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Title: Vulnerability of tropical forest ecosystems and forest dependent communities to droughts

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Abstract

Energy captured by and flowing through a forest ecosystem can be indexed by its total Net Primary Productivity (NPP). This forest NPP can also be a reflection of its sensitivity to, and its ability to adapt to, any climate change while also being harvested by humans. However detecting and identifying the vulnerability of forest and human ecosystems to climate change requires information on whether these coupled social and ecological systems are able to maintain functionality while responding to environmental variability.

To better understand what parameters might be representative of environmental variability, we compiled a metadata analysis of 96 tropical forest sites. We found that three soil textural classes (i.e., sand, sandy loam and clay) had significant but different relationships between NPP and precipitation levels. Therefore, assessing the vulnerability of forests and forest dependent communities to drought was carried out using data from those sites that had one of those three soil textural classes. For example, forests growing on soil textures of sand and clay had NPP levels decreasing as precipitation levels increased, in contrast to those forest sites that had sandy loam soils where NPP levels increased. Also, forests growing on sandy loam soil textures appeared better adapted to grow at lower precipitation levels compared to the sand and clay textured soils. In fact in our tropical database the lowest precipitation level found for the sandy loam soils was 821 mm yr⁻¹ compared to sand at 1739 mm yr⁻¹ and clay at 1771 mm yr⁻¹. Soil texture also determined the level of NPP reached by a forest, i.e., forest growing on sandy loam and clay reached low-medium NPP levels while higher NPP levels (i.e., medium, high) were found on sand-textured soils. Intermediate precipitation levels (>1800 to 3000 mm yr⁻¹) were needed to grow forests at the medium and high NPP levels. Low thresholds of NPP were identified at both low (~750 mm) and high precipitation (>3,500 mm) levels.

By combining data on the ratios of precipitation to the amount of biomass produced in a year with how much less precipitation input occurs during a drought year, it is possible to estimate whether productivity levels are sufficient to support forest growth and forest dependent communities following a drought. In this study, the ratios of annual precipitation inputs required to produce 1 Mg ha⁻¹ yr⁻¹ biomass by soil texture class varied across the three soil textural classes. By using a conservative estimate of 20% of productivity collected or harvested by people and 30% precipitation reduction level as triggering a drought, it was possible to estimate a potential loss of annual productivity due to a drought. In this study, the total NPP unavailable due to drought and harvest by forest dependent communities per year was 10.2 Mg ha⁻¹ yr⁻¹ for the sandy textured soils (64% of NPP still available), 8.4 Mg ha⁻¹ yr⁻¹ for the sandy loam textured soils (60% available) and 12.7 Mg ha⁻¹ yr⁻¹ for the clay textured soils (29% available). Forests growing on clay textured soils would be most vulnerable to drought triggered reductions in productivity so NPP levels would be inadequate to maintain ecosystem functions and would potentially cause a forest-to-savanna shift. Further, these forests would not be able to provide sufficient NPP to satisfy the requirements of forest dependent communities. By predicting the productivity responses of different tropical forest ecosystems to changes in precipitation patterns coupled with edaphic data, it could be possible to spatially identify where tropical forests are most vulnerable to climate change impacts and where mitigation efforts should be concentrated.

Key words (up to 5): Net Primary Productivity, soil texture, sustainable resource consumption, edaphic, climate change

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1.0 Introduction

Many studies have focused on measuring the vulnerability of coupled human and natural systems to climate change (e.g., IPCC 2012) by integrating information from the social and natural sciences (e.g., Chuvieco et al. 2014; Downing et al. 2014; Mumby et al. 2014). Despite the multitude of research, it has been challenging to equate social and ecological resilience with vulnerability to climate change. To fully understand these interconnected systems different approaches and methodologies are needed to address our diverging research objectives (Liu et al. 2007). A lack of knowledge of an ecosystem's pre-novel context (Seastedt et al. 2008) or the interconnectivities of complex social drivers of change (Scullion et al. 2014) means that resilience represents the ability of a system to recover after a disturbance. However does it indicate whether ecological and social systems have recovered within their historical range of conditions? Additional knowledge may be needed to identify system parameters that maintain functionality within the "safe operating space" where a stress or disturbance does not trigger the system to cross a threshold of recovery beyond the historical range of variation (Scheffer et al. 2015). In fact identifying the safe operating space for both the social as well as the ecological systems would probably be even more challenging with the multitude and complexity of connections that exist between them. To help decrease some of those challenges of quantifying the sensitive parameters that reflect movement within and between regimes (Scheffer and Carpenter 2003), we try to quantify the parameters remotely rather than locally and also at different spatial and temporal scales to minimize unexplained unique results (Vogt et al. 2002; Gmur et al. 2013; Scullion et al. 2014). Further, one cannot focus on a single part of the coupled socio-ecological system (Maxwell 2014; Silva 2014) and expect to understand the mechanistic links between them. Even when research has effectively linked the complexity of socio-economic interactions with resources, they have been less able to validate what variables should be managed to reduce the impacts on both people and the environment (e.g., Downing et al. 2014; Görg et al. 2014; but see Scullion et al. 2014).

One metric for detecting mechanistic links between the social and ecological systems is to use an indicator such as total Net Primary Production (NPP). NPP reflects the pools and fluxes of materials and energy flowing through the social and ecological systems (Vitousek et al. 1986; Rojstaczer et al. 2001; Haberl et al. 2007). It is analogous to measuring 'virtual water' which tracks total water consumption by integrating water stored in the materials and track the energy consumed by products across different time and spatial scales and organizational units managing water (Liu et al. 2015). When harvesting forest products are required for survival, those dependent people become vulnerable when a drought affects their forest productivity. Therefore, NPP can potentially reflect whether a forest is competitively fit and whether a species may be more adaptable to a changing environment and stresses (Vogt et al. 1996). NPP could also be used to index plant adaptation and response to a changing environment or physiological adaptation of species to drought, soils, insects and pests (Waring 1991; Lambers and Poorter 1992; Davies et al. 2005; Bartlett et al. 2012; Smith 2015). Thus by determining how much biomass a specific landscape produces each year and obtaining information on the amount of ecosystem services (e.g., habitats, water, nutrient cycles, forest products, biodiversity) collected by a group of people, it becomes possible to estimate whether a landscape is capable of sustainably supporting both activities.

