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1 Title: Climate sensitive size-dependent survival in tropical trees

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68

69 **Abstract**

70 Survival rates of large trees determine forest biomass dynamics. Survival rates of small
71 trees have been linked to mechanisms that maintain biodiversity across tropical forests. How
72 species survival strategies change across size globally offers insight into the links between
73 biodiversity and ecosystem function across tropical forests. We tested patterns of size-dependent
74 tree survival across the tropics using data from 1781 species and over two million individuals to
75 assess whether complex and diverse tropical forests can be characterized by size-dependent life-
76 history survival strategies. We found species, across the tropics, were classifiable into four
77 “survival modes” that explain life-history strategies shaping the terrestrial forest ecosystem
78 carbon-cycle budget and also display the full range of life forms in the forest, from shrubs to

79 emergent canopy trees. Frequently collected traits, such as wood density, leaf mass per area, and
80 seed mass, were not generally predictive of these survival modes, suggesting poor alignment
81 between those traits and survival strategies across tropical forests. Mean annual temperature and
82 cumulative water deficit predicted the proportion of biomass of survival modes, indicating
83 important links between evolutionary strategies, climate, and carbon cycling. We also applied
84 survival modes in demographic simulations to accurately predict biomass change over time in
85 sites for which we had long-term data. Our results reveal globally identifiable size-dependent
86 survival strategies that differ across diverse systems in a consistent way. These modes and their
87 interaction with climate ultimately determine forest structure, carbon storage, and can link
88 climate change to future forest states.

89 Tropical forests store an estimated 500-1000 Pg of C in biomass and soils^{1,2}, making this
90 biome the most important component of the terrestrial carbon cycle. Whether intact tropical
91 forests will be sinks or sources of carbon in the future remains a critical question^{1,3} that will
92 fundamentally depend on how different forest species respond to climate change⁴. The great
93 diversity of tropical forests might buffer stands from shifts in standing biomass or might promote
94 changes due to the characteristics of the species that best tolerate novel climate conditions.
95 Forest carbon volume depends exponentially on the annual rate of tree survival, and tree survival
96 rates in turn depend on climate⁵ and the strategies species use to tolerate climate variation. In
97 most forests, survival strategies range from short-lived species that die within decades to long-
98 lived species that retain carbon for centuries. Changes in forest composition due to differential
99 survival responses of species to novel climate variation or new regimes of extreme episodic
100 events (i.e. droughts and storms), may cause large and rapid changes in the terrestrial carbon

101 balance that could potentially persist for centuries because different strategies may prove
102 differentially vulnerable to such changes. Climate-driven impacts on tree survival are potentially
103 more important than impacts on forest productivity (i.e., photosynthesis and allocation to
104 growth), which has a relatively constrained and slower influence on forest carbon dynamics⁶⁻⁹.

105 For species to coexist in diverse forests, they must have roughly equivalent fitness over
106 long time periods^{10,11}, yet differences in achieving that fitness can influence compositional shifts
107 when faced with novel long-term ecological changes. Tree species have evolved resource
108 allocation strategies that, over the course of life-history, emphasize investment in metabolic
109 maintenance, structural, defensive, and reproductive tissues. Variation in these allocation
110 strategies leads to variation in demographic rates (i.e. survival, growth and reproduction). The
111 survival rates that emerge from allocation to maintenance, defense, and structure, can then
112 determine observed population distributions across space¹², size, and age structures¹³. Allocation
113 to tissues that increase survival are typically negatively correlated (or “trade-off”) with allocation
114 to tissues involved in other demographic rates¹⁴. For example, using resources to build defensive
115 structures reduces resources available for growth. Allocation to tissues for increased survival can
116 lead to distinct vulnerabilities to stressors, such as pathogens¹⁵, pests, storms, drought, or
117 extreme temperatures¹⁶, or the reverse. Tolerance of climate change may vary with allocation
118 strategies resulting in important implications for forest biodiversity and carbon stocks. Greater
119 understanding of allocation strategies and how demographic rates vary with size should increase
120 our ability to predict how diverse forests cycle carbon and provide insights into potential shifts in
121 those cycles.

122 Here we quantify tree survival strategies to provide a deeper understanding of basic
123 ecological and evolutionary features of tropical forests. Using an exemplary dataset of more than
124 two million trees across the tropics, we developed models of size-dependent survival. Using a
125 cluster analysis, we aggregated the results of these models into groups of similar survival
126 strategies that we call ‘survival modes’. We then explore how these modes reflect important
127 features of tropical forest carbon and diversity dynamics.

128 To understand the ecological significance of these survival modes, we : 1) investigated
129 how survival modes contribute to carbon fluxes through differences in growth rates and biomass
130 turnover; 2) examined if the modes of survival that emerge from the demographic data are
131 related to the commonly collected plant traits of wood density, leaf mass per area and seed mass;
132 3) tested whether the relative abundance of these survival modes relate to climate variables and
133 4) tested the predictions of our model results against the observed biomass at each site through
134 time.

135 **Results**

136 Survival models were fit for 1781 species occurring across 14 pan-tropical large area forest
137 dynamics plots (ranging from 2 to 52 ha each with 371 ha in total in which all stems ≥ 1 cm
138 diameter at breast height are recorded (Supplementary Table 1). The parameters from these
139 models were included in a principal component analysis (PCA) (Fig. 1 details the workflow).
140 The PCA revealed clear axes of evolved life-history strategies (Supplementary Fig. 1). For
141 example, PCA axis one defines a continuum characterized by relatively stable survival
142 probability across the life-cycle at one extreme (either high or low survival) and at the other by
143 notable increases and decreases in survival probability with size at small and large sizes

144 respectively, i.e. species with more extreme thinning due to competition for resources when
145 relatively small, and senescence or mortality causes related to old age and exposure in the other
146 direction. Axis two differentiates species based on long-term survival rate (i.e. the upper
147 asymptote of the survival curve).

148 Species were hierarchically clustered by loadings of the PCA analysis which creates a
149 dendrogram from a similarity matrix. An optimizing analysis of the inertia of cluster numbers
150 across the dendrogram resolved four survival modes (Fig. 2, Methods). To test the robustness of
151 our survival modes, we bootstrapped the Jaccard similarity index for all clusters which were well
152 above the 0.75 threshold¹⁷ indicating stable clustering for our size-dependent survival modes
153 (Supplementary Table 2).

