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Local-scale changes in topography influence tree growth and mortality in a *terra firme* forest in the Northwestern Amazon

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A mi familia y amigos por su motivación, en especial a mis compañeros, Luisa Gómez, y Carlos Hernández, por el apoyo incondicional y paciencia.

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Resumen

Los cambios en la topografía a escala local influyen en el crecimiento y la mortalidad de los árboles en un bosque de tierra firme del noroeste de la Amazonia

Se cree que la variación espacial en la diversidad y distribución de las especies arbóreas está influenciada por la variación ambiental, incluida la topografía, pero los procesos subyacentes no se comprenden bien. Hábitats más húmedos, como los valles, deberían soportar un mayor crecimiento y supervivencia que hábitats más secos, como las colinas. Sin embargo, pueden ocurrir desviaciones de este patrón debido a las asociaciones de hábitat de las especies, que deben estar alineadas con la estrategia ecológica de las especies a lo largo del espectro adquisitivo-conservador interespecífico: crecimiento rápido a costa de una menor supervivencia y mayor supervivencia a costa de un crecimiento más lento. Aquí, evaluamos la influencia de la topografía en el crecimiento y la mortalidad de 123,977 árboles (1,266 especies) en la Parcela de Dinámica Forestal Amacayacu de 25 ha, en el noroeste de la Amazonía. Específicamente, preguntamos: (1) ¿Varían las tasas de crecimiento y mortalidad de los árboles entre los hábitats topográficos (valles, pendientes y colinas)? (2) ¿Varían el crecimiento y la mortalidad dependiendo de las asociaciones de hábitat de las especies? y (3) ¿los patrones observados de crecimiento y mortalidad de árboles son consistentes con las expectativas basadas en el espectro adquisitivo-conservador? Se utilizaron modelos de efectos mixtos para examinar la variación demográfica entre los hábitats topográficos y las asociaciones de hábitats de especies que controlan el tamaño de los árboles. Los árboles que crecían en valles tenían tasas de mortalidad y crecimiento significativamente más altas en comparación con los árboles que crecían en pendientes y colinas, lo que era consistente con el espectro adquisitivo-conservador. Este patrón se mantuvo independientemente de las asociaciones de hábitat de las especies. Nuestros hallazgos sugieren que incluso pequeñas diferencias en la topografía pueden traducirse en diferencias en el acceso al agua del suelo que afectan el rendimiento de los árboles, lo que tiene implicaciones para

comprender las estrategias ecológicas de las especies y las respuestas de los bosques al cambio climático.

Palabras clave: crecimiento de los árboles; mortalidad de los árboles; bosques tropicales, dinámica forestal, asociaciones de hábitat de las especies; estrategias adquisitivas-conservadoras.

Abstract

Local-scale changes in topography influence tree growth and mortality in a terra firme forest in the Northwestern Amazon

Spatial variation in tree species diversity and distribution is thought to be mediated by environmental variation, including topography, but the underlying processes are not well understood. Wetter habitats like valleys should support higher growth and survival than drier habitats like ridges. However, deviations from this pattern may occur due to species' habitat associations, which should be aligned with species' ecological strategy along the interspecific acquisitive-conservative spectrum: fast growth at the cost of lower survival, and higher survival at the cost of slower growth. Here, we assess the influence of topography on the growth and mortality of 123,977 trees (1,266 species) in the 25-ha Amacayacu Forest Dynamics Plot, Northwestern Amazon. Specifically, we asked: (1) Do tree growth and mortality rates vary across topographic habitats (valleys, slopes, and ridges)? (2) Do growth and mortality vary depending on species' habitat associations? and (3) are the observed patterns of tree growth and mortality consistent with expectations based on the acquisitive-conservative spectrum? Mixed-effects models were used to examine demographic variation across topographic habitats and species habitat associations controlling for tree size. Trees growing on valleys had significantly higher mortality and growth rates compared to trees growing on slopes and ridges, which was consistent with the acquisitive-conservative spectrum. This pattern held true regardless of the species habitat associations. Our findings suggest that even small differences in topography can translate into differences in access to soil water affecting tree performance, which has implications for understanding species' ecological strategies and forest responses to climate change.

Keywords: tree growth; tree mortality; tropical forests, forest dynamics, species habitat associations; acquisitive-conservative strategies.

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Introduction

Tree species are distributed according to the climate and environmental conditions for which they are evolutionarily adapted. However, as climate rapidly changes, forest ecosystems are subjected to new conditions including increasing vapour pressure deficit, increasing temperature, severe droughts, floodings, etc. (Bauman et al., 2022; Brodribb et al., 2020; Malhi et al., 2009; N. McDowell et al., 2022). Species' ability to acclimate, migrate, or adapt to new conditions will shaped future forest composition and functioning (Feeley et al., 2012; Feeley & Zuleta, 2022). Therefore, understanding tree species performance under different environmental conditions is key to improve predictions of forest ecosystems and the ecosystem services they provide.

At local scales, soil hydrological conditions (mainly proxied by topography) play a key role in determining the variation in forest composition (Fortunel et al., 2016; Russo et al., 2005; Zuleta et al., 2020), functioning (Cosme et al., 2017; but see Zuleta et al., In Press), and dynamics (Cushman et al., 2021; Valencia et al., 2004, 2009; Zuleta et al., 2017) of tropical forest (Costa et al., 2022; Jucker et al., 2018). In Amazon upland (terra firme) forests, small-scale variation in topography creates a mosaic of small valleys and ridges that generate a local gradient of soil water availability where valleys are generally wetter than ridges (Costa et al., 2022; Sousa et al., 2020). Trees located in valleys are expected to have resource-acquisitive strategies, while trees located in ridges are expected to have more resource-conservative strategies (Cosme et al., 2017; Costa et al., 2022; Valencia et al., 2004; but see Zuleta et al., In Press). However, species' habitat associations could deliver specific adaptations that are expected to modify species performance along the interspecific acquisitive-conservative spectrum defined by faster growth at the cost of lower survival, and higher survival at the cost of slower growth (i.e. growth-mortality trade-off).

Assuming environmental filtering as a dominant process in ecological communities, species should have demographic variation in different habitats, and in particular, show

demographic advantages when growing in their more suitable or preferred habitats (Fortunel et al., 2016; Kenfack et al., 2014; Russo et al., 2005). Across habitats, species can either (i) perform better (i.e., low mortality and high growth rates) in its preferred habitat (home) than elsewhere (away) (best-at-home hypothesis, Kenfack et al., 2014), or (ii) perform better in their preferred habitat (where they are residents) than species from the regional pool that are not specifically associated with that habitat (foreigners) ((resident-advantage hypothesis, Kenfack et al., 2014). However, other processes not related with environmental filtering could drive species assemblages. For example, spatially aggregated trees could be simply due to dispersal limitations (Hubbell, 2001). In this case, species would not show demographic variation among habitats and nor an advantage in their preferred habitat (Kenfack et al., 2014).

