Vertical niche partitioning of life histories in a tropical forest

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Abstract

Life history variation in trees is a ubiquitous feature of tropical forests that may facilitate the niche partitioning of light. However, many tests have failed to detect light partitioning by saplings in gaps, which may reflect the stochastic nature of understory light penetration and recruitment. We argue that tree size is a critical component of niche partitioning that is more tightly linked to light availability. To account for size, we use a scaling framework to assess patterns of growth, abundance, mortality, and richness across life histories from >114,000 trees in a primary, neotropical forest. Relative abundance, productivity, and richness shift ~1-2 orders of magnitude with tree size: from shade tolerant, slow trees dominating the understory to parity with rapidly growing fast and long-lived pioneer species in the canopy. Life history tradeoffs promote vertical niche partitioning in tropical forests.

1

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JMG conceived the study, JMG developed theory, JMG and QDR wrote the paper, JMG, QDR, NR, SR, and BJE designed the approach, QDR and JMG performed analyses, NR and SPH contributed data. All authors discussed results and edited the manuscript.

Novelty: Despite the ubiquity of *fast-slow* life history variation in diverse tropical forests, its role in contributing to niche partitioning and species diversity is unclear. We provide evidence for a novel *vertical* axis of niche differentiation, with *fast* and *long-lived pioneers* systematically increasing over an order of magnitude in abundance, productivity and richness at larger size classes relative to *slow* shade-tolerant competitors.

Data accessibility: Data, analyses, and results are available at
https://github.com/qdread/forestscalingworkflow/. Upon acceptance the github repository containing both data and code will be given a DOI and archived with Zenodo.

This PDF file includes:
      Abstract
      Main Text
      Main Figures: 1 to 6
      Acknowledgements
      References

Abstract

Life history variation in trees is a ubiquitous feature of tropical forests that may facilitate the niche partitioning of light. However, many tests have failed to detect light partitioning by saplings in gaps, which may reflect the stochastic nature of understory light penetration and recruitment. We argue that tree size is a critical component of niche partitioning that is more tightly linked to light availability. To account for size, we use a scaling framework to assess patterns of growth, abundance, mortality, and richness across life histories from >114,000 trees in a primary, neotropical forest. Relative abundance, productivity, and richness shift ~1−2 orders of magnitude with tree size: from shade tolerant, *slow* trees dominating the understory to parity with rapidly growing *fast* and *long-lived pioneer* species in the canopy. Life history tradeoffs promote vertical niche partitioning in tropical forests.

Introduction

How hundreds of species coexist in tropical forests is a longstanding issue in ecology. Niche partitioning of resources is a classic explanation for species coexistence and the maintenance of diversity (MacArthur & Levins 1967; Wright 2002; Chase & Leibold 2003). A challenge to this hypothesis is that even at local scales – where most environmental gradients are modest – plant diversity is remarkably high in rainforests. For instance, there are over 700 species of woody plants in a single hectare in Amazonian Ecuador (Balslev *et al.* 1998). Substantial variation in soil nutrients or hydrology may be important for niche diversity, but these generally occur over larger, landscape scales (Paoli *et al.* 2006; John *et al.* 2007; Russo *et al.* 2008). Indeed, attention on niches has largely shifted to the role of plant pathogens and predators as the driver of plant densities and niche division (Comita *et al.* 2010), or emphasized the role of neutral and stochastic forces (Hubbell 2001). There is one universal resource, however, that can vary several orders of magnitude from tree to tree and has mechanistic linkages to a variety of plant traits: light.

Gaps in forests create enormous variation in light availability that affect tree growth and survivorship (Poorter 1999; Wright *et al.* 2010). Tolerance of shade is closely linked to broader axes of trait variation known as life histories – correlated patterns of growth, survival, and reproduction that reflect tradeoffs in the allocation of assimilated energy. A widely observed life history tradeoff in high-diversity, humid forests is a growth-mortality or *fast-slow* tradeoff (Reich

2014; Russo *et al.* 2021). Light-demanding, short-lived pioneers have *fast* life histories. In these systems, *fast* trees tend to recruit in gaps, grow quickly, are shade intolerant, and have high mortality, reflecting such features elevated dark respiration (shade intolerance), low wood density (mechanical instability), and poorly defended leaves (Valladares & Niinemets 2008; Rüger *et al.* 2018). Conversely, *slow* trees are slow-growing, long-lived, and shade tolerant, often dominating late successional and primary forests (Reich 2014).

Light varies considerably across the understory, so gap dynamics have long been argued to be an important driver of forest regeneration and niche partitioning of shade-tolerant and shade-intolerant trees (Grime 1977; Ricklefs 1977; Whitmore 1978; Denslow 1980; Pacala & Rees 1998; Kitajima & Poorter 2008; Falster *et al.* 2017). *Fast* trees fare poorly in the shade, but with their rapid growth rates, they may have a competitive advantage in gaps, promoting niche partitioning. Light is such a limiting resource that nearly all tropical forest species show significant increases in seedling or sapling densities in gaps, irrespective of life history. Under a light partitioning scenario, however, if *fast* trees have a competitive advantage, the *relative* abundance and richness should increase in high light gaps and decline the most in shade. Evidence for gap-based niche partitioning, however, is mixed. In analyses of primary neotropical forests, Hubbell (Hubbell *et al.* 1999) and Lieberman (Lieberman *et al.* 1995) failed to find any difference in relative abundance or relative diversity between shade tolerant and pioneer species. Hubbell also observed that only 2-6% of canopy species occurred per 25 m^2, arguing that seedling recruitment limitation precludes most niche-based partitioning of canopy gaps even in the presence of competitive difference between life histories. Similar patterns have been observed in a diverse, primary temperate forest (Busing & White 1997). Lianas appear to be an exception (Schnitzer & Carson 2001), and there is some support of light partitioning in the most shade intolerant species (Schnitzer & Carson 2001; Poorter & Arets 2003), which comprise a small fraction of diversity. A review by (Brokaw & Busing 2000) concluded that "gaps help maintain species diversity mostly by harboring higher densities of stems, not by providing more niches". These high densities are ephemeral, however; growth of a gap cohort leads to inevitable thinning. On the other hand, when (Terborgh *et al.* 2017) focused on smaller saplings and the appearance of new recruits after gap formation (excluding established saplings), they found that post-gap recruitment included relatively more pioneers.

