Research Paper

Title: Global importance of large-diameter trees in forests

Running head: Large-diameter trees in forests

Abstract

Aim: To examine the contribution of large-diameter trees to biomass and species richness.
Location: Global
Methods: We tested the role of large trees as determinants of worldwide forest density, diversity, and biomass using 48 large (2 ha ≤ area ≤60 ha) mapped forest plots with 5,474,048 stems representing 9,407 species and 307 plant families. Large-diameter trees were assessed in three ways: the largest 1% of trees, trees ≥60 cm diameter at breast height (DBH), and those large trees together comprising 50% of forest biomass.
Results: Globally, we found disproportionate contributions of large-diameter trees to biomass. Averaged across these 48 forest plots, the largest 1% of trees comprised 50% of aboveground live biomass, with hectare-scale standard deviation of 26%. Trees ≥60 cm DBH comprised 41% of aboveground live tree biomass. The size of the largest trees correlated with total forest biomass ($r^2 = 0.62$, $P<0.001$), but large-diameter trees in these forests represented far fewer species relative to overall forest richness ($r^2 = 0.45$, $P<0.001$). Forests with more diverse large-diameter tree communities had lower biomass ($r^2 = 0.42$, $P<0.001$). The concentration of biomass in the largest 1% of trees declined with increasing absolute latitude ($r^2 = 0.46$, $P<0.001$). In other words, forests with high biomass had high large-diameter thresholds and relatively low richness of the large-diameter structural class.
Main conclusions: Because large-diameter trees constitute roughly half of the forest biomass worldwide, their climate sensitivities and resilience to change represent potentially large controls on global forest productivity. Understanding the climate sensitivities of large-diameter trees may allow for better prediction of forest biomass with changing climate, and conservation efforts focused on large-diameter trees may provide an effective means of preserving ecosystem function. We recommend managing forests for large-diameter trees as a simple way to preserve ecosystem services.

Keywords: forest biomass, forest structure, ForestGEO, large-diameter trees, latitudinal gradient, resource inequality

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Introduction

Concentration of resources within a few individuals in a community is a pervasive property of biotic systems (West et al., 1997), whether marine (Hixon et al., 2014), terrestrial (Enquist et al., 1998), or even anthropogenic systems (Saez & Zucman, 2016), and the concentration of biomass in forests is no exception (Pan et al., 2013). Forests are the central component of the global terrestrial carbon cycle, and large-diameter trees within forests contribute disproportionately to these functions. They provide structural complexity, long-term carbon storage, contribute importantly to forest biogeochemical and hydrological cycles, and act as a structural and demographic buffer to physical disturbances and climate extremes. Large-diameter trees in forests take many decades or even centuries to develop, but can disappear rapidly due to human or natural disturbances (Van Mantgem et al., 2009). Given the many new threats to forest ecosystems due to global change, quantifying the roles that large trees play in forests is critical to efforts for global forest conservation.

Despite the recognized ecological significance of large-diameter trees within individual forest types, relatively little is known about the distribution and abundance of large-diameter trees at the global scale. Previous studies have showed that large-diameter trees comprise a large fraction of the biomass of many forests (Brown et al., 1995; Clark & Clark, 1996; Lutz et al., 2012; Bastin et al., 2015), and that they modulate stand-level leaf area, microclimate, and water use (Martin et al., 2001, Rambo & North, 2009). Large-diameter trees contribute disproportionately to reproduction (van Wagtendonk & Moore, 2010), influence the rates and patterns of regeneration and succession (Keeton & Franklin, 2005), limit light and water available to smaller trees, and contribute to rates and causes of mortality of smaller individuals by crushing or injuring sub-canopy trees when their bole or branches fall to the ground (Chao et al., 2009; Das et al., 2016). Large-diameter trees (and large-diameter snags and large-diameter down woody debris) make the structure of primary forests and mature secondary forests unique (Spies & Franklin, 1991). The multilayered canopies topped by the largest trees can control forest development and disturbance over long time periods (Swetnam, 1993; Winter et al., 2002). Large-diameter trees occur at low stem densities, yet influence spatial patterns over long inter-tree distances (Enquist et al., 2009; Lutz et al., 2014). Consequently, patterns, mechanisms, and consequences of large-diameter tree ecology require large sample plots (Lutz, 2015; Das et al., 2011). Studies based on smaller plots (≤1 ha) often do not contain enough large-diameter trees to conduct community-level analyses or do not include enough area to gauge the effect of large-diameter trees on the local neighborhood (Das et al., 2011).

Changes in climate or disturbance regimes threaten to continue to contribute to the decline of large-diameter trees globally (e.g., Lindenmayer et al., 2012; Bennett et al., 2015; Lindenmayer & Laurence, 2016). The resilience of large-diameter trees (and by extension, the ability of the forest to sequester carbon) is dependent on two factors: 1) presence of species capable of attaining a large size, and 2) conditions permissive for the development large-diameter trees. If the species richness of the large-diameter cohort is high, a forest may be better able to respond to perturbations (Musavi et al., 2017) and maintain its structure and ecological function. However, if the large-diameter species richness is low, then a forest could be susceptible to any change that affected those few species.

What is a large-diameter tree?

Generally, a large-diameter tree can be considered to be one that is of reproductive stature, is tall enough to reach the upper canopy layer of the forest, and that is larger than the majority of woody stems in the forest. In any forest, the largest trees *relative to the rest of the stand* contribute disproportionately to ecological function and represent some of the longest-lived and most fecund components of their respective forests. The definition of large-diameter inherently depends on species and forest type. In cold, continental forests, a large-diameter tree may only be 20 cm diameter at breast height (1.3 m above the ground; DBH) (Baltzer et al., 2014). In productive temperate or tropical forests, a large-diameter tree may be >100 cm DBH (Lutz et al., 2012; 2013). To compare dissimilar ecosystems, we used three metrics for defining large diameter trees:

1) 99th percentile diameter. The largest 1% of trees in the forest.
2) Fixed diameter. We used a fixed threshold for large-diameter trees of 60 cm DBH, a diameter reached by at least some trees in almost all plots.
3) The *large-diameter threshold.* We defined the large-diameter threshold to be that diameter such that trees greater than or equal to that diameter constituted half of the aboveground live biomass of the plot.

Both the Unified Neutral Theory of Biodiversity (Hubbell, 2001) and Metabolic Scaling Theory (West et al., 2009) propose that plants have a degree of functional equivalency. However, those theories cannot fully explain global patterns of forest species diversity or the larger portion of the size distribution (Coomes et al., 2003; Muller-Landau et al., 2006; Lutz et al., 2012; LaManna et al., 2017). Other studies suggest that a greater generalization of forest structure in the tropical, subtropical, temperate, and boreal forests of the world may indeed be possible (i.e., Gilbert et al., 2010; Slik et al., 2013; Ostertag et al., 2014). To the extent that forests share structural attributes either globally or regionally, it may improve our ability to model forest change by focusing on global patterns in structure rather than individual species life-history traits. Our principal hypothesis was that only a small proportion of the largest trees are responsible for the preponderance of forest biomass globally. Our objectives were to characterize the range of global forest structure and to quantify the relative contribution of large-diameter trees to forest biomass and species richness. We analyzed 48 forest plots spanning 86.4° of latitude (Fig. 1), covering 1,240 ha (median size 24 ha), and including 5,474,048 stems representing 9,407 species and 307 plant families (Fig. 1, Tables 1, S1).

Materials and Methods

We used data from the Forest Global Earth Observatory (ForestGEO; Anderson-Teixeira et al., 2015) network of forest dynamics plots coordinated by the Smithsonian Institution), which includes major forest types in the Köppen climate zones of cold, temperate, and tropical forests (Fig. 1, Table S1). These forest plots feature consistent field methods (Condit, 1998) and data representation (Condit et al., 2014). Importantly, these plots include all woody stems ≥1 cm DBH. ForestGEO includes most major forest types (Anderson-Teixeira et al., 2015).