154 Although annual survival probability across much of the life-cycle was high for most
155 species (greater than 0.95), there were species with much lower long-term survival rates (less
156 than 0.78, Supplementary Table 2). Further, the degree of juvenile mortality varied between
157 modes indicating differences in the strength of mortality mechanisms in small sizes across the
158 four modes. Finally, there were also clear differences between the maximum sizes at which
159 species showed increased mortality (senescence) indicating important mode-dependent life-
160 expectancies (Fig. 2).

161 The four survival modes clustered along multiple axes, but there was a clear delineation
162 among species of size at senescence which allows us to group them by life form. *Understory*
163 species are characterized by their small maximum diameters, with an across-site mean 99th
164 percentile diameter of 9.8 ± 2.4 cm (mean ± 1 sd). *Transient* species are distinguished by their
165 very low overall survival with an across-site mean maximum-survival rate of $78\% \text{ yr}^{-1}$ and an
8

166 across-site mean 99th percentile diameter of 14.3 ± 9.4 cm. There are two groups of large stature
167 tree species or species capable of reaching canopy sizes. *Canopy* species are the group with
168 intermediate maximum size, across-site mean 99th percentile diameter of 27.8 ± 7.0 cm and lower
169 small-diameter survival rates compared to *Large Canopy* species which have larger maximum
170 diameter, across-site mean 99th percentile diameter of 68.4 ± 18.5 cm and relatively higher
171 survival at smaller diameters. Our analysis has an abundance threshold of 200 individuals;
172 species with lower abundance are *Unclassified*, and it is possible that some of them display other
173 survival modes that were too rare to describe statistically.

174 Survival modes varied in abundance (Supplementary Table 3) and dynamics across
175 forested plots (Fig. 3). The *Canopy* mode was typically the most species rich, followed by the
176 *Understory* and *Large Canopy* modes (Supplementary Table 4). The species included in the
177 cluster analysis represented 76.7% (range: 46.9-97.0%) of the biomass on average across the
178 plots (Supplementary Table 3 & Supplementary Fig. 2).

179 We calculated carbon lost to mortality at each site in order to understand the influence of
180 these survival modes on carbon residence times. Total carbon loss from tree mortality ranged
181 from 0.14 - 5.6 Mg C·ha⁻¹·yr⁻¹ with a mean of 2.28 Mg C·ha⁻¹·yr⁻¹ for all survival modes
182 including *Unclassified* (Fig. 3). The Lambir plot in Malaysia had the highest absolute rate of
183 annual carbon loss. The dry tropical forest Palamanui plot in Hawaii had the lowest rate of
184 annual carbon loss due to tree mortality. Somewhat surprisingly, the plots that are commonly
185 struck by typhoons and hurricanes (Luquillo, Palanan and Fushan) had intermediate rates of
186 carbon loss due to mortality even though the plots experienced storms during sampled intervals,
187 demonstrating that species at these sites are potentially selected to tolerate disturbances instead

188 of recover from them. The overall portion of carbon loss due to mortality varied greatly among
189 these forests, though on average Indo-Malaysian forests had the highest rates of absolute carbon
190 loss (Fig. 3); alternately, relative to total biomass neo-tropical forests lost slightly more biomass
191 (Supplementary Table 3).

192 Common plant traits had limited ability to predict survival modes, indicating that species
193 within given survival modes were diverse in these traits. Only the *Transient* mode was
194 significantly less dense wood than the other survival (ANOVA $F=9.65$, $p\text{-value}<0.001$, Fig 4a),
195 when we limited the analysis to sites (7 of 14) that had locally collected wood density values the
196 *Large Canopy* and the *Transient* groups had significantly lower wood density than the
197 *Understory* and *Canopy* survival modes (Supplementary Fig. 3). Leaf mass per area (LMA)
198 varied significantly among survival modes, with the *Transient* and *Large Canopy* species having
199 significantly lower LMA than the *Understory* and *Canopy* species (ANOVA, $F=7.28$, $p\text{-}$
200 $\text{value}<0.001$) (Fig 4b). The relation between the natural log of seed mass and survival mode
201 revealed no significant difference among clusters (ANOVA $F=2.26$, $p\text{-value}=0.086$) (Fig. 4c).
202 These analyses were constrained by the low current availability of functional trait data: LMA
203 was only available for 40.4% and seed mass for only 8.1% of species. This result does, however,
204 support an emerging consensus in the trait literature that using traits as proxies for life-history
205 strategies may be constrained to specific contexts and questions, and does not offer an easy link
206 between measurements and performance¹⁸⁻²⁰.

207 We related mean annual temperature (MAT), mean annual precipitation (MAP) and
208 cumulative water deficit (CWD) at each forest to the relative percent biomass of *Large Canopy*
209 survival mode species (Supplementary Fig. 4) to understand if there were climate dependencies

210 in survival mode composition. Multiple linear tobit regression (p-value = 0.000083, McFadden's
211 pseudo $R^2 = 0.24$, note this is not the same as OLS R^2 and a model with a statistically good fit to
212 the data will have McFadden's pseudo- R^2 between 0.2 and 0.4) indicated that *Large Canopy*
213 biomass relative abundance had a negative relation to MAT, but had a positive relation to CWD
214 and no relation to MAP. The relative percent biomass of *Canopy* and *Large Canopy* survival
215 modes were inversely related (Supplementary Fig. 2). *Transient* survival mode biomass was
216 miniscule and was not modeled. The *Understory* mode relative biomass was positively related to
217 MAT (p-value = 0.031, McFadden's pseudo $R^2 = 0.12$), but lacked any significant relation to
218 CWD or MAP.

219 To further explore the characteristics of the survival modes, especially to understand how
220 survival and growth interact to affect the progression of individuals through their life-cycle, we
221 calculated mean growth rates by survival mode. We found that growth rates significantly differed
222 among survival types where the *Large Canopy* survival mode had the largest mean annual
223 growth rate $2.18 \text{ mm}\cdot\text{yr}^{-1}$, while the *Understory* survival mode was the slowest growing 0.52
224 $\text{mm}\cdot\text{yr}^{-1}$ (Fig. 5). A similar pattern was found when we expressed growth in terms of biomass
225 accumulation (Supplementary Fig. 5). The *Canopy* mode has nearly half the growth rate of the
226 *Large Canopy* mode suggesting carbon residence times of these two groups may be similar, but
227 the *Large Canopy* mode would sequester more carbon in a similar time frame.