Here, we evaluated the demographic variation of tree species across topographic habitats (valleys, slopes, ridges) at the 25 ha Amacayacu Forest Dynamics Plot (AFDP), an aseasonal terra firme forest in the Colombian Amazon. The main research questions are: (1) Do tree growth and mortality rates vary across topographic habitats? (2) Do growth and mortality vary depending on species' habitat associations? (3) Are the observed patterns of tree growth and mortality consistent with expectations based on the acquisitive-conservative spectrum? Given that trees on valleys have access to more resources and are more acquisitive than trees on slopes and ridges, we expect trees growing on valleys to have higher mortality and growth rates compared to trees growing on slopes and ridges (Cosme et al., 2017; Costa et al., 2022; Oliveira et al., 2021; Zuleta et al., 2017). However, we expect these patterns to vary depending on the species' habitat associations, with species performing better on their home habitat than on other habitats (i.e., best-at-home hypothesis), and resident species on a given habitat having better demographic performance than foreigners (i.e., resident-advantage hypothesis) (Fortunel et al., 2016; Kenfack et al., 2014). Likewise, we expect generalist species to perform similarly across habitat types.

1. Methods

1.1 Study area

This study was carried out in the Amacayacu Forest Dynamics Plot (AFDP), located in the Northwestern Amazon (3°48'33.02" S and 70°16'04.29" W). The AFDP is part of the Forest Global Earth Observatory (ForestGEO; Davies et al., 2021), a global network of large forest plots following standardized methods (R Condit, 1998). The life zone of the AFDP corresponds to Tropical wet forest (Holdridge, 1978), with a unimodal rainfall regime and mean annual precipitation of 3,216 mm (with no months below 100 mm). Relative humidity is 86% and mean annual temperature is 25.8 °C. The plot is 25 ha in area (500 m × 500 m) and harbors ~1,200 tree, shrub, and palm species (Duque et al., 2017). The AFDP was established on a transitional area between low dissected tertiary plains and waterlogged soils on low terraces of the alluvial plain (Hoorn, 1994). This creates a depression in a small portion of the plot that occasionally gets swampy for a few months due to poor soil drainage in the lower parts of internal valleys, the drainage of streamlets during the wet season, and the high seasonal level of the water table of the Amazon River (Zuleta et al., 2020). Soils in the AFDP are poor, with high acidity, and low base saturation due to the abundance of minerals like kaolinite and quartz (Chamorro, 1989; Zuleta et al., 2020).

1.2 Forest census

We used two full censuses of the AFDP. The first census was carried out from August 2007 to April 2009, in which all trees, shrubs, palms, and tree ferns with a diameter at breast height (*DBH*; 1.3 m) ≥ 10 mm were mapped, tagged, measured, and collected for taxonomic identification. The second census was carried out between August 2014 and November 2015, in which we visited the trees to determine survival, and measure the *DBH* of surviving trees to quantify growth. Taxonomic voucher and identification were

made by the Herbario Amazónico Colombiano (COAH) of the Instituto Amazónico de Investigaciones Científicas (SINCHI).

1.3 Topographic habitat definition

Three topographic habitats were previously defined in the AFDP: ridges, slopes, and valleys (Zuleta et al., 2017, 2020). These habitats were defined by applying hierarchical clustering of elevation, slope and convexity at the 20 m × 20 m quadrat scale, obtained from a 5 m resolution topographic survey following the standard ForestGEO protocol (Condit 1998). For each quadrat, elevation was calculated as the mean elevation of its four corners. Convexity was estimated as the mean elevation of the quadrat minus the mean elevation of its immediate neighbors. Slope was estimated by dividing each quadrant into four sub-quadrants, calculating the slope within each sub-quadrant, and averaging the resulting slope values. Overall, valleys, slopes and ridges represent 44.2% (11.04 ha), 30.7% (7.68 ha), and 25.1% (6.28 ha) of the plot. Quadrats classified as valleys have elevation lower than 95 m a.s.l., slope lower than 5°, and convexity between -1.4 and 0.3 (i.e., concave). The slope habitat included quadrats with mean elevation lower than 95 m a.s.l., slopes higher than 5°, and convexity between -1.6 and 1.2. Ridges included quadrats with mean elevation higher than 95 m. a.s.l., slopes between 1.7° and 14.4°, and convexity between -0.9 and 2.4. Despite the relatively small changes in elevation in the AFDP (~20 m total elevation change), tree species distributions are associated with elevation and topography, more so than with soil chemistry (Zuleta et al., 2020).

1.4 Species' topographic habitat associations

We performed a Torus Translation (TT) test to determine the species' preference to each of the three topographic habitats defined above. This test was performed for species with at least 50 individuals in the first census of the plot using the *tt.test* function in the *fgeo.analyze* R package (Chuyong et al., 2011; Harms et al., 2000; Zuleta et al., 2020). For each species, the TT test compares its observed relative density in a given habitat to the expected random density obtained from a null distribution based on the torus translation. Species with observed relative densities on a given habitat greater than or equal to the 97.5 percentile of the null distribution were considered significantly positively

associated. Species with observed relative densities on a given habitat between the 2.5 and 97.5 percentiles of the null distribution were considered neutrally distributed. Species neutrally distributed across the three topographic habitats were defined as generalists. We excluded from our analysis species with less than 10 individuals per habitat to avoid issues related to small sample sizes. After filtering, we tested species' habitat associations for a total of 106,230 trees of 441 species. Of these species, 41, 47, and 99 were significantly associated with ridges, slopes, and valleys, respectively; and 168 species were neutrally distributed across the three topographic habitats (i.e., hereafter generalists). The rest of the species (56) were not significantly positively associated with any habitats or neutrally distributed across the three habitats and were not considered in the analysis.

1.5 Growth estimates

We calculated the growth rate (G) of survivor trees as $\frac{DBH_2 - DBH_1}{t_2 - t_1}$, where DBH_1 and DBH_2 correspond to the diameter measurement in the first and second census, respectively; $t_2 - t_1$ is the time difference in years between the censuses. For trees for which the diameter measurement was not made at a height of 1.3 m, we applied a taper correction to obtain the *DBH sensu* Cushman et al. (2021). The *DBH* of those trees was obtained as $DAB * \exp(B*(HOM - 1.3))$ (Metcalf et al., 2009), where *DAB* is the diameter (in cm) at the height of measurement (*HOM*, in meters), and *B* is the tapering factor. The tapering factor was adjusted by Cushman et al. (2021) for trees in the AFDP as $B = 0.14939 - 0.025 * \log(DAB) - 0.02 * \log(HOM) - 0.021 * \log(WSG)$. The wood specific gravity (*WSG*) was obtained for each tree, based on its taxonomic identity, from the literature (Chave et al., 2009; Zanne et al., 2009). When species-level values were not available, we used genus- or family-level averages (Zanne et al., 2009).