We argue that these methods obscure stronger, underlying patterns of relative diversity and niche partitioning. Because the vast majority of trees are small seedlings and saplings, assessment of total relative abundance or richness are effectively measurements of saplings occupying a low, horizontal layer of the forest floor. However, the most sustained, non-

stochastic changes in light intensity — where light limitation, differential growth, and mortality should be most pronounced and persistent — is *vertical*, as tree size and light intensity increase systematically toward the canopy. In a tropical humid forest, light intensity increases approximately fiftyfold from the ground floor to upper canopy (Muller-Landau *et al.* 2006a) found that the probability of access to direct light increased with stem diameter as a power law in Barro Colorado Island, Panama (BCI). Using LiDAR, (Stark *et al.* 2012) showed that the transmission of light and the amount intercepted per leaf scaled linearly with tree height, or equivalently as a power function with stem diameter, since height is an allometric function of stem diameter (Feldpausch *et al.* 2011)). Therefore, if light partitioning is occurring in forests, we might expect a power law shift in relative abundance and richness of pioneer and shade tolerant species with size.

Light is an obvious resource that changes with size, but other variables relevant to vertical niche partitioning are also size-dependent. Water and heat stress, windthrow, and vulnerability to lightning increase vertically toward the canopy (Canham *et al.* 2001; Bennett *et al.* 2015; Gora *et al.* 2020). Humidity declines with height (Graham *et al.* 2014), which may affect vulnerability to pathogens and the strength of negative density-dependent effects. For instance, there is evidence that fast-growing species have higher rates of negative density dependence at the seedling stage than other size classes (Zhu *et al.* 2018).

To evaluate possible vertical niche partitioning across life histories, we examine the relative abundance, productivity, and richness of *fast* and *slow* trees in a humid neotropical primary forest at Barro Colorado Island, Panama. We include a more recently identified life history axis orthogonal to the *fast-slow* axis: *long-lived pioneers (LL pioneers)* and *short-lived recruiters (SL recruiters)*. *LL pioneers* have poor recruitment but, once established, grow quickly to large stature, have low mortality, and persist for long periods. Conversely, *short-lived recruiters* are shrubs and small trees that have slow growth and high mortality, but recruit abundantly. Under our vertical niche partitioning hypothesis, we expect shade-tolerant, *slow* trees to dominate the understory in diverse forests, but decline in relative abundance, productivity and richness toward the well-lit canopy as trees as faster-growing *fast* and *LL pioneers* outpace them. A preliminary examination supports this prediction. We use life history data from (Rüger *et al.* 2018) from BCI of a 50-hectare plot at demographic equilibrium to

classify woody plant life histories (Fig. 1A, Fig. S1; 1995 census, Methods). *Slow* trees decline steadily in abundance from ~70% at 3 cm dbh (diameter at breast height) to ~50% at 10 cm dbh, and then <8 % at 100 cm dbh (Fig. 1B). This decline is offset by a rapid increase in the relative abundance of *fast* and *LL pioneers,* which achieve numerical parity or superiority in the upper canopy.

The Scaling of Niche Partitioning

To quantify the role of size in niche partitioning, we take a scaling approach to the demography of trees across life histories. Many aspects of physiological rates and demography, such as abundance, change or scale with size following a power law, $y \propto x^a$, where y is a quantity, x is organismal size (e.g. stem diameter) and a is an exponent that is the slope on a log-log plot, where $\log(y) = ax + \text{intercept}$. Deviation from a single power law at upper and lower bounds can be accommodated by fitting piecewise power law distributions.

We focus on three key axes of niche partitioning that scale with tree size: population density, richness, and productivity. Scaling analyses permit straightforward inferences when considering niches and demographic change. For instance, the population density of virtually all trees declines with size, but differences in the steepness of slopes will lead to shifts in relative abundance with size. Thus, if *slow* trees have a
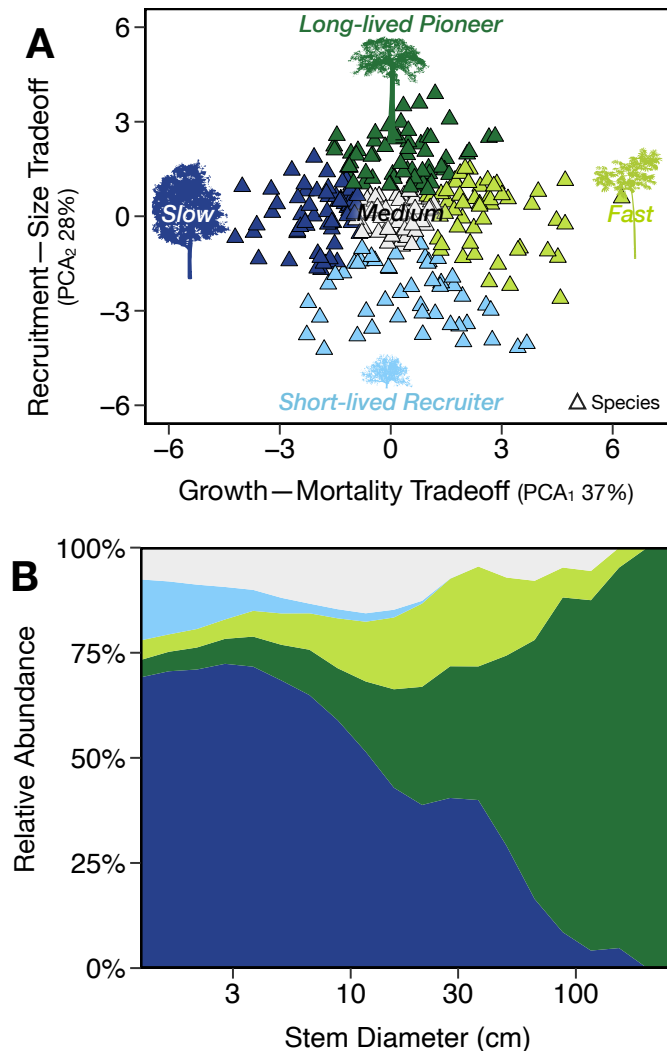
Figure 1. Life history variation in Barro Colorado Island, Panama. A. Species vary along two orthogonal life history axes, generating distinct life history groups: long-lived pioneers (represented by a *Cavanillesia* sp.), *slow* species (*Andira* sp.), *fast* (*Cecropia* sp.) and *short-lived recruiter* (*Piper* sp.), and an intermediate *medium*. **B**. Observed relative abundance of life history groups as a function of tree size (n = 114,120). <3% of species are unclassified and are not shown. Life histories were based on traits including maximum height, wood density, seed mass, leaf mass per area, leaf dry matter content, leaf phosphorus, leaf nitrogen, and leaf area assessed at multiple size stages.