228 We found strong correlation (marginal R^2 0.97) between observed biomass in each
229 survival mode and biomass predicted from an Individual Based Model (IBM) run at each site, in
230 which individuals were classified by survival mode (Fig. 6). Biomass was small and changed
231 little across census intervals, particularly for the *Understory* and *Transient* survival modes. The

232 accuracy of predictions of biomass varied for the *Large Canopy* and *Canopy* modes. Predicted
233 biomass was underestimated in the *Large Canopy* mode at Lambir and Laupahoehoe by 47.68
234 and 42.15 Mg·hectare⁻¹, respectively. In contrast, expected biomass was overestimated in the
235 *Canopy* and *Large Canopy* modes at BCI, by 14.45 and 26.62 Mg·hectare⁻¹ respectively.

236 **Discussion**

237 Our results provide objective and quantitative descriptions of global size-dependent tropical tree
238 survival that reflect some of the classic descriptors of tree species demographic strategies²¹. We
239 discovered groups of species that differ in how they survive as they grow. We found mortality at
240 small sizes varies among the survival modes, likely reflecting the tradeoffs inherent in competing
241 for limited resources (e.g. light) in the understory²², or susceptibility to pests²³ and
242 pathogens^{24,25}. We also found that survival modes varied in their senescence phase, where causes
243 of mortality are likely driven by reallocation of resources from resistance or tolerance of
244 structural damage²⁶, water limitation¹⁶ and accumulation of pathogens²⁷ to increased investment
245 in reproduction. Our contention that this difference in survival at large sizes is a life-history
246 strategy and not simply a product of a lower average survival rate for earlier senescing modes is
247 supported by the fact that three of the four modes had very similar maximum survival rates, but
248 differed remarkably in their size at senescence.

249 Past studies have indicated that tree survival under environmental stress can depend on
250 tree size^{16,28}. We discovered that climatic factors correlated well with the relative biomass of
251 survival modes. The climate correlates with different proportions of survival modes suggests
252 differences in carbon residence times and forest structure with climate. Higher relative biomass
253 in the *Large Canopy* survival mode was observed in forests with lower MAT and longer dry

254 seasons and less *Canopy* species biomass. Considering that larger individuals can be more
255 susceptible to drought¹⁶, the cumulative water deficit result seems counter-intuitive at first, but it
256 may be that these species are deciduous or have particular adaptations for water limitation
257 tolerance in forests with intense dry seasons. Alternately, the prevalence of the *Large Canopy*
258 mode may be driven by other environmental factors not considered here, such as soils or
259 biogeographic history. The increase in the prevalence of the *Understory* mode with increasing
260 temperature suggests an advantage to being shaded in warmer forests. Indeed, photosynthetic
261 efficiency and stomatal conductance decline above a temperature threshold²⁷, which may provide
262 an advantage to being shaded in warmer forests though the best fit to the data was linear.
263 Differences in the dominance of these survival modes among tropical forests are likely driven by
264 many mechanisms and understanding those drivers is an important next step towards accurately
265 forecasting the fate of forests.

266 Widely collected plant traits explained some of the differences in size-dependent survival
267 modes in our analysis. Wood density has been previously recognized as a significant predictor of
268 tree survival^{29,30} and growth-survival trade-off in saplings³¹, but variation in size-dependent
269 survival was not explicitly considered in those analyses. We found that clear associations
270 between trait means and survival modes were demonstrated only for the *Transient* mode, which
271 likely describes many aggressive light-dependent pioneering species. Lower LMA in the
272 *Transient* and *Large Canopy* modes combined with mean growth rates of those modes suggests
273 that those species likely have higher metabolic costs, potentially lower leaf nitrogen
274 concentrations, and shorter life leaf-span³². Variation in seed mass may reflect a suite of
275 strategies independent from allocation to size-dependent survival at the sizes we examined. Seed

276 mass among reproductive adults might correlate better with individual growth rates or different
277 species' reproduction life-history strategies³³ and seed mass may correlate with survival in
278 individuals < 1cm diameter at breast height (DBH).

279 Our model predictions fit observed forest biomass well in an IBM. Despite large amounts
280 of demographic data being available globally, few studies have moved beyond descriptions of
281 mortality averaged over species or coarse size classes. Models in which survival probability
282 changes as a continuous function of size are necessary to accurately represent the variation in the
283 way that individuals of different species move through the life-cycle, thus allowing more
284 biologically nuanced forward projection of populations and communities. Even when combined
285 with a relatively simple growth model, the survival modes presented here were able to capture
286 the change in biomass at each site attributed to each survival mode.

287 The IBM projections demonstrate that our survival modes might offer benchmarks for
288 biome models that simulate forest dynamics at a global scale (e.g. terrestrial biome models
289 (TBMs)) or dynamic global vegetation models (DGVMs), where vegetation is coupled with
290 climate. Attempts at modelling carbon fluxes in DGVMs have led to very divergent results due
291 to the potential response of forests, both in estimates of future atmospheric carbon³⁴ and in
292 terrestrial vegetation carbon stocks⁶. The evolutionary strategies of tree survival, integrated
293 within the ecological models of environmental conditions might provide a better pathway
294 towards forecasting these diverse systems^{6,35}. To do so, however, requires integration of field
295 data, statistical models, and size-structured TBMs that can accept demographic data as inputs.
296 We compared the observed mortality rates from our plot data with mortality rates from one size-
297 structured DGVM, Functionally Assembled Terrestrial Ecosystem Simulator (FATES), with one

298 tropical broadleaf evergreen plant functional type³⁶. We found that FATES underestimated small
299 tree survival, but over-estimated large tree survival compared to our data. Specifically, the
300 annual mortality rate of trees larger than 70cm DBH in FATES was 1.47%, while the observed
301 mean annual mortality rate from ForestGEO plots for the same size class was 2.85%
302 (Supplementary Fig. 6), which could result in overestimation of carbon storage in the FATES
303 model. This deviation of the FATES model is not on the surface a large error; however mortality
304 rates compound annually, and this almost two-fold underestimate of annual mortality reflects a
305 significant mismatch to the pace of forest dynamics over decades. Incorporation of size-
306 dependent survival constraints could improve how we assess, and perhaps how we model
307 mortality for the suite of DVGMs that can incorporate size-based survival³⁷.

308 Despite the large range of species diversity and biomass turnover represented in our
309 analysis, we found consistent patterns of size-dependent survival (Supplementary Fig. 7) that are
310 not strongly tied to commonly collected plant traits. The relative abundance of different survival
311 modes varied with temperature and water deficit, which has implications for community
312 composition, dynamics and carbon storage. If the temperature-survival mode relation is
313 mechanistically driven, then as temperature rise forests would shift from dominance by *Large*
314 *Canopy* mode species to *Canopy* mode species resulting in less carbon sequestered. Future work
315 based on our findings should investigate how trade-offs in growth and survival affect the survival
316 modes identified, and how forecasting tropical carbon stocks could be improved by explicitly
317 considering large tree survival mechanism to constrain terrestrial carbon dynamics.

