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ARTICLE

Vegetation Ecology

Demographic rates and diversity vary with tree stature and ontogenetic stage in an African tropical rainforest

Moses B. Libalah[1,2] | **Sabrina E. Russo**[3,4] | **George B. Chuyong**[5] | **Duncan Thomas**[6] | **David Kenfack**[7]

[1]Department of Plant Biology, Faculty of Science, University of Yaoundé I, Yaoundé, Cameroon

[2]Plant Systematics and Ecology Laboratory (LaBosystE), Higher Teacher's Training College, University of Yaoundé I, Yaoundé, Cameroon

[3]School of Biological Science, University of Nebraska, Lincoln, Nebraska, USA

[4]Center for Plant Science Innovation, University of Nebraska, Lincoln, Nebraska, USA

[5]Department of Plant Science, University of Buea, Buea, Cameroon

[6]Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon, USA

[7]Smithsonian Forest Global Earth Observatory, Washington, DC, USA

Correspondence
Moses B. Libalah
Email: libalah_moses@yahoo.com

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Abstract

The vertical gradient of light in closed-canopy forests selects for trees with different adult statures, but our understanding of how stature affects forest diversity and demography is unclear. In a species-rich rainforest in Cameroon, we quantified the contributions of four growth forms of increasing adult stature (treelet, understory, canopy, emergent species) to forest structure and diversity, and investigated variation in life history trade-offs across growth forms. Treelets had the highest stem density, contributed the most to forest diversity, and diverged from larger statured species in terms of demographic trade-offs. Growth rates were slower for smaller statured than for larger statured species, and at the adult stage, treelets had significantly lower mortality than other growth forms. We observed significant interspecific trade-off relationships between staure and demographic rates that often differed between growth forms. Recruitment rate strongly declined with adult stature for all growth forms, but recruitment per reproductive adult declined only for emergents. While we observed a significant growth-mortality trade-off across all species, the trade-off was similar across growth forms. Smaller statured species in our study are not light-demanding but rather treelet and understory species that live entirely in the shaded understory. Differences in how historical biogeography has shaped species pools may ultimately cause variation in how adult stature contributes to tropical forest diversity.

KEYWORDS

demography, growth rate, mortality rate, rain forest, recruitment rate, trade-off

INTRODUCTION

The bottom-to-top stratification of aboveground vegetation in closed-canopy forests has been proposed as an important mechanism promoting species coexistence in diverse forest types (Wright, 2002; Brokaw & Lent, 1999; Kohyama, 1993; Terborgh, 1985; Yoda, 1974;). Yet, how stratification owing to differences in the adult stature of tree species contributes to variation in demographic rates and trade-offs has not been adequately described. Competition for light and adaptations to maximize light interception in the context of complex life histories mean that tree species have evolved to occupy different height strata at adulthood closed canopy forests, ranging from treelets that live their entire lives in the shaded understory to emergent species that ultimately tower over other trees making up the forest canopy. Previous studies have described associations among adult tree stature (or maximum size; Kohyama, 1993), demographic rates (King, Davies, et al., 2006; Thomas, 1996a, 1996b), and trade-offs (Kambach et al., 2022; Rüger et al., 2018; Russo et al., 2021), but have not specifically separated the effects of adult stature from growth form (but see Iida, Kohyama et al., 2014). Here, we investigate variation in demographic rates and life history trade-offs among species of different statures and growth forms in a species-rich closed canopy topical forest in Cameroon.

Two major trade-offs in life history strategies to structure species dynamics and coexistence in closed canopy forests are the stature–recruitment trade-off (Kohyama, 1993; Rüger et al., 2018) and the growth–mortality trade-off (Russo et al., 2021; Wright et al., 2010), which have been found to be orthogonal to each other (Rüger et al., 2018). Trade-offs between adult and demographic rates distinguish long-lived species from short-lived species (Rüger et al., 2018). The trade-off is characterized by longer-lived species that grow to larger statures and maintain faster growth, lower mortality and lower recruitment rates than shorter-lived species that attain smaller statures and slower growth, higher mortality, and higher recruitment rates (King, Davies, et al., 2006; King, Wright, et al., 2006; Kohyama et al., 2003). In the growth–mortality trade-off, species tend to align along a “fast-slow” continuum (Salguero-Gómez et al., 2016) such that faster growing species have shorter life spans whereas slower growing species have longer life spans. However, if adult stature affects species' growth, mortality, and recruitment (Thomas, 1996a, 1996b), then it is possible that it may also affect the strength of the growth–mortality trade-off among tree species, yet most studies of this trade-off in trees have not accounted for stature (e.g., Russo et al., 2021; Wright et al., 2010). It is also important to distinguish trees of different size from species of different stature. Variation in demography among tree size classes is well known and has been described in studies too numerous to cite here (e.g., Bohlman & O'Brien, 2006; LaFrankie et al., 2006). While it is essential to control for tree size effects when assessing demographic rates and trade-offs (LaFrankie et al., 2006; Rüger et al., 2011), it is also important to account for variation in stature among species.

Despite the importance of adult stature and growth forms for forest structure (King et al., 2005; Popma et al., 1988; Smith, 1973; Terborgh, 1985; LaFrankie et al. 2006) we have an incomplete picture of variation in demographic and life history strategies among species of different adult statures and growth forms. Not accounting for growth forms and size class may lead to poor prediction of demographic rates as has been the case with the predictive power of functional traits upon growth and mortality rates (Iida, Kohyama, et al., 2014; Iida, Poorter, et al., 2014). For instance, canopy and emergent species frequently had lower mortality and recruitment rates than smaller growth forms among Amazonian trees (Nascimento et al., 2005) while growth rates increased with trunk diameter across five growth forms in Malaysian forests (King, Davies, et al., 2006). Also, both growth and mortality rates declined with increasing woody density wooded species with faster-growing species being shorter-lived likely owing to investment in light interception rather than mechanical strength (Hietz et al., 2017). Further, growth form appears to be a strong correlate of adult asymptotic height and shade tolerance, such that canopy trees tend to be better competitors for light than understory trees (King, Davies, et al., 2006). Since 24%–45% of tree species in diverse tropical forests constitute species of smaller adult stature (Duque et al., 2017; Kenfack et al., 2007; Memiaghe et al., 2016) which grow, reproduce and die under the forest canpy, it is crucial to control for tree size, adult stature and growth form when assessing demographic rates and trade-offs (Iida, Kohyama, et al., 2014; Rüger et al., 2011).

