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Disentangling competitive versus climatic drivers of tropical forest mortality

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Abstract

1. Tropical forest mortality is controlled by both biotic and abiotic processes, but how these processes interact to determine forest structure is not well understood. Using long-term demography data from permanent forest plots at the Paracou Tropical Forest Research Station in French Guiana, we analyzed the relative influence of competition and climate on tree mortality. We found that self-thinning is evident at the stand level, and is associated with clumped mortality at smaller scales (< 2 m) and regular spacing of living trees at intermediate (2.5-7.5 m) scales. A competition index based on spatial clustering of dead trees was used to build predictive mortality models, which also accounted for climate interactions.

2. The model that most closely fitted observations included both the competition index and climatic variables, with climate-only and competition-only models less informative than the full model. There was strong evidence for U-shaped size-specific mortality, with highest mortality for small and very large trees, as well as sensitivity of trees to drought, especially when temperatures were high, and when soils were water saturated. The effect of the competition index was more complex than expected *a priori*: a higher CI index was associated with lower mortality odds, which we hypothesize is caused by gap-phase dynamics, but there was also evidence for competition-induced mortality at very high CI values.

3. The strong signature of competition as a control over mortality at the stand and individual scales confirms its important role in determining tropical forest structure. The complexity of the competition-mortality relationship and its interaction with climate indicates that a thorough consideration of the scale of analysis is needed when inferring the role of competition in tropical forests, but demonstrates that climate-only mortality models can be significantly improved by including competition effects, even when ignoring species-specific effects.

4. *Synthesis* Empirical models such as the one developed here can help constrain and improve process-based vegetation models, serving both as a benchmark and as a means to disentangle mortality processes. Tropical vegetation dynamic models would benefit greatly from explicitly considering the role of competition in stand development and self-thinning while modeling demography, as well as its interaction with climate.

Introduction

Over the past few decades, reports of increased tree mortality worldwide have raised concern regarding the future of the world's forests under climate change (Breshears *et al.* 2005, 2009; van Mantgem *et al.* 2009; Allen *et al.* 2010, 2015; Peng *et al.* 2011). These reports come from a variety of observational studies (Breshears *et al.* 2005; van Mantgem *et al.* 2009), ranging from tropical ecosystems in South America (Phillips *et al.* 2004; Brienen *et al.* 2015) to semi-arid systems in Australia (Brouwers *et al.* 2013), and are sometimes accompanied by experimental work showing strong sensitivity of forests to drought (Nepstad *et al.* 2007; da Costa *et al.* 2010). Attributing the causality of tree mortality is crucial for understanding as well as predicting the impacts of climate change on forests, in order to conserve and manage ecosystem services, e.g. carbon sequestration, and biodiversity.

The Amazon Basin, as the world's largest and most species-rich rainforest (Garda *et al.* 2010), and one of the largest regional terrestrial carbon sinks (Phillips *et al.* 2008; Brienen *et al.* 2015), has been the focus of several forest mortality studies following droughts in 2005 and 2010. In recent decades, long-term monitoring plots have shown that tree mortality has increased across Amazonia (Phillips *et al.* 2004; Laurance *et al.* 2009; Brienen *et al.* 2015), with net carbon uptake, i.e. the carbon sink, either saturating or weakening as a result (Phillips *et al.* 2008; Lewis *et al.* 2011; Brienen *et al.* 2015). Explanations for increased mortality have focused primarily on climatic drivers such as drought (Nepstad *et al.* 2007; Malhi *et al.* 2009; Phillips *et al.* 2009; Feldpausch *et al.* 2016) and drought-induced fire (Brando *et al.* 2014), often using a trait-based approach (e.g., wood density; Chao *et al.* 2008; Aubry-Kientz *et al.* 2013). However, other studies suggest that factors related to stand-age effects (e.g., disturbance, crowding) have an equally important effect on forest structure (Fisher *et al.* 2008; Gloor *et al.* 2009).

While it is well known that forest mortality is driven by multiple processes and their interactions (McDowell *et al.* 2011), ranging from biotic processes such as competition (Peters 2003; Delbart *et al.* 2010), herbivory (Christensen *et al.* 1995), disease (Logan *et al.* 2010), and senescence, to abiotic ones such as climate-driven death (Breshears *et al.* 2009) and natural disaster, e.g., floods, the ultimate causes of tree mortality in the tropics are poorly understood and vary strongly in intensity (background versus catastrophic mortality), spatial scale (local to large-scale), and temporal scale (gradual to sudden; Lugo & Scatena 1996). In spite of this complexity, ecosystem models such as dynamic global vegetation models (DGVMs) often use a constant mortality rate, and have limited ability to accurately simulate observed forest demography and resulting ecosystem carbon, water and energy fluxes, particularly in the tropics (Fisher *et al.* 2010; Joetzjer *et al.* 2014; Sitch *et al.* 2015). Considering the increasing use of DGVMs for a variety of predictive purposes ranging from coupled global climate models (Sellers *et al.* 1996; Bonan 1998) to understanding the effect of forest management activities (Chang *et al.* 2013), improving the representation of tree mortality in DGVMs is a high priority. A more detailed

understanding of the complexity of drivers of mortality across tropical regions requires studies of all potential drivers, as well as their interactions.

One of the main autogenic drivers of tree mortality is competition (Reineke 1933; Long & Smith 1984; Vanclay 1994; Enquist *et al.* 1998; Taubert *et al.* 2015; Farrior *et al.* 2016). As a forest stand develops, individuals compete for increasingly scarce water, nutrient and light resources; this results in decreasing stand density, while survivors increase in size - a phenomenon referred to as "self-thinning" (Yoda *et al.* 1963; Mohler *et al.* 1978). An extensive body of work supports the occurrence of self-thinning in boreal and temperate forest ecosystems (Reineke 1933; Yoda *et al.* 1963; Mohler *et al.* 1978; Westoby 1984; Pretzsch 2006), with less of an emphasis on tropical forests (but see, e.g., Poorter *et al.* 2016), and a variety of mathematical descriptions of the process have been developed (Reineke 1933; Yoda *et al.* 1963; Westoby 1984; Enquist *et al.* 1998; Taubert *et al.* 2015).

Here, we evaluate how competition and self-thinning affect temporal and spatial patterns of mortality in wet tropical forests across multiple scales, and how these processes interact with climate-induced mortality. Using long-term and large-scale monitoring plots, we investigate if self-thinning-related mortality is verified from data in tropical forests through self-thinning curves based on stand density and average tree biomass. We then analyze the resulting spatial patterns of living and dead trees, since mortality from competition should result in a clumped pattern of dead trees, and overdispersion (regular spacing) of living trees. Finally, a predictive mortality model is developed using logistic regression to evaluate if competition as a predictor of mortality improves accuracy in the presence of temperature and precipitation covariates. With this approach we assess competition for entire stands and for individual trees, as well as quantify climate effects on individual tree mortality. As we do not include data on trees <10 cm diameter in this analysis, we focus on examining well-established trees rather than early ecological filtering processes.

Material and methods

Study area and data set

Our analyses are based on an extensive forest inventory data set collected at the Paracou Tropical

Forest Research Station (5°18' N, 52°53' W; Fig. S1, Fig. S6) in a lowland tropical rainforest close to

Sinnamary, French Guiana. Mean annual precipitation at Paracou equals 2980 mm (30-year period), with

a dry season from August through November (Wagner *et al.* 2011). Inventory data from 1984 through

2014 were analyzed, representing measurements from almost 29,000 individual trees from nearly 600

species. Field data were collected annually in six 6.25-ha plots (numbered 1, 6, 11, 13, 14, 15) between

July and September at the onset of the dry season. Incomplete or missing censuses (1996, 1998, 2000,

2002, 2004, 2006) were not considered. Only individuals ≥ 10 cm diameter at breast height (1.35 m;

DBH) were recorded. For each tree record (~460,000 total) in the data set the circumference was

measured and coordinates were noted. Individual trees were identified to species for 88% of records,

but in some cases only to genus (5%) or family (1%). Six percent of records were not identified to family.

