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RESEARCH ARTICLE

Marked tree demographic variation along subtle elevation differences partially explains species' habitat associations in an Amazonian forest

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Abstract

1. It is widely recognized that large-scale topographic variation affects the distribution of tree diversity, yet the effects of topography at smaller scales are less appreciated but can be no less consequential. We evaluated how small-scale topographic variation affects tree demography and diversity in a hyperdiverse Amazonian forest where species distributions respond strongly to elevation differences as small as 22 m.
2. For topographically structured species distributions to arise, species should grow and survive (perform) better in the topographic habitat they are associated with (*best-at-home* hypothesis), and they should outperform other species that are found, but not strongly aggregated, in that habitat (*resident-advantage* hypothesis). Here, we tested these demographic hypotheses using data on the growth and mortality of 79,911 trees (352 species) among three topographic habitats (valleys, slopes and ridges) in the 25-ha Amacayacu Forest Dynamics Plot.
3. Despite the small variation in elevation, there was significant community-level variation in growth and mortality among topographic habitats: trees growing in valleys, where soil moisture is higher, had significantly higher growth and mortality rates than those growing on slopes and ridges. However, tree growth rates did not depend on, and mortality rates varied inconsistently with, species' habitat association. Our results partially support the *best-at-home* or *resident-advantage* hypotheses for valley-associated species, which grew best in their home habitat (valleys) than elsewhere and had lower mortality there compared to slope-associated or generalist species (foreigners). For slope- and ridge-associated species, our results did not support these hypotheses at the community level.

Species-specific analyses revealed that 73 out of the 352 species analysed at the community level supported either hypothesis.

4. *Synthesis*. Our findings show that even small differences in elevation can lead to biologically meaningful variation in resource access that translates into significant differences in tree growth and survival. However, resource access could not fully explain the patterns of topographically driven demographic variation we observed. While certain species may still exhibit home and resident advantages in specific habitats, even when community-level averages partially reflect this pattern, alternative hypotheses are likely driving the patterns observed at the community level.

KEYWORDS
demographic variation, drought, environmental filtering, forest dynamics, topography, tropical forests, species habitat associations

1 | INTRODUCTION

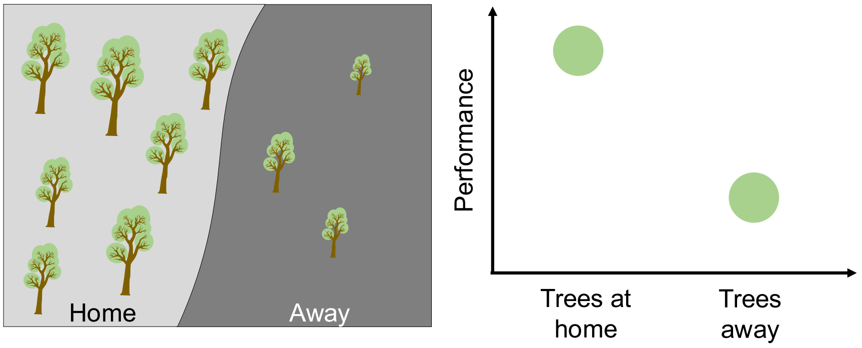
Species turnover structures diversity at a range of spatial scales in tropical forests (Comita et al., 2010; Condit et al., 2002; Tuomisto et al., 2003). Variation in geology, soil fertility and climate creates a mosaic of forest composition at intermediate and regional scales (Duque et al., 2002; John et al., 2007; Kochsiek et al., 2013; Quesada et al., 2011; Tuomisto et al., 2003). Less appreciated, however, is that small-scale variation in topography can drive species turnover at much more local scales ($<1\,km^2$), resulting in tree species being associated with distinct topographic habitats, despite relatively small differences in topographic position (Chuyong et al., 2011; Fortunel et al., 2016; Zuleta et al., 2020). Topography influences environmental conditions and the availability of resources and therefore plays a key role in determining variation in species composition (Fortunel et al., 2016; McNichol et al., 2022; Zuleta et al., 2020), functioning (Cosme et al., 2017; Jucker et al., 2018; Zuleta et al., 2022) and forest response to severe disturbances, like droughts and storms (Cushman et al., 2021; O'Brien & Escudero, 2022; Valencia et al., 2009; Zuleta et al., 2017). However, the specific demographic processes driving these topographic effects are still debated. The goal of this study was to evaluate how small-scale topographic variation structures tree demography and diversity in a hyperdiverse Amazonian forest where tree species are strongly associated with or repelled from topographic habitats differing in as little as 22 m of elevation (Zuleta et al., 2020).

Greater access to resources generally increases the growth and reduces the mortality of individual trees (Chapin III et al., 2011; Kobe et al., 1995; Poorter et al., 2008; Wright, 2002). For example, trees in valleys have been found to grow faster than conspecifics on ridges (Comita & Engelbrecht, 2009; John et al., 2007; Russo et al., 2005). Moreover, individual trees that grow faster generally have higher survival (Kobe, 1996; Kobe et al., 1995; Russo et al., 2021). However, resource availability also shapes the strategies of the tree species found on a habitat (Baltzer et al., 2007; Kraft et al., 2008; Russo et al., 2005). This is because across species, trees align along an interspecific slow-fast continuum, reflecting a trade-off between faster growth with lower survival versus slower growth with higher survival (the growth-survival trade-off) (Harms et al., 2001; Hubbell, 2001; Kitajima & Myers, 2008; Russo et al., 2008, 2021; Wright et al., 2010). Species at the slower end of the growth-survival trade-off are not only often found in more resource-limited habitats, such as ridges (Cosme et al., 2017), but also, individuals of these species tend to grow more slowly and have lower mortality rates (Costa et al., 2022; Oliveira et al., 2021; Russo et al., 2021). Conversely, species at the faster end are often found in less resource-limited habitats (Cosme et al., 2017) and tend to grow faster and have higher mortality rates (Costa et al., 2022; Oliveira et al., 2021; Russo et al., 2021). Both intraspecific and interspecific effects jointly influence demographic variation among habitats.