318 **Methods**

319 We used a global dataset of tree demography to build models of survival probability as a
 320 function of size. We used data from 14 plots that follow the same methodology: all woody stems
 321 ≥ 1 cm in diameter at breast height have been identified to species, mapped, and measured every
 322 five years (following³⁸ and summarized in Supplementary Table 1). All species with > 200
 323 observations across the censuses were included in the following analyses, comprising a total
 324 sample of over two million individuals in 1781 species. All analyses were conducted in R³⁹.

325 We estimated size-dependent survival by fitting a functional form to the data for every
 326 species in each census interval (see Fig.1 for workflow diagram). We used a Bayesian
 327 framework (see Supplementary Table 5 for details of model fitting), and fit the model in R using
 328 Stan⁴⁰. The basic form of the survival function allows for variations in the classic ‘U-shaped’
 329 mortality curve^{13,41-43} (ours is inverted to survival). Because the data are heavily weighted to
 330 small individuals and the mechanisms that cause mortality across size can vary significantly, we
 331 combined two logistic functions to describe mortality across size (see Supplementary Fig. 7 for
 332 examples of the species specific fits and Supplementary Fig. 8 for sites). The probability of
 333 survival is therefore given by

$$334 \quad S = \left(\frac{K}{1 + \exp(-r1((x-p1)))} \right)^t \quad \text{for all } x < \textit{thresh} \quad (\text{Equation 1})$$

335

$$336 \quad S = \left(\frac{K}{1 + \exp(-r2((x-p2)))} \right)^t \quad \text{for all } x \geq \textit{thresh}$$

337 where S is annual survival probability, K , r and p are the upper asymptote, the rate of change and
 338 the inflection point of the survival curve, x is size (DBH in mm), t is the time in years between

339 censuses, and *thresh* is the size threshold at which the two functions meet. The threshold was set
340 at the median DBH size (see Supplementary Fig. 7). This ensured that species had an equal
341 number of observations informing each of the two curves. Subscripts 1 and 2 denote parameters
342 for the curves describing survival in individuals below and above the size threshold respectively.

343 The parameters in these functions hold distinct meanings across tree life-history. K
344 determines the maximum annual survival probability, and usually remains constant over most of
345 the tree's life-history, especially in large statured species. Mortality of small individuals, often
346 due to thinning in the understory is determined by $r1$ and $p1$, and $r2$ and $p2$ define survival at the
347 largest sizes.

348 The five parameters from the joint survival functions ($K, r1, p1, r2, p2$) for each species
349 in each census interval were standardized to unit scale and included in a Principal Components
350 Analysis (PCA). To ensure that species had equal weight in the PCA, species were weighted
351 equal to the inverse of the number of census intervals over which they were modelled. We
352 derived modes of survival across species by performing a hierarchical cluster analysis on the first
353 five dimensions of the PCA using the "HCPC" function for hierarchical cluster analysis from the
354 R package *FactoMineR*⁴⁴. The HCPC function builds a dendrogram of species relatedness from a
355 similarity matrix. It then calculates the within- and between-group sum of squares (also termed
356 "inertia") for a range of potential cluster numbers and selects the number of clusters where the
357 change in between group variance is minimized⁴⁵. Four clusters were selected using this
358 algorithm, and we tested the robustness of the recommended clusters with Jaccard similarity
359 index produced via bootstrapping function, clusterboot in the *fpc* package¹⁷. To visualize these
360 modes (i.e., the four clusters, Fig. 2 and Supplementary Fig. 7), we used the mean values of

361 parameter sets within each cluster and their covariances to randomly draw 1000 simulated
362 survival curves. At each millimeter increment, from 1 to the maximum size, we then selected the
363 median, 50% and 90% quantile values. We also plotted the survival function corresponding to
364 the most representative species of each mode (Supplementary Fig. 8), i.e. the species from each
365 cluster closest to the centroid.

366 In calculations of biomass loss due to mortality for each survival mode, biomass was
367 calculated for the main stem of each tree using general tropical allometries for trees without
368 height measurements⁴⁶, as tree height measurements are not part of the ForestGEO monitoring
369 protocol. These allometries estimate height based on diameter of the stem and an environmental
370 index to ultimately calculate biomass. For each survival mode, annual carbon loss due to
371 mortality was based on tree diameter at the beginning of the census interval and made annual by
372 dividing by the mean census interval time (typically ~5 years) and we also report mean mortality
373 rate by survival mode at each site for comparability (Supplementary Fig. 9). Absolute annual
374 diameter growth rates were calculated for each survival mode by subtracting diameters at the
375 beginning of the census interval from the ending diameter and dividing by the time between
376 censuses for each tree.

377 We tested the correlation between survival modes and three common functional traits:
378 wood density, leaf mass per area (LMA), and seed mass. Trait values for wood density (n=1781,
379 some species were assigned genus or family level values when species specific values were not
380 available) were obtained from compiled databases⁴⁷⁻⁴⁹, half of the plots had locally collected
381 wood density values. Leaf mass per area (n=719) and seed mass (n=144) data were collected
382 locally^{31,50-52}. Differences between trait means among survival modes were compared with a

383 Tukey HSD test. To test associations between survival modes and climate variables, we
384 calculated mean annual temperature⁵³ (MAT), mean annual precipitation⁵³ (MAP) and mean
385 Climatic Water Deficit (CWD) for each plot (1901-2013)⁵³. As a metric of aridity, annual CWD
386 (mm yr⁻¹) was calculated as the sum of monthly deficit values which is the difference between
387 potential and actual evapotranspiration^{46,54}. Because the response variable was a percentage
388 bounded at 0 and 100, multiple tobit regression models were run with backwards selection using
389 the *vglm* function in the VGAM package⁵⁵ on MAT, MAP and CWD. Residual diagnostics
390 indicated that the Palamanui plot data was an outlier and was subsequently removed from the
391 analysis of climate relations; none of the remaining plots data had undue leverage on the
392 regression. The best fit model by AICc contained MAT and CWD as significant predictors.