We calculated structural accumulation curves for each plot, calculating the area required to estimate forest density and aboveground live biomass to within 5% of the entire plot value. Within each plot, for each of density and biomass, we used random sampling of 400 m^2 quadrats, beginning with random sample of n = 1 quadrat and ending with a random sample of n = total number of quadrats in each plot. This process was repeated based on the number of quadrats in each plot which allowed us to calculate a mean and standard deviation for each value of n. A percent deviation metric was calculated as:

$$Percent\ difference = (abs(mean_n - mean_{plot}) + sd_n)/mean_{plot}$$

where $mean_n$ is the mean of a random sampling of n quadrats, $mean_{plot}$ is the mean for the entire plot, and sd_n is the standard deviation for the random sample of n quadrats.

We calculated the density, basal area, and biomass of stems ≥1 cm DBH and tabulated them within each square hectare (100 m × 100 m) of the 48 plots. Because large-diameter trees can strongly structure the local community, we used the one hectare scale to implicitly include variation in structure without introducing the spurious high or low values of biomass that could be associated with small extents (Réjou-Méchain et al., 2014). We calculated biomass for tropical forests by the methods of Chave *et al.* (2014), which uses a generic equation to predict biomass based on diameter, climate, and wood density. We calculated biomass for cold and temperate plots using the composite taxa-specific equations of Chojnacky *et al.* (2014). For both tropical and temperate plots, species not represented by specific biomass equations or wood density values were defaulted to an equation or wood density value for the genus or the family. We used site-specific allometric equations when available (Palamanui, Laupahoehoe, Jianfengling, Lanjenchi, and Changbaishan). We used the fixed metric (≥60 cm DBH) and the two relative metrics (large-diameter threshold and 99th percentile diameter) to examine the species richness of the large-diameter cohort.

We further analyzed the full structural characteristics of each plot based on six tree diameter classes (1 cm ≤ DBH < 5 cm, 5 cm ≤ DBH < 10 cm, 10 cm ≤ DBH < 30 cm, 30 cm ≤ DBH < 60 cm, 60 cm ≤ DBH < 90 cm, and DBH ≥ 90 cm). Diameter classes were selected to include recognized differences in tree life-history traits worldwide. The two smallest diameter classes (DBH < 10 cm) were selected because of the ability of the ForestGEO protocol to capture unique elements of small-diameter trees (Memiaghe et al., 2016). The larger diameter classes were selected based on preliminary analysis of the data and on prior studies (Lutz et al., 2009; 2012). We performed nonmetric multidimensional scaling (NMDS; Kenkel & Orloci, 1986) analyses on the density and biomass of each diameter class of each 100 m × 100 m area, using the environmental correlates of Anderson-Teixeira et al. (2015). Analyses were performed using the version 2.4.2 of the vegan package (Oksanen et al. 2016, Oksanen, 2017) in R version 3.3.1 (R Development Core Team, 2016).

Results

The concentration of biomass in the largest 1% of trees ranged from 13% (Palamanui, USA) to 83% (Ituri Lenda, Democratic Republic of Congo), with the mean of the 48 plots being 45% (SD = 18%)(Table 1). Average stem density in the plots ranged from 608 stems ha^{-1} (Mudumalai, India) to 12,075 stems ha^{-1} (Lanjenchi, Taiwan) with most high-density plots occurring in the tropics (Tables 1, 2). Aboveground live tree biomass ranged from 13 Mg ha^{-1} (Mpala, Kenya) to 559 Mg ha^{-1} (Yosemite, USA). The biomass of trees ≥60 cm DBH ranged from 0 Mg ha^{-1} (Mpala, Kenya, Palamanui, USA, and Scotty Creek, Canada) to 447 Mg ha^{-1} (Yosemite, USA). The large-diameter tree threshold (separating the plot aboveground forest biomass into two equal parts) varied from 2.5 cm (Palamanui, USA) to 106.5 cm (Yosemite, USA). Variation in the abundance of trees of different diameter classes at hectare scales was high globally (Tables S2, S3), and relative variance of the 1-ha stem densities was highest in the cold temperate / boreal plots and lowest in the tropics (Table 2). There was a strong positive relationship between the large-diameter threshold and the overall forest biomass globally ($r^2 = 0.62$, $P<0.001$; Fig. 2A). Results based on basal area were similar to those for biomass (Fig. S1). There was a negative relationship between the large-diameter threshold and large-diameter richness ($r^2 = 0.42$, $P<0.001$; Fig. 2B). There was a strong negative relationship between large-diameter richness and biomass ($r^2 = 0.45$, $P<0.001$; Fig. 2C) and a strong negative relationship between large-diameter richness (relative to the forest as a whole) and concentration of biomass in the largest 1% of trees ($r^2 = 0.61$, $P<0.001$; Fig. 2D). In other words, plots with high biomass had high large-diameter thresholds and relatively low richness of this large-diameter structural class.

The amount of aboveground forest biomass contained within the largest 1% of trees averaged among the 48 plots was 50% (weighted by the forest biomass of each plot, 48% as an unweighted average of the 48 plots), representing an average of 23% of the total species richness (Table 1). The average large-diameter threshold was 47.7 cm DBH (half of global aboveground forest biomass is contained within trees ≥ 47.7 cm DBH) irrespective of total stem density or the high density of small trees (Fig. 4D). The average portion of biomass contained within trees ≥60 cm DBH in the 48 plots was 41%. Forest density gradually decreased with increasing absolute latitude ($r^2 = 0.33$, $P<0.001$; Fig. 3A). The proportion of tree biomass accounted for by the largest 1% of trees declined with absolute latitude ($r^2 = 0.46$, $P<0.001$; Fig. 3C), partially a reflection of the higher stem densities of small-diameter trees in the tropics (Fig. 3A, Tables 1, S2). Latitudinal gradients were not present for biomass (Fig. 3B) or the large-diameter threshold (Fig. 3D).

The absolute numbers of species that reached the local large-diameter threshold varied between two in Laupahoehoe, USA to 343 in Yasuni, Ecuador (Table 1). Temperate plots generally had <10 species that reached the large-diameter threshold (maximum 25 species in SERC, USA). Tropical plots generally had >25 species reaching the large-diameter threshold (minimum nine species in Cocoli, Panama). On a percentage basis, large-diameter richness ranged from 5% (Cocoli, Panama and Bukit Timah, Singapore) to 69% (Palamanui, USA). The relative richness of the large-diameter cohort was highest in plots with low biomass, while plots with high biomass had a lower proportion of richness represented by the large-diameter trees (Fig. 2C, Table 1). In general, forests with lower total richness had a higher proportion of that richness retained in the large-diameter class. Unsurprisingly, plots with lower large-diameter thresholds (<60 cm) had a higher proportion of species represented in the large-diameter guild (mean 34%), whereas plots with large-diameter thresholds ≥60 cm DBH had a lower proportion of species represented in the large-diameter guild (mean 18%).

NMDS ordinations of the abundance of trees in each of the six diameter classes in each 100 m × 100 m area showed that tropical forests have a high degree of structural similarity at the global scale (Fig. 4A, B). The 1-ha scale variation for tropical plots showed a high degree of overlap (Fig. 4C, D). Temperate plots, conversely, showed a wide range in ordination space, indicating greater structural variability at global scale. This phenomenon was also mirrored at local scales - coefficients of variation in density at 1-ha quadrats differed among climate regions and were higher in temperate and boreal forests than in tropical plots (Table 2). The grouping of plots with no trees ≥60 cm DBH (left of Figs. 4A, B; Table S2) shows a structural equivalency of forests growing in stressful environments. Those forests include Scotty Creek, Canada (temperature, nitrogen, and hydrologically limited), Mpala, Kenya (water and herbivory limited) and Palamanui, USA (water limited, soil limited, and with limited species complement). Temperate plots occupied the greatest range of structure. Some 100 m × 100 m areas of temperate forests were structurally unique, but there were 100 m × 100 m areas from temperate plots that were structurally similar to the less dense portions of tropical forests.

