

Forest response to increased disturbance in the Central Amazon

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Forest response to increased disturbance in the Central Amazon and comparison to Western Amazonian forests

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Abstract

Uncertainties surrounding vegetation response to increased disturbance rates associated with climate change remains a major global change issue for Amazon forests. Additionally, turnover rates computed as the average of mortality and recruitment rates in the Western Amazon basin are doubled when compared to the Central Amazon, and notable gradients currently exist in specific wood density and aboveground biomass (AGB) between these two regions. This study investigates the extent to which the variation in disturbance regimes contributes to these regional gradients. To address these issues, we evaluated disturbance-recovery processes under two scenarios of increased disturbance rates in a complex Central Amazon forest using first ZELIG-TROP, a dynamic vegetation gap model which we calibrated using long-term inventory data, and second using the Community Land Model (CLM), a global land surface model that is part of the Community Earth System Model (CESM). Upon doubling the mortality rate in the Central Amazon to mirror the natural disturbance regime in the Western Amazon of $\sim 2\%$ mortality, at steady-state, AGB significantly decreased by 41.9% and there was no significant difference between the modeled AGB of 104 Mg C ha^{-1} and empirical AGB from the western Amazon datasets of 107 Mg C ha^{-1} . We confirm that increases in natural disturbance rates in the Central Amazon will result in terrestrial carbon loss associated with higher turnover. However, different processes were responsible for the reductions in AGB between the models and empirical datasets. We observed that with increased turnover, the subsequent decrease in wood density drives the reduction in AGB in empirical datasets. However, decrease in stand basal area was the driver of the drop in AGB in ZELIG-TROP, and decreased leaf area index (LAI) was the driver in CLM. Further comparisons found that stem density, specific wood density, and basal area growth rates differed between the two Amazonian regions. This suggests that: (1) the variability between regions cannot be entirely explained by the variability in disturbance regime, but rather potentially sensitive to intrinsic environmental factors; or (2) the models are not accurately simulating all forest characteristics in

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response to increased disturbances. Last, to help quantify the impacts of increased disturbances on climate and the earth system, we evaluated the fidelity of tree mortality and disturbance in a global land surface model: CLM. For a 100 % increase in annual mortality rate, both ZELIG-TROP and CLM were in close agreement with each other and predicted a net carbon loss of 41.9 and 49.9 %, respectively, with an insignificant effect on aboveground net primary productivity (ANPP). Likewise, a 20 % increase in mortality every 50 years (i.e. periodic disturbance treatment) resulted in a reciprocal biomass loss of 18.3 and 18.7 % in ZELIG-TROP and CLM respectively.

1 Introduction

One of the largest uncertainties in future terrestrial sources of atmospheric carbon dioxide results from changes to forest disturbance and tree mortality rates, specifically in tropical forests (Cox et al., 2000, 2004; DeFries et al., 2002; Clark, 2007; Pan et al., 2011). There has been evidence that climate change and forest disturbance are linked such that a changing climate can influence the timing, duration, and intensity of disturbance regimes (Overpeck et al., 1990; Dale et al., 2001; Anderegg et al., 2013). In the tropics, climate change related impacts such as water and heat stress, and increased vulnerability to fires could lead to increased forest dieback (i.e. tree mortality notably higher than usual mortality) and increased disturbance rates (Cox et al., 2004; Malhi et al., 2008, 2009; US DOE, 2012). Recent studies have detected that forested ecosystems are already responding to climate change related factors such as drought, temperature stress, and associated hydraulic stress, and insect and pathogen infestation, triggering varying levels of forest diebacks (Cao et al., 2009; Allen et al., 2010; Martinez-Vilalta et al., 2012; Anderegg et al., 2013). Increased mortality from droughts, fires, storms, deforestation, and introduced species can decrease carbon sequestration, ecosystem productivity and climate stabilization (Millennium Ecosystem Assessment, 2005; Bonan, 2008). These effects could then produce large economic costs, ecological impacts, and lead to climate related positive feedback cycles (Canham and

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Marks, 1985; Dale et al., 2001; Laurance and Williamson, 2001). Therefore, due to the connection between climate change and tropical forest disturbance rates, investigations on the consequences of increased disturbance rates on aboveground carbon stocks and fluxes are required.

The effects of large-scale removal of tropical forest leading to changes in global climate and the global carbon balance have been studied within global general circulation models (GCMs) (Shukla et al., 1990; Henderson-Sellers et al., 1993; Hahmann and Dickinson, 1997; Gedney and Valdes, 2000; Avissar and Werth, 2005; Huntingford et al., 2008). For example, a rapid and complete deforestation of the diverse Amazon Basin was predicted to be irreversible (Shukla et al., 1990), losing ~ 180 Gt carbon stock from the tropical forest. In general, these past studies have simulated extreme deforestation, or complete removal of the tropical forest biome, with the goal of evaluating climate impacts (i.e. albedo, evaporation, precipitation, surface boundary conditions). However, instead of sudden and complete removal, gradual increases and spatially heterogeneous patterns of tropical tree mortality due to multiple causes are more likely to occur than complete loss (Fearnside, 2005; Morton et al., 2006). Therefore, it is necessary to improve global climate models in order to simulate dynamic disturbance rates and gradual forest biomass loss in response to increasing mortality rates. This study aims to better understand how shifts in disturbance regimes and background mortality rates will affect ecosystem processes and carbon cycling dynamics for tropical forests.

Disturbance regimes and turnover rates currently vary for different regions of Amazonia (Baker et al., 2004a, b; Lewis et al., 2004; Phillips et al., 2004; Chao et al., 2009), with Central Amazon forests having “slower” turnover rates, and the Western and Southern Amazon forests (which we call “west and south”) exhibiting “faster” turnover rates. This regional variation in turnover rates is connected with differences in carbon stocks, growth rates, specific wood density, and biodiversity. Baker et al. (2004a) investigated the regional-scale comparisons of AGB estimates, concluding that differences in species composition and related specific wood density determine the regional patterns in AGB. Upon including weighting for wood density when estimating AGB,

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western Amazon forests were found to have significantly lower AGB than their eastern counterparts. In contrast basal area varied only slightly across their Amazon plot network (27.5 vs. $29.2 \text{ m}^2 \text{ ha}^{-1}$, Baker et al., 2004a), making wood density, which is a strong indicator of functional traits (e.g., species light demand; Whitmore, 1998) and patterns of family composition, a strong driver in steady-state AGB variation. It is unclear if these regional variations in forest processes are driven by external disturbance (e.g., increased drought, windstorm, forest fragmentation) or internal influences (e.g., soil quality, phosphorus limitation, species composition) (Phillips et al., 2004; Chao et al., 2009; Quesada et al., 2010; Yang et al., 2014). Investigating the causes that drive variation in tree dynamics in the Amazon, in order to understand consequences for future carbon stocks for each region should still be explored. For example, are the differences in forest structure and function between the two regions a result of the disturbance regime? If the Central Amazon forests were subject to a higher disturbance regime and turnover rates similar to that of the “west and south”, would the two regions match in terms of forest dynamics, carbon stocks and fluxes? A goal of this paper is to address these questions, by using model predictions to explore the influence of disturbance regimes on net carbon stocks and fluxes in the Central Amazon, and then compare to observational data from the “west and south” regions of the Amazon.