We removed extreme outliers from the growth distribution. We excluded trees that increased more than 75 mm yr^{-1} and trees that decreased by more than $4 * SD$, where $SD = 0.0062 * DBH_2 + 0.904$ (sensu Condit et al., 2014). We allowed small negative growth rates in the analysis because excluding these growth rates causes considerable bias and can greatly alter the mean (Condit et al., 1993; Davies et al., 2021). Because growth rate distributions are highly skewed (i.e., many trees grow slowly and few trees grow fast), we transformed the growth estimates using the modulus function (G_T , John and Draper

1980): $G_{\tau} = G^{0.39}$ if $G \geq 0$ and $G_{\tau} = -(-G)^{0.39}$ if $G < 0$. The power of 0.39 was used because it was more effective in reducing the asymmetry of growth in the plot (Figure S1). G_{τ} was used to fit statistical models and test our hypotheses but original, back-transformed growth rates are presented in the main text. Because the mean of transformed variables is not the same as the transformation of the mean $\hat{G} \neq \hat{G}_{\tau}^{1/\tau}$, all of our results are based on the median (Kenfack et al., 2014).

1.6 Mortality estimates

We declared a tree as dead if it had no fresh leaves, sprouts, or buds anywhere, and/or had a dry trunk or if it was not found (Condit, 1998). Mortality (M) was analyzed as a binary variable: 1 for dead, and 0 for alive trees. Mean annual mortality ($\%yr^{-1}$) was estimated from the average marginal probability of tree death (p_{death}) between time 1 (t_1) and time 2 (t_2) as: $(-\log(1-p_{\text{death}})/(t_2-t_1))*100$. After filtering the dataset according to the species habitat association tests and the growth and mortality criteria stated above, the final number of species employed for the models was 352, of which 68,380 individual trees were used for growth models and 79,911 individual trees (12,943 dead) were used in mortality models.

1.7 Statistical analysis

Changes in growth and mortality across topographic habitats (Q1) and across topographic habitats depending on the species' habitat associations (Q2) were modeled separately for each demographic attribute using mixed effects models. Individual tree growth (G_{τ}) was modeled using Linear Mixed-Effects Models (LMMs) assuming a normal error distribution. Tree mortality (M) was modeled using the logit link function in Generalized Linear Mixed-Effects Models (GLMMs) assuming binomial errors. All models had species random effects to account for intraspecific variability in growth and the probability of mortality and were fitted using the lme4 R package (Bates et al., 2015). As both growth and the probability of mortality vary with ontogeny, we also included the log-transformed DBH as a fixed effect in the models. In R lme4 notation, the full model to answer Q1 was: *demographic parameter (G_{τ} or M) ~ Habitat * log(DBH) + (1 | Species)*; the full model for Q2 was: *demographic parameter (G_{τ} or M) ~ Habitat *Habitat_association* log(DBH) + (1 | Species)*.

We fitted all possible combinations of the explanatory variables including the second-order interactions among them; that is, a total of 5 models for Q1 and 8 models for Q2, ranging from the full model (all the variables and their second-order interactions) to the null model (only intercept) for each demographic rates. The mixed-effects models were fitted by maximum likelihood estimation (Laplace approximation) using the LME4 package (Bates et al 2015) and the model residuals were evaluated using the DHARMA package (Hartig 2021). We ranked models, selected the best one according to the second-order Akaike's information criterion (AIC) using the AICcmodavg package (Mazerolle, 2020), and calculated the conditional and marginal coefficient of determination using the MuMIn package (Barton, 2022).

1.8 Test for the demographic hypotheses: *best-at-home* and *resident-advantage*

To evaluate the role of species habitat associations in shaping overall growth and mortality patterns, we first tested for the effect the habitat association term in the models and then performed multiple comparison tests using the *lsmeans* package using Tukey test (Lenth, 2016) (**Figure 1-1**). The *best-at-home* hypothesis was evaluated by testing for differences in the demographic performance of species at the habitat to which they are associated (home) versus their performance in habitats to which they are not associated (**Figure 1-1a**). Within each habitat, the *resident-advantage* hypothesis was tested by comparing the performance of species associated to that habitat versus the performance of species that are not associated but are still found in the habitat (**Figure 1-1b**). Finally, we tested for differences in the performance of generalist species across habitat types.

All statistical analyses were performed in R (R Core Team, 2021).

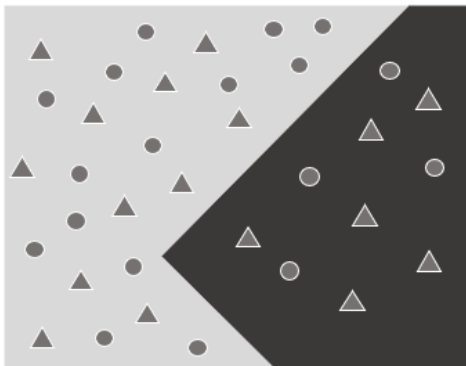
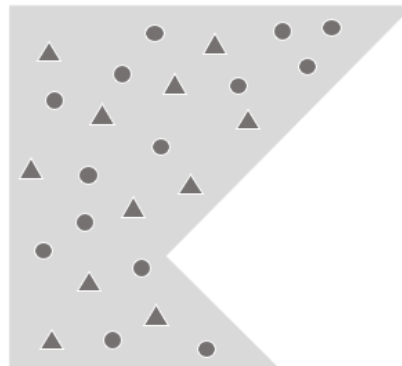
(a) *Best-at-home* hypothesis**(b)** *Resident-advantage* hypothesis

Figure 1-1: Schematic representation of the demographic hypotheses for a single species. Circles represent trees of a species associated with the grey habitat; triangles represent trees of other species. (a) The best-at-home hypothesis states that, trees located on their home (circles on grey) habitat will perform better than trees located away (circles on the black habitat). (b) The resident-advantage hypothesis states that within the grey habitat, trees associated with that habitat (circles) will perform better than trees from other species that are not associated with the habitat (triangles).

2. Results

2.1 Do tree growth and mortality rates vary across topographic habitats?

Both tree growth and mortality were significantly different across topographic habitats and exhibited strong size-dependency (**Table 2-1**). On average, growth and mortality rates were higher for trees on valleys than for trees on slopes and ridges (**Figure 2-1**). The predicted tree growth decreased from 0.56 mm yr^{-1} (95% CI $0.52 - 0.61 \text{ mm yr}^{-1}$) on valleys to 0.47 mm yr^{-1} (95% CI $0.44 - 0.51 \text{ mm yr}^{-1}$) on slopes and 0.41 mm yr^{-1} (95% CI $0.38 - 0.45 \text{ mm yr}^{-1}$) on ridges (**Figure 2-1a**). Likewise, annual mean mortality rates decreased from $3.20\% \text{ yr}^{-1}$ (95% CI $2.97 - 3.45\% \text{ yr}^{-1}$) for trees in valleys to $2.10\% \text{ yr}^{-1}$ (95% CI $1.94 - 2.28\% \text{ yr}^{-1}$) in slopes and $2.12\% \text{ yr}^{-1}$ (95% CI $1.95 - 2.31\% \text{ yr}^{-1}$) in ridges (**Figure 2-1c**). Tree growth increased and mortality decreased with tree diameter consistently across topographic habitats (**Figure 2-1b, d**).

Table 2-1: Comparison of mixed-effects models for tree growth (linear) and mortality (logistic) as a function of the trees' topographic habitat (TopoHab) and size (log(DBH)). Models are ranked according to the difference in the Akaike information criterion value (AICc) compared to the model with the lowest AIC (best model, first row) (Δ AICc) (Burnham and Anderson, 2002). LL: log-likelihood model. All models included a random intercept effect for species (1 | Species).

