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 this issue, we evaluated disturbance-recovery processes in a Central Amazon forest under two scenarios of increased disturbance rates 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 ~2% mortality, the two regions continued to differ in multiple forest processes. With the inclusion of elevated natural disturbances, at steady-state, AGB significantly decreased by 41.9% with no significant difference between modeled AGB and empirical AGB from the Western Amazon datasets (104 vs. 107 Mg C ha^{-1} respectively). However, different processes were responsible for the reductions in AGB between the models and empirical dataset. The empirical dataset suggests that a decrease in wood density drives the reduction in AGB. While decreased stand basal area was the driver of AGB loss in ZELIG-TROP, a forest attribute that does not significantly vary across the Amazon Basin. Further comparisons found that stem density, specific wood density, and basal area growth rates differed between the two Amazonian regions. Last, to help quantify the impacts of increased disturbances on the climate and earth system, we evaluated the fidelity of tree mortality and disturbance in CLM. Similar to ZELIG-TROP, CLM predicted a net carbon loss of 49.9%, with an insignificant effect on aboveground net primary productivity (ANPP). Decreased leaf area index (LAI) was the driver of AGB loss in CLM, another forest attribute that does not significantly vary across the Amazon Basin, and the temporal variability in carbon stock and fluxes was not replicated in CLM. Our results suggest 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 tropical forest characteristics in response to increased disturbances.

Keywords: aboveground biomass, CLM, disturbance-recovery, growth rates, mortality, specific wood density, tropical rain forest, ZELIG-TROP.

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; U.S. DOE 2012). Increased forest dieback in tropical locations could then produce large economic costs, ecological impacts, and lead to climate related positive feedback cycles (Canham and Marks 1985; Dale et al., 2001; Laurance and Williamson 2001, Bonan 2008).

The effects of large-scale removal of tropical forest, leading to changes in global climate 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). 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. 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). In addition, the effectiveness of climate mitigation strategies will be affected by future changes in natural disturbances regimes (IPCC 2014; Le Page et al., 2013), due to the effect of disturbances on the terrestrial carbon balance. By using an economic/energy integrated assessment model, it was found that when natural disturbance rates are doubled and in order to reach a stringent mitigation target, (3.7 W m^{-2} level) the societal, technological, and economic strategies will be up to 2.5 times more costly (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) where an integrated assessment model is coupled with a biogeochemical and biophysical climate model such as CLM/CESM. It is necessary to improve earth system models in order to simulate dynamic disturbance rates and gradual forest biomass loss in response to increasing mortality rates.

Turnover rates currently vary for different regions of Amazonia (Baker et al., 2004a; 2004b; 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 regional-scale AGB estimates, concluding that differences in species composition and related specific wood density determined the regional patterns in AGB. There is a strong west-east gradient in that ‘west and south’ Amazon forests were found to have significantly lower AGB than their eastern counterparts; also confirmed by additional studies (Malhi et al., 2006, Baraloto et al., 2011).

It is unclear if these regional variations in forest processes and carbon stocks are driven by external disturbance (e.g., increased drought, windstorm, forest fragmentation) or internal influences (e.g., soil quality, phosphorus limitation, species composition, wood density) (Phillips et al., 2004; Chao et al. 2009; Quesada et al., 2010; Yang et al., 2013). 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 use modeling tools 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.

We are using an individual-based, demographic, gap-model (Botkin et al., 1972; Shugart, 2002) as a "benchmark" model to 1) evaluate the influence of disturbance on net carbon loss and variations in forest dynamics between two regions (central vs. 'west and south'), 2) evaluate disturbance and mortality in CLM-CN 4.5 (called CLM for remainder of paper), and 3) improve upon representing terrestrial feedbacks more accurately in earth system modeling. We used the dynamic vegetation gap model ZELIG (Cumming and Burton 1993; Urban et al., 1993). ZELIG has been updated and modified to simulate a tropical forest in Puerto Rico with a new versatile disturbance routine (ZELIG-TROP; Holm et al., 2012), making this vegetation dynamic model a good choice for this study.

Vegetation and carbon response to increased disturbance rates resulting from human induced climate change must be examined in more detail. To test how a widely used global land surface model, CLM, forecasts changes in forest carbon sinks and sources we addressed differences in AGB, ANPP, growth rates, and coarse litter production rates as a result of disturbances. The main research questions of the study are: 1) what are the long-term consequences of continual elevated disturbance rates and periodic, large-scale disturbances in the Central Amazon? 2) Can the variability in forest dynamics, carbon stocks and fluxes between the Western and Southern Amazon and the Central Amazon forests be explained by the variability in the natural disturbance regime (i.e., higher mortality rates)? Finally: 3) what are the differences after increasing disturbance rates in ZELIG-TROP vs. CLM for the Central Amazon? We are assuming an independent driver of mortality; therefore 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 Pequisas 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 2,110 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 2,739 mm yr^{-1}.

We quantified demographic data such as stem density, diameter at breast height (DBH, cm), and change in diameter for trees >10 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, Mg C ha^{-1} yr^{-1}) after taking into account loss of tree mass due to tree damage (Chambers et al., 2001). Observed mortality rates (% 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 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 used inventory data collected from 59 plots as reported in Baker et al. (2004a; 2004b), 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. We then compared the Central Amazon forests (both simulated and observed data) to the observed ‘west and south’ datasets.

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 (400m^2 plots, replicated uniquely 100 times). Maximum potential tree behaviors (e.g. 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 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 supplemental material).

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 km^2 (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). We used the canopy classification as described by Laurance et al. (2004) to infer species-specific rankings for tolerance and intolerance to shading. Average monthly precipitation (cm) and temperature (°C) required for the environmental parameters in ZELIG-TROP (Table 2) were based on field data collected from 2002-2004 in the study site (Tribuzy, 2005). Soil field capacity (cm) and soil wilting point (cm) were determined from soil measurements in nearby central Amazon study sites (Laurance et al., 1999).

In order to more accurately simulate the Central Amazonian forest, a few modifications were made to the original ZELIG-TROP model (Holm et al., 2012). First, the allometric equation used to estimate above-ground biomass (Mg C ha^{-1}) was updated to include an equation specific for the Brazilian rainforest in the Central Amazon (Chambers et al., 2001; Eq. 1).

$$\ln(mass) = \alpha + \beta_1 \ln(DBH) + \beta_2[\ln(DBH)]^2 + \beta_3[\ln(DBH)]^3 \tag{1}$$

where above-ground biomass (mass) is in kg, α is -0.370, β_1 is 0.333, β_2 is 0.933, and β_3 is -0.122 (r^2_{adj} = 0.973) based upon data collected from 315 harvested trees. Specific wood density is not taken into account in this model.