The effectiveness of climate mitigation strategies, and the consequential negative or positive effect on carbon pools, will be affected by future changes in natural disturbances regimes (IPCC working group III). A recent study by Le Page et al. (2013) found that future natural disturbance rates can greatly alter climate mitigation strategies due to the effect of disturbance on the terrestrial carbon balance. Specifically, by using this economic/energy integrated assessment model, it was found that in order to reach a stringent mitigation target, (3.7 W m^{-2} level) the societal, technological, and economic strategies will be substantially more costly- up to 2.5 times when disturbance rates are doubled (Le Page et al., 2013). Due to the strong feedbacks from terrestrial processes, there is a need to utilize an integrated Earth System Model approach (i.e. iESM; Jones et al., 2013) with biogeochemical, biophysical, and climate model-

we are not assigning mortality to any particular cause. The final research question will evaluate the accuracy of CLM to predict changes to carbon fluxes due to increased disturbance, a process that is likely to increase with human induced climate change.

2 Methods

2.1 Study area and forest inventory plots

The empirical data used for this study were from two permanent transects inventoried from 1996–2006, located in reserves of the National Institute for Amazon Research (Instituto Nacional de Pesquisas da Amazonia, INPA) in the Central Amazon in Brazil. The forest inventory transects are approximately 60 km north of Manaus, Brazil, in the Central Amazon where vegetation is old-growth closed-canopy tropical evergreen forest. The mean annual precipitation at Manaus was 2110 mm yr^{-1} with a dry season from July–September, and mean annual temperature was 26.7°C (Chambers et al., 2004; National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, N.C., USA). However, during 2003 to 2004, mean annual precipitation in the study area reached 2739 mm yr^{-1} .

We quantified demographic data such as stem density, diameter at breast height (DBH, cm), and change in diameter for trees $> 10 \text{ cm DBH}$ from census data from the two transects. This data was used to calculate above-ground biomass (ABG) estimates (Mg C ha^{-1}) and were determined using region-specific allometric equations after harvesting 315 trees in the Central Amazon (Chambers et al., 2001; see Eq. 1 below). This data was also used to estimate observed values for above-ground net primary productivity (ANPP, $\text{Mg C ha}^{-1} \text{ yr}^{-1}$) after taking into account loss of tree mass due to tree damage (Chambers et al., 2001). Observed mortality rates ($\% \text{ stems yr}^{-1}$) were based on census intervals ranging from 1 to 5 years on 21 1 ha undisturbed plots located in the Biomass and Nutrient Experiment (BIONTE), and the Biological Dynamics

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and Forest Fragments Project (BDFFP), also located in INPA (Chambers et al., 2004). We compared model predictions from ZELIG-TROP to observed field data.

In order to test whether the variability in forest dynamics and carbon stocks between the “west and south” and the Central Amazon forests can be explained by the variability in the natural disturbance regime, we used forest inventory data collected and reported in Baker et al. (2004a) and Phillips et al. (2004). We compared the Central Amazon forests (both simulated and observed data) to the observed “west and south” datasets, using inventory data collected from 59 plots as reported in Baker et al. (2004a, b), and from 97 plots as reported in Phillips et al. (2004) with these plots constituting a large part of the RAINFOR Amazon forest inventory network (Malhi et al., 2002). Sites occur across a large range of environmental gradients, such as varying soil types and level of seasonal flooding, however all sites are considered to be mature tropical forests.

2.2 Description of ZELIG-TROP

ZELIG-TROP is an individual based gap model developed to simulate tropical forests (Holm et al., 2012). It is derived from the gap model ZELIG (Urban, 1990, 2000; Urban et al., 1991, 1993), which is based on the original principles of the JABOWA (Botkin et al., 1972) and FORET forest gap models (Shugart and West, 1977). ZELIG-TROP follows the regeneration, growth, development, and death of each individual tree within dynamic environmental conditions across many plots (400 m² plots, replicated uniquely 100 times). Maximum potential tree behaviors (optimal tree establishment, diameter growth, and survival rates) are reduced as a function of light conditions, soil moisture, level of soil fertility resources, and temperature. Specific details on the ZELIG model modifications to create ZELIG-TROP can be found in Holm et al. (2012). Gap models have been used extensively to forecast forest change from varying types and levels of disturbances, such as windstorms and hurricanes (O’Brien et al., 1992; Mailly et al., 2000); simulate vegetation dynamics in response to global change (Solomon, 1986; Smith and Urban, 1988; Smith and Tirpak, 1989; Overpeck et al., 1990; Shugart et al., 1992); and explore feedbacks between climate change and vegetation cover (Shuman

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et al., 2011; Lutz et al., 2013). ZELIG has been used to simulate forest succession dynamics in many forest types across the globe (O'Brien et al., 1992; Seagle and Liang, 2001; Busing and Solomon, 2004; Larocque et al., 2006; Nakayama, 2008). (Descriptions of the plant mortality algorithm as well as definitions of terms and parameters used in ZELIG-TROP are provided in the Supplement).

2.3 Model parameterization for the Central Amazon

The silvicultural and biological parameters for each of the 90 tropical tree species required for ZELIG-TROP are found in Table 1. The 90 tree species consist of 25 different families, 54 canopy species, 18 emergent species, 12 sub-canopy species, and 6 pioneer species (Table 1). While these tree species do not represent all existing species found in the Central Amazon forest, they represent a diverse array of family types, canopy growth forms, and demographic traits such as growth rates, stress tolerances, and recruitment variations that will produce a robust and reliable result. The majority of the data used to parameterize ZELIG-TROP for the Amazon was derived from a long-term (14–18 years) demographic study to estimate tree longevity (Laurance et al., 2004) located in Central Amazon. Data was collected on 3159 individual trees from 24 permanent, 1 ha plots which span across an area of 1000 km² (Laurance et al., 2004). Wood density data for the 90 species used in this study were gathered from published sources with sites across South America (Fearnside, 1997; Chave et al., 2006).

We used results found by Laurance et al. (2004) to determine several parameters; specifically the maximum age of the species (AGEMAX), the maximum diameter at breast height (DBH_{max}, cm), and the growth-rate scaling coefficient (*G*) for ZELIG-TROP. AGEMAX was found by taking the mean of three longevity estimates. DBH_{max} were scaled to match a more accurate representation of maximum DBH in the simulated field sites (Chambers et al., 2004). Additionally, we used the canopy classification and family traits to infer species-specific rankings related to light, drought, soil nutrient tolerances, and regeneration stocking. Average monthly precipitation (cm) and temperature (°C) required for the environmental parameters in ZELIG-TROP (Table 2) were

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individual, thereby adjusting the ALGF relative to horizontal space occupied by the crown and improving the predictive capacities of ZELIG-TROP for the Amazon. This modification thus affected the light extinction on tree growth, allowed more available light from the top to the bottom of the individual-tree crown, and in turn better predicted observed data of basal area growth and abundance of stems per plot.

2.3.1 Calibration methods

ZELIG-TROP simulations for the Central Amazon forest were run for 500 years and replicated on 100 independent plots, each the size of 400 m². All simulations began from bare ground, and results from ZELIG-TROP were averaged over the final 100 years of simulation. This was the period when forest dynamics (e.g. stem density, AGB, ANPP) were seen to reach a stable state and represent a mature forest stand. The model was verified by comparing the following five simulated forest attributes (average ± SD) to observed field data from the two inventory transects: (1) total basal area (m² ha⁻¹); (2) total AGB (Mg C ha⁻¹); (3) total stem density (ha⁻¹); (4) leaf area index; and (5) ANPP (Mg C ha⁻¹ yr⁻¹). To test model validity for the Central Amazon forest we report percent difference between the observed and simulated results (Table 3).