Trees were also coded every year as alive or dead, with a further description of its state (e.g., death due

to fallen neighboring tree or windthrow).

Pre-processing

We analyzed diameter (d), specific wood gravity or density (ρ), and aboveground biomass (*AGB*) for each

tree record. Tree diameter at breast height was calculated from the field-measured circumference.

Specific wood gravity was obtained from the Global Wood Density Database (GWDD) found on the

Dryad repository (Chave *et al.* 2009; Zanne *et al.* 2009). Species-level median (to avoid potential outliers)

wood density was used when multiple values were available. Where trees were not identified to species

or data on species were not available in the GWDD, genus- or family-level medians were used. For trees

not identified to family, the median density for tropical South America was used (0.625 g/cm^3). Lastly,

AGB was calculated using the allometric equation from Chave *et al.* (2014), recommended for use when data for a local diameter-AGB model is not available, and when height data is not collected:

$$AGB = \exp(-1.803 - 0.976 \times E + 0.976 \times \ln(\rho) + 2.673 \times \ln(d) - 0.0299 \times \ln(d)^2) \qquad \text{(Eq. 1)}$$

Here, *E* represents a metric of environmental stress, incorporating the effects of temperature and precipitation seasonality, and climatic water deficit, and was derived from a global gridded layer of E at 2.5 arc sec resolution (Chave *et al.* 2014). All of the study plots fell within a single grid cell of the raster, and thus a constant value (*E* = -0.1014973) was used.

Self-thinning

We fitted self-thinning curves (Westoby 1984) to the inventory data by calculating the log-transformed (base 10) AGB per individual (kg) and tree density (per ha) for every year and plot. Only living trees with diameter >10 cm were considered. AGB per individual was then modeled as a function of density using simple linear regression, per 6.25 ha plot:

$$\hat{\mu}\{\log_{10} AGB/individual \mid \log_{10} tree\ density\} = \hat{\beta}_0 + \hat{\beta}_1 \log_{10} tree\ density \text{ (Eq. 2)}$$

The estimated slope and its significance was used to evaluate whether or not the plot follows a self-thinning trajectory. To visualize size distributions per plot, we constructed per-plot boxplots of the diameter distributions of trees in the years 1995, 2001, and 2005 (Fig. S2), with years randomly selected using a number generator. This allowed us to explore whether dissimilar size distributions could explain differing self-thinning curve slopes across plots.

Spatial analysis of living and dead trees

Self-thinning mortality should result in clumping of dead trees, as well as the evolution of an overdispersed pattern of living trees (Kenkel 1988). As an additional test for self-thinning, we

investigated spatial patterns of both living and dead trees using second-order spatial statistics, i.e., evaluating spatial dependence between mortality/survival events of trees over a range of spatial scales.

Exact plot boundaries were estimated using the Ripley-Rasson method (Ripley & Rasson 1977) with all tree records from every year as the observed points. This algorithm computes an estimate of the spatial domain delineating the observations, assuming that the domain is a convex set. Using these observational windows, point patterns for dead and living trees were built. First, we used all dead tree records aggregated over all years for each plot, as mortality events tend to be rare in tropical forests (often < 5% per year; Condit *et al.* 1995; Phillips *et al.* 2004; Aubry-Kientz *et al.* 2013; < 2% per year in our dataset) and may extend over the course of several years. Trees that died directly due to physical damage by other (fallen) trees (21% of mortality records) were excluded since these causes of mortality could result in clumping of dead trees even if self-thinning were absent. Second, for the point-pattern of living trees, we used all living tree records partitioned by year for each plot.

For each plot, we compared the point pattern of dead trees to a uniform Poisson pattern using Besag's transformation of Ripley's K-function, also known as the L-function (Besag 1977). Ripley's K-function compares a point pattern at many spatial scales simultaneously to that expected under a homogeneous Poisson process. Besag's transformation is generally used for data analysis, as it stabilizes the variance of the estimator, making the L-function more useful for simulating critical envelopes and hypothesis testing. The transformation also linearizes the expected values of the function under a Poisson process. To facilitate comparisons across plots, the results were normalized by subtracting the expected from the observed L-function values. This allows for an easily interpretable graphical analysis in which $\hat{L}(r)$ is plotted against *r* (neighborhood distance), with positive L-function values indicating clustering, values close to zero suggesting a Poisson process, and negative values implying overdispersion (i.e., regularly-spaced events). To test for complete spatial randomness (CSR), two-sided 90% simultaneous critical

envelopes were computed using a Monte Carlo approach (Ripley 1981). If $\hat{L}(r)$ falls outside of the critical envelope for any value of r, then we reject the null hypothesis of CSR at a significance level (α) of 0.1. Our analysis was identical for living trees, except that the analysis was performed for each year separately. To make the significance of our results more readily comparable with other analyses using Ripley's K-function, we used α = 0.1 because many studies use pointwise methods for quantifying uncertainty for Ripley's K-function at a range of spatial scales, increasing the actual Type I error rate above that expected for the commonly used α = 0.05. Spatial analyses were performed using the R package *spatstat* (Baddeley *et al.* 2015).

Mortality modeling

To explore the role of competition in individual tropical tree mortality, we modeled individual mortality through logistic regression, a common choice for building tree mortality models (Monserud & Sterba 1999; Yao *et al.* 2001; Stephens & Finney 2002). Logistic regression enabled us to test the importance of interaction effects, for example between competition and climate, and yielded model parameters that are more easily interpretable than is the case for more complex machine learning algorithms. We considered a variety of tree-level and climatic variables (Table 2) for inclusion in the mortality model, evaluating climate-competition, climate-size, climate-climate, and competition-size interaction effects and second-order terms when their main effects were included in the model.

Two tree-level variables related to competition were tested: a competition index and DBH. The competition index (CI) was defined from measurements as total basal area of neighboring trees within a 5-meter radius; higher CI should thus indicate a higher potential for competition. Unlike other studies of competition in tropical forests (e.g. Uriarte *et al.* 2004), we chose not to differentiate between competition from conspecific versus heterospecific neighbors. Similarly, we did not use species traits as potential predictors, allowing us to evaluate the performance of mortality models that are naïve with

regard to taxonomic identity. The competition index was not normalized by tree size; instead, we investigated the effect of tree size (DBH) and its interaction with CI as predictors in the logistic regression. The radius of 5 m was chosen based on results from the spatial analysis; this was the scale at which living trees were strongly overdispersed (see *Results* section for further details). However, to investigate the sensitivity of our results to the choice of neighborhood size, we also tested basal area of neighboring trees within 10-m radius. Because the results from this alternative analysis were the same, in terms of variable selection and the sign and magnitude of coefficients, we only discuss models based on the 5-meter radius from the point pattern analysis. To investigate the influence of competition in the past, we also tested a 5-year average of basal area of neighboring trees within a 5-meter radius. This did not improve model performance, likely because CI changes little from year to year, and we therefore opted to use a single-year index here, using only CI from the appropriate census year. We also tested for the presence of lag effects, assessing the significance of previous year climatic variables.

For the climatic mortality component of the model, we extracted preceding wet- (December-July) and dry-season (August-November) temperature and precipitation from the latest version of the University of East Anglia Climatic Research Unit data base (CRU TS 3.23.01; Harris *et al.* 2014).