We studied variation in demographic rates and trade-offs across tree species of different adult statures in a tropical rainforest in Cameroon. We identified a priori four growth forms representing trees with different adult stature (treelet, understory, canopy, emergent; Kenfack et al., 2007), analyzed variation in structural and taxonomic diversities among growth forms, and tested the roles of stature and ontogenetic stage in shaping variation in demographic rates and trade-offs. We hypothesized that (1) growth forms would contribute differently to forest diversity such that smaller stature growth forms would possess higher diversity than larger stature growth forms; (2) demographic rates would differ among growth forms and ontogenetic stages such that mortality rate would be higher while growth rate would be lower for saplings than adults. Furthermore, interspecific trade-offs between adult stature and demographic rates (e.g., stature–growth, stature–mortality, stature–recruitment; Kambach et al., 2022; Kohyama, 1993; Rüger et al., 2018) and between growth and mortality rates (growth–mortality; Wright et al., 2010) are commonly observed in tropical forests. We thus tested whether growth forms have different slopes of the trade-offs (i.e., stature–growth, stature–mortality, stature–recruitment, and growth–mortality) with our null hypothesis for each trade-off being that the slopes of the growth forms are equal. We further examined the correlations between stature and demographics, and between growth and mortality. We expect evidence of a strong stature–growth, stature–mortality, stature–recruitment, and growth--mortality relationships among species of each growth form. However, trees of different growth forms have access to different amounts of light, so we expect that the strength of these relationships would be stronger for sapling than adult ontogenetic stages because of differences in their capacity to capture and use aboveground resources.

METHODS

Study site and tree census

This study was conducted in ForestGEO's 50-ha Korup forest dynamics plot (FDP) in Cameroon (5°03.86′ N, 8°51.17′ E; ~100–1079 m above sea level). The FDP (1000 m × 500 m) is a rugged landscape with natural lowland evergreen rainforest in the southern end of Korup National Park. The topography of the 1000 × 500 m FDP is uneven, fairly flat at the low-lying south end and steep toward the northern third of the plot (Thomas et al., 2003). The climate is characterized by 9 months of rainfall (March to November) with monthly ranges of 220–340 mm, and 3 months of dryness (December to February) with monthly rainfall less than 100 mm. Annual precipitation average is slightly less than 5000 mm and annual temperature averages 27°C (Chuyong et al., 2004; Newbery et al., 1998). Soils are Arenosol or Ferralitic, sandy at the top, and nutrient-poor due to leaching from intense rainfall (Gartlan et al., 1986).

For this study, we used data from two censuses. The censuses of the Korup FDP were realized following the standardized tree census protocol of the Center for Tropical Forest Science (Condit, 1998). During the first census in 1996–1999, all woody stems with dbh ≥10 mm at 1.3 m were permanently tagged, measured to nearest 1.0 mm, assigned to a species which was identified, as much as possible, by attributing a scientific name, and mapped by recording their *X*- and *Y*-coordinates. The second census in 2008–2010 witnessed the remeasurement of all living stems at the same previous dbh, and new stems that attained 10 mm dbh were recruited following the same procedure as in the first census. The floristic composition of these two censuses has been described (Chuyong et al., 2011; Kenfack et al., 2007, 2014) to be comprised of 329,519 trees, 493 species, and morphospecies, including 365 (71%) identified to species level, 96 genera, and 29 families.

Demographic rates

We quantified demographic rates as growth, mortality, and recruitment rates, and their derivatives (i.e., fast growth rate, mortality in shade, recruitment per abundance of reproductive adults) using the standard methods (Condit et al., 1999; Wright et al., 2010) and the *fgeo* *R*-package (Lepore et al., 2019).

Relative growth rate (RGR, mm year^{-1}) was calculated for each tree as $(\log(\text{dbh}_f)\text{-}\log(\text{dbh}_i))/\text{time}$, where subscripts f and i are final and initial values of tree diameter in millimeters, respectively, and time is mean time interval between two censuses in years. Species mean RGR was taken as the average RGR of all trees belonging to the species. Because of potential errors in diameter measurement, tree diameter was trimmed according to Condit et al. (1993a, 1993b). That is, if the (1) second dbh measurement of 2008–2010 was more than 4 SDs below the first dbh measurement of 1996–1999, (2) growth rate was greater than 55 mm year^{-1}, and (3) point of measurement changed by more than 5% between the two censuses. Only species with ≥50 trees (342 species) were considered for the computation of RGR to allow for acceptable annual CLs (Condit et al., 1993a, 1993b). We then calculated the growth rate of fast-growing individuals (RGR_{95}) as the 95th quantiles of the RGR and corresponds to the growth rates realized when resource availability is high and other stresses are low (Wright et al., 2010).

Annual mortality rate (AMR, year^{-1}) was calculated using the logarithmic formula: $(\log(N_t) - \log(S_t))/\text{time}$, where N_t is the number of trees present in the first (1996–1999) census, S_t is the number of trees in the second (2008–2010) census, and time is the mean time interval from the exact census dates of the tree for each 20 m × 20 m quadrant in the plot. Only species with ≥50 trees were considered for the computation of AMR because tree death is a rare event (Condit et al., 1993a, 1993b). We then used the neighborhood density approach or shade tolerance index (Bin et al., 2019, 2022) to calculate the mortality rate in shade (AMR_{50}). This approach assumes that the most shaded trees are those surrounded by trees that have larger dbh than them and should have a smaller neighborhood effect with respect to their larger neighbors. The basal area of each tree was calculated and used as a proxy for neighborhood density. The neighborhood effect was evaluated within a 10 m radius of the focal tree by considering only trees that are larger in dbh and perhaps taller than the focal tree. The AMR_{50} was then determined for those trees that have the upper 50% (50th quantiles) of the neighborhood density. The AMR_{50} corresponds to mortality rates realized when resource availability is low and other stresses are high (Wright et al., 2010). Although we do not have species-specific diameter-height allometries, it is likely that trees with a larger dbh are also taller than the focal tree.

Recruitment rate was the number of trees that entered the census at ≥10 mm dbh between two censuses. It was calculated as $(\log(N_t) - \log(S_t))$/time, where N_t is the number of individuals alive at the second census, S_t is the number of survivors between the beginning and the end of the interval, and time is the time interval in years. For each species, the recruitment rate was determined as the mean number of annual recruits between the two census intervals. Recruitment per abundance of reproductive adults or per capita recruitment (REC_{abun}, year^{-1}) was calculated by dividing the recruitment rate by the total number (abundance) of reproductive trees. Only species and morphospecies with ≥50 trees were considered for the calculation of demographic rates and consequently, unidentified trees were excluded from all calculations.

