# Article (refereed) - postprint

1 **Research Paper**

2 **Title: Global importance of large-diameter trees**

3 **Running head: 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

**Methods:** We examined the contribution of large trees to forest density, richness, and biomass using a global network of 48 large (from 2 ha 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 ≥1 cm diameter at breast height (DBH), all trees ≥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 ≥1 cm DBH 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 ($r^2 = 0.62$, $P<0.001$). Large-diameter trees in high biomass 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 were comprised of smaller trees ($r^2 = 0.33$, $P<0.001$). Lower large-diameter richness was associated with large-diameter trees being individuals of more common species ($r^2 = 0.17$, $P=0.002$).The concentration of biomass in the largest 1% of trees declined with increasing absolute latitude ($r^2 = 0.46$, $P<0.001$), as did forest density ($r^2 = 0.31$, $P<0.001$). Forest structural complexity increased with increasing absolute latitude ($r^2 = 0.26$, $P<0.001$).

**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

48    conservation of existing large-diameter trees or those that can soon reach large diameters as a

49    simple way to conserve and potentially enhance ecosystem services.

50    **Keywords:** forest biomass, forest structure, large-diameter trees, latitudinal gradient, resource

51    inequality, Smithsonian ForestGEO

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53    **Tables:** 2

54    **Figures:** 5

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56    **Data References:** 36

**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 (Saez & Zucman, 2016). The concentration of total forest biomass in a few large-diameter trees is no exception (Pan et al., 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 (Lutz et al. 2009, van Mantgem et al., 2009, Allen et al. 2010, Lindenmayer et al. 2012).

Despite the recognised 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 (Binkley et al. 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 et al., 2009; Das et al., 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 (Enquist et al., 2009; Lutz et al., 2014; Das et al., 2018). Consequently, to elucidate the patterns, mechanisms, and

80    consequences of large-diameter tree ecology requires sample plots ≥1 ha (Das et al., 2011;

81    Réjou-Méchain et al., 2014; Lutz, 2015).

82        Changes in climate, disturbance regimes, and logging are accelerating the decline of

83    large-diameter trees (e.g., Lindenmayer et al., 2012; Bennett et al., 2015; Lindenmayer &

84    Laurence, 2016). The dynamics of large-diameter trees is dependent on at least two factors: 1)

85    presence of species capable of attaining a large size, and 2) conditions, including disturbance

86    regimes, that permit the development of large-diameter individuals. If the species richness of the

87    large-diameter assemblage is high, a forest may be better able to respond to perturbations

88    (Musavi et al., 2017) and maintain its structure and ecological function. However, if the large-

89    diameter species richness is low, then a forest could be susceptible to any change that affected

90    those few species.

91        Surprisingly, the specific roles of large-diameter trees are not well anchored in two

92    widely referenced theories of global vegetation. Both the Unified Neutral Theory of Biodiversity

93    (Hubbell, 2001) and Metabolic Scaling Theory (West et al., 2009) propose that plants have a

94    degree of functional equivalency. The Unified Neutral Theory makes predictions about the rank-

95    order abundance of species in a forest, but it makes no specific predictions about the rank order

96    of large-diameter species or even if large-diameter individuals are members of common or rare

97    species. Metabolic Scaling Theory does predict the abundance of large-diameter trees, and

98    empirical tests of the theory for more abundant, smaller-diameter individuals are generally good.

99    However, Metabolic Scaling Theory often tends to under-predict the abundance of large-

100    diameter trees in temperate forests (Anderson-Teixeira et al. 2015b; their Fig. 2) and rather over-

101    predict the abundance of large-diameter trees in tropical forests (Muller-Landau et al. 2006; their

102    Table 2) and in some temperate forests (Lutz et al. 2012; their Fig. 2). Metabolic Scaling Theory

103    also advances its predictions as continuous functions, and the departure from theory (i.e., the

104    spatial variation) at discrete grain sizes remains unquantified. Accordingly, those theories alone

105    cannot fully explain global patterns of forest species diversity or the larger portion of the size

106    distribution (Coomes et al., 2003; Muller-Landau et al., 2006; Lutz et al., 2012; LaManna et al.,

107    2017).

108        However, studies do suggest that a greater generalization of forest structure in the

109    tropical, subtropical, temperate, and boreal forests of the world may indeed be possible (i.e.,

110    Gilbert et al., 2010; Slik et al., 2013; Ostertag et al., 2014). To the extent that forests share

111    structural attributes either globally or regionally, our ability to model forest change may be

112    improved by focusing on global patterns in structure rather than individual species life-history

113    traits. We expected that latitudinal trends in the concentration of biomass in the largest trees

114    would follow trends in forest density (with more stems in the largest diameter classes, relative

115    biomass should be higher). We also expected that relative richness of the large-diameter cohort

116    would be lower in forests with high stem density because the large trees would be a smaller

117    fraction of stems and thus a smaller fraction of species. Our principal hypothesis was that only a

118    small proportion of the largest trees are responsible for the preponderance of forest biomass, and

119    that the abundance and variation of these large-diameter trees reflect latitudinal gradients of

120    forest structure. Specifically we set out to ask four interrelated questions:

121        1) Are there global relationships between large-diameter trees (defined various ways)

122            and forest biomass?

123        2) Does the richness of the large-diameter cohort depend on the richness or biomass of

124            the forest?

8

125      3) Are there latitudinal gradients in forest density, biomass, concentration of biomass, or

126          structural complexity?

127      4) Are large-diameter trees members of common or rare species in forests?