steeper negative slope in abundance than *fast* trees, *fast* individuals will become relatively more common at larger sizes (Fig. 2A-B). We quantify this demographic shift by taking the ratio of competing life history guilds that overlap in size, i.e. *fast:slow* or *LL pioneer:slow* (Fig. 2B); on log-log plots, the slope of the ratio is the difference in slopes between respective guilds. Shrubby *short-lived recruiters* may be abundant at small sizes but, given their maximum size constraints, they will decline in abundance rapidly with size. Although this contributes to niche
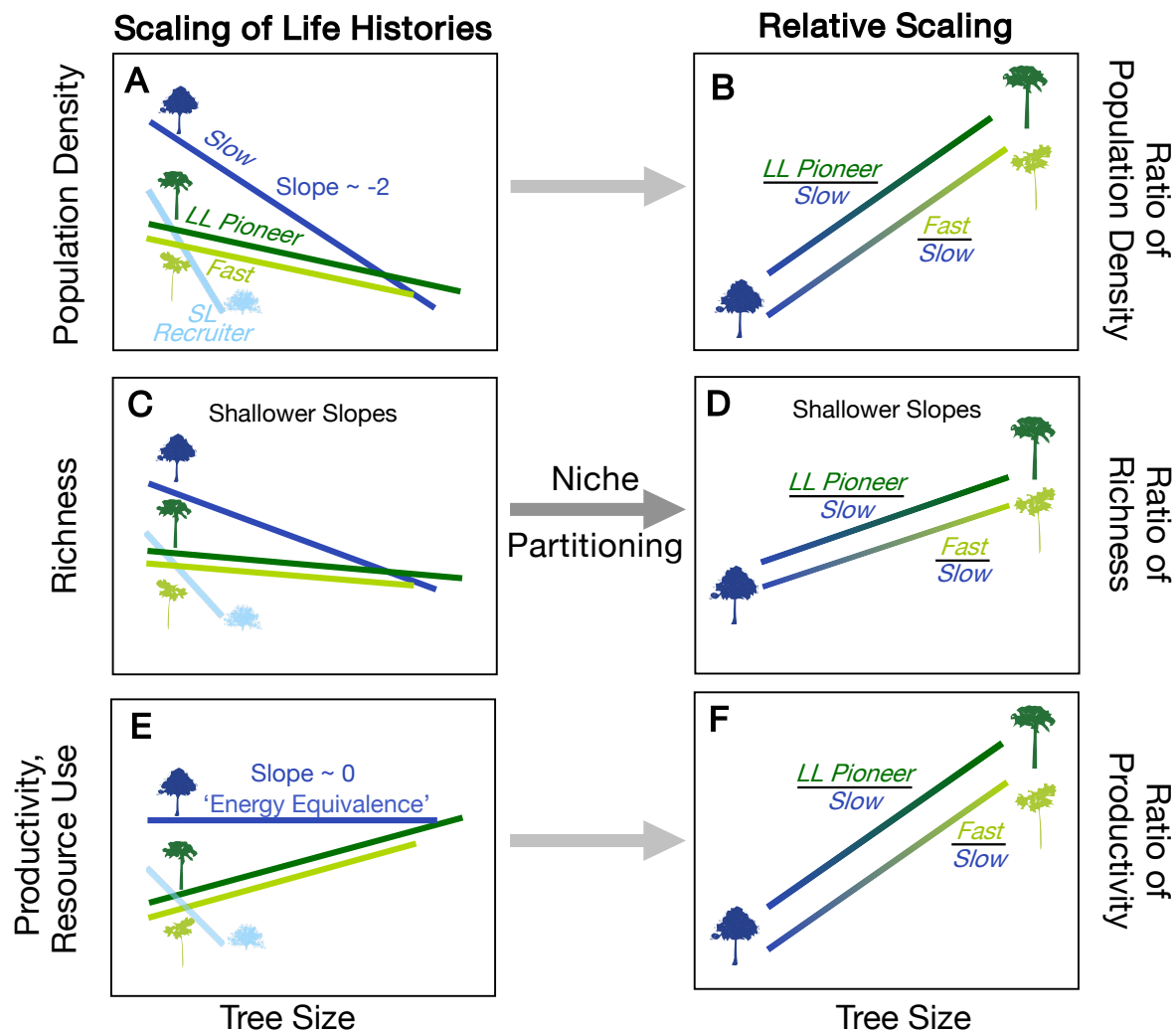
Figure 2. A schematic for niche partitioning with life history and tree size. Different scaling slopes of population density (A), richness (C) and productivity and resource use (E) lead to corresponding shifts in the dimensionless ratio or relative abundance, richness, and productivity between canopy-reaching life history pairs (B, D, F). In particular, shade-tolerant *slow* saplings are predicted to dominate the understory (highest y-intercept), but fast-growing *fast* and *long-lived pioneer* species will become increasingly common toward the canopy; other y-intercepts are arbitrary. Richness scaling (C) is predicted to track abundance (A), but with shallower slopes. Abundant, shade-tolerant *slow* species are expected to be closest to whole community scaling patterns and the least vulnerable to shading in the understory. Total productivity per size class (E) is the product of positive per capita productivity and negative population density (A). Shade tolerant *slow* species are predicted to be closest to equivalent productivity per size class ('energy equivalence). All axes are log-transformed.

partitioning with size, it also implies that direct competition for light with other guilds at larger sizes is not occuring. For this reason, we do not focus on the scaling of relative diversity in *SL recruiters* in Fig. 2 or elsewhere unless stated.

The slope of decline in population density with tree size is ~ –2 for most humid forests, whereby an order of magnitude increase in tree stem diameter leads to a two orders of magnitude decline in population density, though site to site variation is common (Muller-Landau *et al.* 2006a; Muller-Landau *et al.* 2006b; Enquist *et al.* 2009). Specifically, $D = b_0 S^{-2}$, where D is population density, S is stem diameter, and b_0 is a normalization constant. Population density at small size classes reflects recruitment and survivorship in the largely shaded understory. Thus, we expect shade-tolerant *slow* trees to have the highest absolute abundance, particularly at small sizes, and to be closest to typical –2 scaling (Fig. 2A). Conversely, *fast* and *long-lived pioneers* recruit poorly in the understory or suffer high mortality but may perform relatively better toward the well-lit canopy; thus, they will have lower y-intercepts and shallower slopes (Fig. 2A). This leads to a scaling shift in the relative abundance of *slow* vs *fast* or *LL pioneers* with size (Fig. 2B) – a key feature of niche partitioning (Hubbell *et al.* 1999).