Growth forms, adult stature, and ontogenetic stages

All species were assigned to one of four growth forms based on information on maximum tree height at maturity from botanical literature (e.g., Aubreville et al., 1963–2001; Hutchinson et al., 1954–1972) and complemented with field estimates (Kenfack et al., 2007). Species that attained <10, 10 to <20, 20–30, and >30 m maximum height at maturity were categorized as treelets, understory, canopy, and emergent, respectively. To evaluate whether these growth forms represented demographically discrete groups of species, we perform a linear discriminant analysis (LDA) using species' mean wood density (from Dryad database), RGR_{95}, AMR_{50}, and REC_{abun} as implemented in the *lda* function of the *R MASS* package (Vernables & Ripley, 2003). The assignment of species into four growth forms was strongly supported by the LDA with a 34% misclassification rate (Appendix S1: Figure S1). Overlaps were also observed between understory and canopy, and treelet and understory species (Appendix S1: Figure S1). We also estimated continuous variation in adult stature based on the maximum dbh of the species (dbh_{max}).

We used the approach of Visser et al. (2016) to define ontogenetic stages by delimiting saplings from adult (reproductive) trees. A single dbh (often 5 or 10 cm) is often used to categorize trees as saplings or adults, but since ontogenetic variation may occur among growth forms, we delimited sapling from adult trees in a way that captures the differences between growth forms following Visser et al. (2016). This approach assumes that reproductive maturity is attained when a tree grows to 50% of the species' dbh_{max}, which is a reasonable approximation in the absence of tree fecundity data (Minor & Kobe, 2019; Visser et al., 2016). We calculated reproductive threshold (dbh_{rep}) of each species for which a robust estimate of maximum dbh could be made, which we considered to be species with ≥50 trees in the plot. The dbh_{rep} for each species was used to categorize each tree as sapling ($\text{dbh}_{\text{tree}} < \text{dbh}_{\text{rep}}$) or adult ($\text{dbh}_{\text{tree}} \geq \text{dbh}_{\text{rep}}$).

Stature-related variation in diversity, demography, and trade-offs

To evaluate how growth forms and ontogenetic stages contribute to structural diversity, we used two-way ANOVA of the number of trees per hectare with growth forms and ontogenetic stages as predictors, then applied a Tukey honestly significant difference (HSD) test for multiple comparisons.

To evaluate the contribution of growth forms to species diversity (richness and Shannon), we used the Hill numbers rarefaction and extrapolation approach (Hsieh et al., 2016). This approach allows the use of (un-) standardized tree densities (or number of trees) among the growth forms (Chao & Jost, 2012). It should be noted that taxonomic metrics are sensitive to sampling bias of the tree density such that the probability of finding more species increases with the number of trees sampled. We then performed rarefaction and extrapolation of Hill numbers based on species richness and Shannon–Wiener diversity metrics (Chao et al., 2014) using a species abundance data for each growth form. We standardized the number of trees to 5000 trees per growth form. This value corresponds to about 50% of the tree density of emergent trees, the growth form with the lowest tree density. We calculated the bootstrap SE for 50 replication and CI (at probability of 0.95) for each growth form. Finally, we visually inspected the rarefaction graphs and considered two growth forms to be significantly different if the CI of their species diversity does not overlap. The above analyses were performed with the *iNEXT* package (Hsieh et al., 2016). To assess variation in demographic rates among the four growth forms and ontogenetic stages, we used two-way ANOVA with multiple comparisons between growth forms using Tukey HSD tests.

To assess the trade-offs between stature and demographic rates (i.e., dbh_{max} vs. RGR, dbh_{max} vs. RGR_{95}, dbh_{max} vs. AMR, dbh_{max} vs. AMR_{50}, dbh_{max} vs. REC, and dbh_{max} vs. REC_{abun}) and between growth and mortality (i.e., RGR vs. AMR, or RGR_{95} vs. AMR_{50}) among the four growth forms, we applied a standardized major axis (SMA) regression (Warton et al., 2012). Contrary to ordinary least square regression where growth should predict mortality (or vice versa), the SMA builds allometry between the variables and uses single line-fitting (or line-of-best-fit) to describe the two-dimension variables (Warton et al., 2006). The slope and magnitude of the SMA line enable to assess the nature of, and make inferences about, the bivariate relationship (Warton et al., 2006). Since our interests were to understand the behavior of the four growth forms when stature scales with demographic rate (i.e., stature vs. growth; stature vs. mortality; stature vs. recruitment) and when growth scales mortality, we fitted four separate SMAs by first log-transforming RGR, RGR_{95}, AMR, AMR_{50}, recruitment, and diameter prior to analysis. This log–log relationship is expected to linearize on the log-transformed scale and approximately takes the power law form (Warton et al., 2012): $\mathrm{RGR} = a\mathrm{AMR}^b$, where b is the slope and represents the scaling exponent of the log–log axes. The magnitude of the slope determines the steepness of diameter–demographic rate or growth–mortality relationships. a is the intercept of the log–log relationship and determines the demographic rate (RGR, RGR_{95}, AMR, AMR_{50}, recruitment) of a species at a given diameter or the growth of species at a given mortality. To test the significance of growth forms in the relationships, we tested whether the SMA lines have equal slopes (variation in slopes steepness) by means of a likelihood ratio statistic (Warton & Weber, 2002). We tested whether variables were uncorrelated (i.e., similar intercepts). We performed pairwise comparisons between the different growth forms for slope (based on likelihood ratio test) using the *multcomp* command integrated in the *smatr-3* (*v* 3.4-8) R-package (Warton et al., 2012).

RESULTS

A total of 329,519 trees (≥10 mm in diameter) and 493 species and morphospecies were recorded from the 50-ha FDP in Korup in 2010. Exclusion of unidentified trees and morphospecies left 329,319 trees and 387 species. The final dataset used for this study constituted 216,249 trees (Appendix S1: Table S2) and 213 species (Table 1) after applying a sample size cutoff of 50 trees per species for the calculation of demographic rates (e.g., growth and mortality) and trade-offs (e.g., growth–mortality and stature–demographic rates).

Variation of taxonomic and structural diversities among growth forms

Species diversity (species richness and Shannon index) and forest structure (number of trees) varied among the four growth forms in the Korup rainforest. For species diversity, treelets had the highest species diversity (198 for richness; Figure 1A, 39 for Shannon; Figure 1B) compared to other growth forms (Figure 1; Appendix S1: Table S1) and canopy species the second highest diversity (110 for richness, 19 for Shannon; Appendix S1: Table S1). The understory and emergent species had the lower species diversity that did not differ significantly from each other (Figure 1; Appendix S1: Table S1).