128  **Materials and Methods**

129  We used data from the Forest Global Earth Observatory (ForestGEO; Anderson-Teixeira et al.,

130  2015a) network of forest dynamics plots coordinated by the Smithsonian Institution, which

131  includes major forest types in the Köppen climate zones of cold, temperate, and tropical forests

132  (Fig. 1, Table S3.1). Forests included in the ForestGEO network include undisturbed primary

133  forests or older secondary forests meeting the United Nations Food and Agricultural

134  Organization definition of forest (trees >5 m tall and canopy cover >10% occurring in patches

135  >0.5 ha; Forest Resource Assessment 2015). The ForestGEO plots feature consistent field

136  methods (Condit, 1998) and data representation (Condit et al., 2014). Importantly, these plots

137  include all standing woody stems ≥1 cm diameter at breast height (1.3 m along the main stem;

138  DBH). A representativeness analysis showed that the ForestGEO includes most major forest

139  types of the world, albeit with some exceptions (see Anderson-Teixeira et al., 2015a for details).

140  We analyzed 48 plots in primary or older secondary forest spanning 86.4° of latitude (Fig. 1),

141  covering 1,278 ha (median size 24 ha), and including 5,601,473 stems representing 9,298 species

142  and 210 plant families (Fig. 1, Tables 1, S3.1).

143      There is no universal definition for what constitutes a large-diameter tree. Generally, a

144  large-diameter tree is of reproductive stature, is tall enough to reach the upper canopy layer of

145  the forest, and that is larger than the majority of woody stems in the forest. In any forest, the

146  largest trees *relative to the rest of the stand* contribute disproportionately to ecological function

147  and represent some of the longest-lived and most fecund components of their respective forests.

148    The definition of large-diameter inherently depends on species and forest type. In cold,

149    continental forests, a large-diameter tree may only be 20 cm DBH (Baltzer et al., 2014). In

150    productive temperate or tropical forests, a large-diameter tree may be >100 cm DBH (Lutz et al.,

151    2012; 2013). To compare dissimilar ecosystems, we used three metrics for defining large

152    diameter trees:

153        1)  99th percentile diameter (the largest 1% of trees ≥1 cm DBH in the forest).

154        2)  Fixed diameter. We used a fixed threshold for large-diameter trees of 60 cm DBH, a

155            diameter reached by at least some trees in almost all plots.

156        3)  The large-diameter threshold. We defined the large-diameter threshold to be that diameter

157            such that trees greater than or equal to that diameter constituted half of the aboveground

158            live biomass of the plot.

159        We calculated the density, basal area, and biomass of stems ≥1 cm DBH and tabulated

160    them within each square hectare (100 m × 100 m) of the 48 plots. Because the distribution of

161    large-diameter trees within forests is often not homogeneous (e.g., Lutz et al. 2013), we used the

162    one-hectare scale to capture variation in structure across the plots without introducing the

163    spurious high or low values of biomass that could be associated with small extents (Réjou-

164    Méchain et al., 2014). We calculated biomass for tropical forests (absolute latitude ≤23.5°) by

165    the methods of Chave *et al.* (2014), which uses a generic equation to predict biomass based on

166    diameter, climate, and wood density. The Chave et al. (2014) equations are of the form:

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

168    where ρ is wood density and $E$ is the environmental parameter. Wood specific gravity was taken

169    from Zanne et al. (2009), and we used the values hierarchically, taking species-specific values

170    where defined, then genus-specific values, then family-specific values. If there was no wood

171    specific gravity data for the plant family, or if the stem was unidentified, we used the global

172    average of 0.615 g cm$^{-3}$. Values for the environmental parameter $E$ are listed in Table S3.1.

173    We calculated biomass for cold and temperate plots (absolute latitude >23.5°) using the

174    composite taxa-specific equations of Chojnacky *et al.* (2014). Those equations are of the form

175                $\ln(biomass) = \beta_0 + \beta_1 \times \ln(DBH)$                       Eq. 2

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

177    Species not represented by specific biomass equations were defaulted to an equation or

178    wood density value for the genus or the family. We used site-specific allometric equations for

179    Palamanui (Ostertag et al., 2014), Laupahoehoe (Ostertag et al., 2014), Lanjenchi (Aiba &

180    Nakashizuka, 2009), and Changbaishan (Wang, 2006).

181    We further analyzed the diameter-abundance relationships of each plot based on six tree

182    diameter classes (1 cm ≤ DBH < 5 cm, 5 cm ≤ DBH < 10 cm, 10 cm ≤ DBH < 30 cm, 30 cm ≤

183    DBH < 60 cm, 60 cm ≤ DBH < 90 cm, and DBH ≥ 90 cm). Diameter classes were selected to

184    include recognised differences in tree life-history traits (Memiaghe et al., 2016). We performed

185    nonmetric multidimensional scaling (NMDS; Kenkel & Orloci, 1986) analyses on the density of

186    each diameter class of each 100 m × 100 m area.  We used the Bray-Curtis dissimilarity index

187    and performed the NMDS ordinations in three dimensions using the version 2.4-4 of the vegan

188    package (Oksanen et al. 2016) in R version 3.3.1 (R Development Core Team, 2016). We used

189    the three-dimensional coordinates of each 1-ha in NMDS space to create a metric for structural

190    complexity. For the 1-ha structural ordination values for each plot, we fit a one standard

191    deviation ellipsoid using the orglellipse function from the vegan3d package (Oksanen, 2017). We

192    then calculated the volume of that ellipsoid as a metric of structural difference (i.e., complexity)

193    to compare the relative differences between 100 m × 100 m areas within the plot.

194        To examine commonness of species that can reach large diameters, we ranked all species

195    according to their abundance within each plot. We then identified large-diameter species as

196    species which had ≥1 individual with a DBH greater than or equal to the large-diameter

197    threshold, and determined the species rank for each of these large-diameter species (i.e., if the

198    third most abundant species was a 'large-diameter species', it would receive rank = 3). We then

199    used the median rank for all large-diameter species ranks within each plot, and normalised this

200    value across plots by dividing rank by the total number of species (i.e., in a plot with 60 species,

201    a median rank of 18 becomes 0.3).