Across communities in many taxa, abundance is postively correlated with richness, although there is considerable variability. This relationship may take the form of an allometric power law, where richness increases more slowly than abundance (Šímová *et al.* 2011; Storch *et al.* 2018), and may reflect joint power law scaling of richness and abundance with area, e.g., (He *et al.* 1996; He *et al.* 2002). This relationship, to our knowledge, has not been examined *within* forests in a scaling framework. Extending this pattern within a community, we predict scaling patterns of absolute and relative life history richness of trees to largely track scaling patterns of abundance, but with shallower slopes (Fig. 2C). Thus, we expect to observe a power law increase in the ratio of richness of *slow*:*fast* and *slow*:*LL pioneers* with tree size (Fig. 2D).

Productivity is a metabolic process that requires light and nutrients to drive carbon assimilation and growth. There are general stoichiometric linkages between productivity, respiration, and resource uptake within a forest that suggest an approximately proportional relationship between them (Niklas & Enquist 2001; Reich *et al.* 2006; Enquist *et al.* 2007; Mori *et al.* 2010). Further, more individuals in a size cohort should correspond to proportionally more productivity for that cohort. Given these relationships, the scaling of a size cohort's total productivity will broadly reflect that cohort's scaling patterns of light capture and resource use. For instance, as *slow* trees become rare in the canopy, their share of light capture, nutrient flux and productivity will likewise diminish relative to *fast* and *LL pioneer* competitors. Because total per capita productivity P is challenging to measure for all trees in a large plot, we focus on a

significant component — biomass stem growth per size class i (a measure of aboveground net stem productivity) — as a proxy. Thus, scaling differences in P_i should broadly reflect life history differences in resource uptake and assimilation.

Scaling patterns of biomass productivity are qualitatively different than population density and richness, which decline with tree size. In a variety of forests, individual biomass growth G (kg yr^{-1}) increases at roughly ~2 slope with tree diameter on a log-log scale, approximately the inverse of population density. Since total productivity per size cohort i is the product of per capita productivity (growth) and abundance ($P_i = \overline{G_i} \times A_i$), size classes have been predicted to be equally productive whether small or large (West $et\ al.$ 2009), where stem diameter^2 * stem diameter^{-2} = stem diameter^0, although variation is observed across forests (Zhang $et\ al.$ 2015). This flat scaling of productivity matches "energy equivalence" patterns observed in many autotroph communities where total respiration per size class is invariant with size (Perkins $et\ al.$ 2019). We expect $slow$ species to be closest to productivity equivalence (Fig. 2E, blue), because $slow$ species comprise much of the individuals driving whole community equivalence, and because they can tolerate the shade understory that may limit other life histories. In contrast, $fast$ and $LL\ pioneer$ species recruit poorly and/or have high mortality in the understory, depressing population density scaling (Fig. 2A) and causing size class productivity to increase with size (Fig. 2E). Thus, relative productivity of $fast$ and LL $pioneer$ species are expected to increase with size as $slow$ species decline (Fig. 2F).

Overall, across three dimensions – abundance, productivity, and richness — we quantify life history scaling and test whether patterns are consistent with niche partitioning with size. Because demographic shifts with size may also reflect historical, non-equilibrial processes (e.g., large-scale succession) (Bazzaz 1979), we focus on a primary forest in Panama that lacks a history of major disturbance (Hubbell & Foster 1992) and was found to be near demographic equilibrium, with 1-2% disturbance annually (Rüger $et\ al.$ 2020).

Materials and Methods

Site and Demographic Data. We used long-term demographic data from a moist neotropical forest on Barro Colorado Island (BCI), Panama (9º9'N, 79º51'W). The forest at BCI is semideciduous, with a four-month dry season. Censuses of all free-standing woody stems ≥1 cm dbh, (diameter at breast height, measured 1.3 m from ground), at 0.1 cm resolution, excluding tree ferns and lianas, have been conducted on a 50 ha portion of the island at five-year intervals since 1980; see (Condit 1998) (Condit 1998) for full description. Growth analyses were based on the ~114,000 trees tagged in both 1990 and 1995. We also included the ~18,000

new recruits from the 1995 census when fitting the abundance distributions for 1995, for a total of ~132,000 individuals. We use life history data from (Rüger *et al.* 2018), following their classification scheme of *fast*, *medium, slow*, *short-lived recruiter* (aka "short-lived breeder"), and *long-lived pioneer*. Rüger *et al.* analyzed 282 species at BCI, using demographic data across four canopy layers. Species scores in weighted PCA, including growth, survival, and recruitment rates, were used to classify life histories (Fig. 1A, Fig. S1).

Binning and Plot Presentation The wealth of data at long-term monitoring sites is invaluable but can present challenges for presentation. First, it is difficult to visually assess variation between life history groups when there are >100,000 data points overlapping on a plot. Even a heat map of individual growth rates can only convey the general trends and variation, but not differences between life history guilds (Fig. 3). Second, nonlinearities are also obscured by such an abundance of overlapping data. Finally, despite drawing from the same large data pool, collective attributes like population density and total production per size class do not have individual data values for presentation. For these reasons, we show regression fits and 95% credible interval bands without raw data, as well as binned mean or summed quantities per size class to indicate empirical central tendency patterns, including nonlinearities (Fig. 3, black circles). Thus, observed deviation from a regression fit — such as curvilinearity near the upper or lower bounds of the data — is apparent to the viewer (note Fig. 3, upper right). Using binned data, we can plot and compare trees from different life histories. Where appropriate, the use of two- or three-part piecewise regression and distribution fits helps capture shifts in slope at the upper and lower bounds. Error associated with regression fits is provided in the supplementary data.

