



# Altitude and community traits explain rain forest stand dynamics over a 2370-m altitudinal gradient in Costa Rica

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**Abstract.** Stand dynamic rates in Earth's vitally important tropical mountain rain forests are a central component of the response of these forests to global change, but their relationships to environmental gradients are poorly understood. We worked in mature forests on a 440–2810 m asl altitudinal gradient on Costa Rica's Talamanca Cordillera, making five censuses of 29 0.25-ha permanent sample plots during 2012–2019. We determined mortality and recruitment rates, as well as basal area ( $G$ ) increments, for individuals  $\geq 10$  cm diameter at breast height. Our main hypothesis was that stand dynamic rates decrease with altitude (therefore temperature); we also tested the hypotheses that rates increase with plot community-weighted mean specific leaf area (CWM SLA) and decrease with CWM wood specific gravity (WSG). We developed regressions using generalized additive models to test our hypotheses. Mortality and recruitment rates decreased with altitude in line with our main hypothesis, though the strongly non-linear mortality trend may be driven by extreme weather and temperature. Also, the best model for recruitment rates included plot CWM SLA with a negative relationship. Gross basal area increment  $\Delta G_{\text{gross}}$ , the annual basal area increment of trees that survived the study period, had a hump-shaped relationship to altitude, possibly related to the low CWM WSG of mid-altitude forests.  $\Delta G_{\text{gross}}$  was indeed negatively related to CWM WSG. However, net basal area growth ( $\Delta G_{\text{net}}$ , the annualized difference between initial and final plot basal areas) was *positively* related to altitude due to low mortality in montane forests, in a model with CWM WSG with a negative relationship.  $\Delta G_{\text{net}}$  was negative in nine of the 29 plots at  $< 1500$  m asl. Patterns of rain forest stand dynamics on this long altitudinal gradient go beyond a direct response to temperature, and further work is required to improve scenarios of forest response to climate change. CWM traits should be measured to improve understanding. The effects of storms and lightning on low- and middle-altitude forest and the potentially high resilience of montane Fagaceae-dominated forests require attention. Diversity, not generality, should be expected on comparing tropical forest altitudinal transects.

**Key words:** climate change; Fagaceae; lightning; mortality; recruitment; specific leaf area; stand growth; wood specific gravity.

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## INTRODUCTION

Tropical mountain rain forests (rain forests at altitudes  $> 300$  m asl; Körner 2007) are highly

vulnerable to the effects of climate change (Malhi et al. 2010, Delgado et al. 2016, Feeley et al. 2020). Thermophilization, through which the composition of a forest stand changes toward a greater

representation of species adapted to higher temperatures (Feeley et al. 2020), is a possible consequence of climate change in these forests. If thermophilization represents the natural adaptation of the stand to rising temperatures, it seems plausible that adaptation rates are positively correlated with stand dynamic rates (Duque et al. 2015). However, the relationship between forest stand dynamic rates and altitude, as a surrogate of temperature, is not well documented. Nor are the relationships of rates to factors other than temperature.

Plausible hypotheses about dynamic rates in tropical mountain rain forests can be derived from knowledge of latitudinal patterns of ecological processes in forests. Globally, there is strong support for a negative relationship between latitude and forest net primary productivity, in models that besides latitude include the length of a growing season, mean annual temperature (MAT), mean annual precipitation, and mean growing season temperature and precipitation (Gillman et al. 2015, Chu et al. 2016). Inferred declines in productivity with altitude, therefore temperature, in tropical mountain rain forests (Malhi et al. 2010) may involve several factors reviewed by Malhi et al. (2017) and Muller-Landau et al. (2021). As water availability is not limiting in these forests (Malhi et al. 2010, Clark et al. 2015), these factors include declining photosynthetic rates and changes in carbon use efficiency. Positive correlations between altitude and belowground allocation of net primary productivity have been observed in some studies (e.g., Leuschner et al. 2007). The factor most strongly supported by a study in the Andean mountain rain forest was declining gross primary productivity (Malhi et al. 2017). Notably, however, in some places, AGB on long altitudinal gradients peaks in montane rain forests (Venter et al. 2017). This may occur because specific combinations of climatic variables—high water availability, moderate temperatures, and small intra-annual temperature variations—and natural disturbance regimes favor the development of very large trees (Keith et al. 2009, Venter et al. 2017). Indeed, basal area peaks in old-growth montane rain forests at altitudes >2000 m asl on our Costa Rican gradient (Muñoz Mazón et al. 2020) as it does at 2800 m on another Costa Rican Cordillera (Heaney and Proctor 1990, Clark et al. 2015).