Growth			
Model	AICc	Δ AICc	LL
G _T ~ TopoHab + log(DBH)	115,400.0	0.0	-57,694.0
G _T ~ TopoHab * log(DBH)	115,402.4	2.4	-57,693.2
G _T ~ log(DBH)	115,654.5	254.5	-57,823.3
G _T ~ TopoHab	119,841.5	4441.5	-59,915.8
G _T ~ 1	120,120.6	4720.6	-60,057.31
Mortality			
M ~ TopoHab * log(DBH)	65,293.3	0.0	-32,639.6
M ~ TopoHab + log(DBH)	65,311.2	17.9	-32,650.6
M ~ log(DBH)	65,697.7	404.4	-32,845.8
M ~ TopoHab	65,731.2	437.9	-32,861.6
M ~ 1	66,098.4	805.1	-33,047.2

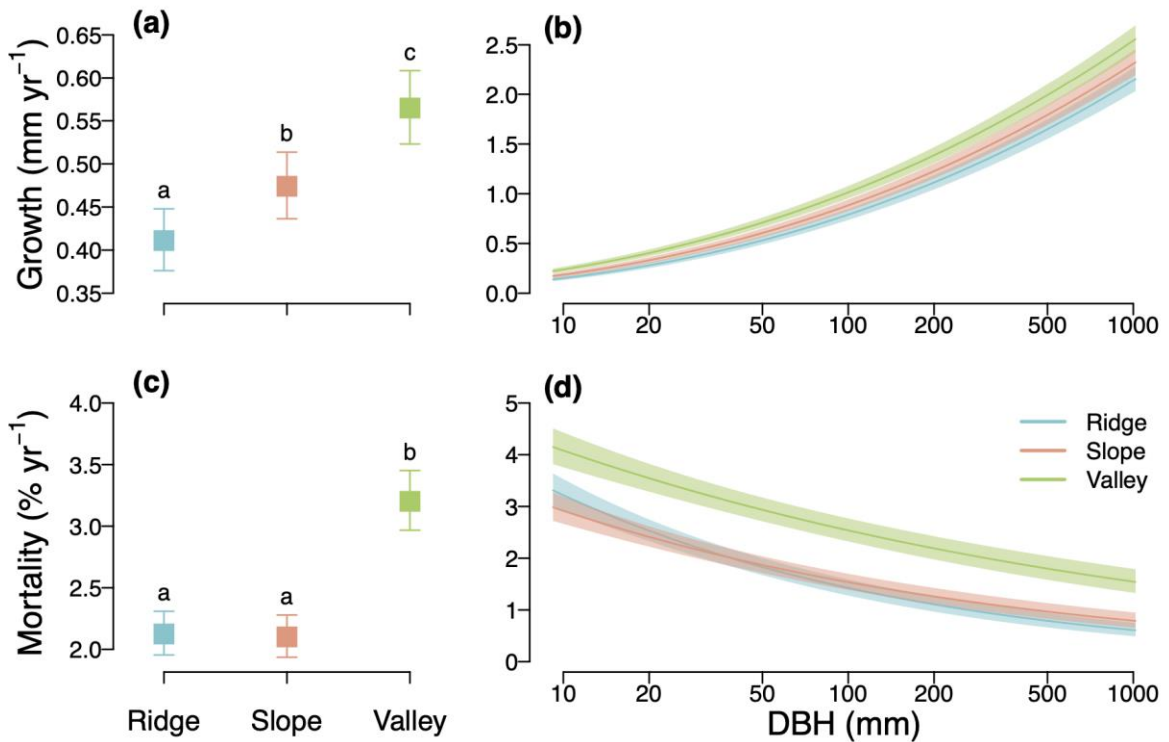


Figure 2-1: Annual tree growth (a,b) and mortality rates (c,d) varied across trees' topographic habitats (valleys, slopes, and ridges) and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon. In all cases the back-transformed predicted growth and mortality rates are shown from the best models (Table 1). Squares in (a,c) and lines in (b,d) correspond to predicted means from the best models (see Methods). The error bars in (a,c) and envelopes in (b,d) correspond to 95% confidence intervals. Different letters indicate significant differences across topographic habitats (Tukey test).

2.2 Are patterns across topographic habitats maintained when species' habitat associations are included?

When the species habitat association term was included in the models, it was maintained in the best models for both demographic rates (Table 2-2). However, its inclusion did not affect the overall trend across topographic habitats (i.e., higher tree mortality and growth in the valleys compared to slopes and ridges) or their size dependency (Figure 3). Overall, tree growth did not vary across species' habitat associations (Figure 3a) whereas tree mortality was significantly higher for generalists and for species associated with slopes than for species associated with valleys and ridges (Figure 3b).

Table 2-2: Comparison of the Mixed-Effects Models to predict tree mortality (with GLMMs) and growth rate (with LMMs) as a function of the trees' topographic habitat (TopoHab), size (log(DBH)), and the topographic habitat association (HabAss). Models are ranked according to the difference in Akaike information criterion value the second-order ($\Delta AICc$) compared to the best model (Burnham and Anderson, 2002). LL: log-likelihood of each model. All models included a random intercept effect for species (1 | Species). Note that the AICc for the null models and the models as a function of the Log(DBH) as a single fixed effect are the same as in Table 1-1.

Growth			
Model	AICc	$\Delta AICc$	LL
G _T ~ HabAss * TopoHab * log(DBH)	115,389.7	0.0	-57,668.8
G _T ~ HabAss * TopoHab + log(DBH)	115,398.8	9.1	-57,684.4
G _T ~ HabAss + TopoHab + log(DBH)	115,402.0	12.3	-57,692.0
G _T ~ HabAss * log(DBH)	115,644.3	254.6	-57,812.2
G _T ~ HabAss + log(DBH)	115,654.6	264.9	-57,820.3
G _T ~ HabAss * TopoHab	119,842.2	4,452.5	-59,907.1
G _T ~ HabAss + TopoHab	119,844.1	4,454.4	-59,914.0
G _T ~ HabAss	120,120.8	4,731.1	-60,054.4
Mortality			
M ~ HabAss * TopoHab * log(DBH)	65,185.8	0.0	-32,567.9
M ~ HabAss * TopoHab + log(DBH)	65,212.6	26.8	-32,592.3
M ~ HabAss + TopoHab + log(DBH)	65,287.5	101.7	-32,635.7
M ~ HabAss * TopoHab	65,631.3	445.5	-32,802.7
M ~ HabAss + TopoHab	65,680.4	494.6	-32,834.2
M ~ HabAss + log(DBH)	65,685.1	499.3	-32,833.6
M ~ HabAss * log(DBH)	65,707.3	521.5	-32,846.7
M ~ HabAss	66,081.4	895.6	-33,035.7

