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Research article

Canopy openness modifies tree seedling distributions along a tropical forest elevation gradient

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In theory, canopy openings can influence tree species establishment and resulting distributions over environmental gradients, but evidence concerning the magnitude and direction of such effects remain scarce. In this study we examine how canopy openings influence seedling persistence and growth and resulting elevation range limits. We transplanted 1360 seedlings of eight woody species (trees *Trichilia habanensis*, *Persea caerulea*, *Cedrela tonduzii*, *Cornus disciflora*, *Quercus salicifolia*, *Q. bumelioides*, *Q. costaricensis* and the shrub *Hypericum irazuense*) under the forest canopy and in open areas with understorey vegetation removed in a replicated design along a 2900 m elevation gradient in Costa Rica. We recorded survival, stem diameter and height over 18 months. We used hierarchical generalized additive models to examine relationships of seedling survival and growth with elevation and treatment (inside forest versus open area). We found a clear effect of open versus forest conditions on survival across the elevation gradient for six species. Species planted into open areas with full light exposure survived 100–1000 m below (~ 0.5–5°C warmer), and in one case 300 m above (~ 1.8°C colder) their observed ranges. Above 2900 m, survival of all species was markedly greater under the forest canopy versus open sites, suggesting facilitation from the forest, as frost occurred in open areas above this elevation. The resulting upper range increased between 200 and 1160 m (~ 1–6°C colder) compared to their observed range. At lower elevations, severe insect herbivory occurred on some species likely influencing lower range limits. Open areas influenced how seedling survival and growth varied with elevation for all the studied species. All species survived and grew outside the elevation ranges where they are typically observed. We suggest that the influence of forest gaps and clearings over extended gradients offers novel insights into tree range dynamics, limits and conservation.

Keywords: competition, disturbance, facilitation, frost, herbivory, persistence, range limits, transplant experiment

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Introduction

The influence of canopy shade versus open conditions on seedling establishment and forest regrowth is well established (Whitmore 1986, Brown and Whitmore 1992, Kobe et al. 1995, Bentos et al. 2020, Zhang and Yi 2020). Numerous studies have noted how different tree species possess distinct abilities to establish, grow and survive with and without canopy shade (Chazdon et al. 1988, Clark et al. 1996, Denslow and Guzman 2000, Kitajima et al. 2005, Poorter 2005, Sheil et al. 2006). These abilities distinguish both broad classes of species, such as light-demanding pioneers versus shade-tolerant taxa, along with more subtle differences within them (Turner 2001, Kwit and Platt 2003, Pearson et al. 2003, Poorter et al. 2005). Thus, if seeds or seedlings are present, any event, such as a treefall gap that alters the availability of light, has the potential to influence plant establishment and growth. This 'gap effect' is recognised as a key determinant of where any given tree species is likely to be found (Grubb 1977, Pearson et al. 2003). As such, the study of disturbance and recovery processes have been influential among tropical forest ecologists exploring succession and various forest characteristics (Richards 1952, Whitmore 1986, Poorter 2005, Chou et al. 2018, Sheil and Bongers 2020, Terborgh et al. 2020). Despite widespread interest in the ecology of species range limits, and recognition that past disturbances may explain the presence and abundance of plants along environmental gradients (e.g. for tropical forests see, Van Steenis 1958, Budowski 1965), neither the concepts nor implications of disturbances on species rangeshave been much explored (for exceptions see Huston and Smith 1987, Keddy and MacLellan 1990, Malanson 1997).

Building on previous syntheses (Sheil 2016) and pilot studies (Muñoz Mazón et al. 2019), these ideas on how forest gaps and clearings shape species ranges complement other studies that examined how climate and biotic interactions shape species distributions (Louthan et al. 2015, Defossez et al. 2016, Olsen et al. 2016, Ettinger and HileRisLambers 2017, Putnam and Reich 2017). While it is well known that species tolerance to drought, low temperatures or frost can influence range limits (Ettinger et al. 2011, Anderegg and HilleRisLambers 2015, Korner et al. 2016), the role of plant interactions, such as competition and facilitation, are still debated (HilleRisLambers et al. 2013, Scherrer et al. 2020). Observations of mountain forests leave little doubt that gaps and clearings permit some species to establish well outside the elevations they are typically observed. For example, observations in African mountains have shown that *Polyscias fulva* (Hiern) Harms., a fast growing light demanding tree typical of higher elevations, can also be locally common in open and disturbed sites at lower elevations (Morrison and Hamilton 1974). Such low elevation occurrences have been noted for various other taxa too, like high elevation Ericaceae (Marchant and Hooghiemstra 2001). Similar observations have also been made in Costa Rica, where young regrowth after clearing of mountain oak forest, contains many species typically restricted to higher elevations (Kappelle et al.

1995b). This reflects a more general pattern when the treeline (the upper forest limit) is lowered by fires or other disturbances thus permitting high elevation vegetation, comprising species that cannot persist under tree cover, to occur at lower elevations and warmer temperatures than otherwise (for further examples see Sheil 2016).

We assume that open areas provide additional light permitting the growth and survival of species that cannot establish in closed forest. We know that the presence or absence of canopy cover has additional consequences that may influence seedling growth and survival, for example by influencing the local microclimate and the prevalence of herbivores. Indeed, under certain conditions, forest canopy cover can facilitate the establishment, survival and growth of species that may otherwise be unable to survive in open conditions (Bertness and Callaway 1994, He and Bertness 2014). Thus, how the occurrence of open areas influences species establishment and distributions will likely depend not only on the tolerances and needs of the species but on local conditions.

Understanding how the presence and absence of forest canopy shape species elevation ranges may help predict, and perhaps even manage, the ecological consequences of climate change on species distributions. The characterization of these relationships is difficult due to the multiple factors that may influence distributions, including the complexity of natural disturbance regimes and multiple processes governing dispersal, establishment and survival (Sheil 2016). Experimental transplanting of tree seedlings under controlled conditions can clarify some effects of open areas versus forest canopy on the performance of this crucial life stage outside their typical elevation ranges (Muñoz Mazón et al. 2019).