202        To validate our results, we calculated structural accumulation curves for each plot,

203    calculating the area required to estimate forest density and aboveground live biomass to within

204    5% of the entire plot value. Within each plot, for each of density and biomass, we used random

205    sampling of 400 m$^2$ quadrats with replacement (from the available quadrats), beginning with a

206    random sample of n = 1 quadrat and ending with a random sample of n = total number of

207    quadrats in each plot. This process was repeated based on the number of quadrats in each plot

208    which allowed us to calculate a mean and standard deviation for each value of n. A percent

209    deviation metric was calculated as:

210        $Percent\ difference = (abs(mean_n - mean_{plot}) + sd_n)/mean_{plot}$        Eq. 3

211    where $mean_n$ is the mean of a random sampling of n quadrats, $mean_{plot}$ is the mean for the entire

212    plot, and $sd_n$ is the standard deviation for the random sample of n quadrats.

213    **Results**

214   Average stem density in the plots ranged from 608 stems ha$^{-1}$ (Mudumalai, India) to 12,075

215   stems ha$^{-1}$ (Lanjenchi, Taiwan) with most high-density plots occurring in the tropics (Tables 1,

216   2). Aboveground live tree biomass ranged from 13 Mg ha$^{-1}$ (Mpala, Kenya) to 559 Mg ha$^{-1}$

217   (Yosemite, USA). The biomass of trees ≥60 cm DBH ranged from 0 Mg ha$^{-1}$ (Mpala, Kenya,

218   Palamanui, USA, and Scotty Creek, Canada) to 447 Mg ha$^{-1}$ (Yosemite, USA). The large-

219   diameter tree threshold (separating the plot aboveground forest biomass into two equal parts)

220   varied from 2.5 cm (Palamanui, USA) to 106.5 cm (Yosemite, USA). Variation in the abundance

221   of trees of different diameter classes at the 1-ha scale was high globally (Tables S3.2, S3.3), and

222   CV of the 1-ha stem densities was highest in the cold temperate / boreal plots and lowest in the

223   tropics (Table 2).

224       There was a strong positive relationship between the large-diameter threshold and overall

225   forest biomass ($r^2 = 0.62$, $P<0.001$; Fig. 2A). This relationship held for all three of our

226   definitions for large diameter trees (Fig. 2A-C). The relationship for large-diameter threshold

227   was strongest, but the biomass of the largest 1% of trees also predicted total biomass ($r^2 = 0.35$,

228   $P<0.001$; Fig. 2B) as did the density of stems ≥60 cm DBH ($r^2 = 0.49$, $P<0.001$; Fig. 2C).

229   Results based on basal area were similar to those for biomass (Fig. S1.1). There was a negative

230   relationship between large-diameter species richness and total biomass ($r^2 = 0.45$, $P<0.001$; Fig.

231   2D) which was consistent with the negative relationship between large-diameter threshold and

232   large-diameter richness ($r^2 = 0.33$, $P<0.001$; Fig. 2E) and the negative relationship between

233   large-diameter richness and the biomass of the largest 1% of trees ($r^2 = 0.61$, $P<0.001$; Fig. 2F).

234   In other words, plots with high biomass had high large-diameter thresholds and relatively low

235   species richness within this large-diameter structural class.

236     The amount of aboveground forest biomass contained within the largest 1% of trees

237     averaged among the 48 plots was 50% (weighted by the forest biomass of each plot, 45% as an

238     unweighted average of the 48 plots), representing an average of 23% of the total species richness

239     (Table 1). The average large-diameter threshold was 47.7 cm DBH (half of the biomass of the 48

240     plots was contained within trees ≥47.7 cm DBH). The average portion of biomass contained

241     within trees ≥60 cm DBH in the 48 plots was 41%. Forest density gradually decreased with

242     increasing absolute latitude ($r^2 = 0.31$, $P<0.001$; Fig. 3A), as did the proportion of tree biomass

243     accounted for by the largest 1% of trees  ($r^2 = 0.46$, $P<0.001$; Fig. 3C), following our

244     expectations and partially a reflection of the higher stem densities  in the tropics (Fig. 3A, Tables

245     1, S3.2). However, latitudinal gradients were not present for biomass (Fig. 3B) or the large-

246     diameter threshold (Fig. 3D).

247     The three metrics for large-diameter trees were not perfectly correlated (Fig. S1.2). The

248     large-diameter threshold and the density of stems ≥60 cm DBH had a linear relationship ($r^2 =$

249     $0.80$, $P<0.001$), even though some forests did not have trees ≥60 cm DBH. The relationship

250     between the biomass of the 1% of largest diameter trees and both the density of stems ≥60 cm

251     DBH and the large-diameter threshold was significant for tropical plots but not for temperate

252     plots.

253     NMDS ordinations of the abundance of trees in the six diameter classes in each 100 m ×

254     100 m area showed that tropical forests have a higher degree of structural similarity based on

255     their positions in the ordination (Fig. 4A, B). The 1-ha scale variation for tropical plots also

256     showed a high degree of similarity both globally (clustering and high overlap of red ellipses in

257     Fig. 4C, D) and locally (smaller size of individual red ellipses). The volumes occupied by the 1-

258     ha NMDS points of temperate plots, conversely, covered a wide range in ordination space,

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259    indicating greater structural variability both among and within the plots (greater size and

260    dispersion of green ellipses in Fig. 4C, D, three-dimensional animation in S2). This phenomenon

261    was also mirrored by coefficients of variation of density and biomass of 1-ha quadrats, which

262    differed among regions and were higher in temperate and boreal forests than in tropical plots

263    (Table 2). The grouping of plots with no trees ≥60 cm DBH (left of Figs. 4A, B; Table S3.2)

264    shows a structural equivalency of forests growing in stressful environments. Those forests

265    include Scotty Creek, Canada (temperature, nitrogen, and hydrologically limited), Mpala, Kenya

266    (water and herbivory limited) and Palamanui, USA (water limited, limited soil development, and

267    with limited species complement). The structural complexity of forests (variation in abundance

268    of the six diameter classes) at 1-ha scale increased with increasing absolute latitude (Fig. 5A).

