2011; Zhu et al., 2012; Rehm, 2014; Parmesan and Hanley, 2015).

Tropical Montane Cloud Forest (CF) is one of the ecosystems most affected by global climate change due to increased temperatures and alterations in the patterns of precipitation and cloud distribution (Feeley et al., 2013; Lutz et al., 2013). Under climate change scenarios, the climatically suitable areas for CF distribution in Mexico are

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projected to have reduced by 68% by 2080 (Ponce-Reyes et al., 2012). Recent studies report shifts in the distributions of tree species in response to temperature increases, including natural migrations to higher elevations and mortality at lower elevations for many CF tree species in Costa Rica, Peru and Colombia (Feeley et al., 2011, 2013; Rehm, 2014; Duque et al., 2015). However, these studies are all based on analyses of the distributions or composition of established individuals (primarily large adult trees > 10 cm diameter) and very limited information exists regarding the impacts of increasing temperatures on tree recruitment. Recruitment is a critical phase in tree population dynamics given that seedlings can be affected to a greater extent than adults by extreme climatic events (Wenny, 2000; Fisichelli et al., 2014). Numerous CF tree species could be limited by dispersal barriers, both natural and anthropogenic, such as the considerable distances between isolated mountain ranges, rivers, valleys, cities, roads and farms (Foster, 2001; Feeley et al., 2012) that act to limit shifts in species distribution towards higher elevations (Lenoir and Svenning, 2015), as well as by low propagule availability caused by selective over-extraction of reproductive trees from the CF (González-Espinosa et al., 2011; Ortiz-Colin et al., 2017). The ability to disperse and track climate change also depends on biotic interactions but defaunation negatively affects dispersal, since a large fraction of tree species rely on animal dispersal agents (Kurten, 2013; Alexander et al., 2018). As a result of these drivers of change, 60% of CF tree species in Mexico have been reported to be under some category of threat (González-Espinosa et al., 2011). The reduced area and highly fragmented distribution of CF add to the factors limiting the migration of native species to climatically suitable areas (Foster, 2001).

Assisted migration of key tree species refers to the intentional moving of species populations to locations outside their current range that are projected to be climatically suitable in the future, in order to mitigate the impact of climate change on biodiversity (Hunter, 2007; McLachlan et al., 2007; Thomas, 2011). The concept of assisted migration has generated intense debate: on one hand, there is concern about the translocated species becoming invasive and potential mismatches in the biotic interactions at the new ranges (Ricciardi and Simberloff, 2009; Bucharova, 2017). On the other hand, it is considered justified to assist the migration of vulnerable species that are confined to disappearing habitats and where the occurrence of natural migration is improbable (McLachlan et al., 2007; Hoegh-Guldberg et al., 2008). However there is limited experimental evidence to support such initiatives and the benefits and drawbacks of assisted migration in tropical forests are largely unknown (Malcolm et al., 2002; Richardson et al., 2009).

Species that occur in areas of high climatic vulnerability, with small populations, fragmented ranges, low fecundity, and those in decline, are considered suitable candidates for assisted migration (Aitken et al., 2008; Hoegh-Guldberg et al., 2008). Several CF species fulfil these criteria (González-Espinosa et al., 2011). However, species selection for assisted migration demands a quantitative assessment of the ecological success of individuals in the new colonization environments, given that these impose different microclimatic conditions, which could be far from the physiological optimum for the species. Since the operation of assisted migration programs are in principle technically feasible when conducted with young plants (McLane and Aitken, 2012; Otis Prud'homme et al., 2018), and tree seedlings are particularly sensitive to environmental changes (Fisichelli et al., 2014), research into the ecological performance of seedlings becomes critical. In temperate forests, the translocation of seedlings of pines, oak and spruce from their current ranges into areas at higher latitudes and elevations has produced positive effects on seedling growth (McLane and Aitken, 2012; Castellanos-Acuña et al., 2015; Otis Prud'homme et al., 2018).

Evaluation of seedling establishment along a gradient of elevation can contribute to our understanding of the capacity of species to respond to observed or predicted effects of climate change, the influence of environmental factors on early seedling establishment and the potential response of species to assisted migration to higher elevations (Körner, 2007; Malhi et al., 2010). In this study, we experimentally examined the early establishment of CF tree species in enrichment plantings along an elevation gradient. The aim of enrichment planting is to introduce ecologically or commercially valuable species into degraded forests, under the existing forest canopy, where natural regeneration is insufficient (Paquette et al., 2006). Since variations in environmental factors along elevation gradients can act as filters for seedling establishment, we assessed the influence of site-level variables such as temperature, canopy cover, herbaceous layer cover and humidity, on seedling performance. Temperature influences rates of assimilation and carbon loss (Way and Oren, 2010); low temperatures reduce carbon assimilation rates (Moser et al., 2011) and can decrease the probability of survival, especially if tissue damage occurs due to freezing (Vitasse et al., 2014; Rehm and Feeley, 2015). While high temperatures can initially increase growth rates (Perumal et al., 2014), they can also have a negative impact on the hydric balance and survival of seedlings (Will et al., 2013; Adams et al., 2017). Along an elevation gradient, it is expected that extreme temperatures will have a negative effect on the survival and growth of seedlings (Way and Oren, 2010; Rehm and Feeley, 2015). Under these conditions, canopy cover can play a key role as a buffer of extreme temperatures and acts to increase humidity in the understory (Lamb et al., 2005; Rehm and Feeley, 2013, 2015; Lusk and Laughlin, 2017). On the other hand, higher canopy and understory coverage is associated with reduced light availability, which can negatively affect tree seedling growth (George and Bazzaz, 1999; Dupuy and Chazdon, 2008). Since CF species depend on high levels of humidity (Pounds et al., 1999; Foster, 2001; Boehmer, 2011), drier conditions could reduce both the probability of survival and growth rates in the tree seedlings.

Given the evidence that many CF species in the Neotropics are shifting their ranges upslope in response to increased temperatures (Feeley et al., 2011, 2013; Rehm, 2014; Duque et al., 2015), and the projected changes in the location of areas climatically suitable for CF in Mexico due to climate change (Ponce-Reyes et al., 2012), we experimentally evaluated the establishment success and seedling growth of 12 CF tree species in sites located above the upper limit of CF distribution in the study region. This knowledge will make a valuable contribution to the design of management strategies for CF tree species that incorporate climate change mitigation efforts.

2. Methods

2.1. Species

Twelve CF tree species were selected based on seed availability and shade tolerance (Table 1). All of these species are associated with advanced successional phases and are reported as intermediate to shade tolerant (Ramírez-Marcial et al., 2012; Toledo-Aceves et al., 2017). Nine of the species are in a category of threat in the Red List of Mexican Cloud Forest Trees (González-Espinosa et al., 2011; see status in Table 1). As a result of traditional selective extraction, some species have suffered an important reduction in their populations in the study region (Paré and Gerez, 2012; Ortiz-Colin et al., 2017). The reported elevation distribution differed greatly among species (Table 2).

Seeds of at least three individuals per species were collected from CF fragments in the region in 2014. The number of trees available for collection was limited due to the scarcity of certain species or, where they were abundant, because of the lack of reproductive individuals at the time of collection. Seeds were collected directly from the trees. Immediately after collection, the seeds were cleaned and sown on seed beds with forest soil from the same location in a common garden environment. The resulting seedlings were transplanted into polythene bags (30 × 16 cm), with forest soil, approximately two months after germination. Plants were kept in a rustic nursery (located at 2088 m a.s.l.) covered with 30% shade mesh and no chemicals were applied.