Using NPP data to integrate the social and natural science requires an ability to detect the scale at which these productivity changes occur. For some forests, significant correlations between precipitation and NPP across soil textural-class levels exist suggesting these variable combinations could be used to identify locations where NPP and ecosystem services may be at critical risk to droughts (Slik et al. 2014; Wooster et al. 2012; Xu et al. 2011). Further, there is considerable research reporting the importance of soil texture in defining the nutrient and water holding capacity of soils - both key factors controlling plant growth rates (Waring and Franklin 1979; Gentry and

Terborgh 1990; DeWalt and Chave 2004; Sotta et al. 2007). Soil texture therefore not only influences soil moisture retention capacity and soil available nutrient supplies but they impact how a plant adapts to its growing environment and whether NPP levels will decrease during a drought.

By identifying how a forest maintains functionality for NPP as it is related to its soil texture, it is possible to estimate what levels of NPP are needed to safeguard sustainable harvests of ecosystem services against drought. To demonstrate one possible approach, we used a database populated with metadata from 96 different tropical forest sites to determine if any soil textural class had significant correlates between NPP and precipitation levels. Of 12 soil textural classes, forests growing on three textural classes (i.e., sand, sandy loam and clay) had productivity levels changing in response to precipitation levels. Since these three textural classes are found in over half of the tropical forest sites (Sanchez et al. 1982), relationships between NPP and precipitation (e.g., NPP per precipitation amounts) were examined to search for any potential trends and/or thresholds. A by-product of this exercise generated an estimate of the potential drought impact on productivity as well on the amount of productivity capacity available for harvest by humans. By identifying NPP thresholds, an evidence-based decision-making framework for spatially disparate natural resources could be provided for tropical forests that are potentially vulnerable to drought.

2.0 Methods

2.1 Database creation and description.

This study was based on a compilation of NPP, edaphic and climatic information for 96 published plot-level data entries that had been characterized as natural tropical forests. The geographic distribution of the selected field sites are presented in Figure 1. The database was populated by information collected in natural tropical forests reported as mature or closed canopy stands. For each site, data were separately recorded by forest region, forest age, climatic variables, elevation and elevation groupings, soil type (i.e., taxonomic soil orders) and soil textural classes according to the USDA soil taxonomy system (Table 1).

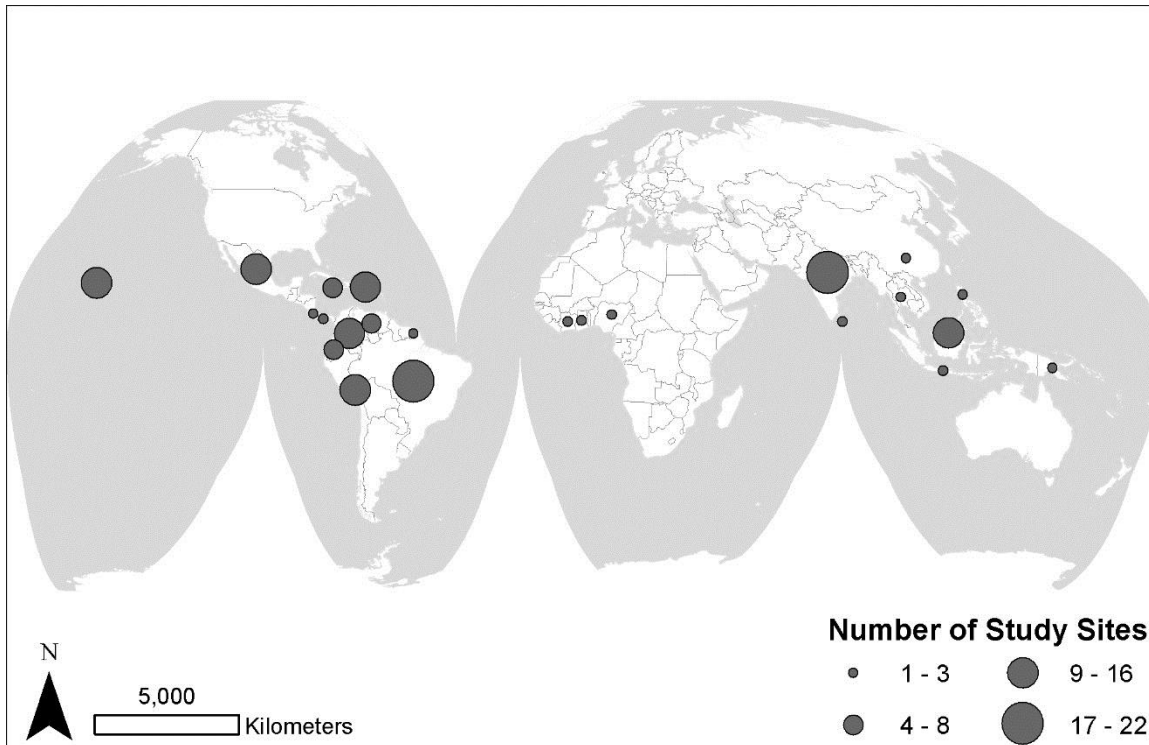


Figure 1. Geographic distribution of pan-tropical forest studies' field sites used in our database.

Table 1. Variables and groupings used in our database to create tree-like regression models using data reported by the cited authors of research reports from 96 pan-tropical forest field-sites.

