Norwegian University of Life Sciences
Faculty of Environmental Sciences
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2021:99

Forest disturbance and tree species elevation ranges in Costa Rica

Skogforstyrrelser og høyder på treslag i Costa Rica

Miguel Muñoz Mazón

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“Nature does not hurry, yet everything is accomplished”

Lao Tzu

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Table of Contents

1 Abbreviations and definitions

Term	Definition
Disturbance	Any event that disrupts the structure of an ecosystem, modifying the availability of resources and that alters the physical environment.
Niche	The range of abiotic and biotic conditions where a species can persist.
Fundamental niche	The range of abiotic condition under which a species can persist.
Realized niche	The abiotic condition in which a species can persist in presence of other species.
Competition	A species interaction that results in a decrease in fitness (growth and reproduction).
Competitive exclusion	When the presence of a species determines the persistence of another species.
Trade-off	When the investment in a trait involves a decreased investment of another trait. This inverse correlation among physiological characteristics prevents any given species to be optimally adapted to all conditions.
Life-history traits	The combination of physiological characteristics that allow us to distinguish between early and late successional species. In this thesis I consider these as a continuum of strategies rather than a clear dichotomy between species adapted to persist in early successional vs late successional environments.

2 List of papers

Paper I

Muñoz Mazón, M., Klanderud, K., Finegan, B., Veintimilla, D., Bermeo, D., Murrieta, E., ... & Sheil, D. (2020). How forest structure varies with elevation in old growth and secondary forest in Costa Rica. *Forest Ecology and Management*, *469*, 118191.

Paper II

Muñoz Mazón, M., Klanderud, K., Finegan, B., Veintimilla, D., Bermeo, D., Murrieta, E., ... & Sheil, D. (2019). Disturbance and the elevation ranges of woody plant species in the mountains of Costa Rica*. Ecology and evolution*, 9(24), 14330-14340.

Paper III

Muñoz Mazón, M., Klanderud, K., Sheil, D. Disturbance and light availability determine the elevation ranges of paramo and cloud forest tree species. *Manuscript*

Paper IV

Muñoz Mazón, M., Klanderud, K., Sheil, D. Canopy openness modifies tree seedling distributions along a tropical forest elevation gradient. *Under review in Journal of Ecology.*

3 Abstract

The role of disturbance in influencing interspecific competition and species persistence and distributions remains surprisingly unexplored. Disturbance may increase elevation ranges, especially at the lower range limits, through reduced competitive exclusion. Nevertheless, to date this relationship remains unclear. This thesis contributes to fill that knowledge gap and understand how disturbance can shape tropical trees distributions along elevation gradients.

To explore these ideas, I went to the mountains of Costa Rica and used three different methodological approaches. First, I explored broad scale tree distribution patterns in relation to forest succession by analysing tree species composition in a network of plots along a 2900 meters elevation gradient. Second, I used distance sampling transects to explore the small-scale distribution in relation to forest structure and light availability of ten cloud forest trees along a 1500-meter elevation gradient. Third, I stablished a transplant experiment along an elevation gradient to understand how temperature, competition for light and disturbance influence the persistence of eight species.

I found a context dependant role of disturbance on forest structure (Paper I) and tree distributions (Papers II, III and IV) along elevation gradients. The distribution of multiple species along their elevation gradient depended on forest structure and light availability. For example, species that arrived first after succession and scaped exclusion had broader ranges than those arriving later in succession (Paper II). Some high elevation species showed a clear light demanding strategy and expanded their ranges when competition for light was reduced. Others showed a context dependant role of competition and disturbance, shifting from a shade tolerant to a light demanding distribution between their upper and lower range limits (Paper III and IV). Often these species had their lower range limits in areas with lower basal area and greater light availability (Paper II, III and IV), with extensions between 100 and 1000 meters below their range limit (equivalent to 5 C^0 warmer). On the other hand, the upper most distribution depended more on tolerance to frost, being facilitation a key for the persistence of the studied species (Paper II and IV).

These results suggest that disturbance relaxes the constraints imposed by competition and extends effective elevation ranges of species to warmer and cooler climates, offering novel

insights into tree range dynamics, limits, and conservation. Depending on the environmental context, disturbance may catalyse or slow down tree range shifts in the future. Suitable disturbances may be key reducing the indirect effect of novel competitors on species persistence in a warmer world.

4 Norsk sammendrag

Betydningen av forstyrrelser for interspesifikk konkurranse, artssammensetning og utbredelse er overraskende lite studert. Forstyrrelser kan øke arters høydegrenser, spesielt i de nedre grensene for utbredelse, gjennom redusert konkurranseekskludering. Likevel er dette forholdet til dags dato uklart. Denne oppgaven bidrar til å fylle dette kunnskapshullet og forstå hvordan forstyrrelser kan påvirke utbredelsen av tropiske trær langs høydegradienter.

For å utforske dettebrukte jeg tre forskjellige metodiske tilnærminger i fjellene i Costa Rica. Først studerte jeg trærnes utbredelse i forhold til suksesjon, ved å analysere artssammensetningen av trær i et nettverk av ruter langs en høydegradient på 2900 meter. Deretter brukte jeg 'distance sampling' langs transekter for å studere utbredelsen av trærpå en mindre skala i forhold til skogstruktur og lystilgang for ti 'cloudforest' trær langs en 1500 meter høydegradient. Til slutt gjennomførte jeg et transplanteringseksperiment langs en høydegradient for å forstå hvordan temperatur, konkurranse om lys, og forstyrrelser påvirker vekst og overlevelse av åtte arter.

Jeg fant at effekten av forstyrrelser på skogstruktur (artikkel I) og utbredelsen av trær (artikkel II, III og IV) er kontekstavhengig langs høydegradienter. Utbredelsen av flere arter langs høydegradienten var avhengig av skogstruktur og lystilgang. For eksempel hadde arter som ankom tidlig i suksesjonen og dermed unnslappkonkurranseekskludering en videre utbredelse enn dem som ankom senere i suksesjonen (artikkel II). Noen arter med utbredelse øverst i høydegradienten var klart lyskrevende og utvidet utbredelsesområdet når konkurransen om lys ble redusert. Andre arter viste en kontekstavhengigheti forhold til konkurranse og forstyrrelse, og skiftet fra å ha en skygge tolerant til en lyskrevende fordeling mellom øvre og nedre utbredelsesgrenser (artikkel III og IV). Ofte hadde disse artene sin nedre grense for utbredelse i områder med lavere basalareal av trær og større lystilgjengelighet (artikkel II, III og IV), med utvidelse av utbredelsesområdet mellom 100 og 1000 meter lavere (tilsvarende 5 C^0 varmere). På den annen side var utbredelsen i de høyereliggende områdene mer avhengig av frosttoleranse, og fasilitering var viktig for vekst og overlevelse av de studerte artene (artikkel II og IV).

Disse resultatene antyder at forstyrrelse kan frigjøre begrensningene som konkurranse kan gi og utvide leveområder for arter til varmere og kjøligere klima, og gir ny innsikt i dynamikk, grenser og bevaring av trærs leveområder. Avhengig av miljøkonteksten kan forstyrrelser katalysere eller bremse endringer i trærs leveområder i fremtiden. Forstyrrelser kan være viktige for å redusere den indirekte effekten av nye konkurrenter på arters utbredelse i en varmere verden.

5 Synopsis

5.1 Introduction

How and why species are distributed remain major themes in ecological sciences. Nonetheless, some aspects are still uncertain. For example, there is no consensus on when biotic interactions impact the range limits of species, particularly in the tropics. While ecologists have long known that the fundamental and realized niche of any organism can be very different, we still do not completely understand the implications of these differences on species' distributions. Such gaps are concerning if we consider current topics, such as the influence of climate and climate change, on how species are distributed. Disentangling the climatic and biotic conditions that shape species ranges is key to predicting how their distributions will shift in the face of both climate change and human impact on species interactions. Climate change is an imminent threat to biodiversity (Urban, 2015). Whether climate change threatens species' potential to persist depends on direct climate impacts on the extent and suitability of habitats (Román-Palacios & Wiens, 2020) and indirect impacts of a reshuffling of species interactions (Cahill et al., 2013; Klanderud & Totland, 2005). Tropical montane ecosystems with high levels of endemism and narrowly distributed species are particularly vulnerable (Laurance et al., 2011). For many of these species, there will be no option but to disperse to higher elevations or latitudes to stay within their current thermal ranges and avoid being excluded.

The outcomes of these novel biotic conditions in terms of species persistence have been little explored, particularly in the tropics. Ecologists predict that climate change will alter species' competitive environments through both shifts in the performance of their current competitors and the arrival of new ones (Alexander et al., 2015; Corlett & Westcott, 2013a; Ettinger & HilleRisLambers, 2013). While current conservation efforts focus on preserving and increasing landscape connectivity to help species escape the direct and indirect effects of climate change, many species are not moving fast enough (Alexander et al., 2018; Corlett & Westcott, 2013b). Thus, it is reasonable to think that competitive exclusion represents a real threat to those species not able to move fast enough. This situation highlights the need to find and explore any means to preserve species under novel biotic and climatic conditions.

Managed disturbances that slow or prevent competition could be an option. While climate limits where tree species can potentially live and grow, their current distribution is often determined by biotic interactions (Araújo & Luoto, 2007; Bocsi et al., 2016). For example, a tree species may be excluded from an area it can climatically tolerate due to competition for light by another species, potentially establishing a range limit. This implies that the geographical distributions of species in nature represents their realized niche. Disturbance can modify a species' realized niche and resulting distribution. For example, disturbance may promote changes in forest stand structure (e.g., canopy openings, reductions in basal area), increasing light availability and opportunities to establish (Denslow & Guzman, 2000). However, scientists still lack a minimal understanding of how competition and disturbances can shape species distribution. This thesis is a contribution to fill that knowledge gap.

After disturbance, the composition of the community will depend on how tree species establish and compete with new arrivals, which is a function of their life history traits (Pickett et al., 1987). The species that are competitive dominants under the most benign conditions are seldom the same as those that dominate in less benign conditions (Huston & Smith, 1987; Shipley & Keddy, 1994; Wisheu, 1998). For example, along elevation gradients, species' tolerance of colder (higher elevation) conditions may imply a cost in terms of reduced competitive abilities under warmer (lower elevation) conditions. Such trade-offs generate a competitive hierarchy, in which inferior competitors are excluded from elevations with an optimum environment for their growth. Often, these latter species will also become established and grow well in more benign sites if the other species are absent or eliminated through disturbances. Thus, what appear to be colonizing species in some locations seem to behave as late successional species in other generally less hospitable environments (Budowski, 1965; van Steenis, 1958). A trade-off between species' abilities to colonize and compete, such as poor competitors being better colonizers, also allows excluded species to arrive first. This mechanism grants a short-term advantage to the inferior competitors in terms of access to new sites, as arriving and emerging first allows them to grow and scape separately from other species. This advantage influences their distributions (Amarasekare, 2003; Morin & Chuine, 2006).

The role of disturbance on species ranges likely depends on the specific environmental context. Along elevation gradients, for example, competition is predicted to be more important in explaining species range limits at lower elevations than at higher elevations, where tolerance to cold temperatures is more fundamental. At the lower elevation range limits, disturbances might protect some tree species from the encroachment of more competitive lower elevation species (Alexander et al., 2015; Kopp & Cleland, 2014). At higher elevations, where plant cover may facilitate species' survival and growth (Cáceres et al., 2019), disturbance can have a negative impact. The implication is that upper elevation range limits depend more on environmental tolerance, and lower elevation limits depend more on competition. This context-dependent role of biotic interactions along gradients has been long discussed (Darwin, 1859) with more recent contributions from the stress gradient hypothesis (Bertness & Callaway, 1994). Despite this extensive theoretical work and multiple evidence on temperate ecosystems (Callaway et al., 2002; Ettinger & HilleRisLambers, 2017; Olsen et al., 2016), the role of biotic interactions and disturbance on tree distributions remains little explored in the tropics.

Predicting species' responses to novel climates and biotic conditions is challenging because we often lack sufficient observational and experimental data to fully determine the conditions that allow a species to grow. Elevation gradients in mountains offer a unique opportunity to test how changes in competitors and climate will affect species' performance and potential distribution. The advantage of using elevation gradients to explore these ideas is that the novel competitors that species will face following climate warming are those already occurring only hundreds of meters away.

Using a combination of observational and experimental approaches, I explored the degree to which competition and disturbance determine the upper- and lower-elevation distribution ranges of multiple tropical tree species in Costa Rica. More specifically, I examined 1) how disturbance and tree species' life histories influence forest structure and thus, potentially, elevation distributions (Chapters 1 & 2); 2) how disturbance influences cloud forest and paramo plant species' elevation range limits (Chapter 3), and 3) the ability of disturbance, and interventions based on disturbance, to modify tree elevation ranges and seedling persistence under a warmer climate (Chapter 4).

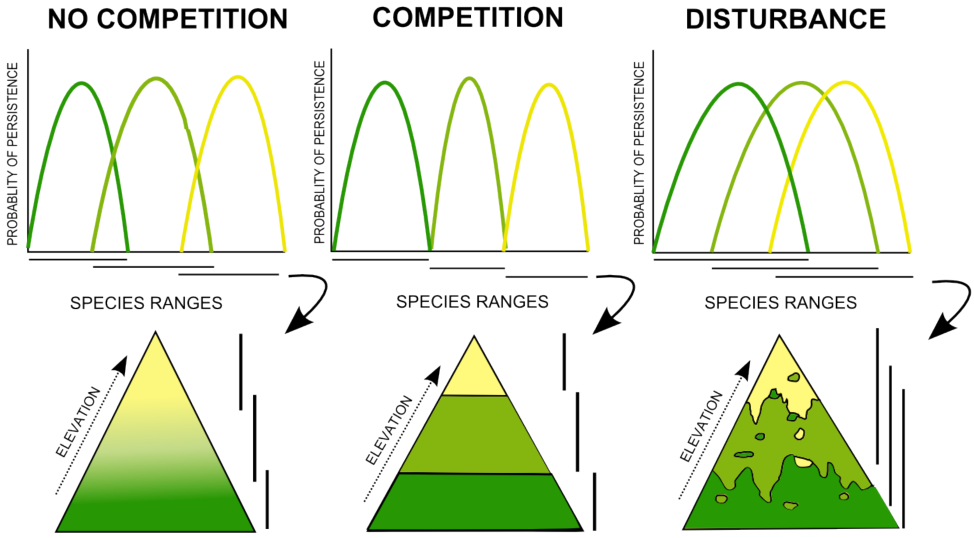

Figure 1: Theoretical framework modified from Paper II (Muñoz Mazón et al., 2019, based on Sheil, 2016). Schematic representation of how competitive hierarchies and disturbance may influence the elevation range of three species. The upper row represents the probability of persistence of three species along a gradient in three different scenarios (no competition, competition, and disturbance). The lower row shows how their ranges would be distributed along an elevation gradient. Under a theoretical scenario of no competition between the three species, their ranges will follow the environmental conditions corresponding to each species' fundamental niche. Competitive interactions would constrain their distributions along elevation gradients, particularly their lower range limits, and the realized niche is smaller than the fundamental niche. Disturbance may allow these three species to expand their ranges to upper and lower elevations by altering the already established competitive hierarchies and reducing priority effects so that the realized niche is larger.

5.2 Materials and Methods

5.2.1 Study Area

The fieldwork was carried out in the montane forest and paramos along the Atlantic slopes of the Talamanca Mountains and the slopes of volcano Turrialba in Costa Rica. While the Talamanca Mountains originated from ancient volcanic activity, marine sedimentary process, and more recently Pleistocene glacial activity; Turrialba Volcano originated from recent volcanic activity. This volcano is still active with its uppermost part of the cone currently depleted of vegetation. Despite the different geomorphological origins, both mountain ranges share similar soil compositions. At elevations above 1,500 meters, soils are typically dark, rich in organic matter, and deep. Below that elevation, soils tend to be heavily weathered, belonging to the Ultisol category (Kappelle & Lobo, 2016; Lawton et al., 2016).

Both mountain ranges span similar elevations up to 3,400 m.a.s.l. and support similar climate gradients. The climate is tropical, wet, and seasonal in the lowlands, with annual rainfall of 3,500 mm and mean annual temperature of 24°C. At higher elevations, precipitation becomes more seasonal, with a mild, dry season from January to March. Temperature decreases at a rate of approximately 0.56°C per 100 m of elevation (Muñoz Mazón et al., 2019; Veintimilla et al., 2019). The climate of these mountain ranges is highly influenced by the trade wind patterns that blow from the Caribbean/Atlantic lowlands. Indeed, much of the environmental variation among these mountain ranges is due to the patterns of wind flow that cross them. The trade winds are responsible for the amount of orographic rainfall, the frequency of immersion in the clouds, and the levels of exposure to mechanical stress from wind. Windspeeds reach their maximum around January and February, progressively decreasing throughout the year. During these months, the constant influx of clouds brought by the trade winds helps to alleviate the scarcity of rainfall in the highlands (Kappelle & Lobo, 2016; Lawton et al., 2016).

Most of the study area lies within the Barbilla, Tapanti, and Cerro de la Muerte National Parks. Tropical rainforest covers the lowland areas, transitioning to Quercus spp.-dominated cloud forests at the higher parts of the gradient (Kappelle et al., 1995). Floristically, the

Talamanca Mountain range is one of the four areas with the greatest levels of endemism in Costa Rica, with approximately 30% to 40% of its flora endemic to the region (Kappelle & Lobo, 2016). Some examples of the endemic flora are the study species in this thesis, such as *Prumnopty standleyi*, *Quercus costarricensis*, *Schefflera rodriguesiana*, *Vaccinium consanguineum*, *Hypericum irazeuense,* and *Rhamnus oreodendron*.

From 700 to approximately 1,700 m.a.s.l, premontane forests dominate the landscape (Figure 2A). These forests are dominated by species from the Lauraceae, Melastomataceae, and Euphorbiaceae families, with an increasing abundance of Fagaceae and Juglandaceae, such as the oak *Quercus seemani* and *Oreomunea mexicana,* respectively, toward higher elevations. Some of the species studied in Papers III and IV are characteristic of this ecosystem, such as *Cedrela tonduzii*, *Quercus seemani,* and *Trichilia habanensis*. From 1,800 m.a.s.l, coinciding with the cloud belt, to 2,400 meters, we can find the lower montane cloud forest (Figure 2B). Here, oak species, such as *Quercus bumelioides*, start to become more important in terms of numbers of individuals and basal area. Members of the Lauraceae (Ocotea spp. and Persea spp.) and Araliaceae (*Oreopanax spp*., *Schefflera spp*., *Dendropanax spp*.) families are abundant. The upper cloud forest (Figure 2C) is characterized by the clear dominance of *Quercus bumelioides* and, closer to the tree line, by the endemic *Quercus costarricensis*. Trees of these two species dominate the canopy, with individuals as high as 50 meters and several meters in diameter. Scattered in the landscape and much less abundant than the oaks are other giant trees, such as *Podocarpus oleifolius* and the rare endemic *Prumnopitys standleyi* (both from the Podocarpaceae family). Another element that characterizes these montane cloud forests is the abundance and diversity of bamboo species from the genera, *Chusquea spp*. Other characteristic tree species present in the upper montane cloud forest are *Weinmannia pinnata* and *Styrax argenteus*, both studied in Paper III. Finally, above the tree line (around 3,000 m.a.s.l), we find the Paramos (Figure 2D), a grass/shrub-dominated ecosystem characteristic of the wet and cool upper slopes of many tropical mountains in America. Its small extent (Paramos only occupy 0.3% of Costa Rica's total surface) and high levels of plant endemism (up to 35% of their flora is endemic to that ecosystem) makes it a conservation priority (Kappelle & Horn, 2005). Three characteristic species are the bamboo, *Chusquea subtesselata*, and the shrubs, *Vaccinium consanguineum* and *Hypericum irazuense*. These last two species are studied in Paper III and Paper IV.

Figure 2: A) Premontane forest. B) Lower montane cloud forest. C) Upper montane cloud forest with huge individual of *Q. bumelioides*. D) Paramo shrubland with some individuals of *Hypericum irazuense* and the bamboo *Chusquea subtesselata*.

Treefalls were the most common natural disturbance that I encountered during the different surveys carried out (Figure 3A). The frequency of treefalls increases during the rainy season due to the cold winds from the north, which bring heavy rainfall around October and November (Lawton et al., 2016). A less common disturbance event is fire, which occurs more frequently at higher elevations in the transition between paramos and cloud forest (Horn & Kappelle, 2009). Despite landslides being quite conspicuous in other tropical mountains and even in other regions of Costa Rica (Crausbay & Martin, 2016; Garwood et al., 1979; Martin et al., 2011; Quesada-Román et al., 2019), I did not encounter any patch of forest affected by this disturbance type while collecting data in the field.

Most of the studied secondary forest patches were recovering from human disturbances. These ecosystems have been exposed to human disturbances for thousands of years. Records of human artifacts found along the Arenal Volcano suggest human presence dating back to 10,000 BP (Sheets et al., 1991). However, it is not until 1,500 BP that swidden agriculture appears in these landscapes, according to charcoal and pollen records. Along the slopes of the Turrialba volcano, the Guayabo archaeological site evidences the presence of humans since at least 2,300 years BP (Amighetti et al., 2016). However, the influence of pre-Colombian people on modern vegetation in the studied region is not very well known. In the neighboring Panama, pollen and charcoal records suggest that human-ignited fires were the cause of oak species (Quercus spp.) disappearing from the lowlands 5,000 years ago. We know better how humans impacted Costa Rican forest during modern times. It is estimated that between the 1940s and 1990s, almost 80% of the forest was cut down for agriculture and pastures (Sanchez-Azofeifa et al., 2001), particularly in the more accessible lowlands and premontane forest in the Central Valley. This is the case for the Turrialba area, where milk farms substituted most of the highland's forest, and sugar cane the lowland ones. According to landowners, the secondary forest studied along the Turrialba Volcano previously comprised pastures, such as the one presented in Figure 3B. The impact of past and recent human activities could explain why oaks are almost absent from the Turrialba Volcano cloud forest. Deforestation and land use change occurred at a slower pace in the Talamanca mountain range due to its isolation from the big urban areas of the Central Valley. The construction of the Inter-American highway in the late 1970s facilitated the arrival of settlers and the transformation of those ecosystems. Forest was transformed into potato and blackberry fields and, to a lesser extent, into pastures. However, the greatest impact of humans in this mountainous forest was logging for firewood, construction, and production of charcoal. Before the protection of these cloud forests under the creation of both the Tapanti and Cerro de la Muerte National Park and Reserva Forestal Rio Macho in 2000, this area provided two thirds of the total charcoal produced in Costa Rica (Kappelle & Lobo, 2016; Pedroni, 1991). Most of the secondary forest in this area is recovering from the logging activities that the charcoal industry required.