Phylogenetic and biogeographical factors may also play a role: Culmsee et al. (2010) found that the dominance of Fagaceae species—in the case of Central America, *Quercus* spp.—is also associated with high AGB and basal area in high-elevation tropical rain forests (see also Whitmore 1984). Finally, litter decomposition rates decline with altitude on our gradient (Esquivel et al. 2020). This slowdown of process rates, if demonstrated at the forest stand level, may be associated with reduced mortality rates and long basal area residence times (Clark et al. 2015).

But do stand dynamic rates in tropical mountain rain forests decline with altitudes such as NPP and decomposition rates? What factors other than altitude drive dynamic rates? These are key questions because climate-driven changes in forest ecosystem functional properties, structure, and composition (Feeley et al. 2013, Duque et al. 2015) are all in some way linked to the underlying stand dynamic rates: first, of recruitment and mortality of individuals of the tree species that make up the stand, and second, of stand growth, which can be estimated in terms of increments of AGB or measured in terms of basal area increments. It is well known that the composition and taxonomic diversity of rain forest stands change markedly over the long altitudinal gradients that characterize the mountain ranges of Central and South America (Tello et al. 2015, Veintimilla et al. 2019). But the ways in which forest stand dynamics vary over these gradients have only recently come to the attention of researchers. On a rain forest transect in Costa Rica, Clark et al. (2015) found that individual and basal area turnover rates decreased with altitude, while Báez et al. (2015) found declines in mortality and recruitment rates with altitude across north Andean sites under a wide range of precipitation regimes. Net increases of aboveground carbon predominated between 1991 and 2017 in forests across an Andean plot network covering a 500–3500 m asl altitudinal range (Duque et al. 2021), suggesting that these forests are currently acting as strong carbon sinks. Aboveground carbon dynamics were not related to altitude in that study, however.

In tropical American lowland rain forest, the possible effect of climatic and non-climatic drivers on stand dynamic rates is relatively well documented. Tree mortality rates are

substantially higher than in temperate or boreal forests but are increasing due to climate variability in all these biomes, with a major effect on aboveground carbon storage (McDowell et al. 2018). In lowland Neotropical forests, biomass productivity and stocks are positively related to climatic water availability (Poorter et al. 2015) and are well predicted by community-weighted mean values of functional traits (Finegan et al. 2015, Poorter et al. 2015). Yet, while these tropical lowland studies illustrate the important relationship of climate and forest functional properties to forest stand growth, they cover only short temperature gradients and in terms of climate primarily illustrate precipitation effects on stand dynamics.

Temperature changes markedly over short geographical distances on tropical altitudinal gradients, often under quite uniform water availability regimes, thus permitting testing of hypotheses about temperature effects on forest ecological processes (Malhi et al. 2010, Clark et al. 2015). However, although community-weighted mean leaf trait values can also vary strongly and predictably over altitudinal gradients in tropical mountain rain forests (Asner et al. 2015), it is not known whether they are correlated with ecological process rates as in lowland forests. Finally, strong correlations between climate and other environmental factors, especially soil, continue to represent a major challenge to understanding the response of forest vegetation to altitude (Grubb 1977, Malhi et al. 2010, Asner et al. 2015).

Here, we explore the variation of rates of recruitment, basal area growth, and mortality of tropical rain forests over a long altitudinal gradient in the Costa Rican tropical mountain rain forest. We ask how this variation is associated with altitude (as a temperature surrogate), forest functional properties, and other predictors. Our data set includes five censuses of individuals  $\geq 10$  cm dbh carried out over a seven-year period (2012–2019) in 29 permanent sample plots of 0.25 ha. We characterize forest functional properties using community-weighted mean values of functional traits that are expected to be correlated with stand dynamic rates: specific leaf area (SLA), with a hypothesized positive correlation, and wood specific gravity (WSG), with a hypothesized negative correlation (cf. Unger et al. 2012, Finegan et al. 2015, Poorter et al. 2015). Leaf-level

SLA tends to decrease with altitude in a tropical mountain rain forest, perhaps representing increased leaf conservatism due to decreasing temperatures and solar radiation (Grubb 1977, Asner et al. 2015), which would be linked to declining photosynthetic rates (Malhi et al. 2017). Altitudinal trends of wood specific gravity (WSG), on the contrary, are not well known.

To determine stand dynamic rates, we measured a total of 4008 trees belonging to 450 species over the seven-year study period. We measured community-weighted mean (CWM) functional trait values for a total of 162 dominant tree species, selected on the basis of their contribution to the total stand basal area.