In model development of the original ZELIG-TROP (modified for a subtropical dry forest), death caused by natural mortality (age-related) was killing tropical trees prematurely. This was also seen in initial model testing for the wet tropical forest. In contrast to tropical dry forests, individuals in tropical wet forests have a longer life potential and a higher likelihood of reaching their potential size. For example, the Central Amazon is able to support trees >1000 years old (Chambers et al., 1998; 2001; Laurance et al., 2004), where a dry forest may only be able to support trees to a maximum of 400 years. To adjust for this variation, the natural survivorship rate was increased from 1.5% to 6% of trees surviving to their maximum age (Table 1). This was a conservative value, with one study estimating about 15% of species in Central Amazon attaining their maximum ages (Laurance et al., 2004). Lastly, we also modified ZELIG-TROP's mean available light growing factor algorithm, which in part was used to accurately calculate tree height and crown interaction effects, as developed in ZELIG-CFS (Larocque et al., 2011). To best portray tree growth and crown development typical of an individual within a tropical canopy, we used an earlier algorithm version developed for ZELIG-CFS. This algorithm was the ratio of available growing light factor (ALGF) to a doubled crown width for each 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 Verification Methods

ZELIG-TROP simulations for the Central Amazon forest were run for 500 years and replicated on 100 independent plots, each the size of 400m^2. 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 (m^2 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 supplementary materials. Predicting the impacts of increased mortality is critical since other recent studies have found that tree mortality in the Central Amazon has been undersampled 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 canopy trees with a large percentage of gaps having relatively small areas of <200 m^2 (Uhl, 1982; Denslow, 1987; Stanford, 1990). However, some windthrow events will create large gaps that then initiate secondary succession processes (Brokaw, 1985, Chambers et al., 2013). Since there can be multiple spatial scales and drivers of tree mortality, we are simulating mortality as a stochastic, independent event within ZELIG-TROP, using the new versatile disturbance routine implemented in Holm et al. (2012). Most mortality events in the Central Amazon occur on individual trees (Chambers et al., 2004; 2013). Therefore, this phenomenon was replicated in the model. Specifically, any one tree >10cm DBH was randomly selected to die and be removed from the forest canopy on an annual basis at the gap scale, in addition to the existing selection of trees removed by natural senescence. This ‘high disturbance’ treatment for the Central Amazon forests is representative of the current turnover rates in ‘west and south’ (Phillips et al., 2004), thus creating an opportunity 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. Variables compared between the two regions included AGB, wood density (Baker et al., 2004a), recruitment rates, and stem density (Phillips et al., 2004), and stand-level BA growth rates (Lewis et al., 2004).

A second treatment has been applied in order to improve understanding of periodic large-scale disturbance and recovery events. This treatment consisted of removing 20% of stems >10cm DBH every 50 years (i.e. periodic treatment). It has recently been noted that patch-scale ($400m^2$) succession-inducing disturbances exhibit a return frequency of about 50 years within the Central Amazon region (Chambers et al., 2013). Therefore we have set our large-scale disturbance event to repeat four times over a 200 year period (every 50 years) after the forest has reached a mature stable state. This treatment was also conducted in both ZELIG-TROP and CLM. An important metric in determining the forest carbon balance as a result of disturbance is the total change in stand biomass over time (ΔAGB, Mg C ha^{-1}), defined as $AGB_{t2} - AGB_{t1}$ over the simulation period.

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 m^2 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}). ZELIG-TROP was also successful at accurately predicting stem density and AGB by DBH (cm) size class (Fig. 1a, 1c). 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 consists of many tree crowns, large trees, and usually a dense area of biodiversity (Wirth et al., 2001). For example, 63% of the 90 tree species simulated were categorized as a canopy growth form. However, there was also an even mixture 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% ± 1.72% (Chambers et al. 2004). As estimated by ZELIG-TROP, the no-disturbance annual mortality rates were near to observed values (1.27% ± 0.21%) but had a smaller distribution around the mean (Fig. 3). As expected, annual mortality rate doubled (2.66% ± 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 to mirror the ~2% yr^{-1} mortality rates in the 'west and south', the two Amazon regions continued to differ in forest structure and function. Stem density, specific wood density, basal area growth rates, and AGB 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, there was a significant difference in both wood density and basal area growth rates between the two regions in the empirical dataset, but no significant difference in the model results (Fig. 4). Alternatively when comparing stem density there was no significant difference between the two regions in the empirical dataset, but there was a significant increase in the model results (Fig. 4).

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. The AGB from the higher disturbed Central Amazon was similar (104 Mg C ha^{-1}) to AGB values in the 'west and south' RAINFOR network plots, but only when comparing to biomass equations that included weighting for wood density (Chave et al., 2001; Chambers et al., 2001). For example, AGB predicted by the Chave et al. (2001) equation (107 Mg C ha^{-1}), had no significant difference between the two disturbed regions (two sample t-test, $t_{(38,\ 2.7)} = 2.29$, considering alpha=0.01, p=0.03) (Fig. 4a). 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). However, 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) and Malhi et al. (2006). 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 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=0.4077, 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=0.1260), only decreasing ANPP by 0.04 (from 5.39 to 5.35 Mg C ha^{-1} 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 (i.e., 10 cm DBH size class) in newly opened gaps. When comparing the stand-level BA growth rates (proxy for productivity) in the RAINFOR network there was a significant increase in growth rates in the 'west and south' compared to the Central Amazon, 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 m^2 ha^{-1} yr^{-1}, Fig. 4e or 0.20 Mg C ha^{-1} yr^{-1}, Fig. 5c). The model might be inaccurately representing 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 m^2 ha^{-1} yr^{-1}).

The recruitment rates (% 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% yr^{-1}, constituting a 69.1% increase above no-disturbance recruitment rates (Table 4, Fig. 6a). Pre-treatment, modeled recruitment rates were 0.9% 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 ~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, Mg C ha^{-1} yr^{-1}, Fig. 6b) compared to the no-disturbance scenario, but rather a significant decrease (two sample t-test, $t_{(99,1.97)} = 2.70$, $p<0.01$). Under a high disturbance treatment, the production of coarse litter decreased by an average of 0.25 Mg C ha^{-1} yr^{-1} (8.3%, Table 4). However it is unclear if this decrease in production of coarse litter is biologically or atmospherically significant.

Once the forest reached a mature stable state (after 500 years) the periodic disturbance treatment was applied, removing 20% of stems in the mature forest every 50 years (for a duration of 200 years). The carbon loss over the 200-year period, including the four large-scale disturbances, was less severe than the high-disturbance treatment, but was still a significant decrease (two sample t-test, $t_{(99,1.97)} = 22.73$, $p<0.001$). Compared to the no-disturbance scenario, average AGB net carbon loss was 40 Mg C ha^{-1} (from 178 to 138 Mg C ha^{-1}, 22.7%, Fig. 7c) and ANPP significantly decreased from an average of 5.39 to 5.06 Mg C ha^{-1} yr^{-1} (6.1%, two sample t-test, $t_{(99,1.97)} = 7.65$, $p<0.001$). For the periodic treatment, the decrease in biomass was roughly half the decrease observed in the high-disturbance treatment, however the decrease in ANPP was more severe.

3.2.2 Community Composition Changes

The individual-based dynamic vegetation model approach was able to explore the long-term changes to community composition and fate of each species with increased disturbance. A high disturbance treatment shifted species composition towards a more even canopy structure, and increased the species evenness and diversity (Fig. 2b). The largest basal area reduction occurred in the most common species; specifically the top two emergent species, followed by the most common canopy species. With an increase in disturbance, the species originally occupying the largest basal area on the plot, *Parkia multijuga*, decreased by 94.8% in relative difference in basal area compared to all species averaged over the last 100 years. The 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).

The empirical dataset 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). This trend was not seen between the no-disturbance and high disturbance treatment in the central Amazon, with no significant difference between the treatments (Fig. 4c). 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.