In this study, we aim to understand how open areas (versus closed forest) with full overhead light influence the survival and growth of tree seedlings along an elevation gradient in Costa Rica. We recognise four alternative and not mutually exclusive hypotheses (H0–H3): under the null hypothesis we expect similar range limits in forest versus open area (H0, Fig. 1a). Under this hypothesis, the physiological tolerance of species to different climatological conditions is what explains their elevation ranges. H0 assumes no effect of light availability nor facilitation by other tree species on the hypothetical elevation range. The competition hypothesis suggests that forest shade reduces the growth and survival of seedlings compared to open areas, and thus restrict species to a narrower upper and lower elevation range (H1, Fig. 1b). The facilitation hypothesis assumes that positive interactions favour survival and growth, and thus leading to broader upper and lower ranges in the forest (H2, Fig. 1c). Under this hypothesis forest cover may buffer environmental extremes allowing the species to persist at elevation otherwise inaccessible given its physiological limitations. Finally, in our combined hypothesis, both competition and facilitation influence range limits depending on biotic and abiotic conditions along the elevation gradient (Bertness and Callaway 1994, Louthan et al. 2015, Olsen et al. 2016). According to the 'stress gradient hypothesis' the importance of competition along an environmental gradient would increase
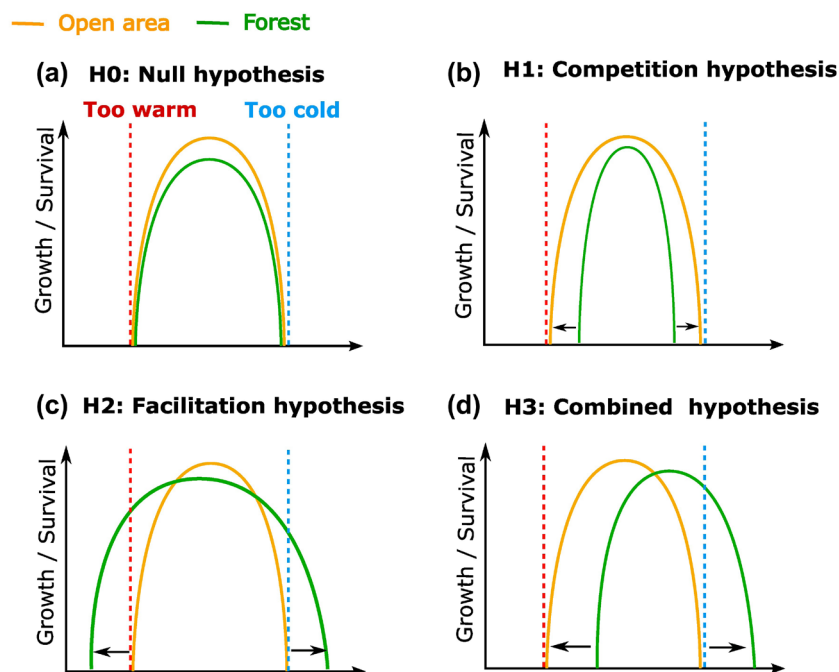
Figure 1. Tree seedling survival and growth along an elevation gradient inside the forest (green) and in open areas (orange) under four alternative hypotheses. The red dotted line (too warm) represents the potential highest temperature a given species can tolerate. The blue dotted line (too cold) represents the lowest most temperature a species can tolerate. (a) H_0: climate determines the elevation distribution regardless of forest cover; (b) H_1: forest cover reduces light and limit the upper and lower range limits compared to open areas where competition is released. (c) H_2: forest cover facilitates the survival and growth of tree species at its upper and lower range limits; (d) H_3: forest cover inhibits and facilitates growth and survival at different elevations leading to distinct changes at the upper and lower range limits (this pattern could also be reversed).

when abiotic stress is relatively low and the environmental conditions allow a rapid resource acquisition (Bertness and Callaway 1994). Here we predict that the consequences of competition (the negative impacts associated with a closed forest) are more important at lower elevations, whereas the consequences of facilitation (the positive impacts associated with a closed forest) are more important at higher and colder elevations where cover under the Paramo vegetation could offer protection against freezing temperatures (Kappelle and Horn 2005). Therefore species may be able to extend their ranges towards lower elevations in open areas, where asymmetric competition for light is reduced. This pattern could be reversed if facilitation were to dominate only at the lowest elevations (H3, Fig. 1d). This could happen if lower elevations are dryer than mid and high elevations, for example, and forest cover improves water availability.

Material and methods

We established and maintained a replicated experiment with eight species (seven tree and one shrub) (Table 1) at ten locations spanning a 2900 m elevation gradient in the Talamanca Mountains, Costa Rica. We maintained it for 18 months from February 2017 to August 2018. Temperature declines from an annual mean of 24°C to 10°C from low to high elevation, while precipitation follows a unimodal shape,

from around 3400 mm a year at the lowest elevations, then rises until it peaks at almost 4200 mm at 1500 m and then declines again to around 2000 mm at the highest elevations (Muñoz Mazón et al. 2019, 2020, Veintimilla et al. 2019). The lowest parts of the elevation gradient are 'premontane forest' a floristic transition between lowland and cloud forest. There, Holarctic tree species dominate, such as *Oreomunnea mexicana* (Standl.) J.-F. Leroy, mixed with more generalist taxa such as *Billia rosea* (Planch. & Linden) C. Ulloa & P. Jörg., *Cecropia insignis* Liebm. and *Alchorenea latifolia* Klotzsch (Venteimilla et al. 2019). With increasing elevation (around 2000 m a.s.l.), the vegetation transitions to an oak dominated cloud forest (primarily *Quercus bumelioides* (Liebm.) and *Quercus costaricensis* (Liebm.)). The highest locations (above 3000 m a.s.l.) are in the paramo, dominated by shrubs such as *Hypericum irazuense* (Kuntze.), *Vaccinium consaguineum* (Klotzsch.) and a bamboo, *Chusquea subtesellata* (Hitchc.) (Kappelle et al. 1995a).