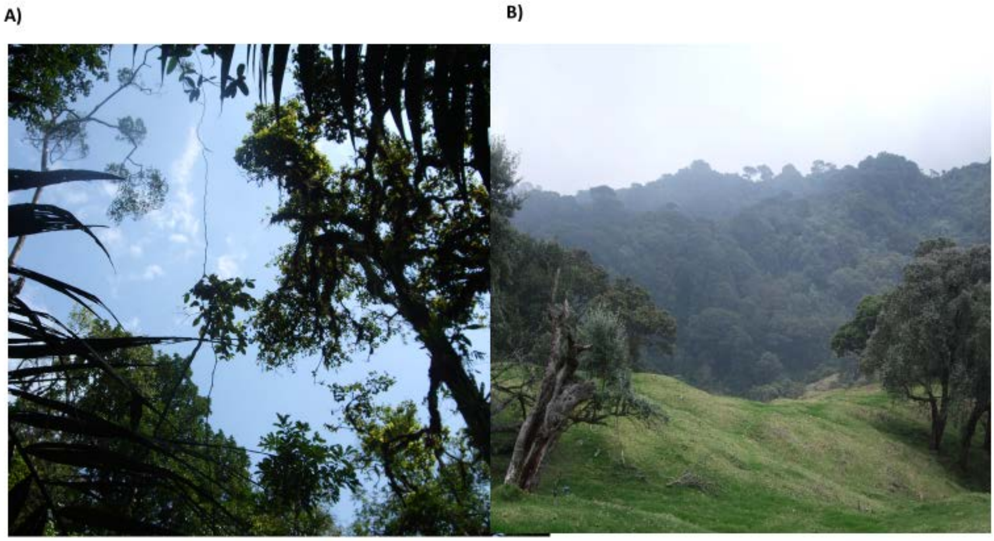

Figure 3. A) Gap created in the canopy due to a tree fall. B) Pastures next to a secondary forest in the Volcano Turrialba.

5.2.2 Study design

I used three different approaches to explore the role of disturbance on tree species' elevation ranges:

1) <u>Vegetation plots:</u> A network was established of 68 plots of 0.25 and 0.1 ha in secondary and old growth forest (Figure 4.) along an elevation gradient from 400 to 2,900 m.a.s.l. I explored existing data from this network to understand how succession and elevation interact and shape the structure of the studied forest (Paper I) and how changes in forest structure may impact the broad-scale patterns of tree species' elevation ranges in relation to succession (Paper II). The geographical extent of this network allowed me to explore coarse patterns across a relatively broad scale for multiple tree species. See Paper I (Muñoz Mazón et al., 2020) and Paper II (Muñoz Mazón et al., 2019) for greater detail about the sampling methodologies and selection of the locations.

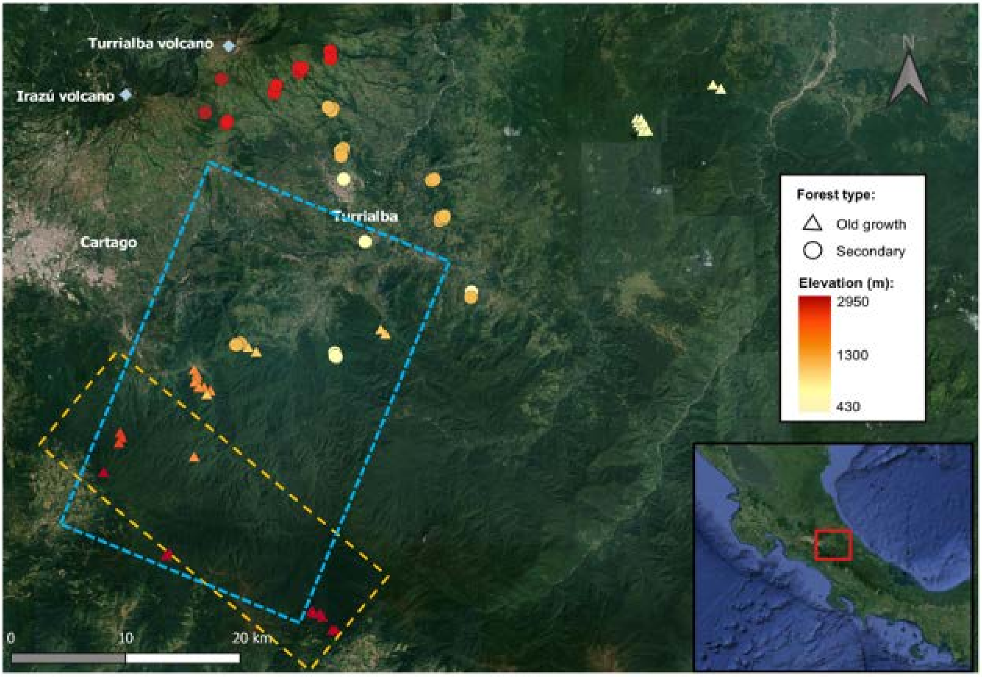

Figure 4: Map of the study area of each of the three different sampling approaches. The plot network (1) is represented by triangles (old growth plots) and circles (secondary forest plots). The study area of the distance sampling (2) corresponds to the yellow dashed rectangle. The blue dashed rectangle corresponds to the area covered by the transplant experiment (3).

2) <u>Distance sampling transects:</u> To understand the small-scale changes of tree distributions due to disturbances, I inventoried the individuals of ten species of trees along 1,200 meters (from 3,200 to 2,000 m.a.s.l.) elevation gradient. I established 22 distance sampling transects of 500 meters length (Figure 5). This method consists of establishing a transect perpendicular to the slope and inventory any individual of the target species seen from the transect and its distance to the transect. It assumes that all individuals located on the line are detected, the probability of detection decreases with distance from the transect, and objects are immobile. Then, using the distribution of the distances, it is possible to estimate the probability of detecting an individual given a distance through a detection function (Buckland et al., 2005). To improve the model fit, it is possible to include any variable that may affect detection (Marques et al., 2007). In my case, for each individual tree detected, I recorded its diameter at breast height, basal area around the individual using the relascope method (Phillip, 1994), approximate tree

height, and crown illumination index (Dawkins & Field, 1978). The same variables were recorded within the transect at intervals of 50 meters. This allowed me to characterize the transect for later predictions of species' densities in relation to the variables recorded. With that probability, it is possible to estimate densities. At each transect, I recorded the presence of the following species: *Vaccinium consanguineum*, *Hypericum irazuense*, *Escallonia myrtilloides*, *Schefflera rodriguesiana*, *Weinmannia pinnata*, *Rhamnus oreodendron*, *Magnolia poasana*, *Podocarpus oleifolius*, *Prumnopity standleyi*, and *Styrax argenteus*. More details about the sampling design and method can be found in Paper III.

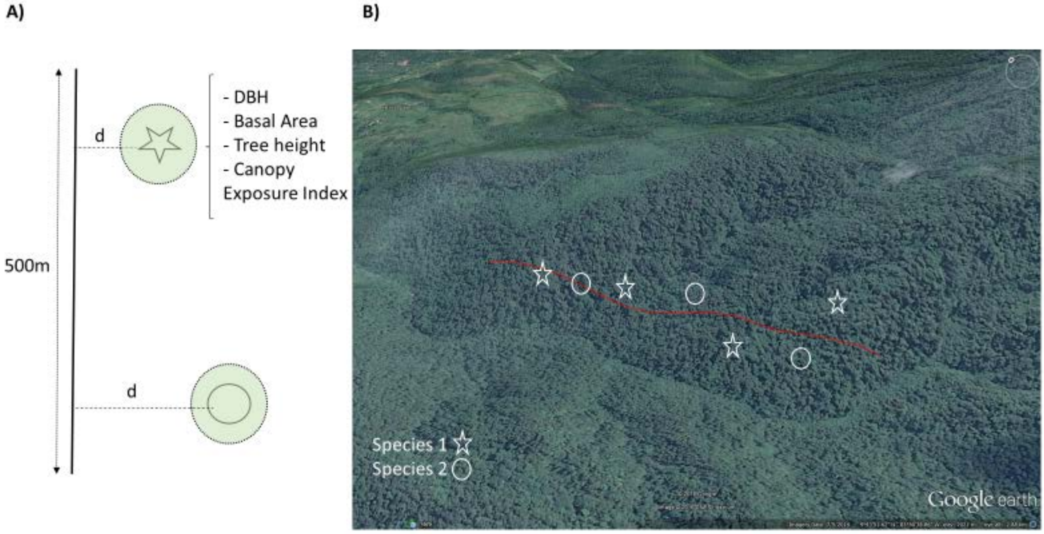

Figure 5: A) Schematic representation of a distance sampling transect with the variables measured for each recorded individual; d = distance in meters. B) Example of a transect in the landscape.

3) A transplant experiment (Figure 6). The previous surveys allowed me to explore at two different scales how current species distributions have been influenced by past disturbances. However, the results of these approaches will always be confounded by species' ability to disperse. Transplanting of species to areas beyond their geographic range limits is key to disentangle the determinants of their range limits. To understand how disturbance may influence species' seedling growth, survival, and persistence in a warmer future, I performed a transplant experiment along the same elevation gradient covered in the previous approaches. I selected nine locations between 600 m.a.s.l. and 3,400 m.a.s.l. In each location, I selected two sites in which I established ten 1x1-meter plots. In each site, five plots were established under the shade of trees inside the forest and the other five in an adjacent open area. In each plot, I transplanted one individual of eight different species. These included one Paramo endemic shrub (*Hypericum irazuense*), four montane cloud forest trees (*Quercus bumelioides*, *Q. costarricensis*, *Cornus discifloral*, *Persea schiediana*), and three premontane forest trees species (*Q. seemani*, *Cedrela odorata* and *Trichilia habanensis*).

The seedlings of these species were transplanted with standardized soil (from the forest where the seedling was collected) at the end of the dry season, between April and May in 2017. The data presented in this thesis corresponds to the growth and survival of the seedlings 18 months after the transplanting. At the center of one plot per treatment (open area and forest) per site, I installed a HOBO pendant datalogger to record luminosity and temperature every 30 minutes during the length of the study.

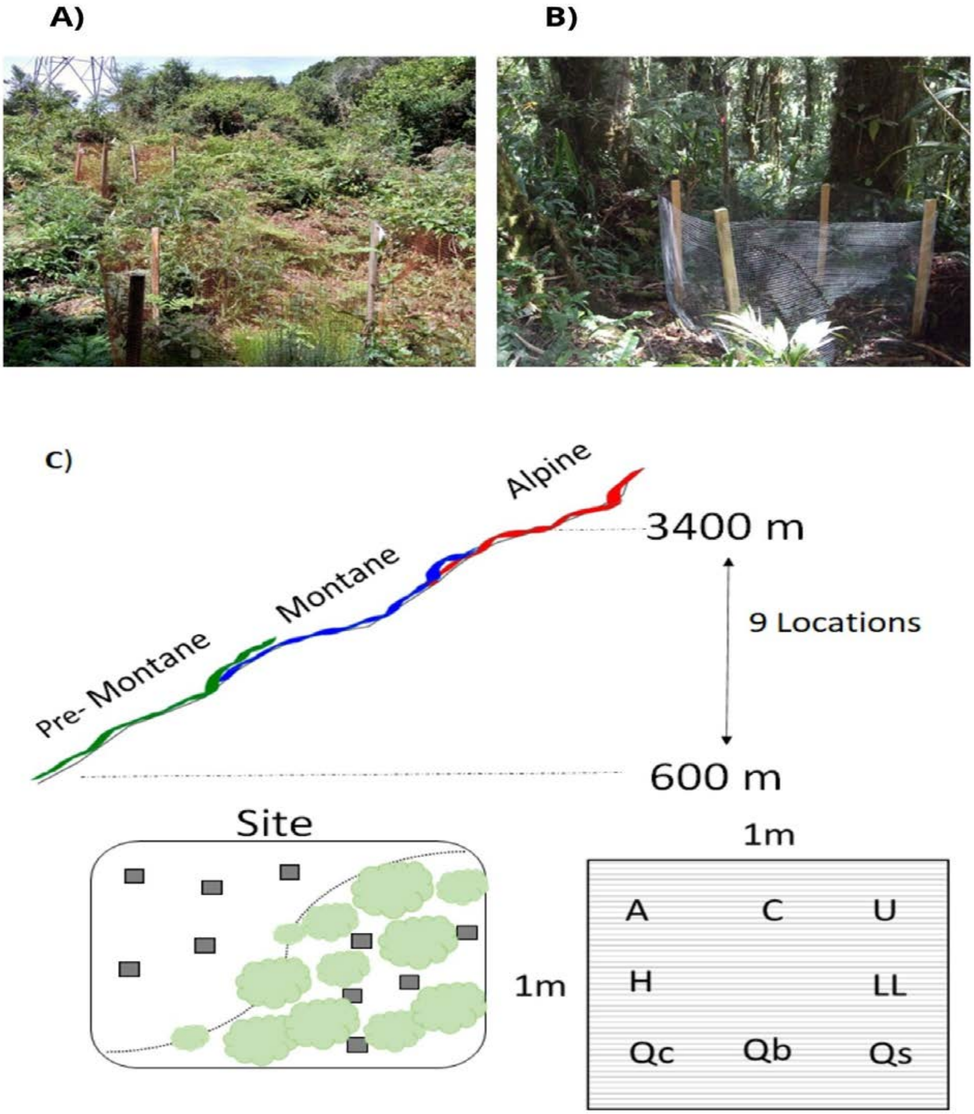

Figure 6: A) Transplant plots in the open treatment. B) Plots in the forest treatment. C) Schematic representation of the transplant experiment. The dark squares inside the site rectangle represent plots in each of the treatments. Each plot consists of a 1x1-meter square, fenced up to 1.5 meters to avoid herbivory from large animals.

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5.2.3 Data Analyses:

The statistical analyses used in this thesis are detailed in each Paper. Here, I present a table that summarizes the analyses performed and the variables used.

Table 1. Summary of main statistical analyses performed in each Paper.

Paper	Response variable	Explanatory variables	Analyses
I	Basal Area, N umber of stems, N of stems > 30 cm dbh, Wood Specific Gravity	Elevation, PCA axis 1,PCA axis 2, Wood Specific gravity (Weighted means and dispersion)	GLM
	Wood Specific Gravity	Elevation	GAM
II	Species elevation range size	Elevation Range Midpoint	Pearson Correlation
	Species elevation range size	Forest categories: Old growth vs Secondary	Wilcoxon test
	Species elevation range size	Tree diameter size categories: 10-15 cm vs 15-30 cm vs > 30 cm	Kruskal–Wallis test
	Basal Area	Elevation	GLM (Gamma)
	Number of range limits per Basal area category	Expected values under two assumptions: 1) equal probability in both categories; 2) Greater change of range limit where there are more individuals	Chi square
III	Species density	Light availability, Basal area, Elevation	Density Surface Models (DSM) (Miller, Burt, Rexstad, & Thomas, 2013)
IV	Seedling survival, growth	Treatment (Open vs Forest) x Elevation	Hierarchical Generalized Additive Model (Pedersen, Miller, Simpson, & Ross, 2019)

5.3 Results and discussion

Disturbance through altering the structure of the forest and affecting the availability of resources, such as light, influences the elevation ranges of multiple tropical tree species. The results of this thesis highlight the relevance of biotic interactions in shaping the elevation ranges of tropical trees. I also found evidence of a context-dependent role of competition and facilitation on tropical trees' elevation ranges in line with the stress gradient hypothesis (Bertness & Callaway, 1994). Competition seems to be more important when setting the warmer lower elevation range limits of multiple species, while facilitation influences mainly their upper and colder range limits. Thus, depending on the dominant interaction, disturbance can promote tree species' range expansions or contractions. Most importantly, managed disturbance could be a fundamental strategy to prevent tree species being excluded by novel competitors in a warmer future. These ideas and their implications for biodiversity conservation are discussed in the sections below.

5.3.1 Disturbance explains variation in forest structure and dynamics across elevation gradients.

In Paper I, I observed a pattern of increasing basal area and density of large trees with elevation in both secondary and old-growth forests. I interpreted these patterns through the existence of a positive feedback loop in which disturbances, such as windstorms or droughts, kill vulnerable canopy trees and promote the regrowth of fast-growing species, which remain vulnerable to further damage. Similar positive feedback between disturbances has been observed in boreal, temperate, and tropical forest (Aleixo et al., 2019; Liang et al., 2018; Thom et al., 2017; Uriarte et al., 2016). However, there is still little knowledge on the importance of these feedback loops across gradients. Two observations from Paper I suggest that this feedback could be more prevalent in lowland forest. First, there is a greater variability of wood density at lower elevations and in secondary forest. This implies that there is a greater chance of a vulnerable (to drought and wind) species recruiting after disturbance in the lowlands, particularly in secondary forest. Second, in these forests, the basal area and number of individuals decrease with increasing water scarcity. The studied high elevation montane forest recovers faster, at least structurally, than the lowland ones. This faster recovery seems to rely on survival and resistance to disturbance. It is possible that the whole community of trees in the studied montane forest are adapted to cope better with rainfall seasonality. Higher values of wood specific gravity are commonly associated with security against hydraulic failure (Hacke et al., 2001). In this study, trees at high elevations tend to have a more similar and higher wood specific gravity than their lowland counterparts. It has been shown that tropical tree vulnerability to climate extremes is generally inversely related to long-term exposure to extreme weather events (Ciemer et al., 2019; Uriarte et al., 2016), supporting the idea of high elevation trees being better adapted to rainfall seasonality. The impact of severe El Niño–related droughts on the forests' dynamics is huge, affecting both canopy trees and their regeneration (Browne et al., 2021), which in turn can slow down the recovery of these forests.

It is interesting that other studies in Costa Rica suggested that extreme droughts could accelerate succession in tropical lowland forest (Uriarte et al., 2016). The idea is that by killing vulnerable trees, droughts "filter" the community toward more resistant late successional species. After several extreme events, the dominance of these species increases, and the community becomes more resistant with time. This is likely the case in many secondary forests well connected to old growth forest patches. In my case, the opposite pattern could be explained by dispersal limitation of late successional species due to the relative isolation of the secondary forest patched from old growth forests.

Another non-mutually exclusive hypothesis is that both extreme dry events and windstorms are more severe in the lowland areas compared to the higher elevations. For example, fog and cloud immersion in the montane forest could alleviate rainfall scarcity during drought. At global scales, basal area peaks in temperate rainforest, such as Redwoods in California, the Valdivian forest in Chile, or Eucalyptus forest in Australia (Larjavaara, 2014). These regions have in common the influx of humidity in the form of fog from the ocean and mild mean annual temperatures (approximately 12–16°C) (Keith et al., 2009). These same variables seem to explain forest structure along elevation gradients in some tropical forest, too (Venter et al., 2017). However, in my study area, this hypothesis should remain unexplored. The role of climate extremes on forest dynamics across elevation gradients should be a matter of future studies.

5.3.2 Disturbance shapes the elevation ranges of multiple tropical tree species—potential mechanisms.

To understand how disturbance shapes species' distributions along elevation gradients, we must understand the context-dependent role of competition on species ranges. The relative competitive abilities of species depend on the abiotic condition (Huston & Smith, 1987; Usinowicz & Levine, 2018). Under specific environmental conditions, a superior competitor can exclude the inferior competitor to areas not physiologically tolerable to the superior competitor. These competitive displacements along a gradient imply that species' competitive abilities trade off with their abilities to tolerate certain environmental conditions and colonize new areas. Under this assumption, competition should be more intense at physiologically optimal areas for growth along an elevation range. In our case, it is the low elevation limit, as the weather is warmer and wetter toward lower elevations. The presence of these trade-offs has been well documented and described (Coomes & Grubb, 2003; D'Andrea & O'Dwyer, 2021; Uriarte et al., 2012; Zhu et al., 2018). However, the role of these trade-offs in shaping species distributions and the contribution of disturbance to these processes have been poorly documented, particularly in the tropics. Some of the observations in this thesis suggest the presence of these trade-offs among the studied species. For example, results from Paper II show how the species that establish themselves first after disturbance in secondary forest benefit most from the temporary absence of competition and have broader elevation ranges. In the same paper, we observe a greater frequency of species with low-range limits in plots with lower basal area and thus reduced competition. In a similar way, we observe in Paper III how multiple species have a greater density in areas with more light availability and less basal area toward their lower range limit. The results from the transplant experiment in Paper IV point to the same direction, showing that seedling survival and growth increases at the low elevation range limits when competition for light is reduced. All these observations support the idea that any species is optimally adapted to all conditions and that their competitive ability shifts along the elevation gradient. In this context, disturbance can improve species' persistence where competition represents a greater risk for long-term survival, such as at species' warmer range limits. The role of disturbance on species distributions has important implications for species conservation in a warmer world.

Some of our results suggest a potential role of competition also limiting the upper range distribution of some trees, particularly below the tree line, where frost occurs. This is supported by observations from Paper II of a greater number of species in the old growth forest having their upper range limit in low basal area plots, where we presume there is less competition. In addition, the greater survival in open vs forest areas described for *Trichillia habanensis* in Paper IV suggests a role of competition just below the tree line. Although these observations contradict predictions of the stress gradient hypothesis, any species is likely to be less competitive close to their physiological upper range limits (McGill, 2012). Under this scenario of competition limiting the upper range limits of tree species, disturbance can catalyze species' range shifts toward higher elevations. Similar patterns have been observed in the boreal/temperate forest transition, where disturbance promoted the encroachment of broadleaved tree species into the conifer-dominated taigas (Brice et al., 2019; Brice et al., 2020) or in The Alps (Scherrer et al., 2021; Shepard et al., 2021). However, in the tropics, these patterns have not been so well described. Thus, disturbance could be important to avoid cases of biotic attrition in the future. It is possible that some of the observed elevation shifts of tree species in the tropics (Duque et al., 2015; Feeley et al., 2013) are amplified by disturbances and do not necessarily correspond to a shift in their thermal optimum due to climate change.

Above the tree line, exposure to frost determines the survival of tree seedlings (Paper IV). At these elevations, disturbances can have a negative impact and contract species ranges through reducing any potential facilitative interactions trees and shrubs may offer. The observed patterns in Paper II and Paper IV are good examples of facilitative interactions at the upper range limits of tropical trees. There are multiple examples where facilitation shapes the upper range limits of trees, both in temperate and tropical ecosystems (Cáceres et al., 2019; Farji-Brener et al., 2009; Rehm & Feeley, 2015). However, one consequence less discussed in the literature is how facilitative interactions can advance the arrival of novel competitors to higher elevation. For example, in Paper IV, paramo shrubs facilitated the survival of oak trees, which, in the future, with increasing temperatures, could grow and exclude them. Depending on conservation goals, favoring facilitative interactions could do more harm than good.

5.3.3 How relevant is dispersal limitation to the observed patterns?

Dispersal is a fundamental element to understand species distributions. Indeed, the geographic ranges of most species are, in a way, limited (Gaston, 2009). Consequently, the outcome of disturbance on elevation ranges and forest dynamics depends not only on establishment but also on each species' ability to reach suitable locations. The observed slower rate of recovery after disturbances in the studied secondary forest could be related to a slower arrival of resistant late successional species due to dispersal limitation and forest isolation. In Papers II and III, since we cannot distinguish the influence of propagule availability and dispersal limitation from environmental limitations, the observed patterns are likely a minimum estimate. This underestimation appears particularly important for species with short, localized dispersal and short-lived seeds, such as late successional species. Some patterns observed in Paper IV, such as the great survival of *Cedrela tonduzii* and *Hypericum irazuense* outside their typical ranges, suggest that these species are highly limited by dispersal. These species are dispersed by wind and gravity respectively. However, in the context of the thesis, dispersal limitation is less important than the role of competition and disturbance. The future persistence of many species may often depend on enduring a changed climate and associated novel competitors rather than on dispersal to suitable areas. Indeed, many observed elevational range shifts relate to range reductions (Elsen et al., 2020) and changes in abundance within their current elevational range (Rumpf et al., 2018) and not by dispersal and colonization beyond the range limits.