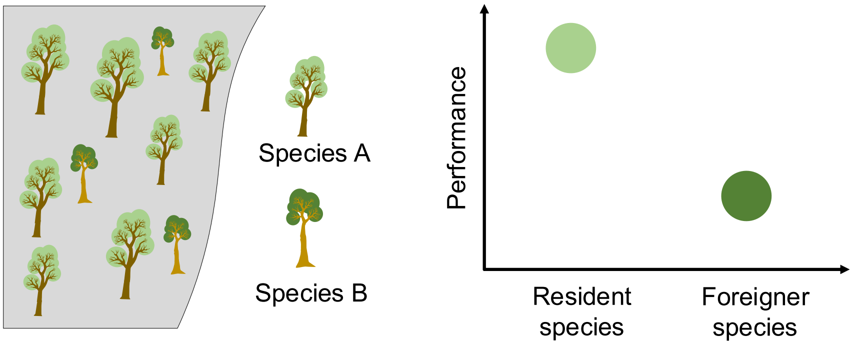
The interaction between interspecific strategies (slow-fast) and intraspecific responses to topographically driven below-ground resource availability should act to filter species based on their phenotypes, favouring those suited to local conditions and limiting those less suited (Chesson, 1985; Kraft et al., 2015; Wright, 2002). If so, then species associated with a given habitat should become locally abundant in that habitat because of two reasons. First, at the intraspecific level, individuals of a species perform better (lower mortality and faster growth rates) in their preferred habitat (home) than in other habitats to which they are not associated (away) (hereafter the *best-at-home* hypothesis; Figure 1a). And second, at the interspecific level, within a specific habitat, the species associated with that habitat (resident) performs better than other species that are present, but not specifically associated with that habitat (foreigner) (hereafter the *resident-advantage* hypothesis; Figure 1b) (Chesson, 1985; Fortunel et al., 2016; Kenfack et al., 2014). The *best-at-home* hypothesis addresses how performance varies within species among habitats (intraspecific),

FIGURE 1 Schematic representation of the hypotheses for the demographic mechanisms enabling species associations with topographic habitats. Species A (trees with light green foliage and dark brown wood) represents a species associated with the light grey habitat (home), and species B (trees with dark green foliage and light brown wood) represent individuals of another species that is not associated with the grey habitat. Tree size symbolizes performance, with larger trees performing better.
(a) Best-at-home hypothesis: Within a species, trees located in their home habitat (species A, a resident on light grey) will perform better (higher survival and growth rates) than trees of the same species located in less habitats (away).
(b) Resident-advantage hypothesis: A species associated with a particular habitat (a resident species—species A) will perform better than a species not associated with that habitat (a foreigner species—species B).

(a) *Best-at-home* hypothesis: intraspecific performance across habitats



(b) *Resident-advantage* hypothesis: interspecific performance in a given habitat



whereas the *resident–foreign* hypothesis compares performance between species in a given habitat (interspecific).

We investigated the demographic drivers of tree species distributions among three topographic habitats (valleys, slopes, ridges) in the 25-ha Amacayacu Forest Dynamics Plot (AFDP), an aseasonal *terra firme* forest in the Colombian Amazon. In this forest plot, valleys are generally non-flooded but wetter than slopes and ridges (Figure S1 in Zuleta et al., 2022). We focused on the demographic (tree growth and mortality) mechanisms of habitat filtering after juvenile trees (>1 cm in diameter at breast height, DBH) are established, rather than the mechanisms determining where trees are initially established (seed dispersal, seedling establishment). We asked: (1) At the community level, do tree growth and mortality rates vary among topographic habitats? (2) Do species' growth and mortality rates depend on species' habitat associations? (3) Are the observed patterns of species growth and mortality among habitats consistent with either the *best-at-home* or the *resident-advantage* hypotheses? We expected individual trees growing in valleys to have better performance (faster growth and lower mortality) than trees growing on slopes and ridges, due to the higher soil water availability in valleys. We also expected species associated with valleys to have higher growth and mortality than species associated with slopes and ridges. However, we expected these patterns to vary depending on both the habitat where an individual tree is growing and species' habitat associations. Within a species, trees will perform better in their home habitat than in other habitats due to preferred environmental conditions, in line with the *best-at-home* hypothesis. Additionally, resident species—that is, species in their home habitats—will have better performance than foreigners as per the *resident-advantage* hypothesis.

2 | MATERIALS AND METHODS

2.1 | 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 (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 3216 mm (with no months below 100 mm). Relative humidity is 86% and mean annual temperature is 25.8°C (Zuleta et al., 2020). The plot is 25 ha in area (500 m × 500 m) and harbours ~1200 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), all of them used in this study. 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). In general, soils in the AFDP are poor, with high acidity and low base saturation due to the abundance of minerals like kaolinite and quartz and are not correlated with topographic habitats (Zuleta et al., 2020). Fieldwork permits were granted through the 'Parcela Permanente Amacayacu – Convenio No. 16' agreement held between Parques Nacionales Naturales de Colombia, the Instituto Amazónico de Investigaciones Científicas SINCHI and Universidad Nacional de Colombia sede Medellín.

2.2 | Forest censuses

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

2.3 | Topographic habitat definition

Three topographic habitats—ridges, slopes and valleys—were defined in previous studies by Zuleta et al. (2017, 2020) in the AFDP. These three habitats were chosen because they best explain tree species distributions in this forest, even after testing multiple habitat arrangements based on soil chemistry and topography (Zuleta et al., 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 neighbours. Quadrat slope was estimated by dividing each quadrat into four sub-quadrats, calculating the slope within each sub-quadrat 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, respectively. 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.

2.4 | Species' topographic habitat associations

We performed a Torus Translation test (TT) to determine the species' preference for each of the three topographic habitats defined above. We tested species' habitat associations for a total of 106,230 trees of 441 species. We excluded from our analysis species with less than 10 individuals per habitat to avoid issues related to small sample sizes. 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.analyse R package (Chuyong et al., 2011; Harms et al., 2001; Zuleta et al., 2020). For each species, the TT test compares its observed relative density in each habitat to the expected random density obtained from a null distribution based on the torus translation. Species with observed relative densities in 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 in a given habitat between the 2.5 and 97.5 percentiles of the null distribution were considered neutrally distributed. Among the 441 species, 41, 47 and 99 were significantly associated with ridges, slopes and valleys, respectively; and 168 species were neutrally distributed among the three topographic habitats (i.e. hereafter generalists). The rest of the species were not considered for testing the demographic hypotheses because they were either neutrally distributed among two habitats and repelled from the other (79 species) or associated with two habitats and repelled from the other (seven species).

2.5 | Growth estimates

We calculated the growth rate (G) of survivor trees as $\frac{\mathrm{DBH}_2 - \mathrm{DBH}_1}{t_2 - t_1}$, 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 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 $\mathrm{DAB} \times \exp(B \times (\mathrm{HOM} - 1.3))$ (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 $B = 0.14939 – 0.025 \times \log(\mathrm{DAB}) - 0.02 \times \log(\mathrm{HOM}) - 0.021 \times \log(\mathrm{WSG})$. 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 year^{-1} and trees that decreased by more than 4 × SD in growth, where $\mathrm{SD} = 0.0062 \times \mathrm{DBH}_2 + 0.904$ (sensu Condit et al., 2014). We allowed small negative growth rates in the analysis because they can be caused by herbivory (Delissio & Primack, 2003), pathogens or drought (Gerhardt, 1996), not necessarily due to measurement errors. Excluding these growth rates can cause 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 ($G\tau$, John & Draper, 1980). We tested in the range $t \in (0.3, 0.54)$, and we found the transformed growth rates have the lowest skewness (Sk) at the power of $t=0.39$ (Figure S1): $G\tau=G^{0.39}$ if $G\geq 0$ and $G\tau=-(-G)^{0.39}$ if $G<0$. $G\tau$ was used in statistical models and tests our hypotheses, but figures and tables present back-transformed growth rates. 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 our results are based on the median (Kenfack et al., 2014).