Species selection

We selected eight woody species (seven trees and a shrub), representing different elevation distribution ranges (Table 1). Apart from *Hypericum irazuense* and *Quercus costaricensis* (below) seeds were collected directly from the mother trees in 2016. These seeds were collected by technicians from the Cachi's tree nursery from the Instituto Costarricense

Table 1. Species observed elevation distribution ranges in the experiment.

Species	Family	Elevation range m a.s.l.*	Maximum tree height (m)**
Persea caerulea (Ruiz & Pav.) Mez	Lauraceae	700–1900	20
Cedrela tonduzii C.DC.	Meliaceae	990–2025	40
Trichillia havanensis Jacq.	Meliaceae	400–2600	15
Cornus disciflora Sessé & Moc. ex DC.	Cornaceae	550–3200	30
Hypericum irazuense Kuntze ex N.Robson	Hypericaceae	2900–3560	3
Quercus costaricensis Liebm.	Fagaceae	2388–3600	45
Quercus bumelioides Liebm.	Fagaceae	1250–2895	45
Quercus salicifolia Nee	Fagaceae	650–2560	25

*Ranges were estimated from GBIF observations in Costa Rica using the 2.5 and the 97.5 quantiles to reduce the impact of outliers due to misidentifications, or errors in the georeferencing. Additionally, we selected observation with preserved specimens and without geospatial issues (coordinates with errors or invalid, such as locations in the middle of ocean for trees). Data source: <https://doi.org/10.15468/dl.7ywanm>.
**References: Zamora-Villalobos et al. (2017) and Tropicos data base (<www.tropicos.org>).

de Electricidad (ICE). The exact elevations from where the seeds were collected was not recorded. However according to personal communications with the technicians, all seedlings were collected in the same area/landscape were we carried out the experiment (Atlantic slope of the Talamanca Mountain Range, along the slopes of Tapantí and Cerro de la Muerte National Park). They were immediately sown on seed beds comprising a standardized soil mix (60% forest soil, 40% sand). Once germinated, seedlings were planted into individual plastic bag-pots (30 × 16 cm), with homogenised forest soil (from a different forest than the seeds where collected) and kept under shade netting in a nursery at 1300 m a.s.l. until transplantation. At the time of transplantation seedling age varied from 6 to 10 months depending on their germination time. For *Q. costaricensis* and *H. irazuense* seeds were unavailable so we collected and used naturally growing seedlings (all 10–15 cm height) from forest and paramo sites around 3000 m a.s.l. These were collected with soil from the same forest (including soil attached to their root system) and planted into plastic bag-pots (30 × 16 cm) within the same day. These plants were kept in a nursery at 2800 m a.s.l. covered with a shade net for a month before being transplanted. This was to acclimatize the seedlings to the transplant bags and thus reduce a potential effect of a transplant shock.

Design and measurements

We established 170 plots with 1360 seedlings. This included two experimental sites, separated by at least 1 km at each

elevation (580–640, 1050–1140, 1400–1500, 2100–2200, 2300–2400, 2600–2700, 2900–3000 a.s.l.; at elevations 1670, 3200, 3400 a.s.l. there was only one site). When possible, sites were established inside protected areas in old growth forest (though the two lower sites were located in mature (30+ years) secondary forest, according to the landowners). In each site we established five replicated plots in an open area (open treatment) and five under nearby (200 m or less) forest canopy (forest treatment). Plots were 1 × 1 m, fenced up to 150 cm height and contained one transplanted individual of each species. The fencing aimed to reduce any impact from herbivores. The disturbed 'open' treatment are areas where all trees and understory vegetation have been removed. In most cases, we could use cleared areas under power lines or comparable areas kept open through mechanical cutting and removal of plants. In order to avoid interactions with neighbour vegetation, we carefully cleared and removed all the vegetation, except the transplanted species, within one meter of each side of each plot. The weeding (by both clipping and uprooting) was performed every four months during the experiment. In the forest treatment we did not clear the understorey but avoided locations with a dense understorey or pre-existing vegetation aside from trees over several meters tall. To reduce impact of transplant shock in the first month of experiment, we watered all the plots at establishment. One month after the transplantation we examined all the seedlings with the intention to replace those already dead, but initial survival was good and replacement was only necessary for four *H. irazuense* in the open area treatment at the highest elevation (3400 m a.s.l.). Survival was measured as the percentage of individuals alive at the end of the experiment at each site–elevation–treatment combination. Seedling height was measured as the distance from the ground where the seedling was planted, to the apical bud of each individual. Height growth was calculated by subtracting the height at the start of the experiment from height at the end. The diameter of each seedling was measured with a precision calliper at the base of each seedling. Diameter growth was calculated by subtracting the diameter size at the start from the diameter at the end for all the surviving individuals.

Climatic variables

To compare temperature and light conditions under the different treatments, we placed a datalogger (Onset HOBO Pendant Temperature/Light 64K Data Loggers) mounted on a stick at 30 cm above ground in the centre of one of the undisturbed 'forest' and disturbed 'open' treatment plots at each elevation (a total of 20 loggers). The dataloggers recorded temperature and light every 30 min. After 18 months we collected the data loggers and extracted temperature and light data. The datalogger at the 1000 m a.s.l. site in the open treatment had failed. For each treatment we calculated the mean annual maximum temperature, annual mean temperature, mean annual minimum temperature, lowest temperature, number of days with at least one temperature record < 0°C, mean daily range, mean annual range, annual

mean and mean maximum night temperatures. Since we used the data loggers to record light intensity, they were exposed to direct sunlight, which influences temperature measurements. To clarify and control this bias, we explored the data in different ways, each having potential advantages. First, we used only temperature records during the night. Second, we excluded temperatures recorded under strong light conditions (> 30 000 lux). The latter approach provides maximum temperatures close to those recorded by a sheltered weather station near the plot locations during 2017 (CATIE public data <www.catie.ac.cr/productos-y-servicios/estacion-meteorologica/estacion-meteorologica-catie.html/>). Nevertheless, this approach has obvious biases. We also used data excluding the warmer hours of the day (from 10 to 15). With this approach the highest temperatures remain equal to the sheltered weather station and it removes the same amount of data all along the elevation gradient. Both methods exclude temperature records during the brightest conditions and associated variation.