We performed variable selection and model comparison using the following principles:

1) The inclusion of variables that can be used to test common mortality hypotheses (Table 2)
2) The relative quality and parsimony of candidate models (assessed with model AIC; Akaike Information Criterion, which rewards higher model likelihood but penalizes overfitting)
3) The performance of a candidate model on a validation data set (assessed using model AUC; area under the receiver operating characteristic – ROC – curve; Fawcett 2006)

Models were fitted by randomly-selecting training data to generate a dataset representing 60% of the full record, while retaining a balance between dead and alive individuals, and then validated on the

remaining test set of the withheld 40% of records. We discuss the highest-performing model in each of three categories in the Results section: a competition-only model, a climate-only model, and a model including both competition and climate. All calculations and analyses were performed in R 3.2.2-3.3.1 (R Core Team 2016).

Results

Self-thinning

All plot-level regressions of tree density and individual biomass (Fig. 1) showed negative slopes, i.e., an increase in mean AGB per individual associated with a decrease in tree density, as predicted by self-thinning theory. Slopes varied from -1.13 (plots 1 and 14) to -1.81 (plot 15), and were significantly different from zero (p < 0.001; Table 1). Only the 95% confidence interval for plots 1 and 11 did not include -3/2 as a slope for self-thinning, a value often suggested in the literature (see, e.g., Zeide 1987), though this value was not predicted specifically for tropical forests. The regressions explained much of the variation in mean AGB per individual, ranging from 40% (plot 6) to 94% (plot 11). Diameter distributions for 1995, 2001, and 2005 were very similar across all plots (Fig. S2), with standard deviations of tree diameter only differing up to 2 cm between plots (Table S1), suggesting size distribution did not explain between-plot variation in self-thinning slopes.

Spatial analysis of living and dead trees

Dead trees (Fig. 2) were clustered in all six plots at short distances up to 2 meters. Plots 6 and 11 show additional, but weaker, clustering of mortality at intermediate distances of 3 to 8 meters. Given the use of two-sided 90% simultaneous critical envelopes, there is clear evidence in all plots against the hypothesis of a point pattern resulting from a random Poisson process.

For living trees (Fig. 3), there was evidence for overdispersion at intermediate spatial scales from 2.5 to 7.5 meters for all plots in nearly every year, as expected when competition results in more regularly-spaced trees (Kenkel 1988). At longer distances of up to 10 meters, spatial patterns tended towards more random distributions. At short distances up to 2.5 meters, all plots showed evidence for clustering of living trees. Plots 13, 14, and 15 also have a strong overdispersion peak near zero meters. The 5-meter neighborhood radius used for the competition index was chosen based on the overdispersion of living trees between the 2.5 m and 7.5 m found here.

Mortality modeling

We compared three alternative empirical models (Table 3): a model with competition, DBH, and climatic variables (model A), one with competition and DBH only (model B), and another with DBH and climatic variables only (model C). Models B and C can therefore be considered subsets of model A. In terms of AIC, model A (competition, DBH, and climatic variables; AIC = 40,510) outperforms models B (competition and DBH only; AIC = 40,865) and C (climatic variables and DBH only; AIC = 40,744), indicating a better fit to data even after adjusting for model complexity. In terms of predictive ability, model A (AUC = 58.15%) has greater predictive ability than models B (AUC = 57.87%) and C (AUC = 55.35%) using the withheld validation data. Interestingly, the climate-only model had a lower AIC (better) than the competition-only model, but lower predictive ability (AUC).

We present the covariate-mortality relationships for models A, B, and C graphically to aid interpretation (Figs. 4, S4, S5). All covariate-mortality relationships discussed here are strongly significant (p < 0.01; Table 3). CI and its quadratic term were included as predictors in models A and B, and we found significant interactions between CI and both precipitation variables, as well as with dry-season temperature in model A. Mortality initially declined with increasing CI (Figs. 4A-C, S4A), but the relationship flattened out at higher CI and eventually reverses (not shown). Because there are few records with very high CI we have limited confidence in the sharp increase of mortality at very high CI

(>100 m^2 ha^{-1}). Mortality at low CI was highest when dry-season precipitation was low (Fig. 4A), or when wet-season precipitation/temperature were low to moderate (Figs. 4B-C). The mortality-size relationship was also U-shaped in all three models, including a second-order term, with highest mortality for small and large trees (Figs. 4D, S4B, S5A). No size-CI or size-climate interactions were detected in any model.

In both models A and C, mortality increased with higher wet-season temperature and low wet-season precipitation, but decreased with increasing temperatures when precipitation was moderate to high (Figs. 4E-F, S5D-E). Mortality initially increased with increasing dry-season temperatures, but decreased at higher temperatures (Figs. 4H, S5B). However, the observed range of dry-season temperature is less than a single degree C, reflecting limited variation in dry-season temperatures and limiting confidence in the relationship between mortality and this variable. Finally, mortality varied strongly with dry-season precipitation, initially decreasing but then increasing (Figs. 4I, S5C). Dry-season precipitation varied significantly from year to year, ranging from less than 200 to more than 400 mm. We found no evidence for climate lag effects.

Discussion

Self-thinning

While competition, and the resulting self-thinning curve, have long been known to play an important role in shaping forest structure and development, a variety of approaches has been used to describe these processes, ranging from empirical geometric approaches (Reineke 1933; Yoda *et al.* 1963), which remain actively debated both in terms of slope, functional form, and even validity of the rules themselves (Zeide 1987; Lonsdale 1990; Weller 1991; Hamilton 1995), to the more mechanistic packing models of Enquist *et al.* (1998) and Taubert *et al.* (2015), explicitly considering three-dimensional forest structure (Taubert *et al.* 2015; Farrior *et al.* 2016). Historically, studies of self-thinning and competition

have focused on temperate biomes and within these, monospecific, even-aged stands (e.g., Aikman & Watkinson 1980; Lonsdale & Watkinson 1982; Kenkel 1988; Hynynen 1993; de Kroon & Kalliola 1995), with little work on uneven-aged stands of multiple species typical of tropical forests (but see, e.g., Kohyama 1992; Vanclay 1994, Taubert *et al.* 2015). Our results show that even simple empirical approaches can be useful to investigate self-thinning and competition in structurally complex tropical forests.

In our analysis, all six plots showed a strong power-law relationship between stem density in the standard average individual aboveground biomass. R^2 for the linear regressions of log-transformed biomass vs. log-transformed density varied from 40% (plot 6) to 94% (plot 11), indicating a good fit of observations to the self-thinning lines. All the forest monitoring plots had self-thinning slopes significantly different from zero (p < 0.001) and also showed an evolution over time from a pattern of high tree density and low individual biomass to lower density and higher biomass, as expected under self-thinning. While this supports the generalization of Yoda's law to non-temperate, uneven-aged stands of multiple species, the slopes of the self-thinning lines varied widely from -1.13 (plots 1 and 14) to -1.81 (plot 15) and thus were not in close agreement with Yoda's slope of -3/2 suggested for even-aged temperate stands. However, self-thinning slopes tend to be quite variable between species even in monospecific stands (Pretzsch 2006), and given the species diversity of trees in tropical forests it is not surprising that slopes for tropical stands could differ widely among plots, even if diameter distributions are very similar (Fig. S2) and plots are in close proximity to one another.

If self-thinning in the tropics indeed takes the form of a power-law relationship, as supported by our analysis, then this also supports the concept of a carbon carrying capacity (*sensu* Gupta & Rao 1994; Keith *et al.* 2009), which tends to be stable in the absence of anthropogenic disturbance and where climate change is limited. However, given that the plots studied here were not selectively logged in the past, yet a consistent "ageing" trend, with increased mean biomass per individual over time (Fig. 1), is

observed in the self-thinning curves, either the plots are still recovering from historical natural disturbance, or we are seeing increasing carbon packing efficiency due to climate/environmental changes. The latter hypothesis is supported by an observed increase in biomass at Paracou (Rutishauser *et al.* 2010), and the increasing, but slowing, tropical carbon sink (Brienen *et al.* 2015), and therefore has important implications for carbon sequestration trends in the tropics. However, recent work suggests that even if carbon storage capacity is reached faster in a changing environment, the capacity itself will not change (Körner 2017). The latter would support the disturbance recovery hypothesis.