2.6 | 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 analysed as a binary variable: 1 for dead and 0 for living trees. The instantaneous mortality rate (%year^{-1}) was estimated from the average marginal probability of tree death (p_{death}) between time 1 (t_1) and time 2 (t_2) as: $(-\log(1-p_{death})/(t_2-t_1))\times 100$ (Kohyama et al., 2018).

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.

2.7 | Statistical analysis

Variation in growth and mortality among topographic habitats (Q1) and depending on the species' habitat associations (Q2 and Q3) were modelled separately for each demographic attribute using mixed-effects models. Individual tree growth (Gτ) was modelled using linear mixed-effects models (LMMs) assuming a normal error distribution. Tree mortality (M) was modelled 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 (Gτ or M) ~ Habitat × log(dbh) + (1|Species)*; the full model for Q2 and Q3 was: *demographic parameter (Gτ or M) ~ Habitat × Habitat_association × log(dbh) + (1|Species)*. The explanatory variable *Habitat* was a tree-level factor with three levels: located on ridge, slope or valley, while *Habitat_association* was a species-level factor with four levels: associated with ridges, associated with slopes, associated with valleys and generalist. We fitted all possible combinations of the explanatory variables including the second-order interactions among them; that is, a total of five models for Q1 (Table S1) and eight models for Q2 and Q3 (Table S4), ranging from the full model (all the variables and their second-order interactions) to the null model (only intercept) for each demographic rate.

To assess whether tree growth and mortality rates vary among topographic habitats (Q1) and among species' habitat associations (Q2) we first tested for the significance of the *Habitat* and the *Habitat_association* terms in our mixed-effects models, respectively. We then conducted multiple comparison tests using the *lsmeans* package with Tukey's Honest Significant Difference (HSD) test (Lenth, 2016) (Figure 1). Tukey's HSD was used to compare the demographic performance between the three topographic habitats (Q1) and the four species' habitat association levels (Q2) to determine which ones are significantly different from each other.

To assess whether the observed patterns of species growth and mortality among habitats were consistent with the *best-at-home* and *resident-advantage* hypotheses (Q3), we used the same models fitted to answer Q2 (i.e. *demographic parameter (Gτ or M) ~ Habitat × Habitat_association × log(dbh) + (1|Species)*) and tested for multiple comparisons based on the *Habitat × Habitat_association* interaction. These multiple comparisons allowed us to assess whether their demographic performance was higher in the habitat to which they were associated (home) than in habitats to which they were not associated (away)—as predicted by the *best-at-home* hypothesis. Similarly, these multiple comparisons allowed us to test whether, within each habitat, the performance of species associated with that habitat was higher than that of species not associated with it but still present there—as predicted by the *resident-advantage* hypothesis. Finally, we also tested for differences in the performance of generalist species among habitat types.

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, 2020). We ranked models based on the second-order Akaike's information criterion (AIC) using the AICcmodavg package (Mazerolle, 2020), and calculated the conditional and marginal coefficients of determination using the MuMIn package (Barton, 2012).

All statistical analyses were performed in R (R Core Team, 2021). Processed data used in this study are archived at the Dryad Digital Repository: https://doi.org/10.5061/dryad.b2rbnzst1 (Jaramillo et al., 2025).

3 | RESULTS

3.1 | Do tree growth and mortality rates vary among topographic habitats?

Both tree growth and mortality were significantly different among topographic habitats and exhibited strong size dependency (Table S1; Figure 2). On average, growth and mortality rates were higher for trees in valleys than for trees on slopes and ridges (Figure 2; Tables S2 and S3). The predicted median tree growth varied from 0.56 mm year^{-1} (95% CI 0.52–0.61 mm year^{-1}) in valleys to 0.47 mm year^{-1} (95% CI 0.44–0.51 mm year^{-1}) on slopes and 0.41 mm year^{-1} (95% CI 0.38–0.45 mm year^{-1}) on ridges (Figure 2A). Likewise, annual mean mortality rates decreased from 3.20% year^{-1} (95% CI 2.97–3.45% year^{-1}) for trees in valleys to 2.10% year^{-1} (95% CI 1.94–2.28% year^{-1}) on slopes and 2.12% year^{-1} (95% CI 1.95–2.31% year^{-1}) on ridges (Figure 2C). Tree growth increased,

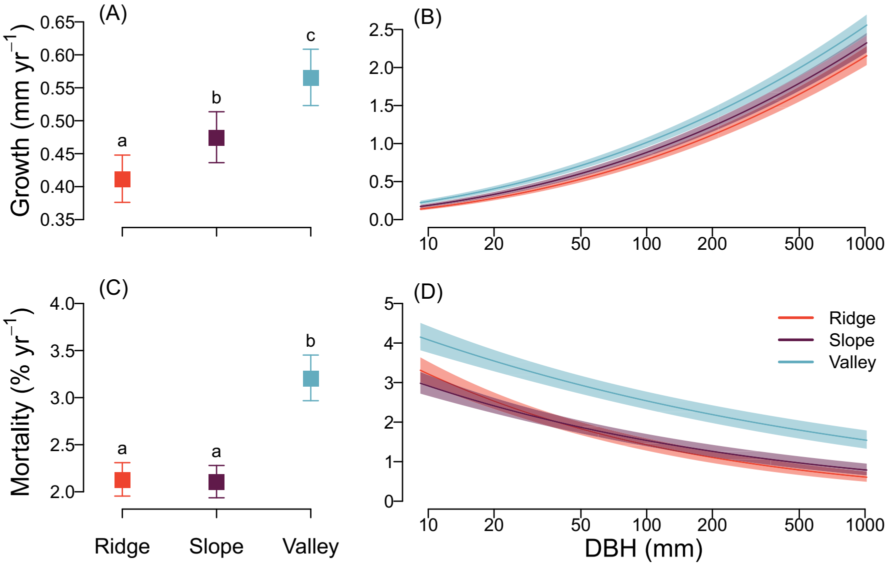


FIGURE 2 Annual tree growth (A, B) and mortality rates (C, D) varied among trees' topographic habitats (valleys, slopes and ridges) and size (DBH) in the 25-ha Amacayacu Forest Dynamics Plot, Northwestern Amazon. In all cases, the back-transformed predicted median growth and predicted mean mortality rates are shown from the best models (Table S1). Squares in (A, C) and lines in (B, D) correspond to predicted means from the best models. The error bars in (A, C) and envelopes in (B, D) correspond to 95% confidence intervals (CIs) obtained from the model prediction and reflect the uncertainty around the mean. Different letters indicate significant differences among topographic habitats based on Tukey's HSD test. Note that the confidence intervals (CIs) of two groups may overlap, but the CI for the difference between their means can still exclude zero, indicating a statistically significant difference according to Tukey's HSD.

and mortality decreased with tree diameter consistently among topographic habitats (Figure 2B,D).

