Landsc Ecol (2023) 38:2005–2018
https://doi.org/10.1007/s10980-023-01670-6

RESEARCH ARTICLE

# Exploring how disturbance and light availability shape the elevation ranges of multiple mountain tree and shrub species in the tropics

**Miguel Muñoz Mazon · Kari Klanderud ·**
**Douglas Sheil**

Received: 1 June 2022 / Accepted: 24 April 2023 / Published online: 8 May 2023

## Abstract

*Context* Tropical mountains are hotspots of plant diversity, with a remarkable density of narrow ranged and endemic species. To develop effective in situ strategies for the conservation of species under changing climatic conditions we need to understand the mechanisms that shape their distributions.

*Objectives* We explore how disturbance shapes the elevation ranges of two shrubs and eight tree species (*Hypericum irazuense*, *Vacciunium consanguineum*, *Escallonia myrtilloides*, *Schefflera rodriguesiana*, *Weinmannia pinnata*, *Rhamnus* (Frangula) *oreodendron*, *Styrax argenteus*, *Podocarpus oleifolius*, *Prumnopitys standleyi*, *Magnolia poasana*) characteristic of the paramos and cloud forest of the Talamanca Mountains, Costa Rica.

*Methods* We used distance sampling transects along a 1400 m elevation range and "density surface models" to explore how the distribution of the selected species responds to changes in basal area and light availability after disturbance, across their elevation range.

*Results* The legacies of disturbance on forest structure and light availability clearly shaped the elevation ranges of seven species. *H. irazuense* had a clear light demanding strategy, only occurring at well-lit sites throughout their range. *V. consanguineum*, *E. myrtilloides* and *S. rodriguesiana* shifted from a shade tolerant to strictly light demanding distribution between their upper and lower range limit, showing a context dependent role of light availability along their elevation range. *R. oreodendron*, *S. argenteus* and *W. pinnata* occurred mainly under shaded and crowded conditions. The density of *M. poasana*, *P. oleifolius* and *P. standleyi* species was related only to elevation.

*Conclusions* Our study illustrates how light availability and disturbance are key to understand the elevation range dynamics of high elevation tropical trees and shrubs. Canopy openings after disturbances provide habitat for paramo and high elevation woody plant species to persist under warmer conditions. These findings can inform conservation efforts aimed at preserving high elevation plants species in the future.

---

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s10980-023-01670-6.

---

M. Muñoz Mazon (✉)
Ecosystem Dynamics and Forest Management Group, School of Life Sciences, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
e-mail: mmunozmazon@gmail.com

K. Klanderud
Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences (NMBU), Ås, Norway

D. Sheil
Forest Ecology and Forest Management Group, Wageningen University & Research, PO Box 47, 6700 AA Wageningen, The Netherlands

**Keywords** Costa Rica · Light availability · Distance sampling · Elevation ranges · Disturbance

## Introduction

By shaping forest structure and light availability, disturbance can create novel opportunities for tree and shrub species to stablish, affecting their abundance and distribution along environmental gradients. Any reduction in competition for light or other biotic interactions after disturbance may modify the upper and lower elevation and temperature ranges of plant species (Fig. 1) (Sheil 2016; Muñoz Mazón et al. 2019), leaving long lasting legacies in the community (Turner 2010; Cuddington 2011). Although ecologists have long noted how competition and disturbance may influence the presence and abundance of tree species along environmental gradients (see Van Steenis 1958; Budowski 1965; Huston and Smith 1987; Keddy and MacLellan 1990; Malanson 1997) these insights appear neglected in recent studies concerning plant distributions (e.g. Corlett & Westcott 2013), particularly in the tropics (Feeley et al. 2020). Nonetheless, theory and observations in mountain ecosystems indicate, that release from assumed competition via disturbance improves plants performance at their lower range limit (Chardon et al. 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 et al. 2016; Wang et al. 2019).

