

RESEARCH ARTICLE

Consistency of demographic trade-offs across 13 (sub)tropical forests

Stephan Kambach^{1,2}  | Richard Condit^{3,4} | Salomón Aguilar⁵ | Helge Bruehlheide^{1,2}  | Sarayudh Bunyavejchewin⁶  | Chia-Hao Chang-Yang⁷  | Yu-Yun Chen⁸  | George Chuyong⁹ | Stuart J. Davies¹⁰  | Sisira Ediriweera¹¹  | Corneille E. N. Ewango^{12,13,14} | Edwino S. Fernando¹⁵  | Nimal Gunatilleke¹⁶  | Savitri Gunatilleke¹⁶ | Stephen P. Hubbell^{4,17} | Akira Itoh¹⁸  | David Kenfack¹⁰  | Somboon Kiratiprayoon¹⁹ | Yi-Ching Lin²⁰  | Jean-Remy Makana²¹  | Mohizah Bt. Mohamad²²  | Nantachai Pongpattananurak²³ | Rolando Pérez⁴ | Lillian Jennifer V. Rodriguez²⁴ | I-Fang Sun²⁵  | Sylvester Tan¹⁰ | Duncan Thomas²⁶  | Jill Thompson²⁷  | Maria Uriarte²⁸  | Renato Valencia²⁹  | Christian Wirth^{5,30,31}  | S. Joseph Wright⁴  | Shu-Hui Wu^{7,32} | Takuo Yamakura¹⁸ | Tze Leong Yao³³  | Jess Zimmerman³⁴ | Nadja Rüger^{2,4,35}

¹Institute of Biology/Geobotany, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany; ²German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; ³Field Museum of Natural History, Chicago, Illinois, USA; ⁴Morton Arboretum, Lisle, Illinois, USA; ⁵Smithsonian Tropical Research Institute, Balboa, Ancón, Panama; ⁶Forest Research Office, Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand; ⁷Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung, Taiwan; ⁸Department of Natural Resources and Environmental Studies, National Dong Hwa University, Hualien, Taiwan; ⁹Department of Botany and Plant Physiology, University of Buea, Buea, SWP, Cameroon; ¹⁰Global Earth Observatory (ForestGEO), Smithsonian Tropical Research Institute, Washington, USA; ¹¹Department of Science and Technology, Uva Wellassa University, Badulla, Sri Lanka; ¹²Forest Ecology and Forest Management Group, Wageningen University & Research, Wageningen, The Netherlands; ¹³Faculty of Renewable Natural Resources Management, University of Kisangani, Kisangani, Democratic Republic of Congo; ¹⁴Biosystematics Group, Wageningen University, Wageningen, The Netherlands; ¹⁵Department of Forest Biological Sciences, University of the Philippines - Los Baños, Laguna, Philippines; ¹⁶Faculty of Science, Department of Botany, University of Peradeniya, Peradeniya, Sri Lanka; ¹⁷Department of Ecology and Evolutionary Biology, University of California, Los Angeles, California, USA; ¹⁸Graduate School of Science, Osaka City University, Osaka, Japan; ¹⁹Faculty of Science and Technology, Thammasat University (Rangsit), Klongluang, Pathum Thani, Thailand; ²⁰Department of Life Science, Tunghai University, Taichung, Taiwan; ²¹Faculty of Science, University of Kisangani, Kisangani, Democratic Republic of Congo; ²²Forest Department Sarawak, Kuching, Sarawak, Malaysia; ²³Department of Forest Biology, Faculty of Forestry, Kasetsart University, Bangkok, Thailand; ²⁴Institute of Biology, University of the Philippines Diliman, Quezon City, Philippines; ²⁵Center for Interdisciplinary Research on Ecology and Sustainability (CIRES), National Dong Hwa University, Hualien, Taiwan; ²⁶Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon, USA; ²⁷UK Centre for Ecology & Hydrology, Edinburgh, UK; ²⁸Department of Ecology, Evolution & Environmental Biology, Columbia University, New York, New York, USA; ²⁹Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; ³⁰Systematic Botany and Functional Biodiversity, Institute of Biology, University of Leipzig, Leipzig, Germany; ³¹Max-Planck-Institute for Biogeochemistry, Jena, Germany; ³²Taiwan Forestry Research Institute, Council of Agriculture, Executive Yuan, Taiwan; ³³Forest Research Institute Malaysia (FRIM), Kepong, Selangor Darul Ehsan, Malaysia; ³⁴Department of Environmental Sciences, Universidad de Puerto Rico, San Juan, Puerto Rico and ³⁵Department of Economics, University of Leipzig, Leipzig, Germany

Correspondence

Stephan Kambach

Email: stephan.kambach@gmail.com

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Abstract

1. Organisms of all species must balance their allocation to growth, survival and recruitment. Among tree species, evolution has resulted in different life-history strategies for partitioning resources to these key demographic processes.

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Life-history strategies in tropical forests have often been shown to align along a trade-off between fast growth and high survival, that is, the well-known fast-slow continuum. In addition, an orthogonal trade-off has been proposed between tall stature—resulting from fast growth and high survival—and recruitment success, that is, a stature–recruitment trade-off. However, it is not clear whether these two independent dimensions of life-history variation structure tropical forests worldwide.

2. We used data from 13 large-scale and long-term tropical forest monitoring plots in three continents to explore the principal trade-offs in annual growth, survival and recruitment as well as tree stature. These forests included relatively undisturbed forests as well as typhoon-disturbed forests. Life-history variation in 12 forests was structured by two orthogonal trade-offs, the growth–survival trade-off and the stature–recruitment trade-off. Pairwise Procrustes analysis revealed a high similarity of demographic relationships among forests. The small deviations were related to differences between African and Asian plots.
3. *Synthesis.* The fast-slow continuum and tree stature are two independent dimensions structuring many, but not all tropical tree communities. Our discovery of the consistency of demographic trade-offs and life-history strategies across different forest types from three continents substantially improves our ability to predict tropical forest dynamics worldwide.