3.2 | Do tree growth and mortality vary depending on species' habitat associations?

The most supported growth and mortality models always included the interaction between habitat association and habitat (Table S4). However, this interaction did not affect the overall trends in performance among topographic habitats (i.e. higher tree mortality and growth in the valleys compared to slopes and ridges) or their size dependency (Figure 3; Tables S5 and S6). Despite the significant interaction between habitat association and habitat, neither tree growth nor mortality varied significantly among species' habitat associations (Figure 3A,B). This interaction was mostly driven by generalist species having slightly higher growth and significantly higher mortality than specialists in valleys and ridges.

3.3 | Are the observed patterns of tree species growth and mortality among habitats consistent with either the *best-at-home* or the *resident-advantage* hypotheses?

We found limited support for the *best-at-home* or the *resident-advantage* hypotheses at the community level. Tree species associated with a given habitat did not perform better on their home habitat than elsewhere (Figure 4), and resident species did not perform better than foreign species within any given habitat (Figure 5). The only exception was species associated with valleys, which grew the most in their home habitat than elsewhere (Figure 4C) and died less in valleys (resident) than species associated with slope or generalists (foreigners) (Figure 5F). Generalist species did not perform similarly among habitat types (Figure 4D,H) nor did they have better performance within a given habitat compared to other species (Figure 5); they all performed better in valleys.

4 | DISCUSSION

4.1 | Limited support for *best-at-home* and *resident-foreigner* hypotheses

Topographically driven niche heterogeneity has been shown to strongly influence forest structure, functioning and composition (Cosme et al., 2017; Jucker et al., 2018; McNichol et al., 2024; Zuleta et al., 2017, 2022), and many tree species have been observed to associate with distinct topographic habitats at local scales (<1 km^2) (e.g. Chuyong et al., 2011; McNichol et al., 2024; Zuleta et al., 2020). In this Amazonian *terra firme* forest, we found marked demographic variation among topographic habitats differing in as little as 22 m of elevation. Across size classes, the greatest differences were between trees located in the valley, which had the highest growth and mortality rates, versus those located on slope and ridge habitats. However, valley-associated species did not have the highest growth

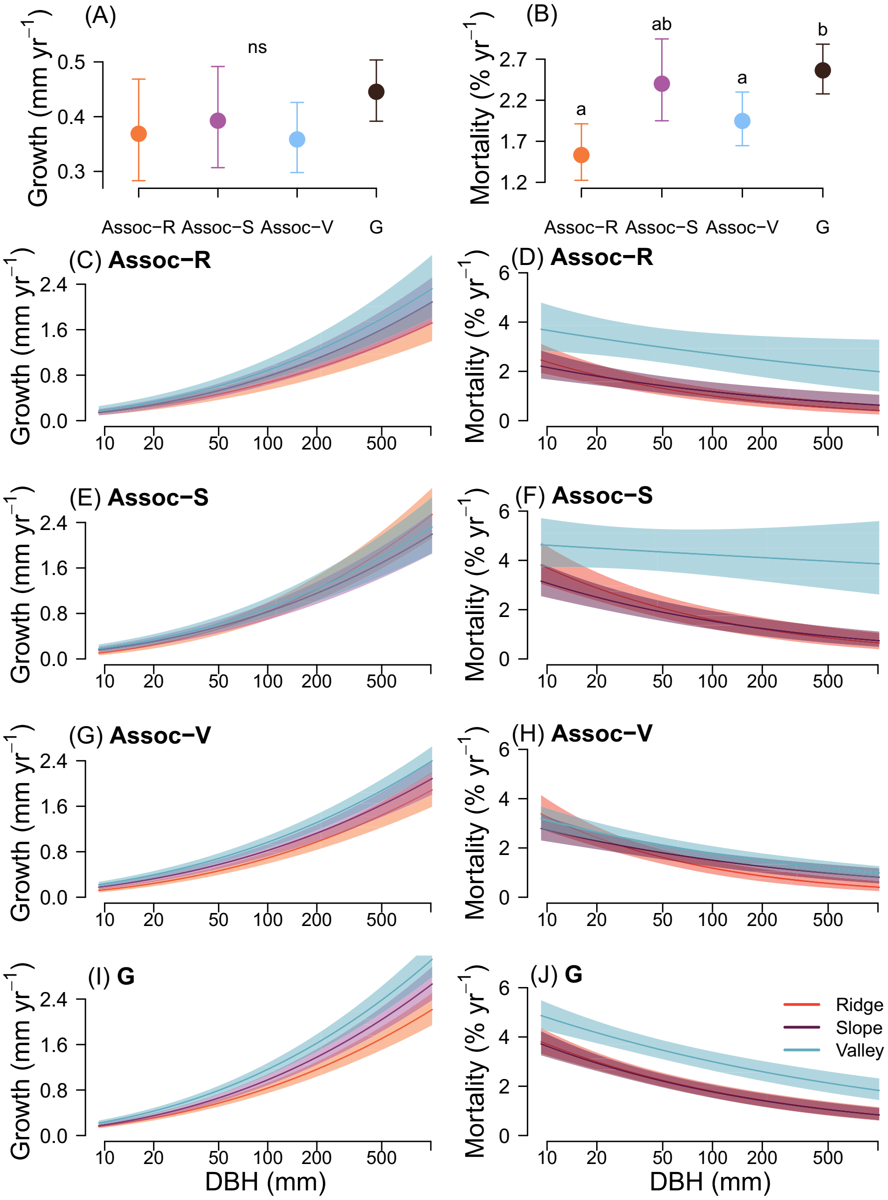


FIGURE 3 Variation in annual tree growth (A, C, E, G, I) and mortality rates (B, D, F, H, J) among species association habitats (Assoc-R, associated with ridges; Assoc-S, associated with slopes; Assoc-V, associated with valleys; G, generalist), habitats (valleys, slopes and ridges) and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon. In all cases the back-transformed predicted median growth and predicted mean mortality rates are shown from the best models (Table S4). Circles in (A, B) and lines in (C–I) correspond to predictions from the best models. The error bars in (A, B) and envelopes in (C–I) correspond to 95% confidence intervals (CIs) obtained from the model prediction and reflect the uncertainty around the mean. Different letters indicate significant differences based on Tukey's HSD test. Note that the confidence intervals (CIs) of two groups may overlap, but the CI for the difference between their means can still exclude zero, indicating a statistically significant difference according to Tukey's HSD.

and mortality rates as expected under the interspecific slow-fast continuum. Similarly, within species, the highest growth and mortality for trees in valleys was inconsistent with intraspecific predictions based on resource availability (i.e. higher growth and lower mortality in resource-rich habitats). As a result, we found partial support for the *best-at-home* and *resident-advantage* hypotheses only for valley-associated species, which grew best in their home habitat (valleys) than elsewhere and had lower mortality there compared to slope-associated or generalist species (foreigners).