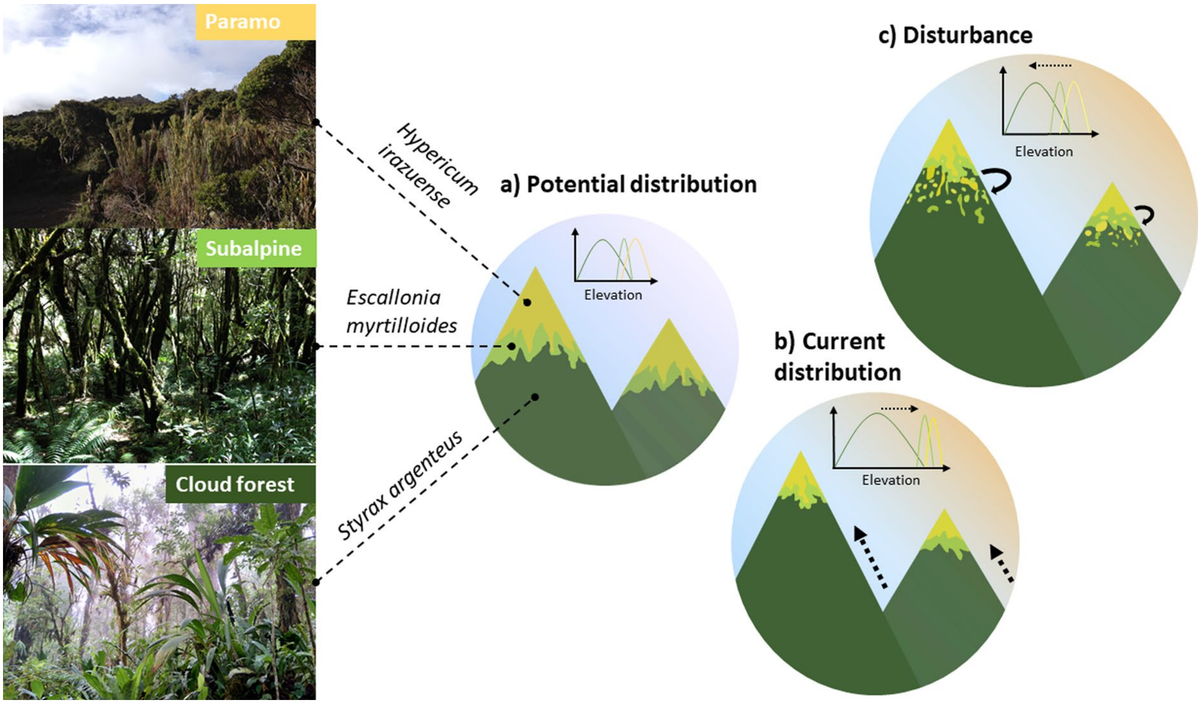

**Fig. 1** Schematic and theoretical representation of how disturbance may influence the elevation ranges of three woody plant species (*H. irazuense*, *E. myrtillodes* and *S. argenteus*) characteristic of the paramo, subalpine and cloud forest life zones in Costa Rica respectively. *H. irazuense* has the highest distribution and is a characteristic paramo species. *E. myrtilloides* occurs in the subalpine zone between the paramo and the cloud forest. *S. argenteus* is a characteristic sub canopy tree species from the cloud forest. **a** In the absence of competitors, these species may be able to follow their physiological tolerances and persist at wide range of elevations following their fundamental niche. The curves of the diagram represent their hypothetical densities across the elevation gradient. **b** Competition for light and other resources may exclude these tree species from the most benign sites, in this case lower elevations, with rage shifts and range reductions. **c** Disturbances can relax any constrain imposed by competition and allow species to persist at a wider range of environmental conditions than otherwise, including lower and warmer elevations

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 (Fig. 1).

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 (Wilson and Keddy 1986; Lusk et al. 2013). For example, along a temperature gradient a species' tolerance of cold conditions may reduce competitive abilities under warmer conditions (Koehler et al. 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 (Fig. 1b). 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 (Uriarte et al. 2012; Bin et al. 2019). Disturbance, by freeing up space and resources such as light, a reduction in the superior competitors gives these species an opportunity to establish populations before competitively superior species can exclude them, potentially expanding their ranges (Fig. 1c).

On the other hand, biotic interactions can be beneficial facilitating the establishment, survival and growth of other species extending the apparent realised niche beyond the fundamental niche (Bertness and Callaway 1994; He and Bertness 2014). Furthermore, it is possible that some species, for example long-lived shade tolerant taxa, are sensitive to recurrent disturbance (Sousa 1984; Shea et al. 2004). For these species and at elevations where positive biotic interactions are necessary for establishment, disturbance may remove these favourable effects and thus reduce species ranges.

The extent to which disturbance affects species distributions depends on the relative influence of biotic and abiotic factors setting their range limits. The significance of these factors can vary with elevation, as seen in trees along elevation gradients (Lyu and Alexander 2022). Generally, biotic interactions play a more important role in setting the range limits of species at lower, warmer elevations, whereas abiotic factors are more significant at higher, colder elevations (Paquette and Hargreaves 2021). Recent evidence in a tropical elevation gradient support the idea that competition for light plays a key role in setting the lower range limits of multiple tropical tree species (Muñoz Mazón et al. 2022). However, most of the evidence comes from manipulative experiments which often focus on the regeneration phase and frequently last for only a couple of years. As a result, it is not yet clear how long-term legacies after disturbance affects the distribution of adult trees in tropical mountains.

The aim of this study is to explore 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 and human interventions on species persistence and distributions. We predict that if species are structured according to a competitive hierarchy in which competition displaces some species towards higher elevations (Fig. 1b), release of competition after disturbance via reductions in forest basal area and increase of light availability, will allow species, insofar as dispersal permits, to establish and thus be observed at lower elevations than within old-growth forest (Fig. 1c). Here we use distance sampling protocol (Buckland et al. 2015) to quantify the presence and abundance of eight trees and two shrub species along an elevation gradient across different levels of recovery after 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 and 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 forest patches with different basal areas and light availability at each elevation, we examine how past disturbance modifies their elevation ranges.

## Methods

### Study area

The study area is located along the Eastern Atlantic slope of the Talamanca Mountains in Costa Rica, from 2000 m a.s.l. in La Esperanza de Tapantí to the hills of Cerro Asunción at 3400 m a.s.l (meters above sea level). Most of the transects where located within the Cerro de la Muerte and Tapantí National Park and the forest reserve Río Macho. 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.; 2022), average annual temperature decreases from 14 °C at the lowest sampled elevation (2000 m a.s.l.) to 9 °C at 3400 m a.s.l. Precipitation remains constant along the elevation gradient, ranging between 2500 and 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 (Kappelle et al. 1995). 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 et al. 1995). Forest structure and light availability remain more or less constant through the studied elevation gradient until the treeline around 3000 m.a.s.l where there is a shift towards a shrubbier and more open ecosystem, the paramo (Muñoz Mazón et al. 2020; Muñoz Mazón et al. 2022). This confirms that, within the studied forest ecosystem, variations in basal area and light availability may be directly driven by past disturbances and not by changes in the environment or forest composition across the elevation gradient. Other studies carried out in the same region also suggest relatively constant stand dynamics (mortality and recruitment) in these forest above 2000 m.a.s.l (Hernandez-Gordillo et al. 2021). The paramo ecosystem is dominated by regional endemics such as the bamboo *Chusquea subtessellata* and the shrubs *Hypericum irazuense* and *Vaccinium consanguineum* (Kappelle and Horn 2005). Between the paramo and the cloud forest, it is possible to find another life zone, sometimes referred as subalpine forest (Kappelle and Horn 2005). This forest shares species characteristic from the paramo, such as *Hypericum irazuense* and *Vaccinium consanguineum*, with cloud forest species such as *Schefflera rodriguesiana* and some exclusive of this formation such as *Camarostaphylus arbutoides* and *Escallonia myrtilloides*.