Considering all ontogenetic stages combined, the number of trees, significantly varies among the four growth forms (Figure 2; Appendix S1: Table S2). Treelets by far comprised the greatest number of stems, followed by canopy, understory, and emergent species. The average number of trees per hectare decreases approximately 19-times as growth forms change from treelet to emergent species (Appendix S1: Table S2). Taking the ontogenetic stages into account, a similar decrease in average number of trees per hectare was observed (Appendix S1: Table S2), and this variation among growth forms was significant for both the adult and sapling (Figure 2) stages. The average number of trees per hectare was 19 times higher for treelet ($3927 \pm 577.2\ \mathrm{ha}^{-1}$) than for emergent ($204 \pm 67.8\ \mathrm{ha}^{-1}$) growth form at the sapling stage and 13 times higher for treelet ($661 \pm 110.5\ \mathrm{ha}^{-1}$) than for emergent ($50 \pm 16.6\ \mathrm{ha}^{-1}$) at the adult stage (Appendix S1: Table S2).

Variation of demographic rates among growth forms and ontogenetic stages

Growth, mortality, and recruitment strongly differed among growth forms and between ontogenetic sapling and adult stages (Figure 3; Appendix S1: Tables S2 and S3). For both ontogenetic stages, growth rates increased with adult stature, with treelets displaying the slowest and emergent species displaying the fastest, growth rates (Figure 3A). Considering all trees together, RGR differed approximately 0.5% to 1% between the growth forms (i.e., on average treelet: $0.0092 \pm 0.0034\ \mathrm{mm\ year}^{-1}$; canopy: $0.0134 \pm 0.0044\ \mathrm{mm\ year}^{-1}$; emergent: $0.0192 \pm 0.0086\ \mathrm{mm\ year}^{-1}$; Figure 3A; Appendix S1: Table S3) and this trend translated to the different ontogenetic stages with treelet having the overall lowest growth rate, but the trend was higher for adult than for sapling stages. Considering all trees together and saplings alone, mortality rate did not differ among growth forms (Figure 3B), but at the adult stage, treelets had significantly lower mortality rates than both canopy and emergent species, which had similar mortality rates (Figure 3B). Recruitment rate showed little significant variation among growth forms except that the lowest recruitment

TABLE 1 Results from standardized major axis (SMA) regression depict demographic and adult stature trade-off relationships among species of four growth forms in a tropical rainforest.

Growth forms	No. species	R^2	p	Slope estimate	95% CI lower	95% CI upper	Pairwise differences
Mean relative growth rate ~ max diameter: $\Lambda = 20.33$, df = 3, $p < 0.001$							
Treelets	98	0.029	<0.136	0.53	0.43	0.65	a
Understory	51	<0.06	0.578	0.73	0.55	0.97	a, b
Canopy	38	<0.01	0.649	1.16	0.84	1.61	b
Emergent	26	<0.01	0.742	−1.09	−1.64	−0.72	b
Mean annual mortality rate ~ max diameter: $\Lambda = 20.59$, df = 3, $p < 0.001$							
Treelets	98	0.03	0.097	−1.1	−1.34	−0.9	a
Understory	51	0.02	0.354	1.69	1.28	2.24	a, b
Canopy	38	<0.01	0.674	2.41	1.73	3.35	b
Emergent	26	<0.01	0.904	−2.16	−3.25	−1.43	b
Recruitment rate ~ max diameter: $\Lambda = 37.72$, df = 3, $p < 0.001$							
Treelets	158	0.31	<0.001	−1.14	−1.3	−0.97	a
Understory	74	<0.01	0.829	−1.98	−2.56	−1.53	b
Canopy	91	<0.01	0.591	−3.63	−2.13	2.78	b
Emergent	64	0.07	0.078	−1.64	−2.24	−1.20	c
Mean growth rate ~ mean mortality rate: $\Lambda = 0.87$, df = 3, $p = 0.675$							
Treelets	98	0.01	0.443	−2.05	−2.52	−1.68	a
Understory	51	0.22	<0.001	2.30	1.79	2.96	a
Canopy	38	0.04	0.198	2.06	1.49	2.86	a
Emergent	26	0.06	0.22	1.97	1.32	2.93	a
Fast growth ~ max diameter: $\Lambda = 21.59$, df = 3, $p < 0.001$							
Treelets	98	0.06	<0.013	0.46	0.38	0.56	a
Understory	51	<0.01	0.935	0.64	0.48	0.85	a, b
Canopy	38	<0.01	0.982	1.034	0.74	1.44	b
Emergent	26	0.01	0.538	−0.95	−0.42	−0.63	b
Mortality in shade ~ max diameter: $\Lambda = 20.46$, df = 3, $p < 0.001$							
Treelets	92	0.07	0.009	−1.22	−1.48	−0.99	a
Understory	48	0.01	0.540	1.75	1.31	2.35	a, b
Canopy	36	0.01	0.625	−2.65	−3.72	−1.88	b
Emergent	21	0.05	0.352	−2.65	−4.17	−1.68	b
Recruitment per number of reproductive adults ~ max diameter: $\Lambda = 25.37$, df = 3, $p < 0.001$							
Treelets	105	0.005	0.466	−2.66	−3.22	−2.19	a
Understory	59	0.002	0.730	−4.48	−5.79	−3.46	b
Canopy	55	<0.01	0.930	−5.65	−7.39	−4.33	c
Emergent	37	0.14	0.017	−2.84	−3.83	−2.10	b
Fast growth ~ mortality in shade: $\Lambda = 0.91$, df = 3, $p = 0.822$							
Treelets	92	0.01	0.438	−2.52	−3.14	−2.07	a
Understory	48	0.28	<0.001	1.77	2.16	3.55	a
Canopy	36	0.25	0.001	2.45	1.82	3.30	a
Emergent	21	0.27	0.013	2.45	1.51	3.34	a

Note: Likelihood ratio tests (Λ) were used to evaluate the importance of growth form in each relationship. R^2 and p values are for the correlation between the two variables, and SMA slope estimates, and CIs are provided for each growth form. Pairwise differences in slopes between growth forms based on the Sidak correction for multiple comparisons are indicated by lowercase letters; pairs that share a letter do not differ significantly. Note that SMA slopes are based on the ratio of the SDs of the two variables, and so cannot overlap zero (Warton et al., 2006).

