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RESEARCH PAPER

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# Global importance of large-diameter trees

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## Abstract

**Aim:** To examine the contribution of large-diameter trees to biomass, stand structure, and species richness across forest biomes.

**Location:** Global.

**Time period:** Early 21st century.

**Major taxa studied:** Woody plants.

**Methods:** We examined the contribution of large trees to forest density, richness and biomass using a global network of 48 large (from 2 to 60 ha) forest plots representing 5,601,473 stems across 9,298 species and 210 plant families. This contribution was assessed using three metrics: the largest 1% of trees $\geq$ 1 cm diameter at breast height (DBH), all trees $\geq$ 60 cm DBH, and those rank-ordered largest trees that cumulatively comprise 50% of forest biomass.

**Results:** Averaged across these 48 forest plots, the largest 1% of trees $\geq$ 1 cm DBH comprised 50% of aboveground live biomass, with hectare-scale standard deviation of 26%. Trees $\geq$ 60 cm DBH comprised 41% of aboveground live tree biomass. The size of the largest trees correlated with total forest biomass ($r^2 = .62$, $p < .001$). Large-diameter trees in high biomass forests represented far fewer species relative to overall forest richness ($r^2 = .45$, $p < .001$). Forests with more diverse large-diameter tree communities were comprised of smaller trees ($r^2 = .33$, $p < .001$). Lower large-diameter richness was associated with large-diameter trees being individuals of more common species ($r^2 = .17$, $p = .002$). The concentration of biomass in the largest 1% of trees declined with increasing absolute latitude ($r^2 = .46$, $p < .001$), as did forest density ($r^2 = .31$, $p < .001$). Forest structural complexity increased with increasing absolute latitude ($r^2 = .26$, $p < .001$).

**Main conclusions:** Because large-diameter trees constitute roughly half of the mature forest biomass worldwide, their dynamics and sensitivities to environmental change represent potentially large controls on global forest carbon cycling. We recommend managing forests for conservation of existing large-diameter trees or those that can soon reach large diameters as a simple way to conserve and potentially enhance ecosystem services.

**KEYWORDS**

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

## 1 | INTRODUCTION

Concentration of resources within a few individuals in a community is a pervasive property of biotic systems (West, Brown, & Enquist, 1997), whether marine (Hixon, Johnson, & Sogard, 2014), terrestrial (Enquist, Brown, & West, 1998) or even anthropogenic (Saez & Zucman, 2016). The concentration of total forest biomass in a few large-diameter trees is no exception (Pan, Birdsley, Phillips, & Jackson, 2013). Large-diameter trees in forests take many decades or even centuries to develop, but human or natural disturbances can decrease their abundance, rapidly changing forest structure (Allen et al., 2010; Lindenmayer, Laurance, & Franklin, 2012; Lutz, van Wagtendonk, & Franklin, 2009; van Mantgem et al., 2009).

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 (Bastin et al., 2015; Brown et al., 1995; Clark & Clark, 1996; Lutz, Larson, Swanson, & Freund, 2012) 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 (Binkley, Stape, Bauerle, & Ryan, 2010), 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, Phillips, Monteagudo, Torres-Lezama, & Vásquez Martínez, 2009; Das, Stephenson, & Davis, 2016). Large-diameter trees (and large-diameter snags and large-diameter fallen woody debris) make the structure of primary forests and mature secondary forests unique (Spies & Franklin, 1991). Large-diameter trees occur at low stem densities, yet influence spatial patterns over long inter-tree distances (Das, Larson, & Lutz, 2018; Enquist, West, & Brown, 2009; Lutz et al., 2014). Consequently, to elucidate the patterns, mechanisms and consequences of large-diameter tree ecology requires sample plots $\geq$ 1 ha (Das, Battles, Stephenson, & van Mantgem, 2011; Lutz, 2015; Réjou-Méchain et al., 2014).

Changes in climate, disturbance regimes and logging are accelerating the decline of large-diameter trees (e.g., Bennett, McDowell, Allen, & Anderson-Teixeira, 2015; Lindenmayer & Laurence, 2016; Lindenmayer et al., 2012). The dynamics of large-diameter trees is dependent on at least two factors: (a) presence of species capable of attaining a large size, and (b) conditions, including disturbance regimes, that permit the development of large-diameter individuals. If the species richness of the large-diameter assemblage 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.

Surprisingly, the specific roles of large-diameter trees are not well anchored in two widely referenced theories of global vegetation. Both the unified neutral theory of biodiversity (Hubbell, 2001) and metabolic scaling theory (West, Enquist, & Brown, 2009) propose that plants have a degree of functional equivalency. The unified neutral theory makes predictions about the rank-order abundance of species in a forest, but it makes no specific predictions about the rank order of large-diameter species or even if large-diameter individuals are members of common or rare species. Metabolic scaling theory does predict the abundance of large-diameter trees, and empirical tests of the theory for more abundant, smaller-diameter individuals are generally good. However, metabolic scaling theory often tends to under-predict the abundance of large-diameter trees in temperate forests (Anderson-Teixeira, McGarvey, et al., 2015; their fig. 2) and rather over-predict the abundance of large-diameter trees in tropical forests (Muller-Landau et al., 2006; their table 2) and in some temperate forests (Lutz et al., 2012; their fig. 2). Metabolic scaling theory also advances its predictions as continuous functions, and the departure from theory (i.e., the spatial variation) at discrete grain sizes remains unquantified. Accordingly, these theories alone cannot fully explain global patterns of forest species diversity or the larger portion of the size distribution (Coomes, Duncan, Allen, & Truscott, 2003; LaManna et al., 2017; Lutz et al., 2012; Muller-Landau et al., 2006).

However, studies do 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; Ostertag, Inman-Narahari, Cordell, Giardina, & Sack, 2014; Slik et al., 2013). To the extent that forests share structural attributes either globally or regionally, our ability to model forest change may be improved by focusing on global patterns in structure rather than individual species life-history traits. We expected that latitudinal trends in the concentration of biomass in the largest trees would follow trends in forest

density (with more stems in the largest diameter classes, relative biomass should be higher). We also expected that relative richness of the large-diameter cohort would be lower in forests with high stem density because the large trees would be a smaller fraction of stems and thus a smaller fraction of species. Our principal hypothesis was that only a small proportion of the largest trees are responsible for the preponderance of forest biomass, and that the abundance and variation of these large-diameter trees reflect latitudinal gradients of forest structure. Specifically we set out to ask four interrelated questions:

1. Are there global relationships between large-diameter trees (defined various ways) and forest biomass?
2. Does the richness of the large-diameter cohort depend on the richness or biomass of the forest?
3. Are there latitudinal gradients in forest density, biomass, concentration of biomass, or structural complexity?
4. Are large-diameter trees members of common or rare species in forests?

## 2 | MATERIALS AND METHODS

We used data from the Forest Global Earth Observatory (ForestGEO; Anderson-Teixeira, Davies, 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 (Figure 1, Supporting Information Table S3.1). Forests included in the ForestGEO network include undisturbed primary forests or older secondary forests meeting the United Nations Food and Agricultural Organization definition of forest (trees $>$ 5 m tall and canopy cover $>$ 10% occurring in patches $>$ 0.5 ha; Forest Resource Assessment, 2015). The ForestGEO plots feature consistent field methods (Condit, 1998) and data representation (Condit, Lao, Singh, Esufali, & Dolins, 2014). Importantly, these plots include all standing woody stems $\geq$ 1 cm diameter at breast height (1.3 m along the main stem; DBH). A representativeness analysis showed that the ForestGEO includes most major forest types of the world, albeit with some exceptions (see Anderson-Teixeira, Davies, et al., 2015 for details). We analysed 48 plots in primary or older secondary forest spanning 86.4° of latitude (Figure 1), covering 1,278 ha (median size 24 ha), and including 5,601,473 stems representing 9,298 species and 210 plant families (Figure 1, Table 1, Supporting Information Table S3.1).

There is no universal definition for what constitutes a large-diameter tree. Generally, a large-diameter tree is of reproductive stature, is tall enough to reach the upper canopy layer of the forest, and 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 DBH (Baltzer, Venes, Chasmer, Sniderhan, & Quinton, 2014). In productive temperate or tropical forests, a large-diameter tree may be $>$ 100 cm DBH (Lutz et al., 2012; Lutz, Larson, Freund, Swanson, & Bible, 2013). To compare dissimilar ecosystems, we used three metrics for defining large diameter trees:

1. 99th percentile diameter (the largest 1% of trees $\geq$ 1 cm DBH 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.

We calculated the density, basal area, and biomass of stems $\geq$ 1 cm DBH and tabulated them within each square hectare (100 m $\times$ 100 m)


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

of the 48 plots. Because the distribution of large-diameter trees within forests is often not homogeneous (e.g., Lutz et al., 2013), we used the 1-ha scale to capture variation in structure across the plots 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 (absolute latitude $\leq$ 23.5°) by the methods of Chave et al. (2014), which uses a generic equation to predict biomass based on diameter, climate and wood density. The Chave et al. (2014) equations are of the form:

$$AGB = \exp[-1.803 - 0.976E + 0.976\ln(\rho) + 2.676\ln(DBH) - 0.0299\ln(DBH)^2] \quad (1)$$

where $\rho$ is wood density and $E$ is the environmental parameter. Wood specific gravity was taken from Zanne et al. (2009), and we used the values hierarchically, taking species-specific values where defined, then genus-specific values, then family-specific values. If there was no wood specific gravity data for the plant family, or if the stem was unidentified, we used the global average of 0.615 g/cm$^3$. Values for the environmental parameter $E$ are listed in Supporting Information Table S3.1.

We calculated biomass for cold and temperate plots (absolute latitude $>$ 23.5°) using the composite taxa-specific equations of Chojnacky, Heath, & Jenkins (2014). Those equations are of the form

$$\ln(\text{biomass}) = \beta_0 + \beta_1 \times \ln(\text{DBH}) \quad (2)$$

where $\beta_0$ and $\beta_1$ are listed in Chojnacky et al. (2014; their table 5).

Species not represented by specific biomass equations were defaulted to an equation or wood density value for the genus or the family. We used site-specific allometric equations for Palamanui (Ostertag et al., 2014), Laupahoehoe (Ostertag et al., 2014), Lanjenchi (Aiba & Nakashizuka, 2009) and Changbaishan (Wang, 2006).