2.4 Disturbance treatments

To better understand the long-term consequences of high disturbance in a Central Amazon rainforest, we crafted a simulation that doubled annual background tree mortality in both ZELIG-TROP and CLM assuming an independent mechanism as the driver of mortality. A description of the Community Land Model (CLM) can be found in the Supplement. Predicting the impacts of increased mortality is critical since other recent studies have found that tree mortality in the Central Amazon has been under-sampled in plot-based approaches, and after analyzing a larger range of gap sizes (including larger gaps), ~ 9.1 to 16.9 % of tree mortality was missing (Chambers et al., 2013). The majority of gaps created in Amazonian rainforests are from windthrow of

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3 Results

3.1 Model verification results

Results simulated by ZELIG-TROP for the mature Central Amazon tropical forest (pre-disturbance treatment) were in close range (e.g., within 17%) to empirical data (Table 3), making ZELIG-TROP successful at predicting stand dynamics of a complex tropical forest. Average basal area was 9.7% higher than the observed value (32.96 vs. 30.06 m² ha⁻¹), average AGB was 5.0% higher (178.38 vs. 169.84 Mg C ha⁻¹), and average leaf area index (LAI) was 1.8% higher (5.8 vs. 5.7). ZELIG-TROP predicted average stem density to be 12.5% lower (574 vs. 656 stems ha⁻¹), and ANPP was 17.1% lower than observed values reported by Chambers et al. (2001) (5.4 vs. 6.5 Mg C ha⁻¹ yr⁻¹). All simulated values were reported once the forest reached a stable, mature forest. ZELIG-TROP was also successful at accurately predicting stem density and AGB by DBH (cm) size class (Fig. 1a and c). The model over predicted the number of stems in the lowest size class (10–20 cm), by an additional 84 stems per hectare, and in the eighth size class (80–90 cm), but for the remaining size classes values were near to the observed data. Even with these slight over predictions in certain DBH size classes, the model predicted AGB to be within a reasonable range (8.5 Mg C ha⁻¹) of the observed values ($r^2 = 0.60$).

ZELIG-TROP was also able to predict a realistic community composition (Fig. 2a). After initiating the model from bare ground, there was a sudden increase in basal area per species, followed by a typical jigsaw pattern of die-offs and growth increases, with the model reaching a steady-state during the last 100 years. The dominant species in terms of basal area, (*Parkia multijuga*), a large, fast-growing emergent species from the Leguminosae family accounted for 17% of the total basal area in the last 100 years of simulation. The next four dominant species were all canopy-level species. This was an accurate representation of the forest, as the canopy layer holds large trees and usually the densest area of biodiversity. For example, 63% of the 90 tree species simulated were categorized as a canopy growth form. However, there was also an even mixture

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of emergent, sub-canopy, and pioneer species as dominant and rare species, typical of a diverse Central Amazon forest. There was no one single species that dominated the canopy throughout the course of the simulation. Instead, we saw a diverse species representation (Fig. 2a). During the last 100 years of simulation, emergent species represented 29.6% of the total basal area, sub-canopy species represented 1.7%, and pioneer species represented 5.5% of the total basal area.

Empirical mortality rates (% stems yr^{-1}) from BDFFP and BIONTE data were log-normally distributed averaging $1.02\% \pm 1.72\%$ (Chambers et al., 2004). As estimated by ZELIG-TROP, the no-disturbance annual mortality rates were near to observed values ($1.27\% \pm 0.21\%$) but had a smaller distribution around the mean (Fig. 3). As expected, annual mortality rate doubled ($2.66\% \pm 0.26\%$) for the high disturbance treatment.

3.2 Central and Western Amazon disturbance comparisons

3.2.1 AGB, stem density, growth and recruitment rates

Upon increasing the turnover rates of the Central Amazon forest by manually doubling background tree mortality rates to mirror the $2\% \text{yr}^{-1}$ mortality rates in the “west and south”, the two Amazon regions continued to differ in multiple forest structure and functional traits. Stem density, specific wood density, basal area growth rates, and AGB when excluding weighting for wood density in biomass equations from the treatment site did not match the trends observed in the “west and south” plot network. Using a Tukey’s multiple comparison procedure following a one-way ANOVA, the empirical dataset showed a significant difference in both wood density and basal area growth rates between the two regions, but no significant difference between the two regions in the model results (Fig. 4). Plus there were slight opposite responses in the wood density and basal area growth rate values predicted by the model compared to the observed trends (discussed below). Alternatively when comparing stem density there was no significant difference between the two regions in the empirical dataset, but there was

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a significant increase between the Central and “west and south” regions in the model results.

In contrast, the high disturbance treatment did significantly reduce AGB in the Central Amazon to values similar to the “west and south” counterpart, but wood density was not included in the biomass allometric equation for the Central Amazon therefore this reduction in AGB was a “false-positive”. Specifically, when the Central Amazon was subjected to faster turnover rates there was a significant reduction in AGB (two sample t test, $t_{(99,1.97)} = 108.98$, $p < 0.001$) and net carbon loss was 74 Mg C ha^{-1} (from 178 to 104 Mg C ha^{-1}) averaged over the last 100 years of simulation (Fig. 1d) equivalent to a 41.9% decrease. AGB in the Central Amazon was impacted the most by the high disturbance treatment. This new value of AGB for the higher disturbed Central Amazon (104 Mg C ha^{-1}) was similar to AGB values in the “west and south” RAINFOR network plots when: (1) using the Chave et al. (2001) biomass equation (107 Mg C ha^{-1}), which had no significant difference between the two regions (two sample t test, $t_{(38,2.7)} = 2.29$, considering $\alpha = 0.01$, $p = 0.03$), and (2) using the Chambers et al. (2001) biomass equation (123 Mg C ha^{-1}) (Fig. 4a). Therefore, similar to the empirical dataset, the demographic vegetation model captured the net carbon loss in biomass associated with higher turnover caused by higher disturbance. However both the Chave et al. (2001) and Chambers et al. (2001) biomass equations included weighting for wood density. The significant reduction in stand basal area, and not variation in wood density, was the main driver of decrease in AGB in ZELIG-TROP (Fig. 5e). There was no significant difference in stand basal area between the empirical datasets in the Central and “west and south” plots ($p = 0.368$), a finding also confirmed by Baker et al. (2004a). While net carbon loss was the expected result, it constitutes a “false positive” resulting from omitting wood density in the model estimate of biomass and from an absence of significant difference in stand basal area across the Amazonia field network.

The high disturbance treatment in the Central Amazon led to a significant increase in stem density by 197 stems from 574 to 771 stems ha^{-1} (34.3% increase, Fig. 1b, two sample t test, $t_{(99,1.97)} = 28.06$, $p < 0.001$). Compared to the regional gradient

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in the RAINFOR network there was no significant difference between the higher disturbed and the Central Amazon empirical dataset (573 stems ha^{-1} vs. 589 stems ha^{-1}) (two sample t test, $t_{(46,2.01)} = 0.84$, $p = 0.407$, Fig. 4d). ANPP did not significantly alter in the Central Amazon forest under a high disturbance treatment (two sample t test, $t_{(99,1.97)} = 1.54$, $p = 0.126$), only decreasing ANPP by 0.04 (from 5.39 to 5.35 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$, 1.0%, Fig. 5a). Even with increased disturbance events, ANPP did not decrease in the same manner as biomass due to recovery episodes from more frequent thinning and the increase in smaller stems (10 cm DBH size class) in newly opened gaps. When comparing the stand-level BA growth rates (proxy for productivity) there was a significant increase in growth rates as you moved across the RAINFOR network from the Central Amazon to the “west and south”, but there was no significant difference between the modeled treatments. In fact, an opposite response was seen, and there was a slight decrease as a result of higher disturbance (by 0.21 $\text{m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$, Fig. 4e or 0.20 $\text{Mg C ha}^{-1} \text{ yr}^{-1}$, Fig. 5c). The model might not accurately represent growth rates because prior to applying a higher disturbance regime in the Central Amazon, ZELIG-TROP significantly over-estimated the stand-level growth compared to empirical data (3.2 vs. 1.4 $\text{m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$).