Inconsistencies between species habitat associations and expected demographic variation among habitats have also been observed in other studies along a topographic gradient in Cameroon (Kenfack et al., 2014) and along a marked soil fertility gradient in Malaysia (Russo et al., 2005), whereas the strongest support has come from studies at the seedling stage across a soil gradient (Comita & Engelbrecht, 2009; Fortunel et al., 2016). Ultimately, there must be a demographic cause for species' habitat associations, albeit over the long run, so the lack of support for the best-at-home and resident-advantage hypotheses in many studies remains a conundrum. How strongly these hypotheses hold at all time periods for species that live hundreds of years, for all species and for all life stages, as well as how conspecific negative density dependence and neutral dynamics moderate these effects, are potential explanations for the overall lack of support for these demographic hypotheses at the community level.

4.2 | Drought effects reinforced patterns for valleys-associated species

Trees live through many catastrophic disturbances such as droughts or windthrows during their long lives, and these disturbances leave topographic fingerprints (Costa et al., 2022; Emmert et al., 2024). The 2010 Amazon drought occurred between the

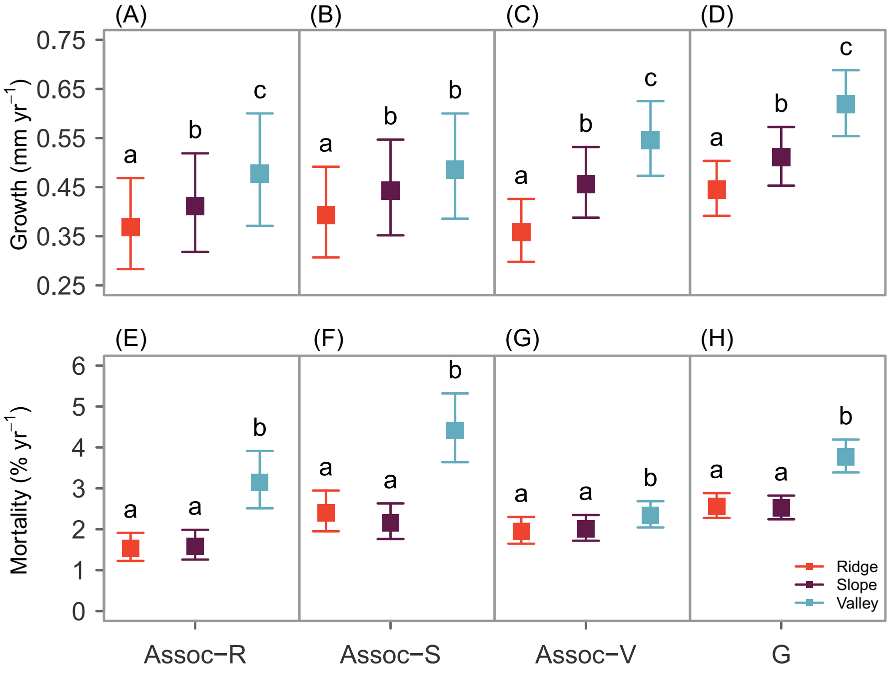


FIGURE 4 Evaluation of the best-at-home hypothesis. Predicted median annual growth (A–D) and predicted mean mortality rates (E–H) of trees by habitat association categories (Assoc-R, associated with ridges; Assoc-S, associated with slopes; Assoc-V, associated with valleys; G, generalist) among each habitat (ridges, slopes or valleys) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon (*best-at-home* hypothesis). Error bars correspond to 95% confidence intervals (CIs) obtained from the model prediction and reflect the uncertainty around the mean. Within each habitat association category (panels), different letters indicate significant differences among topographic habitats based on Tukey HSD test. Note that the confidence intervals (CIs) of two groups may overlap, but the CI for the difference between their means can still exclude zero, indicating a statistically significant difference according to Tukey's HSD.

two censuses conducted in this study and killed more trees in the valleys than in the ridges in this forest (Zuleta et al., 2017). Consequently, we found consistently higher mortality in valleys compared to slopes and ridges at the community level (Figure 2C). Species associated with valleys did not have the highest growth or mortality as expected based on the slow-fast continuum (Figure 3A,B), but tended to have lower mortality rates in valleys than species associated with other habitats (Figure 5F). Thus, species associated with valleys fared better than non-valley species in the valley during drought. The consistently higher mortality observed in valleys compared to slopes and ridges at the community level was mostly driven by non-valley associated species (i.e. 'foreigners') present in valley habitats. These species accounted for 42.4% of the trees in valleys and experienced higher mortality than valley species in the same environment (Figure 3D,F,H,J). The high mortality of ridge- and slope-associated species present in valleys may be explained by plasticity toward a faster strategy when in valleys, making them more susceptible to drought (Zuleta et al., 2022). In contrast, in their home habitats, these species remain 'slow' and thus more stress-tolerant. Droughts have also been shown to promote growth in trees located in valleys (defined as sites with shallow water-tables <5 m) in central Amazon forests (Costa et al., 2022; Esteban et al., 2021; Sousa et al., 2020), presumably due to reduced competition and alleviation of anoxic conditions in flooded habitats. Experimental studies in other tropical forests have demonstrated that differential species' performance under droughts results in species habitat associations (Baltzer et al., 2008; Comita & Engelbrecht, 2009; Engelbrecht et al., 2007). The differential effect of the Amazon 2010 drought on the growth and mortality of trees among topographic habitats may have reinforced the expected demographic advantages of valley-associated species.

4.3 | Few, yet dominant, species fulfil the *best-at-home* and *resident-foreigner* hypotheses

Considering the high diversity of tropical forests, one obvious question is the extent to which the *best-at-home* and *resident-advantage* hypotheses apply to all species. A post hoc analysis comparing species performance among habitats showed that 29 species had significantly faster growth and/or lower mortality in their home habitat compared to other habitats (*best-at-home*), and 65 species outperformed other species (faster growth or lower mortality) in the habitat where they were residents (*resident-advantage*) (Figure 6; Tables S7 and S8). Based on these estimates, a total of 73 species fulfilled either the *best-at-home* or the *resident-advantage* hypothesis. These 73 species represented 21% of the 352 species analysed here, 6% of the tree species in the plot (currently estimated at 1232 species), and accounted for 25% of the total number of individuals and 33% of the