To bin summed data, we follow (White *et al.* 2008) by plotting summed abundance and total growth that is measured over stem diameter or light intensity bin increments in logarithmic space and then divided by the bin range to show arithmetic mean densities and growth rates per unit cm diameter. Thus, sums such as population density or richness at a given size are per unit cm stem diameter. Population density is per ha, but richness is per plot (44 ha), since richness scales allometrically with plot size. All plotted points have a minimum of 20 individuals per bin.
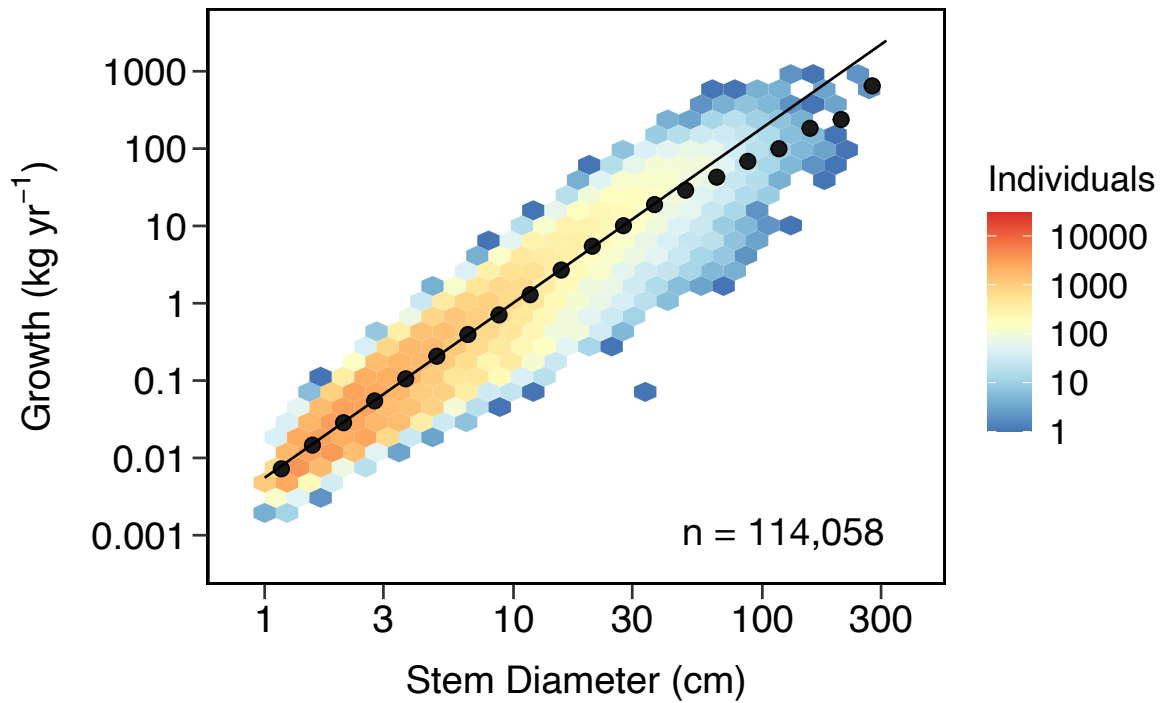
Figure 3. Heat map of biomass growth in trees. Individual growth rates from >110 k individuals in a 50 ha plot at BCI, with the most common growth rates are in red and the least common in blue. Filled circles represent the mean growth rate at a given size class; each point is limited to at least 20 individuals. A fitted regression line is shown with 95% credible bands; however, these are not visible due to the large sample size and low standard error. The quantity of data makes plotting individual data points and different life histories challenging, so we limit subsequent plots to regression fits and empirically binned values.

Piecewise Regressions We used hierarchical Bayesian models to model the scaling of growth, abundance, richness, and productivity for respective life histories. We evaluated fits with one, two, and three segments, fitting piecewise log-log regressions to biomass growth, individual diameter growth and richness data and piecewise Pareto (power law) distributions to abundance data. We used the widely applicable information criterion (WAIC (Gelman *et al.* 2019) to select the optimal number of segments. A single segment was best suited for growth and three-part segments for abundance following a Pareto distribution. To calculate the modeled estimate of aboveground productivity at each sample from the posterior distribution, we took the product of the fitted values for abundance and individual growth across the range of sizes. For three-part regression fits in abundance and productivity, we report the middle regression fit, which covers most of the tree size range. Lastly, to model the scaling of mortality with tree size, we fit a nonlinear logistic mixed-effects model with a J-curve functional form to capture the trend of mortality decreasing with increasing diameter for small trees but flatlining or increasing with increasing diameter at large sizes.

Code and data availability All models were coded in the Stan language. In all cases, we used Hamiltonian Monte Carlo to sample from the posterior distribution, with three chains, 5000 warmup samples per chain that we discarded, and 1000 post-warmup samples per chain that we retained. We assessed convergence of posterior distributions by visually examining trace plots and by ensuring that $\hat{R}<1.1$ for all parameters (Gelman & Rubin 1992). All R and Stan scripts required to reproduce our analysis are available at https://github.com/qdread/forestscalingworkflow. BCI survey data are publicly available through the Smithsonian Institution (https://repository.si.edu/handle/10088/20925)

See supplemental information for complete methods description.

Results

Slow species are by far the most abundant saplings in the understory, with shrubby, short-lived recruiters a distant second (Fig. 4A). As expected, slow trees decline in abundance with size at a faster rate than LL pioneer and fast trees, (slope$_{slow}$ = −2.40, 95% quantile credible interval (CI) = −2.38, −2.42; slope$_{Fast}$ = −1.71, CI: −1.60, −1.82; slope$_{LLPioneer}$ = −1.45, CI: −1.40, −1.50). This leads to ~order of magnitude decline in the relative abundance of slow species toward the canopy, where they are equaled by fast species and surpassed by LL pioneers (Fig. 4B). At smaller size classes, slow trees effectively drive the scaling patterns of population density, but toward the canopy the no more common than fast and LL pioneer trees (Fig. 4A-B). Reflecting size limitations, SL recruiter relative abundance declines rapidly at larger size classes.