269         Large-diameter trees consisted primarily of common species (rank <0.5; Fig. 5B), and

270    rarer species reached large diameter in plots with higher large-diameter richness ($r^2 = 0.17$; $P =$

271    0.002). The absolute numbers of species that reached the local large-diameter threshold ranged

272    from two in tropical Laupahoehoe, USA to 343 in Yasuni, Ecuador (Table 1). Tropical plots

273    generally had >25 species reaching the large-diameter threshold (minimum nine species in

274    Cocoli, Panama). Temperate plots generally had <10 species that reached the large-diameter

275    threshold (maximum 25 species in SERC, USA). On a percentage basis, large-diameter richness

276    ranged from 5% (Cocoli, Panama and Bukit Timah, Singapore) to 69% (Palamanui, USA). The

277    relative richness of the large-diameter assemblage was highest in plots with low biomass, while

278    plots with high biomass had a lower proportion of richness represented by the large-diameter

279    trees (Fig. 2D, Table 1). In general, forests with lower total richness had a higher proportion of

280    that richness retained in the large-diameter class. Unsurprisingly, plots with lower large-diameter

281    thresholds (<60 cm DBH) had a higher proportion of species represented in the large-diameter

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282    assemblage (mean 34%), whereas plots with large-diameter thresholds ≥60 cm DBH had a lower

283    proportion of species represented in the large-diameter guild (mean 18%).

284    **Discussion**

285    The relationship between the large-diameter threshold and overall biomass (Fig. 2A) suggests

286    that forests cannot sequester large amounts of aboveground carbon without large trees,

287    irrespective of the richness or density of large-diameter trees. Species capable of attaining large

288    diameters are relatively few (Fig. 2) but individuals of these species are relatively abundant (Fig.

289    5B). The relationships among biomass and richness across plots held over a range of stem

290    densities (608 stems ha$^{-1}$ to 12,075 stems ha$^{-1}$) and among trees of varying wood densities (0.10 g

291    cm$^{-3}$ to 1.08 g cm$^{-3}$). A linear relation of biomass to large-diameter threshold (Fig. 2A) best

292    explained the correlation among the 48 plots, although we would expect an upper limit based on

293    maximum tree heights (Koch et al., 2004) or biomass (Sillett et al., 2015; Van Pelt et al., 2016).

294    The generally high proportion of biomass represented by the largest 1% of trees reinforces the

295    importance of these individuals to carbon sequestration and productivity (e.g., Stephenson et al.,

296    2014). Larger numbers of small and medium-diameter trees cannot provide equivalent biomass

297    to a few large-diameter trees, although small and medium sized trees can contribute significantly

298    to carbon cycling (Fauset et al., 2015; Meakem et al., 2017). The implication from scaling theory

299    (West et al., 2009) is that large-diameter trees are taller and have heavier crowns, and occupy

300    growing space not available to smaller trees (i.e., at the top of the canopy; West et al., 2009; Van

301    Pelt et al., 2016).

302        Temperate forests featured a higher density of trees ≥60 cm DBH (Table 1), consistent

303    with the presence of the very largest species of trees in cool, temperate forests (Sillett et al.,

304    2015; Van Pelt et al., 2016). Temperate forests also exhibited considerably lower densities of

305    small trees (e.g., 1 cm ≤ DBH < 5 cm; Table S3.2) and lower total stem density, which is mainly

306    comprised of small trees than tropical forests (Tables 2, S3.2). Metabolic Scaling Theory does

307    predict the diameter-abundance relationship throughout much of the middle of the diameter

308    range in many forest types (Muller-Landau et al., 2006; Lutz et al., 2012; Anderson-Teixeira et

309    al. 2015b). However, the dichotomy between temperate forests and tropical forests, where

310    temperate forests have lower densities of small trees and higher densities of large trees (and

311    tropical forests the reverse), reinforces the need to examine departures from the theory's

312    predictions. In tropical forests, the lower proportional richness of large-diameter trees likely has

313    at least two explanations. First, tropical forests contain many more stems per ha (Table S3.2)

314    with much higher small-diameter understory diversity (LaFrankie et al., 2006). Secondly, not all

315    of the species capable of reaching large-diameters in that region may be present even in the large

316    ForestGEO plots, and thus even the extensive ForestGEO network may have sampling

317    limitations.

318        The grouping of plots with only small-diameter trees (Fig. 4A) shows that forests in

319    markedly different environments can exhibit convergent structure based on different limiting

320    factors. Large-diameter trees can be abundant in any region (Table S3.1), but different factors

321    may limit the ability of an ecosystem to support a high level of aboveground live biomass. In

322    addition to environmental limits, ecosystems that are environmentally quite productive in terms

323    of annual growth may be limited by frequent, severe disturbance (e.g., typhoons in Fushan,

324    Taiwan and hurricanes in Luquillo). Finally, the regional species pool may not contain species

325    that can attain large diameters in the local combination of climate and resource availability (e.g.,

326    Palamanui, USA). The higher levels of structural complexity at 1-ha scales in temperate forests

327    may be due to higher proportions of the forests where small trees predominate and large-

328 diameter trees are generally excluded (i.e., swamps, rocky outcrops), supported by the higher

329 coefficient of variation of density in temperate and cold forests (Table 2). The trend of increasing

330 structural complexity (i.e., 1-ha heterogeneity) with increasing absolute latitude (Fig. 5A) may in

331 fact be hump-shaped, with decreasing complexity at higher latitudes than the 61.3°N of the

332 Scotty Creek, Canada plot.

333     There is still considerable uncertainty as to what will happen to large-diameter trees in

334 the Anthropocene when so much forest is being felled for timber and farming, or is being

335 affected by climate change. Bennett et al. (2015) suggested that the current large-diameter trees

336 are more susceptible to drought mortality. Larger trees, because of their height, are susceptible to

337 sapwood cavitation and are also exposed to high radiation loads (Allen et al., 2010; Allen et al.,

338 2015), but vigorous large-diameter individuals may also still be sequestering more carbon than

339 smaller trees (Stephenson et al., 2014). Both Allen et al. (2015) and Bennett et al. (2015)