Variable Key	Groups
Global forest region	1 = America; 2 = Asia; 3 = Africa
Stand age classes, yrs	1 = Age reported in a paper; 2 = Mature or closed canopy forest
Elevation groups, m asl (e.g., Hertel et al. 2009)	1 = Lowland zone = <400 m; 2 = Pre-montane zone = 400-1200 m, 3 = Montane = >1200 m
Precipitation, mm yr ⁻¹	<p><u>Forest groups by rainfall</u> (Chave et al. 2005):</p> <p>1 = <u>Wet</u> - evapotranspiration exceeds rainfall during <1 month; usually high-rainfall lowland forests (rainfall >3,500 mm yr⁻¹ and no seasonality;</p> <p>2 = <u>Moist</u> - evapotranspiration exceeds rainfall during more than a month but <5 months; forests with marked dry season (1-4 months), sometimes semi-deciduous canopy and 1,500-3500 mm yr⁻¹ rainfall for lowland forests;</p> <p>3 = <u>Dry</u> - pronounced dry season, plants suffer serious water stresses <1,500 mm yr⁻¹, and >5 months dry season)</p> <p><u>Additional subgroups by rainfall:</u></p> <p>1 = H wet, >4500 mm yr⁻¹;</p> <p>2 = L wet, >3500-4500 mm yr⁻¹;</p> <p>3 = H moist, >3000-3500 mm yr⁻¹;</p> <p>4 = M moist, >2000-3000 mm yr⁻¹;</p> <p>5 = L moist, 1500-2000 mm yr⁻¹;</p> <p>6 = moist-dry, 1000-<1500 mm yr⁻¹;</p> <p>7 = dry-dry, <1000 mm yr⁻¹</p>

Air temperatures, °C	1 = Mean annual air temperature; 2 = Minimum air temperature; 3 = Maximum air temperature
Soil texture classes - standard soil texture class matrices based on proportion of sand, silt, clay (Soil Survey Staff 2010)	1= sand; 2= loamy sand; 3= sandy loam; 4= fine sandy loam; 5= very fine sandy loam; 6= loam; 7= silt loam; 8= silt; 9= sandy clay loam; 10= silty clay loam; 11= clay loam; 12= sandy clay; 13= silty clay; 14= clay [S2 Percent sand, silt and clay in each soil texture class]
Soil types; Soil orders in the US Soil Taxonomy system (Soil Survey Staff 2010)	1= Mollisols; 2= Alfisols; 3= Andisols; 4= Histosols; 5= Inceptisols; 6= Ultisols; 7= Entisols; 8= Spodosols; 9= Oxisols; 10= Aridisols; 11= Vertisols
Net Primary Productivity, Mg ha ⁻¹ yr ⁻¹	1 = Aboveground NPP (NPP _a); 2 = Belowground NPP (NPP _b); 3 = Total NPP (NPP _t)

We appreciate that many tropical areas may have at least three distinct climatic seasons because of monsoons, but the analyses in this study were limited to the mean annual data since that is what is most commonly reported in published papers. To further tease apart the impact of climatic seasonality on productivity, data were aggregated by precipitation groups and subgroups (see Chave et al. 2005). The precipitation groups consisted of: Dry (<1500 mm yr⁻¹ of precipitation), Moist (1500-3500 mm yr⁻¹) and Wet (>3500 mm yr⁻¹). Precipitation grouping or categorization is a common approach used to search for patterns in tropical data since the variance in precipitation rates, in contrast to temperature, is high in this climatic zone (Holdridge 1947). This precipitation grouping is particularly useful because the coarse-scale climatic constraints indirectly integrate differences in soil development rates and their varying nutrient delivery capacities (Brown and Lugo 1982; Sanchez et al. 2003; Chave et al. 2005).

The database in this study, including the soil-type data, originated from Vogt et al. (1986) which was then expanded upon using other published global databases on total forest productivity and site characteristics (e.g., Vogt et al. 1995, 1996; Phillips et al. 1998; Clark et al. 2001; Malhi et al. 2011). If Vogt et al. (1986) did not provide complete site information, then the missing data were searched for using the University of Washington Library's Search Tools (Articles and Research Databases, Academic Search Complete - EBSCO, Web of Science) as well as Google Scholar and JSTOR to complete the database used in this study. Data on site characteristics were frequently found in non-refereed publications, reports or theses and dissertations.

If a publication did not report both direct field estimates of above- (NPP_a) and below-ground (NPP_b) net primary productivity data for a research site, that site was not included in the database. The belowground root productivity in this database is a combination of coarse (generally >2mm diameter) as well as fine root (generally <2mm diameter) data. Most estimates of coarse root biomass and productivity are a ratio developed from allometric relationships developed for a particular species (e.g., Kenzo et al. 2009). However fine root NPP data were obtained from direct measures of fine root growth using a diversity of field sampling methods (e.g., root cores, in-growth cores, mini-rhizotrons, etc). We also used site characteristic and NPP_t data provided by Clark et al. (2001) for the 39 sites they summarized in their paper. But we did not use the ORNL dataset (Olson et al., 2001) since the core of those data are from the empirically determined NPP_b data of Clark et al. (2001) which we had already used. When source authors reported NPP_t as Mg C ha⁻¹

yr⁻¹, the value was doubled in the database to estimate dry biomass productivity (i.e., mass of C was assumed to be 50% of the dry biomass).

2.2 Regression-tree prediction model

When collating data from research plots scattered across different regions of the world, the productivity relationships to site-scale edaphic and climatic conditions may not be immediately apparent using standard multivariate regression models. Therefore, this study used a multivariate statistical method that utilizes a binary division of sample populations to create tree-like regression models (Therneau et al. 2011) to determine the correlations and thresholds of total productivity. Since binary regression trees are a non-parametric technique, they do not suffer from linear regression requirements for normalized distributions and the initial distribution of the data can be used without the constraints of traditional transformation of any non-normal data (Lemon 2003).