We further analysed the diameter–abundance relationships of each plot based on six tree diameter classes (1 cm $\leq$ DBH $<$ 5 cm, 5 cm $\leq$ DBH $<$ 10 cm, 10 cm $\leq$ DBH $<$ 30 cm, 30 cm $\leq$ DBH $<$ 60 cm, 60 cm $\leq$ DBH $<$ 90 cm and DBH $\geq$ 90 cm). Diameter classes were selected to include recognized differences in tree life-history traits (Memiaghe, Lutz, Korte, Alonso, & Kenfack, 2016). We performed non-metric multidimensional scaling (NMDS; Kenkel & Orloci, 1986) analyses on the density of each diameter class of each 100 m $\times$ 100 m area. We used the Bray–Curtis dissimilarity index and performed the NMDS ordinations in three dimensions using the version 2.4-4 of the vegan package (Oksanen, Kindt, & Simpson, 2016) in R version 3.3.1 (R Development Core Team, 2016). We used the three-dimensional coordinates of each 1-ha in NMDS space to create a metric for structural complexity. For the 1-ha structural ordination values for each plot, we fit a one standard deviation ellipsoid using the orglellipse function from the vegan3d package (Oksanen, 2017). We then calculated the volume of that ellipsoid as a metric of structural difference (i.e., complexity) to compare the relative differences between 100 m $\times$ 100 m areas within the plot.

To examine commonness of species that can reach large diameters, we ranked all species according to their abundance within each plot. We then identified large-diameter species as species that had $\geq$ 1 individual with a DBH greater than or equal to the large-diameter threshold, and determined the species rank for each of these large-diameter species (i.e., if the third most abundant species was a 'large-diameter species', it would receive rank = 3). We then used the median rank for all large-diameter species ranks within each plot, and normalized this value across plots by dividing rank by the total number of species (i.e., in a plot with 60 species, a median rank of 18 becomes 0.3).

To validate our results, 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 with replacement (from the available quadrats), beginning with a 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:

$$\text{Percent difference} = \left(\text{abs}\left(\text{mean}_n - \text{mean}_{\text{plot}}\right) + SD_n\right)/\text{mean}_{\text{plot}} \quad (3)$$

where $\text{mean}_n$ is the mean of a random sampling of $n$ quadrats, $\text{mean}_{\text{plot}}$ is the mean for the entire plot, and $SD_n$ is the standard deviation for the random sample of $n$ quadrats.

## 3 | RESULTS

Average stem density in the plots ranged from 608 stems/ha (Mudumalai, India) to 12,075 stems/ha (Lanjenchi, Taiwan) with most high-density plots occurring in the tropics (Tables 1 and 2, plot characteristics in Table S3.1 and Appendix). Aboveground live tree biomass ranged from 13 Mg/ha (Mpala, Kenya) to 559 Mg/ha (Yosemite, USA). The biomass of trees $\geq$ 60 cm DBH ranged from 0 Mg/ha (Mpala, Kenya, Palamanui, USA, and Scotty Creek, Canada) to 447 Mg/ha (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 the 1-ha scale was high globally (Supporting Information Tables S3.2 and S3.3), and coefficient of variation (CV) 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 overall forest biomass ($r^2 = .62$, $p < .001$; Figure 2a). This relationship held for all three of our definitions for large-diameter trees (Figure 2a–c). The relationship for large-diameter threshold was strongest, but the biomass of the largest 1% of trees also predicted total biomass ($r^2 = .35$, $p < .001$; Figure 2b) as did the density of stems $\geq$ 60 cm DBH ($r^2 = .49$, $p < .001$; Figure 2c). Results based on basal area were similar to those for biomass (Supporting Information Figure S1.1). There was a negative relationship between large-diameter species richness and total biomass ($r^2 = .45$, $p < .001$; Figure 2d), which was consistent with the negative relationship between large-diameter threshold and large-diameter richness ($r^2 = .33$, $p < .001$; Figure 2e) and the negative relationship between large-diameter richness and the biomass of the largest 1% of trees ($r^2 = .61$, $p < .001$; Figure 2f). In other words, plots with high biomass

**TABLE 1** Structural characteristics of global forests

| Plot | Large-diameter threshold (cm) | Density (stems/ha) (*SD*) | Biomass (Mg/ha) (*SD*) | Total species (*n*) | Large-diameter species (*n*) | Large-diameter richness (%) | Biomass of the 1% (%) | Density ≥ 60 cm DBH (stems/ha) |
|---|---|---|---|---|---|---|---|---|
| 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[a] | 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[a] | 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[a] | 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[a] | 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[a] | 45.4 | 1601 (751) | 176 (16) | 45 | 18 | 40 | 24 | 10 |
| Wytham Woods[a] | 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[a] | 35.5 | 3104 (2600) | 260 (66) | 55 | 17 | 31 | 23 | 7 |
| Luquillo | 35.5 | 2903 (626) | 283 (53) | 133 | 47 | 35 | 39 | 12 |

(Continues)

**TABLE 1** (Continued)

| Plot | Large-diameter threshold (cm) | Density (stems/ha) (*SD*) | Biomass (Mg/ha) (*SD*) | Total species (*n*) | Large-diameter species (*n*) | Large-diameter richness (%) | Biomass of the 1% (%) | Density ≥ 60 cm DBH (stems/ha) |
|---|---|---|---|---|---|---|---|---|
| Heishiding | 34.5 | 5277 (706) | 149 (27) | 213 | 59 | 28 | 43 | 12 |
| Wabikon[a] | 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[a] | 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 |

*Note*. Values for density and biomass include trees ≥ 1 cm diameter at breast height (DBH) within each square hectare (100 m × 100 m) of the plots, with the mean and *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 ≥ 1 cm DBH. Plots are listed by declining large-diameter threshold. For additional details of the plots and forest characteristics, see Supporting Information Tables S3.1-S3.3 and references in the Appendix.

[a]Mature secondary forest. SERC - Smithsonian Environmental Research Center; SCBI - Smithsonian Conservation Biology Institute.

had high large-diameter thresholds and relatively low species richness within 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, 45% 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 the biomass of the 48 plots was contained within trees ≥ 47.7 cm DBH). 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 ($r^2 = .31$, $p < .001$; Figure 3a), as did the proportion of tree biomass accounted for by the largest 1% of trees ($r^2 = .46$, $p < .001$; Figure 3c), following our expectations and partially a reflection of the higher stem densities in the tropics (Figure 3a, Table 1, Supporting Information Table S3.2). However, latitudinal gradients were not present for biomass (Figure 3b) or the large-diameter threshold (Figure 3d).

The three metrics for large-diameter trees were not perfectly correlated (Supporting Information Figure S1.2). The large-diameter threshold and the density of stems ≥ 60 cm DBH had a linear relationship ($r^2 = .80$, $p < .001$), even though some forests did not have trees ≥ 60 cm DBH. The relationship between the biomass of the 1% of largest diameter trees and both the density of stems ≥ 60 cm DBH and the large-diameter threshold was significant for tropical plots but not for temperate plots.

NMDS ordinations of the abundance of trees in the six diameter classes in each 100 m × 100 m area showed that tropical forests have a higher degree of structural similarity than temperate or boreal forests

**TABLE 2** The effect of geographical region on tree density and biomass and their variation at 1-ha scale and the abundance of large-diameter trees as measured by the three metrics of proportion of biomass in the largest 1% of trees, density of trees ≥ 60 cm diameter at breast height (DBH), and large-diameter threshold

| Zone | Plots (*n*) | Density (trees/ ha) | Density *SD* | Density CV | Biomass (Mg/ha) | Biomass *SD* | Biomass CV | Biomass of the 1% (%) | Density trees ≥ 60 cm DBH (trees/ha) | Large-diameter threshold (cm) |
|---|---|---|---|---|---|---|---|---|---|---|
| Cold temperate/boreal | 6 | 2,281 | 1,114 | 47 | 174 | 98 | 24 | 23 | 11 | 37 |
| Temperate | 16 | 3,339 | 2,193 | 31 | 266 | 126 | 18 | 38 | 24 | 53 |
| All Tropics | 26 | 5,735 | 1,072 | 18 | 278 | 57 | 20 | 61 | 16 | 44 |
| Tropical Africa | 5 | 6,949 | 2,317 | 29 | 305 | 172 | 27 | 76 | 16 | 48 |
| Tropical Asia | 10 | 5,767 | 3,149 | 16 | 330 | 124 | 21 | 53 | 18 | 47 |
| Tropical Latin America | 8 | 4,339 | 1,410 | 12 | 280 | 27 | 15 | 54 | 13 | 42 |
| Tropical Oceania | 3 | 5,884 | 2,162 | 15 | 198 | 152 | 18 | 61 | 17 | 38 |

*SD* = standard deviation; CV = coefficient of variation.

*Note*. The *SD* of density and the *SD* of biomass represent the within-region (between-plot) variation. The CV of density and CV of biomass represent the average of the individual plot 1-ha CVs, with each plot weighted equally.