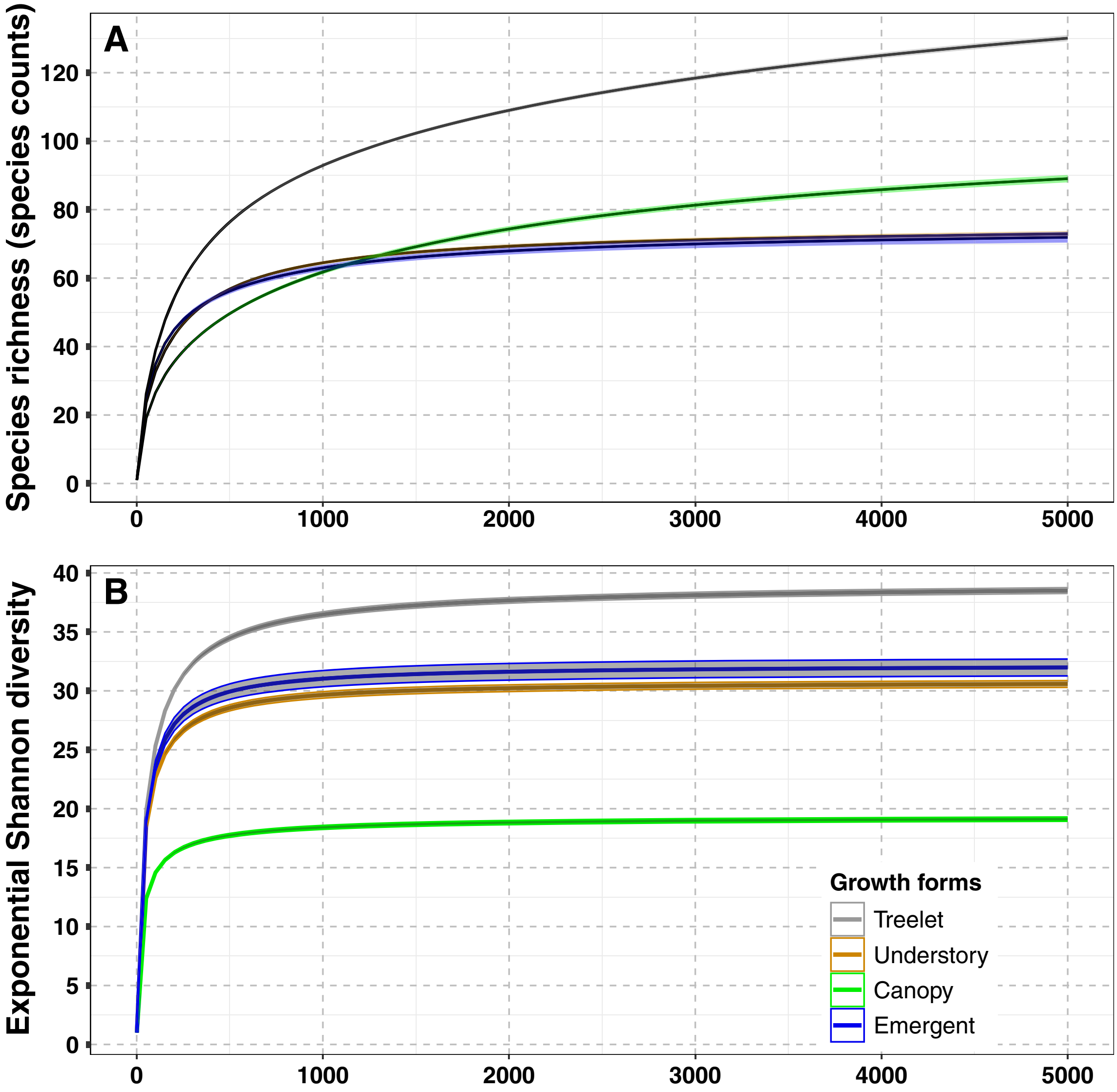

FIGURE 1 Rarefaction curves for (A) the accumulation of species richness and (B) Shannon–Wiener diversity for four growth forms. Lines denote sample-size-based rarefaction, and shaded regions around each line denote 95% CIs (not visible for all groups at this resolution). The number of individuals was standardized to 5000 trees for each growth form (treelet: <10 m, understory: 10 to <20 m, canopy: 20–30 m, and emergent: >30 m height).

rate was recorded for understory trees (Figure 3C). The average recruitment rate was 0.0209 ± 0.0198 year^{-1} with maximum recruitment rate of 0.198 year^{-1} recorded for a treelet species, RGR95 and minimum of 0.0022 year^{-1} recorded for an understory species.

Stature–demography and growth–mortality trade-offs

Overall, there were some significant interspecific relationships among adult stature (dbh_{max}) and demographic rates (RGR, RGR_{95}, AMR, AMR_{50}, REC, and REC_{abun}) that consistently differed across growth forms (Figure 4, Table 1; Appendix S1: Figure S2). Mean and fast relative growth rates (RGR, RGR_{95}) became progressively faster with larger adult stature (dbh_{max}), and the slopes of these relationships were different among growth forms (Figure 4A, Table 1; Appendix S1: Figure S2A). The rate of increase in RGR_{95} with maximum size was lower for species of smaller stature, especially for treelets. Specifically, treelets exhibited shallower slopes than understory, canopy, and emergent species and did differ from those of any other growth form (Table 1). The relationships between mean AMR, mortality in shade (AMR_{50}), and adult stature (dbh_{max}) were weak across all species but exhibited variations across growth forms (Figure 4B, Table 1; Appendix S1: Figure S2B). Mortality