The binary regression-tree statistical method was used as the conceptual framework to identify significant splits within the compiled dataset. The binary regression-tree statistical tree method revealed relationships between multiple variables within the data that might have been ignored using other analytic techniques. This approach was chosen to easily convey results of the statistical model and quickly identify significant splits in a complex dataset. Continuing development and wide use of this statistical method - not just within the environmental sciences but within health sciences, social sciences, statistics, computer science and other fields - speaks to its general acceptance as an exploratory regression method.

To build a regression tree, the sample population was split into two distinct groups based on an identified significant division of the data by choosing one of the predictive factors. This process was then applied again, treating each new group as its own distinct entity and finding the next set of variables which best divides the input population into another two new groups for each initial grouping. The process was carried out continually or recursively until a minimum size was reached or a subgroup could no longer be significantly subdivided (Therneau et al. 2011). It can be said that each successive split adds a new level which isolates each node making it resistant to multi-collinearity among the predictor variables (Loh 2006).

The model's relative error was used to assess and ensure that a regression was not over-fitted to the data. Regression trees with a relative error close to zero produce a good prediction while a relative error around or greater than one produces a poorer prediction (Cukjati et al. 2001). The number of nodes or splits to be used within the regression tree is determined by choosing a complexity parameter which minimizes the cross-validation prediction error. The complexity parameter may increase as additional splits are introduced to the fitted tree. This value is expressed within the RPART library (Therneau and Atkinson 2011) using the `printcp` command which will print a table showing the distinct complexity parameter, the number of splits and the associated cross-validation error (Everitt and Torsten 2010). Each regression tree was cross-validated 10,000 times and pruned to ensure the replication in trees fit for all response variables. Classification and regression trees are non-parametric with no assumptions made about the underlying distribution of the predictor variables (Lewis 2000; TITTONELL et al. 2008).

For the database, the multivariate statistical method identified significant NPP thresholds and a range of productivities within three NPP groupings: Low NPP group had NPP that ranged from 4 to 18 Mg ha⁻¹ yr⁻¹; Medium NPP grouping NPP ranged from 19 to 26 Mg ha⁻¹ yr⁻¹ and the High NPP grouping had NPP ranging from 27 to 43.4 Mg ha⁻¹ yr⁻¹. Data shown in Figure 1 includes information for the entire database. The remaining statistical analyses by soil texture classes selected only sites where mean annual air temperatures were higher than 25°C. The multivariate

statistical approach showed that the selected sites had significant relationships between precipitation and productivity that was not found for forests growing below a mean annual air temperature of 25°C. When the initial multivariate statistical method identified significant relationships between precipitation and NPP by a soil texture class, these data were further explored statistically by soil texture class using the least significant difference (LSD) post-hoc test using SAS (version 9.2, SAS Institute, Inc., Cary, NC).

3.0 Results

NPP levels in relationship to precipitation groups are shown in Figure 2. This figure shows how several soil texture groups may contribute to similar productivities found in an NPP grouping. It is also apparent that specific soil textures do not determine whether NPP would be in the low, medium or high NPP grouping. It also shows that NPP data exist for a diversity of soil texture classes and also that the NPP levels are highly variable in tropical forests.