5.4 Biodiversity conservation and management implications

With the projected increase of temperatures, global biodiversity is expected to decline (Urban, 2015). Among the most threatened species are those with limited dispersal, narrow ranges, narrow climate tolerance, and low population sizes (Laurance et al., 2011). This is the case of many high elevation tropical plant species, such as those found in the Costa Rican Cloud forests and Paramos. Shifts in species interactions may ultimately result in the greatest impacts of climate change on the range dynamics and persistence of individual species (Alexander et al., 2015). Either because of a shift in the competitive hierarchies within communities or due to the arrival of novel competitors, increases in competition could imply greater extinction risks for many species. Therefore, a complete mapping of a species' positive and negative interactions along a gradient could help identify where and how these interactions affect its distribution and persistence more strongly. This could help us recognize where interventions are needed. For example, this thesis suggests that reductions of competition for light through managed disturbances may be needed in a warmer future to grant the persistence of paramo species, such as *Hypericum irazuense* or *Vaccinium consanguineum*. Paramo ecosystems represent “islands” threatened by a rising sea of trees. Disturbance could both help maintain the size of the current Paramo “islands” and to create new islands if needed, which may act as corridors and increase the connectivity of these ecosystems. Although these ideas may seem extreme, ecologist have traditionally associated the extent of paramos in Costa Rica to pre- colonial human activities.

Based on observations of paramo species recruiting below the tree line after fires, Janzen (1973b, 1983) suggested that over time human set fires had extended paramos towards lower elevation, explaining the distribution of this ecosystem in Costa Rica. These ideas have been currently discarded. The existence of several endemic species in these paramos suggests an origin of the ecosystem that predates human presence (Cleef & Chaverri, 1992). However, all these observations suggest that disturbances, particularly fire, is a key element explaining the current distribution of paramos. Despite evidence, management interventions are rarely considered in Costa Rican protected areas. Under a potential future scenario of increasing competitive exclusion, it is unlikely that solely protecting the landscape will be an effective measure to grant the persistence of many tree and plant species.

Mapping the distribution and ecological requirements of rare and low abundant species is a challenge. Furthermore, the abundance of many species decreases towards their range limit, making it difficult to establish the causes that determine their distribution. In this thesis, I show how distance sampling could be a practical method for both conservation managers and researchers interested in understanding both the local distributions of tree species and the mechanisms that determine their range limits. Indeed, standard inventory methods such as plots have been shown to be very ineffective for sampling low abundant species, such as the two podocarpaceae studied (Dalling et al. 2011). Distance sampling methods could be a better option for rare and low abundant species. Previous studies show that distance sampling methods applied to trees could be more efficient than plots in terms of time invested per stem (Kissa & Sheil, 2012). Here, by establishing 22 line transects of 500 meters, I inventoried 5,121 individuals, which is very close to the number recorded in the 68-plot network. I completed work with the support of one person in approximately 360 hours. Although I do not have an estimate of the effort invested in the plot network, I believe it is much more than the time spent in the distance sampling transects.

The patterns observed in this thesis also have implications regarding the recovery and restoration of tropical forest along elevation gradients in Costa Rica. We note that, given the recognized link between basal area, stand biomass, and carbon, natural regeneration of high-elevation rather than low-elevation forest is, hectare for hectare, likely a more rapid means to capture carbon. Implementing successful restoration strategies is key to consider the potential effect of recurrent disturbance and how vulnerable the planted trees are to those events. Typically, few tree species are used in lowland forest restoration projects in Costa Rica. Most of the time, these species are early successional fast-growing trees that are most vulnerable to disturbances. Planting multiple species with different adaptations could improve the resilience and long-term recovery of lowland forests. In the lowlands, planting nursery-raised seedlings of native long-lived species, such as *Brosmium utile*, *Terminalia amazonia,* or *Vochysia guatemalensis* (Guariguata et al., 1995; Guariguata & Ostertag, 2001; Holl et al., 2017; Leopold et al., 2001), could help establish a less vulnerable canopy cover that can slow down or even stop the feedback loops described in this thesis. These strategies may be particularly important in the future given that the frequency and intensity of extreme weather events, such as windstorms and droughts, is expected to increase (Dale et al., 2001; Depsky & Pons, 2020; Seidl et al., 2017)

5.5 Future steps

1) A key assumption in ecology and biogeography is that species are most common where the conditions are optimal for their growth. However, theory and preliminary observations show that the positive relationship between growth and abundance often does not hold true (McGill, 2012). The results from the transplant experiment in this thesis represented a first step to shed some light on these patterns in tropical ecosystems, the context-dependent role of competition, and the existence of competition–environmental tolerance trade-offs. However, the experiment is limited to the seedling-to-sapling transition. To completely understand the impacts of climate change on species diversity, we need to incorporate competitive interactions into predictions of species' range dynamics and persistence. Therefore, we need to explore how adult tree persistence is influenced by competition along environmental gradients. Some authors (Usinowicz & Levine, 2018) suggest using the spatial low-density growth rate along a climate gradient. In relation to the topic of this thesis, this could be done only with long-term growth data along elevation gradients. Once we have the growth abundance relationship for different species along a gradient, we could test whether the slope of this relationship changes between species with different life histories. I would expect the slope to be negative for those species excluded and positive for those being superior competitors. This metric could help detect which species may be more vulnerable to being excluded in the future.

2) Competition for light may reduce species' fitness through reducing the amount of energy a species can invest in reproduction and thus negatively affecting its long-term population growth (Lee & Bazzaz, 1980). We still have limited knowledge about how competition may set range limits through this mechanism in the tropics. In other ecosystems, such understory forbs, it has been observed that competition for light can interact with warming temperatures and influence the reproductive output of species (De Frenne et al., 2011; Vanneste et al., 2021). However, with tropical trees, it is a much more difficult task to explore their flowering, fruiting, seed production, and germination success in different environmental conditions. Perhaps Paramo ecosystems with many shrubs and grass species, or any other tropical alpine ecosystem, would be a good place to explore the role of competition on the reproductive success of plant species at different elevations. Furthermore, we do not know how the interactive effect of increasing competition and temperatures could influence the population growth of many species. This should be explored in the future.

3) Another important knowledge gap is the role of extreme weather events, particularly droughts and heatwaves, on forest dynamics along gradients. With the transplant experiment, I managed to observe the persistence of seedlings and saplings under warmer temperatures when competition for light was reduced. However, there was no remarkable extreme drought or heatwave during that time (2017–2018). These events could have altered the outcome of the experiment. I speculate that during heatwaves and droughts, competition for light from trees to understory plants shifts to facilitation, as the shade from trees could alleviate extreme temperatures and reduce water stress.

4) Finally, the role of natural enemies seems to also be key in determining the elevation range limits of some of the studied species. Leafcutter ants are some of the most important herbivores in tropical American forests (Costa et al., 2008). Their distribution is highly dependent on the thermal ranges of the fungi they cultivate as a food source (Mueller et al., 2011). I suspect that with increasing temperatures, leafcutter ants will be able to move to higher elevations and feed on tree species that have not coexisted before with them. High elevation trees could therefore be more vulnerable to novel herbivores. Tree and plant species with their full ranges above 1,800 m.a.s.l. (the maximum elevation of leafcutter ants in Costa Rica) may not have the adaptations required to avoid damage from ants since their ranges have probably never before

overlapped. In addition, it is known that leafcutter ants select leaves with greater nutritional contents (Mundim et al., 2008). The greater leaf nitrogen content with increasing elevation could increase predation towards highland tree species. Furthermore, with increasing temperatures, high elevation trees could be more stressed and thus be targeted more frequently by ants. This could be related to a greater mobilization of proteins to repair damaged tissues and to a greater concentration of nutrients in dehydrated leaves.

5.6 Conclusions

The result of this thesis supports the increasing evidence of other mechanisms than species' tolerance to the environment, such as biotic interactions (Greiser et al., 2021; Neuschulz et al., 2018) and disturbance (Muñoz Mazón et al., 2019; Sheil, 2016) shape the distribution of tree species. Here, we extend these observations to the tropics. In addition, this thesis shows the context-dependent role of disturbance along elevation gradients on forest dynamics and tree species ranges. Disturbance events can extend contract species' range limits and even grant their persistence within their ranges in a warmer future. Managed and controlled disturbance could be used to grant the persistence of tropical tree species in the future.

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Paper I

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How forest structure varies with elevation in old growth and secondary forest in Costa Rica

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ABSTRACT

Clarifying how forests vary with elevation can inform our understanding of forests and their responses to climate. Despite the prevalence of secondary forests (defined as regrowth after disturbance), few studies have examined how their structure and recovery vary with elevation. Here, in apparently the first study of its kind, we explored how basal area, stem density and community wood specific gravity of stems ≥ 10 cm diameter vary along an old growth and a 25–30 years old secondary forest transect, each spanning over 2000 m of elevation in Costa Rica. The old growth transect comprises 29 plots of 0.25 ha from 440 to 2900 m.asl. and the secondary 28 plots of 0.1 ha and 10 plots of 0.25 ha from 600 to 2750 m.asl. We characterized how stand characteristics vary with elevation using linear and generaled additive models. To our surprise basal area increased with elevation not only in the old growth (from 24 to 56 m^2/ha) but also in the secondary forest (11 to 59 m^2/ha). This increase reflected the greater density of larger trees (≥40 cm diameter) at higher elevations. Basal area decreased with inferred water availability (global aridity index) in the secondary, but not the old growth forest. Surprisingly, wood specific gravity revealed no clear pattern with elevation in either transect though within stand variation decreased with elevation in both. In both forests, basal area is positively correlated with mean wood specific gravity, being significantly greater in stands with less variation in wood specific gravity. We interpret these patterns as resulting from reduced mortality of larger trees at higher versus lower elevations in both old-growth and secondary forest. Our results imply that planting trees to enhance recovery would be more beneficial in lowland than in high elevation forests.

1. Introduction

Elevation and associated environmental and climatic conditions influence forest processes, properties and outcomes including stand dynamics and recovery, composition and structure (Lieberman et al., 1996; Clark et al., 2015). Nonetheless, the relation between many forest properties and elevation remain poorly understood—in either old growth, or especially in the secondary forests, that regrow after large scale clearing or other disturbance. This is true even if we consider simple and widely used structural measures such as basal area (BA)—the summed cross-sectional area of tree stems, usually ≥ 10 cm diameter, at breast height (1.3 m or “diameter at breast height”) per hectare (Table 1).

Basal area is used in both ecology and forest management as a fundamental measure of stand structure and is closely related to stand volume and tree competition (Rozendaal et al., 2020). Furthermore, when combined with wood density, basal area is a key measure in stand biomass, productivity, carbon storage and dynamics. Curiously, while the basal area of mature natural forests worldwide varies remarkably little between the tropics and the boreal forests (Huston and Wolverton, 2009) there are often distinct patterns of difference over elevation gradients. While the patterns of this local variation tend to be relatively consistent within a region, published accounts from different regions reveal a range of distinct patterns (see Table 1). The implication is that multiple mechanisms combine to influence stand structure, and these vary in different ways over different elevation gradients (Clark et al., 2015; Culmsee et al., 2010; Jucker et al., 2018; Körner, 2007). Given that every forest represents the momentary outcome of tree recruitment, growth and mortality, stand processes are clearly key. Nonetheless, our understanding of how structure relates to post-disturbance

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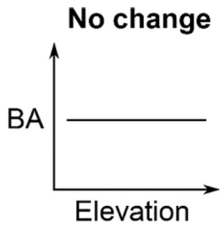
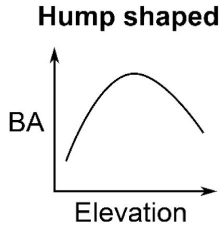
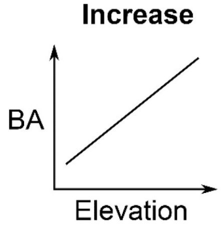
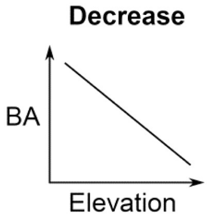
Table 1
Example of patterns of how basal area changes with elevation in tropical mountains.

Pattern	Elevation (m. asl)	Location	Reference
	60–3116	Ecuador, Bolivia, Peru	Girardin et al. (2014)
	2000–3300	Kenya, Uganda	Hamilton and Perrott (1981)
	1050–3050	Ecuador	Leuschner et al. (2007)
	50–3100	Papua New Guinea	Venter et al. (2017)
	2000–3300	Kenya, Uganda	Hamilton and Perrott (1981)
	2400–4250	Nepal	Carpenter (2005)
	272–2021	Tanzania	Marshall et al. (2012)
	32–2600	Costa Rica	Lieberman et al. (1996)
	1050–2400	Sulawesi	Culmsee et al. (2010)
	700–3100	Borneo	Aiba and Kitayama (1999)
	1500–2500	Mexico	Antonio-Vasquez and Givnish (1998)
	470–1700	Tanzania	Lovett et al. (2006)
	500–2000	Ecuador	Unger et al. (2012)
	1800–2600	Ecuador	Homeier et al. (2010)
	700–3100	Borneo	Aiba and Kitayama (1999)

stand recovery and dynamics with elevation is limited (Brokaw and Grear, 1991; Crausbay and Martin, 2016). Disentangling how intact old growth and previously disturbed regrowth secondary forests differ from each other and vary with elevation can help clarify how climate, disturbance and recovery determine forest properties.

Forest structure is known to vary with temperature and water availability. At global scales, tree height and basal area peak in regions with mild mean annual temperatures (around 12–16 °C), low water stress, and low seasonality (Keith et al., 2009; Larjavaara, 2014; Larjavaara and Muller-Landau, 2012). These variables seem to explain forest structure along elevation gradients too (e.g., Venter et al., 2017). Nonetheless, while certain elevations in the tropics should be optimal for the growth of big trees (Álvarez-Dávila et al., 2017; Venter et al., 2017), such a peak is not always observed (Table 1). This suggests that factors other than climate also influence forest structure.

Species composition may be influential (Ashton, 2017; Mitchard et al., 2014; Rodríguez-Correa et al., 2018; Stegen et al., 2011). For example, the presence of trees of the Fagaceae family has been suggested as a key determinant on biomass and basal area increases with elevation in tropical mountains (Culmsee et al., 2010), though this is debated (Phillips et al., 2019a). Composition can also influence the community's wood density and related properties (Phillips et al., 2019b). For example, observations in Amazonia show that forests dominated by dense wooded trees typically possess a greater basal area and a greater density of large trees than others (Baker et al., 2004; Malhi et al., 2006).

Disturbance influences stand properties through multiple processes (Finegan, 1996; Sheil and Bongers, 2020). In relatively moist conditions, disturbance facilitates the establishment of fast growing pioneer species with characteristics such as low-density wood and large short-lived leaves (Adler et al., 2014). These tree characteristics also increase their vulnerability to drought, stem breakage and herbivory (Meakem et al., 2018). In contrast, late successional species with typically denser wood and longer-lived better defended leaves, are less vulnerable to drought, breakage or herbivory. Thus, any event that permits the establishment of pioneers—a "disturbance"—can, under conditions that selectively kill such pioneer trees, slow stand recovery and basal area accumulation. Such disturbance feedbacks have been observed in Amazonia (Aleixo et al., 2019). Such feedbacks and outcomes may vary with elevation (Peters et al., 2019) likely depending also on climate and the local species composition. Few, if any, studies have addressed the role of forest disturbance and recovery on forest structure along extended elevation gradients.

In this study our goal is to describe and contrast the structure (basal area, tree sizes, and wood densities) of old growth and regrowth ("post disturbance" or secondary) forests over an elevation range, from 400–600 to 2700–2900 m.asl in Costa Rica. These forests differ in their histories (old growth vs. recovering from disturbance) and species composition (Murrieta et al., 2007; Veintimilla et al., 2019). These differences allowed us to explore how elevation, associated climate, disturbance (old growth vs. secondary forest) and the presence of oaks (*Quercus* spp.) relate to forest structure. Based on previous observations in Costa Rica (Lieberman, 1996) we expect that in the old growth forest, basal area will peak at mid to high elevations, where forests are dominated by Fagaceae (i.e. *Quercus* spp.) (Veintimilla et al., 2019). Expectations for the secondary forest are more uncertain as they have not previously been examined, but we hypothesized that basal area would be greater at lower elevations due to more favorable growth conditions and the presence of many species capable of rapid growth. Although wood density (measured here as wood specific gravity or "WSG") (Williamson and Wiemann, 2010) is considered useful for understanding species life history, strength and physiological strategies (Swenson and Enquist, 2007), the relationship with elevation is poorly known. We expect that wood specific gravity would increase at the highest elevations, as this is recognized as a protective strategy where the vascular system endures freezing (Hacke et al., 2001; Swenson and Enquist, 2007). Regardless of elevation, we also expect a positive relationship between basal area and wood density in the old growth forest, since wood density is positively correlated with greater shade tolerance and denser stands (Phillips et al., 2019b). In the secondary forest we do not expect a clear relationship between basal area and wood density, since fast growing species with soft woods are expected to dominate during early stages of succession in all sites (Chazdon et al., 2010).

2. Methods

2.1. Study area

We used data from two elevation transects in the mountains of Costa

Rica, one in old growth forest and another in thirty-year secondary forest (Appendix 1). The old growth transect was located along the eastern Atlantic slope of the Talamanca Mountains, from 400 to 2900 m above sea level ("asl"). Soils in the old growth forest change from heavily weathered ultisols at lower elevations to andosols in the higher parts of the gradient (Veintimilla et al., 2019). The climate is tropical wet aseasonal in the lowlands, with an annual rainfall of 3500 mm and mean annual temperature of 24 °C. At higher elevations, precipitation becomes more seasonal and temperature decreases at a rate of approximately 0.56 °C per 100 m of elevation (Muñoz Mazón et al., 2019; Veintimilla et al., 2019). Most of the old growth forest transect lies within the Barbilla, Tapanti and Cerro de la Muerte National Parks. Rain forest covers the lowland areas, transitioning to *Quercus* spp. dominated cloud forests at the higher parts of the gradient (Holdridge, 1987; Kappelle et al., 1995). The secondary forest transect is located along the slopes of the Turrialba Volcano, from 600 to 2700 m asl. In this transect soils are volcanic (Meijer and Buurman, 2003). Climatic conditions along the transect are similar to the old growth forest transect. Rain forest also dominates the lowland areas of the secondary elevation, but in this transect oaks (*Quercus* spp.) do not dominate at higher elevations, being almost absent (Murrieta et al., 2007; Bermeo, 2010). According to landowners, the age of the secondary forests is 25–30 years since abandonment. The previous land uses are not recorded, but pastures were likely common all along the gradient, dominating at middle and higher elevations. Most forests at the lower and middle elevations in the area are believed to have regrown from abandoned sugar cane and coffee plantations.

2.2. Vegetation sampling

We established 29 plots of 0.25 ha in the old growth forest in 2013. In the secondary forest we used plots of different sizes, 29 plots of 0.1 ha and 10 plots of 0.25 ha, depending on the size of the forest patch in order to avoid any edge effect (Appendix 1). All plots were located in areas of similar slope (< 100%) and topographic position, avoiding ridges and valley bottoms. When establishing the plots, we avoided swamps, riverine forest, or areas recently disturbed. Plots were located at least 150 m from the forest edge. All stems greater than 10 cm diameter at breast height (dbh) were recorded and identified at species or morpho-species levels. The recorded stems included palms, trees, ferns and lianas. Further details about the sampling design, and vegetation along these gradients can be found in Murrieta et al. (2007); Bermeo (2010) and Veintimilla et al. (2019).

2.3. Wood specific gravity

We measured the wood specific gravity of the dominant species in both transects. The specific gravity is the density of wood relative to the density of water and therefore is unitless (Williamson and Wiemann, 2010). We selected all the species that made up 80% of the total basal area per plot, resulting in 170 and 108 species in the old growth and secondary forest, respectively. We collected wood core samples of five different individuals per species, using a corer of 5.5 mm diameter and 25.5 cm length. The individuals where located outside the plots, in the surrounding area at similar elevations. Wood specific gravity was measured following standard methods by drying of wood cores at 100 °C for 48 h and using water displacement for measuring the volume (Williamson and Wiemann, 2010).

2.4. Data analyses

We used linear models to explore the relationships between basal area, number of individuals, elevation, and climatic variables (Zuur et al., 2007). To understand the density of “big” trees in both forest we chose 40 cm dbh as cut off limit since larger diameters are not expected among 30-year-old trees in the re growth secondary forest. We extracted from WorldClim (Hijmans et al., 2005) maps at 5 arcsec of mean annual precipitation, the coefficient of variation of precipitation, precipitation of the driest month, precipitation of the warmest month, mean temperature, mean annual range of temperature and mean diurnal range of temperature. The ratio between annual precipitation and potential evapotranspiration, a measure of available water, was extracted from the CGIAR-CSI Global-PET and Global Aridity Index (Global-Aridity) database (http://www.cgiar-csi.org) also at 5 arcsec. Basal area was log transformed when it did not meet the assumptions of normality and homogeneity of variance of the linear model. We fitted generalized additive models to explore nonlinear relationships. To avoid collinearity between the environmental variables, we performed a PCA of the climatic variables and used the PCA axes as independent variables in the general additive model. The first axis of the PCA explained 40% of the variation and was strongly correlated with elevation. The second axis of the PCA explained 30% of the total variation and was strongly correlated with annual precipitation and the ratio between annual precipitation to evapotranspiration.

We estimated the community means of wood specific gravity per plot weighted by the relative basal area and abundance of each species in each plot. We also calculated the functional dispersion of wood specific gravity per plot. The functional dispersion of a trait reflects the mean distance of a species trait to the centroid of the community, weighted by the abundances of the species in the community (Laliberté and Legendre, 2010). We chose this measure due to its relative independence from species richness and outliers. A decrease in functional dispersion can reflect community level convergence in an environmental response (Weiher and Keddy, 1995).

We further explored the interactive effect of elevation and wood specific gravity on basal area with a linear model. For this model we combined plots from both secondary and old growth forest since we expect their communities to have very different wood specific gravities.

All analyses were performed with R. We used the R package gam (Hastie, 2018) to fit the general additive models and the FD package (Laliberté et al., 2014) to calculate the means and functional dispersion.

3. Results

3.1. Forest structural changes with elevation

Though there is considerable variation at all elevations, mean basal area increases with elevation in both old growth and secondary forest (Fig. 1a). The number of stems per hectare decreases at higher elevations in the old growth forest and suggests a hump-shaped pattern in the secondary forest, though the considerable variation among these (smaller) plots makes this uncertain (Fig. 1b). The basal area and number of stems bigger than 40 cm dbh increase at higher elevations in both gradients (Fig. 1c and d).

3.2. Environmental variables and forest structure

The first two axes of the PCA explained 90% of the total variation. Axis 1 was negatively correlated with elevation and temperature, and positively correlated with precipitation seasonality (coefficient of variation). Axis 2 was negatively correlated with mean annual precipitation, precipitation of the warmest quarter and precipitation of the driest quarter. The relation between annual precipitation and potential evapotranspiration (Aridity Index) correlated with both PCA axes, so we decided to examine its relationship with basal area separately (Appendix A). Basal area increases with decreasing temperature and increasing precipitation seasonality in both forests (Fig. 2a). We found no clear relation between the other precipitation variables and basal area along either gradient (Fig. 2b), even after the omission of the extremely wet plot on the left side of Fig. 2b. Nevertheless, in secondary

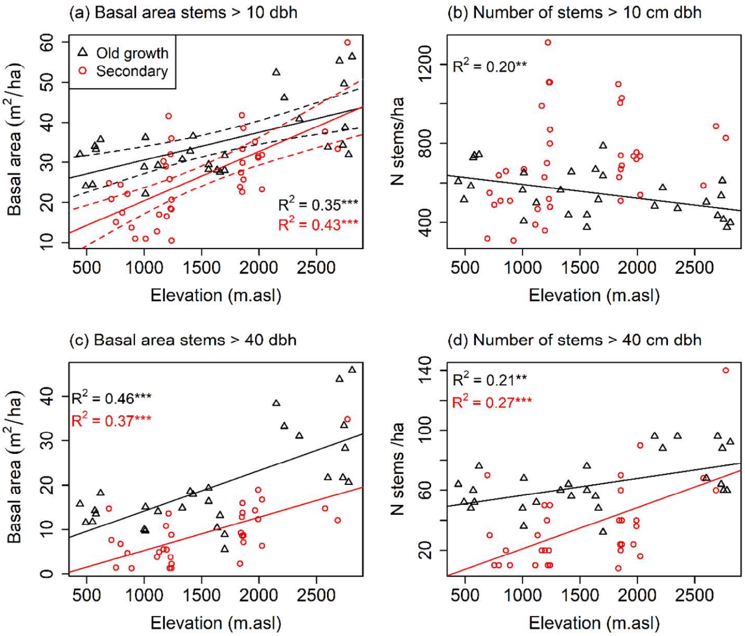


Fig. 1. Relationships between basal area and the number of stems along elevation gradients in old growth and secondary forest for all the inventoried individuals greater than 10 cm dbh (a and b) and for stems greater than 40 cm dbh (c and d). Black triangles represent old growth forest plots. Red circles and lower line represent secondary forest plots. (For interpretation of the references to colour in this and the following figure legends, the reader is refered to the online version ofthis article).

forest, both the total number of individuals and basal area increase with greater ratios of precipitation to evapotranspiration (and thus with implied water availability) (Appendix 2).