Statistical analyses

Because of the nested design (plots within sites) and the non-linear responses between survival/growth and elevation we used generalized additive mixed effects models with the gam function (Wood 2001), which allow for specification of the data structure as random effects, in our case plots nested within sites. We examined the survival, height and diameter growth for each species separately in 'open' versus 'forest' (treatment) plots along the elevation gradient by comparing three different models (Table 2) following (Pedersen et al. 2019). This hierarchical approach allowed us to examine the interaction between elevation and treatment in our additive models. Model 1 assumes there is no effect of treatments on survival and growth. Model 2 is equivalent to a random intercept mixed effects models, were the response variables have similar relationship ('slope') with elevation in both treatments, but a different 'intercept'. Model 2 allows both groups (treatment open and forest) to have similar functional responses to elevation, but intergroup variation is allowed. This approach works by allowing each grouping level to have its own functional response with 'elevation' (hence the 'elevation × treatment' formula in Table 2), but penalizing functions that are too far from the main trend (elevation). Model 3 is equivalent to a random slope and intercept model, in which the relationship between the response variable and elevation can change between treatments. We selected the model with lowest AIC value, in the case the difference between AIC was < 2, we selected the one with greatest deviance explained. To

model the survival, we used the combination of both survival and mortality of each species as response variable using the cbind function and a binomial distribution as suggested by Zuur et al. (2009). We included the negative growth values in our models it will bias the error estimation (will only remove error in the negative values) rounding them to 0 gave the same results in the model selection as the inclusion of negative values). For example, negative height growth values could result from herbivory. All analyses were performed with R ver. 4.0.0.

Results

Climate

Among all nineteen selected plots with functioning data loggers, mean temperature decreased with elevation (Supporting information). The decline is greater for the mean minimum than the mean maximum temperature due to the increasing annual and daily variation with elevation (Supporting information). Temperatures below 0°C occur occasionally at 2900 m a.s.l. in the open treatment and above 3000 m a.s.l. in the forest (Fig. 2), becoming more frequent in both open areas and inside forest above those elevations. In general, open areas have more extreme maximum and minimum temperatures compared to the forest at all elevations, but mean temperatures are slightly lower inside the forest. Therefore, both annual and daily ranges are also lower inside the forest. We observed no distinction between night temperatures in open and forested areas (Supporting information). Available light increases with elevation in both open and forest sites (Fig. 2). All measures vary seasonally with some differences among sites (Supporting information).

Seedling survival

Of 1360 seedlings, 706 (52%) survived the full 18 months. *C. tonduzii* had the best overall survival (81%) and *Q. costaricensis* the worst (21%). Survival for the other species was: *P. caerulea* (42%), *T. habanensis* (59%), *C. disciflora* (51%), *Q. salicifolia* (61%), *Q. bumelioides* (63%) and *H. irazuense* (33%). While we were unable to identify the cause of each death – thus precluding confident quantification – damage was frequent. Notably, below 2000 m a.s.l. we often observed leaf removal by ants (likely *Atta* spp. and/or *Acromirmex* spp.) particularly on *H. irazuense* and *Q. costaricensis*. For seven species (not *Q. costaricensis*) survival between open areas versus intact forest (Fig. 3) are sufficiently distinct to require separate models as indicated by lower AICs (Model 3 versus

Table 2. Models used to test if survival and growth of the transplanted species changes with elevation and treatment.