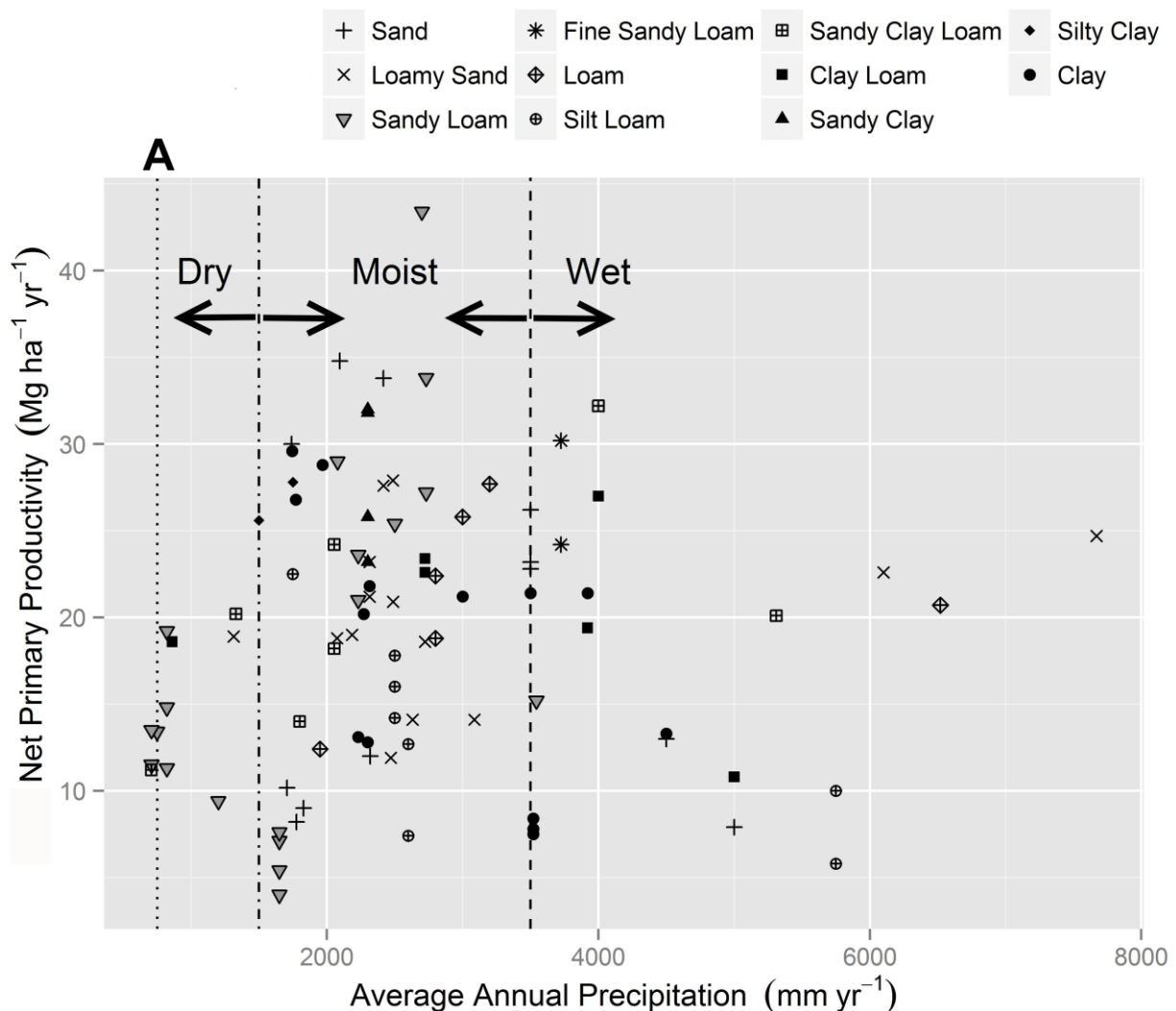


Figure 2. Associations between net primary productivity (above and belowground), average annual precipitation, and soil texture reported from tropical forest sites around the world. The annual precipitation level shown at 'A' is the level assumed in which tropical forest regimes may transition

to the savanna regimes if the precipitation falls below this line. Using multivariate regression analysis, splits were determined for NPP groupings: Low = 4 to 18 Mg ha⁻¹ yr⁻¹; Medium = 19 to 26 Mg ha⁻¹ yr⁻¹ and High = 27 to 43.4 Mg ha⁻¹ yr⁻¹.

When regression analyses of data within aggregated NPP groupings (High, Medium, Low) compared annual precipitation levels to NPP, precipitation levels did not explain any of the variance in NPP for forests growing in the High and Medium NPP groupings. In the Low NPP grouping, only 33% of the variance in NPP was explained by annual precipitation levels. Since none of these comparisons were statistically significant, these data are not discussed here.

The NPP grouping analysis did provide information on the amount of precipitation needed to produce 1 Mg ha⁻¹ yr⁻¹ of biomass each year. For example, in the High NPP grouping, 79 mm of annual precipitation is needed to grow 1 Mg ha⁻¹ yr⁻¹ of biomass. In the Medium NPP grouping, the ratio of precipitation to NPP was 125 mm of annual precipitation to grow 1 Mg ha⁻¹ yr⁻¹ of biomass. Whereas the Low NPP grouping showed that 177 mm of annual precipitation is needed to grow 1 Mg ha⁻¹ yr⁻¹ of biomass.

For sites with mean annual air temperatures above 25°C, three out of the 12 soil texture classes had significant relationships between forest NPP and precipitation (Table 2). Forests growing on sand, sandy loam and clay textured soils had 61%, 81% and 86% of the variation in NPP explained by precipitation levels, respectively (Table 2). Further, sites with sandy loam and clay textured soils reached NPP levels found in each of the three NPP groupings while those growing on sand textured soils reached NPP levels found in the Medium and High NPP groupings. When using the average of all the plots by soil texture class, the amount of annual precipitation needed to produce 1 Mg ha⁻¹ yr⁻¹ biomass was 65 mm yr⁻¹ for the sandy loam textured soils, 105 for sand textured soils and 229 for the clay textured soils. However, developing a ratio of precipitation to productivity levels using an average of all plots resulted in differed ratios and trends for how much precipitation was needed to produce 1 Mg of biomass per year compared to developing regression equations by each soil texture class. The regression equation resulted in the sand textured soils needing almost twice as much rainfall to produce the 1 Mg ha⁻¹ yr⁻¹ compared to the sandy loam and clay textured soils (Table 2).

Table 2. Data summary of NPP, precipitation levels, amount of precipitation (mm yr⁻¹) needed to produce 1 Mg ha⁻¹ yr⁻¹ of NPP by soil texture for forests growing at mean annual air temperatures >25°C.

Soil texture class	NPP \bar{x} [range]	Precipitation \bar{x} [range]	Precipitation levels needed
			to produce 1 Mg of biomass per year (mm yr ⁻¹) [range]
Sand	28.5 [22.8-34.8]	2792 [1739-3500]	105 [58-154]
Sandy loam	20.9 [11.5-43.4]	1421 [821-2730]	65 [43-100]
Clay	17.8 [7.5-28.8]	2736 [1771-3521]	229 [66-469]

The data for both the sand and sandy loam textured soils, but not the clay textured soils, are clustered due to a lack of site data across a broader range of precipitation levels. Despite this

clustering, these plots are useful to develop insights on what might be the lower and upper limits of NPP by soil texture class and to explore how productivity levels change along a precipitation gradient. For both the sand and clay textured soils, an inverse relationship existed between precipitation input levels and NPP (Figures 3a-c). These patterns for the sand and clay textured soils contrasted with the positive correlation that resulted for the sandy loam textured soils. For both the sand and clay textured soils, the higher NPP occurred at precipitation levels around 1500 mm rainfall per year in contrast to the sandy loam soils were forests with high NPP needed between 2500 and 3000 mm yr⁻¹ of rainfall. Further these correlations resulted in sand textured soils needing ~180 mm precipitation for each 1 Mg ha⁻¹ yr⁻¹ of biomass produced, ~100 mm precipitation for each 1 Mg ha⁻¹ yr⁻¹ of biomass when forests grew on sandy loam textured soils and ~90 mm precipitation for each 1 Mg ha⁻¹ yr⁻¹ of biomass on the clay textured soils.