Discussion

Forests with high biomass were characterized by relatively low species richness of the large-diameter trees with respect to overall richness (Fig. 2B), although the density of large-diameter trees was higher (Tables 1, S1). The forests with highest biomass ($\geq$400 Mg ha^{-1}) included temperate forests with low absolute richness of the large-diameter class and tropical forests with high absolute richness of the large-diameter class (Table 1). This relationship suggests that some forests with the highest biomass may be more vulnerable to species declines. The loss of a single species from a high-biomass, low richness forest, whether by changing climate, disturbance, or anthropogenic influence, may have a large impact total forest biomass, making the sequestered carbon less stable over time. Forests with lower biomass had higher relative species richness in the large-diameter classes, and therefore are potentially less sensitive to changes in species composition.

The relation between the large-diameter threshold and overall biomass (Fig. 2A) suggests that forests cannot sequester large amounts of aboveground carbon without large trees, irrespective of large-diameter tree richness. The 48 forests in this study have all passed beyond the developmental stage of intense self-thinning (Yoda et al., 1963) and are composed of large-diameter trees interspersed among more numerous smaller diameter trees (Table S2). Almost all forests have some species that grow to relatively large sizes. In high biomass forests across the globe, these species grow to large absolute sizes. Species capable of attaining large diameters are relatively few (Fig. 2), and their richness does not scale with the diversity of the system globally. The species that reach large sizes are likely able to do this not because of luck or access to resources, but based on allocation adaptations that invest in the types of tissue structures and maintenance that allow long life and large stature. This relationship held across plots with a range of stem densities and among trees of varying wood densities (wood density values from 0.10 g cm^{-3} to 1.08 g cm^{-3}). A linear relation (Fig. 2A) best explained the correlation among 48 plots, although we would expect an upper limit based on maximum tree heights (Koch et al., 2004) or biomass (Sillett et al., 2015; Van Pelt et al., 2016). The generally high proportion of biomass represented by the largest 1% of trees reinforces the importance of these individuals to carbon sequestration. Larger numbers of small and medium-diameter trees cannot provide equivalent biomass, although they may contribute to the majority of carbon cycling (Meakem et al., in press). The implication from scaling theory (West et al., 2009) being that large-diameter trees are taller and have heavier crowns, and occupy space not available to smaller trees (West et al., 2009; Van Pelt et al., 2016). Temperate forests featured higher density of trees $\geq$60 cm DBH (Table 1), consistent with the presence of the very largest species of trees (*Sequoia sempervirens*, *Sequoiadendron giganteum*, and *Eucalyptus regnans*) in cool, temperate forests (Sillett et al., 2015; Van Pelt et al., 2016). As a consequence, temperate forests exhibited also considerably lower density of small trees (e.g., 1 cm $\leq$ DBH < 5 cm; Table S2) and in effect also total stem density, which is largely formed by the density of small trees (Tables 2, S2). The lower proportional richness of large-diameter trees in tropical forests likely has at least two explanations. First, tropical forests contain many more stems (Table S3) with much higher understory diversity (LaFrankie et al., 2006). Second, not all species capable of reaching large-diameters may be represented in even the large ForestGEO plots.

Large-diameter trees can be abundant in a variety of climates (Table S1), but different mechanisms may limit the ability of an ecosystem to support a high level of aboveground live biomass. Environmental limits to the growing season imposed by cold temperatures and nutrient limitations (e.g., Scotty Creek, Canada) or drought and herbivory (Mpala, Kenya) may preclude the development of large-diameter trees. Conversely, ecosystems that are environmentally quite productive in terms of annual growth can be limited by frequent, severe disturbance (e.g., typhoons in Fushan, Taiwan). And finally, the regional species pool may not contain species that can attain large diameters in the combination of local climate and resource availability (e.g., Palamanui, USA). The grouping of plots with only small-diameter trees (Fig. 4A) shows that forests in markedly different environments can exhibit convergent structure based on different limiting factors. Primary forests and older secondary forests exhibited similar distribution of diameter classes overall (Table 1) even though individual species diameter distributions and the history of disturbance varied. Within some older secondary forests, abundances of individuals of shade-intolerant pioneer species exhibited unimodal diameter-abundance relationships as opposed to the reverse-J distribution of shade-tolerant species. In at least some forests (i.e., Wind River, USA), the shade-intolerant cohort was still apparent after five centuries (Lutz et al., 2013). Forest structure clearly depends on climate (Fig. 4), however the relatively low correlations between significant climate variables and the first NMDS axis suggests that either the important climate correlates are not functions of univariate physical or biophysical factors, or that structural similarity between forests depends more significantly on the diversity of the species present and their life-history traits.

The climate sensitivities of larger-diameter trees may provide a more straight-forward path to predicting changes in forest biomass because the large-diameter trees contain about half of forest biomass worldwide. Larger trees are susceptible to sapwood cavitation and are exposed to high radiation loads (Allen et al., 2010). Although location-specific climate models may be the best way to examine potential trends in biomass, at the global scale, it may be more important to understand the environmental sensitivities of large-diameter trees. Any decline in temperate zone large-diameter tree abundance may be compounded by the low large-diameter tree diversity in temperate forests. Large-diameter tree richness in tropical forests suggest more resilience to projected climate warming in two ways. First, large-diameter tree richness was highest in tropical forests, suggesting that the large-diameter tree guild may have different adaptations that will allow at least some species to persist. And second, the pool of species that can reach large diameters may have been undersampled, implying an even higher level of richness.

Characterizing forest structural variation and the abundance and diversity of large-diameter trees required these large plots (Fig. S2), a finding consistent with other studies examining forest biomass (Réjou-Méchain et al., 2014). In particular, the relatively large area required (6.5 ha, on average) to estimate biomass to within 5% of the entire plot value reinforces conclusions that the distribution of large-diameter trees is not uniform throughout the forest (e.g., Lutz et al., 2012; 2013; Furniss et al., 2017), and that the influence that these individuals can have on the local neighborhood is high. We note that this calculation of the size of the plot required is a measure of spatial variation within the forest, and does not depend on the accuracy of the allometric equations themselves. Allometric equations are well known to be imprecise for large-diameter trees, and therefore our estimates of overall biomass could be off by ±15% (Lutz et al. 2016). Although temperate plots had much lower overall species diversity compared to the tropical plots, tropical plots had much more homogeneous structure (Fig. 4). With large plot sizes and global distribution, ForestGEO is uniquely suited to capture structural variation (i.e., the heterogeneity in the abundance of trees of all diameter classes) in addition to their utility in examining species diversity (Hubbell, 2001; Anderson-Teixeira et al., 2015).

Our principal hypothesis that the largest 1% of trees ≥1 cm DBH constitute almost 50% of the biomass (and hence, carbon) was supported worldwide. The maintenance of large-diameter trees is therefore imperative to maintain full ecosystem function, as the time necessary for individual trees to develop large sizes could preclude restoration of full function for centuries following the loss of the oldest and largest trees from forests. The fact that the largest individuals belong to relatively few species (at least in temperate forests) means that the loss of large-diameter trees may alter forest function. If species that can attain large diameter disappear, forests will feature greatly reduced biomass and structural heterogeneity that will take decades to centuries to recover. Recovery may never occur if those species are extirpated, or if continuous climate change over the coming centuries prevents trees from living long enough to attain large sizes. Policies to conserve the tree species whose individuals can develop into large, old trees (Lindenmayer et al., 2014) could promote retention of aboveground biomass globally as well as maintaining ecosystem functions provided by large trees.