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 model outputs from CLM for the disturbed Central Amazon 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 ΔAGB (-0.15 and -0.46 Mg C ha^{-1} yr^{-1} for ZELIG-TROP and CLM respectively, Table 4). The negative total ΔAGB was less in ZELIG-TROP, and was likely attributed to ZELIG-TROP predicting growth rates to significantly increase (by 0.20 Mg C ha^{-1} yr^{-1}, two sample t-test, $t_{(99,1.97)} = 2.14$, $p<0.05$), most likely due to 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).

There were discrepancies with the response of ANPP to the periodic 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 captured 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 heterogeneous landscape (Fig. 5d, 7d). While the relative change in AGB was consistent between the two models, there was a large overestimation in the absolute values. With the inclusion of the high disturbance treatment CLM predicted that average AGB net carbon loss was 134 Mg C ha^{-1} (from 269 to 135 Mg C ha^{-1}) vs. 74 Mg C ha^{-1} in ZELIG-TROP.

4 Discussion

4.1 Elevated forest disturbance and long-term impacts

Disturbance is likely to increase in Amazon forests. Since the mid-1970’s observed tree mortality and recruitment rates have been increasing in the Amazon (Phillips et al., 2004), and higher than usual mortality rates have also been associated with droughts and strong windstorm events (Nepstad et al., 2007; Chambers et al., 2009; Phillips et al, 2009; Negron-Juarez et al., 2010; Lewis et al., 2011), each of which could increase with human-induced climate change. In addition, reported mortality rates might be underestimated as 9.1-16.9% of tree mortality was missing from plot-based estimates in the Amazon (Chambers et al., 2013). We first investigated the impact of continual high disturbance (100 years) in a Central Amazonian forest using a demographic forest model as a benchmark model due to operating at finer scales and having mechanistic mortality algorithms. The elevated disturbance resulted in a decrease in AGB by 41.9%, with essentially no change in ANPP (1.0% decrease), and an increase in recruitment rates by 69.1%. As a result of higher proportion of smaller stems (20.7% increase in the 10-30cm DBH size classes), and decrease in large stems, there was a significant decrease in coarse litter production rate by 8.3%.

We compared empirical data from the higher disturbed 'west and south' Amazon plots ('fast dynamics'), to the modeled Central Amazon forest with mirrored tree mortality to evaluate if the models used in this study could predict similar forest dynamics and characteristics. Only one attribute that is tightly linked with disturbances (i.e., 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 growth rates and specific wood density; forest processes and traits that have been shown to differ with varying turnover rates (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' in the models because 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 are not found to be drivers of AGB loss, or patterns of biomass, in empirical datasets (Baker et al., 2004a;

Malhi et al., 2006). In contrast basal area varied only slightly across the Amazon plot network (27.5 vs. 29.9 m^2 ha^{-1}, Baker et al., 2004a). This indicates that wood density, which is a strong indicator of functional traits (Whitmore, 1998); along with patterns of family composition are strong drivers in steady-state AGB variation.

One study using the RAINFOR network found that variation in wood density drives the pattern in regional-scale AGB (Baker et al., 2004a), a trend that was not captured in ZELIG-TROP. While wood density is typically found to be higher in the central Amazon and lower in the 'west and south' (Baker et al., 2004a; ter Steege et al., 2006; Saatchi et al., 2009), high wood density is also found in northern Peru (Patino et al., 2009; Saatchi et al., 2009). 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. 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.

After applying continual and periodic higher disturbance treatments, we did not observe a continual decrease in forest structure or biomass that lead to a new forest successional trajectory. Instead, we found that the Amazon forest shifted to a new equilibrium state. The outcome of a continual higher disturbance rate generated a stable forest but with less biomass, faster turnover, higher stem density consisting of smaller stems, as well as less emergent species, less ANPP, and less contribution of coarse litter inputs. Inventory studies have reported that with increased turnover, there is a change in community composition, less wood density, and when these traits are taken into account there is also less AGB (Baker et al., 2004a). We conclude that including wood density in dynamic vegetation models is needed. While we have shown that terrestrial biomass will decrease with increased disturbances, the interacting affects from potential CO_2 fertilization should be explored.

4.1.1 Disturbance, biomass accumulation, and CO_2 fertilization

Demographic vegetation models are useful tools at predicting long-term temporal trends related to changes in carbon stocks and fluxes. The offsetting interactions between possible CO_2 fertilization and disturbances are an important next step to evaluate. Based on observational studies from permanent plots there has been an increase in tree biomass in Amazonian forests by ~0.4-0.5 t C yr^{-1} over the past three decades (Lewis et al., 2004; Phillips et al., 1998; 2008). CO_2 fertilization effects might be an explanation (Fan et al., 1998; Norby et al., 2005), but this is unknown or refuted (Canadell et al., 2007, Norby et al. 2010), and manipulation experiments of enhanced CO_2 in the tropics is untested (Zhou et al., 2013). Due to the magnitude of forest growth, CO_2 fertilization may not be a causal factor but instead driven by interacting agents such as biogeography and changing environmental site conditions (Lewis et al., 2004; Malhi and Phillips, 2004). The role of widespread recovery from past disturbances still needs to be explored as an explanation for biomass accumulation.

In a study evaluating the risk of Amazonian forest dieback, Rammig et al. (2010) used rainfall projections from 24 GCMs and a dynamic vegetation model (LPJmL) and predicted that Amazon forest biomass is increasing due to strong CO_2 fertilization effects (3.9 to 6.2 kg C m^{-2}), and out ways the biomass loss due to projected precipitation changes, however larger uncertainties are associated with the effect of CO_2 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 CO_2 (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 CO_2 concentrations, warming temperatures, and changing rainfall patterns (Cox et al., 2013).

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), 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). One explanation could be due to atmospheric CO_2 being held constant. 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 observed 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

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 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 ± SD: 169 ± 27.6 Mg C ha^{-1}, and additional field-based measurements from nearby sites in the Central Amazon (FLONA Tapajós plots) range 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 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 growth rates were determined internally within ZELIG-TROP based on species-specific parameters and environmental conditions.

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 (i.e., 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 wou,ld 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). Upon modeling a Central Amazon forest with disturbance 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. Our results further confirm that environmental and/or stand factors explain the regional variation of AGB and wood density. Even with elevated disturbance in the central Amazon the species that persisted and increased in basal area had on average high wood density (0.7 g cm^{-3}). The growth rate scaling coefficients, G, used in ZELIG-

TROP were inversely correlated with wood density, matching the robust signal observed from inventory data, but was not correlated (R^2=0.13), leading to a 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 community shifts, plant competition, and dynamic changes in carbon stocks and fluxes, and should be considered being incorporated into CLM. The version of CLM used here 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 due to natural death, stress related death, or 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 versus 134 Mg C ha^{-1} in CLM as a result of doubling background mortality, and 2) 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 ~40-50% reduction in carbon stocks, however the drivers that lead to biomass reduction are inconsistent with the empirical driver. 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 and Summary

To constrain the future concentration of CO_2 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), 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 CO_2 and climate change using six DGVMs with varying degrees of functionalities. Including transient changes in vegetation structure while accounting for changes due to elevated disturbance rates requires models to include vegetation dynamics, succession processes, and biogeochemical processes. 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 a fully integrated human system component. The capability of tropical forests to act as a carbon sink with and without the inclusion of disturbances needs to be corrected in some models. If not, incorrect predictions of the land uptake 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.