Spatial analysis of living and dead trees

Our spatial analysis allowed us to test for expected spatial patterns resulting from self-thinning within stands. We found that tree mortality was significantly clustered at small scales – below 2 meters – implying that competition plays out strongly at this scale. Interestingly, this is smaller than the area of influence of 3.5 m reported for jack pine in boreal forest (Kenkel 1988), but not surprising given the strength of competition for resources such as light, water, and nutrients in structurally-diverse tropical forests. Such clumped mortality supports that self-thinning processes are removing individuals through competition.

While this clumped mortality pattern could also be produced by the presence of inhospitable micro-habitats with elevated rates of mortality, we found strong evidence for overdispersion of living trees at intermediate spatial scales (2.5 to 7.5 m). Self-thinning is expected to lead to overdispersion or regular spacing of living trees through negative density-dependence (e.g., Cooper 1961; Laessle 1965; Ford 1975; Kenkel 1988; Kenkel *et al.* 1997), in a process similar to anthropogenic thinning in managed forests, where resources and microhabitat quality tend to be more spatially homogeneous. The evolution of such a regularly-spaced pattern has been previously observed in tropical forests (Sterner *et al.* 1986).

Three plots (1, 6, 11) showed very strong clustering of living trees at distances near zero, while plots 13, 14, and 15 showed strong overdispersion at this scale. However, as individuals <10 cm DBH were not inventoried, we were unable to further explore spatial patterns at this very small spatial scale. Furthermore, given that coordinates for the inventory are only accurate to 0.5 meters, and trees have non-zero diameters, it is likely that analysis at such small scales causes artifacts (Cox 1987; Martens *et al.* 1997). It is not clear why the overdispersion of living trees seems to play out at larger spatial scales (2.5 to 7.5 meters) than mortality (clustered below 2 meters). While we chose to base our competition index on the scale of overdispersion (5 m neighborhood size), repeating this analysis using data from a site with higher numerical accuracy of coordinates, as well available data for trees below 10 cm DBH, would be very informative.

We note that the clustering of dead trees and overdispersion of living trees are also consistent with the Janzen-Connell hypothesis, which explains high plant species diversity in the tropics as a consequence of positive density-dependent juvenile mortality in the presence of conspecific adults (e.g., due to specialist predators), opening up more space for species coexistence and implying overdispersion within a given species (Janzen 1970; Clark & Clark 1984; Condit 2000; Nathan & Casagrandi 2004), as well as gap phase dynamics (see, e.g., Hunter *et al.* 2015). However, here we provide evidence that density-dependent mortality processes in tropical forests can be explained by competition rather than only disease or predation processes as proposed by Janzen-Connell.

Mortality modeling

Model A (competition index, DBH, and climatic variables) performed much better than models B and C (the competition-only and climate-only models) both in terms of fit to the data and predictive ability on a validation data set. This indicates that both competition and climate play an important role in determining mortality dynamics. Interestingly, the competition-only model had a poorer fit to the data

than the climate-only model, but had a higher predictive performance. This implies that competition may be more important in determining mortality than climate for the period of observation, but that the way we represented competition in the models may not capture the complexity of this process. This may not be true when climate-induced catastrophic mortality events occur, which were not observed in Paracou during the study period. It is important to emphasize that even model A, with both competition and climate covariates, had limited predictive ability. Given the difficulty of predicting background mortality, especially when species have very different traits that strongly affect mortality risk (e.g., Aubry-Kientz et al. 2013), this is to be expected. Overall, the evidence from the self-thinning curves, spatial analyses, and mortality models indicate that competition and self-thinning are a complex but important driver of tropical forest mortality beyond climate alone. Importantly, it is likely that mortality from climate and competition interact, e.g. competitive interactions are likely to be altered by climate-induced mortality.

The complexity of the mortality-competition relationship is highlighted by the functional relationship between the two in models that included the competition index (A and B). While mortality was predicted to increase with increasing competition index at very high densities, as expected with typical competitive dynamics, the models predicted a strong initial decline of mortality with a higher competition index. One hypothesis to explain this pattern is that the competition index represents differences in quality, i.e., nutrients and water-holding capacity, between individual tree sites. For example, increasing basal area could indicate that a tree is situated in a favorable microenvironment, e.g. a site with high water availability, thus decreasing mortality and increasing the carrying capacity of that site. However, there was no evidence that CTI (compound topographic index), a topographic wetness index, was different between living and dead trees (paired t-test, $p = 0.96$), and a logistic regression of mortality on CTI also showed no significant relationship ($p = 0.11$). We therefore reject this hypothesis, and instead propose that the observed relationship is a combined result of the processes of

gap-phase dynamics, competition, and increased mortality of large trees in older stands. Under gap-phase dynamics, basal area is low initially after the gap has formed, with many small trees, but mortality is high due to competition and the presence of pioneer, shade-intolerant species (Lang & Knight 1983; Brokaw 1985; Condit *et al.* 1995). As gaps recover to closed canopy, basal area increases, with an increase in tree size and decrease in mortality, as well as the gradual elimination of pioneer species. Eventually, when stand age and neighborhood basal area increases, competition and senescence strongly drive individual and stand-level mortality. It bears repeating that we only found evidence for such an increase in mortality at the very highest CI values, which were not frequently observed. The hypothesis for gap-phase dynamics agrees with observations that multiple density-dependent processes structure tropical forests (Peters 2003), and that the outcomes of density-dependent processes for forests are species-specific (Sterner *et al.* 1986; Martens *et al.* 1997; Peters 2003; Gray & He 2009) and differ between life stages (Sterner *et al.* 1986; Martens *et al.* 1997). Under gap-phase dynamics, we would expect mortality to be concentrated during early gap phases for small trees. Indeed, we found that small trees near the threshold of 10 cm DBH represent the majority of mortality events (Fig. S7), and this was corroborated by the DBH-mortality relationship in the individual mortality models. Furthermore, the mortality model results are also compatible with the results from the self-thinning curves and spatial analysis - whereas the mortality models are analyses at the individual-tree level and are suitable to capture ongoing gap dynamics, the self-thinning curves describe the biomass-density trajectory of the stand as a whole.

Importantly, the census data used here only included trees with a DBH above 10 cm, and a significant component of stand development could therefore not be investigated. In one tropical forest, ninety percent of all mortality observed was for stems below 10 cm DBH (Lang & Knight 1983), and collecting survivorship data for such small trees is therefore of high priority. Interestingly, we found no evidence for size-dependent sensitivity to competition (in trees >10 cm DBH), as is typically found in studies of

competition (e.g., Bella 1971), again showing the importance of collecting data for very small trees. However, there was strong evidence for size-dependence of mortality risk. Tall trees, and especially very small trees, were at much higher risk of mortality than trees of intermediate size, as was found in Lines *et al.* (2010) (also see Figs. S3 and S7 for mortality rate and count per 10-cm diameter class). With data for <10 cm DBH trees, the gap-phase dynamics explanation for the CI-mortality relationship could be further explored. Under these dynamics, we would expect to see most mortality happening in gaps where the neighborhood consists of small trees rather than large individuals.