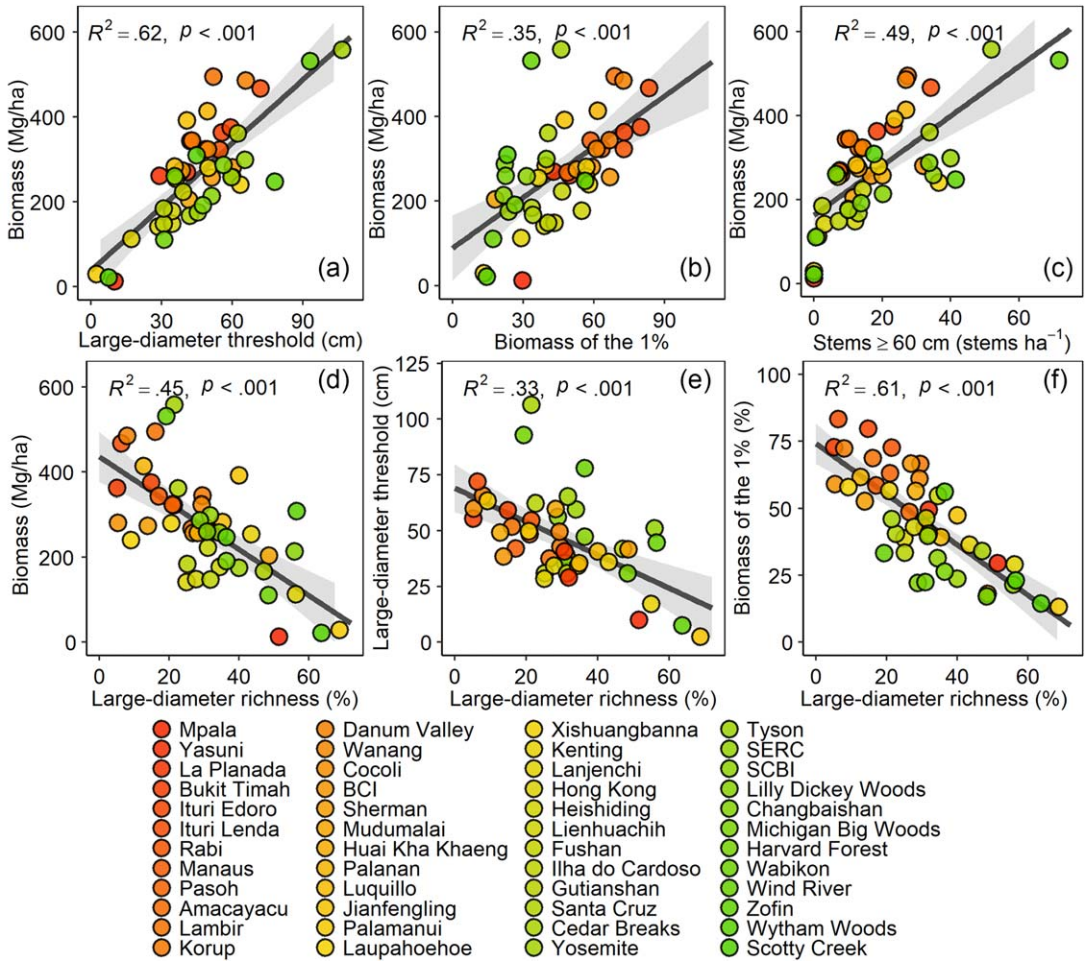


**FIGURE 2** Contribution of large-diameter trees to forest structure of 48 large forest plots. Aboveground live tree biomass increases with increasing large-diameter threshold (a). The large-diameter threshold reflects the tree diameter that segments biomass into two equal parts. Below the large-diameter 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 also increases with the concentration of biomass in the largest 1% of trees (b) and the density of stems ≥ 60 cm diameter at breast height (DBH; c). Large-diameter richness declines with increasing biomass (d), which is consistent with the declining relationship between large-diameter threshold and large-diameter richness (e). The concentration of biomass in the largest 1% of trees has a strong negative relationship with large-diameter richness (f). Colours indicate increasing absolute latitude from red to green. Grey areas around regression lines indicate 95th percentile confidence intervals

based on their position in the ordination (Figure 4a,b). The 1-ha scale variation for tropical plots also showed a high degree of similarity both globally (clustering and high overlap of red ellipses in Figure 4c,d) and locally (smaller size of individual red ellipses). The volumes occupied by the 1-ha NMDS points of temperate plots, conversely, covered a wide range in ordination space, indicating greater structural variability both among and within the plots (greater size and dispersion of green ellipses in Figure 4c,d, three-dimensional animation in Supporting Information Figure S2). This phenomenon was also mirrored by coefficients of variation of density and biomass of 1-ha quadrats, which differed among 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 Figure 4a,b; Supporting Information Table S3.2) 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, limited soil development and with limited species complement). The structural complexity of forests (variation in abundance of the six diameter classes) at 1-ha scale increased with increasing absolute latitude (Figure 5a).

Large-diameter trees consisted primarily of common species (rank < 0.5; Figure 5b), and rarer species reached large diameter in plots with higher large-diameter richness ($r^2 = .17$; $p = .002$). The absolute numbers of species that reached the local large-diameter threshold ranged from two in tropical Laupahoehoe, USA, to 343 in Yasuni, Ecuador (Table 1). Tropical plots generally had > 25 species reaching the large-diameter threshold (minimum nine species in Cocoli, Panama). Temperate plots generally had < 10 species that reached the large-diameter threshold (maximum 25 species in Smithsonian Ecological Research Center (SERC), USA). On a percentage basis, large-diameter richness ranged from 5% (Cocoli, Panama and Bukit Timah, Singapore) to 69% (Palamanui, USA). The relative

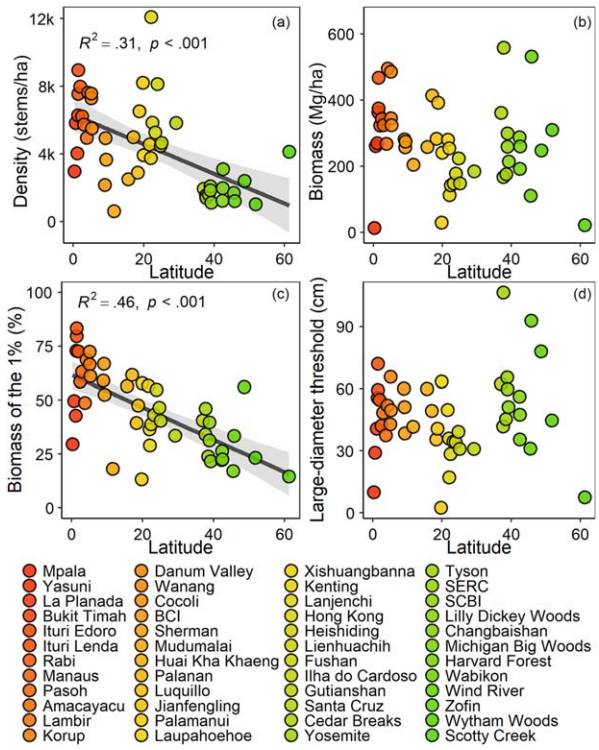


**FIGURE 3** Gradients of forest structural attributes by absolute latitude for 48 forest plots in the ForestGEO network. Absolute latitudinal gradients in density (a) and concentration of biomass in the largest 1% of trees (c) were significant. The relationships for biomass (b; $r^2 = .04$, $p = .106$) and the large-diameter threshold (d; $r^2 = .01$, $p = .551$) were not. Colours indicate increasing absolute latitude from red to green. Grey areas around regression lines indicate 95th percentile confidence intervals

richness of the large-diameter assemblage was highest in plots with low biomass, while plots with high biomass had a lower proportion of richness represented by the large-diameter trees (Figure 2d, 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 DBH) had a higher proportion of species represented in the large-diameter assemblage (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%).

## 4 | DISCUSSION

The relationship between the large-diameter threshold and overall biomass (Figure 2a) suggests that forests cannot sequester large amounts of aboveground carbon without large trees, irrespective of the richness or density of large-diameter trees. Species capable of attaining large diameters are relatively few (Figure 2) but individuals of these species are relatively abundant (Figure 5b). The relationships among biomass and richness across plots held over a range of stem densities (608 to 12,075 stems/ha) and among trees of varying wood densities (0.10 to 1.08 g/cm$^3$). A linear relation of biomass to large-diameter threshold (Figure 2a) best explained the correlation among the 48 plots, although we would expect an upper limit based on maximum tree heights (Koch, Sillett, Jennings, & Davis, 2004) or biomass (Sillett, Van Pelt, Kramer, Carroll, & Koch, 2015; Van Pelt, Sillett, Kruse, Freund, & Kramer, 2016). The generally high proportion of biomass represented by the largest 1% of trees reinforces the importance of these individuals to carbon sequestration and productivity (e.g., Stephenson et al., 2014). Larger numbers of small- and medium-diameter trees cannot provide equivalent biomass to a few large-diameter trees, although small and medium sized trees can contribute significantly to carbon cycling (Fauset et al., 2015; Meakem et al., 2017). The implication from scaling theory (West et al., 2009) is that large-diameter trees are taller and have heavier crowns, and occupy growing space not available to smaller trees (i.e., at the top of the canopy; Van Pelt et al., 2016; West et al., 2009).

Temperate forests featured a higher density of trees ≥ 60 cm DBH (Table 1), consistent with the presence of the very largest species of trees in cool, temperate forests (Sillett et al., 2015; Van Pelt et al., 2016). Temperate forests also exhibited considerably lower densities of small trees (e.g., 1 cm ≤ DBH < 5 cm; Supporting Information Table S3.2) and lower total stem density. In tropical forests, high overall stem densities are mostly due to trees with diameters ≤ 10 cm DBH (Table 2, Supporting Information Table S3.2). Metabolic scaling theory does predict the diameter–abundance relationship throughout much of the middle of the diameter range in many forest types (Anderson-Teixeira, McGarvey, et al., 2015; Lutz et al., 2012; Muller-Landau et al., 2006). However, the dichotomy between temperate forests and tropical forests, where temperate forests have lower densities of small trees and higher densities of large trees (and tropical forests the reverse), reinforces the need to examine departures from the theory's predictions. In tropical forests, the lower proportional richness of large-diameter trees likely has at least two explanations. First, tropical forests contain many more stems per ha (Supporting Information Table S3.2) with much higher small-diameter understorey diversity (LaFrankie et al., 2006). Secondly, not all of the species capable of reaching large diameters in that region may be present even in the large ForestGEO plots, and thus even the extensive ForestGEO network may have sampling limitations.