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 two models are different compared to drivers in empirical datasets, 2) predicted that not all differences in tropical forest attributes (e.g., AGB, basal area growth, stem density, and wood density) can be explained by the disturbance regime alone, and also 3) 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 majority of disturbance studies that have simulated a one-time total deforestation of the Amazon (Shukla et al., 1990; Henderson-Sellers et al., 1993; Hahmann and Dickinson, 1997; Gedney and Valdes, 2000; Avissar and Werth, 2005). We conclude the following two possibilities in addressing the variations in carbon stocks across the Amazon, but disentangling the contribution of each was beyond the scope of this study. The two models used here incorrectly captured the loss in AGB associated with elevated disturbance, because they attributed the reduced biomass to changes in either basal area or LAI, which is not well supported in the literature. A second possibility is that disturbance is not a strong indicator of regional variation in AGB, but environmental, community composition, and/or stand structure factors are stronger contributors to regional variation in biomass. Our results showed that a simulated Central Amazon forest that mirrored the turnover of the west and south Amazon continued to differ in multiple forest attributes.

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Table 1. Species-specific allometric and ecological parameters for the 90 tree species used in ZELIG-TROP, representing species found in central Amazonian (Laurance et al. 2004). All species were assigned a probability factor of stress mortality of 0.369, probability factor of natural mortality of 2.813, zone of seed influence of 200, relative seedling establishment rate (RSER) of 0.9, a crown shape value of 4.0, tolerance to drought a ranking of 3, tolerance to low soil nutrients a ranking of 2, minimum growing degree-day of 5000, and a maximum growing degree-day of 12,229.50.

Species	Growth Form	AGE-MAX (yr)	DBH max (cm)	HT max (cm)	G.	L.	Stock (%)	Wood Density (g cm^{-3})
Anacardium spruceanum	Canopy	175	69.1	3620.4	75.2	2	0.8	0.46
Aniba canelilla	Canopy	226	37.8	2032.8	38.7	2	0.5	0.94
Aspidosperma marcgravianum	Emergent	544	90.0	4680.4	30.8	4	0.5	0.72
Aspidosperma oblongum	Emergent	331	80.0	4173.2	59.5	4	0.5	0.87
Astronium le-cointei	Canopy	335	50.0	2651.6	34.7	2	0.5	0.77
Bocageopsis multiflora	Canopy	152	33.1	1794.5	51.3	2	0.5	0.65
Brosimum acutifolium	Canopy	264	58.3	3072.6	36.2	2	0.5	0.62
Brosimum guianense	Canopy	477	60.0	3158.8	22.3	2	0.5	0.89
Brosimum parinarioides	Canopy	483	60.0	3158.8	24.9	2	0.5	0.62
Brosimum rubescens	Canopy	450	60.0	3158.8	27.1	2	0.5	0.84
Cariniana micrantha	Emergent	223	80.0	4173.2	76.5	4	0.5	0.60
Caryocar glabrum	Canopy	527	110.0	5694.8	32.1	2	0.5	0.71
Casearia arborea	Canopy	91	20.1	1135.1	39.1	2	0.8	0.57
Casearia sylvestris	Canopy	201	25.5	1409.0	23.7	2	0.5	0.71
Clarisia racemosa	Canopy	323	80.0	4173.2	44.7	2	0.5	0.57
Cordia sagotli	Subcanopy	260	26.3	1449.6	14.6	1	0.8	0.43
Corythophora rimosa	Canopy	235	50.0	2651.6	48.1	2	0.5	0.81
Couepia longipendula	Canopy	260	46.6	2479.2	37.7	2	0.5	0.94
Couma macrocarpa	Canopy	233	51.8	2742.9	56.8	2	0.8	0.50
Couratari stellata	Emergent	592	53.5	2829.1	13.4	4	0.5	0.63
Dipteryx odorata	Emergent	323	78.4	4092.1	47.7	4	0.5	0.92
Drypetes variabilis	Subcanopy	252	30.0	1637.2	23.7	1	0.5	0.73
Duckeodendron cestroides	Emergent	818	140.0	7216.4	18.8	4	0.5	0.63
Ecclinusa guianensis	Canopy	448	69.7	3650.8	28.5	2	0.5	0.63
Endopleura uchi	Canopy	223	57.6	3037.1	52.5	2	0.5	0.79
Eriotheca globosa	Canopy	135	20.1	1135.1	28.3	2	0.8	0.41
Eschweilera amazoniciformis	Emergent	369	56.1	2961.0	30.5	4	0.5	0.82

Eschweilera coriacea	Canopy	767	110.0	5694.8	25.7	2	0.5	0.84
Fusaea longifolia	Subcanopy	413	26.5	1459.7	11.5	1	0.5	0.74
Glycydendron amazonicum	Canopy	386	44.0	2347.3	23.8	2	0.5	0.67
Goupia glabra	Emergent	398	100.0	5187.6	44.7	4	0.5	0.72
Guatteria olivacea	Canopy	54	30.0	1637.2	126.4	2	0.8	0.47
Gustavia elliptica	Subcanopy	301	24.7	1368.4	16.8	1	0.5	0.67
Helicostylis tomentosa	Canopy	311	44.7	2382.8	24.0	2	0.5	0.63
Hevea guianensis	Canopy	288	45.7	2433.5	29.3	2	0.5	0.55
Inga capitata	Pioneer	162	26.4	1454.6	27.6	3	0.7	0.60
Inga paraensis	Pioneer	78	40.0	2144.4	95.2	3	0.7	0.82
Inga splendens	Pioneer	52	38.2	2053.1	157.6	3	0.7	0.58
Iryanthera juruensis	Subcanopy	569	26.9	1480.0	8.8	1	0.5	0.66
Iryanthera laevis	Subcanopy	331	27.2	1495.2	15.4	1	0.5	0.63
Jacaranda copaia	Pioneer	225	30.0	1637.2	21.0	3	0.8	0.35
Lecythis barnebyi	Subcanopy	336	28.7	1571.3	19.9	1	0.5	0.82
Lecythis poiteaui	Canopy	747	34.4	1860.4	7.7	2	0.5	0.80
Lecythis zabucajo	Emergent	628	130.0	6709.2	27.0	4	0.5	0.86
Licania apetala	Canopy	199	38.4	2063.3	37.8	2	0.5	0.76
Licania oblongifolia	Canopy	196	54.2	2864.6	65.7	2	0.5	0.88
Licania octandra	Subcanopy	339	35.0	1890.8	21.7	1	0.5	0.81
Licania cannella	Canopy	359	56.5	2981.3	29.0	2	0.5	0.79
Macrolobium angustifolium	Canopy	335	40.0	2144.4	27.7	2	0.5	0.68
Manilkara bidentata	Emergent	773	90.0	4680.4	20.6	4	0.5	0.87
Manilkara huberi	Emergent	349	100.0	5187.6	55.9	4	0.5	0.93
Maquira sclerophylla	Emergent	420	60.0	3158.8	24.0	4	0.5	0.53
Mezilaurus itauba	Canopy	684	44.0	2347.3	12.9	2	0.5	0.74
Micropholis guyanensis	Canopy	248	55.5	2930.6	45.9	2	0.5	0.66
Micropholis venulosa	Canopy	491	60.0	3158.8	22.9	2	0.5	0.67
Minquartia guianensis	Emergent	490	70.0	3666.0	30.4	4	0.5	0.77
Myrciaria floribunda	Subcanopy	490	29.1	1591.6	11.7	1	0.5	0.77
Onychopetalum amazonicum	Canopy	195	29.9	1632.1	33.0	2	0.5	0.61
Parkia multijuga	Emergent	206	119.0	6151.3	101.7	4	0.8	0.39
Peltogyne paniculata	Canopy	251	40.0	2144.4	28.0	2	0.5	0.80
Pourouma bicolor	Pioneer	48	29.8	1627.1	124.6	3	0.8	0.38
Pourouma guianensis	Pioneer	58	31.3	1703.2	112.8	3	0.8	0.38
Pouteria ambelaniifolia	Canopy	296	38.0	2043.0	21.0	2	0.5	0.70
Pouteria anomala	Emergent	452	70.0	3666.0	31.6	4	0.5	0.78
Pouteria caimito	Canopy	240	43.2	2306.7	36.4	2	0.5	0.82
Pouteria eugeniifolia	Canopy	329	44.1	2352.4	25.8	2	0.5	1.10
Pouteria guianensis	Canopy	720	80.0	4173.2	17.5	2	0.5	0.94
Pouteria macrophylla	Canopy	387	29.6	1616.9	13.2	2	0.5	0.86
Pouteria manaosensis	Canopy	981	50.0	2651.6	8.4	2	0.5	0.64
Pouteria multiflora	Canopy	547	35.5	1916.2	9.5	2	0.5	0.75