KEYWORDS

demographic rates, demographic trade-offs, ForestGeo, growth, life-history strategies, mortality, PCA, recruitment, size, stature, survival, tropical forests

1 | INTRODUCTION

Organisms must apportion limited resources among growth, survival and reproduction (Metcalf & Pavard, 2007; Stearns, 1992), and physiological and morphological constraints force trade-offs among these three demographic components. Life-history theory examines these trade-offs and predicts how demographic strategies depend on limited resources and which strategies can coexist in a community (Lande, 1982; Stearns, 1992). Empirical tests of the theory across a wide variety of plant growth forms have uncovered two orthogonal demographic axes (Salguero-Gómez et al., 2016), a trade-off between fast growth and long life, that is, the fast–slow continuum (Reich, 2014), and a trade-off between highly reproductive, iteroparous species at one extreme, and poorly reproductive, semelparous species at the other extreme (Salguero-Gómez et al., 2016).

Tropical forests harbour high numbers of tree species and life-history strategies in small areas (Condit et al., 2006), allowing the exploration of demographic trade-offs within local communities of the same growth form under similar environmental constraints. Several demographic trade-offs have been described from single sites, including trade-offs between growth and survival (Poorter et al., 2008; Wright et al., 2010), between survival and reproduction (Uriarte et al., 2012), between fecundity and dispersal (Uriarte et al., 2012),

between demographic rates during different ontogenetic stages (Baraloto et al., 2005), and between sapling recruitment and maximum tree size (hereafter 'stature', Kohyama, 1993). However, these explorations of the demographic trade-offs typically only include two demographic components and have not provided a holistic assessment of how tropical tree communities are structured in terms of their life-history strategies including growth, survival, reproduction and stature.

A multivariate analysis of tree growth and survival rates in different canopy layers and sapling recruitment rates across 282 coexisting tree species at Barro Colorado Island in Panama (BCI) revealed two orthogonal trade-offs in life-history variation (Figure 1, Rüger et al., 2018). The first one reflected the familiar trade-off between growth and survival rates, which is related to a species' shade tolerance (Rüger et al., 2018; Russo et al., 2021; Wright et al., 2010). The second one described a trade-off between jointly high growth and survival rates, resulting in tall tree statures, with high recruitment rates, a measure of reproductive success (Kohyama, 1993; Kohyama et al., 2003; Rüger et al., 2018). Thus, pace of life (i.e. the growth–survival trade-off) and tree stature (i.e. the stature–recruitment trade-off) present independent axes of life-history differentiation in tropical trees in Panama. This independence has often been assumed (Turner, 2009), especially when classifying tropical tree species into plant functional types for modelling purposes (Gourlet-Fleury et al., 2005; Kazmierczak

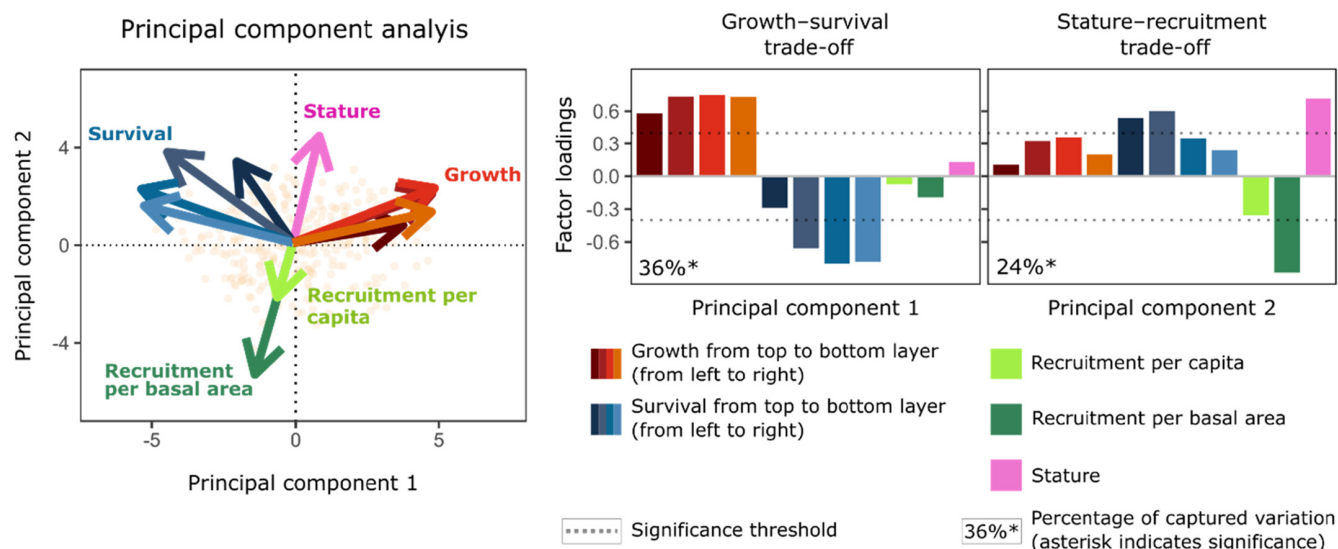


FIGURE 1 Multivariate analysis of variation in demographic rates, exemplified by data from the Barro Colorado Island forest. (Left side) Principal component analysis determines the axes (principal components) of maximum interspecific demographic variation between species' annual growth and survival rates from the top to the bottom canopy layer, recruitment rates and stature. (Right side) Significant loadings of demographic characteristics on the axes show the main demographic trade-offs. Here, the most important trade-off is between growth in all canopy layers and per-capita recruitment versus survival in canopy layers 2–4. The second trade-off is mainly a trade-off between stature (associated with fast growth and high survival) versus recruitment (per-capita and per-basal-area)

et al., 2014), but has rarely been substantiated by empirical data. It is unclear whether the two orthogonal trade-offs emerge across tropical forests that occur under different climate conditions or disturbance regimes. The growth–survival trade-off, for instance, was found to structure only eight, mostly undisturbed, out of 10 globally distributed (sub)tropical forests (Russo et al., 2021).