Our main hypothesis was that rates of recruitment, basal area growth, and mortality decrease with altitude, therefore temperature, over the gradient. Given the expected variation of CWM traits over the gradient, complementary hypotheses were that stand dynamic rates show a negative relationship to CWM WSG and a positive relationship to CWM SLA.

## METHODS

### *Study area and permanent sample plots*

This study was conducted in an old-growth forest on the Caribbean slope of the Cordillera de Talamanca, Costa Rica (plot locations are shown in Appendix S1: Fig. S1). The altitudinal gradient sampled goes from 440 m asl in the north to 2810 m asl in the south close to the continental divide. We sampled in four Holdridge life zones (Holdridge 1967): tropical wet forest, and premontane, lower montane and montane rain forests. Water availability is not a limiting factor in these forest ecosystems, in which annual precipitation is greater than potential evapotranspiration (Holdridge 1967). Mean annual temperatures from WorldClim climate surfaces (<https://www.worldclim.org/>) range from 24.4°C at 440 m asl to ca. 11°C at 2950 m asl. WorldClim mean annual rainfall ranges from 2500 mm at 2810 m asl to 4146 mm at 1635 m asl in Tapantí National Park. Frost can be frequent during January–April in the montane rain forest (personal observations).

Much of the area is underlain by tertiary volcanic rock, though there are patches of intrusive rock of the same geological age, as well as

quaternary glacial sediments in the highlands (Chinchilla et al. 2011). Soils are mainly Ultisols at lower elevations and Inceptisols at higher (Veintimilla et al. 2019). Principally in the montane zone, Andepts have developed in areas covered by ash from the active volcanoes of the Central Volcanic Cordillera of Costa Rica (Chinchilla et al. 2011) and possibly also from Barú Volcano, in the Panamanian sector of the Cordillera (Anchukaitis and Horn 2005).

The Talamanca Cordillera has experienced substantial climatic and possibly also anthropogenic change during the Pleistocene and Holocene periods, and Holocene montane and lowland vegetation became established between 9000 and 8000 B.P. (Islebe and Hooghiemstra 1997, Piperno and Jones 2003). Humans have probably been present in our study area since 7000–4000  $^{14}\text{C}$  yr B.P. (Anchukaitis and Horn 2005).

For individuals  $\geq 10$  cm dbh, forest composition was characterized by Veintimilla et al. (2019) as a lowland zone (tropical wet forest and premontane rain forest, 440–1120 m asl), a transitional zone at 1400–1600 m asl (lower montane rain forest), and the Fagaceae (*Quercus*)-dominated montane rain forest at altitudes  $>2100$  m asl. Alpha diversity on this gradient has a strong negative relationship to altitude (Veintimilla et al. 2019) as do litter decomposition rates (Esquivel et al. 2020). Stand basal area, however, increases linearly with altitude to approach 50  $\text{m}^2/\text{ha}$  in montane forests (Muñoz Mazón et al. 2020).

We analyzed data for individuals  $\geq 10$  cm dbh from 29 permanent sample plots of 0.25 ha distributed along the altitudinal gradient. The plots are separated from each other by a minimum distance of 300 m. All the plots were measured five times over a seven-year period, 2012–2019. To set up plots, homogeneous areas of primary forests located on hillsides without evidence of recent human intervention were entered. Plots were positioned by walking a transect from the access point in such areas until a site meeting the following criteria was reached: We avoided recent large tree fall gaps and steep slopes, to reduce possible slope effects on the testing of our main hypotheses: median slope of plots measured with a clinometer was  $25^\circ$ , with a minimum of  $15^\circ$  and a maximum of  $36^\circ$ . Understory bamboo (*Chusquea* spp.) is a characteristic element of

montane rain forest (Kappelle and Brown 2001) and was not taken into account in plot location. Nor were large trees ( $>60$  cm dbh) that are found throughout the gradient. Finally, we maintained a distance  $>50$  m from water bodies.

We measured stem diameter of all trees, palms, and tree ferns  $\geq 10$  cm diameter using a metal tape. Stem diameters were measured at breast height (dbh, 1.3 m) or 20 cm above buttresses or deformations. Of the total of 4008 trees evaluated, 82 (2.04%) had two or three stems  $\geq 10$  cm dbh. These multiple-stemmed trees were treated as single individuals for mortality and recruitment rate calculations. For basal area increments, the increment of each stem was determined separately. We excluded palms and tree ferns from the analysis of stand dynamics. All individuals were identified as species using procedures described by Veintimilla et al. (2019), who present the full list of species and their distributions across the four life zones (their Appendix 4). Nomenclature is that of the Missouri Botanical Garden (<https://www.tropicos.org/>). In Appendix S1: Table S1, we provide the response variables analyzed in this study.