The grouping of plots with only small-diameter trees (Figure 4a) shows that forests in markedly different environments can exhibit convergent structure based on different limiting factors. Large-diameter trees can be abundant in any region (Supporting Information Table S3.1), but different factors may limit the ability of an ecosystem to support a high level of aboveground live biomass. In addition to environmental limits, ecosystems that are environmentally quite productive in terms of annual growth may be limited by frequent, severe disturbance (e.g., typhoons in Fushan and hurricanes in Luquillo). Finally, the regional species pool may not contain species that can attain large diameters in the local combination of climate and resource availability (e.g., Palamanui, USA). The higher levels of structural complexity at 1-ha scales in temperate forests may be due to higher proportions of the forests where small trees predominate and large-diameter trees are

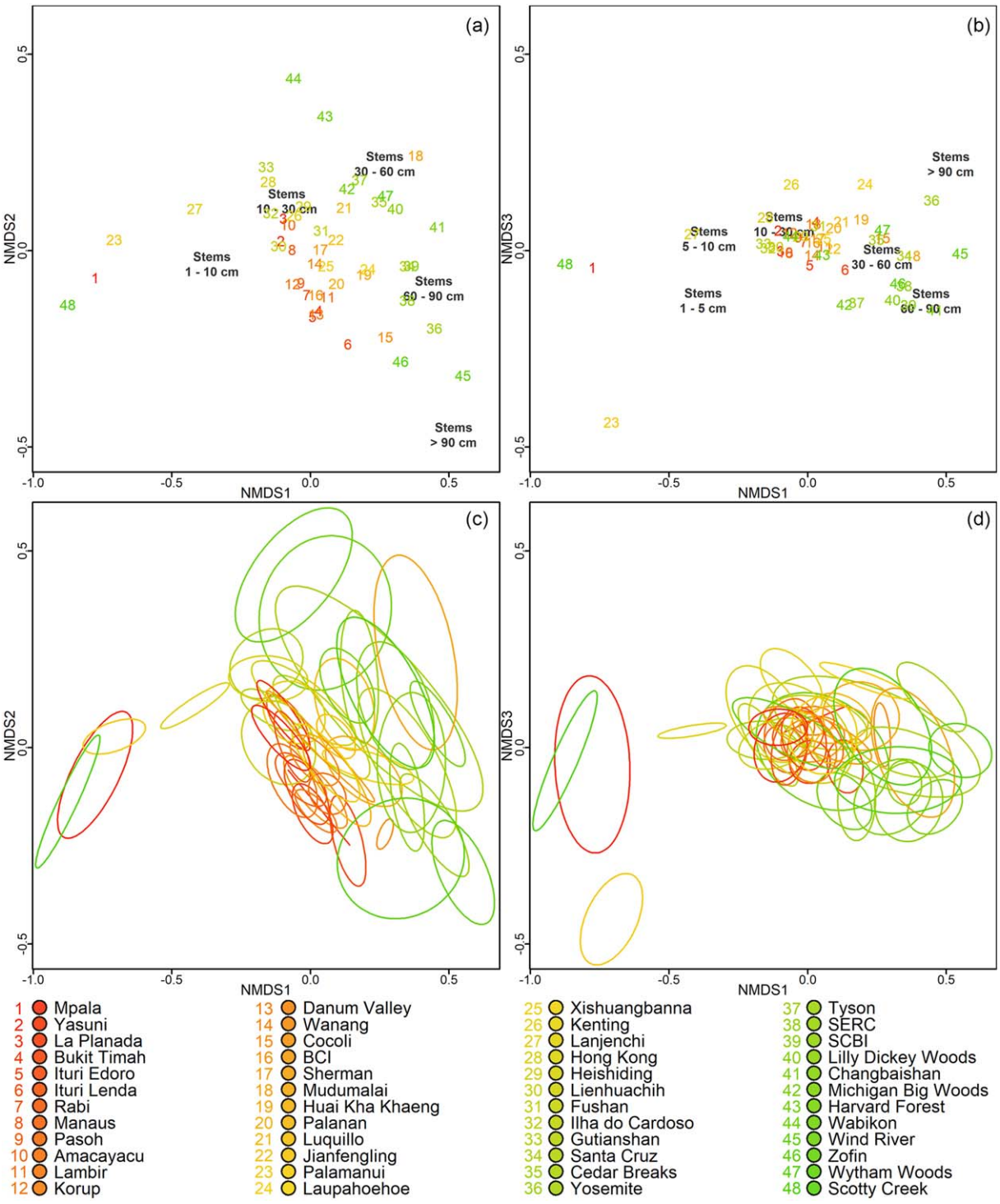


**FIGURE 4** Three-dimensional non-metric multidimensional scaling (NMDS) results for density of trees organized into six diameter classes in 1260, 100 m × 100 m hectares of 48 forest plots in the ForestGEO network (a, b). The structural classes (diameter bins) used in the NMDS ordination are superimposed in black text (a, b). The within-plot variation in structure for each plot is shown by depiction of the *SD* ellipses of the individual 100 m × 100 m hectares within each plot [c, d; where (c) reflects the variation of NMDS1 versus NMDS2 (a) and (d) reflects the variation of NMDS1 versus NMDS3 (b)]. Ordination stress = 0.047. Colours indicate increasing absolute latitude from red to green, with plot centroids numbered (a, b). See Supporting Information Figure S2 for a three-dimensional animation of the structural ordination

generally excluded (i.e., swamps, rocky outcrops), supported by the higher coefficient of variation of density in temperate and cold forests (Table 2). The trend of increasing structural complexity (i.e., 1-ha heterogeneity) with increasing absolute latitude (Figure 5a) may in fact be hump-shaped, with decreasing complexity at higher latitudes than the 61.3°N of the Scotty Creek, Canada, plot.

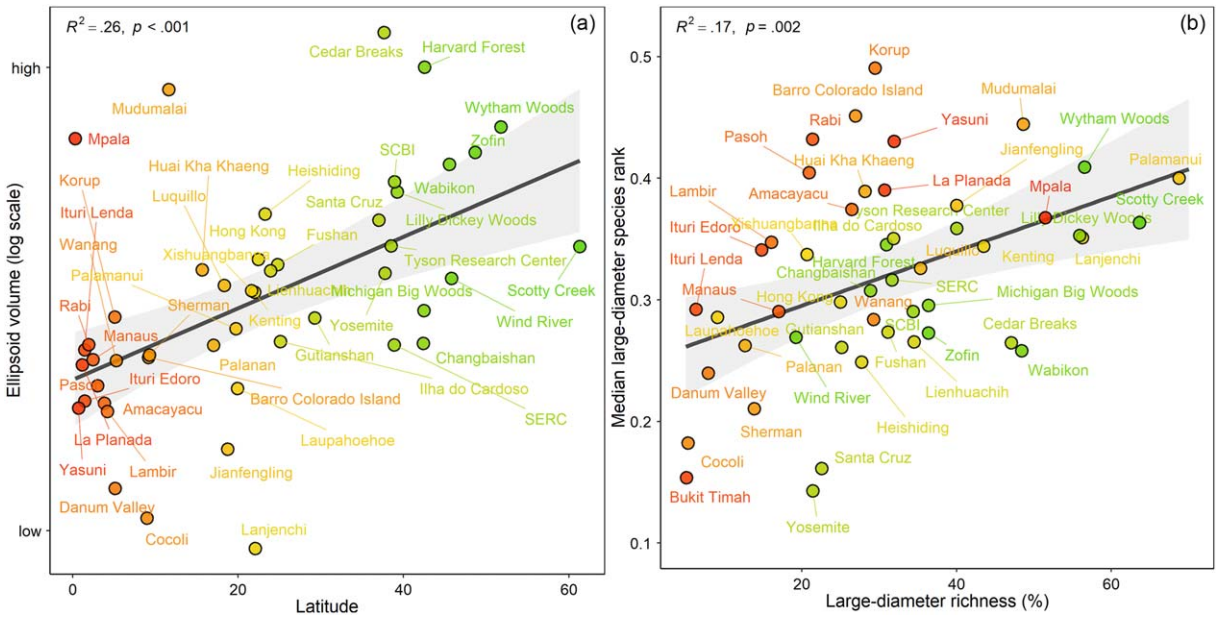


**FIGURE 5** The 1-ha scale structural complexity of 48 forest plots in the ForestGEO network as a function of absolute latitude (a). The metric of structural complexity is the volume of the three-dimensional ellipsoid generated from the non-metric multidimensional scaling (NMDS) ordination of abundance in structural classes (see Figure 4 for two-dimensional projections and Supporting Information Figure S2 for a three-dimensional animation). The rank order of large-diameter species in 48 forest plots (b). Rank order is normalized to the range from zero to one to compare plots with differing species richness. Lower proportions of large-diameter species rank correspond to more abundant species (median large-diameter species rank $< 0.5$ for all 48 forest plots). Species attaining large-diameters were the more common species in the forest plots. Colours indicate increasing absolute latitude from red to green

There is still considerable uncertainty as to what will happen to large-diameter trees in the Anthropocene when so much forest is being felled for timber and farming, or is being affected by climate change. Bennett et al. (2015) suggested that the current large-diameter trees are more susceptible to drought mortality than smaller-diameter trees. Larger trees, because of their height, are susceptible to sapwood cavitation and are also exposed to high radiation loads (Allen, Breshears, & McDowell, 2015; Allen et al., 2010), but vigorous large-diameter individuals may also still be sequestering more carbon than smaller trees (Stephenson et al., 2014). Both Allen et al. (2015) and Bennett et al. (2015) suggested that larger trees will be more vulnerable to increasing drought than small trees, and Luo and Chen (2013) suggested that although the rate of mortality of larger trees will continue to increase because of global climate change, smaller trees will experience more drought-related mortality. These last two conclusions need not be in conflict as the background mortality rates for smaller trees are higher than those of larger trees within mature and old-growth forests (Larson & Franklin, 2010). What remains generally unanswered is whether the increasing mortality rates of large-diameter trees will eventually be offset by regrowth of different individuals of those same (or functionally similar) species. Any reduction in temperate zone large-diameter tree abundance may be compounded by the low large-diameter tree diversity in temperate forests (temperate forests had high relative large-diameter richness, but low absolute large-diameter richness). Large-diameter tree richness in tropical forests suggests more resilience to projected climate warming in two ways. First, absolute 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 (Musavi et al., 2017). Secondly, the pool of species that can reach large diameters may have been undersampled in the plots used here, implying an even higher level of richness may exist in some forests than captured in these analyses.

The finding that large-diameter trees are members of common species groups (Figure 5b) contradicts the neutral theory's assumption of functional equivalency (Hubbell, 2001). Similarly the different structural complexity of forests worldwide (Figure 5a) contradicts the assumptions of universal size–abundance relationships of metabolic scaling theory (Enquist et al., 1998, 2009). The presence of a latitudinal gradient in forest density (Figure 3a) and the lack of a latitudinal gradient in forest biomass (Figure 3b) suggest that size–abundance relationships are not universal but depend on region or site conditions (Table 2).

Characterizing forest structural variation did require these large plots (Supporting Information Figure S1.3), a finding consistent with other studies examining forest biomass (Réjou-Méchain et al., 2014). 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). 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 homogeneous within forests (e.g., Table 2; Furniss, Larson, & Lutz, 2017; Lutz et al., 2012, 2013). 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 used for calculating each tree's biomass. Allometric equations can be imprecise for large-diameter trees, both because of their structural variability and the enormous sampling effort, and therefore our estimates of overall biomass could be off by ± 15% (Lutz et al., 2017).