Here, our objective was to evaluate whether the growth–survival trade-off and the stature–recruitment trade-off are orthogonal demographic dimensions that consistently structure tropical forests from three continents. To do this, we collated demographic information from 13 (sub)tropical large-scale forest dynamics plots that together include more than 5000 species and 2,500,000 individuals and accounted for local differences in growth and survival due to tree size and light availability. We used principal component analyses to investigate the local relationships among species' demographic rates and to see whether trade-offs in life-history strategies could be detected (according to Figure 1). We then used Procrustes analyses to quantify the similarities and differences in demographic relationships among the forests, to investigate whether these differences in local demographic relationships were related to the biogeographic region, species richness, basal area or the occurrence of major disturbance events.

2 | MATERIALS AND METHODS

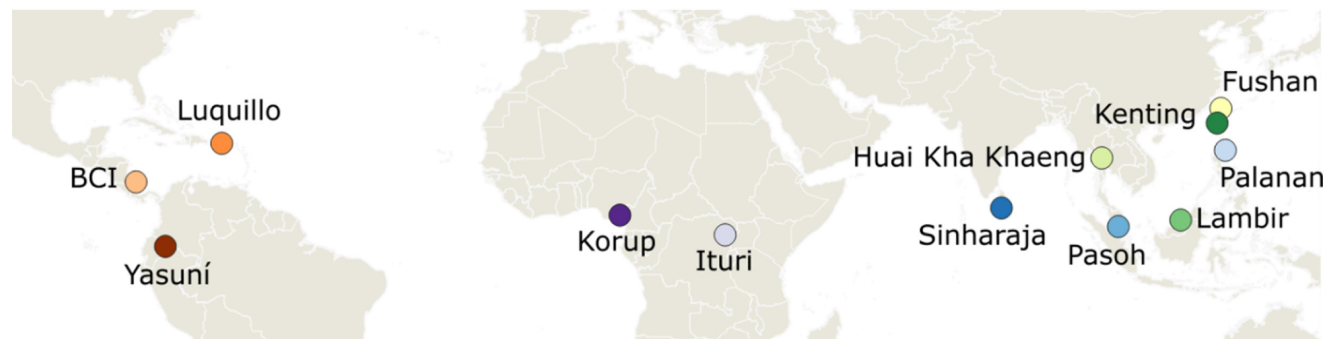
2.1 | Study sites

We collated woody plant census data from 13 tropical and subtropical forest dynamics plots from the Forest Global Earth Observatory network (Anderson-Teixeira et al., 2015; Davies et al., 2021, forestgeo.

si.edu). Site locations, climate, forest types, principal investigators and references are summarized in Figure 2; Tables S1 and S2). Forests were distributed across South America (two sites), Africa (three sites) and Asia (eight sites). Mean annual temperatures ranged from 18.3 to 28.3 °C of. Annual precipitation ranged from 1682 to 5272 mm. Plot sizes ranged from nine to 52 ha and tree species richness ranged from 111 to 1475 species. Four out of the 13 forests experienced regular hurricane disturbances (Fushan, Kenting, Luquillo and Palanan) and one forest experienced regular fires (Huai Kha Khaeng—HKK).

2.2 | Data collection

Each site has been re-censused approximately every 5 years. In every census, the main stem of every woody plant individual (hereafter 'tree') with a diameter at breast height of 1.3 m from the ground (dbh) ≥ 1 cm was mapped, identified to species or morphospecies and measured for dbh with an accuracy of up to 1 millimetre (following the measurement protocol presented in Condit, 1998). We deemed all trees not explicitly marked as alive to be dead, including trees that were previously alive but missing in the next census (average proportions of missing trees are shown in Table S1). Trees with unknown spatial coordinates were omitted from the analyses. Trees with unknown status or morphospecies that might represent more than one species and palms (*Arecaceae*) were retained for the assignment of canopy layers but omitted from the demographic analyses. Growth rates for trees were not calculated if the height of the dbh measurement changed between consecutive censuses. In case of multiple-stemmed trees, only the largest stem was used for the calculation of growth rates. In the first and second censuses of the BCI and the



Research site	Census Range	Forest type (plot size)	Dominant soil order(s)	Nr of species analysed (all)	Basal area (m ² ha ⁻¹)	Major disturbances	Growth–survival trade-off	Stature–recruitment trade-off
BCI (Barro Colorado Island)	1982 - 2015	Broadleaf drought deciduous (50 ha)	Ox	286 (325)	31.2	-	On PC 1	On PC 2
Fushan	2004 - 2013	Broadleaf evergreen (25 ha)	Ult; In	103 (111)	37.1	Typhoons	On PC 2	On PC 1
HKK (Huai Kha Khaeng)	1993 - 2004	Broadleaf drought deciduous (50 ha)	Alf	274 (300)	30.7	Fire	On PC 2	On PC 1
Ituri-Edoro	1995 - 2007	Broadleaf evergreen (19 ha)	Ox	339 (511)	30.9	-	On PC 1	On PC 2
Ituri-Lenda	1995 - 2007	Broadleaf evergreen (19 ha)	Ox	330 (511)	36.0	-	On PC 1	On PC 2
Kenting	2001 - 2013	Broadleaf evergreen (10 ha)		91 (129)	38.0	Typhoons	On PC 1	On PC 2
Korup	1998 - 2008	Broadleaf evergreen (50 ha)	Ult, Ox	437 (490)	31.3	-	On PC 1	On PC 2
Lambir	1992 - 2008	Mixed dipterocarp evergreen (52 ha)	Ult	1,195 (1,475)	42.7	-	On PC 1	On PC 2
Luquillo	1992 - 2016	Broadleaf evergreen (15 ha)	Ox; Ult	133 (163)	30.7	Hurricanes		
Palanan	1994 - 2010	Mixed dipterocarp evergreen (14 ha)	Ult; In	301 (330)	37.3	Typhoons	On PC 1	On PC 2
Pasoh	1987 - 2010	Mixed dipterocarp evergreen (50 ha)	Ult	820 (937)	31.8	-	On PC 1	On PC 2
Sinharaja	1995 - 2007	Mixed dipterocarp evergreen (25 ha)	Ult	226 (239)	44.4	-	On PC 1	On PC 2
Yasuní	1996 - 2008	Broadleaf evergreen (25 ha)	Ult	1,017 (1,100)	29.6	-	On PC 1	On PC 2