3.3. *Basal area and community wood specific gravity*

Basal area increases with increasing wood specific gravity in the old growth forest (Fig. 3a and b). Along the secondary forest gradient, there is only a weak trend when wood specific gravity is weighted by species abundance (Fig. 3b). Along both gradients, basal area decreases with increasing functional dispersion of wood specific gravity (Fig. 3c).

3.4. *Elevation and community wood specific gravity*

When weighted by the basal area of each species, the community mean of wood specific gravity does not change along the elevation gradient (Fig. 4a) but indicates a U-shape when weighed by species abundance (Fig. 4b). The dispersion of wood specific gravity decreases with elevation in both forest gradients (Fig. 4c).

Elevation and community wood specific gravity both appear to be linked to basal area but not independently. To test if the relation between elevation and basal area depends on the wood specific gravity, we performed a multiple linear regression to predict basal area based on elevation and wood specific gravity of the communities (F (3,63) = 25.56, p-value < 0.001, with an R^2 = 0.52). Elevation and wood specific gravity revealed a positive relationship to basal area but their interaction was negative, suggesting that wood specific gravity is less important as a predictor of basal area with increasing elevation. This is also apparent in the observed convergence of basal area in both old-growth and secondary forest as elevation increases (Fig. 1a) despite secondary forest having lower mean community wood specific gravity at all elevations (Fig. 4a and b). When tested seperately within secondary and old growth transect data, the interaction between elevation and wood specific gravity was insignificant in both.

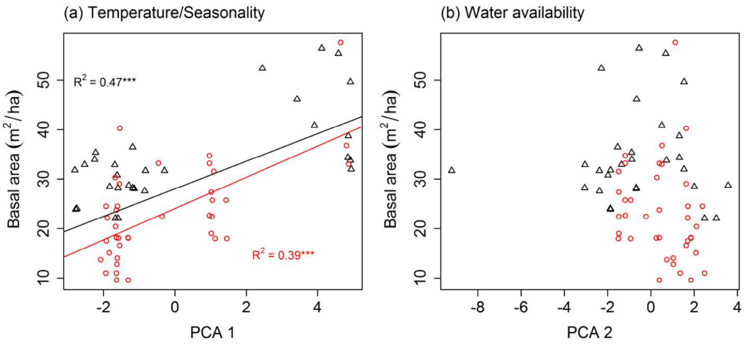


Fig. 2. Relationships between basal area per ha (all stems ≥ 10 cm dbh) and the two most explanatory axes of the environmental PCA. Black triangles represent old growth forest plots. Red circles and lower line represent secondary forest plots.

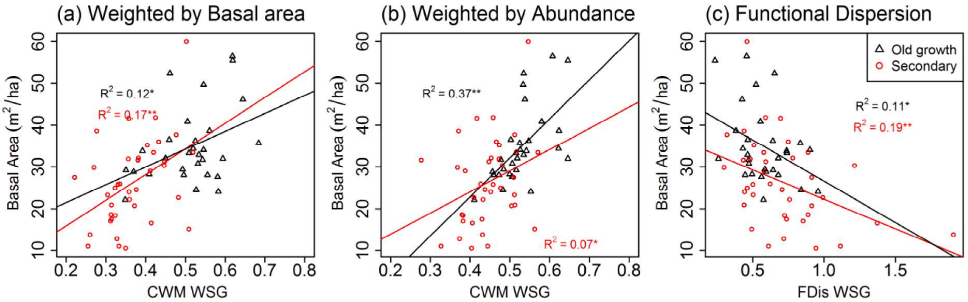


Fig. 3. Relationship between basal area and community wood specific mean weighted by the basal area (a) and by the abundance of each species (b), and relation between basal area and dispersion of wood specific gravity (c).

4. Discussion

Our study appears to be the first examining how forest structure and community wood density change with elevation in both old growth and secondary forest. The observed increase in basal area and larger trees with elevation in the old growth forest agrees with previous studies elsewhere in Costa Rica (Lieberman et al., 1996; Clark et al., 2015) and confirms our hypothesis that basal area peaks where oak species (*Quercus* spp.) dominate. However, to our surprise, we found the same pattern in three decades old secondary forest, where oaks are absent. Interestingly, both forests transects indicate a greater abundance of larger stems and smaller variation in wood specific gravities of trees with increasing elevation. These observations suggest that trees in lower elevation forests achieve large sizes less frequently than in higher elevations. This limited recovery at low elevations contrasts with the rapid tree growth seen in other studies in the region (Letcher and Chazdon, 2009; Piotto, 2007). Moreover, other studies have observed that tree growth declines with increasing elevation elsewhere in Costa Rica (Clark et al., 2015). Although elevation associated differences in either tree growth or survival, or both, could generate these patterns, we find differences in survival the most plausible explanation. In the next sections we examine these ideas in more detail.

The role of Fagaceae as a key determinant on biomass and basal area increases with elevation in tropical mountains remains ambiguous. While our observations confirm that *Quercus* spp. occur in high basal area sites in the old-growth forests they are clearly not essential to explaining the patterns seen in the secondary forest where such species are absent. Furthermore, while Fagaceae may play such a role it remains plausible that other taxa do too as seen with Araucariaceae in the highlands of New Guinea (Enright, 1982) or Lauraceae such as *Ocotea* spp. in Tanzania (Ensslin et al., 2015). For example, in our secondary forest plots members of the family Lauraceae such as *Ocotea austinii*, Araliaceae such as *Oreopanax xalapensis* or Verbenceae such as *Citharexylum donnell-smithii* tend to dominate in the highest plots. Clearly other mechanisms than the presence or absence of a specific plant family can also contribute to these patterns, and these explanations need not be exclusive.

Our interpretation of the observed increase in basal area and density of large trees is that events that kill trees before they reach large sizes occur more frequently, or more severely at lower versus higher elevations. The reduced rainfall associated with ENSO events (El Niño Southern Oscillation), have been seen to increase tree mortality both regionally and elsewhere in the tropics (Clark et al., 2010; Uriarte et al., 2016; Powers et al., 2020), and can have a particularly severe impact on larger stems (Phillips et al., 2010; van Nieuwstadt and Sheil, 2005). Multiple mechanisms including hydraulic failure, carbon starvation and a greater vulnerability to pathogens could contribute to greater tree mortality due to water scarcity (McDowell et al., 2008; Powers et al., 2020). Cloud and fog are typically more frequent at higher elevations in mountains (Bruijnzeel et al., 2011) and can reduce water stress by decreasing transpiration and increasing water uptake (Oliveira et al., 2014). This seems relevant in our transects where fog is common at higher elevations (2500–2900 m.asl) where basal area peaked. Transect observations in New Guinea have also described an increasing density of large trees with elevation that appears related to water availability (Venter et al., 2016). Another possibility is high temperature "heat events", particularly at night, implicated in increased tree mortality elsewhere in Costa Rica (Clark et al., 2010). Such temperature extremes

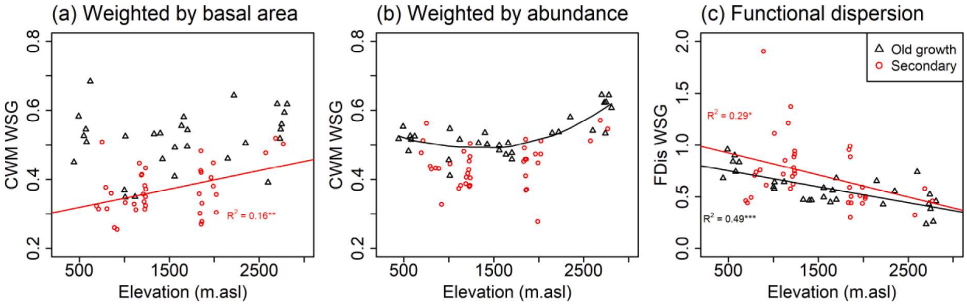


Fig. 4. Relationship between elevation and community wood specific mean weighted by the basal area of each species (a) and by its abundance (b). Relationship between dispersion of wood specific gravity and elevation (c).

may be more frequent, or more lethal, at lower elevations though we lack data to asses this. Finally, other studies have linked increases in forest basal area with elevation to wind damage, as in the old growth subtropical forests of Taiwan (Chi et al., 2015) and Puerto Rico (Brokaw and Grear, 1991). Winds appear more destructive at lower elevations (Brokaw and Grear, 1991; Crausbay and Martin, 2016) potentially influencing stand properties by selectively impacting taller and more weak stemmed trees (Lugo, 2000; Yih et al., 1991). Windstorms may be particularly important if soil properties, shallow rooting, wider crowns or other factors, reduce tree stability in the lowland versus the upland formations (Tanner et al., 1991; Mitchell, 2013; Peterson et al., 2019). Such differences should be the subject of future studies.

The observed positive relation between wood specific gravity and basal area may also reflect differential tree survival. Wood properties may influence the ability of trees to survive events, such as water scarcity (Greenwood et al., 2017) and windthrows (King et al., 2006). Other studies have shown that species with denser wood have a greater resistance to breakage from windstorms in high elevation forests of Jamaica (Tanner and Bellingham, 2006). However, in our study, the community weighted mean of wood specific gravity did not show a clear pattern with elevation, though stand level variation declines with increasing elevation in both forests. We suspect that some proportion of the species at lower elevations may be more vulnerable than those at higher elevations.

Trees in young secondary forest may be more vulnerable to disturbances than in older forest (Canham et al., 2010; Uriarte et al., 2016). Early successional tree species in wet forests generally possess adaptations favoring rapid growth, like big leaves and low wood densities that reduce resistance to breakage (Bellingham et al., 1995) and increase susceptibility to embolism (Greenwood et al., 2017). Indeed, in our study we observed a decrease in basal area and number of individuals with decreasing water availability in the secondary forest gradient (Appendix 2). We propose that these observations reflect a positive feedback in which episodes of water scarcity, and disturbances like wind storms, kill vunerable canopy trees and promote the regrowth of fast-growing species which remain vulnerable to further events (Zimmerman et al., 1994; Aleixo et al., 2019). The greater variability of wood density at lower elevations and in secondary forest, together with the decrease in basal area and number of individuals with increasing water scarcity, suggest that this feedback is more important at lower, versus higher, elevations.

Our study has limitations. The two transects though similar, are imperfectly matched and lack broader replication. Forest structure, and associated elevation trends, may be influenced by differences in soils (Fisher et al., 2013; Grubb, 1977). Furthermore, in the secondary transect, different site histories may result in distinct legacies, though we note that large stems ≥ 60 cm dbh that might be pre-disturbance are scarce (just 40 trees out of 3339). The exclusion of these larger stems in the analyses does not change the has little influence on thepatterns observed in the secondary forest. Furthermore, we know little about the history and impact of the local disturbance regimes along either elevation gradients. The different patterns in Table 1 can depend on what part of a more complete curve is observed. For example, we did not include plots close to the region's high elevation tree-line. If this upper-limit had been included, with good coverage at 3000 m and above, we would likely have recorded an ultimate decline in basal area, as this decline is a global phenomenon (Körner and Riedl, 2012). Thus, if such higher elevation sites had been included, we would likely have seen a unimodal pattern in basal area.

There are implications for forest management and conservation. The slow recovery of basal area in the lowlands indicates a greater potential benefit from any management that can bolster regeneration and recovery (Holl and Zahawi, 2014). For example, planting nursery-raised seedlings of native long-lived species, such as *Brosmium utile*, *Terminalia amazonia* or *Vochysia guatemalensis* (Guariguata et al., 1995; Leopold et al., 2001; Holl et al., 2017), could be an effective strategy to rapidly establish a less vulnerable canopy cover that could enhance the dispersal of seeds (Holl et al., 2018). On the other hand, we see less need for active interventions to bolster recovery in higher-elevation forests, where the natural recovery of basal area is comparatively fast. We also note that, given the recognized link between basal area, stand biomass and carbon, permitting forest recovery in previously cleared areas in high elevation rather than in low-elevation sites is, hectare for hectare, likely a more rapid means to capture carbon.

5. Conclusion

We naively expected that forest recovery from disturbances would be faster in the lowland forest. Nevertheless, we have shown how basal area increases with elevation in both old growth and thirty-years-old secondary forest in Costa Rica. These structural changes were associated with reduced variation in community level wood density. We also noted likely interactions among wood specific gravity, stand recovery, water availability and elevation. We see that disturbance and recovery are important to understanding how climate impacts forest structure and dynamics. Our observations suggest that interventions to bolster forest recovery are likely to be more necessary in lowland than in montane forests. There is need for more studies to determine the interactions between climate and forest recovery along elevation gradients.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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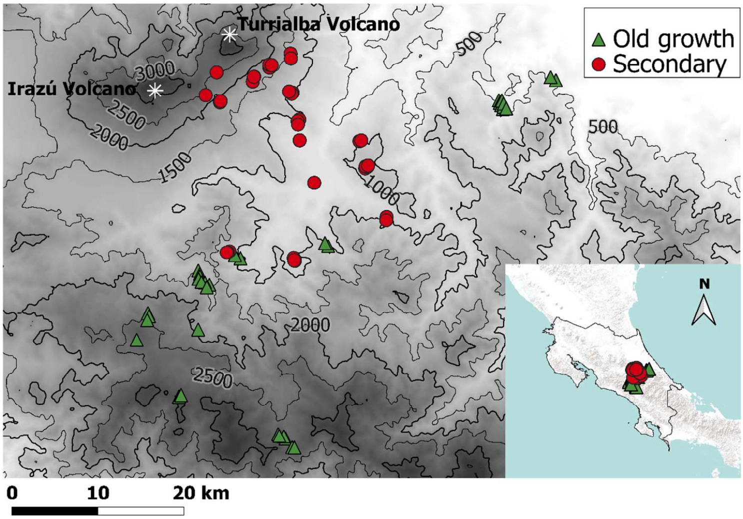
Author Statements

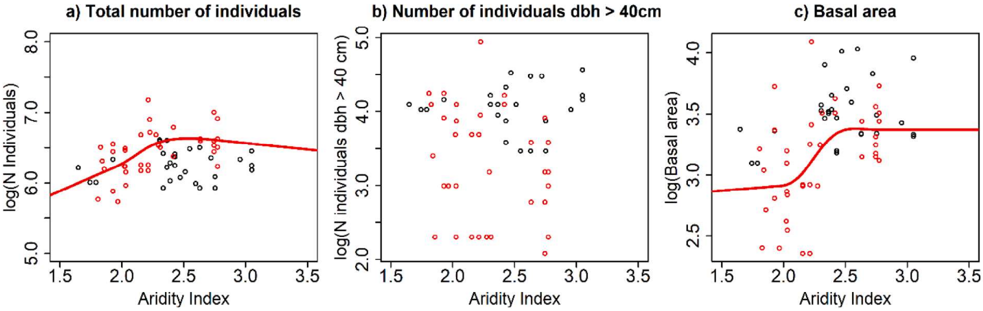
Biosketch: Miguel Muñoz Mazón is a PhD student studying the role of competition and disturbance on the distribution of trees along tropical elevation gradients. Authors contributions: DS proposed the study and identified suitable data with BF; MMM, KK and DS designed the study; BF, DD, DV, DB and EM collected the data; MMM analysed the data and wrote the paper with guidance and support from KK, BF and DS. All authors reviewed and agreed on the final manuscript.

Appendix A



Appendix 1. Locations of plots in old growth (triangles) and secondary forest (circles). Contour lines every 500 m. asl.

In order to better understand the relationships among the environment, basal area and forest age, we explored how basal area changes with the ratio between Annual precipitation and Potential Evapotranspiration (Aridity index). We used a generalized additive mixed model (or "gamm") (Wood, 2017), with a smoother for each forest. Elevation in this case was used as a random effect. The models only fitted a smoother for the secondary forest. The basal area model explained 56.8% of the variation. The total number of individuals model explained 40.6% of the variation.



Appendix 2. Relation between the log transformed a) total number of individuals, b) individuals > 40 cm dbh and c) basal area and the aridity index (Annual Precipitation/Evapotranspiration). Red open circles represent secondary forest plots and black open triangles represent old growth forest. The trend lines represent statistically significant smoothers, in this case for the secondary forest plots

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ORIGINAL RESEARCH

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Disturbance and the elevation ranges of woody plant species in the mountains of Costa Rica

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Abstract

Aim: To understand how disturbance—here defined as a transient reduction in competition—can shape plant distributions along elevation gradients. Theory suggests that disturbance may increase elevation ranges, especially at the lower range limits, through reduced competitive exclusion. Nevertheless, to date this relationship remains unclear.

Location: Mountains of Costa Rica.

Methods: We compared the elevation range of woody stems over 10 cm dbh ("trees") observed in plots along two transects spanning a range of elevations in secondary (regrowth) and old-growth forest (409 and 249 species, respectively). We also estimated these elevation ranges using nationwide data. In addition, we examined the influence of stem size and plot scale basal area (as a measure of competition) on species elevation range limits in the two gradients.

Results: In general, tree species ranges increased with elevation. Species in the secondary forest had broader elevation ranges (100–318 m broader than species in the old-growth forest; Wilcoxon: *p*-value <.001). Also, in the secondary transect, individuals with greater diameters had broader elevation ranges than those observed as smaller trees (137 m broader; Kruskal–Wallis: *p*-value = .03). The lower range limit of species occurred more frequently in plots with lower (vs. higher) basal area than expected by chance in both forest types. We also observed higher elevation upper limits in old growth, but not in secondary forests, with lower (vs. higher) basal area.

Main conclusion: Disturbance relaxes the constraints imposed by competition and extends effective elevation ranges of species, particularly those in secondary forest, to warmer and cooler climates (minimum increase equivalent to about 0.6–1.4°C). Thus, suitable disturbance may assist species persistence under climate change. We believe this is the first study indicating a consistent relation between disturbance and woody plant species distributions along elevation gradients.

KEYWORDS

biotic interactions, competition, distributions, disturbance, elevation ranges, range boundaries, secondary forest, succession

1 | INTRODUCTION

The idea that tree species distribution patterns in tropical forest are influenced by disturbance is long established—many observations indicate a context-dependent effect of competition on species persistence along environmental gradients (Budowski, 1965, Van Steenis, 1958 see further examples in Sheil, 2016). Disturbance events, which we define as a transient reduction in competition (resulting from vegetation death or removal), can reduce or slow competition and the resulting exclusion of inferior competitors by freeing up space or resources and by eliminating superior competitors (Sheil, 2016). The role of disturbance in promoting species diversity and (temporary) coexistence is generally accepted at local scales (Fox, 2013; Sheil & Burslem, 2003, 2013), though there is little agreement on how and in what contexts disturbance affects distributions at larger scales (Liang, Duveneck, Gustafson, Serra-Diaz, & Thompson, 2018; Sheil, 2016; Vayreda, Martinez-Vilalta, Gracia, Canadell, & Retana, 2016). In theory at least, disturbance might promote the establishment and persistence of species at elevations where they would otherwise be excluded by competitors (e.g., lowlands, see Figure 1). These range expansions imply that some species may be able to persist "in situ" in a warmer future if competition is reduced through a suitable disturbance regime (Johansson, Frisk, Nemomissa, & Hylander, 2018; Sheil, 2016). Predictions of extinctions through contractions in the elevation range of species (e.g., Dirnböck, Essl, & Rabitsch, 2011) highlight the importance of considering disturbance as a conservation tool (Sheil, 2016). However, as far as we know, nobody has quantified the influence of disturbance on species distributions along elevation gradients and estimated how they may influence potential persistence under warmer (or colder) conditions.

Biotic interactions can constrain species distributions and influence range limits (Araújo & Luoto, 2007; Louthan, Doak, & Angert, 2015; Svenning et al., 2014). For example, there is evidence from temperate and boreal locations that competitive exclusion affects the distribution of plant species along elevation gradients (Ettinger & HilleRisLambers, 2017; Olsen, Töpper, Skarpaas, Vandvik, & Klanderud, 2016; Sheil, 2016). While climate often appears to impose a physiological limit to growth and survival at the upper distribution limit (Ettinger, Ford, & HilleRisLambers, 2011; Körner et al., 2016; Normand et al., 2009; Wen, Qin, Leng, Zhu, & Cao, 2018), this is less clear for lower range limits where competition may play a greater role (Choler, Michalet, & Callaway, 2001; Defossez, Courbaud, Lasbouygues, Schiffers, & Kunstler, 2016; HilleRisLambers, Harsch, Ettinger, Ford, & Theobald, 2013; Pellissier et al., 2013). Such relationships between competition and species elevation ranges are potentially important for conservation as distributions may respond to managed disturbances (reviewed in Sheil, 2016). Currently, as disturbance processes are seldom incorporated in formal distribution studies, we know little about such influences and their wider implications.

Managed disturbance offers a potential means to manipulate and extend species range limits, slowing the arrival of more competitive lower elevation species and facilitating species migrations to new areas with suitable environment (Sheil, 2016). As in managed habitats that are already burned, grazed, or mown so as to facilitate certain species and communities over others, practices may be adjusted in various ways. Of course, not all species will respond to disturbance in the same way. The nature, intensity, frequency, scales, and timing of the disturbance regime would be adapted to favor target species. There are likely to be other factors to consider too, for example in a changing climate disturbance will influence replacement processes and influence how species can spread and track both biotic and environmental conditions (Royo & Carson, 2006; Serra-Diaz, Scheller, Syphard, & Franklin, 2015; Thom, Rammer, & Seidl, 2017). Furthermore, disturbance could accentuate climatic extremes, promoting the persistence of those species more tolerant to drought or frost. There may also be undesirable persistent vegetation states that are favored by certain disturbance processes (Ssali, Moe, & Sheil, 2018). In any case, the use of disturbance would need to be guided by the best available information and would need to be reevaluated locally. Thus, it is crucial to understand how disturbance can modify species range limits so that we know if these options can be adopted for landscape management and conservation.

Plant species distributed over an extended environmental gradient, such as elevation, are typically thought to sort themselves according to a competitive hierarchy in which inferior competitors are displaced to sites supporting less optimal growth (i.e., higher or lower elevations; Sheil, 2016; Shipley & Keddy, 1994; Wisheu, 1998). This reasoning follows from observations that a trade-off occurs between the competitive ability of a species and its ability to persist under limiting environmental conditions (Michalet et al., 2006; Morin & Chuine, 2006; Salguero-Gómez et al., 2016). At the same time, this trade-off implies that species are seldom good competitors over their entire fundamental range (Grime, 1973; Wilson & Keddy, 1986), depending on disturbance events to establish and persist at the less stressful parts of the gradient (Figure 1; Sheil, 2016). Even if several species have similar competitive ability, colonization and priority effects are likely to favor some over others so that few can thrive throughout their fundamental range. In this context, disturbance allows species to expand their range by temporarily removing competitors and priority effects.