These ecosystems are exposed to different disturbance types. In the studied forest, treefalls are the most common natural disturbance. These occur mainly during the rainy season in October and November. Previous studies in other montane cloud forest of Costa Rica estimate a frequency between 4 and 5 gaps per hectare per year, mainly below 15 $m^2$ (Lawton and Putz 1988). The basal area residence time in this forest is relatively higher than lowland tropical forest (Hernandez-Gordillo et al. 2021), which has been linked to both a greater resistance and lower exposure to disturbance (Muñoz Mazon et al. 2020). Fire is the dominant disturbance agent in the Costa Rican paramos. There is evidence of natural and human fires in this ecosystem for thousands of years. These fires often consume all the biomass present. Although the long-term frequency of fires is not very well understood, in the last century, the recurrence interval has been estimated between 6 and 23 years. The extent of these fires is often small ($<1$ $km^2$), however, extreme dry years have led to a couple of fires larger than 10 $km^2$ (Horn 1991; Horn and Sanford 1992). 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. Since then, the extraction of wood and production of charcoal has been banned within the national park and thus, disturbances are mainly from natural origins.

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** Life form, conservation status and distribution of the studied species

| Name, authority | Lifeform | IUCN conservation status | Distribution |
|---|---|---|---|
| *Hypericum irazuense* Kuntze ex N. Robson | Shrub to 3m[a] | Not assessed | Endemic (CR PN) |
| *Vacciunium consanguineum* Klotzsch | Shrub—small tree to 2.3 (10) m[b] | Not assessed | Endemic (CR PN) |
| *Escallonia myrtilloides* L. | Shrub—medium sized tree to 20 m[c] | Not assessed | Broad |
| *Schefflera rodriguesiana* Frodin ex M.J. Cannon & Cannon | Small—medium size tree to 20 m[d] | Least concern | Endemic (CR and Panama) |
| *Weinmannia pinnata* L. | Medium tree to 15 m[e] | Least concern | Broad |
| *Rhamnus (Frangula) oreodendron* L.O. Williams | Small tree from 2 to 10 m[f] | Least concern | Endemic (CR and Panama) |
| *Styrax argenteus* C. Presl | Small-medium tree from 6 to 16 mg | Least concern | Broad |
| *Podocarpus oleifolius* D. Don ex Lamb | Tree to 25 m[h] | Least concern | Broad |
| *Prumnopitys standleyi* (J. Buchholz & N.E. Gray) de Laub | Tree to 35 m[h] | Endangered | Endemic (CR and Panama) |
| *Magnolia poasana* (Pittier) Dandy | Tree to 30 m[i] | Near threatened | Endemic (CR and Panama) |

[a] Hammel (2007)

[b] Luteyn and Wilbur (2010)

[c] Morales (2010a)

[d] Morales, Cannon and Cannon

[e] Morales (2010b)

[f] Davidse et al. (2015)

[g] Zamora (2015)

[h] Merello (2003)

[i] Gonzalez (2007)

### 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 et al. 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 m each across the elevation gradient (Table S1) from October to November 2016. Every transect was located perpendicular to the slope and at approximately a single elevation. Every transect covered forest with varying basal area and light availability. To characterize the relationship between the observed changes in forest structure and the density of the selected species we measured for every individual observation (trees and saplings) the diameter at breast height (1.3 m above the ground), tree height, crown illumination index (CII) 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 m were calculated from clinometer measurements. The crown illumination index is a rapid visual method to estimate the exposure to light of a tree (Dawkins 1956). Assessing crown exposure directly has been shown to be a plausible estimate of competition for light and shade tolerance in tropical forest. It is known that competition for light between trees is often asymmetric and that plants diminish each other's light through placing their canopies above each other (Schwinning and Weiner 1998). The relascope method allowed us to estimate the basal area around every observation (Philip 1994). 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 our case, a gauge of (18 mm attached to a string of 580 mm to obtain a multiplication factor of 2,4. The number of stems counted multiplied by the factor represents an estimate of basal area. We summarized the relationship of basal area and CII with a PCA analysis (See Fig. S1 in the Supplementary materials).

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

### Analyses

To examine the relationship of light availability and basal area on the estimated density of the selected tree species along the elevation gradient we used Density Surface Models (DSM) (Miller et al. 2013a, b). 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 to relate the density estimations to the different environmental variables measured (Wood 2006).

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 m based on visual inspection of the distance histogram (Fig. 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. 2013a, b). We explored the density of each species along the elevation gradient in relation to basal area and CII separately. Also, to test their combined effect we used the resulting main axis from the PCA analyses described above. We tested the interactive effect of basal area, CII and the PCA 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 (Wood 2006).

**Table 2** Observed and estimated number of individuals per species in the 11-ha analysed with a truncation distance of 10 m

| 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 |

## 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.

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 (Fig. 2a) and a later check of the goodness of fit of the selected

**Table 3** Detection models explored in this study

| Model | Function | Formula | ΔAIC |
|---|---|---|---|
| 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 | 1.055.177 |
| 11 | Half-normal | BA | 1.056.589 |

*D.b.h* diameter at breast height, *BA* Basal area

detection model, we used a truncation distance of 10 m (Fig. 2b). After the truncation, the sampled area had 11 ha of forest and 4862 individuals (Table 2).