FIGURE 2 Location, characteristics and the observed trade-offs in principal component analyses of growth, survival, recruitment and stature in 13 (sub)tropical forests. Principal components (PC) that captured a significant proportion of variation in demographic rates (compared to a broken-stick criterion) are highlighted in bold. Soil order(s) follow the USDA soil taxonomy system (soil survey staff, 1999): Alf—Alfisols; in—Inceptisols; ox, Oxisols, Ult—Ultisols

Pasoh forest, the recorded dbh values had been rounded down to the nearest 5 mm for all stems with <5 cm dbh. Those observations were not used to calculate growth rates.

To assign trees to discrete canopy layers, we first estimated the crown area based on the allometric equation from Bohlman and Pacala (2012).

$$\text{BCI: crown area (m}^2\text{)} = 0.036 \times \text{dbh (mm)}^{1.281}.$$

As crown area is a monotonic function of dbh, size hierarchies are assumed to be consistent between tree diameter and crown area. Since crown area allometries vary between tropical forests (Blanchard

et al., 2016; Loubota Panzou et al., 2021), we checked for the sensitivity of our results to the applied allometric equation by repeating all analyses with an equation from a lowland evergreen tropical rainforest in French Guiana (FG) that yielded relatively lower crown area estimates (Blanchard et al., 2016).

$$\text{FG: crown area (m}^2\text{)} = 0.811 \times \text{dbh (cm)}^{1.212}.$$

We assigned trees to canopy layers following the approach of Bohlman and Pacala (2012). We divided forest plots into subplots of 31.25 by 31.25 m (following to Bohlman & Pacala, 2012) and omitted those edge areas that would not fill a complete subplot. Within each subplot, we sorted trees by estimated crown area and added trees (starting from the largest crown area) to the top canopy layer until the cumulative crown area of added trees exceeded the subplot area. If <50% of the crown area of a tree fitted into the remaining subplot area, this tree was assigned to the next lower canopy layer. This way, all canopy layers were filled. To ensure a sufficiently high number of species per canopy layer, we truncated the maximum number of canopy layers used in subsequent analyses for each forest plot so that the lowest canopy layer had at least half the number of species than the most species-rich canopy layer. The number of canopy layers ranged between four layers in BCI, Ituri-Lenda, Pasoh and HKK and seven layers in Fushan and Sinharaja (see Figure S3 for the distribution of dbh sizes within the different canopy layers).

2.3 | Demographic rates

For every forest plot, we determined species' annual growth and survival rates in each canopy layer and annual recruitment rates per reproductive capita and per unit (m²) of reproductive basal area (modified from Rüger et al., 2018).

Between consecutive censuses, we quantified for all the trees, that were alive in the first (t_1) and the second censuses (t_2), the observed annual increment in dbh as $\frac{\text{dbh}_{t_2} - \text{dbh}_{t_1}}{t}$ (t = time between t_2 and t_1 in years). To balance the dataset and reduce computation time, we pooled observations from different census intervals, discarded the highest and lowest 1% of observed growth rates (for all species with more than 100 observations) and randomly selected up to 100 observations per species and canopy layer. Including repeated measurements of the same tree across different census intervals does not bias the results (Rüger et al., 2018). To achieve approximate normality, we first added the absolute of the observed minimum growth rate plus a constant of 0.001 to every growth rate (to yield positive values) and then log transformed all values. To foster model convergence, we centred and scaled the transformed values. Average transformed growth rates ($g_{j,k}$) of species j in canopy layer k were then estimated using hierarchical Bayesian models that were separately fitted for every canopy layer. The likelihood of the observed transformed growth rate ($\text{growth}_{i,j,k}$) of tree i of species j in canopy layer k was

$$\text{growth}_{i,j,k} = \text{Normal}(g_{j,k}, \text{sigma}_{j,k}),$$

with $\text{sigma}_{j,k}$ being the standard deviation of growth of species j in layer k .

Across species, layer-specific transformed growth rates ($g_{j,k}$) were assumed to follow normal distributions with the mean g_k and standard deviation $\sigma_{g,k}$ and layer-specific standard deviations in growth rates ($\text{sigma}_{j,k}$) were assumed to follow log-normal distributions with the mean sigma_k and the standard deviation $\sigma_{\text{sigma},k}$.

$$g_{j,k} = \text{Normal}(g_k, \sigma_{g,k}),$$

$$\text{sigma}_{j,k} = \text{Lognormal}(\text{sigma}_k, \sigma_{\text{sigma},k}).$$

We chose flat priors for g_k , $\sigma_{g,k}$, sigma_k and $\sigma_{\text{sigma},k}$. To speed up computations, we imposed the following restrictions on the distributions of the parameters and priors: (i) $g_{j,k}$ must be larger than zero and lower than the 95th percentile of the observed species-specific growth rates $\text{growth}_{i,j,k}$, (ii) $\sigma_{g,k}$ must be between one and five, (iii) $\text{sigma}_{j,k}$ must be between the 5th and the 95th percentiles of the observed species-specific standard deviations and (iv) $\sigma_{\text{sigma},k}$ must be between 0 and 2. These restrictions guaranteed that demographic estimates for species with low sample size were more strongly drawn towards canopy-layer mean values and associated with larger uncertainty (95% credible interval). That is, growth rates of species without observations in a given canopy layer were assumed to be equal to the mean of all species in that layer and associated with large uncertainty.