Pouteria oppositifolia	Canopy	277	35.8	1931.4	21.7	2	0.5	0.65
Pouteria venosa	Canopy	702	45.8	2438.6	10.0	2	0.5	0.92
Protium altsonii	Emergent	238	70.0	3666.0	56.4	4	0.5	0.68
Protium decandrum	Canopy	158	32.8	1779.2	40.3	2	0.5	0.52
Protium heptaphyllum	Canopy	96	26.2	1444.5	60.0	2	0.8	0.62
Protium tenuifolium	Canopy	170	38.2	2053.1	49.1	2	0.5	0.57
Qualea paraensis	Emergent	379	70.0	3666.0	31.9	4	0.5	0.67
Scleronema micranthum	Emergent	353	90.0	4680.4	50.3	4	0.5	0.60
Sloanea guianensis	Subcanopy	179	28.5	1561.1	26.8	1	0.5	0.82
Swartzia corrugata	Subcanopy	407	21.1	1185.8	7.7	1	0.5	1.06
Swartzia recurva	Canopy	177	38.4	2063.3	45.5	2	0.5	0.97
Swartzia ulei	Canopy	293	50.0	2651.6	39.1	2	0.5	1.00
Tachigali paniculata	Canopy	91	27.7	1520.6	60.1	2	0.8	0.56
Tapirira guianensis	Canopy	54	41.6	2225.6	188.0	2	0.8	0.45
Tetragastris panamensis	Canopy	320	38.4	2063.3	25.1	2	0.5	0.72
Vantanea parviflora	Canopy	205	69.6	3645.7	65.1	2	0.5	0.84
Virola calophylla	Subcanopy	293	30.8	1677.8	18.6	3	0.8	0.51
Virola multinervia	Canopy	373	32.0	1738.7	14.0	2	0.8	0.45
Virola sebifera	Canopy	161	30.2	1647.4	44.4	2	0.8	0.46
Vochysia obidensis	Canopy	92	47.4	2519.7	109.1	2	0.8	0.50

Key: AGEMAX, maximum age for the species (yr); DBHmax, maximum diameter at breast height (cm); HTmax, maximum height (cm); G, growth rate scaling coefficient (unitless); Light (L): light/shade tolerance class (ranking 1-5); Stock, regeneration stocking (%), wood density (g cm^{-3}); (full parameter explanation found in original ZELIG paper: Urban 1990).

Table 2. Environmental parameters used in ZELIG-TROP for the central Amazon basin. Values reported in a range were monthly low and high averages. *Lawrence et al., (1999).

Lat./Long./Alt. (m)	Plot Area (m^2)	Mean monthly temperature (˚C)	Mean monthly precipitation (cm)	Soil field capacity (cm)*	Soil wilting point (cm)*	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

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 (m^2 ha^{-1})	Avg. Biomass (Mg C ha^{-1})	Avg. Stem Density (ha^{-1})	Avg. LAI	Avg. ANPP (Mg C ha^{-1} yr^{-1})
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

Table 4. Comparison of empirical data and stand model data from Chambers et al. (2004) unless otherwise noted, ZELIG-TROP pre- and post-disturbance treatments, and CLM pre- and post-disturbance treatments for the pool of carbon in live trees, and the annual flux of carbon from stem growth, coarse litter production rates from mortality, ANPP; and recruitment rate of stems, mean DBH, and average ΔAGB.

Positive = sink	Live Trees (Mg C ha^{-1})	Growth (Mg C ha^{-1} yr^{-1})	Coarse Litter (Mg C ha^{-1} yr^{-1})	ANPP (Mg C ha^{-1} yr^{-1})	Recruit ment (% yr^{-1})	Mean DBH (cm)	AGB change (Mg C ha^{-1} yr^{-1})
Empirical§	156	1.70	-2.10	6.50*	1.38**	21.1	NA
Stand Model§	160	1.60	-1.70	6.60	NA	20.4	NA
ZELIG-TROP^1	178	3.09	-3.03	5.39	2.33	22.3	0.02
ZELIG-TROP^2	104	2.89	-2.78	5.35	3.94	18.3	0.01
ZELIG-TROP^3	138	3.29	-3.49	5.06	3.41	26.9	-0.15
CLM-CN^1	269	4.88	-4.82	7.81	NA	NA	0.04
CLM-CN^2	135	4.91	-4.93	7.83	NA	NA	0.00
CLM-CN^3	230	4.71	-4.95	7.54	NA	NA	-0.46
ZELIG Diff. $^{(1\&2)}$	-74	-0.20	0.25	-0.04	1.61	-4.0	0.01
ZELIG Diff. $^{(1\&3)}$	-40	0.20	-0.46	-0.33	1.08	4.6	-0.17
CLM Diff. $^{(1\&2)}$	-134	0.03	-0.11	0.02	NA	NA	-0.04
CLM Diff. $^{(1\&3)}$	-39	-0.17	-0.15	-0.27	NA	NA	-0.50

1 = No Disturbance, 2 = High Disturbance, 3 = Periodic Disturbance, § Chambers et al. (2004), * Chambers et al. (2001), ** Phillips et al. (2004).