The first axis of the PCA explained 76% of the variation and correlated positively with basal area (0.7) and negatively with CII (− 0.7). Thus, it separates areas with a high density of neighbouring trees, where individuals are heavily 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 implied competition for light (hereafter called light-crowding 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 light-crowding 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 basal area (Figs. 3 and 4).

The other six species (*H.irazuense, S.argenteus, W. pinnata, M. poasana*, R. oreodendron and *P. standleyi*) respond in distinct ways to elevation and light-crowding index (Supplementary information, FigureS1). For example, *H.irazuensis* only occurs in low basal area and high light availability subtransects (Figs. 2a, 3a). Indeed, for this species neither the elevation smoother, nor the interaction between elevation was significant (Table 4, Supplementary information: Figs. S2 and S3). 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 basal area, though it also persist under the shade (Supplementary information 1; Fig. S2). We detected an effect of elevation, but not not the light-crowding index, on the density of *M. poasana, Podocarpus oleifolius* and *P. standleyi* (Supplementary information, Fig. S3). 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.

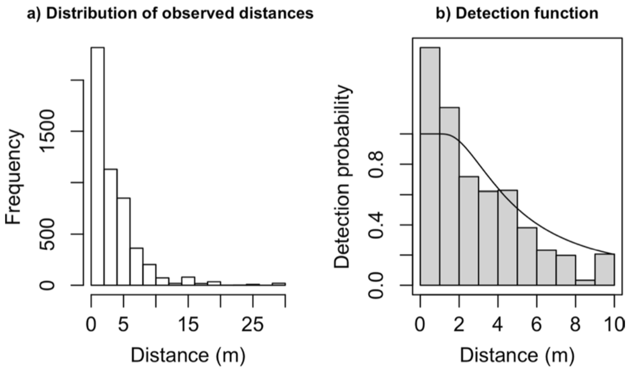

**Fig. 2** **a** Distribution of observed distances; **b** Fit of the selected detection function

**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(Light-crowding_ Index) | … | . | … | … | … | … | … | n.s | n.s | 0.09 |
| ti(Elevation, Light-crowding_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

## Discussion

Our results indicate how past disturbance, by reducing basal area and increasing light availability, influence the elevation ranges of several woody species. 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 elevation ranges.

One species occurred, almost exclusively, in locations with high light availability and low neighbour density. For *Hypericum*, sufficient light availability and low neighbour crowding, likely explain where it occurs (Table 3, Fig. 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. Indeed, the density of this species in the region seems to be exclusively influenced by light availability and not by elevation. *Hypericum irazuense* is notable among our species for being common at the highest elevations in the paramo, 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 endemic and narrow ranged tropical high elevation species will depend on canopy opening disturbances.

For three species (*V. consaguineum*, *E. myrtilloides*, *S. rodriguesiana*), 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 extending 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

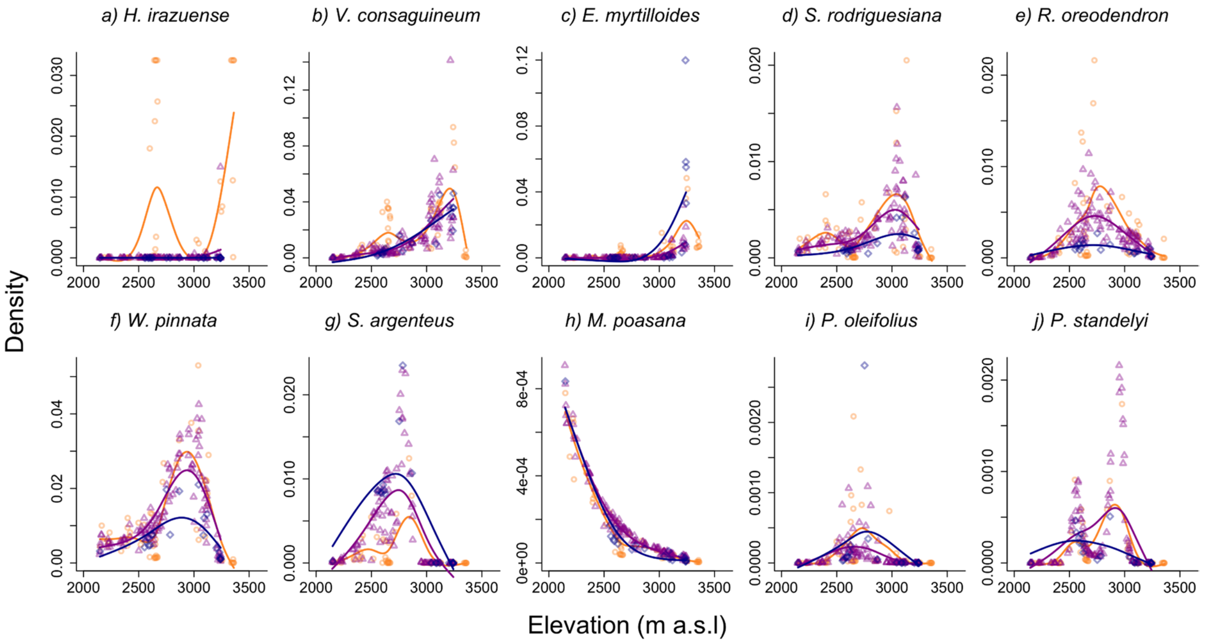

**Fig. 3** Density estimation from dsm model for the selected species. The different colours represent sub transect estimation under three different basal area categories. Yellow and circles are for the lower third (0–9 $m^2$/ha, purple triangles are for the middle third (9–17 $m^2$/ha) and blue diamonds are for basal area values (17–37 $m^2$/ha) in the higher third basal area category