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Tables

Table 1. Structural characteristics of global forests. Values for density and biomass include trees ≥1 cm DBH within each square hectare (100 m × 100 m) of the plots, with the mean and standard deviation (SD) calculated for each full hectare. The large-diameter threshold represents the diameter where half the biomass is contained within trees above that threshold. The biomass of the 1% indicates the proportion of total live aboveground tree biomass contributed by the largest 1% of trees by DBH. Plots are listed by declining large-diameter threshold.

Plot	Large-diameter threshold (cm)	Density (stems ha^{-1}) (SD)	Biomass (Mg ha^{-1}) (SD)	Total species (n)	Large-diameter species (n)	Large-diameter richness (%)	Biomass of the 1% (%)	Density ≥60 cm DBH (stems ha^{-1})
Yosemite	106.5	1399 (266)	559(130)	14	3	21	46	52
Wind River	92.9	1207 (273)	532(161)	26	5	19	33	72
Žofín	78.0	2404 (982)	248 (66)	11	4	36	56	41
Ituri Lenda	72.0	7553 (829)	467 (62)	396	25	6	83	34
Danum Valley	65.7	7573 (526)	486(152)	784	62	8	72	27
SERC†	65.4	2086 (792)	299 (49)	79	25	32	40	40
Laupahoehoe	63.4	3925 (859)	241 (45)	22	2	9	58	37
Santa Cruz†	62.3	1945 (593)	361(102)	31	7	23	41	34
Cocoli	60.1	2164 (248)	281 (37)	170	9	5	59	32
Huai KhaKhaeng	59.9	2506 (674)	258 (65)	284	80	28	57	20
SCBI†	59.7	1850(1637)	259 (43)	64	22	34	31	35
Ituri Edoro	59.3	8956(1270)	375 (46)	426	63	15	80	23
Changbaishan	56.2	1230 (188)	288 (33)	52	15	29	22	34
Bukit Timah	55.6	6273 (180)	363(140)	353	18	5	73	19
Rabi	54.7	7988 (926)	323 (74)	346	74	21	73	14
Lambir	51.9	7635(1233)	495 (99)	1387	223	16	69	27
Barro Colorado	51.2	4938 (463)	257 (49)	297	80	27	67	17
Lilly Dickey	51.2	1112 (441)	214 (29)	34	19	56	22	20
Xishuangbanna	49.8	4565 (650)	280 (81)	450	93	21	57	19
Wanang	49.6	5523 (520)	324 (61)	581	170	29	61	14
Palanan	49.4	4981 (489)	414(119)	324	41	13	62	27
Pasoh	48.5	5735 (631)	324 (55)	926	194	21	63	13
Michigan Woods	47.5	1981 (515)	192 (25)	44	16	36	26	14
Tyson	45.4	1601 (751)	176 (16)	45	18	40	24	10
Wytham Woods†	44.8	1016 (309)	310 (46)	23	13	57	23	18
Korup	42.9	7283 (920)	345 (88)	485	143	29	67	10
Manaus	42.2	6234 (441)	344 (54)	1529	260	17	59	9
Cedar Breaks	41.9	1542 (961)	168 (53)	17	8	47	34	13
Mudumalai	41.7	608 (210)	205 (33)	72	35	49	18	12
Jianfengling	40.8	6526 (993)	392 (37)	290	116	40	48	24
La Planada	40.8	4030 (243)	270 (30)	241	74	31	43	8
Fushan	39.2	4478(1139)	224 (25)	106	33	31	46	14
Sherman	38.5	3662 (550)	275 (41)	224	31	14	53	13
Amacayacu	37.6	4948 (518)	268 (33)	1233	326	26	49	7

Kenting	36.1	3760 (410)	255 (38)	92	40	43	36	7
Lienhuachih	35.7	6131(1760)	170 (25)	145	49	34	51	10
Harvard Forest	35.5	3104(2600)	260 (66)	55	17	31	23	7
Luquillo	35.5	2903 (626)	283 (53)	133	47	35	39	12
Heishiding	34.5	5277 (706)	149 (27)	213	59	28	43	12
Wabikon	31.1	1692(1017)	111 (14)	31	15	48	17	1
Gutianshan	31.0	5833(1580)	185 (27)	159	40	25	34	2
Ilha do Cardoso	31.0	4660 (578)	148 (17)	135	43	32	41	7
Yasuni	29.1	5834 (692)	261 (48)	1075	343	32	50	8
Hong Kong†	28.6	5860(1056)	142 (20)	172	43	25	39	3
Lanjenchi	17.2	12075(2795)	113 (7)	128	72	56	29	1
Mpala	10.0	2963(2902)	13 (8)	68	35	51	30	0
Scotty Creek	7.6	4136(1407)	22 (11)	11	7	64	15	0
Palamanui	2.5	8205(1084)	30 (5)	16	11	69	13	0

†Mature secondary forest

Table 2. The effect of climate zone on tree density and coefficient of variation of density at 1 ha scale and the proportion of biomass in the largest 1% of trees with all 48 plots weighted equally.

Climate zone	Mean tree density per hectare (trees ha^{-1})	Coefficient of variation of density at 1 ha scale	Biomass proportion of the 1% (%)
Cold temperate / boreal	2,281	47	23
Temperate	3,527	32	38
All Tropics	5,904	12	61
Tropical Africa	7,945	12	76
Tropical Asia	5,767	16	53
Tropical Latin America	4,383	12	54
Tropical Oceania	5,523	9	61

Figures

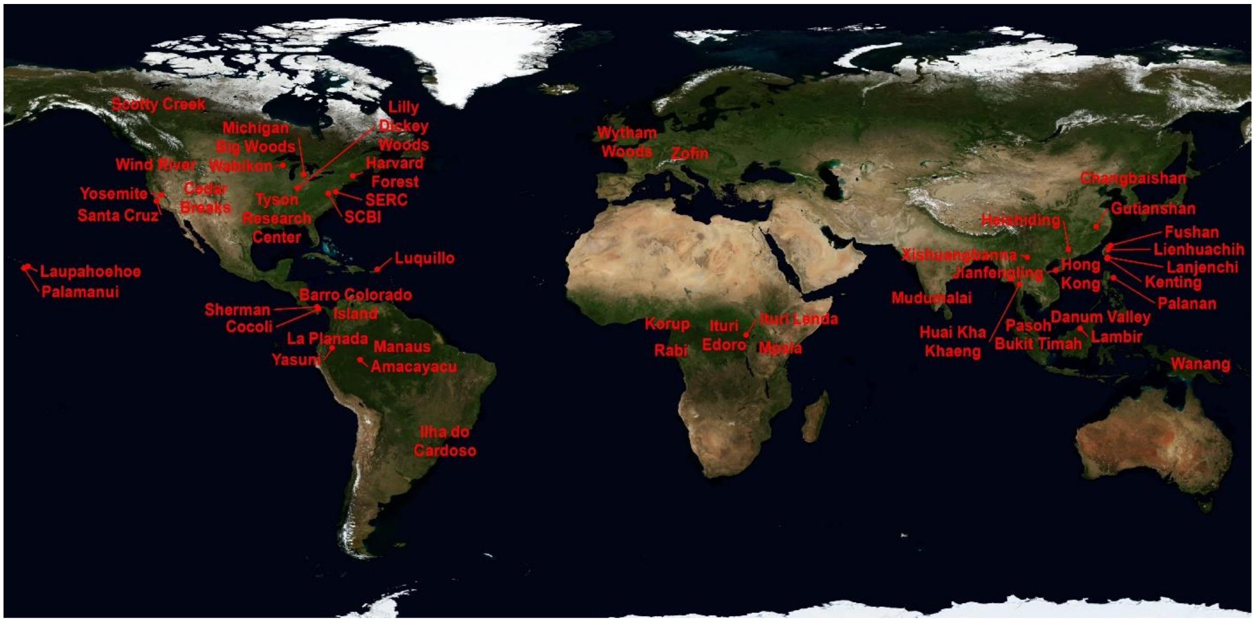

Fig. 1. Location of the 48 plots affiliated with the Smithsonian Forest Global Earth Observatory (ForestGEO) plots used in this study.