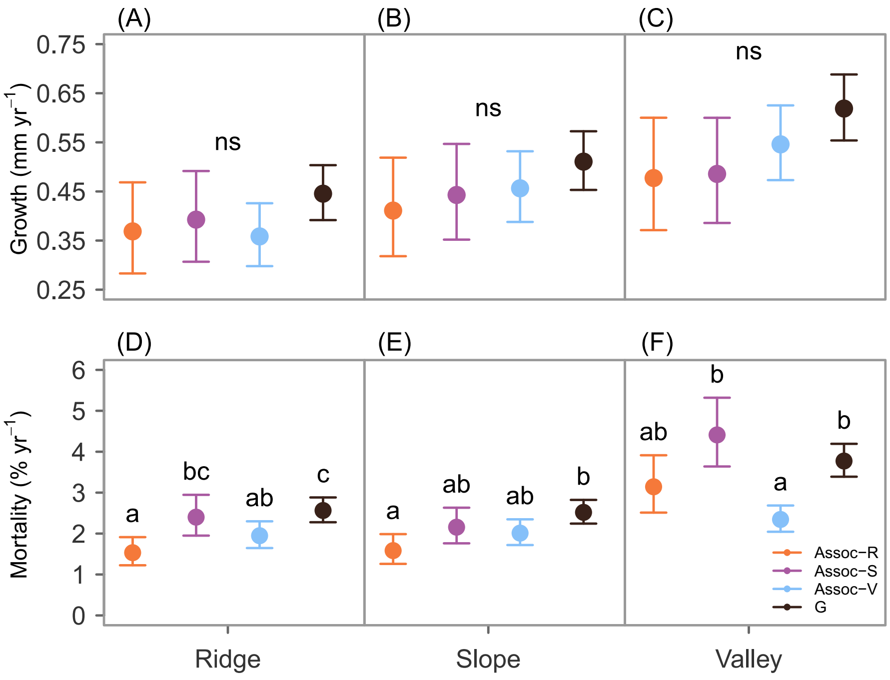


FIGURE 5 Evaluation of the resident-advantage hypothesis. Predicted median annual growth (A–C) and predicted mean mortality rates (D–F) of trees by topographic habitat (ridges, slopes or valleys) among each habitat association category (Assoc-R, associated with ridges; Assoc-S, associated with slopes; Assoc-V, associated with valleys; G, generalist) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon (*resident-advantage* hypothesis). Error bars correspond to 95% confidence intervals (CIs) obtained from the model prediction and reflect the uncertainty around the mean. Within each habitat (panels), different letters indicate significant differences among habitat association categories based on Tukey HSD test. Note that the confidence intervals (CIs) of two groups may overlap, but the CI for the difference between their means can still exclude zero, indicating a statistically significant difference according to Tukey's HSD.

total accumulated basal area in the plot. These results suggest that despite the overall lack of evidence for the *best-at-home* and *resident-advantage* hypotheses at the community level, the species that do fulfil these demographic hypotheses of habitat association still make significant contributions to the forest's structure and functioning.

Beyond this forest, 16 out of the 73 species that fulfil either of the demographic hypotheses in this study have been reported to disproportionately account for a large fraction of tree biomass and abundance across the Amazon basin (i.e. hyperdominant species; ter Steege et al., 2013). Of these 16 hyperdominant species, 11 were associated with valleys, three with slopes and two with ridges. The high dominance of these species is likely due to their competitive success in persisting in and colonising specific, yet conspicuous, habitats across the Amazon, such as the valleys (Costa et al., 2022). For example, *Dialium guianense and Zygia latifolia*, both valley-associated species in this study, show improved performance in their home habitats and are classified as hyperdominant across the Amazon basin. In contrast, *Virola calophylla*, associated with ridges, benefits from habitats that are typically well-drained, allowing it to adopt a more conservative strategy (Fern, 2024). These hyperdominant species, as well as those fulfilling the demographic hypotheses at the local scale (Figure 6; Tables S7 and S8), can be further used to investigate the biogeographical, functional and physiological mechanisms underlying species' habitat association patterns in hyperdiverse Amazon forests.

4.4 | Alternative processes influencing demographic responses and species' topographic distributions

The overall lack of support for the *best-at-home* and *resident-advantage* hypotheses at the community level is consistent with the fact that most of the species analysed (279 out of 352) did not fulfil either hypothesis, even when assessed independently. At least three alternative hypotheses may explain this result: negative density dependence in home habitats causing reductions in growth and mortality rates in areas with high conspecific density, environmental filtering at smaller diameter cutoffs and neutral processes.

By definition, a species' home habitat has a higher density of that species compared to other habitats. Therefore, negative effects on a species' performance in its home habitat may be expected due to competition among conspecifics (Adler et al., 2018) and pest- and pathogen-driven mortality (Connell, 1971; Janzen, 1970). Species may thus exhibit demographic variation among habitats, but not necessarily a demographic advantage in their home habitat. Assuming species have similar sensitivity to conspecific negative density dependence, then, the *best-at-home* hypothesis would be supported for species with low to intermediate abundances in their home habitat, but not for those with high abundance. However, contrary to this expectation, species that supported the best-at-home hypothesis (mean abundance = 276.3) had higher abundances than those that