#### Stand turnover and basal area increment

We calculated mortality rates  $m$  for each plot following Sheil et al. (1995):

$$m = \left[ 1 - \left( \frac{N_s}{N_0} \right)^{1/t} \right] \times 100 \quad (1)$$

where  $m$  is the annual percentage mortality,  $N_0$  is the number of individuals present at the beginning of the measurement period,  $N_s$  is the initial number of individuals minus the number of individuals dying during the 2012–2019 period ( $N_s = N_0 - M$ ), and  $t$  is the time in years.

The recruitment rate  $r$  per plot was calculated following Sheil et al. (2000) as follows:

$$r = \left[ 1 - \left( 1 - \frac{R}{N_t} \right)^{1/t} \right] \times 100 \quad (2)$$

where  $r$  is the recruitment rate expressed as an annual percentage,  $R$  is the total number of recruits,  $N_t$  is the final number of individuals, and  $t$  is the time interval in years.

For each plot, we calculated gross periodic mean annual increments ( $\Delta G_{\text{gross}}$ ) of basal area,

in  $\text{m}^2\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ , for the trees that survived the seven-year measurement period, a total of 3209 for the whole data set. Net annual basal area increment ( $\Delta G_{\text{net}}$ ) was calculated for the seven-year period as the annualized difference between initial and final total basal areas, therefore taking into account recruits and their growth, growth of survivors, and mortality.

#### Weighted mean trait values and soil variables

We measured functional traits for the species that made up 80% of basal area  $\geq 10$  cm dbh in at least one plot; a total of 162 species distributed across the 29 plots. The mean number of species sampled for traits per 0.25-ha permanent sample plot was 17.25 in tropical wet forest, 8.25 in pre-montane rain forest, 10.5 in lower montane rain forest, and 1.3 in montane rain forest. We used well-known procedures (Pérez-Harguindeguy et al. 2013) for measuring the leaf trait specific leaf area (SLA,  $\text{mm}^2/\text{mg}$ ), leaf concentration of phosphorus (P,  $\text{mg}/\text{g}$ ), and nitrogen (N,  $\text{mg}/\text{g}$ ). We calculated leaf N/P ratio from these data. For the measurement of leaf traits, we sampled five trees per species. In the field, branches with mature foliage fully exposed to sunlight were selected and cut from the canopy. Samples were transported to the laboratory in a cooler, and five leaves from each tree sampled, free from herbivore damage and evidence of pathogens, were selected for measurements. The key stem trait, wood specific gravity (WSG, unitless), was measured from cores taken using a stem borer following Williamson and Wiemann (2010).

Community-weighted mean (CWM) trait values were estimated for each trait separately for the first measurement of each plot using Fdiversity software (Casanoves et al. 2011). We used the basal area as the weighting variable. The mean number of species per plot used to calculate CWM trait values declined from over 20 in tropical wet forest to 15 in lower montane rain forest and 3.5 in montane rain forest (see Appendix S1: Table S1). In three montane plots with a single species, *Quercus bumelioides*, making up  $\geq 80\%$  of the basal area, the CWM was set as the trait value for this species. We used soil data from the same sample plots measured to 30-cm soil depth by Veintimilla et al. (2019).

Physical and chemical analysis of soil was performed as described by Veintimilla et al. (2019),

who provide summary statistics of variables measured. Soil texture (percent of sand, clay, and silt) was obtained by the Bouyoucos method. Total acidity, Ca, and Mg extractions were obtained in 1 M potassium chloride (KCl). Extractable K, P, Zn, Cu, Mn, and Fe were obtained by the modified Olsen extraction method with a 0.5 N sodium bicarbonate ( $\text{NaHCO}_3$ ) solution at a pH 8.5. The percentages of C and N were determined by the autoanalyzer of C/N by dry combustion.

#### Statistical analysis

To test our hypotheses, we developed generalized additive models (GAMs) using the “gam” function of the “mgcv” library in R. Besides the main independent variable, altitude, and the CWM traits, we used initial basal area, soil variables, and slope as predictors in models. To select the best GAMs, we evaluated models with  $>4$  effective degrees of freedom, as well as smoothed graphs (Zuur et al. 2009, Wood 2017). None of the models we selected included initial basal area, CWM N, CWM P, CWM N/P, or soil variables. Plot slope was only significant in one model, as a predictor of  $\Delta G_{\text{net}}$  ( $R^2$  adj: 0.12,  $P = 0.03$ ), and we did not select this model. For these reasons, we do not discuss these predictor variables further.