The recruitment rates ($\% \text{ yr}^{-1}$) from the treatment site constitute the only variable that matched the “west and south” observational dataset. Under a high disturbance treatment in the Central Amazon, as expected, there were subsequent increases in recruitment rate, where recruitment significantly increased from 2.3 to 3.9 $\% \text{ yr}^{-1}$, constituting a 69.1% increase above no-disturbance recruitment rates (Table 4, Fig. 6a). Pre-treatment, modeled recruitment rates were 0.9 $\% \text{ yr}^{-1}$ higher compared to empirical values from the Central Amazon BDFFP plots (Phillips et al., 2004). Recruitment and mortality rates are tightly linked (Lieberman et al., 1985), therefore when tree mortality increased, recruitment also significantly increased. In the “west and south” empirical dataset recruitment rates were $\sim 79\%$ higher compared to the Central region (Fig. 4b). However, while turnover rates increased, there was *not* an increase in coarse litter production rate (trunks and large stems > 10 cm diameter, $\text{Mg C ha}^{-1} \text{ yr}^{-1}$,

next most common emergent species, *Cariniana micrantha*, decreased by 32.6 % with high disturbance, and canopy species filled in as the dominant growth form (Fig. 2b).

Similar to stem density and basal area growth, average wood density differed significantly between the Central Amazon treatment site and the RAINFOR plots from “west and south” regions (both locations having ~ 2 % mortality) (two sample t test, $t_{(23,2.07)} = 9.71$, $p < 0.001$), and displayed opposite patterns (Fig. 4c). Previous studies have found wood density to be higher in the central region (~ 0.68 g cm⁻³), and lower in more disturbed “west and south” (~ 0.57 g cm⁻³) (Baker et al., 2004a). Before implementing the high disturbance treatment average wood density was low for the non-disturbed Central Forest (0.59 g cm⁻³, similar to values of the “west and south”), and with increased disturbances average wood density increased (0.63 g cm⁻³), an opposite response from empirical trends. Taking a closer look at the community composition and representation of species, the emergent canopy class experienced a decrease in basal area, amounting to 7.8 % of total basal area, compared to 29.6 % prior to high disturbances. The three remaining growth forms all increased in basal area. The emergent species had on average the highest wood density (0.72 g cm⁻³), and the pioneer species had on average the lowest wood density (0.52 g cm⁻³). With a decrease in emergent species, it would seem likely that average wood density would decrease, as expected in a forest with higher turnover rates. However the dominant species prior to disturbance (the emergent: *Parkia multijuga*), which experienced the largest decrease in basal area, had a very low wood density (0.39 g cm⁻³). In addition, even though the emergent size class decreased, the canopy species (which also had high average wood density of 0.71 g cm⁻³) basal area increased from 63 % to 79.6 %, and the increase in pioneer species from 5.5 % to 5.9 % was not sufficient to lower the total wood density of the forest. With higher disturbance rates subcanopy species represented 6.7 % of the total basal area, compared to 1.7 % prior to high disturbances.

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3.3 Disturbances and carbon change in CLM-CN 4.5 vs. ZELIG-TROP

After applying a continual disturbance regime within CLM as in ZELIG-TROP, similar patterns in forest biomass in response to disturbance were observed, and both models were in agreement with each other. For example, the relative change in AGB was consistent (41.9% vs. 49.9% decrease) for ZELIG-TROP and CLM respectively (Fig. 5b). In CLM the aboveground carbon storage pools are not determined using allometric equations, but rather through a carbon allocation framework based off of photosynthesis, total GPP, and respiration (Thornton et al., 2002). Including or excluding specific wood density is not considered in CLM. The models outputs from CLM for the disturbed Central Amazon runs also showed a reduction in AGB similar to the “west and south”; which was also a “false-positive” result. The significant loss of LAI with disturbance was the main driver of reduction in AGB (Fig. 5f). There was a weak non-significant difference in LAI between the empirical datasets in the Central and “west and south” Amazon regions ($p = 0.077$). Another similarity between the two models was the non-significant change in ANPP, however ZELIG-TROP predicted a decrease in ANPP while CLM predicted a slight increase in ANPP (Fig. 5a).

With regards to the periodic disturbance treatment of large-scale disturbance events, CLM also replicated analogous patterns in biomass loss and recovery as seen in ZELIG-TROP (Fig. 7c). In both models, the sudden decrease in biomass as well as re-equilibration during the recovery phase matched. During each pulse disturbance, the forest lost on average 18.3% and 18.7% biomass in ZELIG-TROP and CLM respectively, and gained 16.5% and 15.4% biomass during the recovery phase. Both CLM and ZELIG-TROP predicted that the recovering forest biomass, on average, was less than the amount lost in each large-scale disturbance event, therefore generating a negative total Δ AGB (-0.15 and $-0.46 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ for ZELIG-TROP and CLM respectively, Table 4). The negative total Δ AGB was less in ZELIG-TROP, and was likely attributed to ZELIG-TROP predicting growth rates to significantly increase (by $0.20 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, two sample t test, $t_{(99, 1.97)} = 2.14$, $p < 0.05$), most likely due to

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the open gaps from disturbance, therefore losses were damped in ZELIG-TROP. In contrast CLM had growth rates that on average decreased, due to the sharp decrease in growth rates following each large-scale disturbance event (Fig. 7b). Both models also showed that each subsequent recovery period was always greater than the previous period, up to a point where re-growth matched the biomass lost in the disturbance event (Fig. 7c).

With regards to the periodic disturbance treatment, there were discrepancies with the response of ANPP to the large-scale forest mortality and recovery events between CLM and ZELIG-TROP. The immediate decrease in ANPP following the large-scale disturbance event was significantly greater in CLM compared to ZELIG-TROP (4.7 vs. 0.6 Mg C ha⁻¹ yr⁻¹, Fig. 7a). The subsequent shape of ANPP during the 50-year recovery was also different between the two models. CLM predicted that within approximately two years after the disturbance, ANPP returned to pre-disturbance levels and stayed relatively constant until the next disturbance. However, ZELIG-TROP did not display a fast return to pre-disturbance levels, but instead predicted a gradual increase in ANPP after each disturbance. Comparing the no-disturbance scenario and the periodic treatment, both models predicted that overall ANPP significantly decreased with periodic disturbances (two sample *t* test, $p < 0.001$ and $p = 0.002$ for ZELIG-TROP and CLM respectively), however the gap model predicted a greater percent difference in average ANPP; a 6.1 % decrease vs. 3.5 % decrease in CLM.