393 We projected the biomass at each site across census intervals using an Individual Based
394 Model (IBM) parameterized with mean parameters for each survival mode, i.e. stems were
395 assigned a survival mode and each year grew and survived with probabilities corresponding to
396 the 95th% growth rate and the size-dependent survival curve of that mode. The site level IBM
397 was initialized by the diameter distribution for each survival mode in the first census and then
398 projected forward in time the length of the census interval at each site. At the end of the
399 projection, we calculated biomass in each survival mode based on the mean wood density of
400 each mode. We used the 95th percentile of growth rates by survival mode in the model to best
401 capture canopy tree growth rates which are the greatest contributors to biomass, we also present
402 the results using mean growth rate for comparison (Supplementary Fig. 10). Biomass was
403 calculated as above using the mean wood density of each survival mode rather than species
404 specific values.

405

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418 DT, JT, MNU, MU, RV, SY, JZ contributed data, provided site specific information and helped
419 revise the manuscript. All authors contributed to the final version of the manuscript.

420 The authors declare no competing interests.

421 **Data availability:** The data that support the findings of this study are available from the
422 corresponding author upon reasonable request. Individual plot data can be requested from:

423 <http://www.forestgeo.si.edu/group/Data/Access+the+data>

424

425 **References**

426 1 Bonan, G. B. Forests and climate change: forcings, feedbacks, and the climate benefits of forests.
427 *Science* **320**, 1444-1449, doi:10.1126/science.1155121 (2008).

428 2 Pan, Y. *et al.* A large and persistent carbon sink in the world's forests. *Science* **333**, 988-993,
429 doi:10.1126/science.1201609 (2011).

430 3 Wright, S. J. The carbon sink in intact tropical forests. *Global Change Biology* **19**, 337-339,
431 doi:10.1111/gcb.12052 (2013).

432 4 Brienen, R. J. W. *et al.* Long-term decline of the Amazon carbon sink. *Nature* **519**, 344-348,
433 doi:10.1038/nature14283 (2015).

434 5 Allen, C. D., Breshears, D. D. & McDowell, N. G. On underestimation of global vulnerability to
435 tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**, 1-55,
436 doi:10.1890/ES15-00203.1 (2015).

437 6 Friend, A. D. *et al.* Carbon residence time dominates uncertainty in terrestrial vegetation
438 responses to future climate and atmospheric CO₂. *Proceedings of the National Academy of*
439 *Sciences* **111**, 3280-3285, doi:10.1073/pnas.1222477110 (2014).

440 7 McMahon, S. M., Parker, G. G. & Miller, D. R. Evidence for a recent increase in forest growth.
441 *Proceedings of the National Academy of Sciences* **107**, 3611-3615,
442 doi:10.1073/pnas.0912376107 (2010).

443 8 van der Sande, M. T. *et al.* Abiotic and biotic drivers of biomass change in a Neotropical forest.
444 *Journal of Ecology*, n/a-n/a, doi:10.1111/1365-2745.12756 (2017).

445 9 Johnson, M. O. *et al.* Variation in stem mortality rates determines patterns of above-ground
446 biomass in Amazonian forests: implications for dynamic global vegetation models. *Global*
447 *Change Biology* **22**, 3996-4013, doi:10.1111/gcb.13315 (2016).

448 10 Chesson, P. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343-+
449 (2000).

450 11 Adler, P. B., Ellner, S. P. & Levine, J. M. Coexistence of perennial plants: an embarrassment of
451 niches. *Ecol. Lett.* **13**, 1019-1029, doi:10.1111/j.1461-0248.2010.01496.x (2010).

452 12 Purves, D. & Pacala, S. Predictive models of forest dynamics. *Science* **320**, 1452-1453,
453 doi:10.1126/science.1155359 (2008).

454 13 Coomes, D. A. & Allen, R. B. Mortality and tree-size distributions in natural mixed-age forests.
455 *Journal of Ecology* **95**, 27-40, doi:10.1111/j.1365-2745.2006.01179.x (2007).

456 14 Rees, M., Condit, R., Crawley, M., Pacala, S. & Tilman, D. Long-Term studies of vegetation
457 dynamics. *Science* **293**, 650-655, doi:10.1126/science.1062586 (2001).

458 15 Cobb, R. C., Filipe, J. A. N., Meentemeyer, R. K., Gilligan, C. A. & Rizzo, D. M. Ecosystem
459 transformation by emerging infectious disease: loss of large tanoak from California forests.
460 *Journal of Ecology* **100**, 712-722, doi:10.1111/j.1365-2745.2012.01960.x (2012).

461 16 Bennett, A. C., McDowell, N. G., Allen, C. D. & Anderson-Teixeira, K. J. Larger trees suffer most
462 during drought in forests worldwide. *Nature Plants* **1**, 15139, doi:10.1038/nplants.2015.139
463 (2015).

464 17 Hennig, C. Dissolution point and isolation robustness: Robustness criteria for general cluster
465 analysis methods. *Journal of Multivariate Analysis* **99**, 1154-1176,
466 doi:<http://dx.doi.org/10.1016/j.jmva.2007.07.002> (2008).

467 18 Kraft, N. J. B., Godoy, O. & Levine, J. M. Plant functional traits and the multidimensional nature
468 of species coexistence. *Proceedings of the National Academy of Sciences* **112**, 797-802,
469 doi:10.1073/pnas.1413650112 (2015).

470 19 Visser, M. D. *et al.* Functional traits as predictors of vital rates across the life cycle of tropical
471 trees. *Funct. Ecol.* **30**, 168-180, doi:10.1111/1365-2435.12621 (2016).