Responses to disturbance vary among tree species. Such responses depend on their ability to colonize and to compete (Cadotte, 2007; Connell & Slatyer, 1977; Swaine & Whitmore, 1988). Tree responses thus depend on the competition-colonization trade-offs among the species present (Huston & Smith, 1987; Muscarella et al., 2017; Zhang, Qi, & Liu, 2018). In nature, tree species' strategies typically appear scattered along a conceptualized "colonization-competition axis" representing a broad range of competition and dispersal abilities and strategies (Adler et al., 2014; Salguero-Gómez et al., 2016). For simplicity, this range of strategies is often simplified and divided into pioneer (disturbance dependent) and nonpioneer species (e.g., Swaine & Whitmore, 1988).

Our objective is to assess and understand the elevation distribution of tree species, specifically their elevation range limits, and how this is influenced by disturbance histories (and inferred

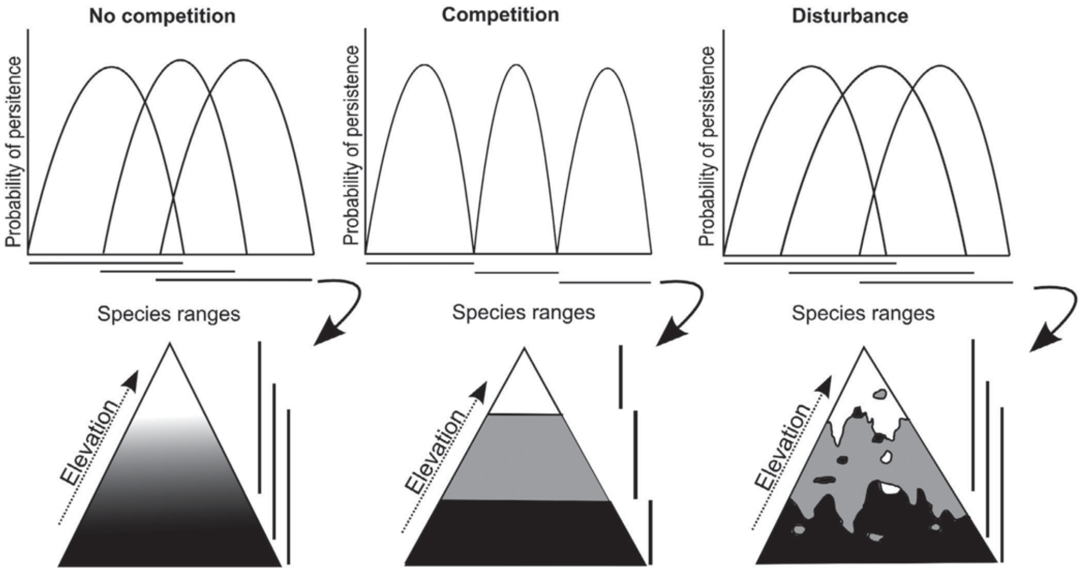


FIGURE 1 Schematic representation of how competitive hierarchies and disturbance may influence the elevation range of three species. The upper row represents the probability of persistence of three species along a gradient at three different scenarios (no competition, competition, and disturbance). The lower row shows how their ranges would be distributed along an elevation gradient. Under a theoretical scenario of no competition between the three species, their ranges will follow the environmental conditions corresponding to each species' fundamental niche. Competitive interactions would constrain their distributions along elevation gradients, particularly their lower range limits and the realized niche are smaller than the fundamental niche. Disturbance may allow these three species to expand their ranges to upper and lower elevations by altering the already established competitive hierarchies and reducing priority effects so that the realized niche is larger (based on Sheil, 2016)

competition). We recognized that there will always be alternative explanations for observed ranges and that good replication of gradients would be needed to distill the effects of disturbance and competition from such observations. Nonetheless, we note that two well sample gradients in the same region offers a “proof of concept” and reveals the ability to detect consistent patterns in real data. We examined distributions over two transects located in old-growth and secondary (regrowth) forests in Costa Rica. Our assumption is that when competitive exclusion restricts species to certain elevations, disturbance may permit them to occur more widely (Figure 1). Thus, we predict that species present in secondary forest will typically have broader elevation ranges than species present in old-growth forest. Moreover, we predict that within the secondary forest, tree species that include large diameter individuals (vs. those without) will tend to have broader elevation ranges since a greater proportion of these will have established sooner after disturbance and were thus able to establish and grow with less competition. We recognize that some species only represented by small-diameter stems may also have established early but believe that the comparison between the range sizes of species with different diameters remains a useful statistical generalization as large stems are seldom young. We also evaluated the relationship between species elevation range limits and local (plot defined) basal area with the prediction that range limits will be more frequent in lower versus higher basal area plots (representing lower vs. higher competition).

2 | METHODS

2.1 | Study area

We used records of trees, palms, ferns, and lianas with diameters (at 1.3 m, “dbh”) >10 cm from plots placed along two elevation transects established in Costa Rica in secondary and old-growth forest during 2013. The old-growth transect comprises 32 0.25 ha plots from 430 to 2,900 m asl along the Atlantic slope of the Talamanca Mountains. The secondary forest comprises 29 0.1 ha plots from 650 to 1,800 m asl and nine 0.25 ha plots from 1,800 to 2,700 m asl along the northern face of the Turrialba Volcano. The height of the mountain ranges where the transects are located is similar (3,324 m asl for the Turrialba Volcano and 3,451 m asl for Talamanca Cordillera transect), with the treeline occurring between 3,000 and 3,200 m asl (B. Finegan & D. Delgado, personal observation). Mean annual temperature varies from 10 to 25 °C along both transects. Precipitation ranges from 2,000 to 5,000 mm per year, peaking at middle elevations (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). There is a short dry season between January and March (Kappelle, Uffelen, &

Cleef, 1995). Although the length of the dry season does not appear to vary along the elevation gradient, the plots at higher elevations typically receive less precipitation than plots at lower elevations during this period (see Appendix S1). Soils at higher elevations tend to be shallower, richer in organic matter and are more often associated with volcanic ash (typically Andosols). At lower elevations, soils are deeper and are typically have a higher proportion of clay (typically Ultisols, CATIE, unpublished data; Veintimilla et al., 2019).

Both transects include Lowland (>700 m. asl), Premontane (700–1,500), Lower montane (1,500–2,200), and Upper montane forest (2,200–2,900; Holdridge, 1987). The lowland old-growth forest includes many palms such as *Euterpe precatoria* and *Welfia regia* (Veintimilla et al., 2019). With increasing elevation, the forest transitions to montane forest, where lianas disappear, palms are scarce and species with more temperate affinities like the oaks (*Quercus bumeloides* and *Quercus costarricensis*) tend to dominate along with *Podocarpus* spp., *Magnolia* spp., *Ilex* spp., *Drymis granadensis* and *Ocotea* spp (Kappelle, Kennis, & Vries, 1995; Kappelle, Uffelen, et al., 1995). Oaks (*Quercus* spp.) are absent in the secondary forest, though other species with temperate affinities still dominate at higher elevations (e.g., *Viburnum costaricanum*, *Cornus schiedianus*, CATIE, unpublished data; Murrieta, Finegan, Delgado, Villalobos, & Campos, 2007).

The secondary forest had 21–30 years regrowth postagriculture, according to interviews with the landowners (see Murrieta et al., 2007). Land use before abandonment was pastured at higher elevations, and coffee and sugar cane plantations at lower elevations. Unfortunately, we lack detailed information about prior land use; but we assume that forest trees were scarce or absent. We also lack information on subsequent disturbance processes in the regrowth. There may have been some low-intensity fuelwood harvesting, but we are confident that there were no fires in this landscape. Secondary forests following coffee plantations likely contain some favored shade trees—typically *Erythrina poepiggiana* and *Cordia alliodora* (Florian, Harvey, Finegan, Benjamin, & Soto, 2008). Although the presence of relic trees along the secondary transect remains uncertain, there are only 41 stems with a dbh >60 cm (of 3,338 stems in total).

Plots were located at least 300 m apart and at least 150 m from the forest edge and avoided obvious disturbances such as larger tree fall gaps. Also, all the plots were established >50 m from watercourses and we avoided very steep areas (slopes >100%). The dominant aspect was east-facing slopes. In each plot, all stems with a diameter at breast height (dbh) >10 cm were measured, identified at least to morphospecies level, and recorded. Records from Costa Rica of all species identified in the field were extracted from the GBIF database on the 24/05/2018. These GBIF records include field observations, herbarium collections, and occurrences reported in the literature.

2.2 | Analyses

The observed elevation range of each species was calculated as the difference between the maximum and the minimum elevation in which they occur in our own plot data and according to national data (GBIF). National data include occurrences of species in all kinds of vegetation and therefore do not represent old-growth forest alone. Nevertheless, the comparison between field versus nationwide elevation ranges is still useful to understand the generality of the observed patterns. The midpoint of the distribution is the halfway point between the highest and lowest record for each species. Due to concerns over uneven sampling, we only consider species with ranges of at least 200 m asl. We tested the relationship between range sizes and their elevation midpoint with a Pearson correlation. In order to compare the different ranges sizes of species present at old-growth versus the ones at secondary forest, we used Wilcoxon test. We also performed these analyses for the species that occur more than twice in both forests and span ranges >200 m asl. For the relationship between range size and dbh, we first divided each dataset into three dbh categories (10–15 cm; 15–30 cm; and >30 cm, note that a species can belong to more than one category). Individuals with a dbh >60 cm (only 41 stems) were excluded from the analysis in the secondary forest since they may represent remnant trees that established before the disturbance. Range sizes of each species were then calculated and compared with Kruskal–Wallis test, and if the *p*-value <.05 we used a Dunn test to check the difference between each of the categories.

We analyzed plot level basal area versus elevation along each transect with a gamma generalized linear model using an identity link for both old-growth and secondary forest gradients. Plots with negative residuals were categorized as "Low" basal area and those with positive residuals as "High" basal area. Then, we determined the number of species with an upper or lower range limit within these categories. We also counted stems in each plot as the null probabilities of finding a stem that is the highest or lowest for its species depends on the number of stems observed. To avoid artifacts, we removed implied range-limit observations in the highest and lowest elevation plots of each gradient from our analysis. Through modeling the basal area changes along the elevation gradient and using the residuals of the regression instead of the real basal area values, we were able to control the effect of any directional change of basal area with elevation on our results. We counted the number of upper and lower range limits in each of the two categories of basal area and compared them to expected values under two different assumptions with a chi-squared goodness of fit test. The first assumption is that the probability of finding a range limit at Low and High basal area is the same. The second assumption considers that the probability of finding a range limit is greater in plots with more individuals. We calculated this probability by dividing the number of stems in each category of basal area by the total number of stems in both categories per transect. All the analyses were performed with R 3.4.3.0.

3 | RESULTS

A total of 4,412 and 3,338 stems were recorded and 491 and 275 tree species identified in the old-growth and secondary transects, respectively. Species with only one record (82 in the old-growth and

26 in the secondary forest) were excluded. After removing species with ranges ≤200 m, 239 and 105 remained for analyses. The old-growth and secondary transects share 21 species that occur at multiple sites and have a range over 200 m in both (None of the species are tree ferns, palms or lianas) .

3.1 | Ranges versus elevation

Though plot observations in the old growth are an exception (Figure 2a), we generally observe a significant positive relation between the range size of a species and their elevation midpoint (field data old growth (Pearson correlation coefficient [*r*] = .153, *p* = .075, field data secondary: *r* = .377, *p* < .001, Figure 2a,b); for nationwide occurrences in old growth: *r* = .464, *p* < .001; and in secondary forest: *r* = .445, *p* < .001, Figure 2c,d). Species with narrow elevation ranges (i.e., spanning <500 m) occur through the entire old-growth elevation gradient (Figure 2a) but appear scarce in secondary forest at higher elevation (Figure 2b).

3.2 | Elevation ranges in secondary versus old growth

Species in the old-growth transect generally had narrower elevation ranges than those in the secondary transect. The pattern is apparent using the observed distributions within the sampled ranges (median values 370 and 675 m for old growth vs. secondary, Wilcoxon, *w* = 40,455, *p*-value = .036) and in the nationwide data (1,603 vs. 1,726 m, *w* = 8,414, *p*-value <.001, Figure 3a,b), though the differences in range size are greater when using the field data (305 m) than the nationwide data (123 m; Figure 3). When we compare the 21 species with ranges >200 m present in both transects, we find that the median range size is about 200 m greater in the secondary transect though there is considerable variation among observations and the difference is not significant (median range size 650 vs. 851 m for old growth vs. secondary, w = 188, *p*-value = .4).

3.3 | Ranges and tree size

The observed elevation ranges of species by tree size show no consistent trend in the old-growth transect (median values 565, 510, 560 m for small, mid, and big sized stems, Kruskal–Wallis w = 1.03, *p*-value = .668). In the secondary transect, trees bigger than 30 cm dbh have broader distributions (137 m broader, median values 787, 762, 920 m for small, mid, and big sized stems; Kruskal–Wallis w = 7.23, *p*-value = .03, see Figure 4). All fifteen species observed to reach sizes over 30 cm dbh in the secondary forest are fast-growing pioneer species (i.e., *Castilla elastica* Sessé ex Cerv., *Cecropia peltata* L., *C. alliodora* [Ruiz & Pav.] Oken, *Croton draco* Schltdl. & Cham, *Hampea apendiculata* [Donn. Sm.] Standl, *Heliocarpus apendiculatus* Turcz., *Inga oerstediana* Benth. ex Seem., *Myrcianthes rhopaloides* [Kunth] McVaugh, *Ocotea austinii* C.K. Allen, *Oreopanax xalapensis* [Kunth] Decne. & Planch, *Symplocos serrulata* Bonpl., *Trema micrantha* [L.] Blume, *Trichospermum grewiifolium* [A. Rich.] Kosterm., and *V. costaricanum* [Oerst.] Hemsl, *Virola koschnyi* Warb.).

3.4 | Range limits and relative basal area

Plot level basal area increases with elevation in both transects (old-growth forest: coef = 0.006, *SE* = 0.001, *t* = 3.973, *p*-value <.001; secondary forest: coef = 0.006, *SE* = 0.003, *t* = 2.826, *p*-value <.001). More species have their lower range limit in plots with below-average versus above-average basal areas in both old-growth (χ^2 = 11.9, *p*-value <.001) and secondary transects (χ^2 = 19.5, *p*-value <.001, Figure 5). We also observe an excess of highest elevation occurrences in below average basal area sites in old growth (χ^2 = 15.7, *p*-value <.001), but this difference decreases in the secondary forest (χ^2 = 5.1, *p*-value <.05; and under the assumption of an effect of the stem number χ^2 = 0.2 *p*-value = .637).

4 | DISCUSSION

We found that typical elevation ranges of the species present tended to increase with elevation. Furthermore, species found in the secondary forest exhibited broader elevation ranges than those in old growth. Within the secondary forest, species present as larger stems also tended to possess broader elevation ranges than species present only as smaller stems. We also found that species tended to have both their upper and lower elevation range-limit occurrences in plots with lower than average basal area at that elevation. This tendency was particularly marked at the lower range limit. Taken together, these results are consistent with our predictions concerning the role of competition constraining (reducing) species elevation ranges and disturbance expanding them (Figure 1). Though there is noise and uncertainty in these data, the implied elevation changes are of the order of hundreds of meters and thus have implications for species occurrence and persistence.

4.1 | Elevation ranges versus elevation

Increasing species elevation ranges with elevation has been noted previously using herbarium records from Costa Rica (see Stevens, 1992) and the Andes (Feeley & Silman, 2010), but see also (Lieberman, Lieberman, Peralta, & Hartshorn, 1996). What determines these patterns? Geometric constraints play a role—we cannot observe a broad range for species that are restricted to the ends of the observed (or available) gradients. While this limits the observed lower elevation species, it is less evident why we lack narrow range species at high elevations (Figure 2). Ranges at higher elevations may reflect the broad climatic tolerances required to persist at

FIGURE 2 Elevation ranges for tree species from the field data (a) and (b) and from occurrences nationwide (GBIF) (c) and (d) versus elevation midpoint for species with ranges >200 m. asl present in the old-growth (a and c) and secondary forest (b and d). Linear trend added to aid interpretation. Dashed lines represent nonsignificant relations. **p*-value ≤.05, ***p*-value ≤.01, ****p*-value ≤.001

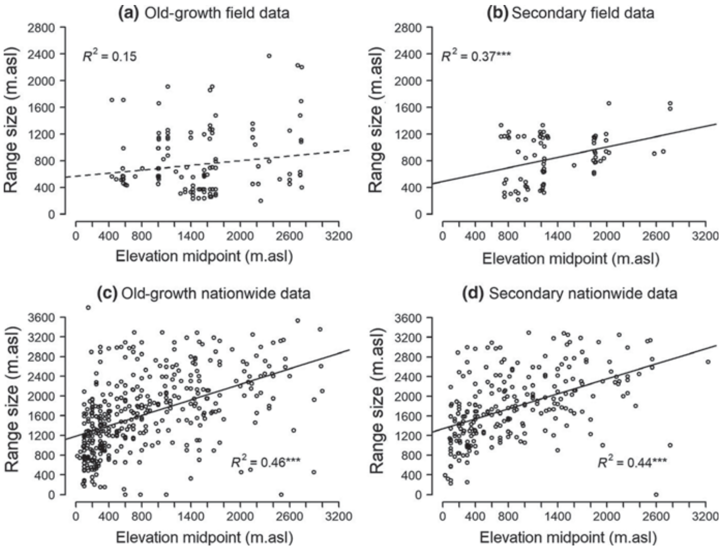
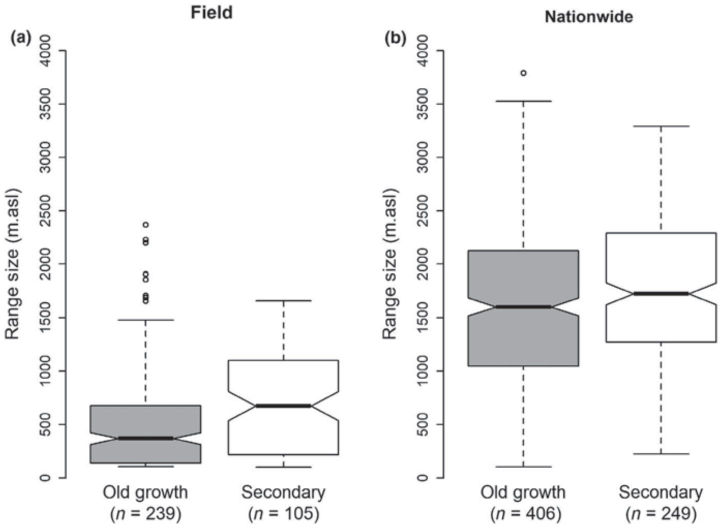


FIGURE 3 Elevation range sizes for old-growth and secondary forest species using field (a) and nation level (nationwide) (b) occurrences data from the two elevation gradients



those elevations (Janzen, 1967; Morin & Lechowicz, 2013; Stevens, 1992). In our study, temperature decrease and precipitation seasonality increases with elevation (see Appendices S1 and S2). Trees with a greater tolerance to frost and seasonal drought have been observed to be more widely distributed than less tolerant species (Anderegg & HilleRisLambers, 2016; Esquivel-Muelbert et al., 2017; Pither, 2003). Nonetheless, the greater investment in tolerance and adaptations required of species able to persist at higher elevation may limit their ability to grow fast and avoid competitors under conditions that do not require such tolerance and adaptations (Koehler, Center, & Cavender-Bares, 2012; Loehle, 1998). The same trade-offs are believed to explain the range size of trees in North America (Ettinger & HilleRisLambers, 2017; Morin & Chuine, 2006; Morin & Lechowicz, 2013) and in the Neotropics (Bemmels et al., 2018). Such patterns and trade-offs are consistent with the presence of a competitive hierarchy.

The presence of narrow-ranged species along the whole elevation gradient in the old-growth forest seems to explain the lack of a marked correlation between elevation range size and elevation midpoint in the old-growth forest (Figure 2). While broad-range species must possess broad environmental tolerances, narrow-ranged species may be constrained by narrow environmental tolerances

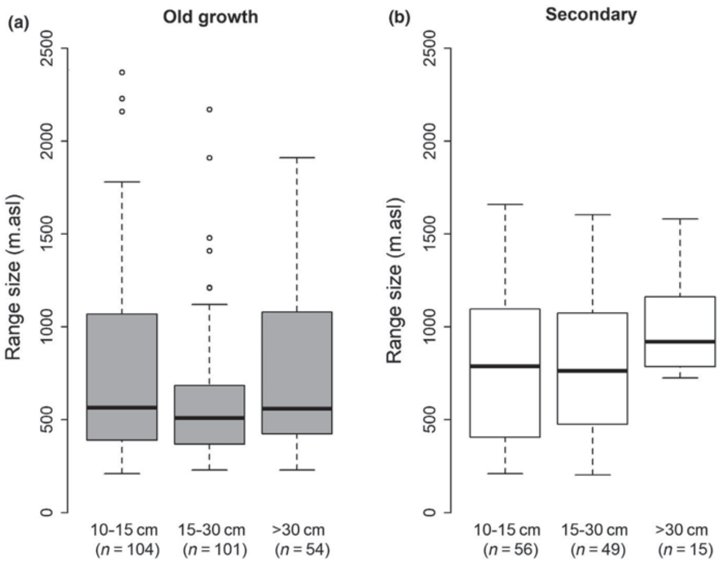


FIGURE 4 Species elevation range size per diameter class (between parentheses the number of species present at each diameter class) for old-growth (a) and secondary forest (b)

or competition (Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006; Kessler, 2001). We also see that species with narrow elevation ranges become less frequent with increasing elevation in the secondary forest, where competition was temporarily reduced. The ability to establish in previously cleared sites may have released some otherwise narrow range species from competitive restrictions, or the history in these areas may have eliminated them, since open sites can accentuate climatic extremes when compared to closed forest, increasing exposure to drought, frost, and other factors (Rehm & Feeley, 2015a).