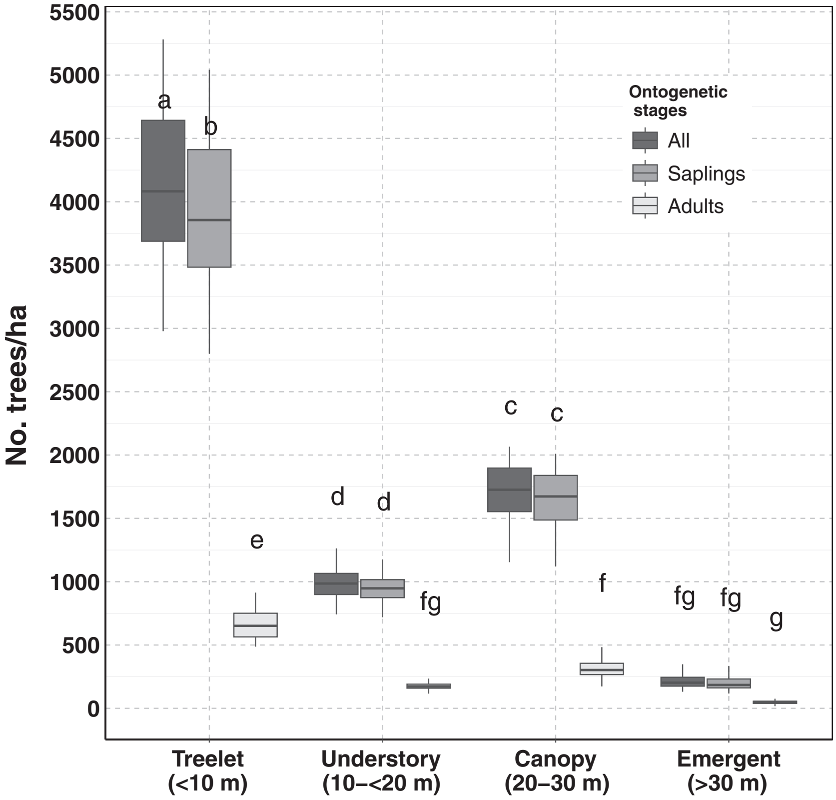

FIGURE 2 Variation of the average number of trees per hectare summed over species among four growth forms and ontogenetic stages. Two-way ANOVA with multiple comparisons based on the Tukey honestly significant difference test. Bottom and top edges of boxes represent the first 25% and third 75%, respectively, of tree density, midline inside of the box represents the median, and the extreme whiskers represent the smallest and largest values of tree density per ontogenetic stage and growth form, respectively. Growth forms with different letters are significantly different at $p < 0.05$.

in shade of treelets declined with increasing adult stature, whereas there were no significant relationships for the other growth forms (Table 1). Across all species, the slope of growth forms exhibited significant variations between recruitment rate (REC), recruitment per reproductive adult ($\mathrm{REC}_{\mathrm{abun}}$), and adult stature (Figure 4C; Appendix S1: Figure S2C) whereas correlations between REC and $\mathrm{REC}_{\mathrm{abun}}$ with adult stature depended on which growth form was analyzed (Figure 4C, Table 1; Appendix S1: Figure S2C). Recruitment and recruitment per reproductive adult declined significantly only for treelet and emergent species, respectively.

Across all species, there was a weak, but statistically significant interspecific growth-mortality trade-off based on all trees (Figure 4D) as well as among saplings only (Appendix S1: Figure S3). Regardless of how the trade-off was modeled, however, there were no significant differences in the slope of this trade-off across growth forms (Figure 4D, Table 1; Appendix S1: Figure S2D). Treelets showed no significant trade-off relationship, whereas understory, canopy, and emergent species showed significant positive correlations between mean growth and mortality and between fast growth and mortality in shade (Figure 4D, Table 1; Appendix S1: Figure S2D). Patterns were similar for analyses using saplings only, except that treelets exhibited a significant negative interspecific growth–mortality relationship (Appendix S1: Figure S3).

DISCUSSION

In this tropical forest of Cameroon, tree stature and growth form influenced patterns of forest diversity, structure, demography, and life history trade-offs. Species of growth forms living their entire lives in the lower forest strata (treelet and understory species) often diverged in these dimensions of forest community structure from species that eventually reach or surpass the forest canopy (canopy and emergent species). Treelet and understory species contributed substantially to taxonomic diversity, more so than larger statured species. Treelets were by far the growth form with the greatest tree density, representing an important component of the physiognomy of this forest. The decline in tree density we observed from

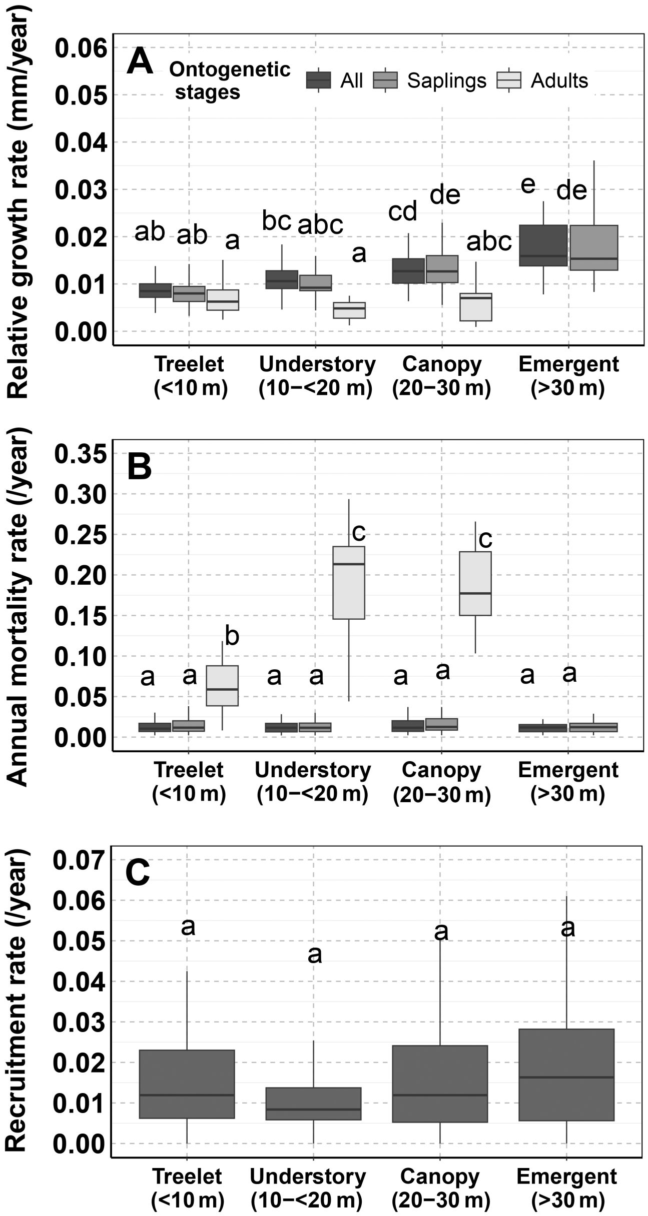

FIGURE 3 Variation of demographic rates among four growth forms and two ontogenetic stages in a tropical rainforest: (A) mean relative growth rate, (B) annual mortality rate, and (C) annual recruitment rate irrespective of ontogenetic stages (all) and per ontogenetic sapling and adult stages. Multiple comparisons by Tukey honestly significant difference test applied on two-way ANOVA. Bottom and top edges of boxes represent the first 25% and third 75%, respectively, of tree density, midline inside of the box represents the median, and the extreme whiskers represent the smallest and largest values of tree density per ontogenetic stage and growth form, respectively. Boxes with similar letters are not significantly different at $p < 0.05$. Adult stage for the emergent growth form is not shown because species had less than the required 50 trees per species.