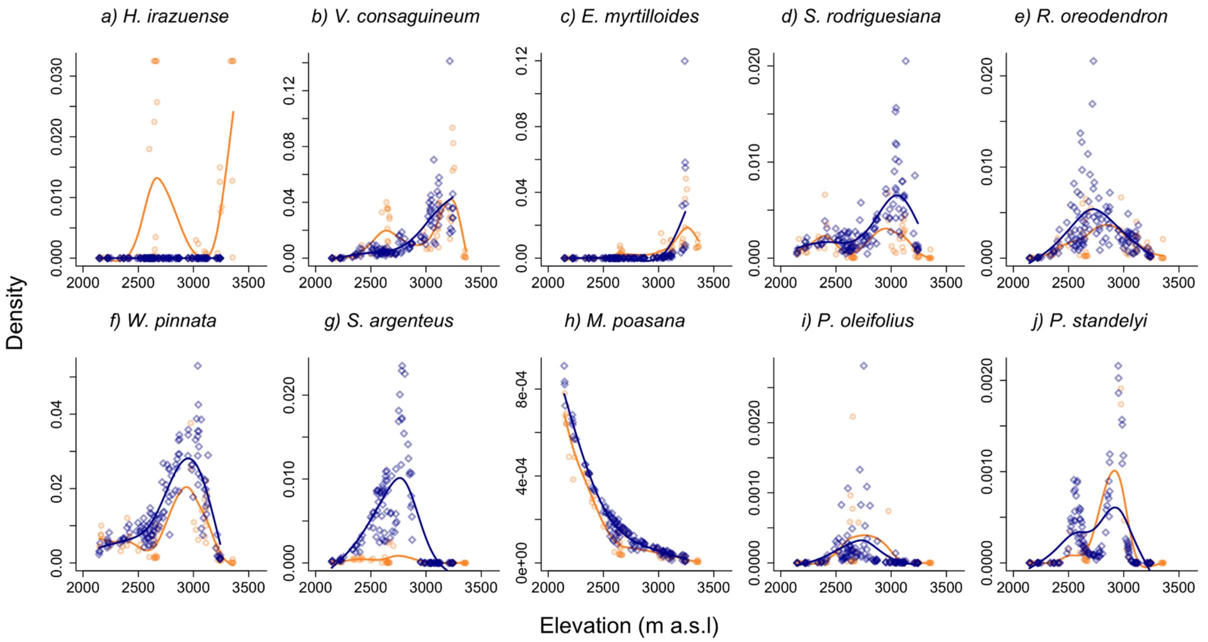

**Fig. 4** Density estimations from dsm models for the selected species. The different colours represent contrasting light and crowding levels categories. The yellow circles are for values in the low crowding and high light availability category. These represent densities of the selected species in sub transects within the lowest half of the light-crowding index. Blue diamond represents values in the high crowding and low light availability category

and benefitting from events that open up the forest canopy. Furthermore, all three 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 (Smith and Huston 1990; Shipley and Keddy 1994), 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 and 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. Three species 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 (*R. oreodendron*, *W. pinnata* and *S. argenteus)*. Interestingly, at least one of these species is also common in early successional forest (*W. pinnata*, Kappelle et al. 1995) and has been consider typically light demanding (Blaser and Camacho 1991). A potential onthogenic shift on the light requirements of the species, were canopy opening disturbances may be more beneficial during the regeneration phase, vanishing as the individuals get taller could explain the observed patterns. A previous study in the same landscape suggested an increased growth and survival of *W. pinnata* seedlings and saplings with increased light availability after selective forestry operations (Saenz and Guariguata. 2001), supporting the idea of disturbance benefiting younger individuals. The interaction between competition and elevation was close to significant for *W. pinnata*, suggesting that continued sampling of this species towards lower elevations could have detected an interaction. Indeed, the density of this species appears to increase in the low competition and basal area categories towards lower elevation (Figs. 3 and 4), as for *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 unable to detect a direct effect of light availability and basal area (sample sizes were small). However, we did detect an interaction between the light -crowding index and elevation for *P. oleifolius* and the smother of the same index was almost significant for *P. standleyi*. The fact that these species appeared mainly as large canopy dominant trees and the extreme scarcity of young individuals and regeneration (Blaser and Camacho 1991), weakens any potential relationship between the abundance of these species and disturbance legacies on forest structure. In the tropics many conifers appear restricted to sites with poorer soils (Palma et al. 2020) or higher elevations (Martin et al. 2007), but these patterns can be modified by disturbance (Coomes and 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 et al. 2011). While both *P. oleifolius* and *P. standleyi* have form and foliage that suggests shade tolerance, it is possible that for these species, disturbances that open the canopy and allow trees to establish without dense shade and competition, likely influence establishment throughout their ranges. This could also be the case for the *Magnolia poasana* regeneration. Other studies in the neotropics have found Magnolia species depending on gaps and good light availability for their regeneration (Weaver 1987, 2001; Gutierrez and Vovides 1997). According to a transplant experiment in Mexico, intermediate levels of canopy openness maximize both survival and growth of other neotropical Magnolia species (Garcia-Hernandez and Toledo-Aceves 2020). The factors that limit the recruitment of these species should be explored in future studies, as it may be the key to develop successful conservation strategies.