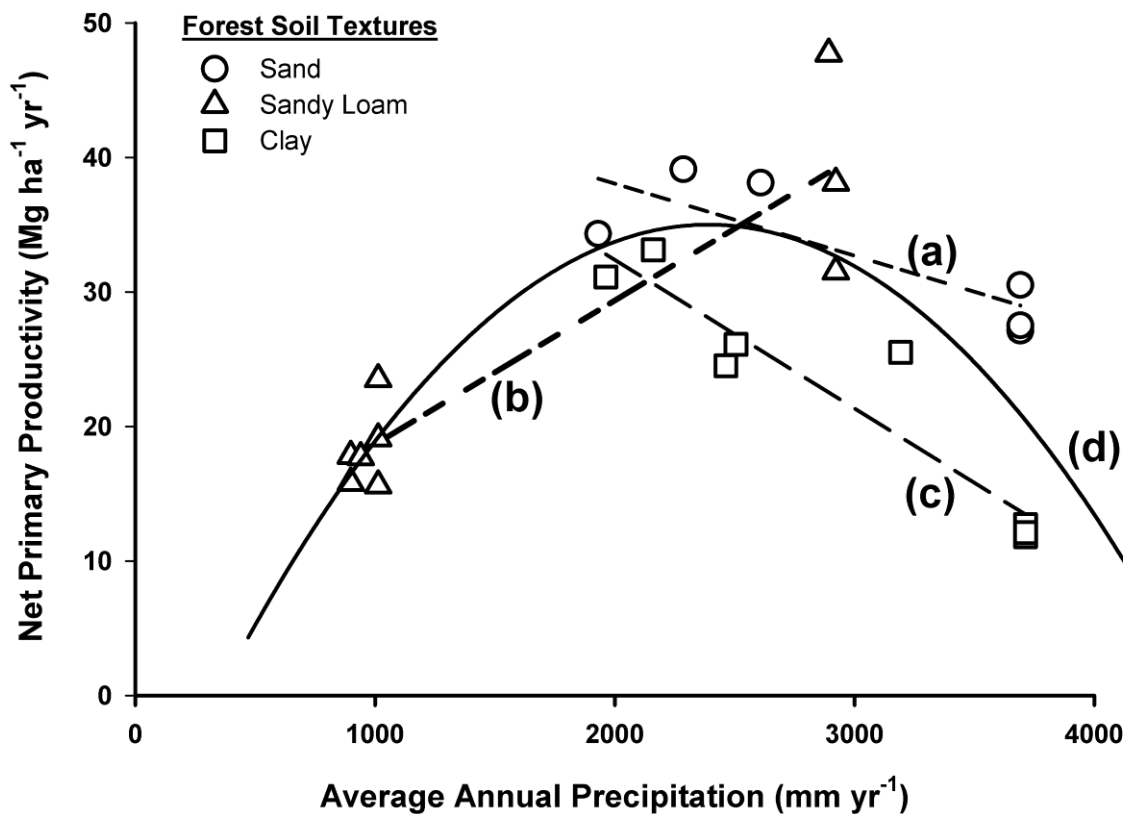


Figure 3. Net primary productivity of tropical forests related to their average annual precipitation levels and their soil textures. The linear regression lines represent forests growing on (a) sand [Adj $R^2 = 0.61$, $P < 0.05$ (clustered), $n=6$]; (b) sandy loam [Adj $R^2 = 0.81$, $P < 0.05$ (clustered), $n=9$]; and (c) clay [Adj $R^2 = 0.86$, $P < 0.05$, $n=8$] textured soils at mean annual air temperatures $>25^\circ\text{C}$. The curvilinear regression line (d) represents data for forests growing at mean annual air temperatures $>25^\circ\text{C}$ on sand, sandy loam and clay textured soils [Adj $R^2 = 0.53$, $P < 0.05$, $n = 23$; $Y = -9.56 + 0.037X - 0.00001X^2$].

3.1 Sand textured soils.

The regression analysis correlating productivity and precipitation resulted by soil texture class did not produce similar upper and lower productivity limits in the database. For example, sand textured soils had the lower limit of NPP at 20 Mg ha⁻¹ yr⁻¹ of biomass since a lower productivity level would occur at precipitation levels higher than 4500 mm yr⁻¹ (Figure 3a). The NPP levels at 4500 mm yr⁻¹ were used to set the lower threshold of NPP since this is where a significant threshold of lower productivity has been detected (Vogt et al. *unpublished data*). The upper limit of NPP for forests growing in the sand textured group was set at 750 mm even though the regression line crossed the Y axis at a higher NPP level. The 750 mm yr⁻¹ was used to set the lower productivity limit since this is considered to be where a forest becomes vulnerable to shifting into a savanna since forests are unable to maintain a positive carbon balance to compete against grasses (Hirota et al. 2011). This approach identified an NPP upper limit of 40 Mg ha⁻¹ yr⁻¹. The study database reported the highest NPP level of 34.8 Mg ha⁻¹ yr⁻¹ which is lower than the upper limit identified using.

3.2 Sandy loam textured soils.

The sandy loam textured soils, which reached the highest NPP compared to the other two soil textures, the regression line crossed the Y axis at 5.7 Mg ha⁻¹ yr⁻¹ of biomass production (Figure 3b). Since the precipitation levels would have been zero, the 750 mm yr⁻¹ lower threshold where forests are vulnerable to being converted to grassland was used to set the lower limit of NPP on the sandy loam textured soils. Using this approach, the lower limit of NPP was 13 Mg ha⁻¹ yr⁻¹. Since the database reported the lowest forest NPP levels around 11.5 Mg ha⁻¹ yr⁻¹, this appears to be a realistic estimate of this lower NPP level.

3.3 Clay textured soils.

Similarly, the upper limits of NPP for forests growing on clay textured soils were determined to be at 38 Mg ha⁻¹ yr⁻¹ of biomass using the same criteria as used for forests growing on the sand textured soils (Figure 3c). Even though the regression line crossed the X axis at a precipitation level of 4500 mm yr⁻¹, this was not a realistic metric to determine the lower limit of NPP for the clay textured soils. Since precipitation levels higher than 4500 mm yr⁻¹ have already been identified as a threshold of significant reductions in NPP (Vogt et al. *unpublished data*) and NPP levels based on the regression equation would have been less than 5 Mg ha⁻¹ yr⁻¹, the lower limit of NPP was selected at 7.5 Mg ha⁻¹ yr⁻¹ since this is the lowest value reported in the study database.