To answer our last research question, what are the differences after increasing disturbance rates in ZELIG-TROP vs. CLM for the Central Amazon, we did find other discrepancies. While the magnitude of change between AGB was similar between the two models, CLM differs greatly from ZELIG-TROP in that it did not capture the inter-annual variability in carbon stocks, while ZELIG-TROP did (Fig. 5b). Therefore, the demographic forest model captured large fluctuations in annual forest biomass and carbon stocks as a result of either gap dynamics, changes in competition for resources, and/or varying size class and age class structure of the forest. In addition, CLM did not produce pulses of coarse litter in response to tree mortality representative of a hetero-

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and characteristics. Only two attributes that are tightly linked with disturbances (i.e. loss in biomass and increase in recruitment) followed the same pattern when shifting from low disturbance to high disturbance. The models were not successful in predicting the shift in basal area growth and specific wood density; forest processes and traits that are known to have strong gradients across the Amazon Basin (Baker et al., 2004a; Lewis et al., 2004; Phillips et al., 2004). Therefore, results showed that the disturbance regime alone might not explain all of the differences in forest dynamics between the two regions, or the models do not accurately capture all disturbance and recovery processes. Furthermore, the net loss in biomass was assumed to be a “false-positive” because empirical data has found that variation in wood density drives the reduction in regional-scale AGB (Baker et al., 2004a), while in ZELIG-TROP AGB loss was driven by basal area loss, and in CLM AGB loss was driven by LAI loss. Basal area and LAI were not found to be drivers in AGB loss in observed data. Next we compared the same disturbance scenario in CLM-CN 4.5 and found with regards to AGB response to disturbance, CLM performed in a very similar behavior to the gap model. However, CLM did not reproduce the temporal variability in coarse litter inputs, and instead remained constant over time. We also compared the response of large-scale periodic disturbances in the two models, and found that CLM captured similar disturbance and recovery patterns as the gap model.

It is predicted that disturbances will increase in the future, and this modeling study was unique in that we: (1) showed that the drivers that lead to the net loss in carbon stocks in models are different compared to drivers in empirical datasets, (2) in order to capture regional-scale variation in life history strategies wood density should be included in estimating biomass, (3) predicted that not all differences in tropical forest attributes (e.g., AGB, basal area growth, stem density, and wood density) can be explained by disturbance regimes alone, and also (4) highlighted some inconsistencies between a detailed gap model and the global community land surface model used in CESM. It was also unique in that we simulated a *continual* high disturbance rate, in addition to background mortality during each time step. This set it apart from the ma-

5 biomass loss due to projected precipitation changes, however larger uncertainties are associated with the effect of CO₂ compared to uncertainties in precipitation. Increasing evidence from an ensemble of updated global climate models are predicting that tropical forests are at a lower risk of forest dieback under climate change, in that they can still retain carbon stocks until 2100 due to fertilization effects of CO₂ (Cox et al., 2013; Huntingford et al., 2013), however there is still large uncertainties between models and how tropical forests will respond to interacting effects of increasing CO₂ concentrations, warming temperatures, and changing rainfall patterns (Cox et al., 2013).

10 Long-term, demographic vegetation models are useful tools at predicting temporal trends related to CO₂ fertilization signals and changes to carbon stocks and fluxes, and the interactions between CO₂ fertilization and varying levels of disturbances are an important next step to evaluate. However, due to the magnitude of forest growth, CO₂ fertilization may not be the only causal factor but instead driven by interacting agents such as biogeography and changing environmental site conditions (Lewis et al., 2004; Malhi and Phillips, 2004). Additionally, the role of widespread recovery from past disturbances still needs to be explored as an explanation for biomass accumulation. The interactions between disturbance-recovery, CO₂ fertilization, and/or changes in forest structure might be a more plausible explanation and could have large effects on future forest productivity and growth patterns.

20 In this study over the period of 100 years there was no significant change in biomass accumulation in both ZELIG-TROP and CLM (Fig. 5b), due to no CO₂ fertilization occurring in the models, and the forest did not act as a carbon sink as predicted by empirical studies across a network of Amazon inventory plots (Phillips et al., 1998, 2004). Upon applying the disturbance treatment, the forest became more stable. With regards to periodic disturbances and sudden tree mortality events both models predicted a negative ΔAGB, -0.15 and -0.46 Mg C ha⁻¹ yr⁻¹ for ZELIG-TROP and CLM respectively, therefore the forest acting as a carbon source (Table 4). CLM predicted a larger decrease in biomass under periodic disturbances, which offsets the current ob-

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served biomass accumulation (lower empirical estimates at 0.20–0.39 Mg C ha⁻¹ yr⁻¹ (Phillips et al., 1998; Chambers and Silver, 2004)).

4.2 Lessons learned from modeling tropical forest disturbance

4.2.1 Model comparison to field data and additional sites

5 We found that using a dynamic vegetation gap model that operates at the species level was successful at replicating the Central Amazon forest. ZELIG-TROP has also been validated for the subtropical dry forest of Puerto Rico (Holm et al., 2012), but this is the first application of a dynamic vegetation model of this kind (i.e. gap model) for the Amazon Basin. As a result of using species-specific traits, the values reported
10 by ZELIG-TROP for average basal area, AGB, stem density, LAI, and ANPP were all close to observed values (e.g. ranging from 1.7 to 17.1 % difference between ZELIG-TROP and observed field results). Field measurements of AGB from the Central Amazon transects averaged \pm SD: 169 ± 27.6 Mg C ha⁻¹, and additional field-based measurements from nearby sites in the Central Amazon (FLONA Tapajós plots) range
15 from 132 to 197 Mg C ha⁻¹ (Miller et al., 2003; Keller et al., 2001). ZELIG-TROP predicted very similar estimates of AGB: 178 ± 10.5 Mg C ha⁻¹, therefore model results were within the expected range. From a single-point grid cell, located in the same latitude and longitude coordinates as observational plots, CLM predicted higher levels of AGB (269 Mg C ha⁻¹). In a study comparable to ours, Chambers et al. (2004) found
20 that upon doubling turnover rates in an individual based stand model, forest biomass for a Central Amazon forest decreased by slightly more than 50 %. This decrease in forest biomass was similar to the response reported in this study (41.9 % and 49.9 %). Unlike the Chambers et al. (2004) study, we did not impose an increase in growth rates in the model parameters in conjunction with elevated turnover rates. Instead, annual
25 growth rates were determined internally within ZELIG-TROP based on species-specific parameters and environmental conditions.

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4.2.2 Growth rates and wood density

Our prediction of average growth rate was higher than field data found in the Central Amazon BDFFP inventory plots (3.1 vs. 1.7 Mg C ha⁻¹ yr⁻¹, Table 4), but similar to other values found in the Central and Eastern Amazon. For example, using a process-based model, Hirsch et al. (2004) found above-ground stem growth to be 3.6 Mg C ha⁻¹ yr⁻¹, and field measurements were 2.9 Mg C ha⁻¹ yr⁻¹ at the Seca Floresta site in the Tapajós National Forest (Rice et al., 2004). During the high disturbance treatment, we did not observe an increase in average growth rates compared to the no-disturbance treatment. In fact, there was a slight decrease in annual growth (Table 4, Fig. 4e). This non-significant change in growth rates could have been due to the nonoccurrence of large increases in available light and resources after each additional death, a result of a continual disturbance treatment as opposed to a dramatic disturbance event. Alternatively the Western Amazon plots, counterparts to the high disturbance treatment, did exhibit an increase in growth rates (Fig. 4e). Differences in environmental gradients between regions, such as higher total phosphorous, less weathered, and more fertile soils in the Western Amazon (Quesada et al., 2010) could be a stronger controlling factor. In the periodic disturbance treatment, growth and productivity *did* increase directly following each large-scale disturbance (removing 20 % of stems). After each pulse disturbance ANPP increased by 14 % over the 50-year recovery phase. The change in community composition under the high disturbance treatment was also representative of what would be expected (i.e. emergent species decreased by the largest percent in basal area, and canopy and subcanopy species increased), however by not capturing expected changes in wood density the model might be missing some shifts in species composition response to disturbance.