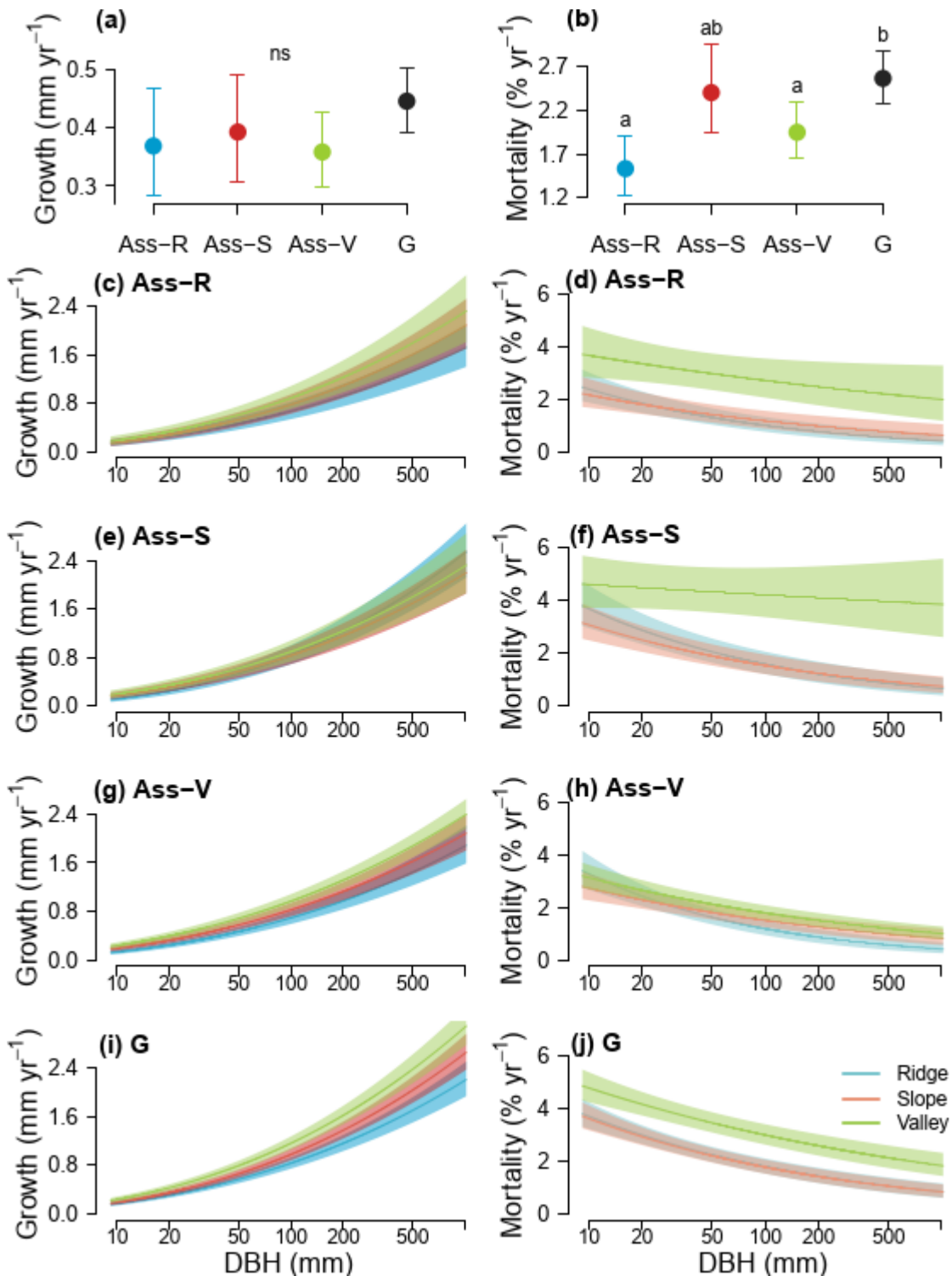


Figure 2-2: Variation in annual tree growth (a,c,e,g,i) and mortality rates (b,d,f,h,g) across species association habitats (Ass-R: associated with ridges; Ass-S: associated with slopes; Ass-V: associated with valleys; G: generalist), topographic habitats (valleys, slopes, and ridges), and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon. In all cases the back-

transformed predicted growth and mortality rates are shown from the best models (Table 2). Circles in (a,b) and lines in (c–i) correspond to predicted means from the best models (see Methods). The error bars in (a,b) and envelopes in (c–i) correspond to 95% confidence intervals. Different letters indicate significant differences across species habitat associations (Tukey test).

We did not find evidence to support the demographic hypotheses. Tree species associated to a given habitat did not perform better on their home habitat than elsewhere (Figure 4); and resident species did not perform better than foreigner species within any given habitat (Figure 5). The only exception was the growth for species associated with valleys, which grew the most on their home habitat than elsewhere (Figure 4c), and died the less in valleys (resident) than species associated with other habitats or generalists (foreigners) (Figure 5f). Generalist species did not perform similarly across habitat types (Figures 4d and 3h) or had higher performance within a given habitat compared to other species (Figure 5).