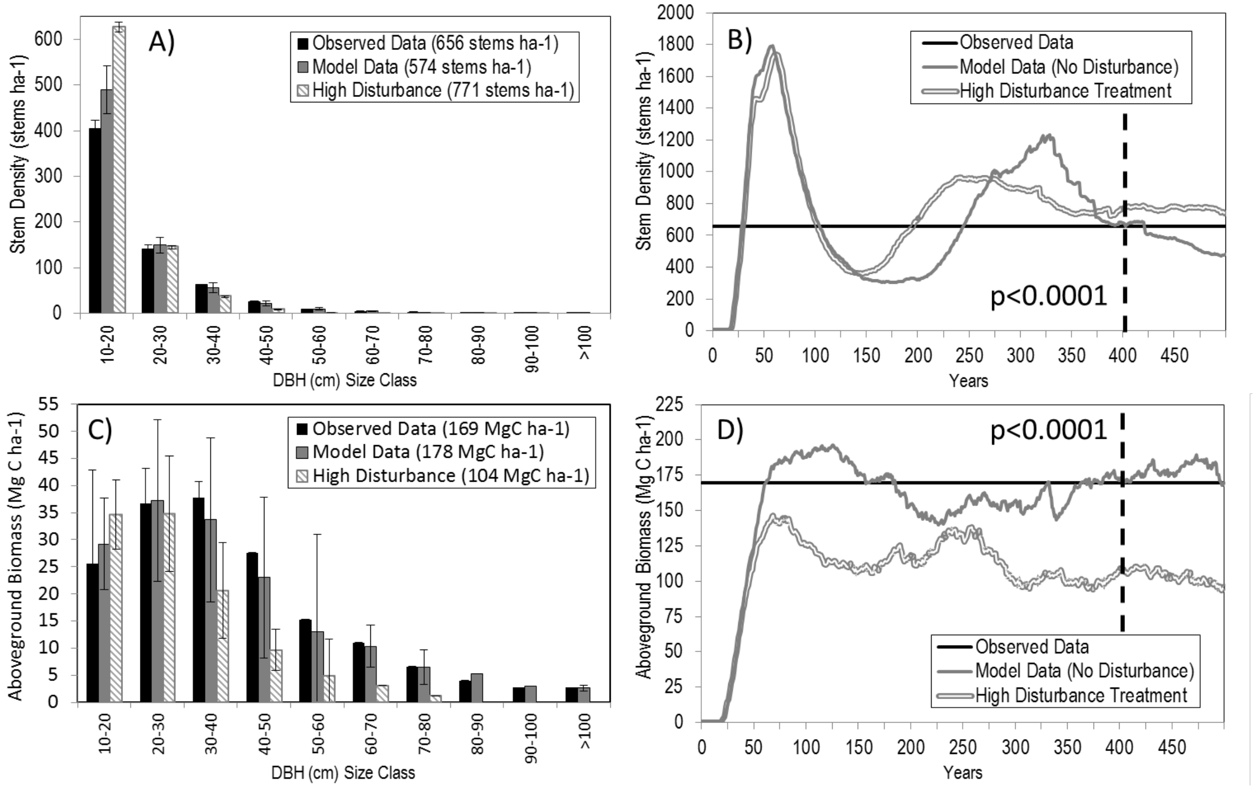

Fig. 1. Comparison between observed field data from "transects" in Central Amazon, ZELIG-TROP model data from no-disturbance scenario, and ZELIG-TROP model data from high-disturbance treatment. **(A)** Average stem density (stems ha^{-1}) and SD by DBH (cm) size class, **(B)** stem density simulated 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.

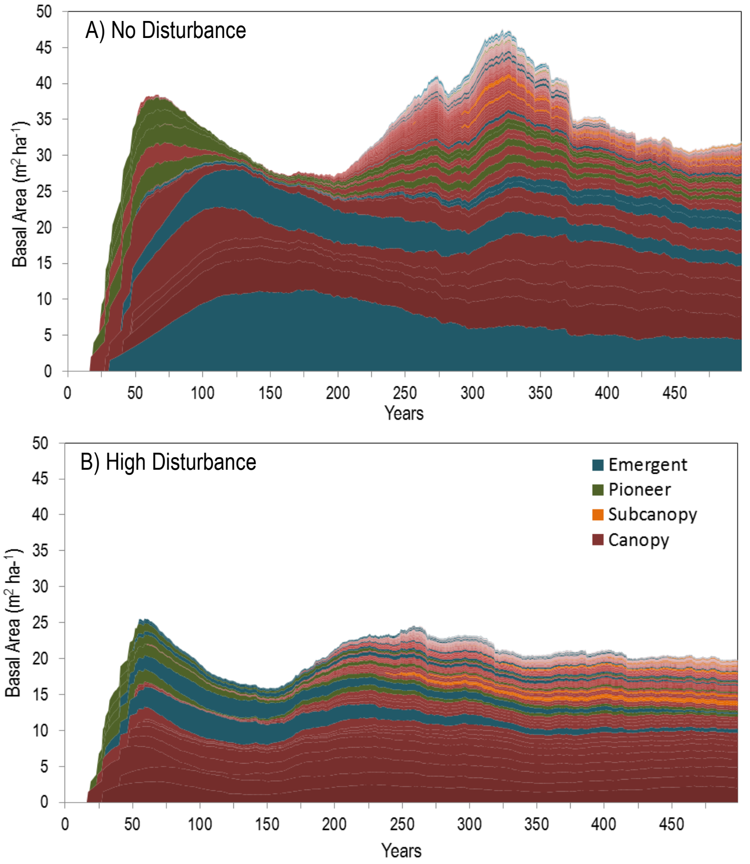

Fig. 2. **(A)** Model simulated successional development for all species modeled in ZELIG-TROP for a Central Amazon forest, separated by canopy growth form (emergent, canopy, sub-canopy, or pioneers). Species composition reported in individual basal area (m^2 ha^{-1}). **(B)** Model simulated successional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

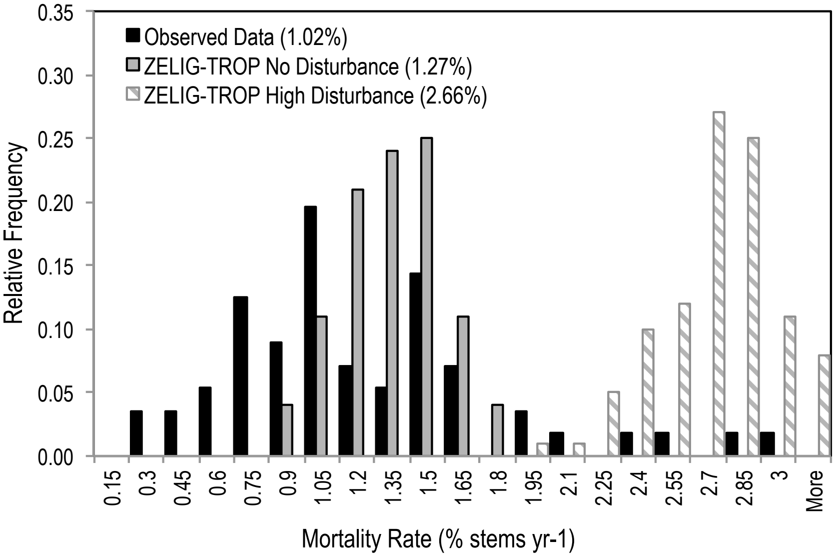

Fig. 3. Comparison of relative frequency of annual mortality rates (% stems year^{-1}) from observed data, ZELIG-TROP no-disturbance, and ZELIG-TROP high-disturbance model data after the disturbance treatment. (Observed data: Chambers et al. 2004).