Although temperate plots had much lower overall species diversity compared to the tropical plots, tropical plots had much more homogeneous structure, both within and across plots (Figure 4), potentially suggesting greater structural equivalency among the many species present. We found that the largest 1% of trees constitute 50% of the biomass (and hence, carbon), supporting our hypothesis of their significance, at least in primary forests or older secondary forests. The conservation of large-diameter trees in tropical and temperate forests is therefore imperative to maintain full ecosystem function, as the time necessary for individual trees to develop large sizes could preclude restoration of full ecosystem function for centuries following the loss of the oldest and largest trees (Lindenmayer et al., 2012). Clearly, areas that have been recently logged lack large-diameter trees, and therefore have less structural heterogeneity than older forests. That the largest individuals belong to relatively few common species in the temperate zone means that the loss of large-diameter trees could alter forest function – if species that can attain large diameters disappear, forests will feature greatly reduced structural heterogeneity (e.g., Needham et al., 2016), biomass, and carbon storage. In the tropical zones, the larger absolute numbers of species reaching large diameters may buffer those forests against structural changes. 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 maintenance of other ecosystem functions.

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## DATA ACCESSIBILITY

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

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## BIOSKETCHES

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**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.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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# APPENDIX

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## S1. Supplemental figures

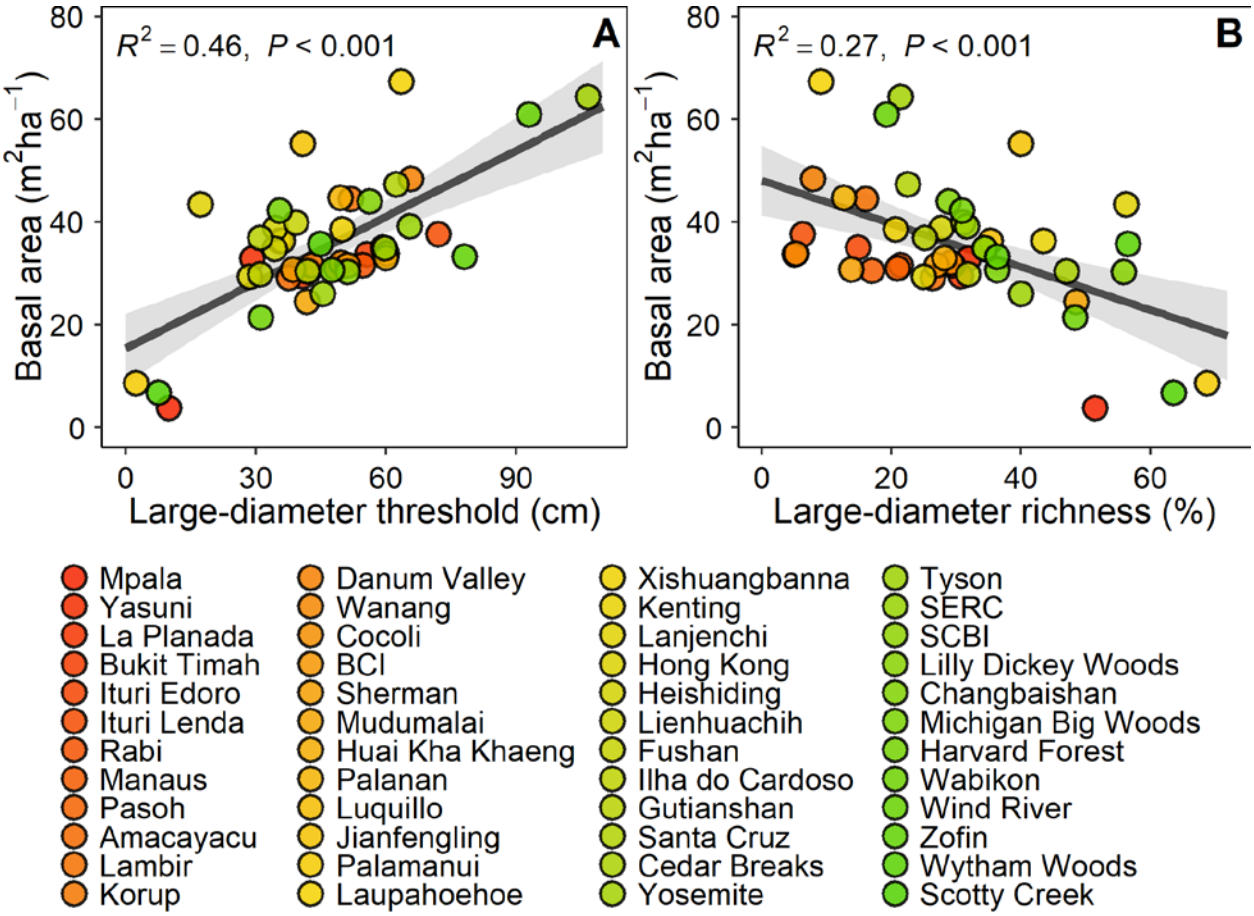


Fig. S1.1. The relationships among basal area and large-diameter threshold and large-diameter richness in 48 Smithsonian ForestGEO plots. This is corollary with Fig. 2, panels A and D, which show biomass instead of basal area. Colours indicate increasing absolute latitude from red to green.

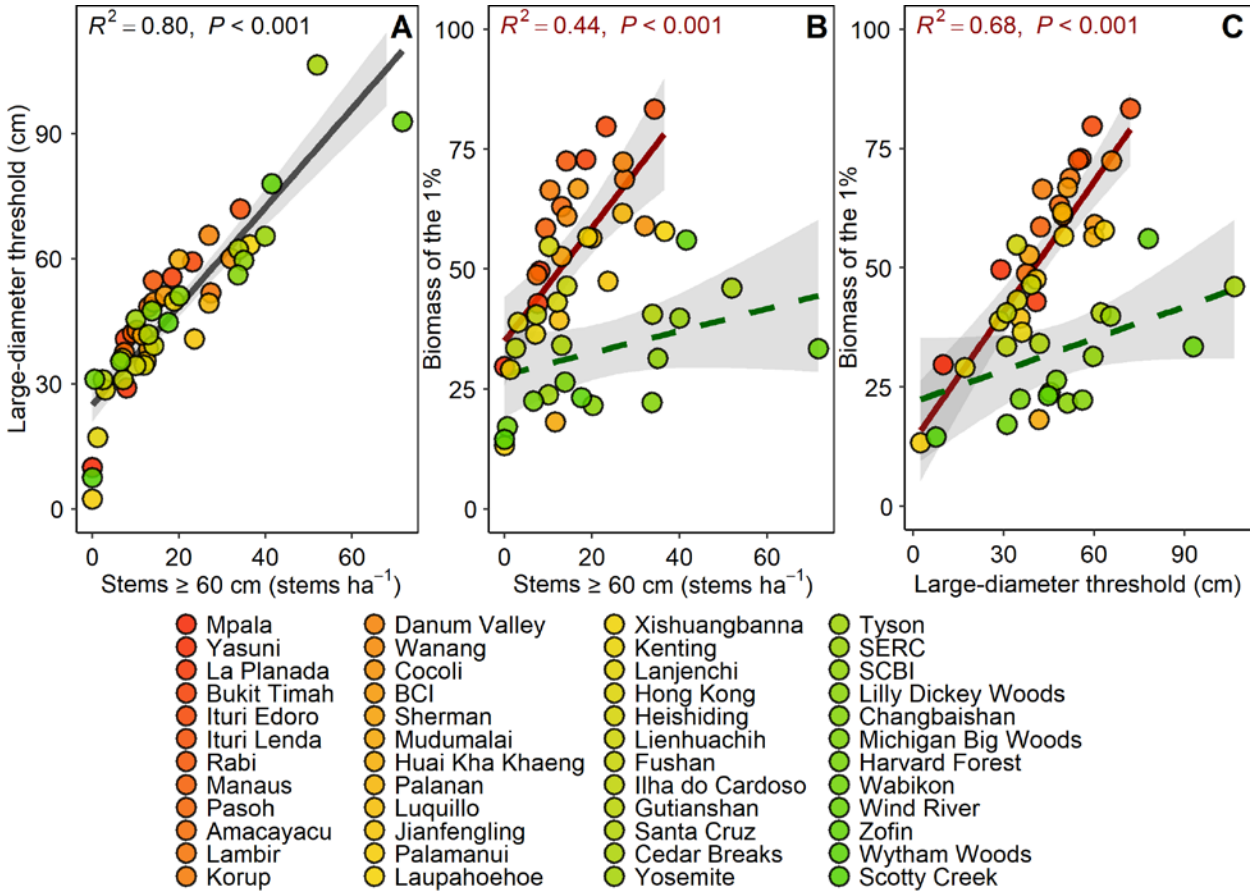


Fig. S1.2. The relationships among the metrics for the abundance of large-diameter trees. The relationship between stems ≥60 cm DBH and the large-diameter threshold was globally applicable (A), even including those plots with no stems ≥60 cm DBH. The relationship between stems and the biomass of the 1% or largest trees was not globally applicable (B), but there was a relationship for tropical plots (absolute latitude ≤23.5°), but not for temperate plots ($P$>0.05). Similarly, the relationship between the large-diameter threshold and the biomass of the 1% of largest trees was not globally applicable (C), although a relationship existed for tropical plots. Colours indicate increasing absolute latitude from red to green.