We were also able to test the relationship between mortality and climatic variables in models A and C. All climatic variables had the same qualitative relationship with mortality in both models. Because inventories were made at the beginning of the dry season, we separated the climatic variables into preceding wet season and preceding dry season. The effect of temperature on tree mortality and growth in Amazonia is controversial, with researchers arguing for (Doughty & Goulden 2008) and against (Lloyd & Farquhar 2008) the existence of a temperature threshold above which tree stress occurs. However, increased mortality and carbon loss due to a combination of higher temperatures, generally associated with high water pressure deficits, and more frequent and prolonged droughts in the Amazon are well-documented (e.g., Condit *et al.* 1995; Williamson *et al.* 2000; Phillips *et al.* 2009, 2010). A combination of warm and dry conditions is reflected in a large vapor pressure deficit, with death from drought resulting from hydraulic failure rather than carbon starvation (Rowland *et al.* 2015). This "hotter drought" (*sensu* Allen *et al.* 2015) phenomenon is corroborated by our model. The effect of wet-season temperature on mortality depended on whether wet or dry conditions prevail. Under dry conditions, mortality increased with temperature, whereas under wet conditions mortality decreased. In other words, mortality was highest during years with hot and dry wet seasons. Surprisingly, dry-season temperature resulted in highest mortality at intermediate values. Further analysis is needed to determine whether this effect is real or is a statistical artifact due to the lack of information for

individuals below 10 cm DBH. We caution that dry-season temperature varied by less than a degree C during our study period, limiting the ability to extrapolate beyond this temperature range, whereas wet-season temperature varied much more and had a stronger effect. Both high and low values of dry-season precipitation were found to increase mortality. The increase in mortality at very high precipitation has been found previously for Paracou (Aubry-Kientz *et al.* 2015b), and has been explained in terms of poor root establishment (lower fine-root productivity and rooting depth) when soils are saturated (Ferry *et al.* 2010; de Toledo *et al.* 2012). We found no interaction between tree size and climatic variables, but this may again be caused by the lack of <10 cm DBH individuals in the data set. There were significant interactions between the competition index and all climate variables except wet-season temperature (in model A). At all observed levels of wet-season precipitation, and dry-season temperature and precipitation, mortality odds were highest under low values of the competition index. If our hypothesis of gap-phase dynamics is correct, this corresponds to the early phases of gap formation, and thus pioneer species and young stands may be disproportionately sensitive to climate-induced mortality. These results underscore that a better understanding of tropical forest dynamics will result from the joint consideration of climate, competition, and tree size.

We detected no evidence for climate lag effects. Given that a mortality analysis of multiple tropical forests found that climatic lag effects are limited to 2 years, and that most mortality effects play out within 9 months of droughts (Phillips *et al.* 2010), our lack of evidence for lag effects is not unexpected. In addition, such lag effects should be most apparent in response to extreme climate events, which were not readily apparent at Paracou during the study period.

Implications

We found convergent evidence at stand, amongst-stand, and individual-tree scales that competition plays an important role in determining forest structure and demography of the tropical forest plots

studied. While species-specific traits are also likely to strongly influence tree mortality in biodiverse tropical forests (e.g., Chao et al. 2008, Aubry-Kientz et al. 2013), our models indicate that mortality prediction can be significantly improved upon, compared to a climate-only model, when a competition index is included, even when species identity is ignored. Because mortality due to competition is often indirect and complex – e.g., due to increased sensitivity to disease, herbivory or, depletion of resources – the use of a simple and easily-derived index of competition to improve mortality prediction offers a promising path forward to capture this complexity phenomenologically. A future analysis could evaluate the generalizability of our results at other forest sites with large plots or at the scale of entire forest site networks, e.g., the Smithsonian Tropical Research Institute's Center for Tropical Forest Science network, though the annual censuses conducted at Paracou make this data set extremely relevant for the types of analysis reported here.

Mortality, especially background mortality, is difficult to predict because effect sizes associated with changes in causative agents, including environmental covariates and competition, may be small, and change slowly over time (e.g., increasing CO_2 concentrations), requiring high sampling power to detect. Though such data are more rare for tropical than temperate forests, there is a need to use long-term tropical inventories to model both background (natural low-intensity) and catastrophic (sudden high-intensity) mortality events. The analyses presented in this study were possible because of the yearly resolution of the Paracou census data; at most other tropical forest sites, censuses take place at longer intervals. Furthermore, catastrophic and background mortality may have very different causes (Lugo & Scatena 1996), with mortality studies in recent years focusing on drought-induced tree death (e.g., Condit *et al.* 1995; Nepstad *et al.* 2007; Phillips *et al.* 2009, 2010; Allen *et al.* 2010; Lewis *et al.* 2011; Brando *et al.* 2014), past patterns of growth (e.g., Wyckoff & Clark 2000; Bigler & Bugmann 2003; Chao *et al.* 2008; Aubry-Kientz *et al.* 2015a), and species-specific traits (e.g., Chao *et al.* 2008; Phillips *et al.* 2009; Kraft *et al.* 2010; Aubry-Kientz *et al.* 2013; Uriarte *et al.* 2016). As there were no extreme climate

events during the course of the Paracou forest inventories, we were limited in our evaluation of the impacts of this type of event on mortality and its interaction with competition. However, the potential for high stem density to increase sensitivity to extreme climate events merits additional analysis. As discussed in the previous section, further data collection for very small trees is also crucial, as the majority of mortality is expected to occur at this stage, influencing long-term stand development. Analysis of such data, when acquired, should focus on the interaction of climate and competition on individual tree mortality, and its potential implications for forest futures and carbon dynamics under ongoing climate change.

While mortality models have been slowly evolving towards more mechanistic approaches, empirical models can be very useful in understanding mortality (Adams *et al.* 2013), especially in complex tropical forest ecosystems. One issue with process-based ecosystem demography models is that it is difficult to understand why a model is performing poorly because of inadequate observations and theory. Poor performance may be caused by incorrect calibration or specification of a process, or can be because of the exclusion of a critical mechanism. Empirical models can thus help constrain mechanistic ones, and rapidly generate testable hypotheses regarding the need for inclusion of specific processes, such as competition. For example, the DGVM ORCHIDEE (Krinner *et al.* 2005) has recently been coupled to a forest growth and management module (together called ORCHIDEE-FM; Bellassen *et al.* 2010). ORCHIDEE-FM implements self-thinning explicitly, as well as tree circumference classes within plant functional types (see Naudts *et al.* 2015), and shifts the focus from stand-level demography to characteristics of distributions of individual trees. This allows the model to simulate both common forestry practices, from clear cutting to selective harvest, and natural demographic processes such as self-thinning. Competition is simulated by allocating stand-level wood increment to individual trees based on an individual growth function (Deleuze *et al.* 2004), with larger trees getting a bigger share of stand growth. Mortality is derived from the relative density index, based on Reineke's theory of limiting

density (Reineke 1933). Quantifying competition from observational data, as done here, can inform both growth and mortality in DGVMs. First, downscaling biomass increment can be based on local neighborhood basal area, and the appropriate area of competitive influence can be approximated using second-order spatial statistics. Second, growth and mortality can be constrained by carbon carrying capacity derived from self-thinning curves. Finally, climate responses can be modified by incorporating within-stand density heterogeneity, indicating competition that varies spatially.

The preceding example shows that disentangling the role of competition and climate in influencing forest mortality based on empirical analysis and modeling is a promising avenue for improving understanding of tropical forest demography and structure.

Author Contributions

MP, EJ, CB, ME, PC, SL and BP conceived the ideas and designed the methodology. JC, AD and BH collected and analyzed the data. All authors contributed critically to the drafts and gave final approval for publication.