- 472 20 Joseph Wright, S. *et al.* Functional traits and the growth-mortality trade-off in tropical trees.
473 *Ecology* **91**, 3664-3674, doi:10.1890/09-2335.1 (2010).
- 474 21 Vanclay, J. K. Mortality functions for north queensland rain forests. *Journal of Tropical Forest*
475 *Science* **4**, 15-36 (1991).
- 476 22 Rüger, N., Huth, A., Hubbell, S. P. & Condit, R. Response of recruitment to light availability across
477 a tropical lowland rain forest community. *Journal of Ecology* **97**, 1360-1368, doi:10.1111/j.1365-
478 2745.2009.01552.x (2009).
- 479 23 Eichhorn, M. P., Nilus, R., Compton, S. G., Hartley, S. E. & Burslem, D. F. R. P. Herbivory of
480 tropical rain forest tree seedlings correlates with future mortality. *Ecology* **91**, 1092-1101,
481 doi:10.1890/09-0300.1 (2010).
- 482 24 Bell, T., Freckleton, R. P. & Lewis, O. T. Plant pathogens drive density-dependent seedling
483 mortality in a tropical tree. *Ecology Letters* **9**, 569-574, doi:10.1111/j.1461-0248.2006.00905.x
484 (2006).
- 485 25 Packer, A. & Clay, K. Soil pathogens and spatial patterns of seedling mortality in a temperate
486 tree. *Nature* **404**, 278-281 (2000).
- 487 26 Chambers, J. Q., Santos, J. d., Ribeiro, R. J. & Higuchi, N. Tree damage, allometric relationships,
488 and above-ground net primary production in central Amazon forest. *Forest Ecology and*
489 *Management* **152**, 73-84, doi:[http://dx.doi.org/10.1016/S0378-1127\(00\)00591-0](http://dx.doi.org/10.1016/S0378-1127(00)00591-0) (2001).
- 490 27 Silver, E. J., Fraver, S., D'Amato, A. W., Aakala, T. & Palik, B. J. Long-term mortality rates and
491 spatial patterns in an old-growth Pinus resinosa forest. *Canadian Journal of Forest Research* **43**,
492 809-816, doi:10.1139/cjfr-2013-0139 (2013).
- 493 28 McDowell, N. G. & Allen, C. D. Darcy's law predicts widespread forest mortality under climate
494 warming. *Nature Clim. Change* **5**, 669-672, doi:10.1038/nclimate2641 (2015).
- 495 29 Kraft, N. J. B., Metz, M. R., Condit, R. S. & Chave, J. The relationship between wood density and
496 mortality in a global tropical forest data set. *New Phytologist* **188**, 1124-1136,
497 doi:10.1111/j.1469-8137.2010.03444.x (2010).
- 498 30 Poorter, L. The relationships of wood-, gas- and water fractions of tree stems to performance
499 and life history variation in tropical trees. *Annals of Botany* **102**, 367-375,
500 doi:10.1093/aob/mcn103 (2008).
- 501 31 Wright, S. J. *et al.* Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*
502 **91**, 3664-3674, doi:10.1890/09-2335.1 (2010).
- 503 32 Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J. & Villar, R. Causes and consequences of
504 variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* **182**, 565-588,
505 doi:10.1111/j.1469-8137.2009.02830.x (2009).
- 506 33 Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. & Wright, I. J. Plant ecological strategies:
507 some leading dimensions of variation between species. *Annual Review of Ecology and*
508 *Systematics* **33**, 125-159 (2002).
- 509 34 Kramer-Schadt, S., Revilla, E., Wiegand, T. & Grimm, V. Patterns for parameters in simulation
510 models. *Ecol. Model.* **204**, 553-556, doi:10.1016/j.ecolmodel.2007.01.018 (2007).
- 511 35 Dietze, M. C. *et al.* A quantitative assessment of a terrestrial biosphere model's data needs
512 across North American biomes. *Journal of Geophysical Research: Biogeosciences* **119**, 286-300,
513 doi:10.1002/2013JG002392 (2014).
- 514 36 Massoud, E. C. *et al.* Identification of key biological controls in forest dynamics based on a
515 sensitivity analysis to the Community Land Model with Ecosystem Demography, CLM4.5(ED).
516 *Journal of Advances in Modeling Earth Systems* ((in review)).

517 37 Fisher, R. A. *et al.* Vegetation Demographics in Earth System Models: a review of progress and
518 priorities. *Global Change Biol.*, n/a-n/a, doi:10.1111/gcb.13910 (2017).

519 38 Condit, R. *Tropical forest census plots: methods and results from Barro Colorado Island, Panama*
520 *and a comparison with other plots.* (Springer Science & Business Media, 1998).

521 39 R: A language and environment for statistical computing (R Foundation for Statistical
522 Computing, Vienna, Austria, 2015).

523 40 Stan: a C++ library for probability and sampling v. 2.10.0 (2015).

524 41 Marod, D., Kutintara, U., Yarwudhi, C., Tanaka, H. & Nakashisuka, T. Structural dynamics of a
525 natural mixed deciduous forest in western Thailand. *Journal of Vegetation Science* **10**, 777-786,
526 doi:10.2307/3237302 (1999).

527 42 Metcalf, C. J. E., Horvitz, C. C., Tuljapurkar, S. & Clark, D. A. A time to grow and a time to die: A
528 new way to analyze the dynamics of size, light, age, and death of tropical trees. *Ecology* **90**,
529 2766-2778 (2009).

530 43 Miura, M., Manabe, T., Nishimura, N. & Yamamoto, S.-i. Forest canopy and community dynamics
531 in a temperate old-growth evergreen broad-leaved forest, south-western Japan: a 7-year study
532 of a 4-ha plot. *Journal of Ecology* **89**, 841-849, doi:10.1046/j.0022-0477.2001.00603.x (2001).

533 44 Lê, S., Josse, J. & Husson, F. FactoMineR: An R package for multivariate analysis. *Journal of*
534 *Statistical Software* **25**, 1-18 (2008).

535 45 Husson, F., Josse, J. & Pages, J. Principal component methods-hierarchical clustering-partitional
536 clustering: why would we need to choose for visualizing data. *Applied Mathematics Department*
537 (2010).

538 46 Chave, J. *et al.* Improved allometric models to estimate the aboveground biomass of tropical
539 trees. *Global Change Biology* **20**, 3177-3190, doi:10.1111/gcb.12629 (2014).

540 47 Chave, J. *et al.* Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351-366,
541 doi:10.1111/j.1461-0248.2009.01285.x (2009).

542 48 Swenson, N. G. *et al.* Temporal turnover in the composition of tropical tree communities:
543 functional determinism and phylogenetic stochasticity. *Ecology* **93**, 490-499, doi:10.1890/11-
544 1180.1 (2012).

545 49 Zanne, A. E. *et al.* (Dryad Digital Repository, Dryad Digital Repository, 2009).

546 50 Katabuchi, M., Kurokawa, H., Davies, S. J., Tan, S. & Nakashizuka, T. Soil resource availability
547 shapes community trait structure in a species-rich dipterocarp forest. *Journal of Ecology* **100**,
548 643-651, doi:10.1111/j.1365-2745.2011.01937.x (2012).

549 51 L. Sack *et al.* (L. Sack, unpublished, 2017).

550 52 L. Sack & Yoshinaga, A. (unpublished, 2017).

551 53 Anderson-Teixeira, K. J. *et al.* CFS-ForestGEO: a worldwide network monitoring forests in an era
552 of global change. *Global Change Biology* **21**, 528-549, doi:10.1111/gcb.12712 (2015).

553 54 Stephenson, N. L. Climatic control of vegetation distribution: The role of the water balance. *The*
554 *American Naturalist* **135**, 649-670 (1990).