## RESULTS

During the period from 2012 to 2019, the annual mortality rate  $m$  varied among plots between 0.56 and 5.17%  $\text{yr}^{-1}$ . Supporting our main hypothesis, the overall trend was a non-linear decrease in mortality rate with increasing altitude, largely leveraged by low rates in montane forests (GAM,  $R^2$  adj: 0.44,  $P = 7.34\text{e}-06$ ; Fig. 1a). Recruitment rates also varied widely, in the range from 0.42 to 3.31%  $\text{yr}^{-1}$ , but they showed no significant bivariate relationship to altitude. However, a GAM recruitment rate in relation to altitude and CWM SLA was highly significant ( $R^2$  adj: 0.30,  $P = 7.34\text{e}-06$ ; Fig. 1b, c). Both these predictors had significant negative relationships to recruitment rates in this model, supporting our main hypothesis but not supporting our hypothesis of a positive relationship between dynamic rates and SLA. CWM SLA declines significantly with altitude (Appendix S2: Fig. S1a).

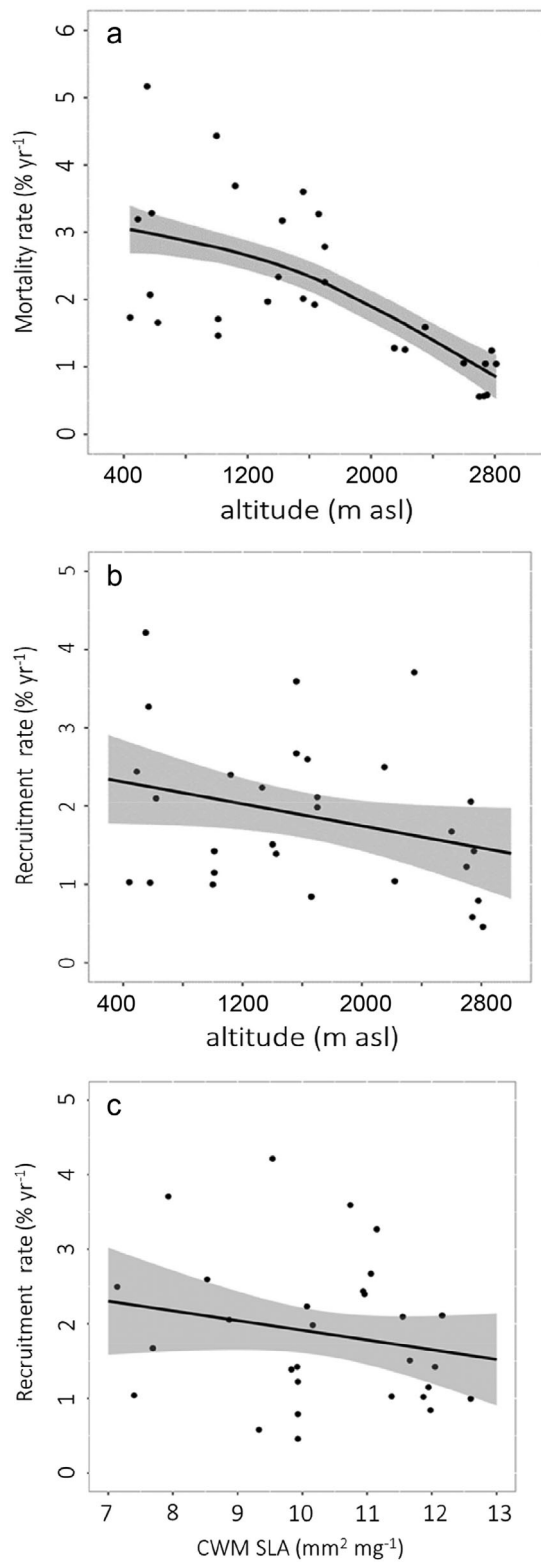


Fig. 1. Relationships of annual rates of mortality ( $m$ )

(Fig. 1. *Continued*)

and recruitment ( $r$ ) to altitude and community-weighted mean (CWM) traits. (a)  $m$ -altitude,  $R^2$  adj: 0.44,  $P=0.00023$ ; (b, c)  $r$ -altitude and  $r$ -CWM specific leaf area (SLA) from model including both these predictors. Model  $R^2$  adj: 0.30,  $P=7.34e-06$ ; altitude,  $F=7.23$ ,  $P=0.008$ ; CWM SLA,  $F=4.64$ ,  $P=0.016$ . Curves are fitted splines from GAMs, and shaded areas represent the 95% confidence limits of the spline.