| Model	Model terms	Random Effects	Hypothesis
1	Elevation	Plot|site	H0: there is no effect of treatment
2	Elevation+elevation × treatment open+elevation × treatment forest	Plot|site	H1 and H2: there is an effect of treatment, but it is the same along the elevation gradient
3	Elevation × treatment open+elevation × treatment forest	Plot|site	H3: the effect of treatment on survival/growth changes with elevation.
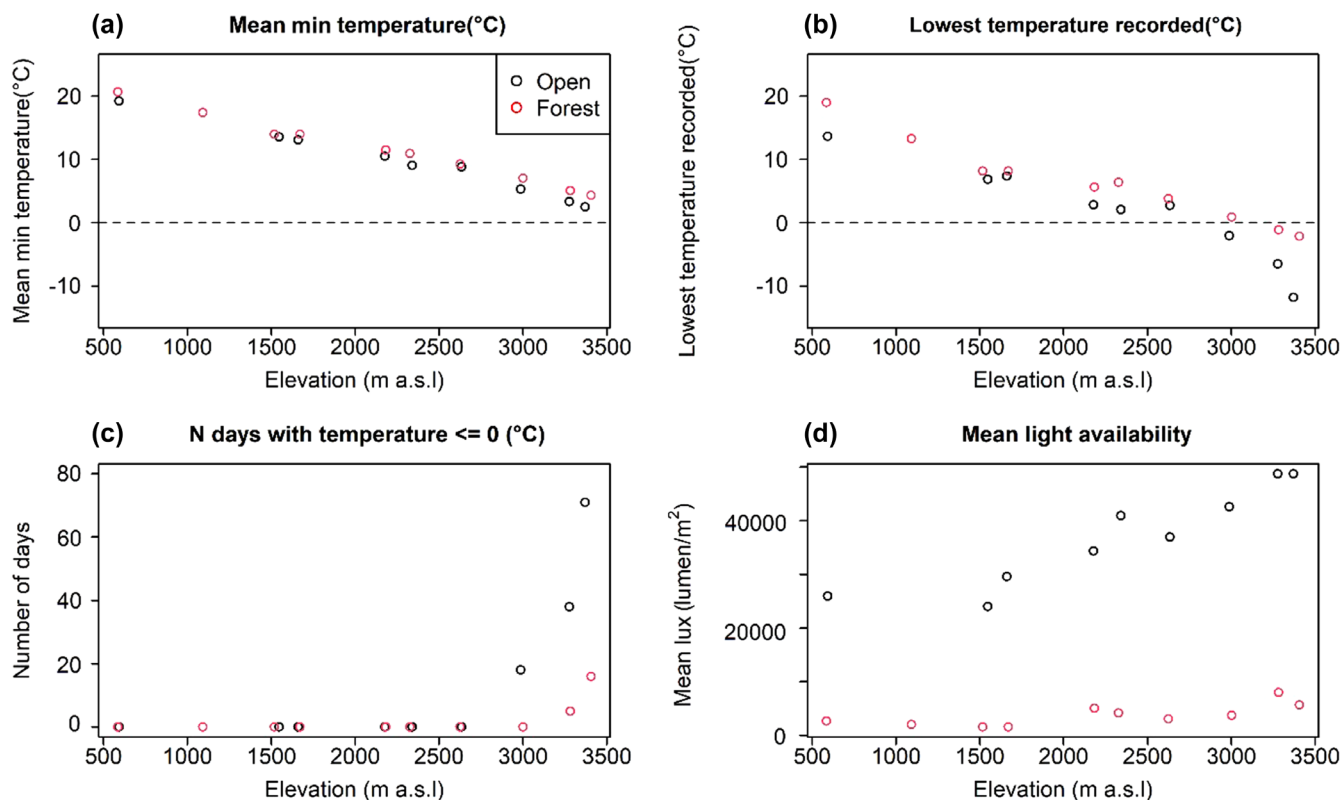
Figure 2. Changes in (a) mean minimum (daily minimum averaged for the year), (b) lowest temperature recorded during the experiment, (c) number of days with temperatures equal or below 0°C. (d) Changes in the light environment along the elevation gradient

Model 2; Fig. 3, Supporting information). At the highest elevations, all the species survive better inside forest. Two species (*T. habanensis* and *P. caerulea*) survive better in open treatment throughout their elevation range except at the highest locations (Fig. 3a, b). Four species (*H. irazuense*, *Q. bumelioidse*, *Q. salicifolia* and *C. disciflora*) have greater survival in the open treatment at their lower range limits, and in the forest treatment at their upper range limits (Fig. 3e–f, h). Finally, *C. tonduzii* has a similar survival between treatments except in the highest elevations, where no individuals survived in the open sites. Overall, for each species, the final selected models explained between 45 and 85 percent of variation.

Growth

Most species showed a difference between treatments for both height and diameter growth. Models that fitted each treatment separately were selected over combined models (by AIC) for the diameter growth of five species (exceptions were *Q. costaricensis*, *P. caerulea* and *C. tonduzii* (Supporting information). In general, both height and diameter growth was greater in the open than in the forest treatment. Also, the relationship between growth and elevation differs between treatments for all species (Supporting information). For most of the species, growth in the open treatment varies much more over the elevation range than growth in the forest treatment. For example, growth in *T. habanensis*, *P. caerulea*, *Q.*

costaricensis and *H. irazuense*, increases towards the lowest elevations (Fig. 4a, b, g– j, o, p). For *C. tonduzii*, *C. disciflora*, *Q. salicifolia* and *Q. bumelioides*, growth follows a unimodal rise-and-fall shape over the elevation gradient (Fig. 4c–f, k–n). The explanatory power of the fitted growth models was markedly lower than for the survival models. For example, the selected height growth model for *C. tonduzii* and *Q. costaricensis* explained only 7.14 and 4.5% of the variation respectively (Supporting information). All species included some negative growth values for both diameter and height in some locations, but we noted no clear patterns.

For three species the deviance explained by the generalised additive model was low for both height and diameter growth, indicating a potentially linear relationship between growth and elevation (*P. caerulea*, *C. tonduzii*, *Q. costaricensis*) (Supporting information). We applied a linear mixed effects model approach, with plot nested in site as a random factor, to examine differences in growth between treatments. In all three cases, diameter growth was significantly greater in the open treatment. Height growth was only significantly greater in the open treatment for *C. tonduzii*.

Discussion

For all eight species investigated, the transplanted seedlings survived and grew well outside the elevation ranges where
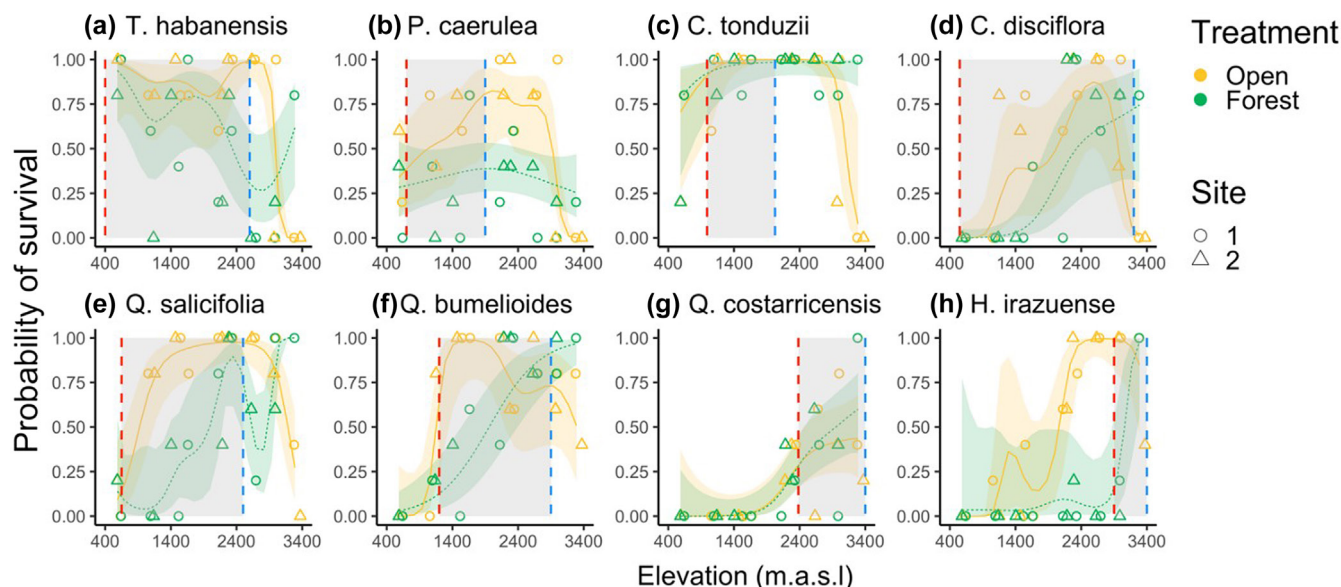
Figure 3. Survival versus elevation for eight species in open (yellow line) and inside (green line) forest. Points represent probability of survival at each studied site. Lines represent predictions form the selected models. The grey shaded area represents the observed elevation range of the species in Costa Rica according to records at GBIF, the red line indicates their lower range limit and blue lines the upper range limit.