Wood density is a robust indicator of life history strategies, growth rates and/or successional status of a forest (Whitmore, 1998; Suzuki, 1999; Baker et al., 2004a). In the “west and south” tree species on average have faster growth rates, faster turnover rates, and lower wood density. Upon modeling a Central Amazon forest with distur-

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bance rates similar to the “west and south”, the higher disturbance did *not* create a community composition dominated by pioneer species or lower the average wood density, but instead created a forest of less emergent species, more canopy species, and higher wood density. The canopy species that decreased in basal area due to disturbance had an average wood density of 0.67 g cm^{-3} , while canopy species that increased in basal area had an average wood density of 0.70 g cm^{-3} , potentially helping to lead to the rise in overall wood density, in addition to the drop in *Parkia multijuga* discussed in the results section. The growth rate scaling coefficient, G , used in ZELIG-TROP did have a negative relationship with wood density, matching the robust signal observed from inventory data, but was not correlated ($R^2 = 0.13$), leading to another possible explanation of the opposite pattern in wood density shifts with increased disturbance. Wood density is not a main parameterization variable in ZELIG-TROP, and other factors in the gap model (e.g., drought or light tolerances, maximum age, availability of light) could be a stronger driver of community composition shifts over wood density.

It should be noted that wood density is difficult to measure accurately in the field, varies between and within species (Chave et al., 2006), varies within a tree across diameter and from the base of the tree to the top (Nogueira et al., 2005), and the Chambers et al. (2001) AGB model without wood density shows that variation of the data explained by the model is strong ($r^2 = 0.973$). Including wood density in AGB allometric equations is not required, but beneficial for accounting for differences in carbon stocks due to changes in species composition, gradients in soil fertility (Muller-Landau, 2004) as opposed to disturbance regimes, and can be a key variable in greenhouse gas emission mitigation programs.

4.2.3 CLM 4.5 vs. dynamic vegetation model

Simulating vegetation demography is beneficial to tracking forest demographics, community shifts, competition, and dynamic changes in carbon stocks and fluxes, and should be considered being incorporated into CLM. The version of CLM used here

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does not take into account differences between plant size, plant age, or all biotic and abiotic stressors. Using demography typical of a gap model will account for these missing factors, will aid in capturing annual carbon variability as a result of heterogeneous mortality across the landscape, and can help improve global land surface models. The exact causes and processes leading to plant mortality are difficult to quantify (Franklin et al., 1987; McDowell et al., 2008, 2011), and additional field research is required in this area, especially in the tropics. However, the gap model approach can quantify the contribution from natural death vs. stress related death vs. disturbance related death under no-disturbance and high-disturbance scenarios.

The major differences between the gap model ZELIG-TROP and CLM in response to higher disturbance rates was, (1) the average AGB net carbon loss was 74 Mg C ha^{-1} in ZELIG-TROP vs. 134 Mg C ha^{-1} in CLM as a result of doubling background mortality, and (2) that the temporal variability in carbon stock and fluxes was not replicated in CLM. While the absolute values in AGB net carbon loss were different between the two models (Fig. 5b), this was due to the fact that ZELIG-TROP was calibrated for a specific location in the Central Amazon and CLM using initial conditions representative of the entire Amazon basin. As a result of this distinction, relative differences should be used as a comparison tool. The two models were consistent in that they both reached new equilibrium steady-states with both continual and periodic disturbances, and therefore the relative change in biomass was analogous between ZELIG-TROP and CLM. Temporal variability in carbon stocks and fluxes over time were also absent from the CLM model due to the inexistence of plant demography (i.e. changes in plant size, structure, and age). Regarding the response to periodic disturbances, the major difference between ZELIG-TROP and CLM was the rapid return to pre-disturbance ANPP levels in CLM after each large-scale disturbance event, while in ZELIG-TROP the recovery of ANPP was gradual.

With the inclusion of higher disturbance rates, the two models tested here do predict a $\sim 40\text{--}50\%$ reduction in carbon stocks, however the driver that lead to this decrease are inconsistent with empirical drivers. Additionally, ZELIG-TROP predicted

lower coarse litter production rates, and gains that exceeded losses. CLM predicted higher coarse litter production rates, and losses that exceeded gains (Table 4), but these differences were minimal. However, these differences that we found in gains minus losses between ZELIG-TROP and CLM can lead to inaccurate predictions of carbon response to increasing disturbance rates in integrated assessment models that use CLM. When taking into account the entire Amazon Basin over many years, this discrepancy can significantly affect predictive outcomes when using the global CLM for mitigation strategies.

4.3 Future directions

To constrain the future concentration of CO₂ into the atmosphere, current mitigation strategies rely heavily on tropical forests to maintain, or increase, as a carbon sink. In order to accurately develop and impose mitigation strategy targets, the land components of earth system models need to more accurately simulate plant mortality, coarse litter inputs, carbon fluxes, and accelerated growth processes associated with disturbance-recovery events. CLM 4.5 has been the model of focus here, however multiple versions of the Lund–Potsdam–Jena Dynamic Global Vegetation Model (LPJ-DGVM; Sitch et al., 2003), such as LPJmL and LPJ-GUESS-SPITFIRE, are notable models to evaluate changes to forest biomass in the Amazon (Rammig et al., 2010, others), and changes to stand structure, plant mortality, and emissions due to fire (Thonicke et al., 2010). Cramer et al. (2001) showed the varying range and uncertainties in ecosystem response and magnitude of the terrestrial carbon sink as a function of rising CO₂ and climate change using six DGVMs with varying degrees of functionalities. Including transient changes in vegetation structure and also accounting for changes due to elevated disturbance rates requires models to include vegetation dynamics and succession processes, biogeochemical processes, and climate and circulation. With the varying degree of capabilities and functionality within vegetation models this study has benchmarked mortality and disturbance processes in CLM and will benefit the iESM project (Integrated Earth System Model; Jones et al., 2013), which combines CLM with

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a fully integrated human system component. To evaluate energy market shifts and carbon policy changes, as a first step we will execute the reduction of the terrestrial carbon sink due to increases in mortality from changes in disturbance regimes, within the fully coupled iESM. In addition, the capability of tropical forests to act as a carbon sink with and without the inclusion of disturbances needs to be corrected in the models, which if not could either diminish the effect of mitigation policy, or force more stringent changes in energy infrastructure in order to meet the same climate stabilization targets. Ultimately the contributions to iESM will create the capabilities to test the carbon market and energy market responses to changes in forest mortality and increased disturbances in the Amazon and on a global scale.

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Table 2. Environmental parameters used in ZELIG-TROP for the central Amazon basin. Values reported in a range were monthly low and high averages.

Lat./Long./ Alt. (m)	Plot Area (m ²)	Mean monthly temperature (°C)	Mean monthly precipitation (cm)	Soil field capacity (cm) ^a	Soil wilting point (cm) ^a	Relative direct and diffuse solar radiation (%)
−2.3/−60.0/ 100.0	400.0	25.18–27.47	8.01–45.16	52.0	32.9	0.6/0.4

^a Lawrence et al. (1999).