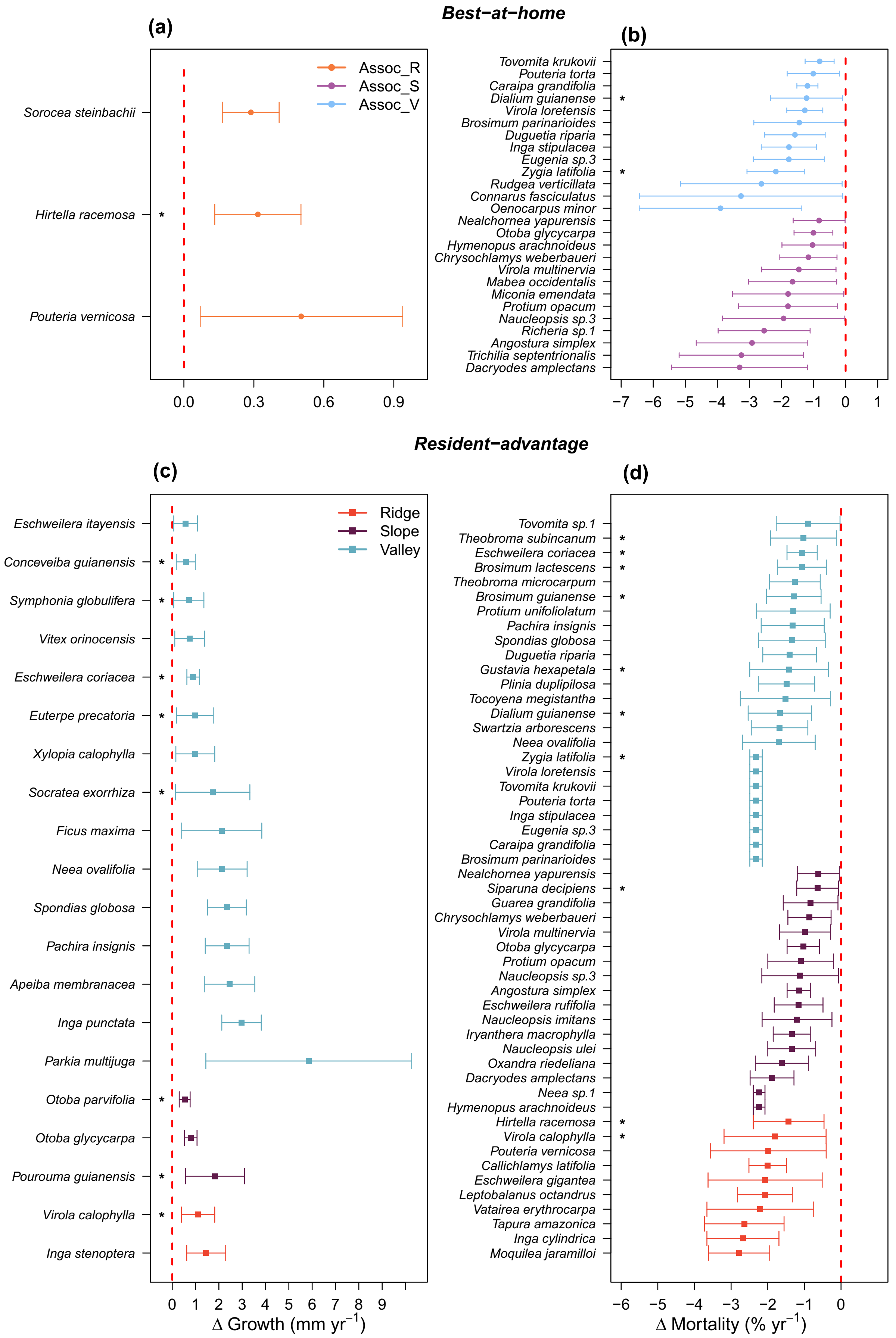

Best−at−home
(a)
Assoc_R
Assoc_S
Assoc_V
Sorocea steinbachii
Hirtella racemosa *
Pouteria vernicosa
0.0
0.3
0.6
0.9
(b)
Tovomita krukovii
Pouteria torta
Caraipa grandifolia
Dialium guianense *
Virola loretensis
Brosimum parinarioides
Duguetia riparia
Inga stipulacea
Eugenia sp.3
Zygia latifolia *
Rudgea verticillata
Connarus fasciculatus
Oenocarpus minor
Nealchornea yapurensis
Otoba glycycarpa
Hymenopus arachnoideus
Chrysochlamys weberbaueri
Virola multinervia
Mabea occidentalis
Miconia emendata
Protium opacum
Naucleopsis sp.3
Richeria sp.1
Angostura simplex
Trichilia septentrionalis
Dacryodes amplectans
−7
−6
−5
−4
−3
−2
−1
0
1
Resident−advantage
(c)
Ridge
Slope
Valley
Eschweilera itayensis
Conceveiba guianensis *
Symphonia globulifera *
Vitex orinocensis
Eschweilera coriacea *
Euterpe precatoria *
Xylopia calophylla
Socratea exorrhiza *
Ficus maxima
Neea ovalifolia
Spondias globosa
Pachira insignis
Apeiba membranacea
Inga punctata
Parkia multijuga
Otoba parvifolia *
Otoba glycycarpa
Pourouma guianensis *
Virola calophylla *
Inga stenoptera
0
1
2
3
4
5
6
7
8
9
Δ Growth (mm yr^{-1})
(d)
Tovomita sp.1
Theobroma subincanum *
Eschweilera coriacea *
Brosimum lactescens *
Theobroma microcarpum
Brosimum guianense *
Protium unifoliolatum
Pachira insignis
Spondias globosa
Duguetia riparia
Gustavia hexapetala *
Plinia duplipilosa
Tocoyena megistantha
Dialium guianense *
Swartzia arborescens
Neea ovalifolia
Zygia latifolia *
Virola loretensis
Tovomita krukovii
Pouteria torta
Inga stipulacea
Eugenia sp.3
Caraipa grandifolia
Brosimum parinarioides
Nealchornea yapurensis
Siparuna decipiens *
Guarea grandifolia
Chrysochlamys weberbaueri
Virola multinervia
Otoba glycycarpa
Protium opacum
Naucleopsis sp.3
Angostura simplex
Eschweilera rufifolia
Naucleopsis imitans
Iryanthera macrophylla
Naucleopsis ulei
Oxandra riedeliana
Dacryodes amplectans
Neea sp.1
Hymenopus arachnoideus
Hirtella racemosa *
Virola calophylla *
Pouteria vernicosa
Callichlamys latifolia
Eschweilera gigantea
Leptobalanus octandrus
Vatairea erythrocarpa
Tapura amazonica
Inga cylindrica
Moquilea jaramilloi
−6
−5
−4
−3
−2
−1
0
Δ Mortality (% yr^{-1})

FIGURE 6 Tree species supporting the *best-at-home* (a, b) and *resident-advantage* (c, d) hypotheses. Panels (a) and (b) show the difference between each species' average growth (a) or mortality (b) in its preferred habitat (i.e. home) and their average values across the other habitats where the species are not associated (i.e. away). Panels (c) and (d) show the difference between each species' average growth (c) or mortality (d) in their home habitat (i.e. residents) and the average values for other species present but not associated to that habitat (i.e. foreigners). Note that, for the *best-at-home* hypothesis, species-specific analyses can only be conducted for non-generalist species with trees growing in at least two habitats (168 out of the 352 species tested in the community-level analysis). To test the *best-at-home* and *resident-advantage* hypotheses, we compared the mean growth and mortality rates using confidence intervals for pairwise differences. Standard errors and confidence intervals were calculated using established methods (Supporting information Methods S1). Only species for which the confidence intervals do not include the zero (red dotted vertical line) are shown. Species depicted as single points without standard error bars in (d) are those with zero mortality rates in their home habitats (i.e. as residents); the point therefore represents the average mortality rate of foreigners in that habitat. Asterisks indicate species classified as hyperdominant across the Amazon Basin. Results for all species are shown in Figure S3 and Tables S7 and S8.

did not (mean abundance = 162.3) (Kruskal test, *p*-value = 0.01011; Figure S2). Conspecific negative density dependence has been widely observed across forests world-wide (Comita et al., 2014), with stronger effects in tropical forests than in temperate ones and differences in the strength of conspecific negative density dependence among species (Hülsmann et al., 2024). Nonetheless, there is no clear evidence that density-dependent processes explain the lack of support for the *best-at-home* hypothesis in this study.

Another possible explanation for the overall lack of support for the demographic hypotheses is that the environmental filtering resulting in habitat association patterns may occur at tree sizes smaller than those considered in this study—that is, when plants are less than 1 cm DBH. At the seedling stage, for example, other studies have found pronounced differences in performance between species habitat association classes that are consistent with the best-at-home and resident-advantage hypotheses (Comita & Engelbrecht, 2009; Fortunel et al., 2016). Altogether, these studies suggest that environmental controls on demography operating at early life stages are important causal factors of the species' habitat association patterns that are observed in adult trees of tropical forests (O'Brien & Escudero, 2022). If so, once habitat associations are established at early life stages, they may persist because survival increases with tree size and once established, reproduction may reinforce these patterns (Comita et al., 2007; Fortunel et al., 2016).