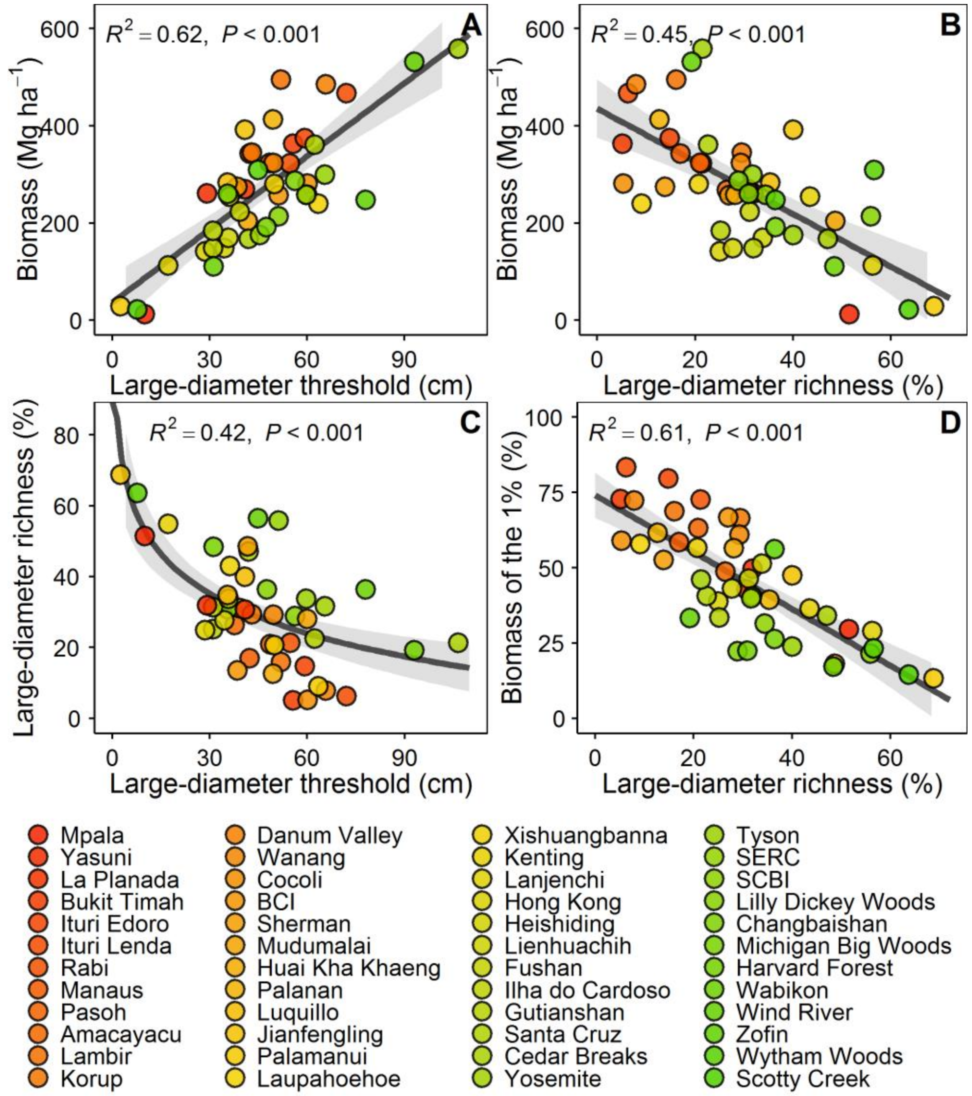

Fig. 2. Contribution of large-diameter trees to forest structure of 48 large forest plots. Aboveground live tree biomass increases with increasing large-diameter threshold (A). The large-diameter threshold reflects the tree diameter that segments biomass into two equal parts. Below the large-diameter threshold are a large number of small-diameter trees, and above the large-diameter threshold are a smaller number of large-diameter trees. Aboveground live biomass declines with the proportion of trees reaching the large-diameter threshold (B). Large-diameter richness also declines with increasing large-diameter threshold (C). The concentration of biomass in the largest 1% of trees has a strong negative relationship with large-diameter richness (D). Grey areas indicate 95th percentile confidence intervals.

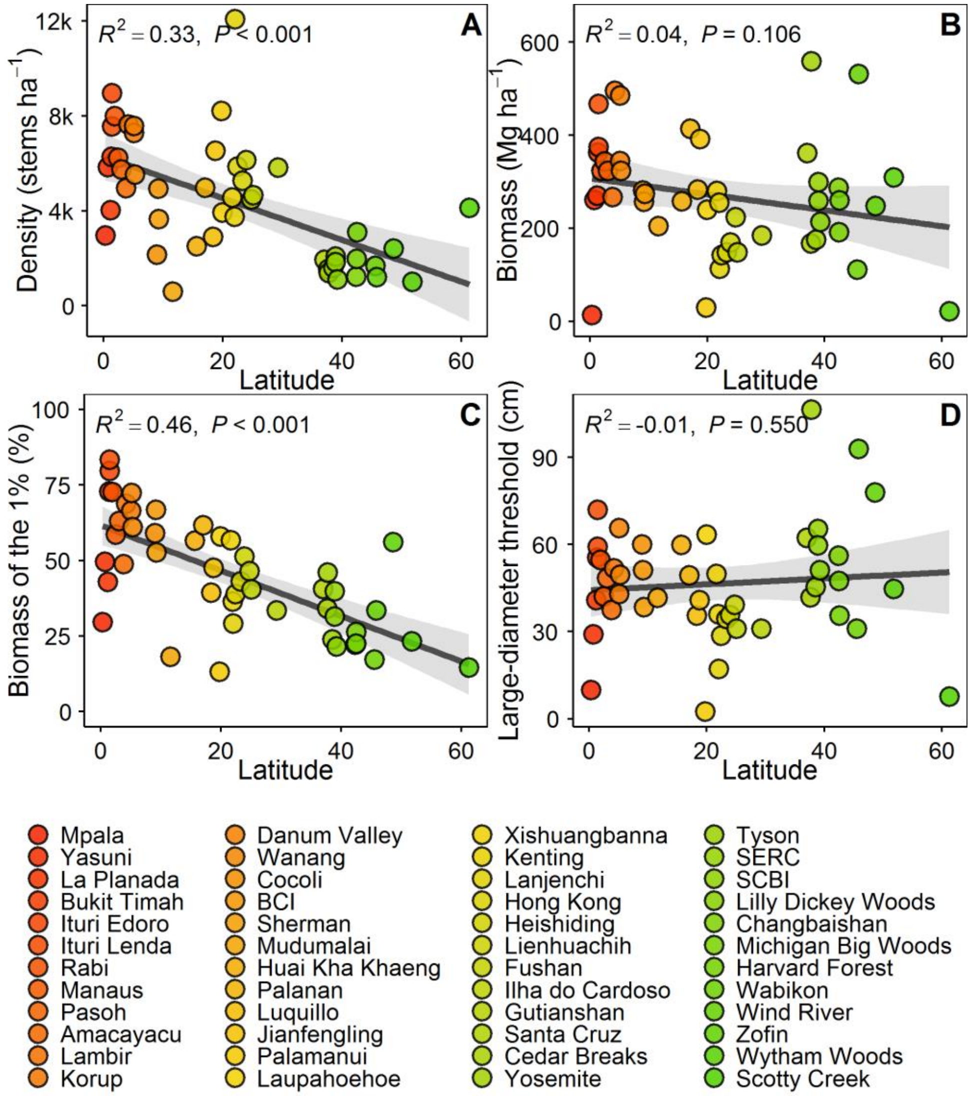

Fig. 3. Gradients of forest structural attributes by absolute latitude for 48 forest plots in the ForestGEO network. Absolute latitudinal gradients in density (A) and concentration of biomass in the largest 1% of trees (C) were significant, whereas those for biomass (B) and the large-diameter threshold (D) were not. Grey areas indicate 95th percentile confidence intervals.