As predicted, slow trees are closest to an 'energy equivalence' of productivity (slope = 0), with a slope of −0.13 (CI: −0.16, −0.12). In all other life histories, there is a much stronger deviation from equivalence, with steady increases in absolute and relative productivity in fast and LL pioneers toward the canopy. (Fig. 4C, 4E; slope$_{Fast}$ = 0.62, CI: 0.49, 0.73; slope$_{LLPioneer}$ = 0.75, CI: 0.70, 0.80; Supp. Table). Consistent with expectations, scaling patterns of absolute and relative richness patterns mirror shifts in abundance, but with shallower slopes (Fig. 4C, 4F, Supp. Table). These shifting patterns of abundance, production and richness are also reflected by a steady increase in the mean life history PCA value for both life history axes with tree size (Fig. S2)
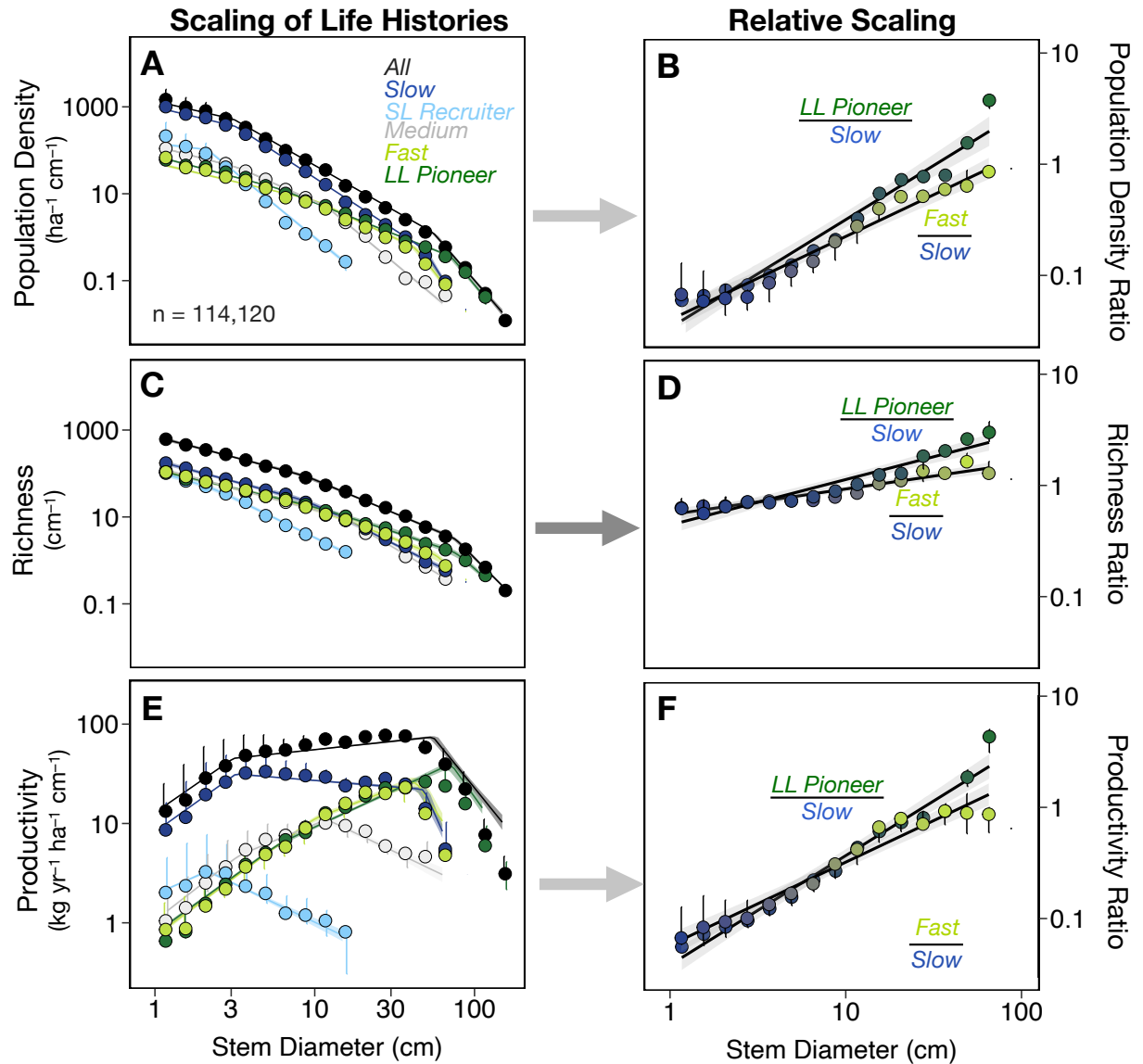
Figure 4. Scaling across life histories. Scaling of population density (**A**), richness (**C**) and productivity (**E**) for each life history (**A**). Relative shifts are shown on right by taking the ratio of *fast* or *LL pioneer* values to *slow* (**B, D, F**). Each point in reflects the summed total per unit plot area (ha) and stem diameter (cm), representing over 114 k individuals, except richness, which is per plot area (48 ha). Regression lines are fit to individual data; 95% credible bands are shown but are often too small to be visible. Data is from a 1995 census; see Fig. S2 for other years. Vertical range bars per bin span 20 years of sampling; some ranges are too small to be visible (see Fig. S1). Each point represents a minimum of 20 individuals per life history guild. Panels A-C and B-D are plotted on the same scale for comparison.

These shifts in relative abundance, richness and productivity are consistent niche partitioning with size. To better understand the drivers of vertical niche partitioning, we analyze components of abundance and productivity, such as diameter growth (a component of the abundance 'gain rate'), biomass growth (a productivity 'gain rate') and mortality (an abundance and production 'loss rate'). Since *fast* trees are, in part, defined by rapid diameter growth and

high mortality, it is unsurprising that *fast* show the greatest diameter growth rates (cm yr^{-1}) for a given size (Fig. 5A, B). However, plotting the scaling patterns shows that these differences are size dependent. Diameter stem growth for all species are approximately equivalent at the smallest size classes but diverge sharply with size, reflecting differences in their slope (slope$_{Fast}$ = 0.73, CI: 0.70–0.75), compared to *LL pioneers* (slope$_{LLPioneers}$ = 0.62 CI: 0.60–0.62) or *slow* species (slope$_{Slow}$ = 0.61 CI: 0.61–0.62). This may reflect a higher sensitivity to light that is increasing toward the canopy among pioneer trees. Again, patterns of mortality broadly fit expectations, but there are shifts in ranking with size: *slow* trees have the lowest mortality and *fast* trees the highest at small sizes, but *LL pioneers* have the lowest mortality and *fast* trees converge with other life histories when large. In contrast, regarding individual biomass growth (kg yr^{-1}), it is striking how similar all groups are, both in terms of absolute values and slopes (Fig. 5B, Supp. Table). *Fast* trees show modestly steeper slopes, but overall there is little difference between guilds (Supp. Table). Mortality rates, however, showed greater divergence (Fig. 5C). As expected, *fast* species have the highest mortality, followed by *short-lived recruiters*. Despite more rapid diameter growth, *long-lived pioneer* mortality is as low as *slow* at ~3 cm dbh (Fig. 5C), and meaningfully lower by 8 cm dbh (Supp. Table).

The visual similarity of abundance and richness scaling in Fig. 4A & 4C is confirmed by regressing richness against abundance (Fig. 5D). Despite notable nonlinearities in abundance and richness on their own (Fig. 4A), when richness is regressed against abundance the results are almost perfectly linear on a log plot (Fig. 5D; Supp. Table). The slopes and intercepts of the regression fits across life histories show some divergences. In particular, *slow* species show the fewest species per individual, at least where abundance is high, while *fast, LL pioneer and medium* have the highest species per size class (Fig. 5D), reflecting significant differences in slopes (Supp. Table). For example, the *LL pioneer slope* is 0.75 (CI:0.72-77) vs. 0.59 for *slow* trees (CI:0.56-0.63). As *LL pioneers* and *fast* are relatively common in the canopy, this pattern may reflect the outsized role of larger reproductive adults on sustaining richness, despite poor recruitment/high mortality pioneer species experience in the understory. Note that abundances and richness reflect size binning shown in Fig. 4A & 4C, such that high abundance generally corresponds to small size classes and vice versa.