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Table 3. Averages (and standard deviations) of five forest attributes for the observed values recorded from sites near Manaus, Brazil, averaged over 5 ha, and the modeled ZELIG-TROP results. ZELIG-TROP results are averaged for the final 100 years, after an initial spin up of 400 years. The remaining values correspond to the percent differences between the observed and simulated values, and the minimum and maximum range of a ZELIG-TROP simulation.

	Avg. Basal Area ($\text{m}^2 \text{ha}^{-1}$)	Avg. Biomass (Mg C ha^{-1})	Avg. Stem Density (ha^{-1})	Avg. LAI ($\text{Mg C ha}^{-1} \text{yr}^{-1}$)	Avg. ANPP
Empirical Data	30.06 (6.61)	169.84 (27.60)	656 (22)	5.7 (0.50)	6.5
ZELIG-TROP	32.96 (1.22)	178.38 (10.53)	574 (70)	5.8 (0.24)	5.4 (0.22)
Percent Diff. (%)	9.66	5.03	-12.49	1.75	-17.08
ZELIG-TROP min./max.	31.14/35.97	167.97/189.26	472/688	5.26/6.48	5.08/5.92

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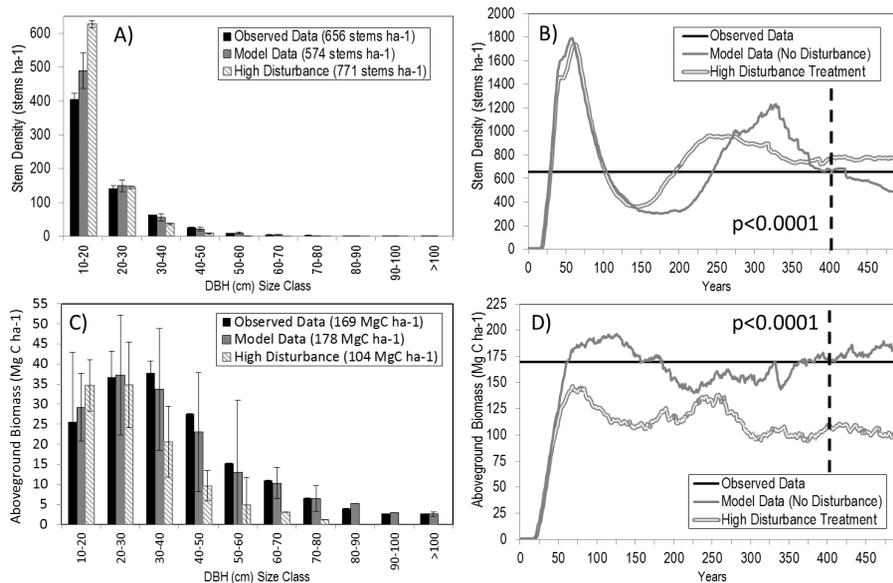


Figure 1. Comparison between observed field data from “transects” in Central Amazon, ZELIG-TROP model data from no-disturbance scenario, and ZELIG-TROP model data from high-disturbance treatment. **(A)** Average stem density (stems ha⁻¹) and SD by DBH (cm) size class, **(B)** stem density simulated over 500 years, **(C)** average above-ground biomass (Mg ha⁻¹) and SD by DBH (cm) size class, and **(D)** above-ground biomass simulated over 500 years. Average results and *t* test between two model results taken once the model reached a steady-state, or the final 100 years of simulation.

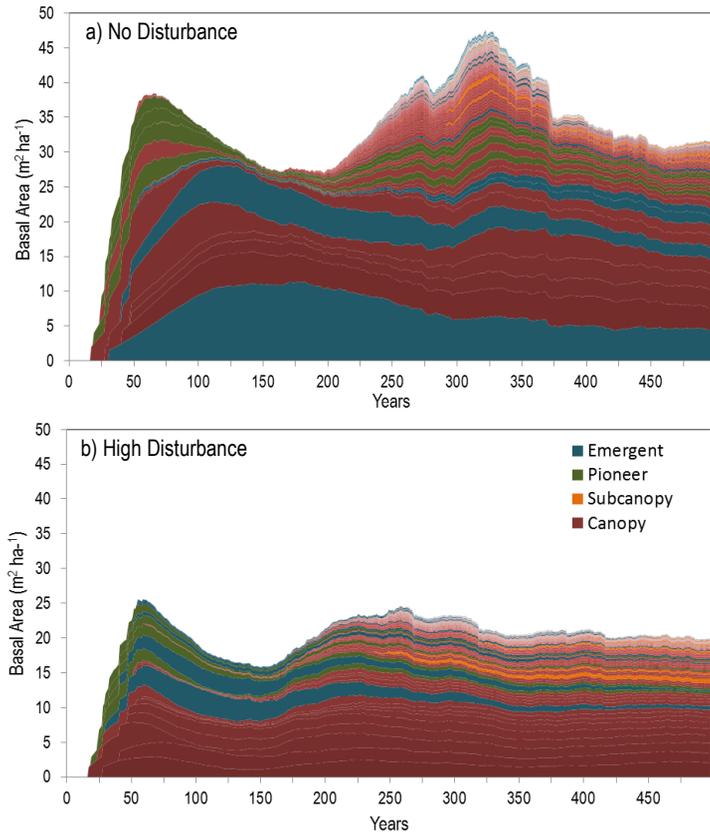


Figure 2. (a) Model simulated successional development for all species modeled in ZELIG-TROP for a Central Amazon forest, separated by canopy growth form (emergent, canopy, sub-canopy, or pioneers). Species composition reported in individual basal area ($\text{m}^2 \text{ha}^{-1}$). (b) Model simulated successional development for all species modeled in ZELIG-TROP after the high-disturbance treatment.

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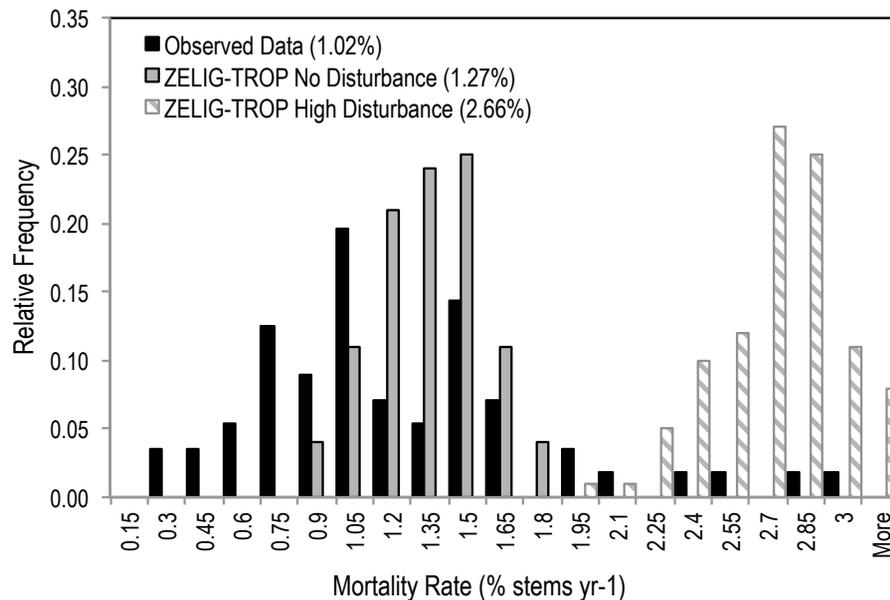


Figure 3. Comparison of relative frequency of annual mortality rates (% stems yr⁻¹) from observed data, ZELIG-TROP no-disturbance, and ZELIG-TROP high-disturbance model data after the disturbance treatment. (Observed data: Chambers et al., 2004.)