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Data Accessibility

The forest inventory data used in this analysis are made available via the Dryad data repository,

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Variable(s)	Symbol(s)	Rationale for consideration for model	References
		Main effects	
Basal area within 5 m radius	CI	Basal area is a proxy for competition. Stronger competition results in higher mortality.	Biging & Dobbertin (1992)
DBH	DBH	Larger trees are more sensitive to mortality from drought and thermal stress.	Nepstad *et al.* (2007)
Temperature	T_w, T_d	Tropical forests may be near a temperature tipping point.	Doughty & Goulden (2009)
Precipitation	PRE_w, PRE_d	Tropical forests may be at risk from increased drought. Conversely, very high precipitation may increase mortality by soil anoxia.	Rowland *et al.* (2015)
		Interaction effects and second-order terms	
(Basal area within 5 m radius)^2	CI^2	The competition-mortality relationship may be non-linear or thresholded.	-
DBH^2	DBH^2	The mortality-DBH relationship may be non-linear.	Lines *et al.* (2010)
Temperature^2	T_w^2, T_d^2	The mortality-temperature relationship may be non-linear or thresholded.	-
Precipitation^2	PRE_w^2, PRE_d^2	The mortality-precipitation relationship may be non-linear or thresholded.	(Allen *et al.* 2015)
Basal area within 5 m radius × temperature	$CI:T_w$, $CI:T_d$	The mortality-competition relationship may be more or less intense under certain climatic conditions.	-
Basal area within 5 m radius × precipitation	$CI:PRE_w$, $CI:PRE_d$		
Temperature × precipitation	$T_w:PRE_w$, $T_d:PRE_d$	Temperature stress may increase at low precipitation, further increasing mortality.	Breshears *et al.* (2005)
Basal area within 5 m radius × DBH	CI:DBH	Smaller individuals may be more sensitive to competition.	Biging & Dobbertin (1992)
Temperature × DBH	T_w:DBH, T_d:DBH	The thermal sensitivity of trees may be related to DBH.	McDowell *et al.* (2008)
Precipitation × DBH	PRE_w:DBH, PRE_d:DBH	Sensitivity of trees to drought or anoxia may be related to DBH.	McDowell *et al.* (2008)

Table 1: Variables considered for mortality model development, along with ecological justifications and references. Subscripts

"w" and "d" refer to wet-season and dry-season variables.

Plot	Intercept	p-value	Slope	p-value	95% C.I.	R^2
1	5.91	< 0.001	-1.13	< 0.001	(-1.38, -0.88)	79%
6	7.60	< 0.001	-1.72	< 0.001	(-2.62, -0.82)	40%
11	6.37	< 0.001	-1.28	< 0.001	(-1.42, -1.14)	94%
13	7.60	< 0.001	-1.72	< 0.001	(-2.06, -1.38)	88%
14	5.96	< 0.001	-1.13	< 0.001	(-1.72, -0.54)	51%
15	7.88	< 0.001	-1.81	< 0.001	(-2.26, -1.36)	82%

Table 2: Summary of self-thinning regression models. p-values are for the test that a regression coefficient is different from zero.

Variable	Exponentiated coefficient estimate (odds ratio)	Exponentiated 95% Wald confidence interval (odds ratio)		p-value
Model A: competition, DBH, and climatic variables		AUC: 58.15%	AIC: 40,510	
CI	0.78	(0.65, 0.92)		0.004
CI^2	1.00	(1.00, 1.00)		< 0.001
DBH	0.98	(0.98, 0.99)		< 0.001
DBH^2	1.00	(1.00, 1.00)		< 0.001
T_w	0.00	(0.00, 0.00)		< 0.001
PRE_w	1.14	(1.11, 1.16)		< 0.001
T_d	9.37×10^{19}	$(5.73 \times 10^8, 1.53 \times 10^{31})$		< 0.001
PRE_d	0.98	(0.97, 0.98)		< 0.001
T_w^2	2.52	(2.02, 3.14)		< 0.001
T_d^2	0.42	(0.26, 0.68)		< 0.001
PRE_w^2	1.00	(1.00, 1.00)		< 0.001
PRE_d^2	1.00	(1.00, 1.00)		< 0.001
$CI:PRE_d$	1.00	(1.00, 1.00)		< 0.001
$CI:PRE_w$	1.00	(1.00, 1.00)		< 0.001
$CI:T_d$	1.01	(1.00, 1.00)		0.004
$T_w:PRE_w$	1.00	(0.99, 1.00)		< 0.001
Model B: competition and DBH only		AUC: 57.87%	AIC: 40,865	
CI	0.98	(0.98, 0.99)		< 0.001
CI^2	1.00	(1.00, 1.00)		< 0.001
DBH	0.98	(0.98, 0.99)		< 0.001
DBH^2	1.00	(1.00, 1.00)		< 0.001
Model C: climatic variables and DBH only		AUC: 55.35%	AIC: 40,744	
DBH	0.99	(0.98, 0.99)		< 0.001
DBH^2	1.00	(1.00, 1.00)		< 0.001

T_w	0.00	(0.00, 0.00)	< 0.001
PRE_w	1.15	(1.12, 1.17)	< 0.001
T_d	9.65×10^{19}	$(5.39 \times 10^8, 1.73 \times 10^{31})$	< 0.001
PRE_d	0.98	(0.97, 0.98)	< 0.001
T_w^2	2.7	(2.16, 3.37)	< 0.001
T_d^2	0.43	(0.26, 0.69)	< 0.001
PRE_w^2	1.00	(1.00, 1.00)	< 0.001
PRE_d^2	1.00	(1.00, 1.00)	< 0.001
$T_w{:}PRE_w$	1.00	(0.99, 1.00)	< 0.001