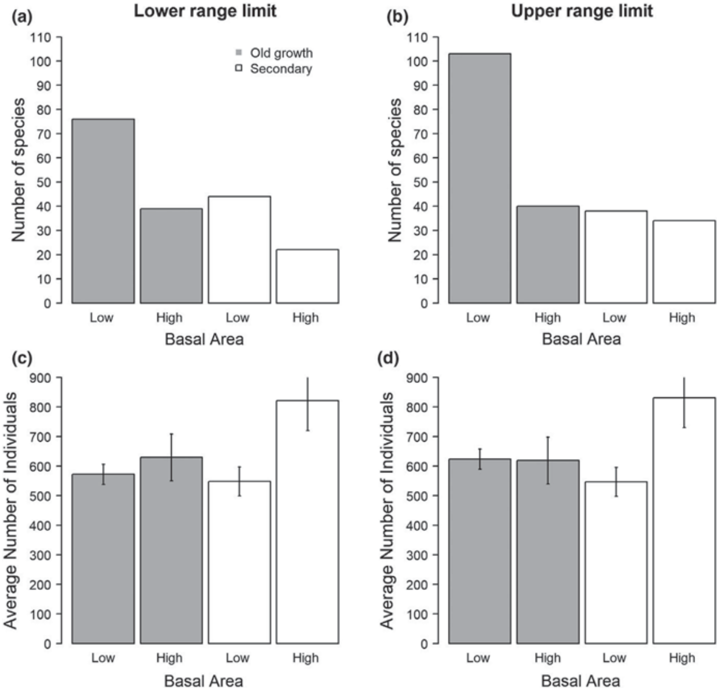


FIGURE 5 Number of species with their lower (a) and upper (b) elevation range limit observed within plots with a basal area higher ("High") or lower ("Low") than predicted by a generalized linear model at that elevation. (c) and (d) show the average number of stems in plots where species have their lower (a and c) and upper (b and d) range limits, respectively

4.2 | Disturbance and elevation ranges

The relation between disturbance and species ranges becomes clearer when comparing old-growth and secondary forest. The broader elevation range sizes (about 100–318 m, equivalent to about 0.6–1.4°C in temperature) of species in the secondary forest, compared to the species in old-growth forest, suggest that the initial period of regrowth when the forest started regrowing from open land allowed them to expand their ranges. Many species observed in secondary forest, especially the larger trees, are pioneers with good dispersal that depend on open habitat to establish. Consequently, in a secondary forest, those species that establish first benefit most from the temporary absence of competition, which permits them to expand their ranges beyond what is observed under more intense competition. For instance, we found that species with stems larger than 30 cm dbh in the secondary forest (but omitting any likely relics with a dbh >60 cm), that is, those species that we assume arrived soonest and grew fastest as a result of limited competition, have broader elevation ranges than those with only smaller stems (averaging 137 m or around 0.6 C^0 broader; Figure 4b). Although the size of a stem does not always reflect when it established, it seems safe to assume that most stems >30 cm dbh in the studied secondary forest represent early arrivals that established when these areas were just abandoned and still open. To our knowledge, only one of the species, *Cordia alliadora*, might plausibly have been transplanted along the elevation gradient, given its use as a shade tree in coffee plantations. Surprisingly, the elevation ranges of the 22 species present in both the old-growth and secondary transects were not statistically different, although on average these species occurred over a broader elevation range in the secondary forest (200 m broader). This group is composed by a small number of pioneer (e.g., *Cecropia* spp., *Hedyosmum* spp., *Schefflera rodriguesiana*) and late successional species (e.g., *Pouteria reticulata*, *Guarea* spp.). The relatively small sample sizes likely explain the lack of a statistical difference. While dispersal plays some role in the patterns, we have observed (discussed below) it is unlikely to be the sole explanation as it fails to account for the high frequency of range-limit observations occurring in low basal area sites. While other authors have noted links between species distributions and competitive abilities (see Sheil, 2016), we believe ours is the first to test a theoretical link with disturbance and elevation ranges in natural communities.

Propagule availability limits potential range expansion. Propagules may only be present in a portion of a range where they would otherwise establish and grow. Since we cannot distinguish the influence of propagule availability and dispersal limitation from environmental limits, the difference in elevation range sizes between species in old-growth and secondary forest provides a minimum estimate of what might be possible if propagule availability were unlimited. This underestimation appears particularly important for species with short localized dispersal and short-lived seeds. We know for example that many old-growth species have median dispersal distances of only a few tens of meters (Muller-Landau, Wright, Calderón, Condit, & Hubbell, 2008) and their seeds lack long-term viability in the soil (Long et al., 2015; Vázquez-Yanes & Orozco-Segovia, 1993). When the climate is changing, we can ask both whether the species can track suitable climates over the landscape (e.g., moving upslope in warming conditions) and also whether they can tolerate the new conditions in situ (Corlett & Westcott, 2013). The first depends on good dispersal, but the second does not. We speculate that in a warmer climate, disturbance may not only facilitate range shifts in species with good dispersal but may also improve the in situ persistence of species with limited dispersal (Sheil, 2016).

4.3 | Competition and range limits

Competition reduces lower elevation range limits. Species in both old-growth and secondary forest had their lower range limit in plots with lower (vs. higher) basal area more frequently than expected if competition was irrelevant (Figure 5a). We infer that reduced basal area favors the establishment of species that are otherwise excluded by competition. Other studies have described a similar relation between high tree cover, competition for light, and elevation range limits in shrub and nonwoody plant species at temperate (Nieto-Lugilde et al., 2015) and tropical ecosystems (Johansson et al., 2018). These studies found that reductions in tree cover helped shrub species to expand their range to lower elevations. Furthermore, observations show that many higher elevation plant species are sometimes observed in disturbed sites at lower elevations (Kappelle, Kennis, et al., 1995; Lovett, 1996; Sheil, 2016; White, 2013). Our observations indicate that many species can establish and persist in lower and warmer conditions if competition is reduced, in this case in the open habitat after land is abandoned, but presumably in any open sites created by disturbance.

Upper range limits appear less clearly influenced by competition than the lower limits. Nonetheless, in the old-growth observations, disturbance appears to increase the upper range limit with species having their upper elevation range limits in plots with lower (vs. higher) basal area more frequently than otherwise expected (Figure 5b). We again infer competitive displacement given that any species is likely to be less competitive near to their physiological range limits (McGill, 2012). On the other hand, competition has less apparent influence on upper limits in the secondary forest (Figure 5b), suggesting that, if competition remains important, opposing positive interactions may also be present. Positive interactions may protect species from drought stress, frost, and other threats that are more severe in more open locations (Callaway et al., 2002; Maestre, Callaway, Valladares, & Lortie, 2009; Rehm & Feeley, 2015b). Our interpretation is that depending on the nature and vulnerability of the biotic interactions (negative or positive) disturbance can modify these relationships with consequences (positive or negative) for each species' upper range limits.

4.4 | Methodological limits and lessons

Our comparison of elevation ranges of tree species in secondary and old-growth forest represents an exceptional opportunity for an initial exploration of how disturbance histories may influence species distributions. From our perspective, it provides a “proof of concept” that these theorized patterns can be detected and explored in these real world data. We acknowledge limitations that should be addressed in future work. Though climatically similar, our two gradients were not perfectly matched and were not replicated at a regional scale: Thus, environmental influences cannot be formally accounted for. For example, we cannot account for the difference in soils while studies elsewhere in the tropics have shown that these can influence species distributions and competition (e.g., Paoli, Curran, & Slik, 2008). Another concern is the influence of sampling effort. The number of stems recorded at each elevation governs the probability of detecting a species. Greater coverage and replication would improve our data and permit broader generalization. Furthermore, we have not examined the many disturbance processes, both natural and human-made, that impact on these forests. Nonetheless, while these uncertainties matter, and robust statistical inferences require greater replication, we remain confident in our general conclusions as they are not readily explained by artifacts, and match our expectations and more ad hoc observations elsewhere (see Sheil, 2016). Finally, we note that while species occurrence is necessary for persistence, it is not sufficient—further work would be required to clarify if these occurrences at range limits contribute to population maintenance and growth (Pulliam, 1988; Sheil, 2016). We encourage others with suitable data to further explore these relationships.

5 | CONCLUSION

We have found patterns that appear largely consistent with how we expect competition may influence (limit) the upper and lower distribution of tree species in the mountains of Costa Rica. We also demonstrate that, as previously suggested (Sheil, 2016), under suitable conditions a release from competition that opens up areas for recolonization (as might result from a disturbance event or from the abandonment of previously cleared land) can expand the elevation ranges that result from these competitive influences (Figure 1). This process can increase the elevation ranges for some species, with a consequent increase in their climatic range of occurrence by 100–300 m in elevation or 0.6°C and 1.6°C. These values may be a substantial underestimate due to the confounding influence of dispersal limitation. Under rapid climate change, any means to improve the persistence of species outside their normal climatic range merits consideration. Our evidence suggests that disturbance, by reducing competitive exclusion, can permit at least some species to occur at lower elevations than otherwise. Therefore, disturbance offers a possible means to manage and maintain distributions and possibly improve species persistence in a warmer future, where competitive exclusion may contribute to local and global extinctions. Although our results are best viewed as a proof of concept, rather than a last word, we underline that of the role of disturbance histories is a vital, though often missing, element in understanding and potentially managing species distributions. To develop these approaches into a practical form of conservation management would require further evaluation of the response of particular species to particular forms, scales, and frequencies of disturbance at their range margins.

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CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY STATEMENT

All the information related to the species composition of the transects is available at CONAGEBIO data repository: http://datos.conagebio.go.cr/collectory/public/showDataResource/dr1. The exact data have been published in the DataverseNO public repository: https://doi.org/10.18710/72JI22

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Paper III

Disturbance and light availability determine the elevation ranges of paramo and cloud forest tree species.

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Abstract:

Aim: We explore how variation in forest cover and light availability after disturbance shape the elevation ranges of ten woody plant species.

Location: Paramos and cloud forest of the Talamanca Mountain Range, Costa Rica

Taxa: Two shrubs: *Hypericum irazuense, Vacciunium consanguineum;* and eight tree species*: Escallonia myrtilloides, Schefflera rodriguesiana, Weinmannia pinnata, Rhamnus (Frangula) oreodendron, Styrax argenteus, Podocarpus oleifolius, Prumnopitys standleyi* and *Magnolia poasana*

Methods: By using distance sampling we recorded the abundance of the selected species along a 1400 m elevation range using 22 500-m transects, each subdivided into 10- sub-transects. For every individual detected we recorded diameter at breast height (DBH), height, canopy exposure to light, and basal area of surrounding forest. These variables allowed us to distinguish between forest at different stages of succession and thus recovery from disturbance. We fitted “density surface models” using a GAM approach to estimate the density of each species along the elevation gradient in relation with light availability and forest structure.

Results: We recorded 5121 stems in total though three of the ten species were represented by less than 100 individuals. We observed a clear relationship between forest structure, crown illumination and the elevation ranges of seven species. One species had a clear light demanding strategy, only occurring at well-lit sites throughout their range. Three species shifted from a shade tolerant to strictly light demanding distribution between their upper and lower range limit. Three species occurred mainly under shaded and crowded conditions. The elevation ranges of three species did not reveal any clear relationship with light availability or forest structure, though its density varied across the elevation gradient.

Main Conclusions: Our study illustrates how distance sampling can clarify the relationship between environmental conditions and tree species distributions. Using this method, we show how competition and disturbance influences the elevation ranges of several species. Our results indicate that competition determines the elevation ranges for some species, in particularly at the lower elevation limit. Disturbance, through altering the distribution of light and structure of the forest can determine the distribution of tropical trees.

Introduction:

Disturbance—a transient or sustained reduction in competition and other biotic interactions—may modify the upper and lower elevation and temperature ranges of plant species (Muñoz Mazón et al., 2019; Sheil, 2016). Ecologists have long noted how competition and disturbance may influence the presence and abundance of tree species along environmental gradients (see Budowski, 1965, Van Steenis, 1958). Nonetheless, despite past efforts to develop and apply suitable theoretical frameworks (Huston & Smith, 1987; Keddy & MacLellan, 1990; Malanson, 1997) these insights appear neglected in recent studies concerning plant distributions (e.g. Corlett & Westcott, 2013). Nonetheless, theory and observations in mountain ecosystems indicate, that release from competition via disturbance improves plants performance at their lower range limit (Chardon, Rixen, Wipf, & Doak, 2019), permitting species to establish in warmer climates at elevations many hundreds of meters below their normal range (Sheil, 2016). One example is the high elevation treeline (the upper boundary of forest), which often occurs at lower elevations following disturbance (Ameztegui, Coll, Brotons, & Ninot, 2016; Wang et al., 2019) Under such conditions, high elevation species that cannot persist under tree cover are able to establish at lower elevations and warmer temperatures than otherwise due to the open areas that result from disturbance.

Disturbance can reduce competitive exclusion in multiple ways (Connell, 1978; Sheil, 2016) . Important processes include, but are not limited to, freeing up space and resources such as light, a reduction in the superior competitors, and/or a greater advantage for the competitively inferior species to arrive first (Sheil & Burslem, 2003). But the effects can also be negative. Some species, especially long-lived shade tolerant taxa, are sensitive to recurrent disturbance(Shea, Roxburgh, & Rauschert, 2004; Sousa, 1984) . Furthermore, biotic interactions can be beneficial facilitating the establishment, survival and growth of other species extending the apparent realised niche beyond the fundamental niche(Bertness & Callaway, 1994; He & Bertness, 2014). Thus, how disturbance influences species range limits may depend on context and vary with elevation.

Trade-offs between competitive abilities and other characteristics, such as dispersal or tolerance to extreme environmental conditions, can explain how disturbance shapes the distribution of species(Lusk, Kaneko, Grierson, & Clearwater, 2013; Wilson & Keddy, 1986) For example, along a temperature gradient a species' tolerance of cold conditions may reduce competitive abilities under warmer conditions (Koehler, Center, & Cavender-Bares, 2012). Such trade-offs can generate competitive hierarchies along gradients where less competitive, but more specialised, species are displaced by superior competitors towards less optimal areas. Improved persistence in or near "optimal" areas may then be possible if there are opportunities to avoid competition (Cadotte, 2007). Often, inferior competitors have a greater fecundity and more effective dispersal than species adapted to be strong competitors (Bin et al., 2019;

Uriarte et al., 2012). Disturbance gives these species an opportunity to establish populations before competitively superior species can exclude them. On the other hand, where positive interactions are necessary for establishment, disturbance may remove these favourable effects and thus reduce species ranges.

We know little about how changes in forest structure and light availability after disturbance can influence species elevation ranges and their ability to establish and persist at higher and lower temperatures. Understanding how disturbance shapes species elevation ranges offers insights that may help predict and manage the ecological consequences of climate change on species distributions. Here we use distance sampling protocol (S. Buckland, Rexstad, Marques, & Oedekoven, 2015) to quantify the presence and abundance of eight trees and two shrub species along an elevation gradient across different levels of disturbance in Costa Rica. Distance sampling, when compared to other plot and transect methods, has been shown to be efficient for detecting uncommon tree species and for assessing their densities, (Kissa & Sheil, 2012). Nonetheless, to our knowledge, such approaches have not been used to assess distributions along gradients, and the ecological factors that determine them. By sampling selected tree and shrub species over a range of successional stages at each elevation, we examine how past disturbance modifies their elevation ranges. We predict that if species are structured according to a competitive hierarchy in which competition displaces some species towards higher elevations, release of competition after disturbance will allow species, insofar as dispersal permits, to establish and thus be observed at lower elevations than within old-growth forest.

Methods:

Study area:

The study area is located along the Eastern Atlantic slope of the Talamanca Mountains in Costa Rica, from the hills of Cerro Asunción at 3400 meters above sea level, down to 2100 m a.s.l. in La Esperanza de Tapantí. According to previous exploration of the area using Worldclim data (Muñoz Mazón et al. 2019) and data loggers installed along the same elevation gradient (Muñoz Mazón et al. in preparation), average annual temperature decreases from 14 °C at the lowest sampled elevation (2100 masl) to 9 °C at 3400 m a.s.l. Precipitation remains constant along the elevation gradient, ranging between 2500 to 3000 mm per year (Muñoz Mazón et al. 2019). There is a mild dry season from December to April.

The vegetation transitions from oak dominated cloud forest in the lowest part of the elevation gradient to a shrubby Paramo above the treeline (approximately 3000 m a.s.l.). The cloud forest is dominated by *Quercus bummelioides*, with an increasing dominance of *Q. costaricenses* towards the tree line (reference). Other common tree species that accompany the oaks are *Schefflera rodriguesiana, Weinmannia pinnata* and *Styrax argenteus*, appearing in early, mid and late stages of succession, respectively (Kappelle, Uffelen, & Cleef, 1995). The paramo ecosystem is dominated by regional endemics such as the bamboo *Chusquea subtesselata* and the shrubs *Hypericum irazuense* and *Vaccinium consanguineum* (Kappelle & Horn, 2005). These ecosystems have been exposed to different disturbance types. The most common was treefalls of different sizes. Some areas of the studied paramo have burnt in the past (Horn, 1997) However, it was difficult to distinguish those areas given that the fires occurred more than 30 years ago (Horn, 1997) and vegetation had fully recovered. Finally, according to previous landowners of sections of what now is the Cerro de la Muerte and Tapantí National Park, some of the studied forest patches where selectively logged for both timber extraction and charcoal production more than 25 years ago.

We recorded the occurrence of ten woody species (eight trees and two shrubs) characteristic of the Paramo and cloud forest ecosystems (Table 1). The species were chosen to represent a variety of life histories (from early successional to late successional species), conservation status and distributions (regional endemic to widespread). Another important factor that determined the selection of species was the ease to identify them visually from a distance.

Table 1. Conservation status, distribution and dispersal mode of the studied species.

Name	IUCN Conservation status	Distribution	Dispersal
Hypericum irazuense	Not assessed	Endemic (CR PN)	Barochory
Vacciunium consanguineum	Not assessed	Endemic (CR PN)	zoochory
Escallonia myrtilloides	Not assessed	Broad	zoochory
Schefflera rodriguesiana	Least concern	Endemic	zoochory
Weinmannia pinnata	Least concern	Broad	zoochory
Rhamnus (Frangula) oreodendron	Least concern	Endemic (CR and Panama	zoochory
Styrax argenteus	Least concern	Broad	zoochory
Podocarpus oleifolius	Least concern	Broad	zoochory
Prumnopitys standleyi	Endangered	Endemic (CR and Panama)	zoochory
Magnolia poasana	Near threatened	Endemic (CR and Panama)	zoochory

Vegetation sampling:

To estimate the density of the selected species along the elevation gradient we used distance sampling (Buckland et al., 2001). This method assumes that all individuals located on a line-transect are detected, that the probability of detection decreases with distance from the transect and that objects are immobile. Then, by using the distribution of the distances it is possible to estimate the probability of detecting an individual given a distance through a detection function. Additionally, it is possible to include variables (e.g. tree height, diameter at breast height) to the detection function to improve the model fit (Marques, Thomas, Fancy, & Buckland, 2007). Finally, the detection function could be used to estimate the density of each species along the transect.

Following this method, we established 22 line- transects of 500 meters each across the elevation gradient. Every transect was located perpendicular to the slope and at approximately a single elevation. Every transect covered forest at different stages of succession. To characterize how recovery form disturbance influenced the density of the selected species we measured for every individual observation (trees and saplings) the diameter at breast height (1.3 meters above the ground), tree height, crown illumination index and an estimate of basal area (through the relascope method). Individuals with multiple stems were considered as one by calculating the cross-sectional area equal to the sum of the individual stems. The heights of trees taller than 2.5 meters were calculated from clinometer measurements. The crown illumination index (CII) is a rapid visual method to estimate the exposure to light of a tree (Dawkins 1956). The relascope method allowed us to estimate the basal area around every observation. This method consists in using gauge of a fixed width, attached to a string of a fixed length; and then turning 360° counting all stems that are wider than the gauge. In my case I used my thumb (18 mm) attached to a string of 580 mm to obtain a multiplication factor of 10. The number of stems counted multiplied by the factor represents an estimate of basal area. We summarized the combined effect of basal area and CII with an PCA analysis.

To characterize the variability of light conditions and basal area across forest at different stages of succession, we divided each transect into 10 sub transects of 50 meters long. We estimated the CII at three different heights (0, 5 and 15 meters), tally, and height of canopy at the beginning of each sub transect. We also estimated the competition index per sub transect averaging the individual values of each observation within each sub transect.

Analyses:

We used Density Surface Models (DSM)(Miller, Burt, Rexstad, & Thomas, 2013) to examine the relationship of light availability and basal area on the estimated density of the selected tree species along the elevation gradient. This method fits first a detection function using the distance data to estimate the density of each species within each sub transect and then builds a generalized additive model (Wood, 2006) to relate the density estimations to the different environmental variables measured.

To fit the detection function, we used half-normal, hazard-rate and uniform models and diameter at breast height, tree height, basal area and species identity as covariates. The data were truncated to 10 meters based on visual inspection of the distance histogram (Figure 1a). We used Akaike's Information Criteria (AIC) to judge the best detection model (Table 2).

To assess the relationship between basal area, CII and elevation and their interactions on the density estimations we used generalized additive models fitted with the DSM package (Miller et al. 2013)). We explored the density of each species along the elevation gradient in relation to basal area and CII separately. Also, to test the combined effect of these variables we used the competition index described above. We tested the interactive effect of basal area, CII and the competition index on the density of each species along the elevation gradient using tensor products (Wood, 2006). Thin plate regression splines were used as the basis for the model's smooth term. Tensor products terms were selected using approximate p-values ($p < 0.05$)

Deviance residuals were checked for normal distribution and constant variance (Woods 2006).

Results:

We recorded a total of 5121 individuals of the ten selected species. Seven species had more than 100 individuals while three had less (*Podocarpus oleifolius* (24), *Prumnopity standleyi* (32) and *Magnolia poasana* (31)). Table 2 summarizes the observed and estimated abundances.

Table 2. Observed and estimated number of individuals per species in the 11-ha analysed.

Species	**Observed N Individuals**	**Estimated N Individuals**
H. irazuense	188	406
V. consanguineum	1582	3298
E. myrtilloides	416	832
S. rodriguesiana	340	556
R. oreodendron	281	537
W. pinnata	1475	2544
S. argenteus	455	686
M. poasana	29	36
P. oleifolius	19	28
P. standleyi	24	49
Total	4862	9059

The best detection model followed a hazard rate distribution and included the covariates, basal area, tree height and dbh (Table 3). The second-best model included also had a hazard rate distribution and only tree height as covariate (Table 2). We selected this simpler model since it had a similar AIC than the best model and a better goodness of fit. Since the models that included the identity of the species were not selected (having a higher AIC), we used a single combined detection function to estimate the density of all the species. Based on a preliminary inspection of the frequency distribution of the distances (Figure 1a) and a later check of the goodness of fit of the selected detection model, we used a truncation distance of 10 meters. After the truncation, the sampled area had 11 ha of forest and 4862 individuals (Table 2).

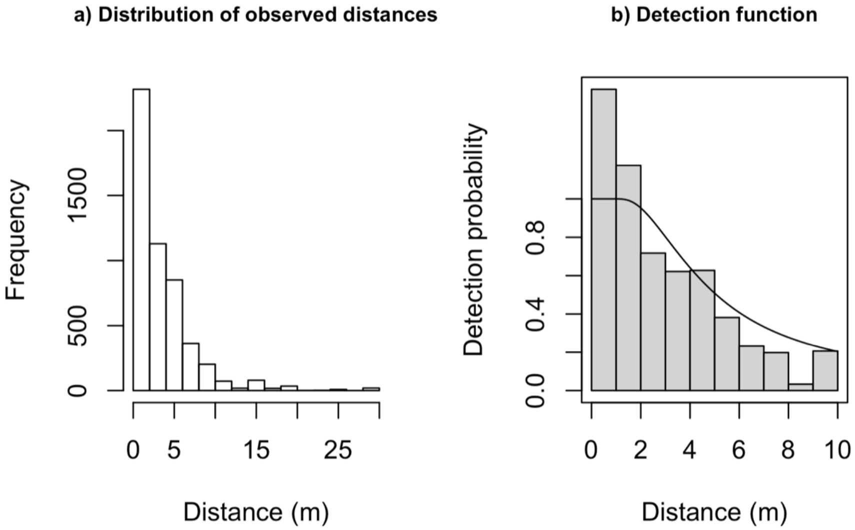

Figure 1: a) Distribution of observed distances; b) Fit of the selected detection function.

Table 3. Detection models explored in this study.

Model	**Function**	**Formula**	**∆AIC**
1	Hazard-rate	d.b.h + BA+ Tree.height	0.000
2	Hazard-rate	Tree.height	0.464
3	Half-normal	d.b.h+BA+Tree.heigth	243.978
4	Half-normal	Tree.height	253.599
5	Hazard-rate	d.b.h	264.238
6	Half-normal	d.b.h	433.762
7	Hazard-rate	Species	502.015
8	Hazard-rate	BA	650.160
9	Hazard-rate	1	664.468
10	Half-normal	1	1055.177
11	Half-normal	BA	1056.589

The first axis of the PCA explained 76% of the variation and correlated positively with basal area and negatively with CII. Thus, it separates crowded areas where individuals are out shaded from open areas where there is more light availability. Furthermore, this axis seems independent of tree size, as it is weakly correlated with tree height (-0.09). Thus, we used this PCA axes as an estimate of competition for light (hereafter called competition index). The other PCA axis explained 24% of the variation and was positively correlated with both basal area and CII. This second axis is likely related with the size and life stage of the individual, as it tends to separate trees located in crowded areas but well illuminated (potentially dominating the canopy) from individuals in less crowded areas but shaded (potentially regenerating). Indeed, this axis is positively correlated with tree height (38%).