Results for basal area increments did not support our main hypothesis.  $\Delta G_{\text{gross}}$  showed a hump-shaped relationship to altitude (GAM:  $R^2$  adj: 0.31,  $P=0.0019$ ; Fig. 2a).  $\Delta G_{\text{gross}}$  tended to be highest in the altitudinal range of 1100–1660 m asl and to decrease in tropical wet forest and montane rain forest at the two extremes of the altitudinal gradient. This relationship of  $\Delta G_{\text{gross}}$  to altitude can possibly be interpreted in terms of its bivariate negative relationship to CWM WSG ( $R^2$  adj=0.19,  $P=0.0096$ ) together with the valley-shaped relationship of CWM WSG to altitude ( $R^2$  adj=0.44,  $P=0.002$ ; Fig. 2b, c)— $\Delta G_{\text{gross}}$  tended to be highest at middle elevations where CWM WSG was lowest. CWM WSG was not, however, significant as a predictor of  $\Delta G_{\text{gross}}$  in models that also included altitude.

Also contrary to our main hypothesis,  $\Delta G_{\text{net}}$  showed a non-linear *positive* relationship to altitude in a GAM with CWM WSG, with which its relationship was negative, as in the case of  $\Delta G_{\text{gross}}$  ( $R^2$  adj: 0.36,  $P=0.0011$ ; Fig. 3a, b).  $\Delta G_{\text{net}}$  showed negative values in ten of the 29 plots, all but one of them located below 1500 m asl, where basal area lost due to mortality was greater than gains from growth of survivors and recruitment.

## DISCUSSION

We tested the main hypothesis that stand dynamic rates in mountain rain forests decrease with altitude. This hypothesis was supported for mortality rates and recruitment rates, though the best model for recruitment included CWM SLA. It was not supported for stand growth. Gross basal area increments  $\Delta G_{\text{gross}}$  had a hump-shaped relationship to altitude, while net basal area increment  $\Delta G_{\text{net}}$  increased with altitude in a best GAM that included CWM WSG. We found

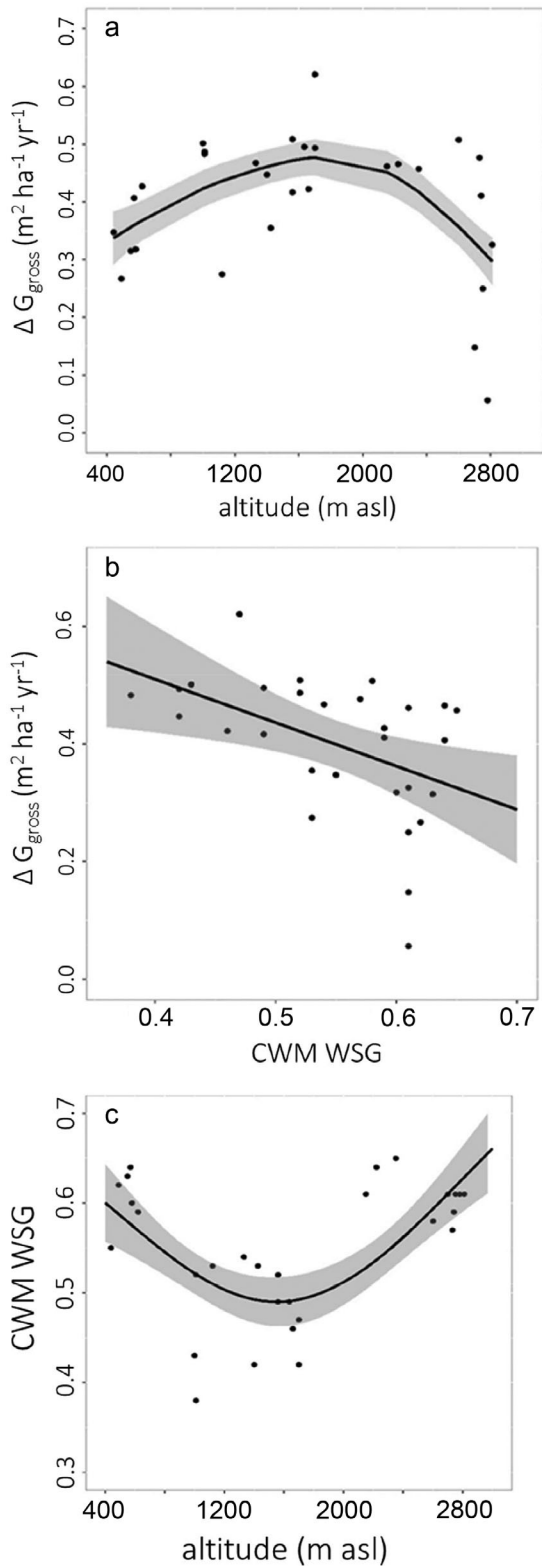


Fig. 2. (a) Relationship of gross basal area increment

(Fig. 2. *Continued*)