Overall, the divergent patterns of abundance, richness, and production across life histories paint a picture of demographic turnover with size (Fig. 6). Life history demographic ratios are consistent with predictions in Fig. 2D-F, including across a thirty-year sampling period (Fig. S3–S5). Despite an almost continuous overlap in size, life history ratios shift ~1-2 orders of magnitude in relative abundance, productivity, and richness from *slow*-dominant on the forest

floor to parity with *fast* and *LL pioneer* in the canopy (Fig. 4).
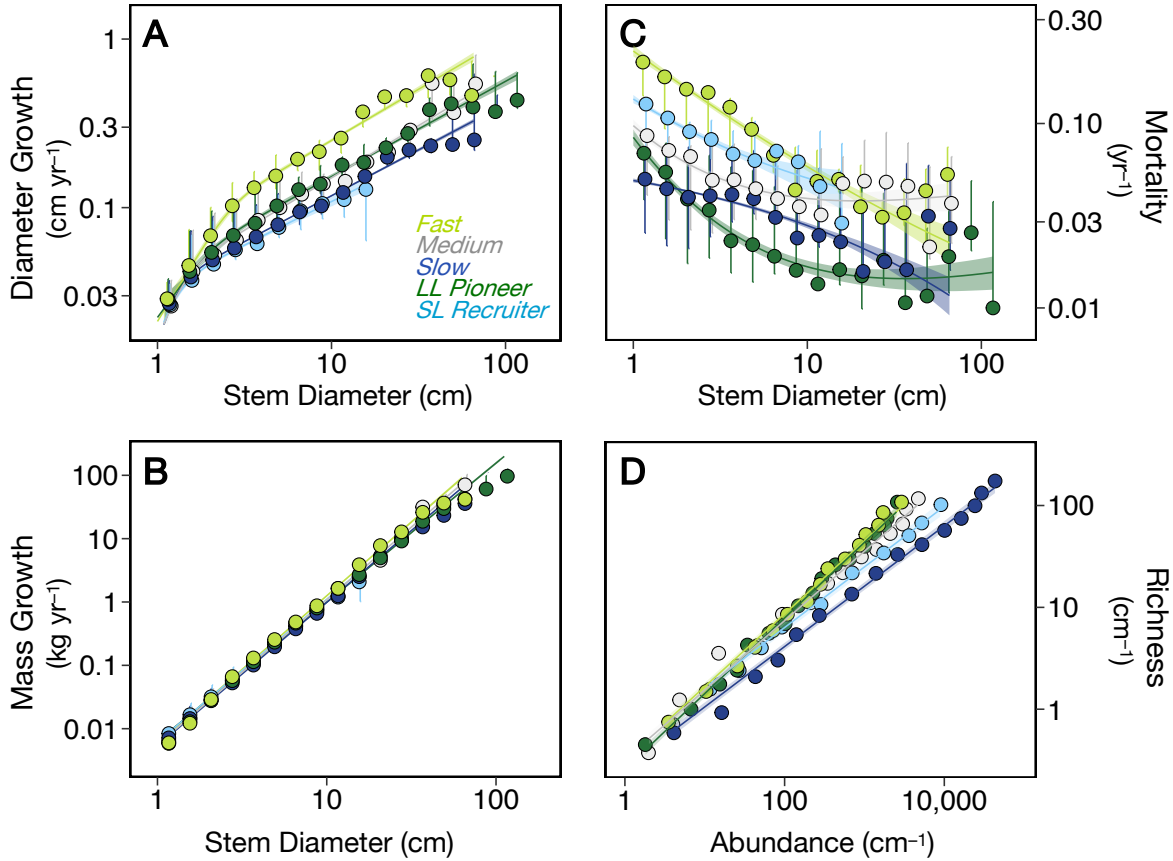
Figure 5. Potential drivers of niche partitioning. Each point has a minimum of 20 individuals per life history guild per bin. In **A-C**, points are mean rates but regression are fit to individual data; in **D** values are totals per plot area (ha) per size class (cm). All regression are plotted with 95% credible intervals.

Discussion

Niche partitioning has been offered as a mechanism to explain a central issue in tropical forest ecology: the origins and maintenance of exceptional species diversity. Given the strong gradient of light across gaps, coupled with species-specific differences in recruitment and growth across this gradient, light has long been theorized to be a key resource for niche differentiation and local diversity in closed forests (Ricklefs 1977; Denslow 1980). Nonetheless, several studies have failed to find shifts in relative abundance or richness in shade-tolerant or pioneer species across canopy gaps, as expected under a light partitioning scenario (e.g, (Lieberman *et al.* 1995; Hubbell *et al.* 1999; Brokaw & Busing 2000)). These assessments, however, often focus on sapling-dominated plots near the forest floor, where stochastic patterns of recruitment may prevail. Our scaling approach explicitly controls for size-based variation to

consider a *vertical* axis of tree demography — where light consistently increases toward the canopy — along three axes that scale with tree size: abundance, productivity, and richness. We find that despite being outnumbered ~ 100:1 in the understory, *fast* and *long-lived pioneers* species rapidly increase their abundance, productivity, and richness relative to shade-tolerant *slow* trees until reaching or exceeding parity in the canopy along each dimension. Indeed, despite representing only 15% of individuals, *fast* and *LL pioneer* species together produce as much annual biomass as *slow* species that are more than four times as abundant.