3.4 Sand, sandy-loam and clay textured soils.

Plotting all the data from the sand, sandy loam and clay textured soils together suggests that the NPP and precipitation data fit a curvilinear relationship (Figure 3d). It shows low NPP levels will be found at low and high precipitation levels while medium and high NPP levels will be found at intermediate precipitation levels (>1800 to 3000 mm yr⁻¹).

4.0 Discussion

4.1 Tropical forests and drought frequency

Lugo and Waide (1993) and Lugo et al. (2012) suggested that tropical wet forests are continually recovering from a previous disturbance because they occur as such a high frequency. Newbery and Lingenfelder (2004) wrote that the occurrence of occasional low intensity droughts is an important part of the climate regimes of moist tropical forests in Borneo where a guild of drought resistant trees grow. Droughts are a common occurrence in the tropics as shown in Table 3 where

representative examples of reported droughts are summarized for five locations in the tropics. This data highlights the high frequency of droughts occurring in tropical forests globally. Indonesia experienced 14 droughts during a 129 year period, Peru at least seven droughts over a 86 period, Brazil at least 14 over 113 years, Puerto Rico nine over a 36 year period, and Kenya and Tanzania 10 droughts during a 34 year period (Table 3). The frequency of droughts is probably higher than what are shown in Table 3 since these only include the documented cases of drought.

Table 3. Drought occurrences in five different areas of tropical forests.

Country	Precipitation Reductions	Reported Dates of Droughts	Reference
Brazil	Mean annual rainfall deficit was 30-40% during drought (Williams et al. 2005)	1900, 1915, 1925, 1926, 1958, 1963, 1964, 1979, 1980, 1981, 1983-1990, 1991-1999, 2005, 2010	Williams et al. 2005, Barbosa et al. 2006, Marengo et al. 2008, Phillips et al. 2009, Marengo et al. 2011, Xu et al. 2011
East Africa (Kenya & Tanzania)	A decrease in total rainfall to 384 mm in March, April, May (from 407 mm average), and to 318 (from 521 mm average) in September to December period (Hastenrath et al. 2007)	1972, 1986, 1993, 1996, 1999, 2000, 2003, 2004, 2005, 2006	Hastenrath et al. 2007, Gereta et al. 2009, Tanaka et al. 2000, Ogotu et al. 2007, Kijazi and Reason 2009
Indonesia	Monthly mean rainfall reduction of up to 110 mm for six consecutive months (Gutman et al. 2000)	1982, 1983, 1987, 1988, 1991, 1992, 1994, 1995, 1997, 1998, 2002, 2003, 2006	Salafsky 1994; Levine 1999; Gutman et al. 2000; Siegert et al. 2001; Slik 2004; Erasmi et al. 2009; Wooster et al. 2012
Peru	A 170 mm instead of 280 mm of rainfall was recorded between July and September 2010 (Espinoza et al. 2012)	1925, 1982, 1983, 1991, 1997, 2010, 2011	Caviedes 1984, Kane 2000, Espinoza et al. 2012
Puerto Rico	Annual rainfall was 20% below normal (Larsen 2000)	1966, 1967, 1968, 1990, 1991, 1994, 1996, 1997, 2002	Beard et al. 2005; Adams et al. 2009; Larsen 2000

There are many well-documented ecological impacts of droughts in the tropics, e.g., decreased NPP levels, higher mortality rates, increase loss of forest cover, and shifts in tree species dominance (Becker et al. 1998; Clark et al. 2003; Beard et al. 2005; Allen et al. 2010; Hirota et al. 2011; Li et al. 2011). Drought induced increases in forest mortality rates are highly variable with reports ranged from 3% to a third of the trees dying (Swaine et al. 1987; Condit et al. 1995; Becker et al. 1998; Potts 2003). Mortality rates also vary based on management practices before the occurrence of the drought; Slik (2004) reported that the 1997/1998 drought in Indonesia led to additional tree mortality of 11.2, 18.1, and 22.7% in undisturbed, old logged and recently logged forest. The high variance in the mortality rates in tropical forests during droughts (Barbosa et al. 2006; Phillips et al. 2009; Xu et al. 2011; NASA 2013) is useful information since it suggests the need to identify other factors to explain the variances reported as well as whether drought imposes different thresholds depending on site conditions. It is difficult to determine whether these mortality rates are within the boundaries of the safe operating space (Scheffer et al. 2015) and whether ecosystems are likely to recover after a drought or not.

What is evident from the summary of precipitation deficits for tropical forests (Table 3) is the high variability in how much precipitation levels need to change to trigger higher mortality rates. For example, Newberry and Lingenfelder (2004) reported how 200 year-old trees growing in Borneo would experience 15 high intensity (rainfall deficit ≥ 200 mm - successive months with < 100 mm mo^{-1} of precipitation) and 30 low intensity droughts (rainfall deficit ranging between 110 and < 200 mm during the drought months). Since the precipitation deficit recorded for each site or region is affected by site edaphic and climatic conditions, drought impacts can be refined by identifying the edaphic scale where changes in NPP are most likely to occur during a drought. The database in this study showed that three soil texture classes (sand, sandy loam, clay) had statistically significant but different relationships between forest NPP and precipitation levels, these results will be examined next.