Table 3: Three alternative individual tree mortality models, including DBH, competition, and climatic variables (model A), DBH and competition only (model B), and DBH and climatic variables only (model C). Coefficient estimates and confidence intervals are expressed as odds ratios. Reported p-values relate to the hypothesis that the odds ratio is different from 1. Note that coefficient estimates should not be used for comparison of effect size.
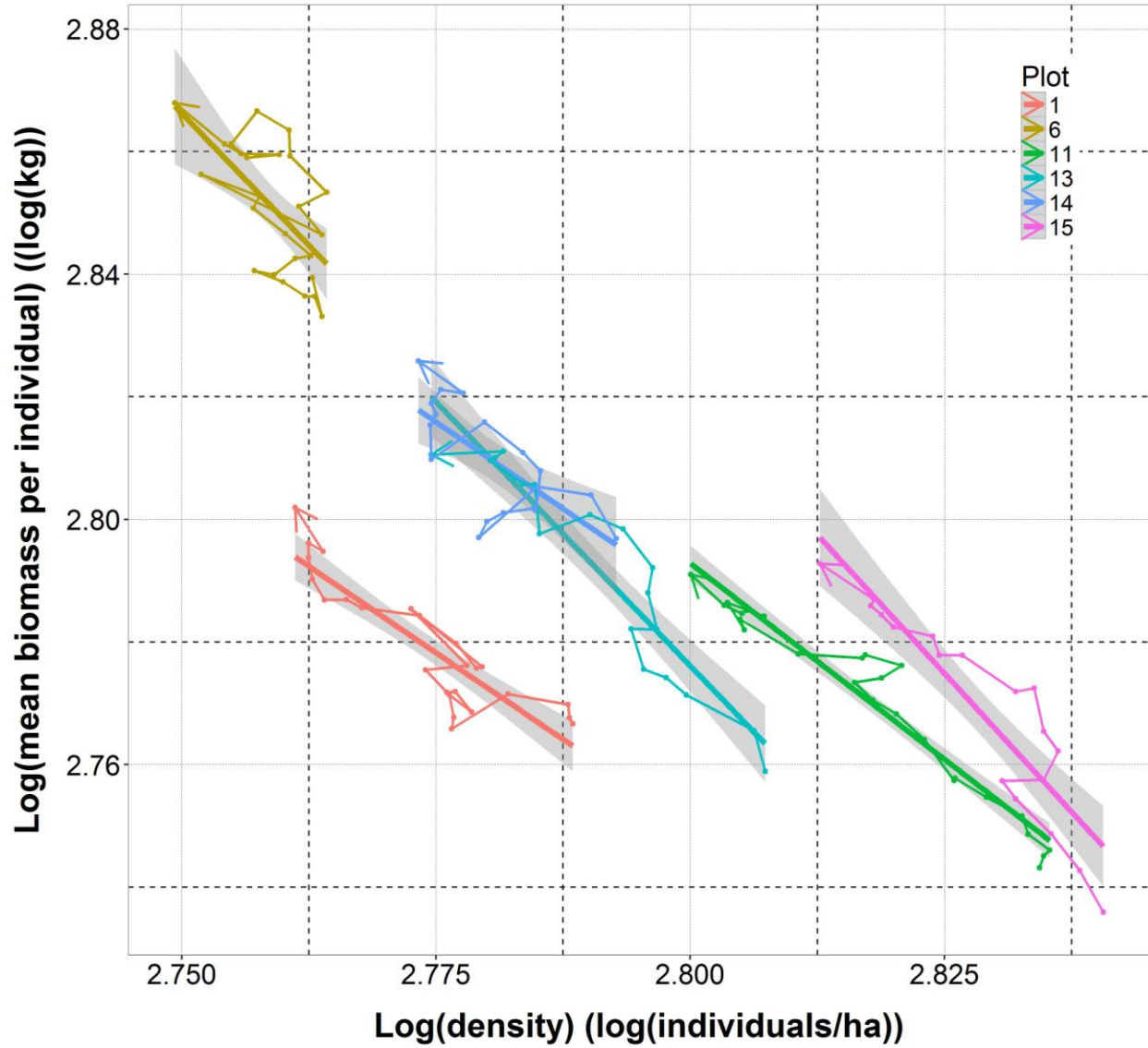
Figure 1: Self-thinning lines (logged biomass per individual versus logged tree density) per plot. The thin lines are the simple linear regression lines. Grey bands indicate 95% confidence bands about the regressions. Individual observations were connected to show the temporal trajectories of the plots, ending at the arrow (2014). Plots 1, 6, and 11 were measured since 1984; plots 13, 14, and 15 since 1991.
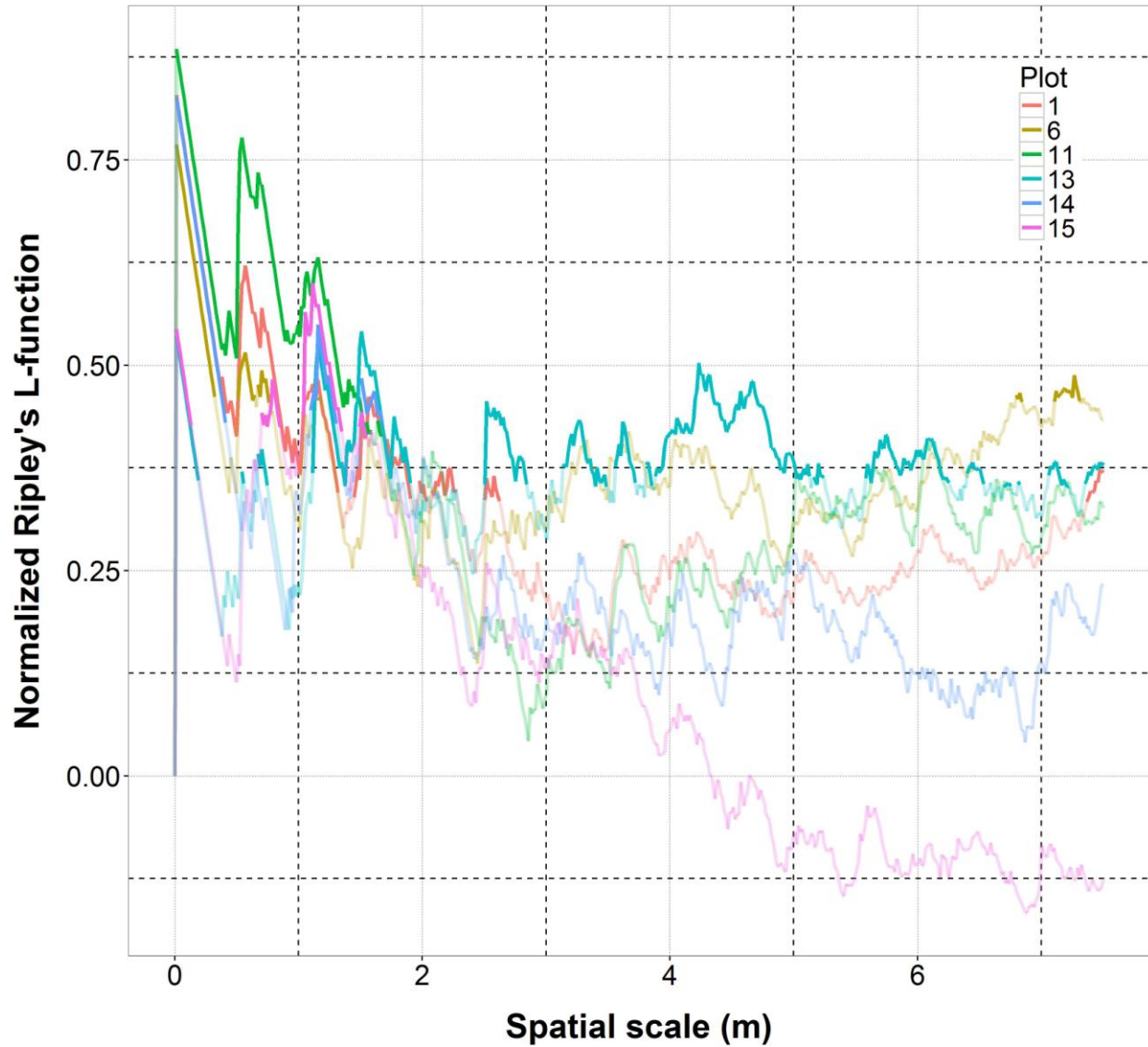
Figure 2: Results of second-order spatial analysis of dead trees, with records from all years combined. Positive L-function values indicate clustering, and negative values overdispersion. Values of zero suggest spatial randomness. Opaque lines indicate point patterns significantly different from a random Poisson process at a specific spatial scale using two-sided 90% simultaneous envelopes.
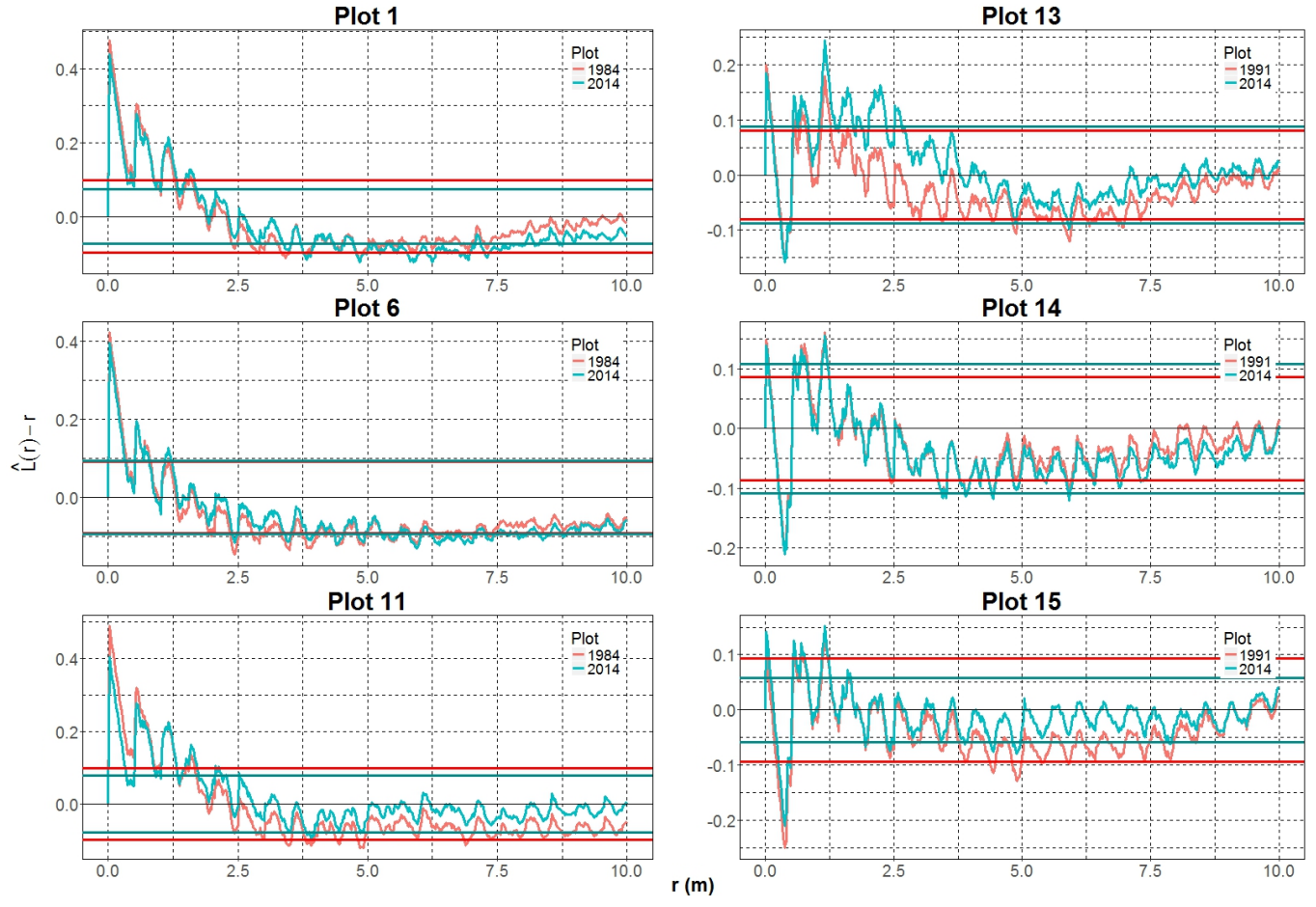
Figure 3: Results of second-order spatial analysis of living trees, with records from all years separated. For clarity, only results