340 suggested that larger trees will be more vulnerable to increasing drought than small trees, and

341 Luo & Chen (2013) suggested that although the rate of mortality of larger trees will continue to

342 increase because of global climate change, smaller trees will experience more drought related

343 mortality. These last two conclusions need not be in conflict as the background mortality rates

344 for smaller trees are higher than those of larger trees within mature and old-growth forests

345 (Larson and Franklin 2010). What remains generally unanswered is whether the increasing

346 mortality rates of large-diameter trees will eventually be offset by regrowth of different

347 individuals of those same (or functionally similar) species. Any reduction in temperate zone

348 large-diameter tree abundance may be compounded by the low large-diameter tree diversity in

349 temperate forests (temperate forests had high relative large-diameter richness, but low absolute

350 large-diameter richness). Large-diameter tree richness in tropical forests suggest more resilience

351  to projected climate warming in two ways. First, absolute large-diameter tree richness was

352  highest in tropical forests, suggesting that the large-diameter tree guild may have different

353  adaptations that will allow at least some species to persist (Musavi et al. 2017). Secondly, the

354  pool of species that can reach large diameters may have been undersampled in the plots used

355  here, implying an even higher level of richness may exist in some forests than captured in these

356  analyses.

357      The finding that large-diameter trees are members of common species groups (Fig. 5B)

358  contradicts the Neutral Theory assumption of functional equivalency (Hubbell, 2001). Similarly

359  the different structural complexity of forests worldwide (Fig. 5A) contradicts the assumptions of

360  universal size-abundance relationships of Metabolic Scaling Theory (Enquist et al., 1998, 2009).

361  The presence of a latitudinal gradient in forest density (Fig. 3A) and the lack of a latitudinal

362  gradient in forest biomass (Fig. 3B) suggests that size-abundance relationships are not universal

363  but depend on region or site conditions (Table 2).

364      Characterizing forest structural variation did require these large plots (Fig. S1.3), a

365  finding consistent with other studies examining forest biomass (Réjou-Méchain et al., 2014).

366  With large plot sizes and global distribution, ForestGEO is uniquely suited to capture structural

367  variation (i.e., the heterogeneity in the abundance of trees of all diameter classes). The relatively

368  large area required (6.5 ha, on average) to estimate biomass to within 5% of the entire plot value

369  reinforces conclusions that the distribution of large-diameter trees is not homogeneous within

370  forests (e.g., Table 2; Lutz et al., 2012; 2013; Furniss et al., 2017. We note that this calculation of

371  the size of the plot required is a measure of spatial variation within the forest, and does not

372  depend on the accuracy of the allometric equations for calculating tree biomass themselves.

373  Allometric equations can be imprecise for large-diameter trees, both because of their structural

374   variability and the enormous sampling effort, and therefore our estimates of overall biomass

375   could be off by ±15% (Lutz et al., 2016).

376        Although temperate plots had much lower overall species diversity compared to the

377   tropical plots, tropical plots had much more homogeneous structure, both within- and across-

378   plots (Fig. 4), potentially suggesting greater structural equivalency among the many species

379   present. We found that the largest 1% of trees constitute 50% of the biomass (and hence, carbon)

380   supporting our hypothesis of their significance, at least in primary forests or older secondary

381   forests. The conservation of large-diameter trees in tropical and temperate forests is therefore

382   imperative to maintain full ecosystem function, as the time necessary for individual trees to

383   develop large sizes could preclude restoration of full ecosystem function for centuries following

384   the loss of the oldest and largest trees (Lindenmayer et al. 2012). Clearly, these large-diameter

385   trees that are now absent from areas that have been recently logged lack the structural

386   heterogeneity of older forests. That the largest individuals belong to relatively few common

387   species in the temperate zone  means that the loss of large-diameter trees could alter forest

388   function - if species that can attain large diameters disappear, forests will feature greatly reduced

389   structural heterogeneity (e.g., Needham et al., 2016), biomass, and carbon storage. In the tropical

390   zones, the larger absolute numbers of species reaching large diameters may buffer those forests

391   against structural changes.. Policies to conserve the tree species whose individuals can develop

392   into large, old trees (Lindenmayer et al., 2014) could promote retention of aboveground biomass

393   globally as well as maintenance of other ecosystem functions.

397    Experiment Station, Utah State University, and approved as journal paper number 8998.

398    Acknowledgements for the global support of the thousands of people needed to establish and

399    maintain these 48 plots can be found in Supplementary Material S4. References to locations refer

400    to geographical features and not to the boundaries of any country or territory.

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## 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.

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664    and human land use. Landscape Ecology **25**, 1099-1111.

**Tables**

666 Table 1. Structural characteristics of global forests. Values for density and biomass include trees
667 ≥1 cm DBH within each square hectare (100 m × 100 m) of the plots, with the mean and
668 standard deviation (SD) calculated for each full hectare. The large-diameter threshold represents
669 the diameter where half the biomass is contained within trees above that threshold. The biomass
670 of the 1% indicates the proportion of total live aboveground tree biomass contributed by the
671 largest 1% of trees ≥1 cm 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 |

672    [†]Mature secondary forest

673   Table 2. The effect of geographical region on tree density and biomass and their variation at 1 ha scale and the abundance of large-
674   diameter trees as measured by the three metrics of proportion of biomass in the largest 1% of trees, density of trees $\geq$60 cm DBH, and
675   large-diameter threshold. The SD of density and the SD of biomass represent the within-region (between-plot) variation. The CV of
676   density and CV of biomass represent the average of the individual plot 1-ha CVs, with each plot weighted equally. SD: standard
677   deviation, CV: coefficient of variation.

| Zone | Plots n | Density (trees ha$^{-1}$) | Density SD | Density CV | Biomass (Mg ha$^{-1}$) | Biomass SD | Biomass CV | Biomass of the 1% (%) | Density trees $\geq$60 cm dbh (trees ha$^{-1}$) | 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 |