While at local scale, species distributions and abundance may be shaped by biotic interactions, at landscape scales dispersal and colonization dynamics play an important role defining the observed patterns (Svenning and Skov 2007). The influence of disturbance on elevation ranges depends not only on establishment but on each species ability to reach suitable locations. In our study, the observed patterns likely underestimate the potential range expansions driven by disturbance, as we cannot distinguish the influence of propagule availability and dispersal limitation from environmental limitations. Although knowledge on the dispersal mode of the study species is limited, studies in Costa Rican and other tropical montane ecosystems suggest strong dispersal limitation of tree species (Holl et al. 2000). Dispersal may be important explaining current distribution patterns, but at longer temporal scales persistence may depend on enduring a changed climate and associated competitors rather than on dispersal. In fact, 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. 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 both at local and landscape scales (Fig. 1b and c).

Our study has implications for the conservation of neotropical montane forests and high elevation ecosystem. Species' responses to climate change will depend on shifts in species interactions, which will play a crucial role in determining the distribution and survival of individual species. (Alexander et al. 2015). For example, future declines in frost frequency at the treeline will cause paramos to shrink due to tree encroachment (Helmer et al. 2019) and the associated shifts in the competitive environment. Species found in paramo and subparamo ecosystems such as the studied Hypericum irazuense, Vaccinium consanguineum, Schefflera rodriguesiana and Escallonia myrtilloides, may require management interventions, such as controlled disturbances, to ensure their persistence in a warmer future. It is important to recognize that protecting the landscape alone may not be enough to ensure the survival of many high elevation species in the face of increasing competitive exclusion. Therefore, we should consider alternative measures to reduce the negative impacts of climate change on species persistence. Overall, our study highlights the importance of taking a holistic approach to conservation, one that considers the complex interactions between species and the biotic and abiotic conditions they face. By understanding these dynamics, we can better anticipate the effects of climate change on biodiversity and take steps to mitigate its impact.

The relationship between disturbance and tree species persistence in the long term is complex and depends on various factors, including the frequency, intensity, and timing of the disturbance event. 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). For example, managed disturbances of a suitable nature could help species with limited dispersal to persist within their current elevation ranges, when their persistence is threatened by novel competitors (Sheil 2016). 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 et al. 2016). Also, uncontrolled disturbances could promote the establishment and dominance of undesirable vegetation (Douterlungne et al. 2013; Ssali et al. 2019) or non-native species (Jauni et al. 2015; Lembrechts et al. 2016).

Finally, our results support the increasing evidences of other mechanisms than species tolerance to the environment, such as biotic interactions (Neuschulz et al. 2018) and disturbance (Sheil 2016; Muñoz Mazón et al. 2019), 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 its effects on forests structure and light availability should be considered when trying to understand tropical tree species range shifts and future distributions in a warmer world.

## 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. In this study we showed that disturbance allows some species to establish at lower elevations than within less disturbed old-growth mature forest. Our results also have implications for conservation of high elevation tropical woody species, 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. Finally, we demonstrated how distance sampling can be used to characterize the populations of tropical tree species across environmental gradients.

**Acknowledgements** We thank SINAC (Sistema Nacional de Áreas de Conservación) for permission. Also, we would like to thank Truchas Selva Madre for their support letting us explore and study the cloud forest within their property. Special thanks to Marvin and Edwin ("Gallo") for sharing their invaluable knowledge about the study area and the species studied. We also thank Bryan Finegan and Diego Delgado for their support and help with the permits and logistics of the research. We thank Margherita Zorgno and Ole Wiggo for their help during fieldwork and data processing, respectively. Finally, thanks to the anonymous reviewers that provided useful feedback and suggestions.

**Author contributions** Conceptualization: DS; Methodology: MMM, KK, DS; Formal analysis and investigation: MMM, DS, KK; Writing—original draft preparation: MMM; Writing—review and editing: MMM, DS, KK; Funding acquisition: DS; Supervision: DS and KK.

**Funding** Open Access funding enabled and organized by Projekt DEAL. This work was supported by The Norwegian University of Life Sciences as part of the PhD of the main author Miguel Muñoz-Mazón.

## Declarations

**Competing interest** The authors have no relevant financial or non-financial interests to disclose.

## References

Alexander JM, Diez JM, Levine JM (2015) Novel competitors shape species' responses to climate change. Nature 525(7570):515–518

Ameztegui A, Coll L, Brotons L, Ninot JM (2016) Land-use legacies rather than climate change are driving the recent upward shift of the mountain tree line in the Pyrenees. Glob Ecol Biogeogr 25(3):263–273

Bertness MD, Callaway R (1994) Positive interactions in communities. Trends Ecol Evol 9:191–193

Bin Y, Lin G, Russo SE, Huang Z, Shen Y, Cao H et al (2019) Testing the competition-colonization trade-off and its correlations with functional trait variations among subtropical tree species. Sci Rep 9(1):1–10

Blaser J, Camacho M (1991) Estructura, composición y aspectos silviculturales de un bosque de roble (Quercus spp.) del piso montano en Costa Rica (Vol. 185). CATIE.

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, Oxford

Buckland S, Rexstad E, Marques T, Oedekoven C (2015) Distance sampling: methods and applications. https://doi.org/10.1007/978-3-319-19219-2.pdf

Budowski, G. (1965). Distribution of tropical American rainforest species in the light of successional processes. Turrialba (Costa Rica)v. 15(1) p. 40–42

Cadotte MW (2007) Competition–colonization trade-offs and disturbance effects at multiple scales. Ecology 88(4):823–829

Chardon NI, Rixen C, Wipf S, Doak DF (2019) Human trampling disturbance exerts different ecological effects at contrasting elevational range limits. J Appl Ecol 56(6):1389–1399

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199(4335):1302–1310

Corlett RT, Westcott DA (2013) Will plant movements keep up with climate change? Trends Ecol Evol 28(8):482–488

Cuddington K (2011) Legacy Effects: the persistent impact of ecological interactions. Biol Theory 6:203–210

Dantas VL, Hirota M, Oliveira RS, Pausas JG (2016) Disturbance maintains alternative biome states. Ecol Lett 19(1):12–19

Davidse G, Sousa Sánchez M, Knapp S, Chiang Cabrera F (2015) Saururaceae a Zygophyllaceae. 2(3): v–xvii, 1–347. In Davidse G, Sousa Sánchez M, Knapp S, Chiang Cabrera F (Eds) Fl. Mesoamer. Missouri Botanical Garden, St. Louis.