(growth of survivors + basal area of recruits) to (a) altitude:  $R^2$  adj: 0.31,  $P=0.0019$  and (b) CWM wood specific gravity (WSG),  $R^2$  adj=0.19,  $P=0.0096$ ; and (c) the relationship of CWM WSG to altitude,  $R^2$  adj=0.44,  $P=0.0002$ . Curves are fitted splines from GAMs, and shaded areas represent the 95% confidence limits of the spline.

net loss of basal area in ten plots, mainly in the lowland wet and premontane rain forests. Overall, stand dynamic rates in these forests show a range of relationships to altitude and therefore temperature, while they also respond to two key forest functional properties, CWM SLA and CWM WSG. After discussing these results, we evaluate their implications regarding the response of tropical mountain rain forest to rising temperatures under climate change.

#### Mortality and recruitment rates

Whole-stand exponential annual mortality rates have been documented in the range from 0.6% to 3% in old-growth lowland tropical forests with “gap” disturbance regimes (Swaine et al. 1987, Lugo and Scatena 1996, Finegan et al. 2001, Lewis et al. 2004). In our study using the improved equation of Sheil et al. (1995), mortality rates were >3.0% in eight plots distributed across tropical wet forest, premontane rain forest, and lower montane rain forest, with a maximum value of 5.2%. However, they declined to 0.56–1.6% at altitudes >2000 m asl. Our sampling protocol was designed to reduce the possibility that steep slopes affect mortality rates (see Methods: statistical analysis). Intense rainfall, high winds, and lightning during the period of our study, associated, for example, with hurricanes Otto (2016) and Nate (2017) and the 2014–2016 el Niño phenomenon (Brenes-Rodriguez et al. 2017), may be the most likely causes of tree mortality in the low and middle elevations of our gradient (cf. Yano-viak et al. 2020). It is notable that although the number of trees  $\geq 60$  cm dbh increases with elevation in our plots (Appendix S2: Fig. S1b), seven of nine tree deaths in this size range occurred in plots at <1120 m asl (10.3% of all trees  $\geq 60$  cm dbh in this altitudinal range). In contrast, in plots located >2000 m asl only two of 95 trees  $\geq 60$  dbh (2.1%) died over the seven years.

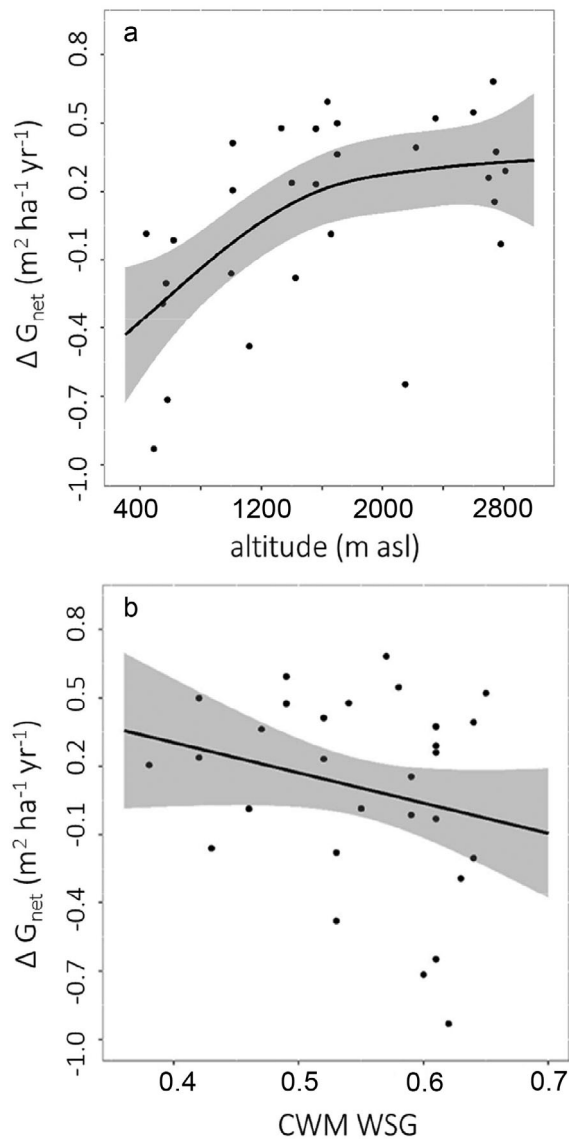


Fig. 3. Relationships between net basal area increment and (a) altitude, (b) CWM wood specific gravity (WSG), from model including both predictors. Model  $R^2$  adj: 0.36,  $P = 0.001$ ; altitude,  $F = 15.1$ ,  $P = 0.0006$ ; CWM WSG,  $F = 6.05$ ,  $P = 0.02$ . Curves are fitted splines from GAMs, and shaded areas represent the 95% confidence limits of the spline.