Finally, the overall lack of topographically structured growth across species may be expected if species are considered ecologically equivalent in terms of their demographic rates (Hubbell, 2001). This implies that no species has a consistent fitness advantage over others across topographic habitats, which would explain the lack of support for the *best-at-home* and *resident-foreigner* hypotheses tested here. Therefore, we cannot dismiss the possibility that the observed distribution across topographic habitats in this forest (Zuleta et al., 2020) may also result from distance-dependent processes, such as dispersal limitation, rather than deterministic, niche-based mechanisms like adaptation to specific habitats, for a significant proportion of species in this study (Condit et al., 2002; Hubbell, 2001).

5 | CONCLUSION

Our research underscores the complex relationships between topographic habitats and species' performance in tropical forests, revealing that even minor differences in topography (22 m of elevation change), and presumably in soil water availability and nutrients, can substantially impact the growth and mortality of trees. The consistently higher growth and mortality of trees in valleys compared to those on slopes and ridges partially support the demographic hypotheses of habitat association for species associated with valleys, potentially due to drought effects. Moreover, certain species may still exhibit home advantages in specific habitats, even when community-level averages do not reflect this pattern. Thus, how the widely observed pattern of tree species' habitat associations in this site and others arises remains an ecological conundrum and is likely an outcome of many processes operating with varying strength throughout the long lives of these Amazonian tree species.

AUTHOR CONTRIBUTIONS

Paola A. Jaramillo, Sabrina E. Russo and Daniel Zuleta designed the study. Paola A. Jaramillo, Nicolas Castaño, Alvaro Duque and Daniel Zuleta conducted the fieldwork. Paola A. Jaramillo analysed the data with the supervision of Daniel Zuleta and Sabrina E. Russo. Paola A. Jaramillo and Daniel Zuleta led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70132.

DATA AVAILABILITY STATEMENT

Processed data used in this study are archived at the Dryad Digital Repository: https://doi.org/10.5061/dryad.b2rbnzst1 (Jaramillo et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. 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 power of $t = 0.39$.

Figure S2. Species abundance (log scale) in their home habitat for species that do not support the 'Best-at-home' hypothesis ($n = 158$ species, mean abundance = 162.3) and those that do ($n = 29$ species, mean abundance = 276.3). Statistical analysis reveals significant difference between these two groups (Kruskal test, $p = 0.01011$).

Figure S3. Species-specific tests for the *best-at-home* (a, b) and *resident-advantage* (c, d) hypotheses. This figure includes all evaluated species. Panels (a) and (b) show the difference between each species' average growth (a) or mortality (b) in its preferred habitat (i.e., home) and their average values across the other habitats where the species are not associated (i.e., away). Panels (c) and (d) show the difference between each species' average growth (c) or mortality (d) in their home habitat (i.e., residents) and the average values for other species present but not associated to that habitat (i.e., foreigners). Note that, for the best-at-home hypothesis, species-specific analyses can only be conducted for non-generalist species with trees growing in at least two habitats (168 out of the 352 species tested in the community-level analysis). To test the *best-at-home* and *resident-advantage* hypotheses, we compared the mean growth and mortality rates using confidence intervals for pairwise differences. Standard errors and confidence intervals were calculated using established methods (Supporting information Methods S1). Species for which the confidence intervals include the zero (red dotted horizontal line) are shown with a transparent color. Species depicted as single points without standard error bars in (d) are those with zero mortality rates in their home habitats (i.e., as residents); the point therefore represents the average mortality rate of foreigners in that habitat.

Table S1. Comparison of mixed-effects models for tree growth (linear) and mortality (logistic) as a function of the trees' topographic habitat (Habitat) and size (log(DBH)) in the 25-ha Amacayacu Forest Dynamics Plot, Northwestern Amazon (Question 1). 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) (ΔAICc). LL, log-likelihood model. All models included a random intercept effect for species (1|Species).

Table S2. Mean estimated parameters and the 95% confidence intervals (CI) of the best linear mixed-effects model predicting tree growth as a function of habitat (ridges, slopes, or valleys) and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon.

Table S3. Mean estimated parameters and the 95% confidence intervals (CI) of the best generalized linear mixed-effects model predicting the probability of death as a function of habitat (ridges, slopes, or valleys) and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon.

Table S4. Comparison of mixed-effects models for tree growth (linear) and mortality (logistic) as a function of the trees' topographic habitat (Habitat), size (log(DBH)), and the topographic habitat association (Hab-Assoc) in the 25-ha Amacayacu Forest Dynamics Plot, Northwestern Amazon (Question 2). 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) (ΔAICc). LL, log-likelihood 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 S1.

Table S5. Mean estimated parameters and the 95% confidence intervals (CI) of the best linear mixed-effects model predicting tree growth as a function of habitat (ridges, slopes, or valleys), species habitat associations (valleys, slopes, ridges, generalist), and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon.

Table S6. Mean estimated parameters and the 95% confidence intervals (CI) of the best generalized linear mixed-effects model predicting the probability of death as a function of habitat (ridges, slopes, or valleys), species habitat associations (valleys, slopes, ridges, generalist), and size (DBH) in the Amacayacu Forest Dynamics Plot, Northwestern Amazon.

Table S7. Tree species supporting the best-at-home hypothesis, based on either growth, mortality, or both. ΔGrowth and ΔMortality represents the difference between a species' average growth or mortality in its preferred habitat and the mean values in the two other habitats where it is not associated. A positive ΔGrowth indicates a greater advantage for the species when growing in its preferred habitat compared to outside it. For mortality, a negative value indicates a higher survival rate in the associated habitat compared to the other two habitats. Note that, for the best-at-home hypothesis, species-specific analyses can only be conducted for non-generalist species with trees growing in at least two habitats (168 out of the 352 species tested in the community-level analysis). Relative abundance refers to the proportion of individuals of a species compared to the total number of individuals in the AFDP (117,101 individuals in total). Relative basal area refers to the total basal area of a species relative to the total basal area of all species within the AFDP (717.3 m^2 in total). A 95% confidence interval was calculated for the difference.

Table S8. Tree species showing higher growth or lower mortality in their home habitat compared to other species (resident-advantage hypothesis). The Performance Index (PI) for growth and mortality quantifies how species associated with specific habitats—ridges, slopes, or valleys—compare to species that are not associated with those habitats. A positive PI for growth indicates that species associated with a particular habitat grow faster on average than those from other habitats. A negative PI for mortality suggests that species associated with that habitat experience lower mortality rates. Relative abundance refers to the proportion of individuals of a species compared to the total number of individuals in the AFDP (117,101 individuals in total). Relative basal area refers to the total basal area of a species relative to the total basal area of all species within the AFDP (717.3 m^2 in total). A 95% confidence interval was calculated for the difference.

Methods S1. Species-specific test for the *best-at-home and resident-foreigner* hypotheses.

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