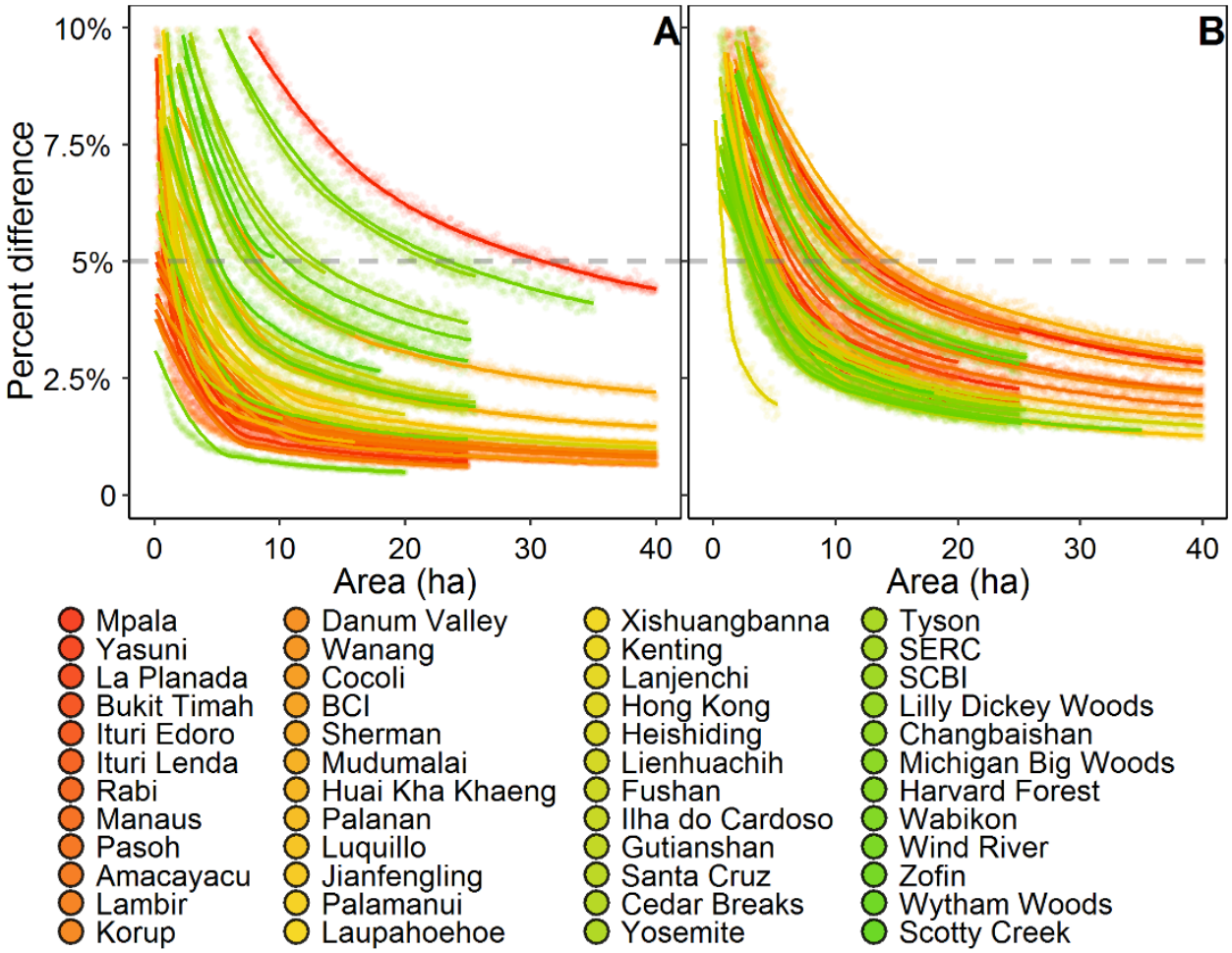


Fig. S1.3. Area needed to estimate biomass (A) and stem density (B) in 48 Smithsonian ForestGEO plots. Each point represents the percent deviation from the mean of a sample size equal to the number of 400 $m^2$ quadrats in each plot. Colours indicate increasing absolute latitude from red to green.

## S3. Supplemental tables

Table S3.1. Characteristics of plots within the Smithsonian ForestGEO network. Stems indicates the number of woody stems ≥1 cm dbh within each plot. *E* represents the latitude derived coefficient for biomass calculation for tropical plots (absolute latitude ≤23.5°) from Chave *et al.* (2014), and extracted from http://chave.ups-tlse.fr/pantropical_allometry.htm#E on 12 December 2017.

| Plot | Region | Latitude (°) | Longitude (°) | Area (ha) | Stems | *E* | Citation |
|---|---|---|---|---|---|---|---|
| Amacayacu | Tropical Latin America | -3.81 | -70.27 | 25 | 123,696 | -0.0792 | Arias-Garcia *et al.* 2009 |
| Barro Colorado Island | Tropical Latin America | 9.15 | -79.85 | 50 | 246,903 | 0.051764 | Hubbell *et al.* 1999 |
| Bukit Timah | Tropical Asia | 1.35 | 103.78 | 2 | 12,546 | -0.0848 | LaFrankie *et al.* 2005 |
| Cedar Breaks | Cold temperate / boreal | 37.66 | -112.85 | 13.64 | 23,238 | – | Furniss *et al.* 2017 |
| Changbaishan | Cold temperate / boreal | 42.38 | 128.08 | 25 | 30,743 | – | Yuan *et al.* 2016 |
| Cocoli | Tropical Latin America | 8.99 | -79.62 | 4 | 8,654 | 0.070899 | Condit *et al.* 2004 |
| Danum Valley | Tropical Asia | 5.1 | 117.69 | 25 | 189,316 | -0.04479 | – |
| Fushan | Temperate | 24.76 | 121.56 | 25 | 111,958 | – | Su *et al.* 2010 |
| Gutianshan | Temperate | 29.25 | 118.12 | 24 | 139,991 | – | Chen *et al.* 2010 |
| Harvard Forest | Cold temperate / boreal | 42.54 | -72.18 | 35 | 108,632 | – | Orwig *et al.* 2015 |
| Heishiding | Temperate | 23.27 | 111.53 | 50 | 263,835 | 0.746412 | Yin & He 2014 |
| Hong Kong | Temperate | 22.43 | 114.18 | 20 | 117,203 | 0.490652 | – |
| Huai Kha Khaeng | Tropical Asia | 15.63 | 99.22 | 50 | 125,296 | 0.319166 | Bunyavejchewin *et al.* 2001 |
| Ilha do Cardoso | Temperate | -25.1 | -47.96 | 10.24 | 47,526 | – | Oliveira *et al.* 2014 |
| Ituri Edoro | Tropical Africa | 1.44 | 28.58 | 20 | 179,120 | 0.003712 | Makana *et al.* 2004 |
| Ituri Lenda | Tropical Africa | 1.44 | 28.58 | 20 | 151,068 | 0.003712 | Makana *et al.* 2004 |
| Jianfengling | Tropical Asia | 18.73 | 108.90 | 60 | 391,628 | 0.280216 | Xu *et al.* 2015 |
| Kenting | Tropical Asia | 21.98 | 120.8 | 9.6 | 36,201 | 0.099318 | Wu *et al.* 2011 |
| Korup | Tropical Africa | 5.07 | 8.85 | 50 | 364,175 | -0.08991 | Kenfack *et al.* 2007 |
| La Planada | Tropical Latin America | 1.16 | -77.99 | 25 | 100,746 | -0.14564 | Vallejo *et al.* 2004 |
| Lambir | Tropical Asia | 4.19 | 114.02 | 52 | 399,234 | -0.1053 | Lee *et al.* 2005 |
| Lanjenchi | Tropical Asia | 22.06 | 120.85 | 5.28 | 66,671 | 0.010925 | Chao *et al.* 2010 |
| Laupahoehoe | Tropical Oceania | 19.93 | -155.29 | 4 | 15,701 | 0.242613 | Ostertag *et al.* 2014 |
| Lienhuachih | Temperate | 23.91 | 120.88 | 25 | 203,313 | 0.225027 | Lin *et al.* 2011 |
| Lilly Dickey Woods | Temperate | 39.24 | -86.22 | 25 | 27,824 | – | Johnson *et al.* 2014 |
| Luquillo | Tropical Latin America | 18.33 | -65.82 | 16 | 46,360 | 0.08761 | Zimmerman *et al.* 2010 |
| Manaus | Tropical Latin America | -2.44 | -59.79 | 25 | 155,908 | -0.11682 | Gomes *et al.* 2013 |
| Michigan Big Woods | Cold temperate / boreal | 42.47 | -84 | 20 | 45,564 | – | Allen *et al.* 2009 |
| Mpala | Tropical Africa | 0.29 | 36.88 | 120 | 355,611 | 0.539807 | Georgiadis *et al.* 2011 |
| Mudumalai | Tropical Asia | 11.6 | 76.53 | 50 | 30,402 | 0.209588 | Sukumar *et al.* 2004 |
| Palamanui | Tropical Oceania | 19.74 | -155.99 | 4 | 32,818 | 0.242613 | Ostertag *et al.* 2014 |
| Palanan | Tropical Asia | 17.04 | 122.39 | 16 | 79,707 | -0.02103 | Co *et al.* 2004 |
| Pasoh | Tropical Asia | 2.98 | 102.31 | 50 | 286,769 | -0.09398 | Manokaran *et al.* 2004 |
| Rabi | Tropical Africa | -1.92 | 9.88 | 25 | 199,703 | 0.012459 | Memiaghe *et al.* 2016 |
| Santa Cruz | Temperate | 37.01 | -122.08 | 6 | 11,708 | – | Gilbert *et al.* 2010 |
| SCBI | Temperate | 38.89 | -78.15 | 25.6 | 45,351 | – | Bourg *et al.* 2013 |
| Scotty Creek | Cold temperate / boreal | 61.3 | -121.3 | 9.6 | 40,391 | – | Baltzer *et al.* 2014 |
| SERC | Temperate | 38.89 | -76.56 | 16 | 33,379 | – | McMahon & Parker 2014 |
| Sherman | Tropical Latin America | 9.28 | -79.97 | 5.96 | 21,911 | -0.04617 | Condit *et al.* 2004 |
| Tyson | Temperate | 38.52 | -90.56 | 20.16 | 30,283 | – | LaManna *et al.* 2016 |
| Wabikon | Cold temperate / boreal | 45.55 | -88.79 | 25.2 | 41,772 | – | Wang *et al.* 2011 |
| Wanang | Tropical Oceania | -5.25 | 145.27 | 50 | 276,139 | -0.17639 | Vincent *et al.* 2014 |
| Wind River | Temperate | 45.82 | -121.96 | 25.6 | 31,005 | – | Lutz *et al.* 2013 |
| Wytham Woods | Temperate | 51.77 | -1.34 | 18 | 18,279 | – | Butt *et al.* 2009 |
| Xishuangbanna | Temperate | 21.61 | 101.57 | 20 | 91,299 | 0.336188 | Cao *et al.* 2008 |
| Yasuni | Tropical Latin America | -0.69 | -76.4 | 25 | 145,859 | -0.02603 | Valencia *et al.* 2004 |
| Yosemite | Temperate | 37.77 | -119.82 | 25.6 | 35,925 | – | Lutz *et al.* 2012 |
| Žofín | Temperate | 48.66 | 14.71 | 25 | 60,112 | – | Janík *et al.* 2016 |
| Total | 48 | | | 1,278 | 5,601,473 | | |