smaller statured growth forms to larger statured ones aligns with a general trend of decreasing tree density with increasing adult stature observed in other tropical forests (King, Wright, et al., 2006; Tchouto et al., 2006). Variation in tree stature and growth form also contributed to demographic diversity. Growth rate consistently increased from treelet to emergent species, whereas mortality and recruitment rates showed weaker or more variable stature-related differences. The only differences in mortality among growth forms were for treelets, which had far lower mortality as adults than the larger growth forms.

Since growth form can influence demographic rates, species of different growth forms may exhibit different strengths of life history trade-offs, such as among adult stature and demographic rates. Our results revealed that growth forms have different slopes for the stature–demographics trade-offs but was independent for the growth–mortality trade-off, implying growth forms should not be considered only for growth–mortality trade-off relationship. A similar result holds broadly across tropical forests meaning faster growing species often experience higher mortality, independent of growth form (Russo et al., 2021). While the interaction of growth forms could mediate the relationship between adult stature and demographic rates, this interaction would not matter for the trade-off between growth and mortality rates.

Like the trend in the number of trees, we also found that small-statured growth forms tended to harbor the highest species richness and Shannon diversity in this Cameroonian forest. These results support the hypothesis that the dominance of small-statured trees evinces high species diversity in the tropics (Niklas et al., 2003a, 2003b). Therefore, predicting tropical forest diversity based only on large trees, usually ≥10 cm in diameter, may induce strong bias in the estimation of species richness. Given the large contribution of smaller statured species (e.g., treelet and understory species) to forest diversity and structure, forest inventories should use tree size cut-offs <10 cm in diameter, in order to avoid biases in the estimation of species richness (Davies et al., 2021) and so as to capture the contribution of small-statured species and young ontogenetic stages to stand diversity and dynamics (Kohyama et al., 2020). Growth forms also often deviated from each other in terms of the strength and slope of interspecific relationships involving demographic rates and adult stature. Not only was there a consistent positive relationship between stature and growth rates across all growth forms, consistent with results from southeast Asian forests (King, Davies, et al., 2006; Thomas, 1996a, 1996b), but also the slope of this relationship was steeper for canopy and emergent species, indicating that larger statured species have even greater growth capacity than smaller statured species. This trend probably reflected the trade-off between stature and fast growth (King, Davies, et al., 2006) that enhances

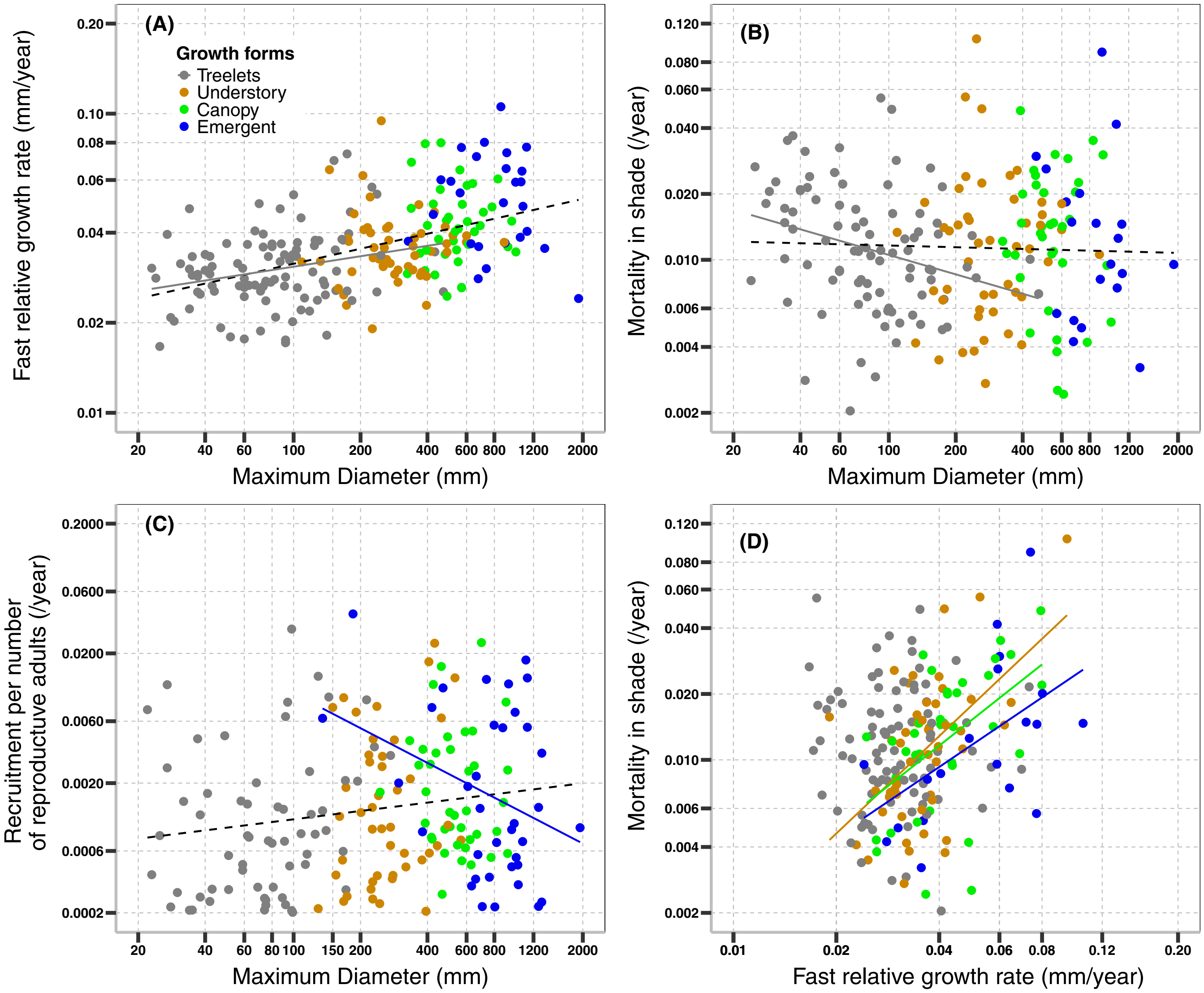

FIGURE 4 Demographic trade-off relationships among species of four growth forms in a tropical rainforest. (A) Fast relative growth rate of species is 95th quantile of the relative growth rate, and (B) mortality in shade is annual mortality rate above the 50th quantile of the neighborhood density; (C) recruitment per number of reproductive adults is plotted against adult stature or maximum diameter; (D) Fast relative growth rate versus mortality in shade. Growth form is defined by species maximum height (treelet: <10 m, understory: 10 to <20 m, canopy: 20–30 m, and emergent >30 m). Dash black line is shown when the hypothesis of equal slopes among the four growth forms is rejected, and solid-colored lines indicate significant correlation for demographic relationship per growth form.