Between consecutive censuses, we quantified for all those trees that were alive in the first census the observed survival status in the second census (alive/dead). To balance the dataset and speed up computations, we pooled observations from different census intervals and randomly selected up to 1000 observations per species and canopy layer. Average annual survival probabilities ($s_{j,k}$) of species j in layer k were estimated using hierarchical Bayesian models that were separately fitted for every canopy layer. The likelihood of the observed survival of tree i of species j in layer k over t years between consecutive censuses, is

$$p(\text{alive}_{i,j,k} | s_{j,k}) = \text{Bernoulli}(\text{alive}_{i,j,k} | s_{j,k}^t),$$

$$s_{j,k} = \text{Beta}(\alpha_k, \beta_k).$$

Across species, survival rates were assumed to follow a beta distribution with flat priors for α_k and β_k .

We quantified recruitment rates as the annual number of trees of each species that entered a census at ≥ 1 cm dbh between consecutive censuses and calculated species-level recruitment rates (r_j) as the mean number of annual recruits across all census intervals. Variability in annual recruitment rates was quantified with the coefficient of variation (CV _{j}). Species without observed recruitment were assigned a recruitment rate equal to half of the minimum observed recruitment rate (per forest site).

Tree stature (maximum diameter) was defined as the mean dbh of the six largest trees of that species in that plot (see Rüger

et al., 2020; Visser et al., 2016). Based on published findings from BCI (Visser et al., 2016), we assumed trees to be reproductive if their dbh was larger than half of the species' maximum diameter (truncated to a maximum of 2 m).

Per-capita recruitment rates were calculated by dividing r_j by the mean number of reproductive trees of species j across all censuses. This measure reflects a population perspective; recruitment needs to offset mortality to maintain a stable population. Recruitment rates per unit of reproductive basal area (per-basal area recruitment) were calculated by dividing r_j by the mean basal area (in m^2) of reproductive trees of species j across all censuses. This measure reflects relative allocation to reproduction because larger trees can invest more resources into reproduction and accommodate more flowers and seeds than smaller trees (Muller-Landau et al., 2008).

The means and 80 percentile range for all species-specific demographic rates within each forest are shown in Figure S4. To account for the uncertainty in demographic rates, especially of rare species, every estimated demographic rate was associated with a credibility weight ranging between zero and one, calculated as $1 - (\text{width of the estimated 95\% credible interval} / \text{width of the 99th percentile of all 95\% credible intervals})$ for growth and survival rates and $1 - (\text{CV}_j / \text{width of the 99th percentile of all CV}_j \text{ values})$ for recruitment rates. Credibility weights were truncated to a minimum value of $1e-6$. Credibility weights for recruitment rates for those species that recruited in less than two census intervals were set to the median value of the credibility weights of the respective forest site.

2.4 | Data analysis

For each forest plot, we used principal component analysis to determine the demographic trade-offs between species-level average annual growth and survival rates per canopy layer, annual per-capita recruitment, annual per-basal area recruitment and stature. To test for the robustness of the results, we also performed a weighted principal component analysis (Delchambre, 2014; R ger et al., 2018), where each demographic rate contributed to the PCA according to its associated credibility weight. This approach allowed us to account for the uncertainty in the demographic estimates. The significance of the resulting principal components was tested against a broken-stick criterion (Legendre & Legendre, 2012). Demographic rates with factor loadings ≥ 0.4 were considered to be significantly related to the respective principal component. We considered the growth–survival trade-off to be associated with a principal component if growth and survival rates were significantly related to it in opposite directions (Figure 1). We considered the stature–recruitment trade-off to be associated with a principal component if stature and recruitment rates were significantly related to it in opposite directions (Figure 1). As species with a tall stature typically have high basal area, and thus tend to have lower per-basal area recruitment, there is a predetermined negative correlation between tree stature and per-basal area recruitment. To check for the robustness of the

results to this predetermined correlation, we also conducted PCAs that excluded tree stature.

We quantified the pairwise similarity between all plots (with regard to the relationships between demographic rates) as the pairwise Procrustes correlation coefficient r (Legendre & Legendre, 2012). These pairwise correlations were summarized in a plot-level correlation matrix that we used to infer the joint similarity between all plots by means of a principal component analysis. To account for the different numbers of canopy layers, we only used growth and survival rates from the highest, second highest, lowest and second lowest canopy layer. In the emerging PCA, the generally high pairwise similarity between all plots (all r values > 0.94) was captured by the first principal component (with 97% of covered variation). To check for differences between plots, we thus extracted their position along the second and third principal components and conducted a post-hoc correlative analyses with 999 permutations to test for the significance of the biogeographical region, the basal area, the species richness and incidence of major hurricane/fire events for the distribution of the plots along these two principal components. In addition, we checked whether the number of canopy layers could have influenced our results but this effect was nonsignificant ($p = 0.56$).

All analyses were conducted in R (R Core Team, 2021) using the following R-packages: *RSTAN* and *CODA* to run Bayesian hierarchical models (Plummer et al., 2006; Stan Development Team, 2018), *FactoMineR* for classical principal component analysis (van der Sande et al., 2020), *vegan* for Procrustes and post-hoc correlative analyses (Oksanen et al., 2020) and *ggplot2* for graphical representations (Wickham, 2009). Stan-models for growth and survival rates are noted in Supplementary Materials S10 and S11. Weighted principal component analyses were calculated with an adapted script from R ger et al. (2018).