678

679
680 **Figures**
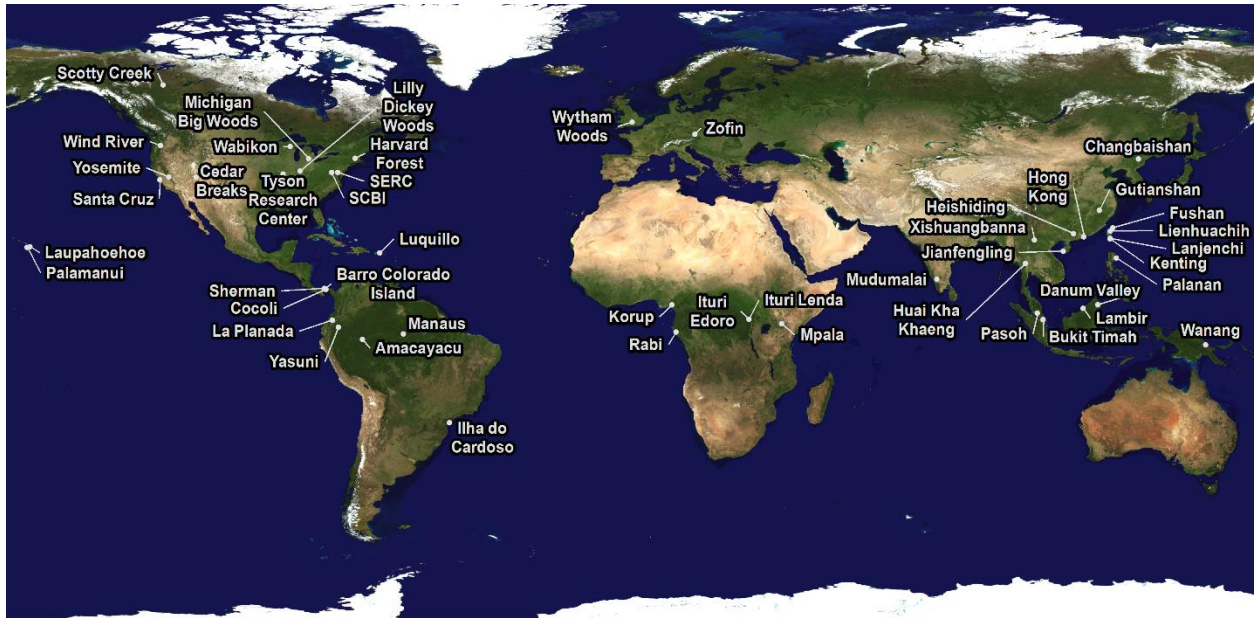


681
682 Fig. 1. Location of the 48 plots affiliated with the Smithsonian Forest Global Earth Observatory
683 (ForestGEO) used in this study.