555 55 Yee, T. W. The VGAM package for categorical data analysis. *Journal of Statistical Software* **32**, 1-
556 34 (2010).

557

558

559 Figure Captions

560 Figure 1. Schematic diagram of the workflow for this analysis.

561 Figure 2. Survival probability as a function of DBH for each of the four identified survival
562 modes. Survival modes were derived from a hierarchical cluster analysis on the parameters from
563 the survival function fit to 1781 species at 14 large area forest plots. In each species, the survival
564 function consists of two curves fit to individuals above and below a species specific size
565 threshold. The means of the size thresholds for species within each mode are shown with the
566 vertical dashed lines. In each mode, the solid line represents the mean of the survival functions
567 from species within the mode and the lighter and darker shaded regions show the 50% and 90%
568 uncertainty range around the mean. Parameters for each mean curve are listed in Supplementary
569 Table 2.

570 Figure 3. Site-level mean annual aboveground carbon loss to mortality for each survival mode
571 across all census intervals including error bars for standard error. Species that did not have
572 enough individuals to model survival are presented as Unclassified. Corollary figure for
573 mortality rates presented in Supplementary Fig. 10.

574 Figure 4. In general, traits do not map strongly onto the four survival modes. A) Natural log
575 transformed wood specific gravity at all sites. B) Leaf mass per area at 6 sites (Lambir, BCI,
576 Luquillo, Laupahoehoe, Palamanui and Fushan), C) Natural log transformed seed mass and
577 survival modes at Luquillo, Laupahoehoe, Palamanui and BCI where there were no significant
578 differences between survival modes. Letters represent significant differences among survival
579 modes in traits at $\alpha=0.05$ by Tukey HSD test.

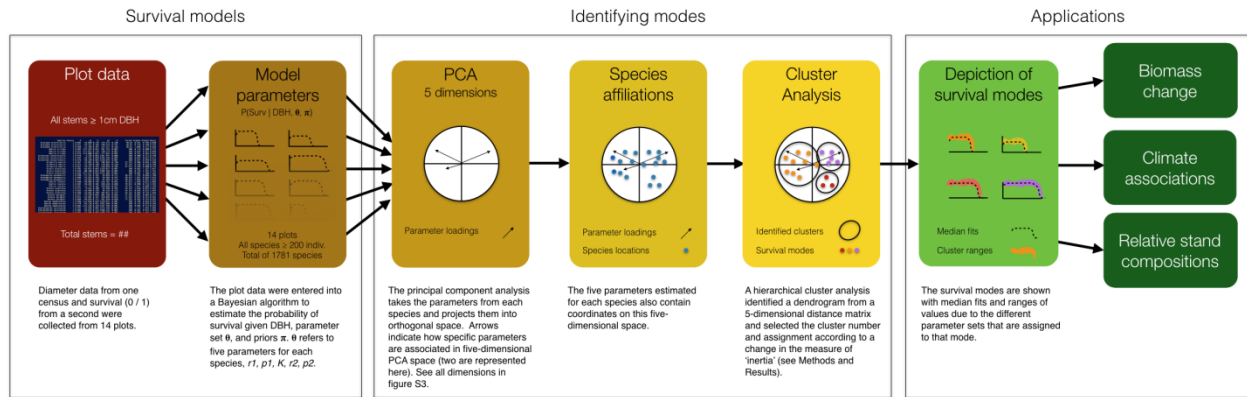
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581 Figure 5. Plot level average annual individual growth rate by survival mode boxplots with the
582 width scaled to the square-root of the number of species that make up the survival mode for all
583 forest plots. Significant differences (n=14, alpha=0.5, Tukey HSD test) denoted by letters above
584 category.

585

586 Figure 6. Observed biomass by survival mode versus predicted biomass from an individual based
587 model at each site (marginal $R^2 = 0.9735$). The line between points traces census interval
588 typically diverging from the dashed line, which represents the 1:1 line, with time.