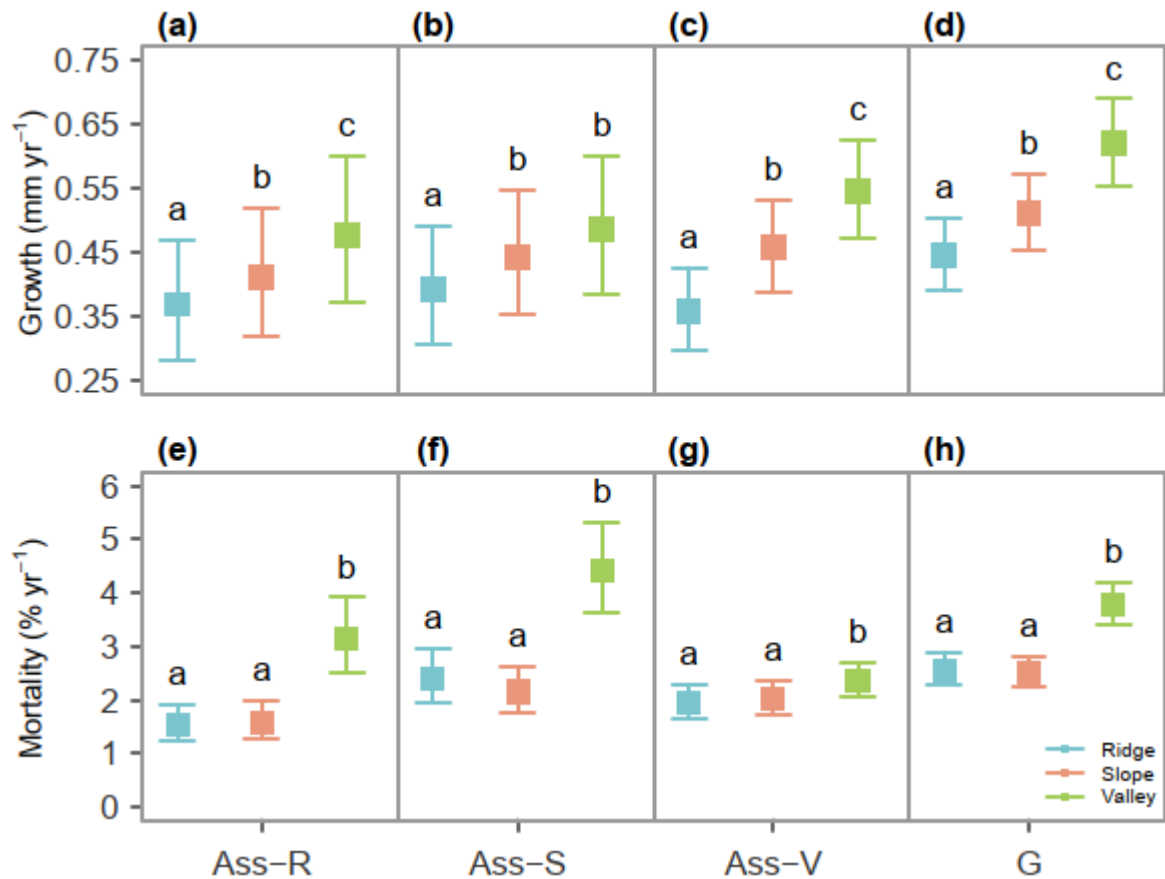


Figure 2-3: Predicted annual growth (a–d) and mortality rates (e–h) of trees by habitat association categories (Ass-R: associated with ridges; Ass-S: associated with slopes; Ass-V: associated with valleys; G: generalist) across each topographic habitat (ridges, slopes, or valleys) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon (*best-at-home* hypothesis). Error bars correspond to 95% confidence intervals. Within each habitat association category (panels), different letters indicate significant differences across topographic habitats (Tukey test).

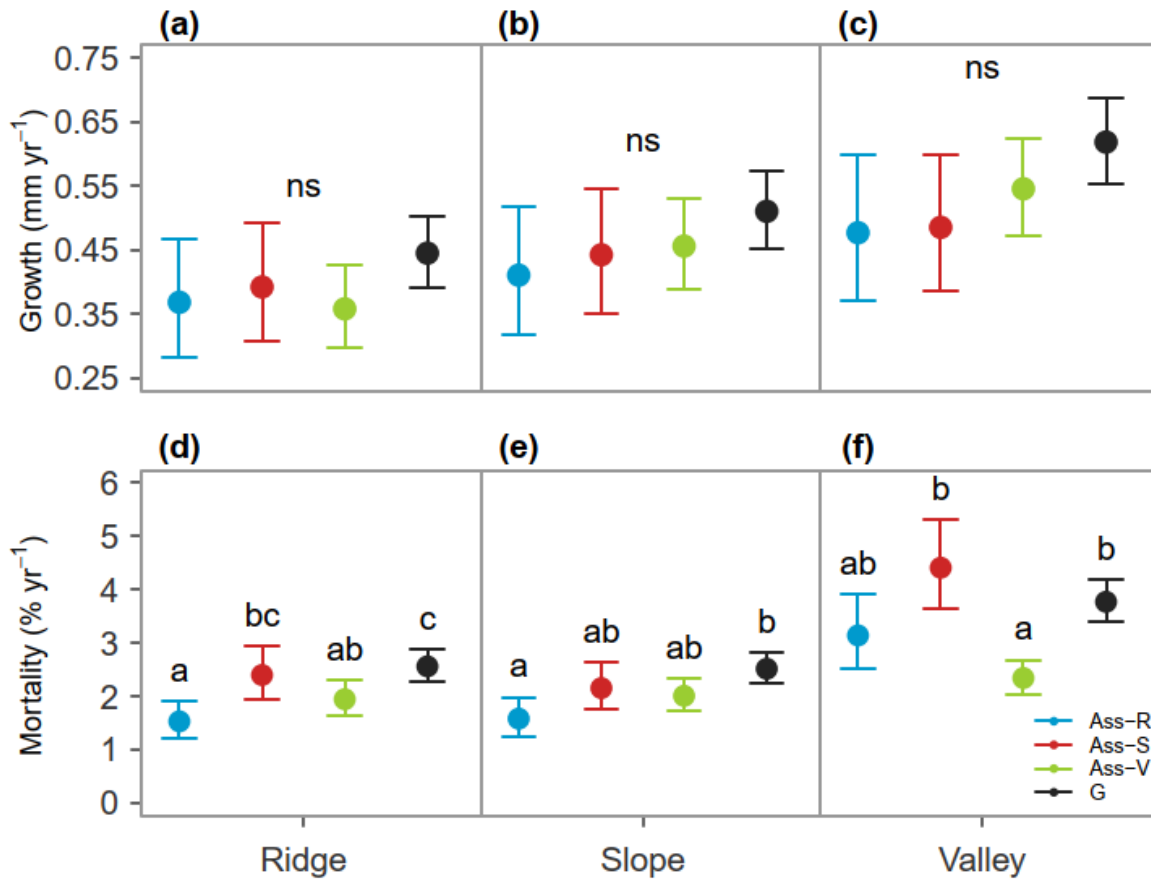


Figure 2-4: Predicted annual growth (a–d) and mortality rates (e–h) of trees by topographic habitat (ridges, slopes, or valleys) across each habitat association category (Ass-R: associated with ridges; Ass-S: associated with slopes; Ass-V: associated with valleys; G: generalist) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon (*resident-advantage* hypothesis). Error bars correspond to 95% confidence intervals. Within each topographic habitat (panels), different letters indicate significant differences across habitat association categories (Tukey test).

3. Discussion

Topography has been shown to control forest structure, functioning and composition (Chuyong et al., 2011; Comita et al., 2007; Harms et al., 2001; Jucker et al., 2018; Russo et al., 2005; Sousa et al., 2020; Zuleta et al., 2017, 2020). Despite little elevational change, our results showed marked variation in tree growth and mortality across topographic habitats that were in line with expectations based on the acquisitive-conservative strategies (Russo et al., 2008, 2021): trees on valleys have consistently high mortality and growth rates than trees on ridges regardless the species habitat associations and tree size. Our findings suggest that even small differences in topography can translate into differences in access to soil water affecting tree performance, which has implications for understanding species' ecological strategies and forest responses to climate change.

Wetter habitats like valleys generally have trees with acquisitive strategies (Costa et al., 2022; Oliveira et al., 2021; Santiago et al., 2018; Wright et al., 2010) meaning that they prioritize growth over safety and are therefore more vulnerable to droughts (Harms et al., 2001; Itoh et al., 2012; Oliveira et al., 2019) or pathogens (J. M. McDowell & Simon, 2008) compared to trees on ridges. Trees with acquisitive strategies also have high risk of embolism by having higher vessel diameter (Oliveira et al., 2021; Poorter et al., 2010), and higher turgor loss points (Santiago et al., 2018). In this study, the high growth and mortality of trees in valleys supports the expectation based on the acquisitive-conservative strategies and could have been exacerbated by the 2010 Amazon drought, which preferentially killed more trees in the valleys than in the ridges of this forest (Zuleta et al., 2017) and has been reported to promote growth in forests with shallow water tables (<5 m) (Costa et al., 2022; Esteban et al., 2021).