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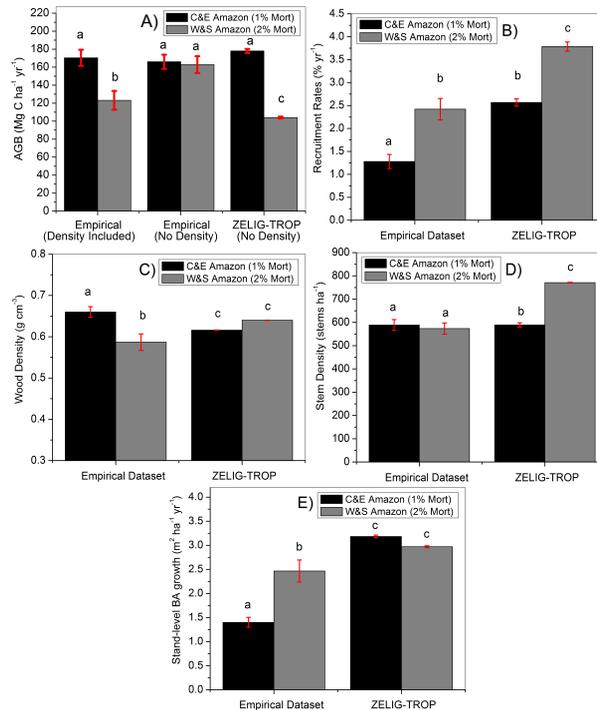


Figure 4. Comparison between “central and east” Amazon (“slow dynamics”) and “west and south” Amazon (“fast dynamics”) between the empirical (RAINFOR dataset) and modeled ZELIG-TROP results for average (A) above-ground biomass (AGB, Mg C ha⁻¹ yr⁻¹) with the observed dataset either including or not including wood density in the Chambers et al. (2001) allometric equation, (B) recruitment rate (% yr⁻¹), (C) average wood density (g cm⁻³), (D) stem density (stems ha⁻¹), and (E) stand-level basal area (BA) growth rate (m² ha⁻¹ yr⁻¹), with 95 % CIs bars included. Different lower case letters represent significantly different values using Tukey’s multiple comparison, following a one-way ANOVA.

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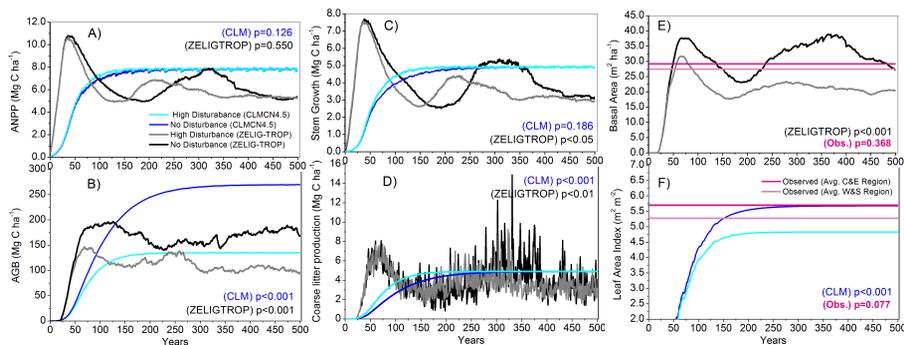


Figure 5. CLM-CN model evaluation and comparisons to ZELIG-TROP for a no-disturbance scenario and a high disturbance treatment: **(A)** ANPP, **(B)** above-ground biomass, **(C)** stem growth, **(D)** coarse litter production rates, all measured in Mg C ha^{-1} , and **(E)** basal area from ZELIG-TROP and observed data reported by Baker et al. (2004a), and **(F)** leaf area index (LAI) from CLM-CN4.5 and observed data reported by McWilliams et al. (1993) and Malhi et al. (2013). Statistical significance test in all panels are two-sample Student's t test between the no-disturbance and high disturbance treatments, separately for each model.

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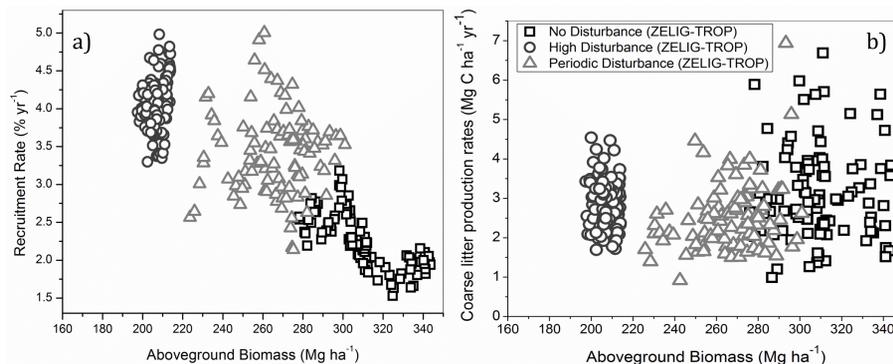


Figure 6. (a) Relationship between above-ground biomass (Mg ha⁻¹) and recruitment rates (% yr⁻¹). (b) Relationship between above-ground biomass (Mg ha⁻¹) and coarse litter production rates as a result of tree mortality (Mg C ha⁻¹ yr⁻¹), during a no-disturbance, high disturbance, and periodic disturbance simulation in ZELIG-TROP for the last 100 years of simulation.

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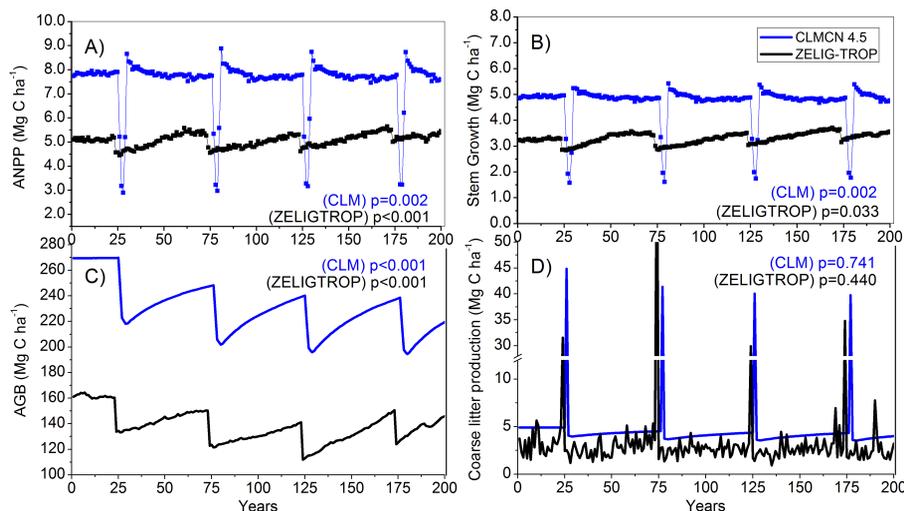


Figure 7. CLM-CN model evaluation and comparisons to ZELIG-TROP for a periodic disturbance treatment: **(A)** ANPP, **(B)** stem growth, **(C)** aboveground biomass (AGB), and **(D)** coarse litter production rates, all measured in Mg C ha^{-1} . Statistical significance test in all panels are two-sample Student's t test between the no-disturbance and high disturbance treatments, separately for each model.

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