589

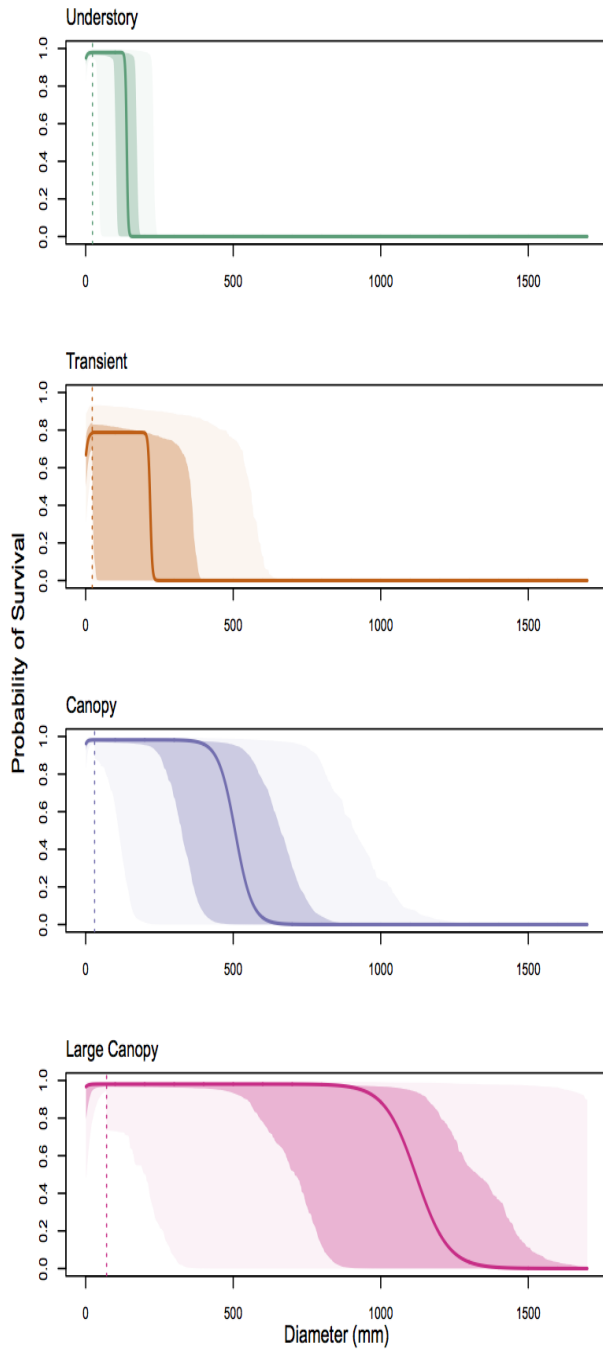


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591 Figure 1

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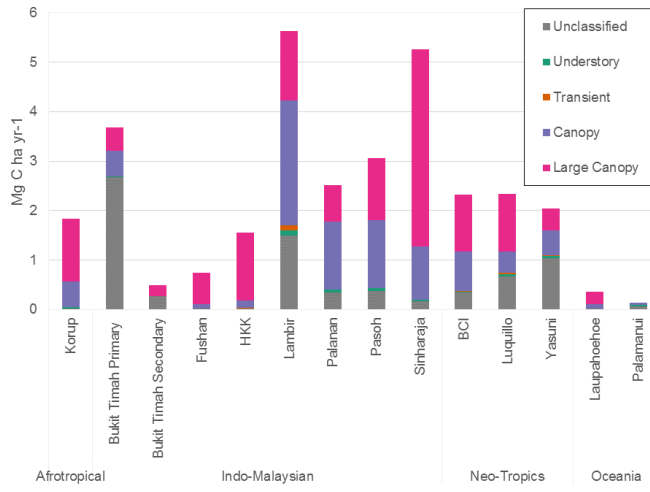


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595 Figure 2

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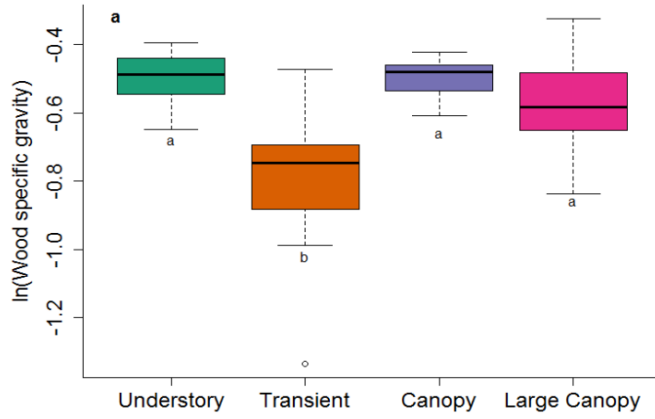


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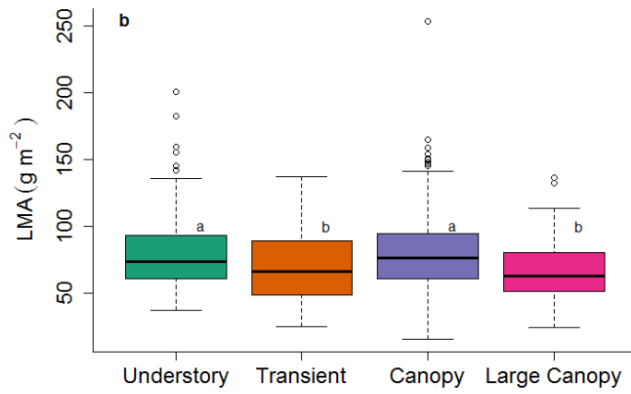
599 Figure 3

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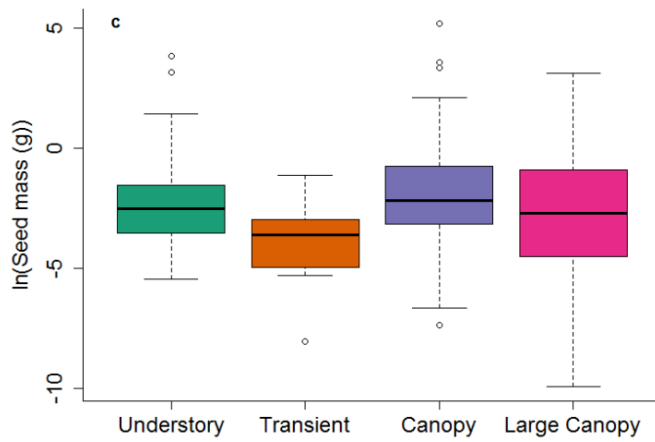
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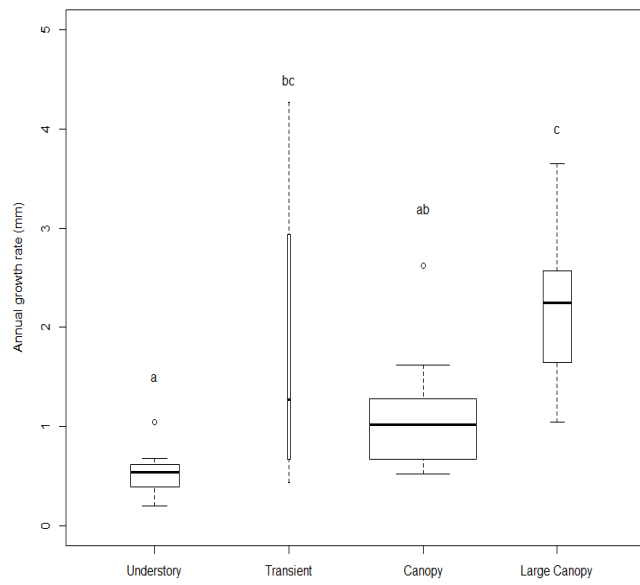
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605 Figure 4

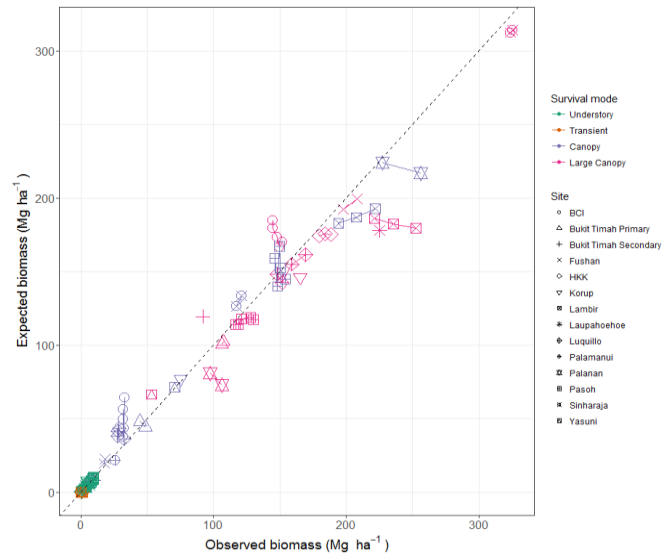
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608 Figure 5

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611 Figure 6

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