The decrease in recruitment rates with altitude in a model with CWM SLA gives some support to our main hypothesis and together with the result for mortality rates suggests that turnover rates of individuals decrease as temperature decreases with altitude. The role of CWM SLA in

the determination of recruitment rates requires further work.

#### Basal area increments

Basal area increments were best explained by GAMs including altitude and CWM WSG. We measured  $\Delta G_{\text{gross}}$  as the increments of trees that survived the whole study period. Values overall were in a similar range to those described by Clark et al. (2015) who, however, reported no clear relationship to altitude. The hump-shaped relationship of  $\Delta G_{\text{gross}}$  to altitude in our study is probably best explained in terms of the contrary, valley-shaped altitudinal pattern of CWM WSG. Stem diameter growth rates increase with decreasing WSG in tropical trees (Héroult et al. 2011), and for lowland forests, negative relationships of CWM WSG to both net and gross biomass increments have been shown by Finegan et al. (2015) and Poorter et al. (2015).  $\Delta G_{\text{gross}}$  on our gradient is negatively related to CWM WSG, possibly because of the high WSG of dominant species in both tropical wet forest and montane rain forest, and the lower values of dominants in the altitudinal range of 1000–1700 m asl (premontane rain forest and lower montane rain forest; see Appendix 1: Table S2), where  $\Delta G_{\text{gross}}$  was highest (Appendix S1: Table S1). Although no soil variables were included in our best models, we are investigating the possibility that higher soil fertility over the 1000–1700 m asl altitudinal range contributes to pattern in basal area increment.

$\Delta G_{\text{net}}$  was quite well explained by altitude in our model, with a non-linear positive relationship, and CWM WSG, with the expected negative relationship. The relationship of  $\Delta G_{\text{net}}$  to altitude is the outcome of two factors: first, the decline with altitude of both mortality rates and the total basal area lost due to mortality (Appendix S2: Fig. S1c); and second, the hump-shaped relationship to altitude of  $\Delta G_{\text{gross}}$ . The improvement of model fit by the incorporation of CWM WSG is probably due to the relationship of this functional property to the higher  $\Delta G_{\text{gross}}$  in middle-elevation premontane and lower montane rain forest.

#### Final comments: a complex forest landscape response to climate change

In the absence of changes in water availability, rising temperatures are expected to bring upslope



species migrations, thermophilization, and changes in carbon fluxes in tropical mountain rain forests (Malhi et al. 2017, Feeley et al. 2020). Climate change is expected to bring increased precipitation in our study area (Delgado et al. 2016). What are the implications of our results in relation to expected consequences of rising temperatures? We propose the following. First, our study suggests that not all rain forest properties and processes are controlled by temperature on altitudinal gradients; not all stand dynamic rates decrease with decreasing temperature. Therefore, understanding and modeling of forest response to climate change must take into account additional predictors. The inclusion of CWM response traits (Pérez-Harguindeguy et al. 2013) in hypothesis testing and modeling is recommendable, and increased understanding of the factors that determine tree species distributions on altitudinal gradients is necessary: On our gradient, for example, it is likely that disturbance extends the altitudinal ranges of tree species (Muñoz Mazón et al. 2019). The climate responses of montane forests dominated by Fagaceae particularly require further study: Species of this family are distributed over broad ranges of altitude and temperature in both Central American (Kappelle and Brown 2001, Veintimilla et al. 2019) and Asian (Culmsee et al. 2010) mountain rain forests. This suggests that montane forests dominated by these species are resilient to rising temperatures, in line with the very low contemporary mortality rates and robust net basal area increments they showed in our study.

Finally, we recommend that forest change scenarios go beyond thermophilization to include responses to storms and lightning (cf. Yanoviak et al. 2020). We agree with Clark et al. (2015) and Fadrique et al. (2018) in not expecting generality on comparing tropical altitudinal transects. Ecological knowledge of TMRF covering a range of pre-warming response and effect scenarios must urgently be included in the evaluation of risk and uncertainty in climate change (Kunreuther et al. 2014).

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