they are typically observed in nature, and our null hypothesis, H0, was rejected. The influence of open versus forest conditions on survival varies with elevation. For example, we observed a greater survival inside forest compared to open areas at higher elevations coupled with the reversed pattern– reduced survival inside forest compared to open areas – at lower elevations for six species (Fig. 1d) supporting H3 (combined hypothesis). For two species (Fig. 1c) we only observed a greater survival inside forest and inferred a facilitative interaction along the whole gradient (supporting H2). Open areas allowed one species, *H. irazuense*, to survive 1000 m below its observed elevation range, assuming an approximate lapse rate of 0.5 per 100 m (as seen in our dataloggers) this is equivalent to growing in a climate 5°C warmer than its current range. Open areas also permitted one species to survive 300 m above its current observed upper range (at an inferred temperature around 1.5°C lower than normal). Survival at the lower range limit was greater in open conditions for three species. Forest conditions boosted survival at higher elevation for six species increasing their upper range limit by 200–1160 m (i.e. from 2 to nearly 6°C colder) indicating that forest cover can favour survival at high elevations. Whereas being inside the forest facilitated survival of most species in the high elevations, growth was always better in open areas. Interestingly, some species achieved maximum growth in open sites both below and above their observed natural range. Our results confirm that whether we have open or closed conditions influences seedling growth and survival and resulting elevation ranges.

Mountain forests, like most forests, are subject to various disturbance processes that create gaps and clearings where seedlings can establish and grow. The presence of such gaps and clearings is expected to provide some release from the understorey conditions where locally superior competitors exclude locally weaker competitors (through shade and

other interactions). Along elevation gradients, excluded species tend to persist at more marginal areas such as higher elevations where they avoid many of the fiercest competitors (Sheil 2016, Muñoz Mazón et al. 2019). In our study, this pattern appears evident for *H. irazuense*, a paramo shrub, which survived 1000 m below its observed distribution range when competition was removed. Indeed, for four of the eight transplanted species, survival and growth is markedly greater towards their lower range limits in the open areas with understorey vegetation removed, indicating that competition influences this limit. Also, the increased survival of the three abundant cloud forest species *Q. salicifolia*, *Q. bumelioides* and *C. disciflora* in open areas at their lower range limits indicates that closed forest restricts establishment at these elevations. Forest cover can also constrain upper range limits, as for *T. habanensis*, where we observed a greater survival in the open areas up to the frostline at 2900 m. These results show thatcanopy opening enhances the survival of species at their lower range limits and under warmer conditions. These observations support the evidence of other conditions than the environment, such as disturbance, shape the elevation ranges of tropical trees.