Dawkins, H.C. (1956) Crown Classification of Natural Forest Trees. Uganda Forest Department Technical Note, No. 17/56.

Douterlungne D, Thomas E, Levy-Tacher SI (2013) Fast-growing pioneer tree stands as a rapid and effective strategy for bracken elimination in the Neotropics. J Appl Ecol 50(5):1257–1265

Elsen PR, Monahan WB, Merenlender AM (2020) Topography and human pressure in mountain ranges alter expected species responses to climate change. Nat Commun 11(1):1–10

Feeley KJ, Bravo-Avila C, Fadrique B, Perez TM, Zuleta D (2020) Climate-driven changes in the composition of New World plant communities. Nat Clim Chang 10(10):965–970

Garcia-Hernandez MA, Toledo-Aceves T (2020) Is there potential in elevational assisted migration for the endangered Magnolia vovidesii? J Nat Conserv 53:125782

Gonzalez J (2007) Magnoliaceae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Eds) Manual de Plantas de Costa Rica. Vol VI, Dicotiledoneas.

Gutierrez L, Vovides AP (1997) An in situ study of Magnolia dealbata Zucc. in Veracruz State: an endangered endemic tree of Mexico. Biodivers Conserv 6:89–97

Hammel BE (2007) Hypericaceae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Eds) Manual de Plantas de Costa Rica. Vol VI, Dicotiledoneas.

He Q, Bertness MD (2014) Extreme stresses, niches, and positive species interactions along stress gradients. Ecology 95(6):1437–1443

Helmer EH, Gerson EA, Baggett LS, Bird BJ, Ruzycki TS, Voggesser SM (2019) Neotropical cloud forests and páramo to contract and dry from declines in cloud immersion and frost. PLoS ONE 14(4):e0213155

Hernández Gordillo AL, Vilchez Mendoza S, Ngo Bieng MA, Delgado D, Finegan B (2021) Altitude and community traits explain rain forest stand dynamics over a 2370-m altitudinal gradient in Costa Rica. Ecosphere 12(12):e03867

Holl KD, Loik ME, Lin EH, Samuels IA (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restor Ecol 8(4):339–349

Horn SP (1997) Postfire resprouting of Hypericum irazuense in the Costa Rican páramos: Cerro Asunción revisited. Biotropica 29:529–531

Horn SP, Sanford RL Jr (1992) Holocene fires in costa rica. Biotropica 24:354–361

Horn SP (1991) Fire history and fire ecology in the Costa Rican páramos. In Fire and the Environment: Ecological and Cultural Perspectives: Proceedings of an International Symposium, Knoxville, Tennessee, March 20–24, 1990 (Vol. 69, p. 289). Southeastern Forest Experiment Station.

Huston M, Smith T (1987) Plant succession: life history and competition. Am Nat 130(2):168–198

Jauni M, Gripenberg S, Ramula S (2015) Non-native plant species benefit from disturbance: a meta-analysis. Oikos 124(2):122–129

Kappelle M, Uffelen J-G, Cleef AM (1995) Altitudinal zonation of montane Quercus forests along two transects in Chirripo National Park. Costa Rica Vegetatio 119(2):119–153

Kappelle M, Horn SP (2005) Páramos de Costa Rica. Editorial INBio.

Keddy PA, MacLellan P (1990) Centrifugal organization in forests. Oikos 59(1):75

Kissa DO, Sheil D (2012) Visual detection based distance sampling offers efficient density estimation for distinctive low abundance tropical forest tree species in complex terrain. For Ecol Manage 263:114–121

Koehler K, Center A, Cavender-Bares J (2012) Evidence for a freezing tolerance-growth rate trade-off in the live oaks (Quercus series Virentes) across the tropical-temperate divide. New Phytol 193(3):730–744

Lawton RO, Putz FE (1988) Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology 69(3):764–777

Lembrechts JJ, Pauchard A, Lenoir J, Nuñez MA, Geron C, Ven A et al (2016) Disturbance is the key to plant invasions in cold environments. Proc Nat Acad Sci USA 113(49):14061–14066

Loehle C (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. J Biogeogr 25(4):735–742

Loehle C (2014) Climate change is unlikely to cause a biodiversity crisis: evidence from Northen latitude tree responses to warming. Energy Environ 25(1):147–153

Lusk CH, Kaneko T, Grierson E, Clearwater M (2013) Correlates of tree species sorting along a temperature gradient in New Zealand rain forests: seedling functional traits, growth and shade tolerance. J Ecol 101(6):1531–1541

Luteyn JL, Wilbur RL (2010) Ericaceae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Eds) Manual de Plantas de Costa Rica. Vol V, Dicotiledoneas

Lyu S, Alexander JM (2022) Competition contributes to both warm and cool range edges. Nat Commun 13(1):2502

Malanson GP (1997) Simulated responses to hypothetical fundamental niches. J Veg Sci 8(2):307–316

Marques TA, Thomas L, Fancy SG, Buckland ST (2007) Improving estimates of bird density using multiple- covariate distance sampling. Auk 124(4):1229–1243

Martin PH, Sherman RE, Fahey TJ (2007) Tropical montane forest ecotones: climate gradients, natural disturbance, and vegetation zonation in the Cordillera Central, Dominican Republic. J Biogeogr 34(10):1792–1806