from two randomly-chosen years are shown here. Positive L-function values indicate clustering, and negative values

overdispersion. Values of zero suggest spatial randomness. A point pattern is significantly different from CSR at a given distance

when it falls above (for positive values) or below (for negative values) the horizontal critical envelopes for that year.
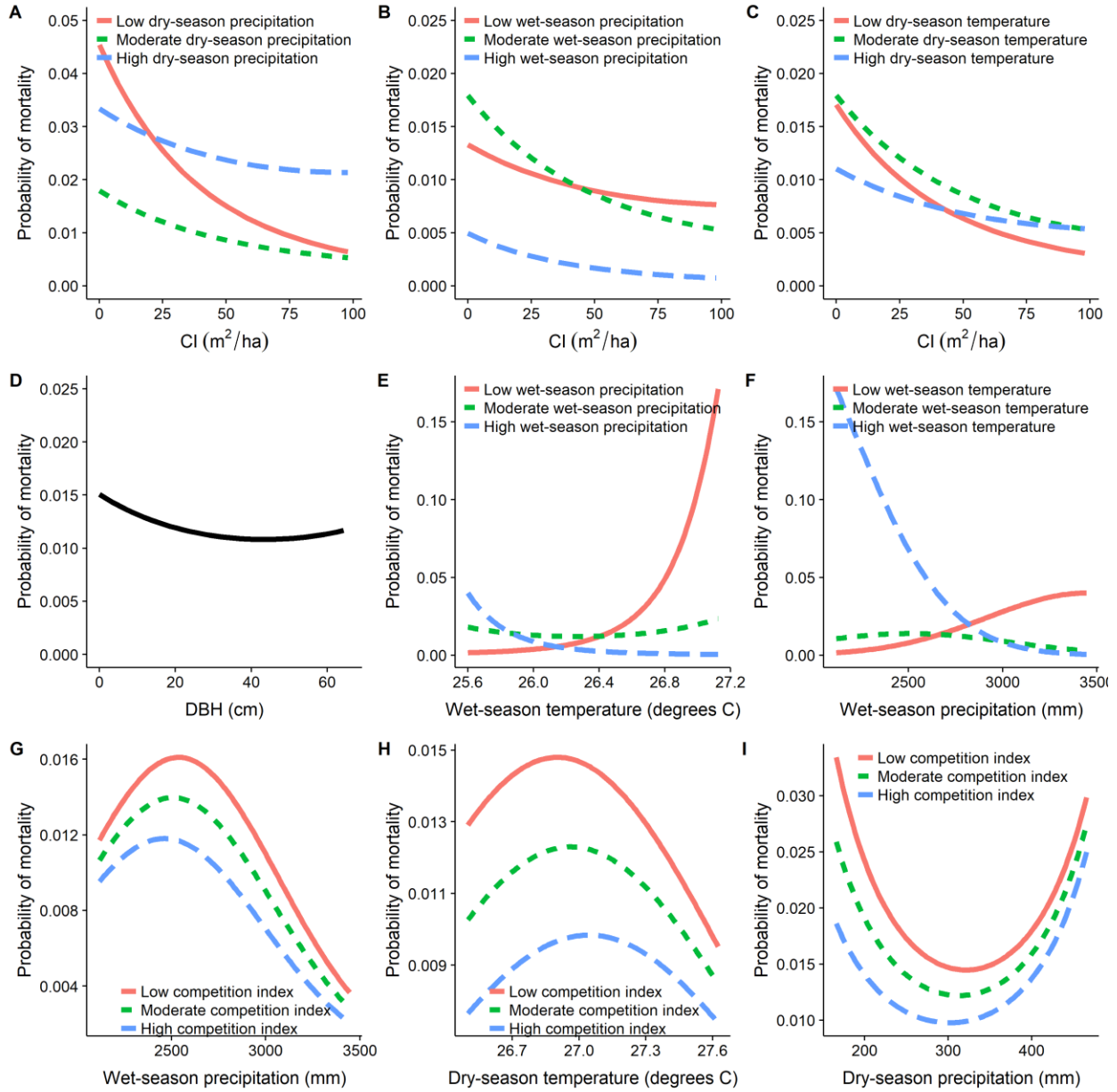
Figure 4: Plots of predicted mortality as a function of the predictors for model A (size, competition, and climate covariates). For each plot all other variables are held constant at their median (CI and DBH) or center of their observed range (precipitation and temperature variables). Low, moderate, and high competition index refer to the 25th, 50th, and 75th percentile of observed values, respectively. Low, moderate, and high precipitation or temperature refer to the observed minimum, center of the observed range, and observed maximum, respectively. x-axis limits represent observed minima and maxima in E-I to avoid extrapolation. In A-D the upper limit was fixed at the 99th percentile of the observed CI and DBH data as there were few trees with very high DBH and neighborhood CI and we therefore have limited confidence in the sharp increase in predicted mortality at high DBH and CI. y-axis represents predicted annual probability of mortality.