Spatial variation in resource availability influence trees' response based on the tolerance–responsiveness strategies (Russo et al., 2021). The higher mortality of slope-affiliated and generalist species compared to ridge- and valley-affiliated species could be in line with other studies carried out in the Barro Colorado Island (BCI), where the mortality of both trees and seedlings was particularly high for slope specialists and generalist during drought events (Comita & Engelbrecht, 2009; Condit 1995). While generalist species are more plastic and responsive to environmental changes among habitats (Fortunel et al., 2019; Oliveira et al., 2019), they also have high costs in terms of fitness or performance as a consequence of limitations to plasticity (Review of DeWitt et al., 1998). In this forest, species associated with slopes and generalists have been recently reported to be more similar in terms of branch, leaf, and stomatal traits and to respond similarly to the topographic gradient than species associated with valleys or ridges (Zuleta et al., In Press). The similarity in functional traits as well as in growth and mortality between slope specialists and generalists in this forest may be due to the small topographic gradient (~22m total elevational change). In such a small elevational change, species associated to slopes will have trees subjected to intermediate environmental factors between ridges and valleys that confer them high plasticity similar to generalist species.

Including the species' habitat associations significantly improved statistical models of growth and mortality in this study. However, the higher mortality and growth for trees in valleys compared to trees in ridges was maintained regardless the species habitat association class. This result do not support the hypothesis that species' habitat associations emerge from a high performance of tree species in their preferred habitat compared to other habitats (best-at-home) and from a high performance of the species compared to other trees in the same habitat (resident-advantage). Similar studies for trees larger than 1 cm in DBH did not find evidence for these demographic hypotheses along a topographic gradient in Cameroon (Kenfack et al., 2014) and a soil texture gradient in Malaysia (Russo et al., 2005). At the seedling stage, however, multiple studies have found pronounced differences in performance between species habitat association classes (Comita & Engelbrecht, 2009; Fortunel et al., 2016). Altogether, these results suggest that environmental controls operating at early life stages are most probably the cause of the species' habitat association patterns observed in adult trees of tropical forests. Alternatively, the lack of support for the demographic hypotheses studied here,

could either be the result of randomness and dispersal limitation (Richard Condit et al., 2002; Hubbell, 2001; Hubbell et al., 1999), or due to unmeasured environmental variation (e.g., light) in this forest (Zuleta et al., 2020).

4. Conclusions

In this study we show that growth and mortality rates varied substantially across topographic habitats. This was a consistent pattern regardless of the species' habitat association and tree size. These results suggest a strong control of hydrological factors on the demography of this Amazon *terra firme* forest. Considering that more severe and frequent droughts are predicted for Amazon forests (Duffy et al., 2015), further studies are needed to better understand the vulnerability of trees along hydrological gradients (e.g., Oliveira et al., 2019), which will improve our ability to predict the fate forests under climate change.

5. Appendix A: Mean estimated parameters and the 95% confidence intervals of the best mixed models.

Table A1: Mean estimated parameters and the 95% confidence intervals (CI) of the best linear mixed models predicting transform annual tree growth rate the growth using a modulus transformation (power 0.39) as a function of topographic habitat (ridges, slopes, or valleys), and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon.

Growth			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p-value</i>
(Intercept)	0.05	0.01 – 0.08	0.004
TopoHab [Slope]	0.04	0.03 – 0.05	<0.001
TopoHab [Valley]	0.09	0.08 – 0.10	<0.001
log(DBH)	0.19	0.18 – 0.19	<0.001
Random Effects			
σ^2	0.31		
T00 spcode	0.04		
ICC	0.12		
N _{spcode}	352		
Observations	68380		
Marginal R ² / Conditional R ²	0.076 / 0.191		

Table A2: Mean estimated parameters and the 95% confidence intervals (CI) of the best general linear mixed models predicting the probability of death among census as a function of topographic habitat (ridges, slopes, or valleys), and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon.

Mortality			
<i>Predictors</i>	<i>Odds Ratios</i>	<i>CI</i>	<i>p_value</i>
(Intercept)	0.57	0.47 – 0.70	<0.001
TopoHab [Slope]	0.74	0.59 – 0.94	0.014
TopoHab [Valley]	0.92	0.74 – 1.15	0.478
log(DBH)	0.68	0.65 – 0.72	<0.001
TopoHab [Slope] * log(DBH)	1.08	1.01 – 1.16	0.022
TopoHab [Valley] * log(DBH)	1.16	1.09 – 1.24	<0.001
Random Effects			
σ^2	3.29		
T ₀₀ spcode	0.52		
ICC	0.14		
N _{spcode}	352		
Observations	79911		
Marginal R ² / Conditional R ²	0.028 / 0.162		

Table A3: Mean estimated parameters and the 95% confidence intervals (CI) of the best linear mixed models predicting transform annual tree growth rate the growth using a modulus transformation (power 0.39) as a function of association habitats (valleys, slopes, ridges, generalist), topographic habitat (ridges, slopes, or valleys), and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon.

Growth			
<i>Predictors</i>	<i>Estimates</i>	<i>CI</i>	<i>p_value</i>
(Intercept)	0.08	0.01 – 0.15	0.030
HabAss [Ridge]	0.03	-0.09 – 0.14	0.651
HabAss [Slope]	-0.15	-0.27 – -0.03	0.016
HabAss [Valley]	-0.04	-0.15 – 0.08	0.535
TopoHab [Slope]	-0.02	-0.10 – 0.05	0.552
TopoHab [Valley]	0.01	-0.07 – 0.09	0.878
log(DBH)	0.19	0.17 – 0.20	<0.001
HabAss [Ridge] * TopoHab [Slope]	-0.02	-0.14 – 0.11	0.794
HabAss [Slope] * TopoHab [Slope]	0.17	0.05 – 0.30	0.006
HabAss [Valley] * TopoHab [Slope]	0.11	-0.02 – 0.23	0.101
HabAss [Ridge] * TopoHab [Valley]	-0.02	-0.17 – 0.13	0.807
HabAss [Slope] * TopoHab [Valley]	0.17	0.02 – 0.31	0.025
HabAss [Valley] * TopoHab [Valley]	0.11	-0.01 – 0.22	0.071
HabAss [Ridge] * log(DBH)	-0.02	-0.05 – 0.00	0.087
HabAss [Slope] * log(DBH)	0.03	0.00 – 0.06	0.022
HabAss [Valley] * log(DBH)	-0.01	-0.03 – 0.02	0.619
TopoHab [Slope] * log(DBH)	0.02	-0.00 – 0.04	0.103
TopoHab [Valley] * log(DBH)	0.03	0.00 – 0.05	0.017

(HabAss [Ridge] * TopoHab [Slope]) * log(DBH)	0.00	-0.03 – 0.04	0.923
(HabAss [Slope] * TopoHab [Slope]) * log(DBH)	-0.05	-0.09 – -0.02	0.004
(HabAss [Valley] * TopoHab [Slope]) * log(DBH)	-0.02	-0.06 – 0.01	0.194
(HabAss [Ridge] * TopoHab [Valley]) * log(DBH)	-0.00	-0.04 – 0.04	0.901
(HabAss [Slope] * TopoHab [Valley]) * log(DBH)	-0.06	-0.10 – -0.02	0.005
(HabAss [Valley] * TopoHab [Valley]) * log(DBH)	-0.02	-0.06 – 0.01	0.121
Random Effects			
σ^2	0.31		
T00 spcode	0.04		
ICC	0.12		
N _{spcode}	352		
Observations	68380		
Marginal R ² / Conditional R ²	0.079 / 0.192		

Table A4: Mean estimated parameters and the 95% confidence intervals (CI) of the best general linear mixed models predicting the probability of death among census as a function of association habitats (valleys, slopes, ridges, generalist), topographic habitat (ridges, slopes, or valleys), and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon.