Intriguingly, this demographic transition with tree size follows an approximate power law (Fig. 5 D-F), matching observed power law shifts in light transmittance and canopy openness with stem diameter (Muller-Landau *et al.* 2006a; Stark *et al.* 2012). Thus, our results are consistent with niche partitioning along a solar gradient. Richness tracks size-class shifts in abundance in a remarkably linear, allometric fashion, offering a version of *within*-community support for the 'more individuals hypothesis' of diversity (Srivastava & Lawton 1998), in which richness increase with higher numbers of individuals in a community. This hypothesis is typically examined across communities and patterns are generally weaker and more variable than observed here (Storch *et al.* 2018). This may indicate that community type or regional variation are important factors that obscure a tighter relationship between abundance and richness when environmental conditions are held constant.
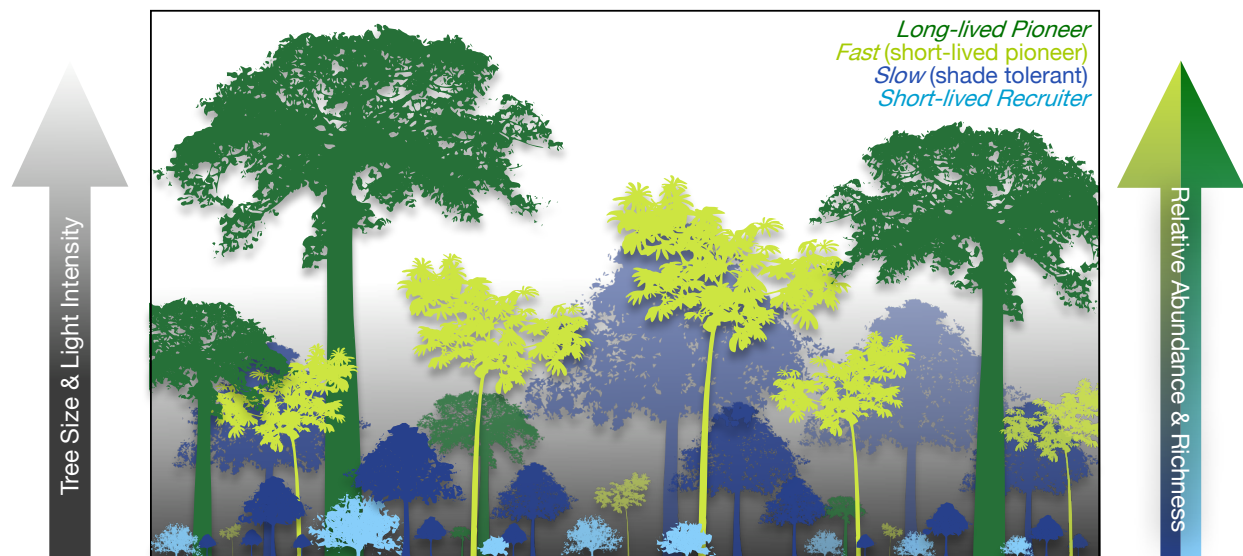
Figure 6. Vertical niche partitioning in humid forests. Shade tolerant trees with a *slow* life history (navy) and *short-lived recruiters* (light blue) dominate the dim forest understory. However, *slow* trees decline in abundance, productivity, and richness relative to fast-growing *fast* (light green) and *long-lived* pioneer trees (dark green) as tree size and light intensity increase toward the canopy.

Vertical demographic turnover likely reflects differences in the scaling and absolute rates of growth and mortality across life histories. Light-demanding *fast* trees and *long-lived pioneers*

have the highest diameter growth rates with size, and *fast* species possess the highest diameter growth *slopes* with size, leading to an acceleration into large size classes (Fig. 5A). By moving quickly through size classes, both short and long-lived pioneers can increase in relative abundance toward the canopy. Intriguingly, at a given tree size, absolute rates of biomass growth converge across all life histories, suggestive of tradeoffs that constrain tree productivity in humid forests (Fig. 5B). Dimensionally, biomass is volume (length^3) × density. Thus, convergence in biomass growth despite differences in diameter growth indicate offsetting wood densities across life histories. For instance, *fast* species have light wood and high diameter growth, facilitating rapid height increase and access to light in gaps, but at the cost of elevated mortality. Conversely, dense wood in *slow* species decreases mortality from mechanical damage. Physiologically, *fast*-growing species typically have higher leaf nitrogen and phosphorus content, permitting greater carbon assimilation rates per leaf at high light intensities (Rüger *et al.* 2018). Elevated maximum assimilation in *fast* trees comes at the cost of higher dark respiration rates and the risk of energy deficit in the shade. Consequently, *fast* trees tend to have few leaves per crown area (Valladares & Niinemets 2008), which limits self-shading but also total carbon intake. Thus, high per capita assimilation trades off with fewer leaves in *fast* trees, constraining total production.

LL pioneers have higher wood density than *fast* trees, increasing structural stability and facilitating larger size attainment that likely plays a role in their high survivorship at larger classes. Like *fast* trees, *LL pioneers* have elevated N and P concentrations in their leaves and elevated growth rates (Rüger *et al.* 2018). Does this also lead to high dark respiration and vulnerability to shade? Although mortality for *LL pioneers* is low at large size classes, it is very high between seedling and sapling size classes (Rüger *et al.* 2018), where shade is greatest. Thus, metabolic tradeoffs between leaf metabolism and shade tolerance may also affect *LL pioneer* demography. *Short-lived recruiters* have slow growth, but rapid absolute growth is likely not as important for plants reaching smaller adult sizes. More research, however, is need to understand the mechanisms underlying the demography of this relatively understudied life history axis. Nonetheless, in both *fast* short-lived pioneers and larger *long-lived pioneers*, a combination of rapid growth and high seedling mortality is likely responsible for depressed sapling numbers in the understory but proportionally higher representation in the canopy.

The scaling of population density and energy use has been a focus of models of forest size structure, including metabolic models. For instance, Metabolic Scaling Theory (MST) predicts –2 scaling slope of tree density, a +2 scaling of biomass growth, and an energy equivalence in total respiration, resource uptake, and productivity across size classes in mature forests (West *et*

al. 2009). Our results at the community level are approximately consistent with these predictions (Supp. Table), but also show that particular functional groups systematically diverge. In particular, pioneer trees (*fast* and *LL pioneers*) consistently deviate from MST, while *slow* species hew closest to model predictions (Fig. 4A, C). One interpretation is that variability in shade tolerance in mixed-species forests leads to scaling patterns that deviate from MST in rarer, shade-intolerant pioneers in the community. In particular, shade-tolerant *slow* species that are so common in humid forests compete for light in the understory and may coexist in a pattern of occupation, mortality, and replacement that fits MST assumptions. However, the available light is too meager for pioneer species in much of the understory, leading to a considerable disadvantage for pioneers at small sizes. Due to their rapid growth and high light penetration in the canopy, pioneer trees are eventually released from shade suppression toward the canopy. This positive shift in total productivity toward the canopy results in a deviation from energy equivalence among pioneer trees. In a monoculture, however, we would expect the scaling of abundance and productivity of pioneers to be closer to MST predictions because their relative shade intolerance will lead to lower total canopy leaf area and greater light penetration into the understory.

Acknowledgements

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