Strikingly, all the transplanted species benefited from forest cover at the highest elevations (above 2900 m a.s.l.), where frost occurs. Frost tolerance is widely recognised as a factor limiting species ranges (Preston and Sandve 2013, Korner et al. 2016, Segovia et al. 2020), as many species fail to establish where frost occurs (Bader et al. 2007, Wesche et al. 2008, Sakai and Larcher 2012, Defossez et al. 2016). The lower frequency and severity of frost in closed forest versus open locations (Fig. 2c), indicate a buffering effect of forest cover on extreme temperatures. Our results are consistent with other transplant experiments that report that forest cover increased survival for some species near their
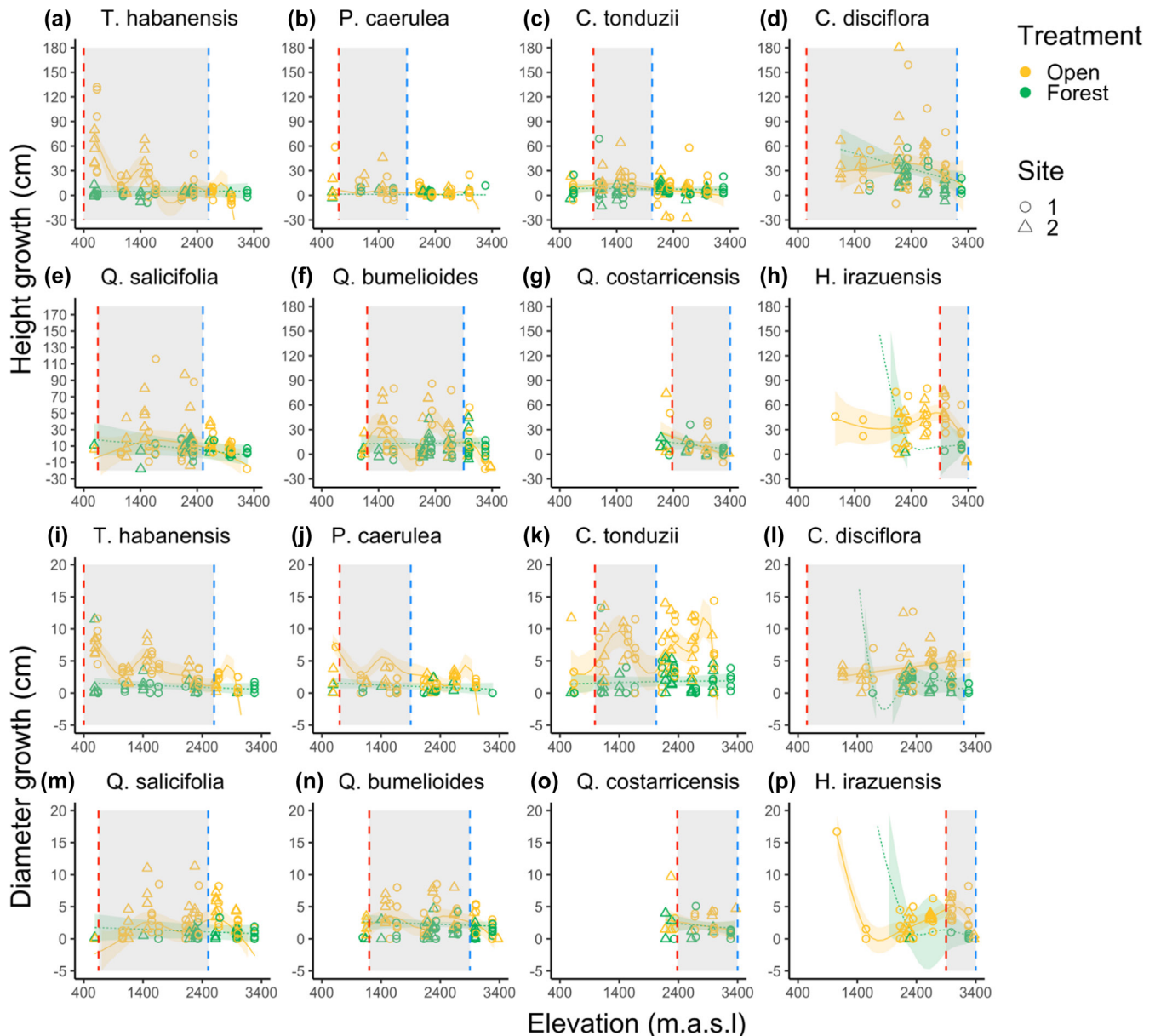
Figure 4. Height (a–h) and diameter (g–p) growth versus elevation for eight species in open (orange lines) and inside forest (green line). Points represent the growth of one surviving individual. Lines represent predictions from the selected models. The grey shaded area represents the observed elevation range of the species in Costa Rica according to records at GBIF, the red line indicates their lower range limit and blue lines indicates the observed elevation range of the species in Costa Rica according to records at GBIF and their upper and lower range limits, respectively. the lower range limit.

upper-range limit, as seen in the Andes (Rehm and Feeley 2015), Mexico (García-Hernández et al. 2019) and elsewhere (Defossez et al. 2016). They are also consistent with studies indicating the survival benefits, or 'nurse effects', of plants on each other in the Costa Rican Páramos (Farji-Brener et al. 2009). Thus, we see that open conditions can constrain species upper ranges through increased exposure to frost.

Our results show that establishment, and persistence in the seedling life-stage is influenced by open areas devoid of dense tree cover. We believe this impacts species distribution. Studies elsewhere have also indicated that both facilitation

and competition influence species persistence and elevation ranges (Olsen et al. 2016, Ettinger and HilleRisLambers 2017, Cáceres et al. 2019). For the tropics, these results are consistent with field observations along the same gradient (Muñoz Mazón et al. 2019). In this study, past disturbance events that permit establishment of seedlings in open sites that subsequently recover to forest, in determining both the upper and lower range limits of tree species. The role of canopy cover in reducing lower elevation range limits and increasing the upper limits conforms to the stress gradient hypothesis predicting greater benefits of facilitation at higher

elevations (Bertness and Callaway 1994). For *H. irazuense*, instead of a gradual change along the elevation gradient, we observed an abrupt shift, from canopy cover exerting a net negative to a net positive impact on seedling survival above 2900 m. This appears to reflect the elevation where frost plays a role. Indeed, no matter what the trends were at lower elevations, all eight of our species survive better under forest cover above the elevation where frost occurs suggesting that frost protection is a key process at these elevations. In any case we see that the presence or absence of open areas can lead to broader or narrower species elevation ranges depending on the local context.

Herbivory may also be important for seedling survival and growth. The translocations of species outside their natural ranges implies changes in the herbivores they are exposed to. While our fenced plots excluded larger vertebrates, they did not exclude smaller herbivores, such as insects. At the lowest elevations we observed severe defoliation from leaf cutter ants (*Atta* spp. and *Acromirmex* spp.), and even witnessed these insects carrying the leaves from our newly planted *Q. costaricensis* and *H. irazuense*, likely contributing to the low survival at these elevations. These ants are generalist herbivores that preferentially target less-defended species (Farji-Brener 2001) and stressed plants (Ribeiro Neto et al. 2012). *Q. costaricensis* and *H. irazuense* appear to be poorly protected against ant herbivory, and in Costa Rica, they occur only at elevations higher than the ants, despite the better growth observed among the temporary surviving seedlings at lower elevations in our study (~ 2000 m a.s.l., Supporting information). Previous observations in the region suggested that survival of *Q. costaricensis* is often determined by herbivory (Calderón-Sanou et al. 2019). Similarly, the good survival of *P. caerulea* above its natural range may reflect an absence of specialized herbivores, such as the avocado moth (*Stenoma catenifer*; Luna et al. 2017), though at these elevations the seedlings grow slowly. Such increases in survival despite the slow growth accord with the life-history tradeoffs expected to sort species along a competition gradient, suggesting that not just growth and competition, but also herbivory, and the resulting mortality, are important in determining observed distributions (Keddy and MacLellan 1990, Sheil 2016).