Mortality			
<i>Predictors</i>	<i>Odds Ratios</i>	<i>CI</i>	<i>p_value</i>
(Intercept)	0.62	0.46 – 0.84	0.002
HabAss [Ridge]	0.69	0.40 – 1.19	0.185
HabAss [Slope]	1.13	0.66 – 1.94	0.659
HabAss [Valley]	1.17	0.67 – 2.04	0.586
TopoHab [Slope]	0.96	0.66 – 1.39	0.840
TopoHab [Valley]	1.03	0.73 – 1.46	0.855
log(DBH)	0.71	0.65 – 0.77	<0.001
HabAss [Ridge] * TopoHab [Slope]	0.71	0.36 – 1.41	0.331
HabAss [Slope] * TopoHab [Slope]	0.72	0.39 – 1.33	0.294
HabAss [Valley] * TopoHab [Slope]	0.54	0.28 – 1.06	0.072
HabAss [Ridge] * TopoHab [Valley]	0.87	0.44 – 1.75	0.705
HabAss [Slope] * TopoHab [Valley]	0.55	0.29 – 1.04	0.065
HabAss [Valley] * TopoHab [Valley]	0.57	0.32 – 1.03	0.062
HabAss [Ridge] * log(DBH)	0.95	0.82 – 1.10	0.485
HabAss [Slope] * log(DBH)	0.95	0.82 – 1.10	0.464
HabAss [Valley] * log(DBH)	0.88	0.75 – 1.03	0.100
TopoHab [Slope] *	1.01	0.90 – 1.12	0.924

log(DBH)			
TopoHab [Valley] * log(DBH)	1.12	1.01 – 1.24	0.028
(HabAss [Ridge] * TopoHab [Slope]) * log(DBH)	1.12	0.91 – 1.37	0.282
(HabAss [Slope] * TopoHab [Slope]) * log(DBH)	1.07	0.89 – 1.29	0.479
(HabAss [Valley] * TopoHab [Slope]) * log(DBH)	1.21	1.00 – 1.47	0.052
(HabAss [Ridge] * TopoHab [Valley]) * log(DBH)	1.15	0.93 – 1.41	0.191
(HabAss [Slope] * TopoHab [Valley]) * log(DBH)	1.27	1.06 – 1.53	0.011
(HabAss [Valley] * TopoHab [Valley]) * log(DBH)	1.10	0.93 – 1.30	0.270
Random Effects			
σ^2	3.29		
T00 _{spcode}	0.47		
ICC	0.13		
N _{spcode}	352		
Observations	79911		
Marginal R ² / Conditional R ²	0.041 / 0.162		

6. Appendix B: Modulus – transformed DBH growth

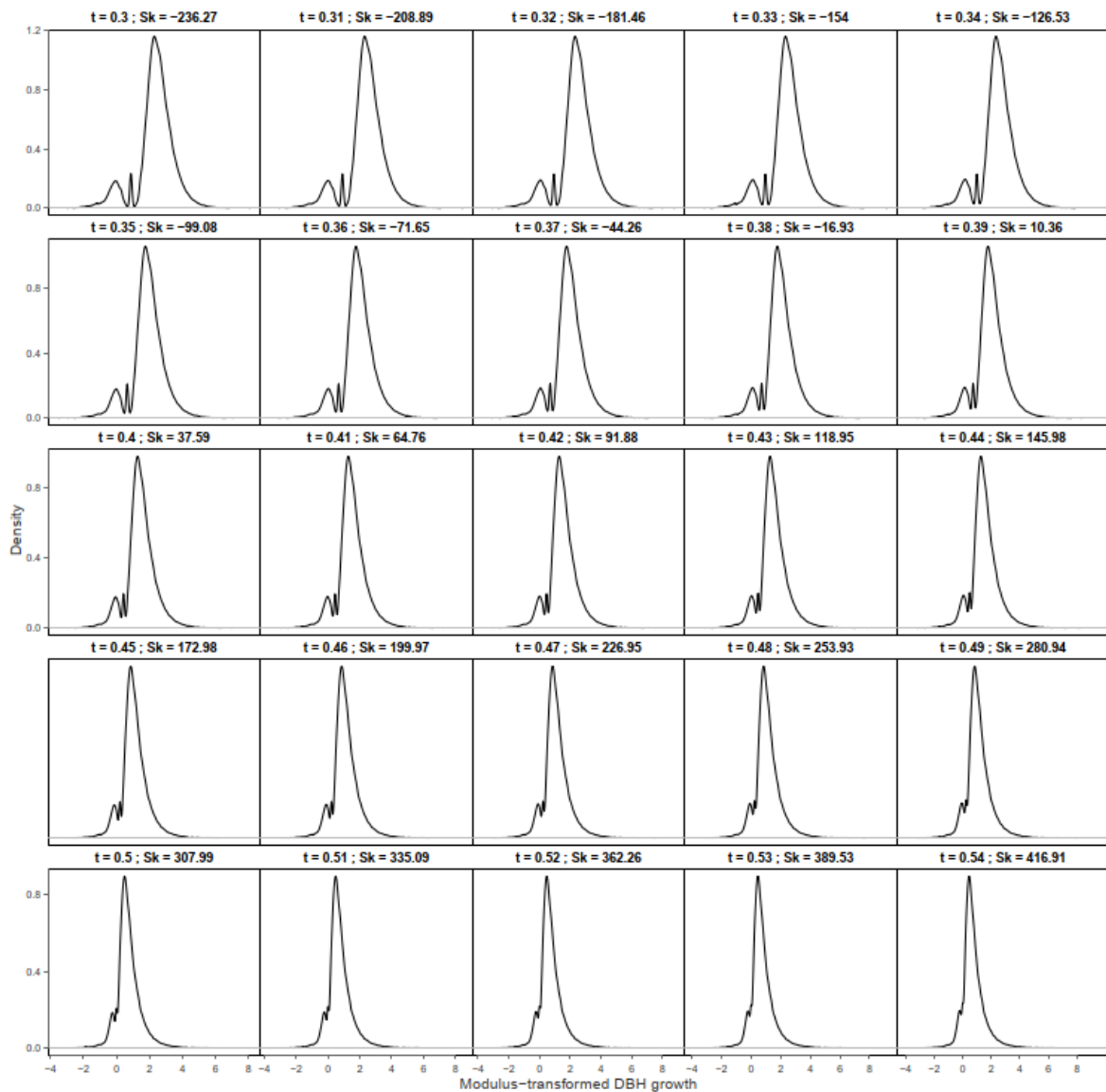


Figure B1. Distribution of modulus-transformed DBH growth values from individual trees in the Amacayacu Forest Dynamics Plot. In the range $t \in (0.3, 0.54)$, the transformed growth rates have the lowest skewness (Sk) at the the power of $t = 0.39$.

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