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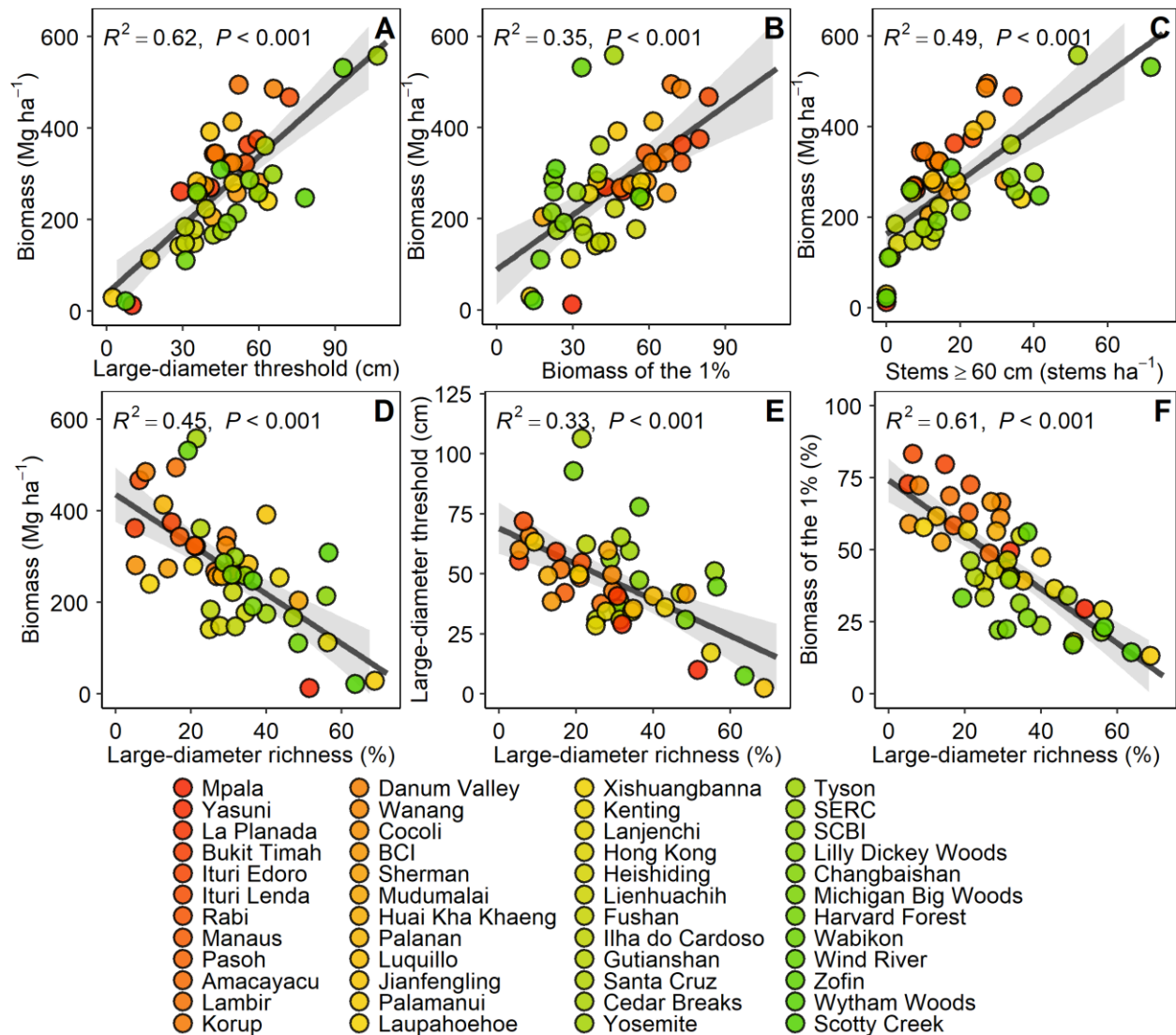
Fig. 2. Contribution of large-diameter trees to forest structure of 48 large forest plots. Aboveground live tree biomass increases with increasing large-diameter threshold (A). The large-diameter threshold reflects the tree diameter that segments biomass into two equal parts. Below the large-diameter 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 also increases with the concentration of biomass in the largest 1% of trees (B) and the density of stems ≥60 cm 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.
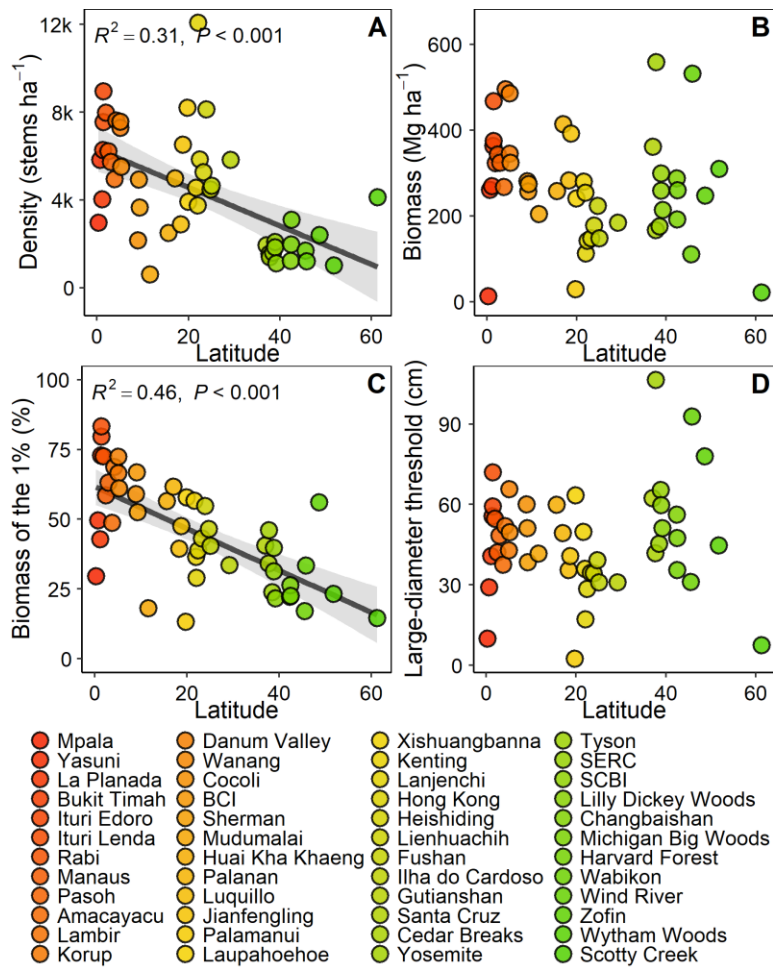
Fig. 3. Gradients of forest structural attributes by absolute latitude for 48 forest plots in the ForestGEO network. Absolute latitudinal gradients in density (A) and concentration of biomass in the largest 1% of trees (C) were significant. The relationships for biomass (B; $r^2 = 0.04$, $P = 0.106$)) and the large-diameter threshold (D; $r^2 = 0.01$, $P = 0.551$) were not. Colours indicate increasing absolute latitude from red to green. Grey areas around regression lines indicate 95th percentile confidence intervals.
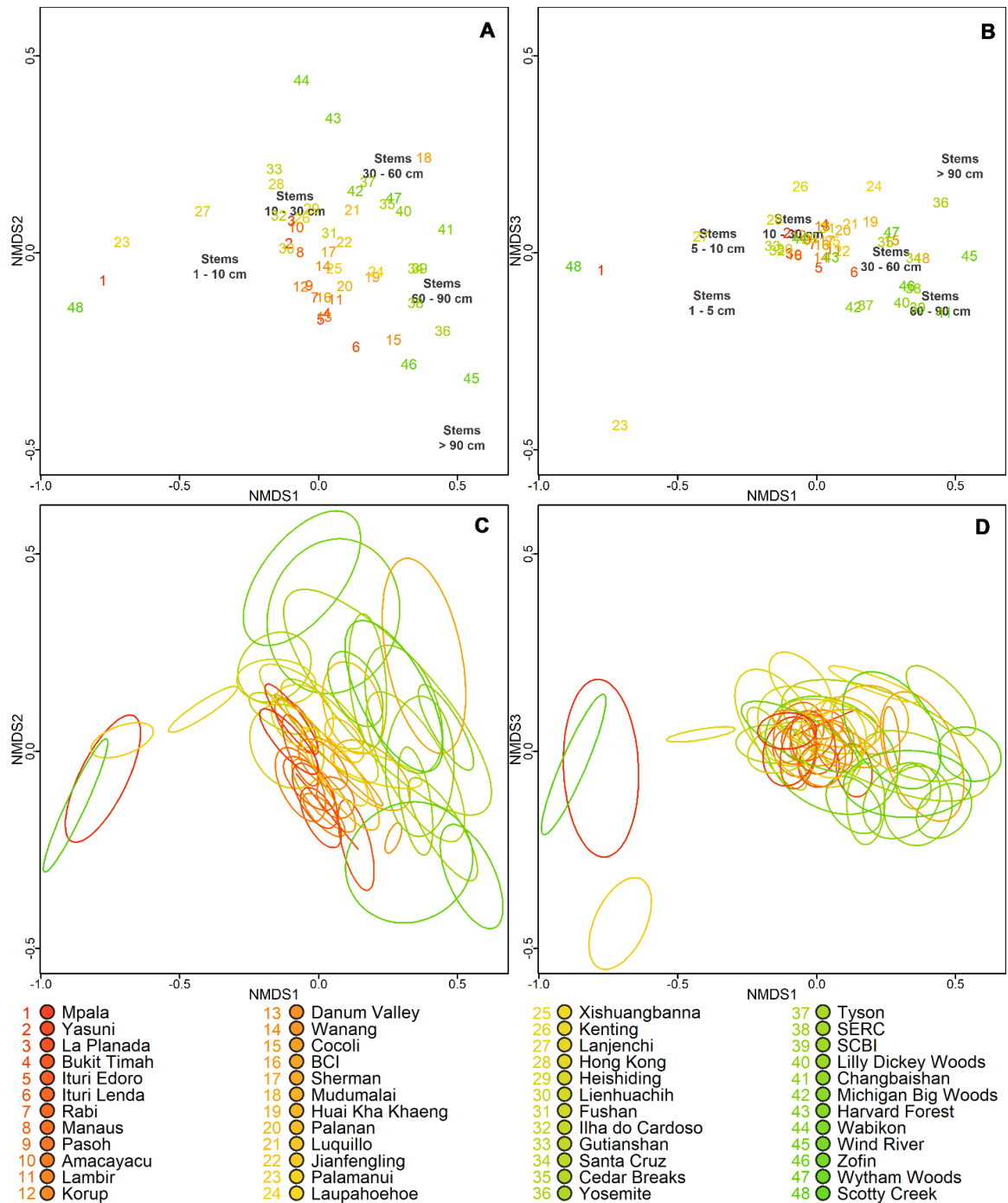
Fig. 4. Three-dimensional nonmetric multidimensional scaling (NMDS) results for density of trees organized into six diameter classes in 1260, 100 m × 100 m hectares of 48 forest plots in the ForestGEO network (A, B). The structural classes (diameter bins) used in the NMDS ordination are superimposed in black text (A, B). The within plot variation of structure for each plot is shown by depiction of the standard deviation ellipses of the individual 100 m × 100 m hectares within each plot (C, D; where C reflects the variation of NMDS1 vs. NMDS2 (A) and D reflects the variation of NMDS1 vs. NMDS3 (B). Ordination stress = 0.047. Colours indicate