Table S3.2. Structural characteristics of stem density for global forests. Values for density (stems $ha^{-1}$) are shown for each diameter class, with mean and standard deviation (SD) given for each 100 m × 100 m of each plot.

| | Diameter class (cm) | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 ≤ DBH < 5 | | 5 ≤ DBH < 10 | | 10 ≤ DBH < 30 | | 30 ≤ DBH < 60 | | 60 ≤ DBH < 90 | | DBH ≥ 90 | | All stems | |
| PLOT | Mean | (SD) | Mean | (SD) | Mean | (SD) | Mean | (SD) | Mean | (SD) | Mean | (SD) | Mean | (SD) |
| Amacayacu | 3667 | (457) | 703 | (68) | 492 | (36) | 80 | (12) | 7 | (3) | 0 | (1) | 4948 | (518) |
| Barro Colorado Island | 3794 | (422) | 702 | (91) | 361 | (46) | 64 | (9) | 12 | (4) | 4 | (2) | 4938 | (463) |
| Bukit Timah | 5210 | (265) | 642 | (55) | 330 | (44) | 73 | (4) | 10 | (4) | 9 | (6) | 6273 | (180) |
| Cedar Breaks | 753 | (537) | 298 | (204) | 378 | (216) | 100 | (53) | 11 | (9) | 2 | (2) | 1542 | (961) |
| Changbaishan | 659 | (148) | 173 | (43) | 214 | (31) | 149 | (15) | 32 | (8) | 2 | (1) | 1230 | (188) |
| Cocoli | 1633 | (242) | 260 | (19) | 190 | (16) | 48 | (9) | 20 | (5) | 12 | (3) | 2164 | (248) |
| Danum Valley | 5853 | (395) | 1078 | (80) | 532 | (45) | 83 | (13) | 15 | (6) | 12 | (6) | 7573 | (526) |
| Fushan | 2975 | (768) | 694 | (242) | 696 | (241) | 100 | (15) | 12 | (5) | 3 | (3) | 4478 | (1139) |
| Gutianshan | 4344 | (1439) | 731 | (183) | 626 | (72) | 130 | (29) | 2 | (2) | 0 | 0 | 5833 | (1580) |
| Harvard Forest | 2011 | (2706) | 334 | (192) | 573 | (226) | 179 | (57) | 6 | (10) | 0 | 0 | 3104 | (2600) |
| Heishiding | 3748 | (643) | 771 | (172) | 638 | (168) | 107 | (22) | 11 | (6) | 1 | (1) | 5277 | (706) |
| Hong Kong | 4618 | (939) | 547 | (141) | 608 | (153) | 83 | (24) | 3 | (2) | 0 | (1) | 5860 | (1056) |
| Huai Kha Khaeng | 1705 | (619) | 341 | (70) | 374 | (48) | 65 | (17) | 14 | (6) | 6 | (3) | 2506 | (674) |
| Ilha do Cardoso | 3121 | (485) | 914 | (107) | 543 | (75) | 75 | (9) | 7 | (5) | 0 | 0 | 4660 | (578) |
| Ituri Edoro | 7588 | (1244) | 885 | (89) | 399 | (34) | 61 | (10) | 18 | (5) | 5 | (3) | 8956 | (1270) |
| Ituri Lenda | 6630 | (804) | 569 | (72) | 259 | (55) | 61 | (19) | 26 | (7) | 9 | (4) | 7553 | (829) |
| Jianfengling | 4866 | (822) | 766 | (144) | 701 | (94) | 169 | (21) | 20 | (5) | 3 | (2) | 6526 | (993) |
| Kenting | 2034 | (262) | 823 | (125) | 807 | (82) | 88 | (17) | 5 | (4) | 2 | (1) | 3760 | (410) |
| Korup | 5923 | (856) | 863 | (156) | 413 | (44) | 74 | (14) | 7 | (3) | 3 | (3) | 7283 | (920) |
| La Planada | 2544 | (189) | 886 | (93) | 514 | (41) | 78 | (9) | 7 | (3) | 0 | (1) | 4030 | (243) |
| Lambir | 6106 | (1118) | 875 | (120) | 535 | (72) | 90 | (21) | 21 | (8) | 7 | (3) | 7635 | (1233) |
| Lanjenchi | 8971 | (2078) | 1919 | (634) | 1108 | (150) | 76 | (31) | 1 | 0 | 0 | 0 | 12075 | (2795) |
| Laupahoehoe | 2036 | (702) | 662 | (140) | 1065 | (88) | 126 | (25) | 28 | (8) | 8 | (4) | 3925 | (859) |
| Lienhuachih | 4668 | (1512) | 802 | (223) | 570 | (95) | 81 | (21) | 9 | (4) | 1 | (1) | 6131 | (1760) |
| Lilly Dickey Woods | 584 | (436) | 199 | (66) | 203 | (30) | 106 | (27) | 19 | (7) | 1 | (1) | 1112 | (441) |
| Luquillo | 1659 | (550) | 429 | (83) | 700 | (62) | 102 | (26) | 10 | (4) | 2 | (1) | 2903 | (626) |
| Manaus | 4908 | (427) | 768 | (60) | 470 | (35) | 79 | (15) | 8 | (3) | 1 | (1) | 6234 | (441) |
| Michigan Big Woods | 1185 | (497) | 395 | (90) | 272 | (72) | 115 | (27) | 14 | (6) | 0 | 0 | 1981 | (515) |
| Mpala | 2525 | (2831) | 353 | (179) | 85 | (69) | 1 | (1) | 0 | 0 | 0 | 0 | 2963 | (2902) |
| Mudumalai | 158 | (154) | 122 | (98) | 225 | (76) | 91 | (18) | 10 | (6) | 1 | (1) | 608 | (210) |
| Palamanui | 7589 | (1200) | 298 | (64) | 316 | (60) | 1 | (2) | 0 | 0 | 0 | 0 | 8204 | (1084) |
| Palanan | 3602 | (429) | 697 | (83) | 573 | (42) | 83 | (14) | 19 | (8) | 8 | (5) | 4981 | (489) |
| Pasoh | 4341 | (584) | 844 | (89) | 476 | (42) | 62 | (10) | 10 | (3) | 3 | (2) | 5735 | (631) |
| Rabi | 6844 | (826) | 663 | (81) | 399 | (54) | 67 | (12) | 10 | (4) | 4 | (3) | 7988 | (926) |
| Santa Cruz | 1238 | (466) | 246 | (65) | 293 | (96) | 133 | (32) | 25 | (9) | 8 | (7) | 1944 | (593) |
| SCBI | 1351 | (1707) | 182 | (56) | 191 | (39) | 90 | (14) | 32 | (11) | 3 | (2) | 1850 | (1637) |
| Scotty Creek | 3079 | (1243) | 921 | (396) | 136 | (129) | 0 | 0 | 0 | 0 | 0 | 0 | 4136 | (1407) |
| SERC | 1514 | (813) | 260 | (42) | 182 | (34) | 90 | (18) | 34 | (7) | 6 | (4) | 2086 | (792) |
| Sherman | 2484 | (356) | 606 | (127) | 482 | (164) | 77 | (6) | 11 | (5) | 2 | (2) | 3662 | (550) |
| Tyson Research Center | 1087 | (803) | 211 | (40) | 184 | (42) | 110 | (24) | 10 | (4) | 0 | (1) | 1601 | (751) |
| Wabikon | 1041 | (674) | 214 | (229) | 343 | (195) | 94 | (28) | 1 | (1) | 0 | 0 | 1692 | (1017) |
| Wanang | 4299 | (460) | 706 | (67) | 420 | (47) | 83 | (15) | 12 | (5) | 2 | (1) | 5523 | (520) |
| Wind River | 660 | (180) | 222 | (78) | 188 | (54) | 64 | (16) | 46 | (10) | 26 | (13) | 1207 | (273) |
| Wytham Woods | 93 | (56) | 384 | (157) | 405 | (158) | 116 | (25) | 15 | (7) | 2 | (2) | 1016 | (309) |
| Xishuangbanna | 3164 | (527) | 789 | (128) | 503 | (53) | 90 | (25) | 15 | (6) | 4 | (3) | 4565 | (650) |
| Yasuni | 4239 | (621) | 898 | (74) | 614 | (38) | 76 | (11) | 7 | (3) | 1 | (1) | 5834 | (692) |
| Yosemite | 539 | (141) | 328 | (86) | 389 | (115) | 91 | (21) | 27 | (9) | 25 | (9) | 1399 | (266) |
| Žofín | 1800 | (724) | 363 | (282) | 156 | (76) | 44 | (17) | 32 | (10) | 10 | (5) | 2404 | (982) |

Table S3.3. Structural characteristics of tree biomass (Mg ha$^{-1}$) for global forests. Values for biomass are shown for each diameter class, with mean and standard deviation (SD) given for each 100 m × 100 m of each plot.