Martin PH, Fahey TJ, Sherman RE (2011) Vegetation Zonation in a neotropical montane forest: environment, disturbance and ecotones. Biotropica 43(5):533–543

Mazón MM, Klanderud K, Finegan B, Veintimilla D, Bermeo D, Murrieta E et al (2020) How forest structure varies with elevation in old growth and secondary forest in Costa Rica. For Ecol Management 469:118191

Merello M (2003) Podocarpaeae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Eds). Manual de Plantas de Costa Rica. Vol II, Gimnospoermas

Miller DL, Burt ML, Rexstad EA, Thomas L (2013a) Spatial models for distance sampling data: recent developments and future directions. Methods Ecol Evol 4(11):1001–1010

Miller DL, Rexstad EA, Burt L, Bravington MV, Hedley S (2013b) dsm: Density surface modelling of distance sampling data. R package version, 2(1)

Morales JF, Cannon MJ, Cannon JFM (2020) Araliaceae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Eds). Manual de Plantas de Costa Rica. Vol IV, Dicotiledoneas

Morales JF (2010a) Grossulariaceae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Eds). Manual de Plantas de Costa Rica. Vol V, Dicotiledoneas

Morales JF (2010b) Winteraceae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Eds) Manual de Plantas de Costa Rica. Vol V, Dicotiledoneas

Muñoz Mazón M, Klanderud K, Finegan B, Veintimilla D, Bermeo D, Murrieta E et al (2019) Disturbance and the elevation ranges of woody plant species in the mountains of Costa Rica. Ecol Evol. https://doi.org/10.1002/ece3.5870

Muñoz Mazón M, Klanderud K, Sheil D (2022) Canopy openness modifies tree seedling distributions along a tropical forest elevation gradient. Oikos 2022(11):e09205

Neuschulz EL, Merges D, Bollmann K, Gugerli F, Böhning-Gaese K (2018) Biotic interactions and seed deposition rather than abiotic factors determine recruitment at elevational range limits of an alpine tree. J Ecol 106(3):948–959

Palma AC, Winter K, Aranda J, Dalling JW, Cheesman AW, Turner BL, Cernusak LA (2020) Why are tropical conifers disadvantaged in fertile soils? Comparison of *Podocarpus guatemalensis* with an angiosperm pioneer. Ficus Insipida Tree Physiol 40(6):810–821

Paquette A, Hargreaves AL (2021) Biotic interactions are more often important at species' warm versus cool range edges. Ecol Lett 24(11):2427–2438

Philip MS (1994) Measuring trees and forests, 2nd edn. CAB International, Wallingford

Rumpf SB, Hülber K, Klonner G, Moser D, Schütz M, Wessely J et al (2018) Range dynamics of mountain plants decrease with elevation. Proc Nat Acad Sci USA 115(8):1848–1853

Saenz GP, Guariguata MR (2001) Demographic response of tree juveniles to reduced-impact logging in a Costa Rican montane forest. For Ecol Manage 140(1):75–84

Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113:447–455

Shea K, Roxburgh SH, Rauschert ESJ (2004) June). Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecol Lett 7:491–508

Sheil D, Burslem DFRP (2003) Disturbing hypotheses in tropical forests. Trends Ecol Evol 18(1):18–26

Sheil D (2016) Disturbance and distributions. Ecol Soc, 21(1). http://www.jstor.org/stable/26270356

Shipley B, Keddy PA (1994) Evaluating the evidence for competitive hierarchies in plant communities. Oikos 69(2):340

Smith T, Huston M (1990) A theory of the spatial and temporal dynamics of plant communities. In *Progress in theoretical vegetation science* (pp. 49–69). https://doi.org/10.1007/978-94-009-1934-1_5

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15(1):353–391

Ssali F, Moe SR, Sheil D (2019) The differential effects of bracken (*Pteridium aquilinum* (L.) Kuhn) on germination and seedling performance of tree species in the African tropics. Plant Ecol 220(1):41–55

Svenning J-C, Skov F (2007) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecol Lett 10(6):453–460

Turner MG (2010) Disturbance and landscape dynamics in a changing world. Ecology 91(10):2833–2849

Uriarte M, Clark JS, Zimmerman JK, Comita LS, Forero-Montaña J, Thompson J (2012) Multidimensional trade-offs in species responses to disturbance: implications for diversity in a subtropical forest. Ecology 93(1):191–205

Van Steenis CGGJ (1958) Rejuvenation as a factor for judging the status of vegetation types: the biological nomad theory. In Proceedings of the symposium on humid tropics vegetation, Kandy. UNESCO, Paris (pp 159–163)

Wang Y, Sylvester SP, Lu X, Dawadi B, Sigdel SR, Liang E, Julio Camarero J (2019) The stability of spruce treelines on the eastern Tibetan Plateau over the last century is explained by pastoral disturbance. For Ecol Manage 442:34–45

Weaver PL (1987) Ecological observations on Magnolia splendens Urban in the Luquillo Mountains of Puerto Rico. Caribbean J Sci 22(1–2):53–70

Weaver PL (2001) Thinning and regeneration in Puerto Rico's colorado forest, with comments about their effect on the Puerto Rican Parrot. Carib J Sci 37(3/4):252–258

Wilson SD, Keddy PA (1986) Species competitive ability and position along a natural stress/disturbance gradient. Ecology 67(5):1236–1242

Wood SN (2006) Low-rank scale-invariant tensor product smooths for generalized additive mixed models. Biometrics 62(4):1025–1036

Zamora N (2015) Styraceae. In: Hammel BE, Grayum MH, Herrera C, Zamora N (Eds). Manual de Plantas de Costa Rica. Vol VIII, Dicotiledoneas