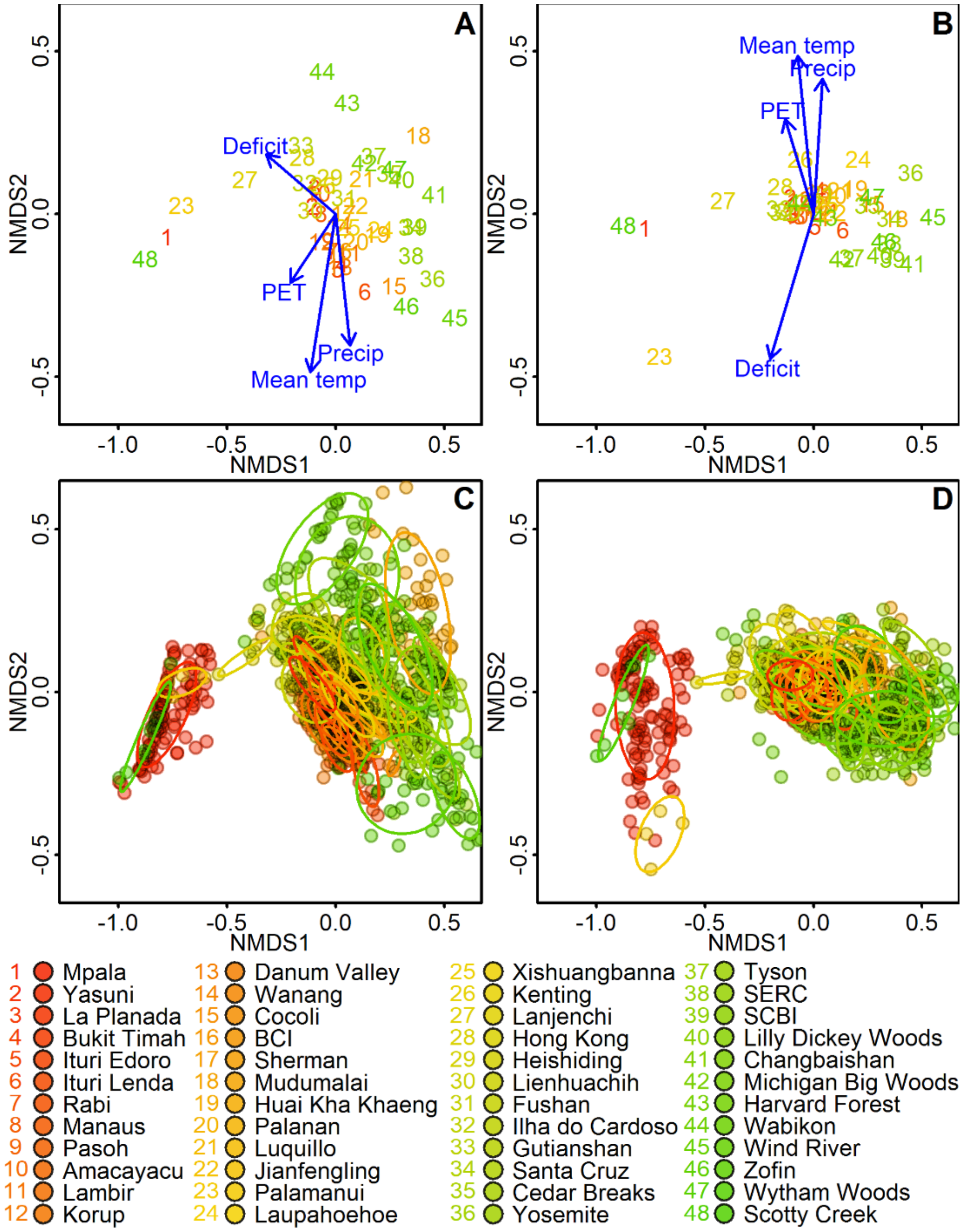

Fig. 4. Three-dimensional nonmetric multidimensional scaling (NMDS) results for density and biomass of trees organized into six diameter classes in 1240 hectares of 48 forest plots in the ForestGEO network (A, B). Plot mean values are shown with environmental predictors from Anderson-Teixeira et al. (2015) (A, B). Significant climate correlates (*P*< 0.001) include months with precipitation less than potential evapotranspiration (Deficit), annual potential evapotranspiration (PET), annual mean temperature (Mean temp), and annual precipitation (Precip). Structure of individual 100 m × 100 m hectares within each plot showed wide variation (C, D; 95th percentile ellipses superimposed). Although plot means are differentiated in the first two ordination axes (A, C), the high degree of structural variation present in each hectare of forest includes considerable structural overlap among forests from very different geographies shown in the third NMDS axis (B, D). Ordination stress = 0.047.

References

Allen, C.D., et al. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management **259**, 660-684.

Anderson-Teixeira, K.J., et al. (2015) CTFS-ForestGEO: A worldwide network monitoring forests in an era of global change. Global Change Biology **21(2)**, 528-549.

Baltzer, J.L., Venes, T., Chasmer, L.E., Sniderhan, A.E. & Quinton, W.L. (2014) Forests on thawing permafrost: fragmentation, edge effects, and net forest loss. Global Change Biology **20**, 824-834.

Bastin, J-F., et al. (2015) Seeing central African forests through their largest trees. Scientific Reports **5**, 13156.

Bennett, A.C., McDowell, N.G., Allen, C.D. & Anderson-Teixeira, K.J. (2015) Larger trees suffer most during drought in forests worldwide. Nature Plants **1(10)**, 15139.

Brown, I.F., et al. (1995) Uncertainty in the biomass of Amazonian forests: An example from Rondônia, Brazil. Forest Ecology and Management **75**, 175–189.

Chao, K-J., Phillips, O.L., Monteagudo, A., Torres-Lezama, A. & Vásquez Martínez, R. (2009) How do trees die? Mode of death in northern Amazonia. Journal of Vegetation Science **20**, 260–268.

Chave, J., et al. (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. Global Change Biology **20(10)**, 3177-3190.

Chojnacky, D.C., Heath, L.S. & Jenkins, J.C. (2014) Updated generalized biomass equations for North American tree species. Forestry **87**, 129-151.

Clark, D.B. & Clark, D.A. (1996) Abundance, growth and mortality of very large trees in Neotropical lowland rain forest. Forest Ecology and Management **80**, 235–244.

Condit, R. (1998) Tropical forest census plots. Berlin: Springer-Verlag, Georgetown: R.G. Landes Company. 211 p.

Condit, R., Lao, S., Singh, A., Esufali, S. & Dolins, S. (2014) Data and database standards for permanent forest plots in a global network. Forest Ecology and Management **316**, 21–31.

Coomes, D.A., Duncan, R.P., Allen, R.B. & Truscott, J. (2003) Disturbances prevent stem size-density distributions in natural forests from following scaling relationships. Ecology Letters **6**, 980–989.

Das, A., Battles, J., Stephenson, N.L. & van Mantgem, P.J. (2011) The contribution of competition to tree mortality in old-growth coniferous forests. Forest Ecology and Management **261**, 1203–1213.

Das, A.J., Stephenson, N.L. & Davis, K.P. (2016) Why do trees die? Characterizing the drivers of background tree mortality. Ecology **97(10)**, 2616-2627.

Enquist, B.J., Brown, J.H. & West, G.B. (1998) Allometric scaling of plant energetics and population density. Nature **395**, 163-165.