3 | RESULTS

The growth–survival trade-off was associated with the first principal component in 10 out of the 13 forest plots, that is, growth and survival rates had significant and opposite loadings on the first principal components (Figures 2 and 3; Figure S5, Table S1). In two more plots (Fushan and HKK), the growth–survival trade-off was associated with the second principal component. In all but one of those plots (Ituri-Lenda), the principal component that was related to the growth–survival trade-off captured a significant amount of demographic variation (as compared against a broken-stick criterion, Legendre and Legendre (2012)). The stature–recruitment trade-off was associated with the second principal component in 10 out of the 13 forest plots, that is, stature and per-basal area recruitment and/or per-capita recruitment rates had significant and opposite loadings on the second principal component (Figures 2 and 3; Figure S5; Table S1). In two more plots (Fushan and HKK), the stature–recruitment trade-off was associated with the first principal component. In nine of those 12 plots (except HKK, Ituri-Edoro and Ituri-Lenda), the stature–recruitment trade-off captured a significant amount of

demographic variation. In Luquillo, growth and survival rates showed a weaker link than in the other plots so that the first principal component corresponded to a survival–recruitment trade-off and the second principal component corresponded to a growth–recruitment trade-off. As a result, the trade-off between stature and recruitment was jointly captured by both principal components. These findings were also confirmed by bivariate relationships between demographic rates and stature (Figure S9).

The principal component associated with the stature–recruitment trade-off was also related to growth at eight sites and, partly matching, survival at eight sites (Figure 3). Only at Ituri-Lenda and Luquillo, a third principal component captured a significant amount of demographic variation (Table S1).

To test for the robustness of our results, we performed several PCAs with different input data. When we excluded tree stature from the PCA (Figure S6), the stature–recruitment trade-off still remained. Species with faster growth and higher survival (and thus taller stature) showed lower per-basal area recruitment. When we excluded per-basal area recruitment from the analysis (Figure S7), the stature–recruitment emerged only in one plot (HKK). When we used the allometric equation from Blanchard et al. (2016), demographic trade-offs were not affected (Figure S8).

Species' annual growth and survival rates were generally strongly related across different canopy layers so that species with relatively high growth or survival in the shaded understorey maintained higher rates in the canopy (Figure 3; Figure S9). Species thus seem unable

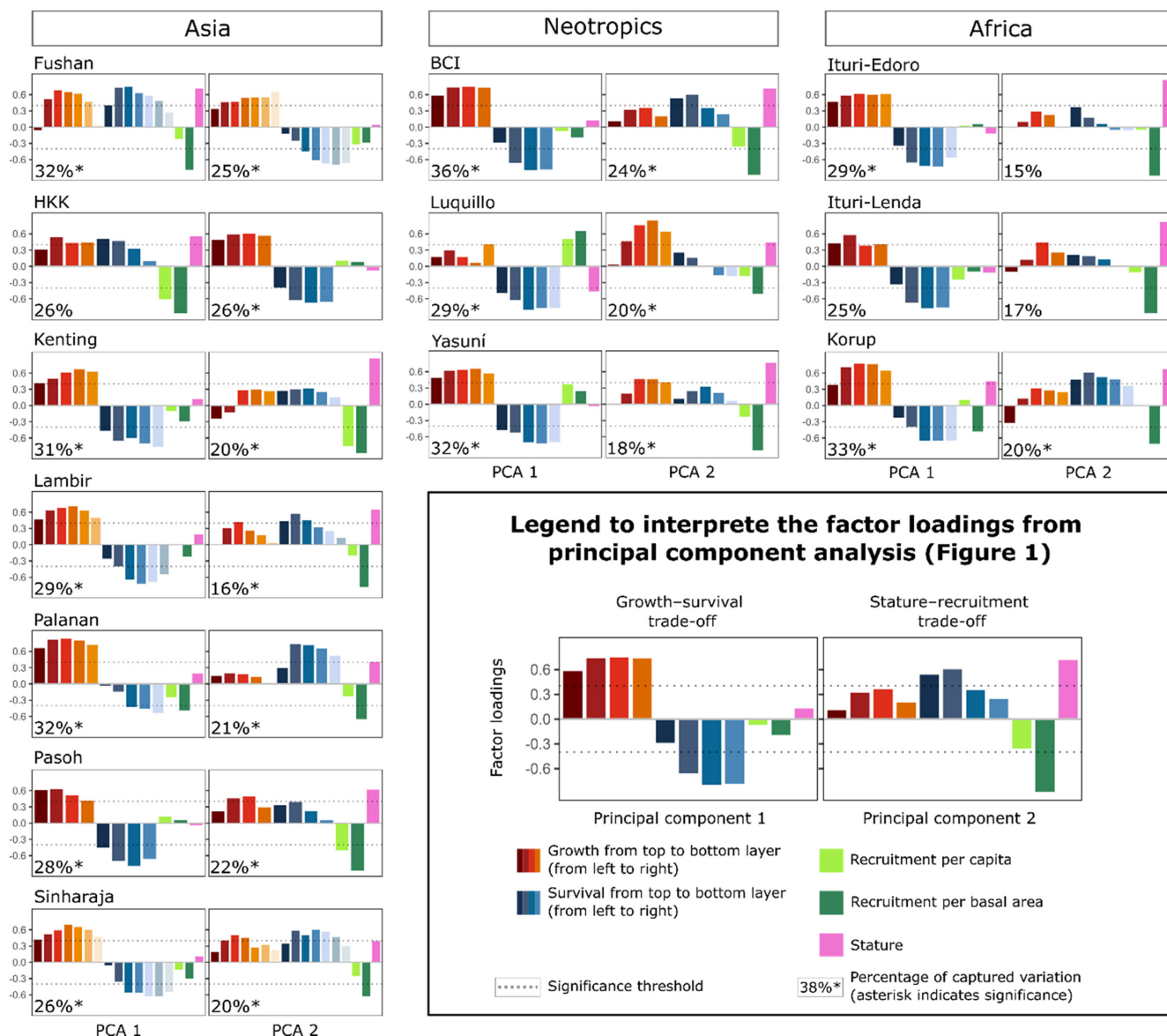


FIGURE 3 Demographic trade-offs between species' annual growth and survival rates from the top to the bottom canopy layer, recruitment rates and stature in 13 (sub)tropical forests. Depicted are the factor loadings of demographic characteristics on the first two principal components (PC) and the proportion of variation captured. Stature refers to the mean diameter at breast height (measured at 1.3 m from the ground) of the six largest individuals. All demographic rates were standardized prior to the PCA

to adapt their relative life-history strategies during ontogeny or to different light conditions. Growth and survival rates in the top canopy layer were less tightly related to the rates of subsequent layers (Figure 3; Figure S9), likely because of the lower number of individuals and species, and thus a higher uncertainty in demographic estimates.