Our model evaluation indicated an interaction between our competition index and elevation on the density of four of the species (*E. myrtilloides, V. consanguineum, S.rodriguesiana, P.oleifolius*) (Table 4). The density of three of these species increased towards lower elevation with more open conditions and decreasing values of competition and basal area (Figure 2 and Figure 3).

The other six species (*H.irazuense, S.argenteus, W. pinnata, M. poasana*, R. oreodendron and *P. standleyi*) respond in distinct ways to elevation and competition (Supplementary information 1). For example, *H.irazuensis* only occurs in low basal area and low-competition subtransects (Figure 2a, Figure 3a). Indeed, for this species neither the elevation smoother, nor the interaction between elevation was significant (Table 4, Supplementary information: Figure S1 and Figure S2). While *W. pinnata* and *S. argenteus* have a greater density under more shaded conditions all over their range, the density of R. oreodendron peaks towards lower levels of competition, though it also persist under the shade (Supplementary information 1; Figure S1). We detected an effect of elevation, but not not competition, on the density of *M. poasana, Podocarpus oleifolius* and *P. standleyi* (Supplementary information, Figure S2). The density of *M. poasana* decreases towards higher elevations, while both *P. oleifolius* and *P. standleyi* have a unimodal distribution peaking approximately between 2500 to 3000 m.a.s.l.

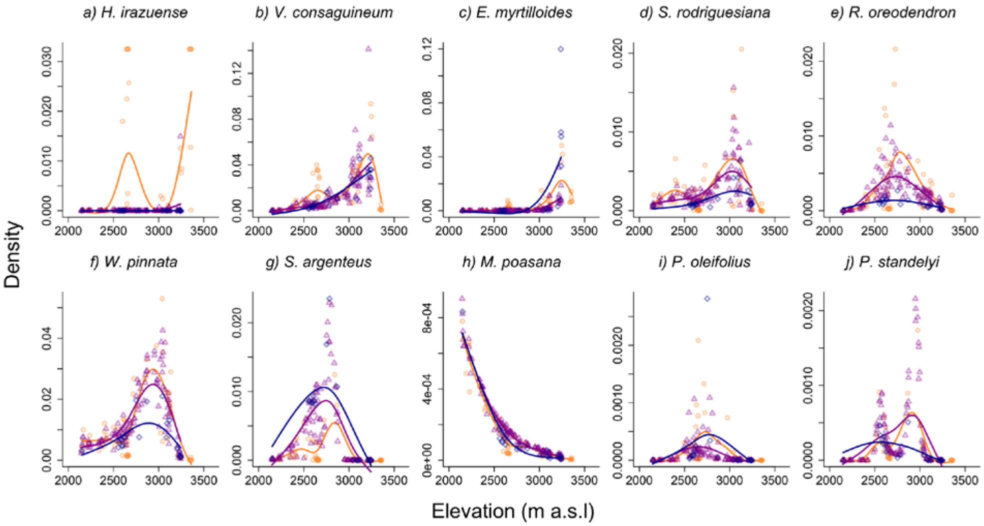

Figure 2: Density estimation from dsm model for the selected species. The different colours represent basal area categories. Yellow and circles are for the lower third, purple triangles are for the middle third and blue diamonds are for basal area values in the lower-, mid- and higher third of the basal area distribution respectively.

Table 4: Selected smoothers and total deviance explained for each species model.

	H. irazuense	***V. consanguineum***	***E. myrtilloides***	***S. rodriguesiana***	***R. oreodendron***	***W. pinnata***	***S. argenteus***	***M. poasana***	***P. oleifolius***	***P. standleyi***
ti(Elevation)	n.s	···	···	···	···	···	···	···	··	···
ti(Comp_Index)	···	·	···	···	···	···	···	n.s	n.s	0.09
ti(Elevation, Comp_Index)	n.s	···	···	·	n.s	n.s	n.s	n.s	···	n.s
Deviance explained	75%	54.3%	84.1%	42.4%	40.7%	41.9%	73.4%	26.7%	66.3%	50%

···: p-value < 0.005; ·· : <0.01; · :<0.05

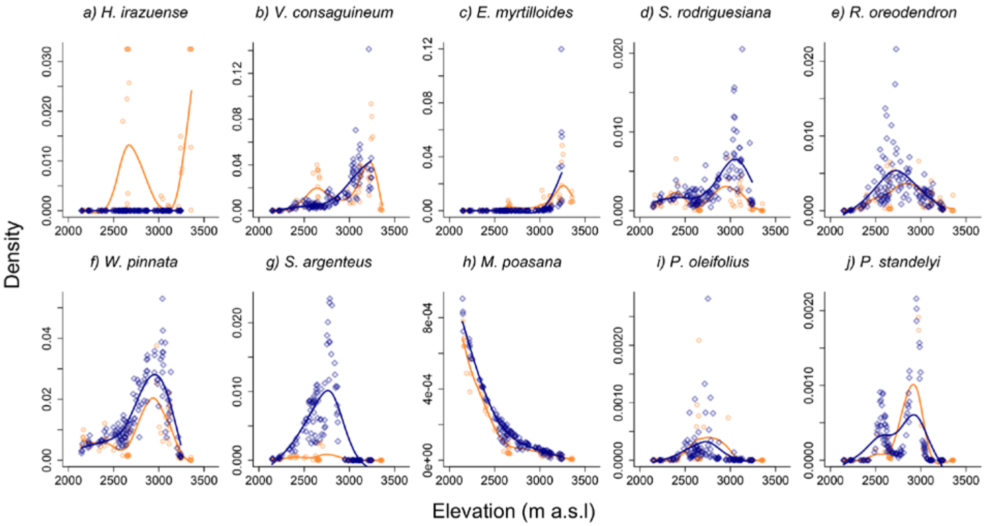

Figure 3: Density estimations from dsm models for the selected species. The different colours represent competition categories. The yellow circles are for values in the low competition category. Blue diamond represent values in the high competition category.

Discussion:

Distance sampling is a promising method to clarify determinants of tree species distributions along environmental gradients. Using this method, we detected an interaction between disturbance and elevation on the density of four species. For these four species, more open sites were associated with increased density towards their lower range limit, suggesting a declining tolerance of more shaded environments under warmer conditions. Additionally, our approach allowed us to better understand the light requirements of the other six species across their ranges. Our results indicate that these methods can help reveal the environmental relationships that shape species distributions, even when densities are low. Moreover, our results indicate how past disturbance, and thus the presence of open and early successional areas, influence the elevation ranges of several woody species.

One species occurred, almost exclusively, in locations with high light availability and low neighbour density. For Hypericums s, sufficient light availability and low competition, likely explain where it occurs (Table 3, Figure S1 in Supplementary material). This species is exclusively present in open locations with full light, indicating little, if any, tolerance of shade along their entire elevation range. *Hypericum irazuense* is notable among our species for being common at the highest elevations where tree cover is often sparse or absent. Previous studies in Costa Rica have reported how the vegetation that establishes following the clearance of high-elevation oak forests is enriched by an influx of even higher-elevation species, such as *Hypericum irazuense* that are normally restricted to above the treeline (Kappelle et al. 1995). In a warmer future, it is likely that the persistence of this and other tropical alpine species will depend on canopy opening disturbances.

For four species, open versus closed forest seem to have a different influence on their abundance depending on range limits. At higher elevations, light and neighbour tree cover has surprisingly little influence on the density of these species, that appear relatively independent of shade. On the other hand, relatively open areas are associated with greater density of four species at lower elevations, suggesting that open conditions favour extend their lower range limits. The implication is that these tree species behave like pioneer species at lower elevations, occurring almost exclusively at early stages of succession and benefitting from events that open up the forest canopy. Furthermore, all four species are common and abundant at elevations where frost occurs (3000 m a.s.l.). A potential mechanism explaining the patterns we observed would be a trade-off between tolerance of the low temperatures needed to establish and persist at higher elevations at the expense of their relative ability to compete for light at lower elevations. Our observations are consistent with the idea of species being sorted along an environmental gradient according to a competitive hierarchy (Shipley & Keddy, 1994; Smith & Huston, 1990), where inferior competitors are excluded to areas of lower productivity such as cold high elevations (Sheil 2016). They are also consistent with the stress gradient hypothesis in the sense that competition appears more important in determining range limits at the low-stress (low elevation) versus the high-stress (high elevation) part of the gradient (Bertness &

Callaway, 1994). Thus, reductions in canopy cover from disturbances could have allowed these four species to escape exclusion and persist at their lower range limits.

Disturbance did not appear to benefit every species. Two appeared more abundant under shaded and crowed conditions over the entire range of our observations. These species include sub canopy trees that are common in mid successional and mature cloud forests (*Weinmannia pinnata* and *Styrax argenteus)*. Interestingly, at least one of these species is also common in early successional forest (*W. pinnata*, Kappelle et al 1995). The interaction between competition and elevation was close to be significant for *W. pinnata*, suggesting that it is likely that if continued the sampling of this species towards lower elevations we could have detected an interaction. Indeed, the pattern observed in Figure 3 it is very similar to the patterns observed for species where the interaction between competition and elevation was significant (*V. consanguineum*, *E. myrtiloides* and *S. rodriguesiana*). Unfortunately, we were unable to explore the lower range limits for these species, which limits our ability to clarify the nature of these with respect to open versus closed areas and to disturbance.

For the conifers *Podocarpus oleifolius* and *Prumnopitys standleyi* and the *Magnolia* we were not able to detect a direct effect of competition for light (though we also note that sample sizes were limited). However, we did detect an interaction between competition and elevation for *P. oleifolius* and the competition smoother was almost significant for *P. standleyi*. In the tropics many conifers appear restricted to sites with poorer soils (Palma et al., 2020) or higher elevations (Martin, Sherman, & Fahey, 2007), but these patterns can be modified by disturbance (Coomes & Bellingham, 2011). For example, pine forest in the Caribbean island of La Hispaniola occurs at lower elevations, in areas otherwise dominated by broad leaved tropical forest, after fires and landslides (Martin, Fahey, & Sherman, 2011). While both *P. oleifolius* and *P. standleyi* have form and foliage that suggests shade tolerance, our results suggest that for these species disturbances that open the canopy and may allow trees to establish without dense shade and competition, likely influencing establishment throughout their ranges.

Dispersal limitation could have influenced the observed relationship between disturbance and the elevation ranges of the studied species. The outcome of disturbance on elevation ranges depends not only on establishment but on each species ability to reach suitable locations. Dispersal has been shown to be a key determinant of tree species distributions and their ability to change (Svenning & Skov, 2007). However, many observed elevational range shifts relate to range reductions (Elsen, Monahan, & Merenlender, 2020) and changes in abundance within their current elevational range (Rumpf et al., 2018), and not by dispersal and colonization beyond the range limits. In the future persistence may often depend on enduring a changed climate and associated novel competitors rather than on dispersal. This would be the case in mountains where ability to ascend and track climate change is limited. We propose that in at least some cases, disturbance processes and their influence on establishment will be key in mediating such persistence. Managed disturbances of a suitable nature could help species with limited dispersal persist within their current elevation ranges. On the other hand, if unmanaged, disturbances could also have a negative impact on species distributions. Disturbances can accelerate unwanted vegetation changes (Loehle, 1998, 2014), triggering shifts from one relatively stable ecological state to another (Dantas, Hirota, Oliveira, & Pausas, 2016). Also, uncontrolled disturbances could promote the establishment and dominance of undesirable vegetation (Douterlungne, Thomas, & Levy-Tacher, 2013; Ssali, Moe, & Sheil, 2019) or non-native species (Jauni, Gripenberg, & Ramula, 2015; Lembrechts et al., 2016). Management of disturbance process, as far as that is possible, through modification of the type of disturbance, intensities, scales, frequencies and timing offers many variables that can be adjusted to favour some species rather than others and, unless already optimal, can be modified to achieve conservation goals (Sheil 2016).

Our results support the increasing evidences of other mechanisms than species tolerance to the environment, such as biotic interactions (Neuschulz, Merges, Bollmann, Gugerli, & Böhning-Gaese, 2018) and disturbance (Muñoz Mazón et al., 2019; Sheil, 2016) , shape the distribution of tree species. Here we extend these observations to the tropics, particularly to the high elevation shrubs and trees.

Through reductions in competitive exclusion, disturbance could both facilitate shifts in distributions and grant species persistence within their current ranges. The role of disturbance and early stages of succession should be considered when trying to understand tropical tree species range shifts and future distributions in a warmer world. Although the current study is small, all ten species belong to genera characteristic of neotropical montane forests and high elevation ecosystems. Furthermore, our results have implications for the conservation of the studied species as more than half occur almost exclusively in the cloud forest and paramos of Costa Rica and include two taxa of conservation concern (Table 1).

Conclusions:

Understanding the relationships and mechanisms, that determine species elevation ranges is key to develop strategies for their conservation in the face of climate change. Exploring the persistence and viability of rear edge populations is essential to advance our ability to better plan for the impacts of environmental change on species range dynamics. Here we show that distance sampling can clarify the relationships and help reveal the mechanisms that shape the ranges of tree species. By this method we showed that disturbance allows some species to establish and be observed at lower elevations than within less disturbed old-growth mature forest. Our results also have implications for conservation of tropical tree species ranges, as they could be managed through controlled disturbance events. Further research should explore how canopy opening can improve species persistence in a warmer climate through manipulative studies, such as transplant experiments.

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Supplementary Information:

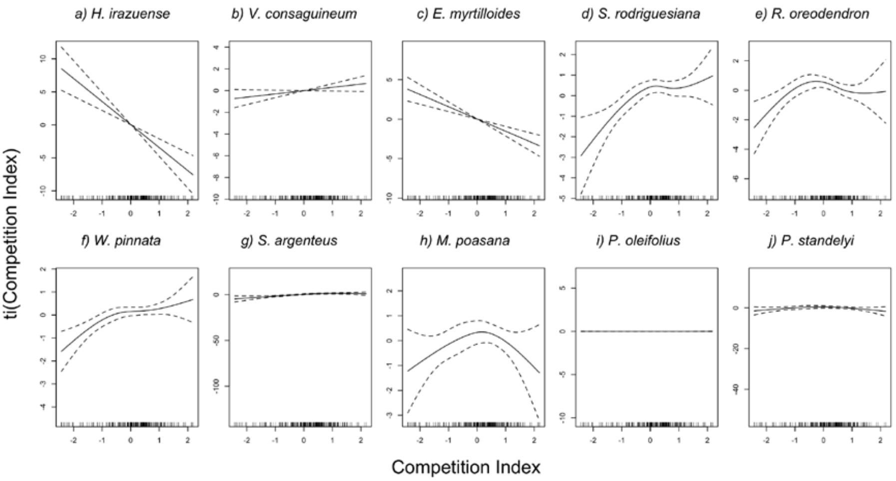

Figure S1: Smooth function for competition index per species

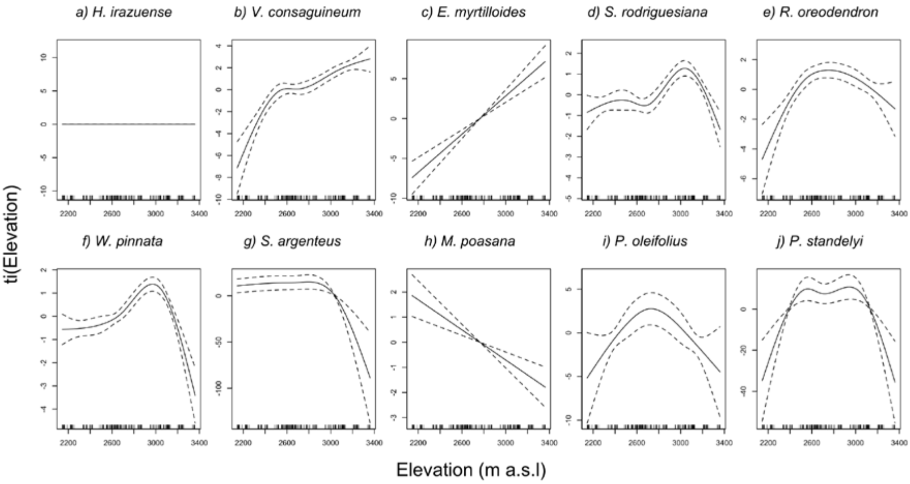

Figure S2: Smooth functions for elevation per species.

Paper IV

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

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ABSTRACT:

1. In theory, canopy cover 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.

2. We transplanted 1360 seedlings of eight woody species (trees *Trichilia habanensis*, *Persea caerulea*, *Cedrela tonduzii*, *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 vs open area).

3. We found a clear effect of open versus forest conditions on survival across the elevation gradient for six species. Species planted into open areas survived 100 -1000 m below (~ 0.5 - 5 C^{o} warmer), and in one case 300 meters above (~ 1.8 C^{o} 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 – 1160 meters (~ 1 - 6 C ^{o} colder) compared to their observed range. At lower elevations, severe insect herbivory occurred on some species (*H. irazuense* and *Q. costaricensis*) likely influencing lower range limits.

4. Synthesis: 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. This suggests that many species may expand their elevation ranges under warmer climates if there are open areas. A contrasting pattern occurs above the frost line where intact forest canopy facilitates survival. 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

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 vs 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 1957, Budowski 1965), neither the concepts nor implications have been much explored (for exceptions see Huston & Smith, 1987; Keddy & MacLellan, 1990; Malanson, 1997).

Building on previous syntheses (Sheil 2016) and pilot studies (Muñoz Mazón et al. 2019), these ideas on the role of forest gaps and clearings complement other studies that examined how climate and biotic interactions shape species distributions (e.g. Defossez et al. 2016; Ettinger and HileRisLambers 2017, Louthan et al 2015, Olsen et al. 2016, Putnam and Reich, 2017). While it is well known that species tolerance to drought, low temperatures or frost can influence range limits (Anderegg and HilleRisLambers 2015, Ettinger et al. 2011, 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 their normal elevation range. 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 & 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 & Callaway, 1994; He & 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 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 hypotheses (H0-H3): under the null hypothesis we expect similar range limits in forest vs. open area (H0, Figure 1a) Under this hypothesis, the physiological tolerance of species to different climatological conditions is what explains their elevation ranges. 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, Figure 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, Figure 1c). Finally, in our combined hypothesis, both competition and facilitation influence range limits depending on biotic and abiotic conditions along the elevation gradient (Bertness & Callaway, 1994; Louthan et al. 2015; Olsen et al. 2016). 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 & Horn, 2005). This pattern could be reversed if facilitation were to dominate only at the lowest elevations (H3, Figure 1d). This could happen if lower elevations are dryer than mid and high elevations, for example, and forest cover improves water availability.

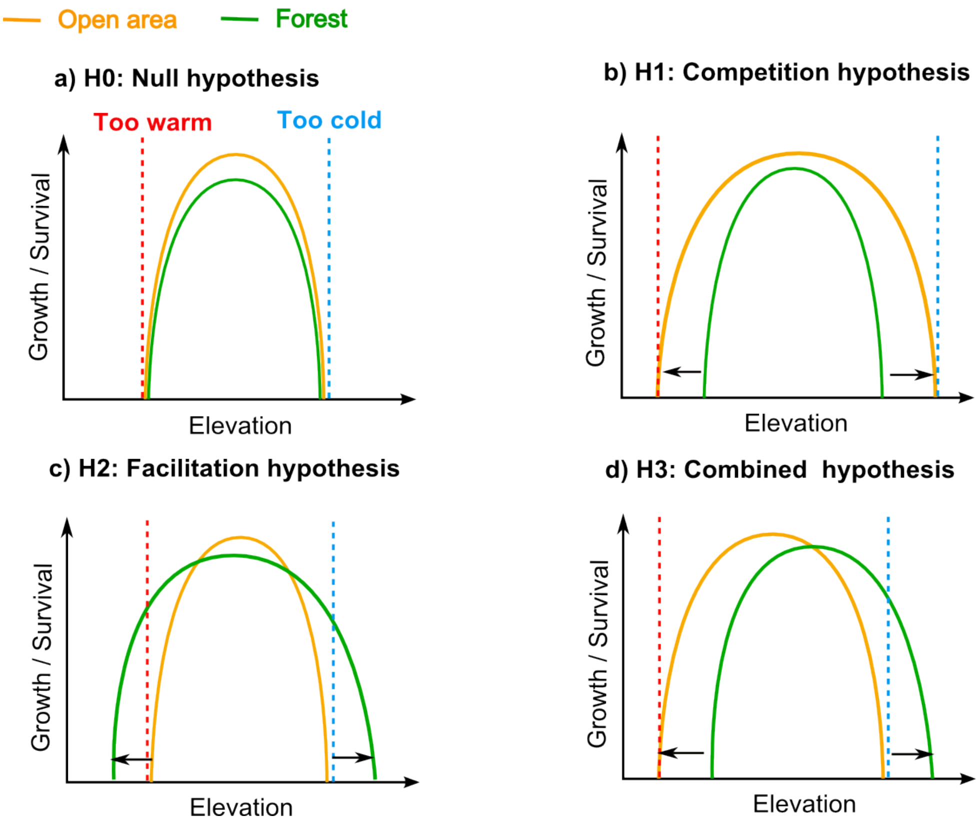

Figure 1. Tree seedling survival and growth along an elevation gradient inside the forest (green) and in open areas (orange) under four alternative hypotheses. The red dotted line (too warm) represents the potential highest temperature a given species can tolerate. The blue dotted line (too cold) represents 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).

MATERIALS 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 meters 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. Jørg*.* , *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* (see below) seeds were collected directly from the mother trees in 2016. 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.

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

Species	Family	Elevation range m a.s.l *	Maximum tree height (meters)**
Persea caerulea (Ruiz & Pav.) Mez	Lauraceae	700-1900	6-20
Cedrela tonduzii C.DC.	Meliaceae	990 -2025	40
Trichillia havanensis Jacq.	Meliaceae	400-2600	10-15
Cornus disciflora Sessé & Moc. ex DC.	Cornaceae	550-3200	30
Hypericum irazuense Kuntze ex N.Robson	Hypericaceae	2900-3560	1-3
Quercus costaricensis Liebm.	Fagaceae	2388-3600	15-45
Quercus bumelioides Liebm.	Fagaceae	1250 - 2895	15-45
Quercus salicifolia Nee	Fagaceae	650-2560	10-25

* 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 issues. Data source: https://doi.org/10.15468/dl.7ywanm

**References: Zamora-Villalobos, N. A., Jiménez-Madrigal, Q., Poveda-Alvarez, L. J., & Aragón-Quesada, C., (2017) and Tropicos data base (www.tropicos.org)

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; at elevations 1670, 3200, 3400 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 1x1 meter, fenced up to 150 cm height and contained one transplanted individual of each species. 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, 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 meters). 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 minutes. 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 ºC, 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 (> 30000 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 https://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" vs "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 O and F) 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 x 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 version 4.0.0

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.

RESULTS

Climate

Among all nineteen selected plots with functioning data loggers, mean temperature decreased with elevation (Supporting information, Figure S1). 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, Figures S2). Temperatures below 0 ºC occur occasionally at 2900 m a.s.l. in the open treatment and above 3000 m a.s.l. in the forest (Figure 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 Figure S3). Available light increases with elevation in both open and forest sites (Figure 2). All measures vary seasonally with some differences among sites (Supporting Information, Figure S4).