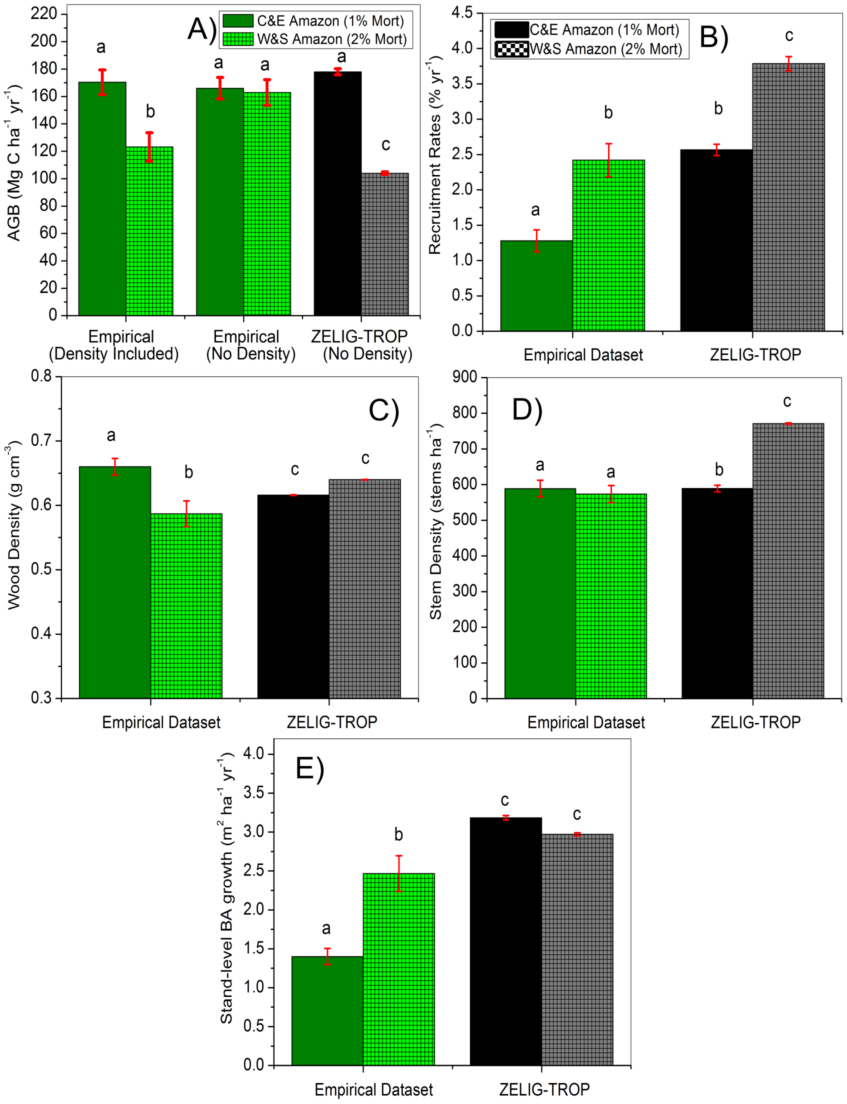

Fig. 4. Comparison between ‘central and east’ Amazon (“slow dynamics”) and ‘west and south’ Amazon (“fast dynamics”) between the empirical (RAINFOR dataset, green columns) and modeled ZELIG-TROP results for average **(A)** above-ground biomass (AGB, Mg C ha^{-1} yr^{-1}) with the observed dataset either 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 (m^2 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.

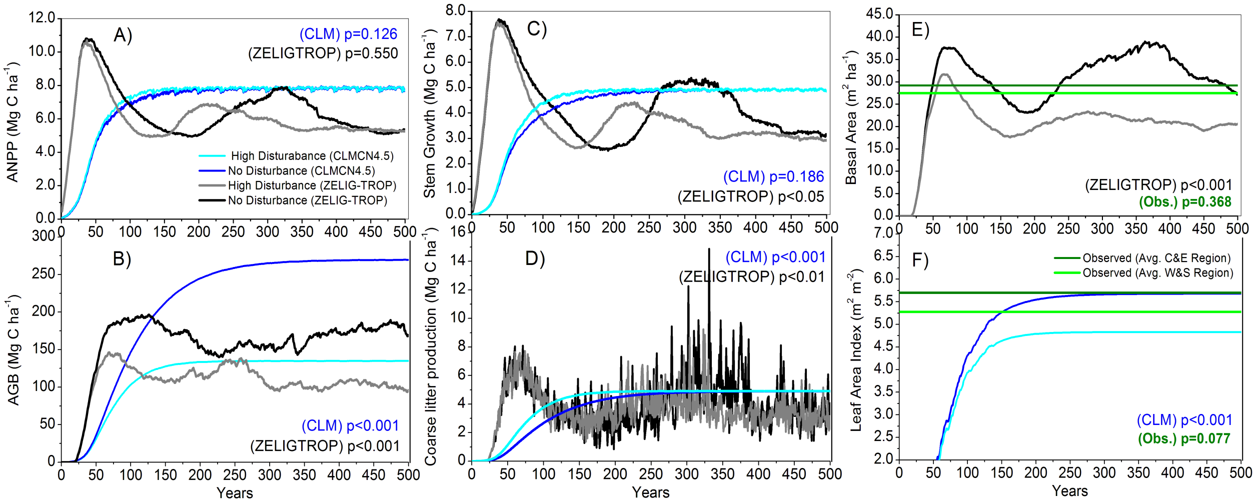

Fig. 5. CLM-CN model evaluation and comparisons to ZELIG-TROP for a no-disturbance scenario and a high disturbance treatment: **(A)** ANPP, **(B)** above-ground biomass, **(C)** stem growth, **(D)** coarse litter production rates, all measured in Mg C ha^{-1}, and **(E)** basal area from ZELIG-TROP and observed data in green as reported by Baker et al. (2004a), and **(F)** leaf area index (LAI) from CLM-CN4.5 and observed data in green as 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.

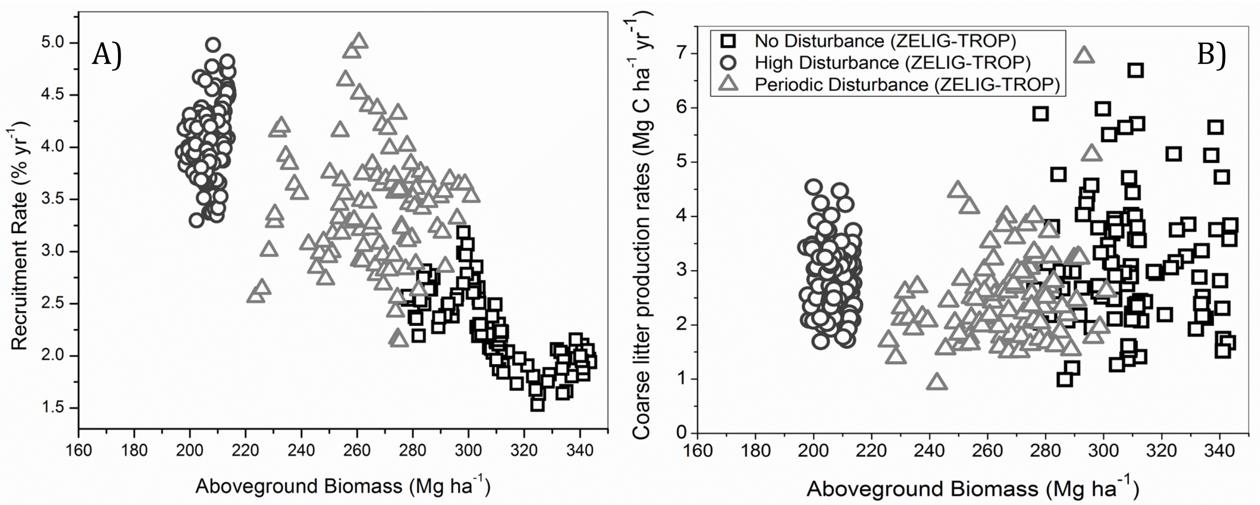

Fig. 6. **(A)** Relationship between above-ground biomass (Mg ha^{-1}) and recruitment rates (% yr^{-1}). **(B)** Relationship between above-ground biomass (Mg ha^{-1}) and coarse litter production rates as a result of tree mortality (Mg C ha^{-1} yr^{-1}), during a no-disturbance, high disturbance,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