Enquist, B.J., West, G.B. & Brown, J.H. (2009) Extensions and evaluations of a general quantitative theory of forest structure and dynamics. Proc Natl Acad Sci USA **106**, 7046–7051.

Furniss, T.J., Larson, A.J. & Lutz, J.A. (2017) Reconciling niches and neutrality in a subalpine temperate forest. Ecosphere **8(6)**, Article01847.

Gilbert, G.S., et al. (2010) Beyond the tropics: forest structure in a temperate forest mapped plot. Journal of Vegetation Science **21(2)**, 388-405.

Hixon, M.A., Johnson, D.W. & Sogard, S.M. (2014) BOFFFFs: on the importance of conserving old-growth structure in fishery populations. ICES Journal of Marine Science **71(8)**, 2171-2185.

Hubbell, S.P. (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press. 375 pp.

Keeton, W.S. & Franklin, J.F. (2005) Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? Ecological Monographs **75,** 103–118.

Kenkel, N.C. & Orloci, L. (1986) Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. Ecology **67(4)**, 919-928.

Koch, G.W., Sillett, S.C., Jennings, G.M. & Davis, S.D. (2004) The limits to tree height. Nature **428**, 851-854.

LaFrankie, J.V., et al. (2006) Contrasting structure and composition of the understory in species-rich tropical rain forests. Ecology **87(9)**, 2298-2305.

LaManna, J.A., et al. (2017) Negative density dependence contributes to global patterns of plant biodiversity. Science **356**, 1389-1392.

Lindenmayer, D.B., Laurence, W.F. & Franklin, J.F. (2012) Global decline in large old trees. Science **338**, 1305–1306.

Lindenmayer, D.B. & Laurence, W.F. (2016) The ecology, distribution, conservation and management of large old trees. Biological Reviews doi: 10.1111/brv.12290

Lindenmayer, D.B., et al. (2014) New policies for old trees: averting a global crisis in a keystone ecological structure. Conservation Letters **7(1)**, 61-69.

Lutz, J.A. (2015) The evolution of long-term data for forestry: large temperate research plots in an era of global change. Northwest Science **89(3)**, 255-269.

Lutz, J.A., Larson, A.J., Freund, J.A., Swanson, M.E. & Bible, K.J. (2013) The importance of large-diameter trees to forest structural heterogeneity. PLoS ONE **8(12)**, e82784.

Lutz, J.A., Larson, A.J., Swanson, M.E. & Freund, J.A. (2012) Ecological importance of large-diameter trees in a temperate mixed-conifer forest. PLoS ONE **7(5)**, e36131.

Lutz, J.A., et al. (2014) Spatially non-random tree mortality and ingrowth maintain equilibrium pattern in an old-growth *Pseudotsuga-Tsuga* forest. Ecology **95(8)**, 2047-2054.

Lutz, J.A., Matchett, J.R., Tarnay, L.W., Smith, D.F., Becker, K.M.L., Furniss, T.J. & Brooks, M.L. 2017. Fire and the distribution and uncertainty of carbon sequestered as aboveground tree biomass in Yosemite and Sequoia & Kings Canyon National Parks. Land **6(10)**, 1-24.

Lutz, J.A., van Wagtendonk, J.W. & Franklin, J.F. (2009) Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA. Forest Ecology and Management **257(11)**, 2296-2307.

Martin, T.A., et al. (2001) Control of transpiration in a 220-year old *Abies amabilis* forest. Forest Ecology and Management **152**, 211–224.

Meakem, V., et al. (In Press) Role of tree size in moist tropical forest carbon cycling and water deficit response. New Phytologist.

Memiaghe, H.M., Lutz, J.A., Korte, L., Alonson, A. & Kenfack, D. (2016) Ecological importance of small-diameter trees to the structure, diversity, and biomass of a tropical evergreen forest at Rabi, Gabon. PLoS ONE **11(5)**, e0154988.

Muller-Landau, H.C., et al. (2006) Comparing tropical forest tree size distributions with the predictions of metabolic ecology and equilibrium models. Ecology Letters **9**, 589–602.

Musavi, T., et al. (2017) Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity. Nature Ecology and Evolution 0048.

Oksanen. J, et al. (2017) vegan: Community Ecology Package. R package version 2.4-2.

Oksanen, J., Kindt, R. & Simpson, G.L. (2016). vegan3d: Static and Dynamic 3D Plots for the 'vegan' Package. R package version 1.0-1.

Ostertag, R., Inman-Narahari, F., Cordell, S., Giardina, C.P., Sack, L. (2014) Forest structure in low-diversity tropical forests: A study of Hawaiian wet and dry forests. PLoS ONE **9(8)**, e103268.

Pan, Y., Birdsley, R.A., Phillips, O.L. & Jackson, R.B. (2013) The structure, distribution, and biomass of the world's forests. Ann Rev Ecol Evol Sys **44**, 593-622.

R Development Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rambo, T. & North, M. (2009) Canopy microclimate response to pattern and density of thinning in a Sierra Nevada forest. Forest Ecology and Management **257**, 435–442.

Réjou-Méchain, M., et al. (2014) Local spatial structure of forest biomass and its consequences for remote sensing of carbon stocks. Biogeosciences **11**, 6827-6840.

Saez, E. & Zucman, G. (2016) Wealth inequality in the United States since 1913: evidence from capitalized income tax data. The Quarterly Journal of Economics **131(2)**, 519-578.

Sillett, S.C., Van Pelt, R., Kramer, R.D., Carroll, A.L. & Koch, G.W. (2015) Biomass and growth potential of *Eucalyptus regnans* up to 100 m tall. Forest Ecology and Management **348**, 78-91.

Slik, J.W., et al. (2013) Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. Global Ecology and Biogeography **22(12)**, 1261-1271.

Spies, T.A. & Franklin, J.F. (1991) The structure of natural young, mature and old-growth Douglas-fir forests in Oregon and Washington. Pages 91-109 in Wildlife and Management of Unmanaged Douglas-fir Forests. USDA Forest Service PNW-GTR-285, Portland, Oregon.

Swetnam, T.W. (1993) Fire history and climate change in giant sequoia groves. Science **262**, 885–889.

Van Mantgem, P.J., et al. (2009) Widespread increase of tree mortality rates in the western United States. Science **323**, 521-524.

Van Pelt, R., Sillett, S.C., Kruse, W.A., Freund, J.A. & Kramer, R.D. (2016) Emergent crowns and light-use complementarity lead to global maximum biomass and leaf area in *Sequoia sempervirens* forests. Forest Ecology and Management **375**, 279-308.

van Wagtendonk, J.W. & Moore, P.E. (2010) Fuel deposition rates of montane and subalpine conifers in the central Sierra Nevada, California, USA. Forest Ecology and Management **259**, 2122–2132.

West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. Science **276**, 122-126.

West, G.B., Enquist, B.J. & Brown, J.H. (2009) A general quantitative theory of forest structure and dynamics. Proc Natl Acad Sci USA **106(17)**, 7040-7045.

Winter, L.E., Brubaker, L.B., Franklin, J.F., Miller, E.A. & DeWitt, D.Q. (2002) Canopy disturbance over the five-century lifetime of an old-growth Douglas-fir stand in the Pacific Northwest. Canadian Journal of Forest Research **32**, 1057–1070.

Yoda, K., Kira, H., Ogawa, H. & Hozumi, K. (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. Journal of Biology of Osaka City University **14**, 107-129.

Data Accessibility

Data for plots in the ForestGEO network is available through the online portal at: http://www.forestgeo.si.edu

Biosketch

James A. Lutz is an Assistant Professor of Forest Ecology at Utah State University. He studies forest ecosystems to contribute to science-based conservation and management with particular emphasis on demography and spatial patterns of tree mortality and the effects of fire on old-growth forest communities.

Tucker J. Furniss is a Ph.D. student at Utah State University. He studies spatial patterns of trees and demographic processes.