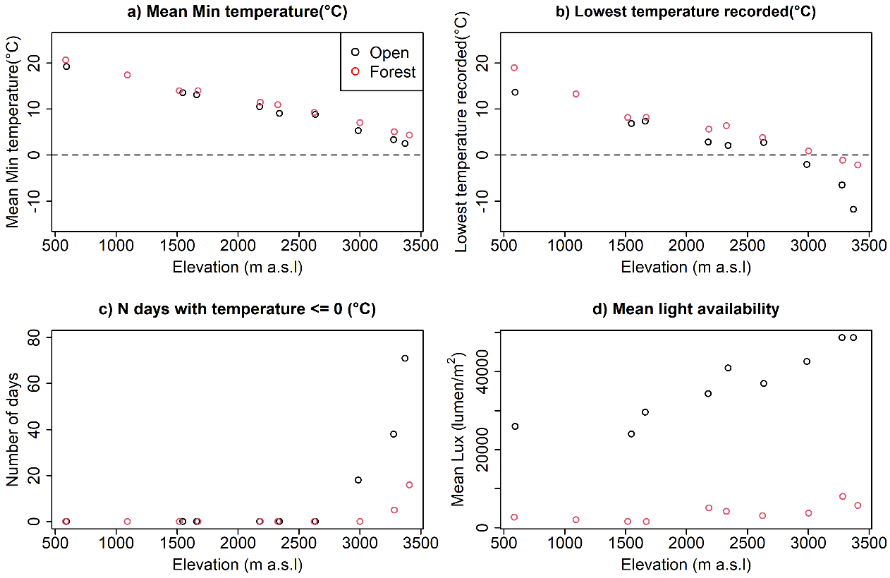

Figure 2. Changes in a) mean minimum (daily minimum averaged for the year), b) lowest temperature recorded during the experiment, c) number of days with temperatures equal or below 0 °C. d) Changes in the light environment along the elevation gradient

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 asl we often observed leaf removal by ants (likely *Atta* spp. and/or *Acromirmex* spp.) particularly on *H. irazuense* and *Q. costarricensis*. For seven species (not *Q. costaricensis*) survival between open areas vs intact forest (Figure 3) are sufficiently distinct to require separate models as indicated by lower AICs (Model 3 versus Model 2; Figure 3, see Table S1 in the 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 (Figure 3a and 3b). Four species (*H. irazuensis*, *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 (Figure 3h, 3f, 3e, 3d). 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.

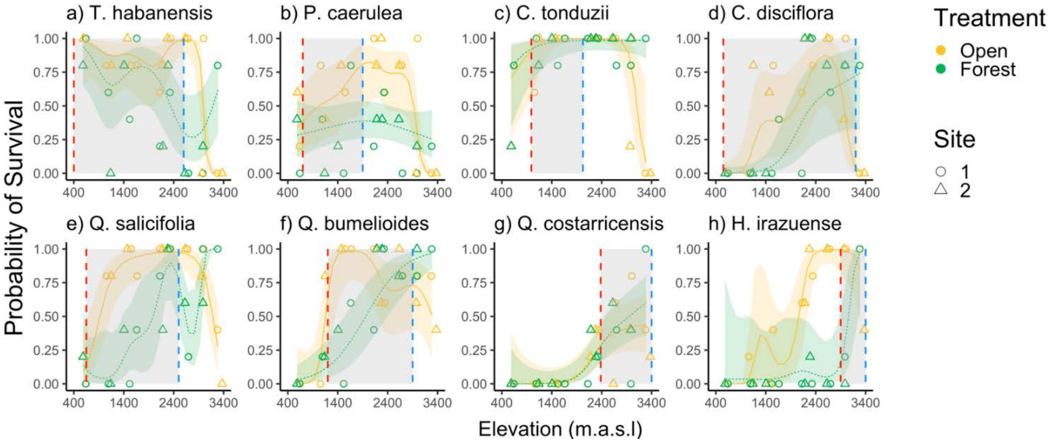

Figure 3. Survival versus elevation for eight species in open (yellow line) and inside (green line) forest. Points represent probability of survival at each studied site. Lines represent predictions form the selected models. The grey shaded area represents the observed elevation range of the species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

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* (Table S3, 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 (Table S3 and S4 in the 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 (Figure 4a, 4b, 4g, 4h, 4i, 4j, 4o, 4p). For *C. tonduzii, C. disciflora, Q. salicifolia ,* and *Q. bumelioides*, growth follows a unimodal rise-and-fall shape over the elevation gradient (Figure 4c,d,e,f,k,l,m,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 (Table S2, Supporting Information). All species included some negative growth values for both diameter and height in some locations, but we noted no clear patterns.

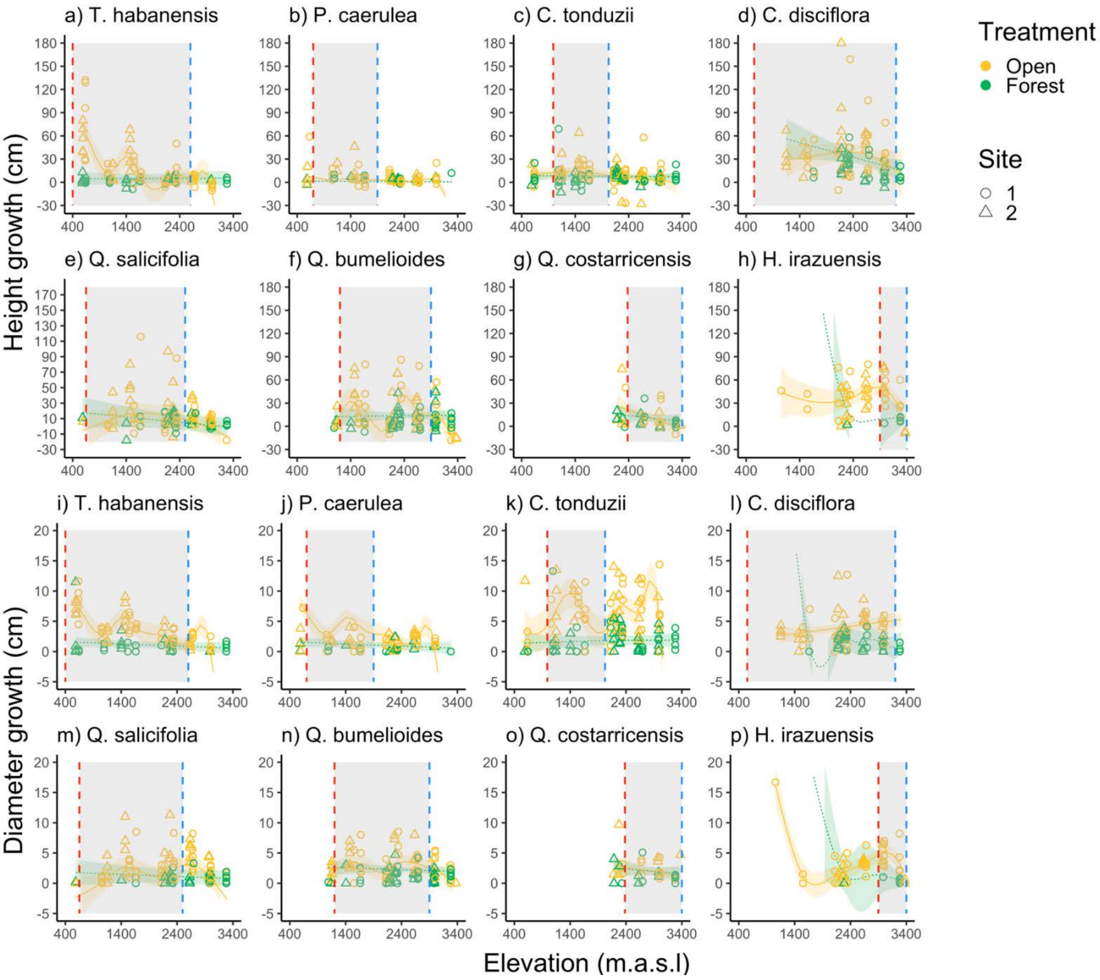

Figure 4. Height (a-h) and diameter (g-p) growth versus elevation for eight species in open (orange lines) and inside forest (green line). Points represent the growth of one surviving individual. Lines represent predictions from the selected models. The grey shaded area represents the observed elevation 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.

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. costarricensis*). 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 also greater in the open treatment for the three species, although statistically significant only for *C. tonduzii* (Table S4, Supporting Information).

DISCUSSION

For all eight species investigated, the transplanted seedlings survived and grew well outside the elevation ranges where 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 (Figure 1d) supporting H3 (combined hypothesis). For two species (Figure 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 ^{o}C warmer than its current range. Open areas also permitted one species to survive 300 meters above its current observed upper range (at an inferred temperature around 1.5 ^{o}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 to 1160 meters (i.e. from 2 to nearly 6 ^{o}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 meters 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 meters. These results show that canopy opening often 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 & Sandve, 2013; Korner et al. 2016; Segovia et al., 2020), as many species fail to establish where frost occurs (Bader et al. 2007; Defossez et al. 2016; Sakai & Larcher, 2012; Wesche et al., 2008). The lower frequency and severity of frost in closed forest versus open locations (Figure 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 upper-range limit, as seen in the Andes (Rehm & 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 (Cáceres et al., 2019; Ettinger & HilleRisLambers, 2017; Olsen et al., 2016). 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 & 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. irazuensis,* 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. irazuensis* 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 see Figure S5, Supporting Information). Previous observations in the region suggested that survival of *Q. costaricenses* 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 trade-offs 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 & 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 & Burslem, 2015; Ssali, Moe & Sheil, 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 don’t 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. 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. 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. 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 (see Corlett & 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).

CONCLUSION:

We have demonstrated how open sites and forest sites exert distinct influences on the survival, growth and resulting elevation range of planted tree seedlings. Our experimental data reveal that the seedlings of multiple species can survive and grow at warmer temperatures (lower elevations) in open areas outside closed forest and can withstand colder temperatures (higher elevations) when forest and understorey vegetation is present. The role of forest gaps, clearings and disturbance processes, in influencing species distributions remains a rich subject for future investigation.

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Authors contributions: DS conceived the study with contributions of KK and MM. MM designed the experiment and collected data with advice from DS and KK. MM leaded the analyses of the data and the writing of the manuscript with contributions from DS and KK. All authors agree on the content of the manuscript.

Data accessibility: We intend to archive the data in the DataverseNO public repository.

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SUPPORTING INFORMATION:

Table S1. Model selection for the survival of the selected species across the elevation gradient at the two treatments.

Species	Model	AIC	Δ AIC	Dev. Expl. (%)
	1	125.62	65.21	37.6
H	2	65.07	4.66	86.5
	3	**60.41**	**0**	**86.5**
	1	**69.63**	**0**	**62.7**
Qc	2	71.32	1.69	64.2
	3	72.02	2.39	63.7
	1	103.2	25.69	53.6
Qb	2	77.54	0.03	78
	3	**77.51**	**0**	**75.7**
	1	134.5	55.01	31.2
Qs	**2**	**79.49**	**0**	**80.4**
	3	98.88	19.39	59
	1	121.2	34.41	47.6
Cd	2	89.71	2.92	73
	3	**86.79**	**0**	**73.2**
	1	89.14	25.72	44
Ct	**2**	63.71	0.29	73
	3	**63.42**	**0**	**73.2**
	1	131.93	13.18	21.4
Pc	**2**	**118.75**	**0**	**45.2**
	3	122.81	4.06	37.1
	1	148.53	37.29	17.5
Th	**2**	**112.04**	**0.8**	**62.8**
	3	111.24	0	58.3

Table S2. Model selection for the height growth of the selected species across the elevation gradient at the two treatments.

Species	Model	AIC	Δ AIC	Dev. Expl. (%)
H	1	512.25	1.35	28.8
	2	510.84	0	42.9
	3	**510.9**	**0.06**	**43**
Qc	1	304.5	0	11.7
	2	306.05	1.55	14.3
	3	**306.05**	**1.55**	**14.3**
Qb	1	965.62	13.72	2.9
	2	952.02	0.12	25.5
	3	**951.9**	**0**	**25.6**
Qs	1	927.2	0.78	12.5
	2	926.42	0	16
	3	**926.42**	**0**	**16**
Cd	1	851.51	0.34	6.24
	2	851.17	0	9.73
	3	**851.18**	**0.01**	**9.78**
Ct	1	1068.17	0	2.93
	2	1068.46	0.29	7.11
	3	**1068.46**	0.29	**7.14**
Pc	1	530.82	2.36	11.4
	2	528.46	0	17.3
	3	**528.46**	**0**	**17.3**
Th	1	919.53	72.39	22
	2	847.14	0	66.5
	3	**847.29**	**0.15**	**66.8**

Table S3. Model selection for the height growth of the selected species across the elevation gradient at the two treatments.

Species	Model	AIC	Δ AIC	Dev. Expl. (%)
H	1	239.85		63.8
	2	230.21		73.6
	3	**229.8**		**73.9**
Qc	**1**	**154.98**		**4.58**
	2	156.83		4.98
	3	156.83		4.98
Qb	1	473.33		5.74
	2	464.36		20
	3	**463.96**		**20.5**
Qs	1	481		16.3
	2	**469.65**		**27.6**
	3	469.63		27.6
Cd	1	415.5		0.376
	2	392.1		34.4
	3	**392.62**		**33.8**
Ct	1	781.98		5.28
	2	709.93		48.4
	3	**709.94**		**48.5**
Pc	**1**	**245.24**		**3.9**
	2	246.35		5.84
	3	246.36		5.87
Th	1	471.13		20
	2	398.92		66.8
	3	**398.87**		**66.8**

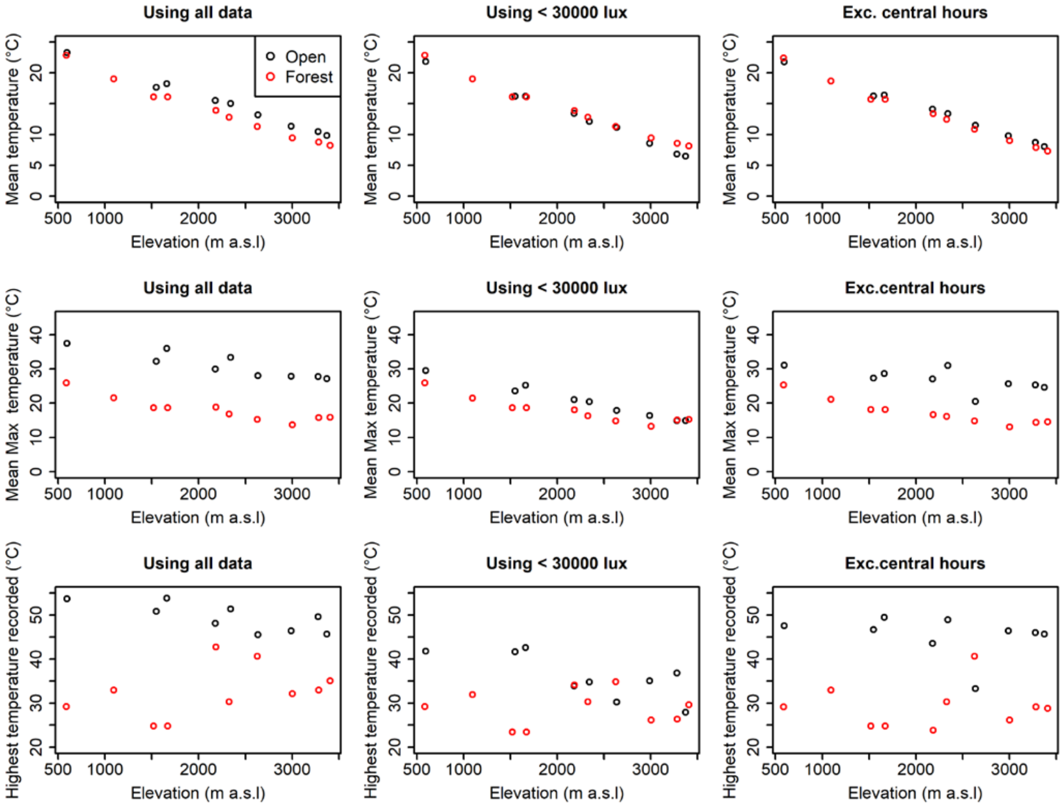

Figure S1. Mean, mean maximum and highest temperatures recorded in the study. The two different methods used to filter the bias caused by the overheating of the logger are plotted ("Using < 30000 lux" and "Exc. Central hours") for its comparison with the raw data.

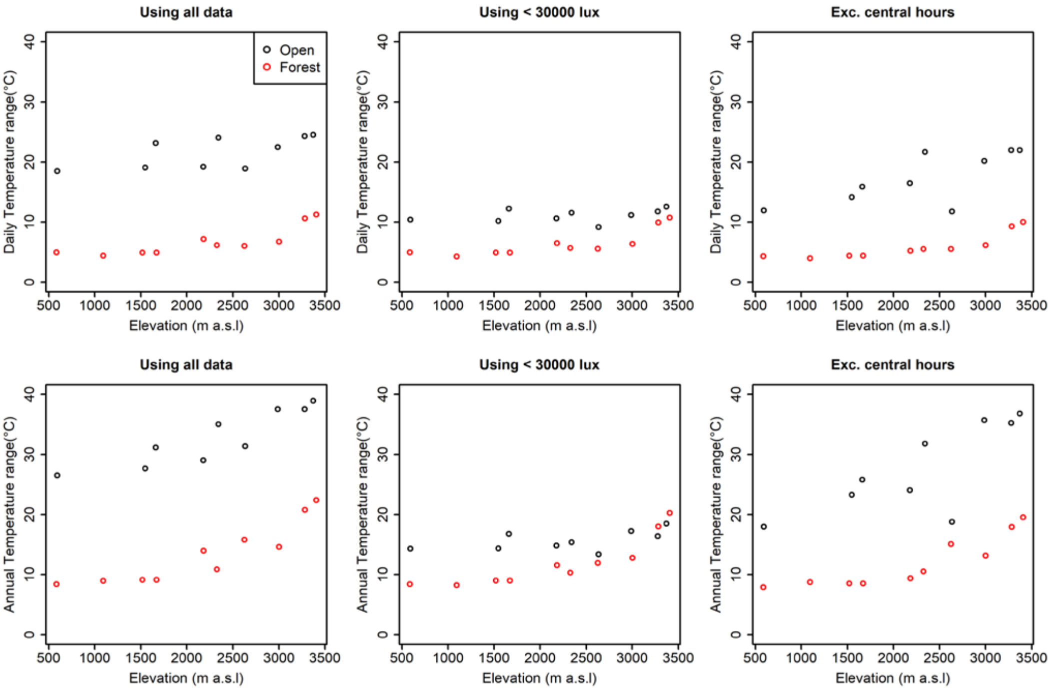

Figure S2. Mean daily and annual temperature ranges along the elevation gradient in both forest and open areas. The two different methods used to filter the bias caused by the overheating of the logger are plotted (“Using < 30000 lux” and “Exc. Central hours”) for its comparison with the raw data.

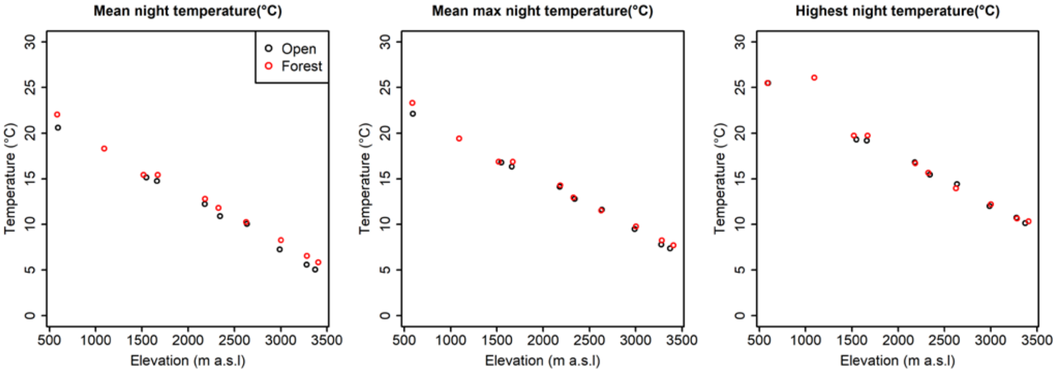

Figure S3. Mean, mean maximum and highest temperature recorded during the night along the gradient, for open and forest areas.

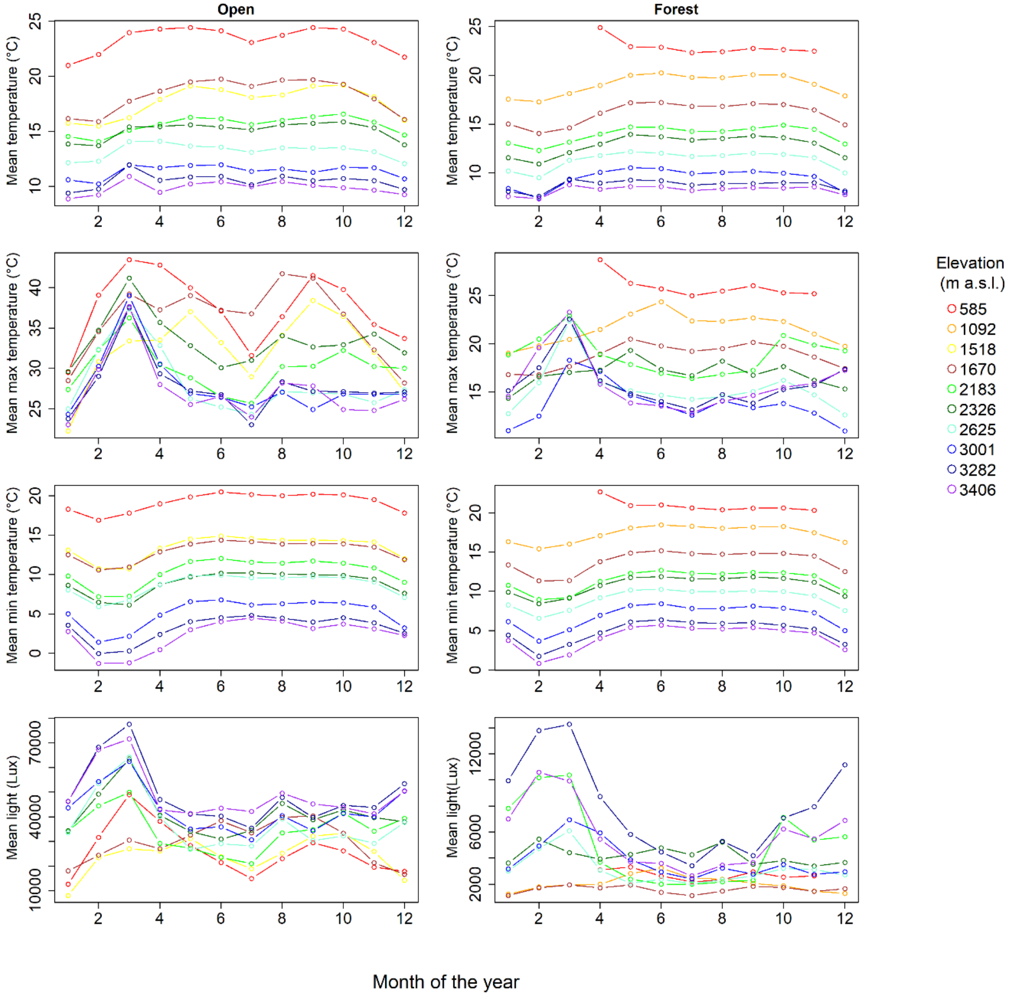

Figure S4. Seasonal variation of temperature and light across the studied elevation gradient inside and outside of the forest. Note that the values of the mean and mean maximum are likely overestimated in the open treatment due to the un

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