| | Diameter class (cm) | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 ≤ DBH < 5 | | 5 ≤ DBH < 10 | | 10 ≤ DBH < 30 | | 30 ≤ DBH < 60 | | 60 ≤ DBH < 90 | | DBH ≥ 90 | | All stems | |
| PLOT | Mean | (SD) | Mean | (SD) | Mean | (SD) | Mean | (SD) | Mean | (SD) | Mean | (SD) | Mean | (SD) |
| Amacayacu | 5.0 | (0.5) | 13.7 | (1.5) | 86.1 | (6.6) | 117.8 | (20.9) | 40.1 | (18.0) | 5.1 | (9.3) | 267.7 | (32.6) |
| Barro Colorado Island | 4.5 | (0.5) | 12.0 | (1.9) | 47.2 | (7.7) | 76.0 | (10.9) | 51.1 | (17.4) | 66.7 | (41.9) | 257.5 | (49.4) |
| Bukit Timah | 6.3 | (0.4) | 11.6 | (0.7) | 58.4 | (1.2) | 107.2 | (22.1) | 44.4 | (17.3) | 135.4 | (102.4) | 363.3 | (140.4) |
| Cedar Breaks | 0.5 | (0.4) | 2.4 | (1.6) | 39.0 | (23.2) | 72.1 | (33.2) | 33.8 | (28.9) | 20.0 | (23.0) | 167.8 | (53.3) |
| Changbaishan | 0.4 | (0.1) | 1.4 | (0.3) | 22.5 | (3.0) | 144.8 | (17.0) | 96.9 | (25.9) | 21.6 | (19.0) | 287.6 | (33.2) |
| Cocoli | 1.9 | (0.3) | 4.1 | (0.5) | 32.4 | (5.2) | 50.3 | (8.5) | 74.5 | (19.0) | 118.0 | (44.1) | 281.3 | (37.0) |
| Danum Valley | 7.5 | (0.5) | 18.8 | (1.5) | 83.1 | (7.4) | 106.6 | (19.0) | 77.0 | (29.6) | 193.0 | (112.3) | 485.8 | (152.4) |
| Fushan | 2.7 | (0.9) | 8.0 | (3.1) | 69.9 | (20.0) | 79.7 | (13.7) | 37.5 | (17.6) | 25.8 | (28.2) | 223.6 | (25.3) |
| Gutianshan | 3.8 | (1.3) | 8.3 | (2.0) | 74.1 | (10.4) | 91.7 | (23.2) | 6.7 | (6.4) | 0.0 | 0.0 | 184.6 | (26.6) |
| Harvard Forest | 1.8 | (1.4) | 5.0 | (3.0) | 85.4 | (27.6) | 148.7 | (53.2) | 19.2 | (29.5) | 0.4 | (2.1) | 260.5 | (65.8) |
| Heishiding | 2.1 | (0.3) | 6.4 | (1.6) | 49.8 | (11.9) | 62.1 | (15.9) | 22.6 | (12.7) | 5.5 | (7.4) | 148.5 | (26.5) |
| Hong Kong | 2.8 | (0.7) | 6.0 | (1.8) | 66.1 | (14.9) | 58.0 | (19.4) | 7.2 | (6.2) | 1.9 | (3.6) | 142.0 | (19.8) |
| Huai Kha Khaeng | 1.3 | (0.4) | 4.5 | (0.9) | 50.3 | (7.2) | 68.8 | (17.4) | 51.2 | (21.6) | 82.3 | (51.4) | 258.4 | (65.4) |
| Ilha do Cardoso | 3.2 | (0.4) | 10.9 | (1.2) | 56.9 | (8.6) | 56.4 | (9.6) | 21.0 | (16.3) | 0.0 | 0.0 | 148.4 | (17.1) |
| Ituri Edoro | 8.0 | (1.4) | 16.1 | (1.2) | 56.3 | (5.6) | 104.9 | (15.5) | 115.1 | (31.1) | 75.0 | (47.4) | 375.3 | (46.0) |
| Ituri Lenda | 6.5 | (0.5) | 9.8 | (1.5) | 43.9 | (8.6) | 111.5 | (31.2) | 166.5 | (50.6) | 129.3 | (64.4) | 467.4 | (61.7) |
| Jianfengling | 4.0 | (0.7) | 9.6 | (1.8) | 94.9 | (12.2) | 170.7 | (21.7) | 80.6 | (18.9) | 32.5 | (21.2) | 392.2 | (37.0) |
| Kenting | 2.9 | (0.5) | 15.1 | (2.0) | 104.7 | (12.9) | 87.4 | (16.4) | 19.7 | (16.3) | 24.9 | (15.1) | 254.7 | (38.0) |
| Korup | 8.1 | (1.3) | 15.2 | (2.3) | 84.3 | (7.0) | 110.4 | (24.2) | 44.9 | (21.1) | 82.1 | (81.8) | 345.0 | (87.9) |
| La Planada | 4.4 | (0.3) | 18.4 | (1.9) | 88.2 | (8.8) | 115.3 | (14.5) | 36.0 | (17.1) | 7.8 | (14.9) | 270.1 | (29.7) |
| Lambir | 7.3 | (1.1) | 16.5 | (2.5) | 93.7 | (14.9) | 143.6 | (39.4) | 127.6 | (46.6) | 106.7 | (43.3) | 495.4 | (99.3) |
| Lanjenchi | 7.7 | (2.6) | 17.2 | (6.0) | 63.1 | (5.4) | 23.5 | (8.8) | 1.4 | (0.5) | 0.0 | 0.0 | 113.0 | (7.1) |
| Laupahoehoe | 2.3 | (0.9) | 8.8 | (1.9) | 32.9 | (3.2) | 63.6 | (17.7) | 76.3 | (21.3) | 56.7 | (25.4) | 240.6 | (45.0) |
| Lienhuachih | 3.9 | (1.2) | 9.3 | (2.5) | 56.1 | (8.5) | 64.4 | (16.1) | 27.7 | (12.1) | 8.5 | (9.5) | 169.9 | (25.4) |
| Lilly Dickey Woods | 0.8 | (0.4) | 2.9 | (1.0) | 27.7 | (4.5) | 113.6 | (31.7) | 60.8 | (24.8) | 8.3 | (10.7) | 214.0 | (28.7) |
| Luquillo | 1.8 | (0.4) | 6.6 | (1.1) | 79.3 | (11.9) | 123.9 | (33.3) | 46.4 | (17.6) | 25.5 | (20.9) | 283.5 | (52.8) |
| Manaus | 6.8 | (0.5) | 15.8 | (1.0) | 96.3 | (9.4) | 141.5 | (32.7) | 56.9 | (21.3) | 26.3 | (47.4) | 343.6 | (53.9) |
| Michigan Big Woods | 1.5 | (0.6) | 5.0 | (1.1) | 28.6 | (6.1) | 118.3 | (26.7) | 37.9 | (17.0) | 0.5 | (1.8) | 191.8 | (24.8) |
| Mpala | 2.2 | (1.4) | 4.6 | (2.5) | 6.0 | (5.4) | 0.4 | (0.8) | 0.0 | 0.0 | 0.0 | 0.0 | 13.2 | (8.4) |
| Mudumalai | 0.2 | (0.2) | 1.4 | (0.8) | 40.5 | (15.5) | 108.6 | (26.8) | 42.7 | (23.7) | 11.3 | (12.3) | 204.7 | (33.2) |
| Palamanui | 18.7 | (2.9) | 3.2 | (0.8) | 6.3 | (1.9) | 1.4 | (2.3) | 0.0 | 0.0 | 0.0 | 0.0 | 29.6 | (4.7) |
| Palanan | 4.9 | (0.5) | 10.4 | (1.4) | 90.4 | (8.4) | 101.7 | (20.9) | 85.1 | (37.2) | 121.6 | (79.0) | 414.0 | (118.8) |
| Pasoh | 7.0 | (0.8) | 15.8 | (1.7) | 82.3 | (7.5) | 98.6 | (16.3) | 60.9 | (21.7) | 59.4 | (42.7) | 324.0 | (55.3) |
| Rabi | 6.9 | (0.7) | 11.6 | (1.5) | 69.9 | (10.6) | 98.6 | (16.3) | 58.2 | (24.6) | 78.1 | (63.6) | 323.2 | (73.7) |
| Santa Cruz | 1.2 | (0.4) | 3.7 | (1.1) | 42.5 | (12.5) | 127.1 | (30.9) | 92.5 | (36.9) | 94.6 | (86.7) | 361.5 | (102.0) |
| SCBI | 1.2 | (1.0) | 2.7 | (0.8) | 25.6 | (5.1) | 102.6 | (18.5) | 103.7 | (35.1) | 23.1 | (17.8) | 258.9 | (43.1) |
| Scotty Creek | 4.3 | (1.9) | 10.9 | (4.9) | 6.8 | (7.7) | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 22.0 | (11.1) |
| SERC | 1.6 | (0.5) | 3.6 | (0.6) | 24.4 | (5.7) | 97.1 | (21.2) | 119.5 | (27.4) | 53.3 | (38.9) | 299.5 | (49.1) |
| Sherman | 3.5 | (0.4) | 10.3 | (2.1) | 71.6 | (22.9) | 100.9 | (25.2) | 54.9 | (23.6) | 33.4 | (24.3) | 274.5 | (40.8) |
| Tyson Research Center | 1.2 | (0.7) | 3.1 | (0.5) | 26.4 | (8.6) | 112.5 | (20.5) | 31.1 | (12.6) | 1.3 | (3.8) | 175.6 | (15.7) |
| Wabikon | 0.9 | (0.8) | 2.6 | (2.8) | 46.9 | (10.8) | 59.2 | (18.9) | 1.5 | (2.9) | 0.0 | 0.0 | 111.1 | (13.6) |
| Wanang | 5.2 | (0.5) | 12.1 | (1.2) | 72.5 | (9.3) | 126.4 | (27.7) | 71.8 | (30.1) | 35.9 | (32.7) | 324.0 | (61.3) |
| Wind River | 0.5 | (0.2) | 1.7 | (0.6) | 17.2 | (4.8) | 62.3 | (17.7) | 171.0 | (37.5) | 279.5 | (174.8) | 532.0 | (161.3) |
| Wytham Woods | 0.4 | (0.2) | 7.5 | (3.0) | 72.1 | (29.2) | 133.4 | (29.7) | 65.6 | (30.8) | 30.5 | (31.0) | 309.5 | (46.4) |
| Xishuangbanna | 3.4 | (0.6) | 10.3 | (1.6) | 61.3 | (9.9) | 93.4 | (26.4) | 58.3 | (27.7) | 53.7 | (44.4) | 280.5 | (80.9) |
| Yasuni | 5.8 | (0.7) | 16.0 | (1.1) | 93.2 | (7.0) | 96.7 | (19.8) | 30.4 | (16.6) | 18.9 | (19.3) | 261.0 | (47.9) |
| Yosemite | 0.4 | (0.1) | 2.7 | (0.7) | 35.8 | (11.1) | 73.0 | (15.8) | 97.2 | (32.2) | 349.7 | (126.0) | 558.8 | (129.9) |
| Žofín | 1.5 | (0.8) | 3.4 | (2.8) | 13.7 | (4.0) | 41.3 | (13.2) | 113.8 | (37.6) | 74.2 | (40.4) | 247.9 | (66.5) |

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