increasing absolute latitude from red to green, with plot centroids numbered (A, B). See
Supplemental Material for a three-dimensional animation of the structural ordination.



716
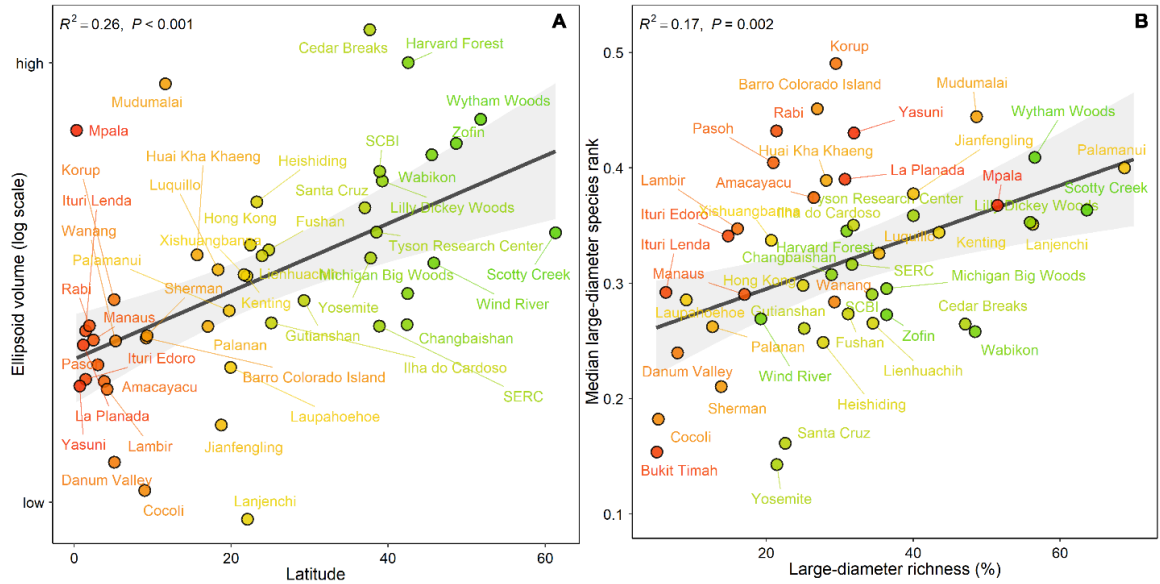
Fig. 5. The 1-ha scale structural complexity of 48 forest plots in the ForestGEO network as a
function of absolute latitude (A). The metric of structural complexity is the volume of the three-
dimensional ellipsoid generated from the NMDS ordination of abundance in structural classes
(see Fig. 4 for two dimensional projections and the Supplementary Material 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.

727 **Supplementary Material**

728 Fig. S1.1. Relationship among basal area, large-diameter threshold, and large-diameter richness

729 Fig. S1.2. Relationships among metrics for large-diameter trees

730 Fig. S1.3. Area needed to estimate structural characteristics of forests

731 Video S2. Animation of the three-dimensional structural NMDS ordination of 48 forest plots
732 [Note: For convenience of review, this animation can also be found at:
733 http://westernforestinitiative.org/Lutz_et_al_S2_20180109.gif

734 Table S3.1. Environmental characteristics of 48 large forest plots

735 Table S3.2. Density data by diameter class for 48 large forest plots

736 Table S3.3. Biomass data by diameter class for 48 large forest plots

737 S4. Acknowledgements for 48 forest plots in the ForestGEO network