Pairwise Procrustes analysis revealed that the joint relationships among all demographic rates were highly consistent between forest plots (with pairwise r values between 0.94 and 0.99). In a joint PCA of all pairwise r values, the second principal component was related to the differences between the Asian and the African plots (with the exception of the Asian plot at Kenting) and the third principal component was related to the uniqueness of the hurricane-impacted plot at Luquillo (Figure 4). The scores of the plots along the second and third principal component were significantly related to the biogeographical region (post-hoc correlation of $p = 0.002$) and unrelated to the species richness, basal area or the occurrence of major disturbances (with $p = 0.82, 0.09$ and 0.12 , respectively).

4 | DISCUSSION

We assembled demographic rates of >5000 tree species from 13 (sub)tropical forest sites to explore demographic trade-offs across tropical forests from three continents. We found that demographic strategies of the tree species in 12 out of the 13 forests were structured along the same two independent demographic dimensions. The growth–survival trade-off distinguished species that grow fast, but die quickly from species that growth slowly, but live long, that is, the well-known fast–slow continuum (e.g. Franco & Silvertown, 1996;

Reich, 2014; Salguero-Gómez et al., 2016). The stature–recruitment trade-off distinguished species that reached a tall stature due to fast growth and high survival, but recruited poorly from species that remained short-statured due to slow growth and low survival, but recruited abundantly (cf. Kohyama, 1993; Rüger et al., 2018).

The relationships between demographic rates were strikingly similar across the different forests. Only the hurricane-impacted forest at Luquillo displayed different trade-offs with stature (Hogan et al., 2018; Russo et al., 2021). This forest experiences infrequent but strong disturbance events so that the range of viable life-history might be restricted and skewed towards shade-intolerant species (>90%, Russo et al., 2021). Severe hurricane disturbances might thus condition a long-term decoupling of growth and survival rates, and thus, preclude the emergence of a growth–survival trade-off. Therefore, we speculate that, beside the short-term effects on adult survival and seedling recruitment at Luquillo (Uriarte et al., 2012) and the long-term effects on tree height, productivity and nutrient cycling in general (Lin et al., 2020), infrequent hurricane events might also cause long-term changes in demographic trade-offs.

We found that per-capita recruitment was generally negatively associated with annual survival across canopy layers. This phenomenon could refer to the well-established trade-off between reproduction and longevity (Stearns, 1992) that should allow species to coexist at the same canopy layer, if a higher mortality can be counterbalanced by a higher fecundity (Kohyama & Takada, 2012). Likewise, in Fushan, another typhoon-impacted forest, >80% of the species were shade-intolerant (Russo et al., 2021). This might also explain why the stature–recruitment trade-off captured more demographic variation than the growth–survival trade-off in this forest. In contrast, the typhoon-impacted forest at Palanan had a

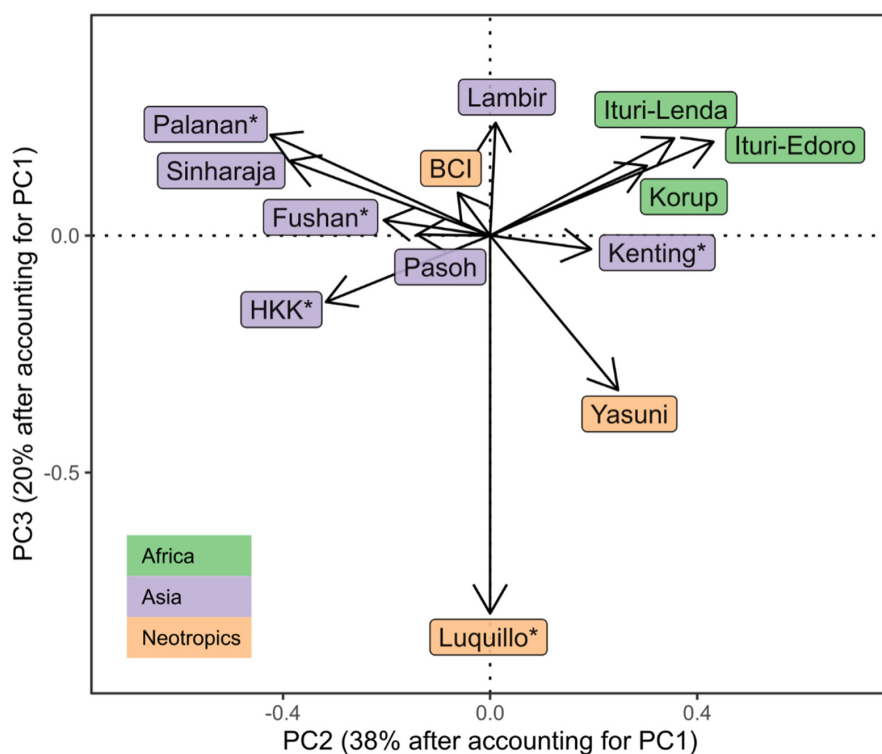


FIGURE 4 Principal component analysis showing the similarity between 13 (sub) tropical forests with regard to the relationships between species' annual growth and survival rates in the two highest and the two lowest canopy layers, species' recruitment rates and maximum dbh. Depicted are the scores of the 13 plots along the second and third principal components calculated from correlation coefficients that were derived from multiple separate pairwise Procrustes analyses

more even representation of demographic strategies, and consequently displayed a growth–survival trade-off (Russo et al., 2021). In Ituri-Lenda, that is not a severely disturbed forest, the principal component related to the growth–survival trade-off was not significant. This forest was dominated by a single species, the mbau tree (*Gilbertiodendron dewevrei* [De Wild.] J. Leonard), which restricted the abundances of other species and potentially skewed the estimated demographic rates.