The ForestGEO Network includes the senior investigators who collaborated on this research. The Smithsonian ForestGEO network conducts long-term, large-scale research on forests around the world. This collaborative effort seeks to increase scientific understanding of forest ecosystems, guide sustainable forest management and natural-resource policies, monitor the impacts of global change, and build capacity in forest science.

Data References

Allen, D., Vandermeer, J. & Perfecto, I. (2009) When are habitat patches really islands? Forest Ecology and Management **258**, 2033–2036.

Arias Garcia, J.C., Duque, A. & Cárdenas, D. (2009) Crecimiento Diamétrico de un bosque del nor occidente Amazónico. Revista Colombia Amazónica **2**, 57–64.

Bourg, N.A., McShea, W.J., Thompson, J.R., McGarvey, J.C. & Shen, X. (2013) Initial census, woody seedling, seed rain, and stand structure data for the SCBI SIGEO Large Forest Dynamics Plot. Ecology **94(9)**, 2111-2112.

Bunyavejchewin, S., Baker, P.J., LaFrankie, J.V. & Ashton, P.S. (2001) Stand structure of a seasonal dry evergreen forest at Huai Kha Khaeng Wildlife Sanctuary, western Thailand. Natural History Bulletin of the Siam Society **49**, 89-106.

Butt, N., et al. (2009) Initial results from establishment of a long-term broadleaf monitoring plot at Wytham Woods, Oxford, UK. University of Oxford Report.

Cao, M., et al. (2008) Xishuangbanna tropical seasonal rainforest dynamics plot: Tree distribution maps, diameter tables and species documentation. Yunnan Science and Technology Press, Kunming. 266 pp.

Chao, W-C., et al. (2010) Lowland rainforests in southern Taiwan and Lanyu, at the northern border of paleotropics and under the influence of monsoon wind. Plant Ecology **210**, 1–17.

Chen, L., et al. (2010) Community-level consequences of density dependence and habitat association in a subtropical broad-leaved forest. Ecology Letters **13**, 695-704.

Co, L., et al. (2004) Palanan Forest Dynamics Plot, Philippines. In: Tropical forest diversity and dynamism: Findings from a large-scale plot network (eds Losos E, Leigh E), pp. 574–584. University of Chicago Press, Chicago.

Condit, R., et al. (2004) Tropical forest dynamics across a rainfall gradient and the impact of an El Nino dry season. Journal of Tropical Ecology **20**, 51–72.

Georgiadis, N.J. (2011) Conserving Wildlife in African Landscapes: Kenya's Ewaso Ecosystem. Smithsonian Contributions to Zoology 1–123.

Gomes, A.C.S., et al. (2013) Local plant species delimitation in a highly diverse Amazonian forest: do we all see the same species? Journal of Vegetation Science **24**, 70-79

Hubbell, S.P., et al. (1999) Light gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science **283**, 554-557.

Kenfack, D., Thomas, D.W., Chuyong, G.B. & Condit, R. (2007). Rarity and abundance in a diverse African forest. Biodiversity Conservation **16**, 2045-2074.

Janík, D., et al. (2016) Tree spatial patterns of *Fagus sylvatica* expansion over 37 years. Forest Ecology and Management **375**, 134–145.

Johnson, D.J., et al. (2014) Conspecific negative density-dependent mortality and the structure of temperate forests. Ecology **95**, 2493-2503.

LaFrankie, J.V., Davies, S.J., Wang, L.K., Lee, S.K. & Lum, S.K.Y. (2005) Forest trees of Bukit Timah: Population ecology in a tropical forest fragment. Simply Green, Singapore. 178 pp.

LaManna, J.A., Walton, M.L., Turner, B.L. & Myers, J.A. (2016) Negative density dependence is stronger in resource-rich environments and diversifies communities when stronger for common but not rare species. Ecology Letters **19(6)**, 657-667.

Lee, H.S., et al. (2005) The 52-hectare Forest Research Plot at Lambir Hills, Sarawak, Malaysia: Tree distribution maps, diameter tables and species documentation. Forest Department Sarawak, The Arnold Arboretum-CTFS Asia Program, Smithsonian Tropical Research Institute, Kuching, Sarawak, Malaysia.

Lin, Y-C., Chang, L-W., Yang, K-C., Wang, H-H. & Sun, I-F. (2011) Point patterns of tree distribution determined by habitat heterogeneity and dispersal limitation. Oecologia **165**, 175–184.

Makana, J., et al. (2004) Ituri Forest Dynamics Plot, Democratic Republic of Congo. In: Tropical forest diversity and dynamism: Findings from a large-scale plot network (eds Losos E, Leigh E), pp. 492–505. University of Chicago Press, Chicago.

Manokaran, N., et al. (2004) Pasoh Forest Dynamics Plot, Malaysia. In: Tropical forest diversity and dynamism: Findings from a large-scale plot network (eds Losos E, Leigh E), pp. 585–598. University of Chicago Press, Chicago.

McMahon, S.M. & Parker, G.G. (2014) A general model of intra-annual tree growth using dendrometer bands. Ecology and Evolution **5(2)**, 243-254.

Oliveira, A.A., et al. (2014) Habitat specialization and phylogenetic structure of tree species in a coastal Brazilian white-sand forest. Journal of Plant Ecology **7**, 134–144.

Orwig, D.A., Foster, D.R. & Ellison, A.M. (2015) Harvard Forest CTFS-ForestGEO Mapped Forest Plot since 2014. Harvard Forest Data Archive: HF253. Available online:http://harvardforest.fas.harvard.edu:8080/exist/apps/datasets/showData.html?id=hf253

Su, S.H., Hsieh, C.F., Chang-Yang, C.H., Lu, C.L. & Guan, B.T. (2010) Micro-topographic differentiation of the tree species composition in a subtropical submontane rainforest in northeastern Taiwan. Taiwan Journal of Forest Science **25(1)**, 63-80.

Sukumar, R., Sathyanarayana, S., Dattaraja, H., John, R. & Joshi, N. (2004) Mudumalai Forest Dynamics Plot, India. In: Tropical forest diversity and dynamism: Findings from a large-scale plot network (eds Losos E, Leigh E), pp. 551–563. University of Chicago Press, Chicago.

Valencia, R., et al. (2004) Yasuni Forest Dynamics Plot, Ecuador. In: Tropical forest diversity and dynamism: Findings from a large-scale plot network (eds Losos E, Leigh E), pp. 609–620. University of Chicago Press, Chicago.

Vallejo, M., Samper, C., Mendoza, H. & Otero, J. (2004) La Planada Forest Dynamics Plot, Colombia. In: Tropical forest diversity and dynamism: Findings from a large---scale plot network (eds Losos E, Leigh E), pp. 517–526. University of Chicago Press, Chicago.

Vincent, J.B., Henning, B., Saulei, S., Sosanika, G. & Weiblen, G.D. (2014) Forest carbon in lowland Papua New Guinea: local variation and the importance of small trees. Austral Ecology **40**, 151-159.

Wang, X., et al. (2011) Spatial patterns of tree species richness in two temperate forests. Journal of Ecology **99**, 1382-1393.

Wu, S-H., et al. (2011) Kenting Karst Forest Dynamics Plot: tree species characteristics and distribution patterns. Taipei: Taiwan Forestry Research Institute. 306 p.

Xu, H., et al. (2015) Community characteristics of a 60 ha dynamics plot in the tropical montane rain forest in Jianfengling, Hainan Island. Biodiversity Science **23**, 192–201.

Yin, D. & He, F. (2014) A simple method for estimating species abundance from occurrence maps. Methods in Ecology and Evolution **5**, 336–343.

Zimmerman, J.K., Comita, L.S., Thompson, J., Uriarte, M. & Brokaw, N. (2010) Patch dynamics and community metastability of a subtropical forest: compound effects of natural disturbance and human land use. Landscape Ecology **25**, 1099-1111.