coexistence of species belonging to the same growth form. The trade-off concerns large-statured species that tend to grow fast in order to reach reproductive size versus small-statured species that tend to grow slowly because they invest more resources toward defense and/or early reproduction in the forests under canopy layer (Thomas, 1996a, 1996b). The positive relationship across all species may be partly explained by the fact that populations of larger statured species often have a greater proportion of larger trees, which tend to grow more quickly due to greater access to resources (Weiner, 1990), all else being equal (King, Davies, et al., 2006; Muller-Landau et al., 2006). However, the facts that the growth–stature slopes were still positive within growth forms, in which the range of adult stature is much smaller, and that they increased significantly from smaller to larger growth forms is consistent with hypothesized trade-offs between adult stature versus fast-growth capacity and mortality driven by interspecific trade-offs related to photosynthetic light-use efficiency (Givnish, 1988; Thomas & Bazzaz, 1999). The physiologies of larger statured species eventually reaching into and beyond the well-lit forest canopy may enable rapid growth that elevates their crowns vertically into better and better light environments, whereas smaller statured, shade-tolerant species living their lifetimes in shaded, lower forest strata are expected to have lower growth capacity and invest in defense (Givnish, 1988; Thomas, 1996a, 1996b; Thomas & Bazzaz, 1999). Our findings that treelets had the lowest mortality rates as adults and that their shade mortality declined with stature are also consistent with these hypothesized trade-offs. Our findings are less consistent with those of Poorter et al. (2008), which proposed that growth and mortality rates should decline with adult stature because light-demanding species should grow fast, reproduce quickly, and die at small adult sizes owing to their dependence on forest gaps, whereas larger statured species should grow more slowly in the shaded understory, where resources are more profitably invested in survival. However, this prediction assumes that smaller statured species are gap-dependent, but in this Cameroonian forest with lower rates of canopy disturbance, many, if not most, smaller statured species are shade-tolerant. Our results are more consistent with those from a Malaysian forest, also with lower rates of canopy gap formation, in which asymptotic height had a positive interspecific relationship with growth rate, but a negative relationship with wood density (King, Davies, et al., 2006; Thomas, 1996a, 1996b). Our findings highlight the need to consider the drivers of stature-related trade-offs with respect to growth form and not only shade tolerance. The higher mortality observed for adult canopy and emergent trees may be associated with the natural cause of aging (Mencuccini et al., 2005). However, the low mortality rate observed for treelet at the adult stage is perhaps an ecological strategy to completely remain in low sunlight conditions for longer time. The negative relationships between adult stature and per capita and mean recruitment for treelets and emergent trees observed in this study are consistent with the stature–recruitment trade-off that Kohyama (1993) proposed could maintain forest diversity even when species have similar growth and mortality rates. The trade-off described here concerns large-statured species that invest in per capita recruitment over canopy performance, as opposed to small-statured species that invest in per capita recruitment over canopy performance. Thus, the generality of the stature–recruitment trade-off (Iida, Poorter, et al., 2014; Kambach et al., 2022; Rüger et al., 2018) is also supported by our findings. Across all species, we also found support for the interspecific growth–mortality trade-off, but the strength and slope of the trade-off did not vary among growth forms. While understory, canopy and emergent species exhibited significant positive correlations, growth and mortality rates were not significantly correlated for treelet nor emergent species, based on trees of all sizes. It has been argued that the trade-off is most strongly exhibited among immature trees (Wright et al., 2010), and our results are consistent with this proposition. Moreover, although analyses using all versus only immature trees yielded similar results for the other growth forms, treelets exhibited a significantly negative growth–mortality trade-off for saplings only. It is possible that for species that live their entire lives in the deeply shaded understory and already have low mortality rates relative to larger growth forms, further reductions in allocation to growth may increase, rather than decrease, mortality risk.

Tropical forests across Asia, the Americas, and Africa differ dramatically in the importance of contrasting growth forms and the tree families responsible for those differences (LaFrankie, 2005; LaFrankie et al., 2006). Our study demonstrates that adult stature should not be conflated with growth form nor shade tolerance, because in this Cameroonian forest, growth form structured life history trade-offs involving adult stature and demography in ways that were not strictly tied to shade tolerance. Small-statured treelets living their entire lives in the shaded understory contributed enormously to forest diversity and physiognomy, and their trade-off relationships often deviated from those of larger growth forms. Thus, the degree to which life history trade-offs involving adult stature and demography differ in strength and direction among forests, and hence the contributions of these trade-offs to diversity maintenance (Kambach et al., 2022; Rüger et al., 2018; Russo et al., 2021; Thomas, 1996a, 1996b; Wright et al., 2010), may be partially explained by how historical biogeography has shaped regional species pools.

AUTHOR CONTRIBUTIONS

Moses B. Libalah, Sabrina E. Russo, and David Kenfack conceived the study. Moses B. Libalah, George B. Chuyong, Duncan Thomas, and David Kenfack collected and compiled the data. Moses B. Libalah and Sabrina E. Russo developed the statistical methods and Moses B. Libalah analyzed the data. All authors contributed to interpreting the results, writing the manuscript, and providing final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data used for this study are available upon request via the ForestGeo Data Request Portal (http://ctfs.si.edu/datarequest/index.php/request/form/4).

ORCID

Moses B. Libalah https://orcid.org/0000-0001-8848-8001
Sabrina E. Russo https://orcid.org/0000-0002-6788-2410
George B. Chuyong https://orcid.org/0000-0002-0235-211X
Duncan Thomas https://orcid.org/0000-0003-1818-0057
David Kenfack https://orcid.org/0000-0001-8208-3388

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SUPPORTING INFORMATION

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

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