Except for Korup and Luquillo, tree stature was only significantly related to the demographic dimension associated with the stature–recruitment trade-off, and not the demographic dimension associated with the growth–survival trade-off (Figure 3). Thus, pace of life (fast–slow continuum) and tree stature are two independent dimensions structuring life-history variation across diverse (sub)tropical forests. The observed consistency in demographic relationships lends empirical support to the common practice of classifying tree species into plant functional types for forest dynamics models based on their stature, as well as shade tolerance (as derived from functional traits or maximum growth rates, Gourlet-Fleury et al., 2005; Kazmierczak et al., 2014).

We are aware that taller tree species have a higher basal area at the stand level (Kohyama et al., 2020). The applied standardization of recruitment rates per basal area might thus have introduced an artefactual negative correlation between stature and per-basal area recruitment. However, the stature–recruitment trade-off also emerged in a PCA excluding stature, where species with faster growth and higher survival (and thus taller stature) showed low per-basal area recruitment. Thus, we are confident, that the second demographic dimension, that is, the stature–recruitment trade-off, is an ecological feature that structures the diversity of life-history strategies of tropical forest trees. To what degree the stature–recruitment trade-off emerges due to allocation differences to seed production, seedling germination or seedling performance remains to be resolved.

Our approach to determining life-history strategies used recruitment of trees (≥ 1 cm dbh) as the measure of reproduction. We assumed that our two measures (recruitment per capita and per unit of basal area) are relevant for population dynamics and are subject to demographic trade-offs. However, neither measures reproductive investment directly, since recruitment integrates over several processes in the earliest life stages, such as flower production, pollination and seed production, germination, and seedling growth and survival. At BCI, the stature–recruitment trade-off also encompassed reduced seedling growth and survival of tall-statured species, hinting at an ontogenetic trade-off between performance in early and later life stages (Rüger et al., 2018). Future studies should specifically quantify the different stages between reproduction effort and recruitment success but currently very little data are available.

Our approach to deriving the principal trade-offs in species' demographic rates can be used to condense demographic diversity by assigning species to groups with similar life-history strategies,

facilitating the prediction of forest dynamics with demographic forest models (e.g. based on the Perfect Plasticity Approximation, PPA, Rüger et al., 2020). The structure and succession of secondary forests in central Panama was accurately predicted when the diversity of life-history strategies BCI (that served as a reference forest) was summarized into five demographic groups that covered the growth–survival and the stature–recruitment trade-off (Rüger et al., 2020). Our results showing the similarity of demographic trade-offs across a number of (sub)tropical forests on three continents suggest that the same approach may work in other forests, and might thus form the basis of generalizable forest dynamics models. Whether and how these demographic trade-offs are shaped by climate (Johnson et al., 2018), soil (Russo et al., 2008), biotic pressure and disturbance regimes (Hogan et al., 2018; Uriarte et al., 2012) cannot be investigated with the currently limited data but this is likely to change with the ongoing expansion of the global network of large-scale and long-term forest research plots.

AUTHORS' CONTRIBUTIONS

The research was designed by S.Ka. and N.R. with input from H.B., R.C., C.W., S.J.D. and S.J.W.; Analyses were performed by S.Ka.; Forest inventory data were collated and provided by S.A., S.B., C.-H.C.-Y., Y.-Y.C., G.C., R.C., S.J.D., S.E., C.E.N.E., E.S.F., N.G., S.G., S.P.H., A.I., D.K., S.Ki., Y.-C.L., J.-R.M., M.B.M., N.P., R.P., L.J.V.R., I.-F.S., S.T., D.T., J.T., M.U., R.V., S.J.W., S.-H.W., T.Y., T.L.Y. and J.Z.; The first draft was written by S.Ka. and R.C. with contributions from N.R. All authors contributed to the final manuscript.

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CONFLICT OF INTEREST

All co-authors declare to have no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13901>.

DATA AVAILABILITY STATEMENT

Observed growth, survival and recruitment rates as well as species-specific maximum dbh and number/basal area of reproductive individuals are archived and available at Dryad Digital Repository <https://doi.org/10.5061/dryad.41ns1rnn> (Kambach et al., 2022).

ORCID

Stephan Kambach  <https://orcid.org/0000-0003-3585-5837>

Helge Bruelheide  <https://orcid.org/0000-0003-3135-0356>

Sarayudh Bunyavejchewin  <https://orcid.org/0000-0002-1976-5041>

Chia-Hao Chang-Yang  <https://orcid.org/0000-0003-3635-4946>

Yu-Yun Chen  <https://orcid.org/0000-0001-8760-8649>

Stuart J. Davies  <https://orcid.org/0000-0002-8596-7522>

Sisira Ediriweera  <https://orcid.org/0000-0002-2270-6085>

Edwino S. Fernando  <https://orcid.org/0000-0001-9422-5451>

Nimal Gunatilleke  <https://orcid.org/0000-0003-3271-2945>

Akira Itoh  <https://orcid.org/0000-0002-2493-1681>

David Kenfack  <https://orcid.org/0000-0001-8208-3388>

Yi-Ching Lin  <https://orcid.org/0000-0003-4604-5063>

Jean-Remy Makana  <https://orcid.org/0000-0002-6006-2938>

Mohizah Bt. Mohamad  <https://orcid.org/0000-0003-1645-2469>

I-Fang Sun  <https://orcid.org/0000-0001-9749-8324>

Duncan Thomas  <https://orcid.org/0000-0003-1818-0057>

Jill Thompson  <https://orcid.org/0000-0002-4370-2593>

Maria Uriarte  <https://orcid.org/0000-0002-0484-0758>

Renato Valencia  <https://orcid.org/0000-0001-9770-6568>

Christian Wirth  <https://orcid.org/0000-0003-2604-8056>

S. Joseph Wright  <https://orcid.org/0000-0003-4260-5676>

Tze Leong Yao  <https://orcid.org/0000-0002-5274-1623>

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