Field experiments are necessary to characterise the determinants of species distributions but invariably involve assumptions and limitations. Our study covers only the seedling life stage, though this early life-stage of establishment and early growth is crucial for species distributions (Grubb 1977, Marques and Burslem 2015, Ssali et al. 2018). Our previous observations in these mountains showed that mature tree species have both upper and lower range limits in more open versus denser forests, as indicated by basal area, supporting the view that forest cover influences the elevation ranges of these tree species (Munoz Mazon et al. 2019). We do not know if our seedlings can persist, mature and reproduce in these conditions thus completing their entire life cycle, so we remain uncertain whether populations of these species might persist outside their typical elevation ranges. Therefore, ontogenic niche differences could also explain the observed patterns for some of the species. Additional work on seed production, dispersal, germination and survival from sapling to mature life stages is needed. Moreover, while our eight species represent a range of life histories and adaptations; they represent a small fraction of the regional species pool. Even so, the selected species are ecologically important. For example, *H. irazuense*, *Q. bumelioides* and *Q. costaricensis* are dominant at certain elevations (Kappelle et al. 1995a, Veinteimilla et al. 2019) and two are regional endemics (*H. irazuense* and *Q. costaricensis* are restricted to Panama and Costa Rica). Additional studies, including many more species, would be required to generalise our results and better clarify which species have elevation ranges that might be modified, under what conditions and to what extent. An important factor we were not able to explore in our study is the role of local adaptation on each species response to warming and shade. Different conspecific populations may have different adaptations to deal with the biotic and abiotic conditions they experience across their range. This topic remains little explored in tropical regions (but see Tito et al. 2020) and deserves to be further explored by multi-population seedling transplants. We reduced the influence of local soil conditions by transplanting the seedlings with homogenized soil but this is imperfect as the roots grow to access the surrounding soil. Finally, we note that by comparing open and closed forest conditions we are neglecting both the intermediate and more ephemeral conditions that also occur in nature. We speculate that elevation ranges and overall persistence will also be influenced by moderate and short-lived changes in cover.

Our results have implications for the understanding of species ranges and the impacts of a warming climate on species coexistence. We have shown that the seedlings of some species survive and grow under warmer temperatures if competition for light is released. All four species with the narrowest current elevation ranges, *H. irazuense*, *Q. costaricensis*, *C. tonduzii* and *P. caerulea*, survived and grew outside these range limits. Some even had their optimum survival or growth outside their natural range (*P. caerulea* and *H. irazuense* respectively). These results support the idea that the upper thermal limit of cold adapted mountain species is in many cases underestimated (Araújo et al. 2013). In addition, our results seem inconsistent with suggestions of mountain species possessing narrow ranges due to narrow environmental tolerances (Boulangeat et al. 2012, Denelle et al. 2020). Other mechanisms, such as biotic interactions or dispersal limitation seem to be at least as important as species thermal tolerance when explaining tree distributions, particularly for those species with the narrowest ranges (Seliger et al. 2021). In this study, we provide a first step towards understanding how climate will influence biotic interactions in and the consequences for species elevation ranges in tropical mountain forest. Based on our observations, we predict that in a warmer future it is very likely that species persistence will be compromised by shifts in their competitive environment before the abiotic conditions become physiologically unsuitable. This is particularly evident for *H. irazuense*, whose future persistence could depend on how fast the treeline moves towards

higher elevations. Indeed, we observed that all of the studied tree species are able to persist above the tree line when transplanted under shrubs. The speed of these changes will be also dictated by the dispersal ability of each species. These indirect effects of climate change on species persistence could be managed locally. Our results indicate that generating or maintaining some open areas could improve the establishment, and perhaps the related persistence, of species well outside their typical range if leaf-cutter ants and other herbivores permit. Thus, weak competitors may benefit most, such as many of the alpine species that appear threatened by a warming climate (Corlett and Westcott 2013, Tovar et al. 2020). Identifying the impacts of canopy openings, created either by natural or anthropogenic disturbance, on species persistence will be vital for developing these insights into improved knowledge of species distributions and providing guidance for conservation management (Sheil 2016).

Speculations and alternative viewpoitns:

Despite the concepts of fundamental and realized niche being central in ecology, there is little consensus on the degree to which biotic interactions impact species range limits. We still lack a complete understanding about how species distributions reflect the transitions between fundamental and realized niche and how competition, facilitation and other factors can modify these resulting patterns. Why? Direct testing requires laborious experiments where species are moved outside of their observed ranges. When examining this for trees, the potential age also becomes a challenge as we cannot easily gauge fitness for adult organisms unless we are willing to wait several decades. However, our results and other evidence highlights the potential role of biotic interactions and disturbance regimes in shaping species ranges. To understand how species persistence may change in a warming climate requires attention to various additional factors such as available light. A climate-only perspective on species distributions neglects the degree to which a species may in fact be able to adapt and persist to future novel biotic conditions. This neglect also leads to overestimation of the vulnerability of many assumed narrow-range thermal specialists to warming temperatures. Such insights are important for developing successful conservation interventions as they indicate that it may be useful to seek and identify novel opportunities to manage and preserve tree species in the future. In particular, managed disturbances appears a promising tool. It is early days. We still need to develop the necessary knowledge base to define an appropriate disturbance regime for sustaining any selected set of species — our results indicate that advances are possible.

Authors contributions

Miguel Muñoz Mazon: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (supporting). **Kari Klanderud**: Conceptualization (equal); Supervision (supporting); Writing – review and editing (equal). **Douglas Sheil**: Conceptualization (equal); Funding acquisition (lead); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are at available from Dryad digital repository: <https://doi.org/10.5061/dryad.sxksn036h>, (Muñoz Mazon et al. 2022).

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