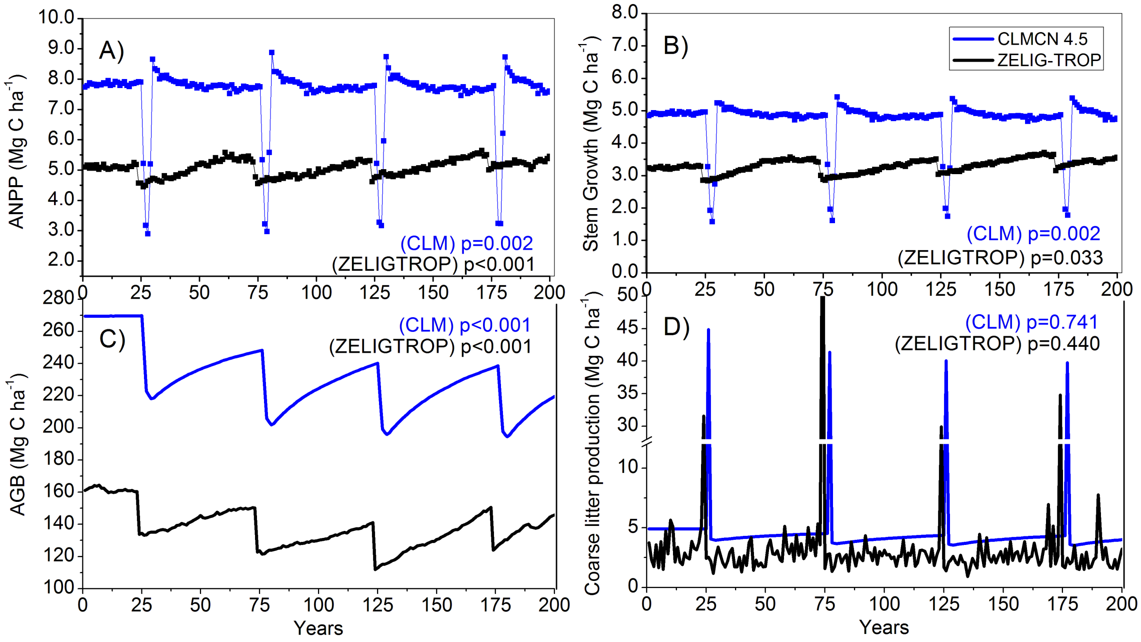

Fig. 7. CLM-CN model evaluation and comparisons to ZELIG-TROP for a periodic disturbance treatment: **(A)** ANPP, **(B)** stem growth, **(C)** aboveground biomass (AGB), and **(D)** coarse litter production rates, all measured in Mg C ha^{-1}. Statistical significance test in all panels are two-sample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

Supplemental Material

Description of the Community Land Model (CLM):

The Community Land Model (CLM) is the land component of the Community Earth System Model (CESM) (Collins et al., 2006; Gent et al., 2011) that models global climate systems and makes projections of future climate change. In this study we used the stand-alone version of CLM4.5. This version used a data atmosphere model, a "stub" ocean, a stub sea-ice model, and the CLM-CN (carbon-nitrogen) version 4.5. Detailed descriptions of updates to version 4.0, algorithms used, and the general structure of CLM can be found in the CLM4.0 Technical Description (www.cesm.ucar.edu/models/cesm1.0/clm/CLM4_Tech_Note; Oleson et al., 2010; and Lawrence et al., 2011). This CN model included a prognostic carbon and nitrogen cycle in vegetation, litter, and soil organic matter (description in Thornton et al., 2007). For model comparisons against the gap model ZELIG-TROP, and observed field data, we used CLM results from a single grid point located at 2°35'S, 60°W, close to exact coordinate as the Central Amazon field transects. (Additional definitions of terms and parameters used in CLM are defined below).

In CLM, disturbance rates and realistically calculated plant mortality rates are ill represented. Currently, CLM includes two independent mechanisms for plant mortality: fire and natural senescence. In this study, mortality caused by fire was turned off. Mortality rates (representing natural senescence) are calculated as a whole-plant mortality that is intended to represent death of plants from all causes other than fire. This annual whole-plant mortality is calculated by removing 2% yr^{-1} of global total vegetation mass, regardless of differences in plant age, size, regional location, distribution of individuals, competition, or plant functional types (PFTs) (Oleson et al., 2010). We believe CLM could benefit from a more mechanistic approach of calculating plant mortality and disturbance. Developing a platform for CLM and CESM to model tropical disturbance in a dynamic approach greatly enhances our understanding of future changes to carbon fluxes and atmospheric carbon dioxide levels. Another benefit of this new development to CESM is the capability to address disturbance within the newly coupled Integrated Earth System Model (iESM) (Jones et al., 2013; description available at http://climatemodeling.science.energy.gov/sites/default/files/iESM_Fact_Sheet.pdf). The iESM model combines the natural-human system with the biophysical and climate system by coupling three models: (1) CESM with the (2) Global Change Assessment Model (GCAM), which focuses on an energy/economic framework, and the (3) Global Land-Use Model (GLM). Therefore, the iESM project creates the capabilities to test the carbon market and energy market response to changes in forest mortality and increased disturbances.

Definition of the mortality algorithm in ZELIG-TROP and terms in each model

Plant mortality is determined in ZELIG-TROP by three separate means: age-related natural death, stress-related death, and external disturbance (evaluation of gap model mortality described in more detail in Keane et al. 2001). Natural mortality, or intrinsic death, is a tree level event that is stochastically determined, based on the assumptions that 1% of trees reach their maximum age, and that mortality was constant with respect to age (Botkin et al., 1972; Shugart, 1984). Stress related death, or growth-dependent mortality, is also a stochastic event in which death occurred to individuals that have a slow growth rate for two years or more due to suppression or environmental stressors. The model assumes that 1% of stressed individuals will live for 10 years (Shugart, 1984; Van Daalen and Shugart, 1989).

Within ZELIG-TROP the production of new organic matter from interval t_1 to t_2 is prognostically determined and given by: growth = $M_{t2} – M_{t1}$, where M_t is woody mass at time t. Growth is a component needed to measure ANPP given by: ANPP = $M_{t2} - M_{t1} + L$, where L is both old and new litter loss. The annual loss of coarse woody material is given by: coarse litter production rate = $W_{L1} + W_{L2} + W_{L3}$, where W_{L1} are losses from natural death, W_{L2} are losses from stress related death, and W_{L3} are losses from disturbance (all trunks and branches >10cm in diameter). All flux values given in Mg C ha^{-1} yr^{-1}.

Within CLM the production of new organic matter from interval t_1 to t_2, is also prognostic, responding to environmental differences and in this study was estimated using the wood carbon allocation variable: woodc_alloc, which is given by: $growth_{CLM}$ = carbon to liveStem + carbon to deadStem + liveStem to storage + deadStem to storage. In CLM, ANPP (leaf, live stem, and dead stem) is given by: $ANPP_{CLM} = GPP - AR$ where AR is autotrophic respiration and is the sum of maintenance and growth respiration. Lastly, the annual loss of coarse woody material was estimated by the wood loss variable: woodc_loss, which is given by: coarse litter production $rate_{CLM}$ = liveStem to litter + deadStem to litter. All flux values given in Mg C ha^{-1} yr^{-1}.