4.2 Productivity levels, soil texture and droughts in the tropical forests

The regression tree-like model showed forests growing on clay, sand, and sandy loam textured soils have significant correlations between precipitation levels and NPP levels. Therefore, the relationships between NPP and precipitation levels were further explored within each of the three soil texture classes especially since they represent more than half (59%) of the soil textures found in the humid tropics. Sanchez et al. (1982) reported that generally 45% of the humid tropical soils are clayey, 23% loamy, 16% loamy over clayey, 13% sandy, 1% sandy over loamy and 2% organic. The results of the remaining nine soil texture classes, with no significant relationships between precipitation levels and NPP, suggest that $\sim 41\%$ of the terrestrial areas are less vulnerable to drought. Many publications have linked factors other than soil texture and soil drought tolerance in controlling forest species dominance, mortality rates and productivity (e.g., nutrient delivery capacity, soil chemistry, aluminum concentrations, rooting depth; e.g., Sanchez et al. 1982, Jha and Singh 1990; Vogt et al. 1995; Palmiotto et al. 2004; Nepstad et al. 2007; Paoli et al. 2008; Quesada et al. 2012; Jiménez et al. 2014; Baldos et al. 2015). It would be worth expanding the database used in this study and to specifically search for other multiple variable(s) combinations to explain NPP levels.

For the three soil texture classes where precipitation levels were linearly correlated with NPP, it was possible to explore how productivity levels would change across a range of precipitation levels without having to conduct an experimental manipulation. In this study, 61%, 81 and 86% of the variance in NPP levels were explained by changes in precipitation levels when data were grouped by sand, sandy loam and clay textured soils, respectively. Both the sand and clay textured soils had inverse relationships between NPP and precipitation where productivity levels decreased as precipitation levels increased. If these forests received < 1700 mm yr^{-1} of rainfall, they are potentially vulnerable to a loss of productivity that may persist beyond the drought event. It would be informative to determine whether the low NPP following the 2005 and 2010 drought in the Brazilian Amazon (Marengo 2005, 2011; Xu et al. 2011; NASA 2013) occurred on forests with sand or clay textured soils.

In contrast to the results produced for the sand and clay textured soils, the sandy loam textured soils had significant positive linear relationships between precipitation and NPP. For the data included in the study database, forests growing in the sandy loam textured soils had a wider range of NPP levels across a large variation in precipitation levels compared to those growing in sand or clay. Also, forests growing in sandy loam soils grew at lower precipitation levels (821 mm yr^{-1}) compared to the sand (1739 mm yr^{-1}) and clay textured (1771 mm yr^{-1}) soils. Forests growing on sandy loam textured soils should be less vulnerable to drought since they are able to maintain their productivity levels at the precipitation levels used to demarcate where the forest-savanna shifts are likely to

occur. Whether forests growing on sandy loam textured soils would have a lower precipitation level that would trigger a forest-savanna biome shift is worth further research. If this scenario is maintained, it would suggest that the forests growing on sandy loam textured soils would have a wider safe operating space for productivity before a threshold is reached compared to the sand and clay textured soils.

When combining data from the three soil texture classes, a curvilinear fit was found for NPP and precipitation (see Figure 3) which suggests that low NPP levels will be found at both the low and high precipitation levels. This database identified the lowest productivity limit for sites receiving too little (the sandy loam textured soils) or too much precipitation (the sand and clay textured soils). Further, the study database suggested the lowest NPP limit for sand textured soils was higher ($\sim 20 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) compared to what was possible when forests grew on sandy loam textured soils ($11.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and clay textured soils ($7.5 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). So productivity thresholds are produced under drought conditions but also in those areas receiving higher rainfall inputs. Two thresholds of lower NPP by soil texture needs further research to verify their occurrence in unmanaged forests. The clustering of data points also suggests that more NPP data need to be collected from a wider range of precipitation levels for each soil texture class to further support these initial analyses. In this study, the three soil textures (i.e., sand, sandy loam and clay) had different relationships between productivity level and precipitation. This database needs to be further expanded to include a greater variance in NPP and precipitation combinations. For example, forests growing on sand textured soils only reported growth rates in the medium and high NPP groupings so there is a lack of data for the low NPP grouping. Therefore, it is not clear whether sand textured soils do not support the growth of forests at these lower NPP levels or this result is an artifact of no data being collected from these sites.

4.3 Tropical forest NPP and biome shifts due to droughts

Even if forests are able to maintain their productivity capacity at low precipitation levels, other factors beyond NPP will determine whether forests will persist, change to another forest type, or be replaced by savannas. Staver et al. (2011) suggested that between 1000 to 2500 mm of annual rainfall, fire disturbances can convert a forests to a savanna system. Also, fire is a positive feedback loop for fire-adapted grasses. However Hirota et al. (2011) suggested that there is a lower precipitation threshold for the conversion of forests into savannas than what was reported by Staver et al. (2011). Hirota et al. (2011) identified precipitation thresholds for savannas between 750 and 2000 mm yr^{-1} . They reported that forest cover dominated when precipitation was greater than 2500 mm annually but no trees were found when precipitation was lower than 750 mm annually. If climate change results in decreases in precipitation inputs in this dry precipitation range, the increased frequency of fires will result in forests being replaced by grasslands since fire frequency is higher at these precipitation levels (Siegert et al. 2001; Staver et al. 2011; Hirota et al. 2011). Staver et al. (2011) did not find any correlations between the existences of forests versus savannas based on edaphic factors but suggested the available data might not have been at the scale needed for such an analysis. This study suggested that in sites where significant correlations resulted between precipitation levels and NPP that soil texture would have a strong influence on NPP thresholds and this information could be used to identify where forest conversion to savannas is likely.

The vulnerability of forests growing on clay textured soils is counter intuitive since abundant research suggests clay textured soils are better growth environments for forests compared to sand textured soils during non-drought periods. Castilho et al. (2006) studying aboveground biomass of

tropical forests in central Amazon reported that soil characteristics (such as nutrients and texture) explained the biomass levels they measured. In the Castilho et al. (2006) study, the percentage of clay found in the soil was significantly related to a larger aboveground biomass. Similarly, Laurance et al. (1999) showed that on the highly weathered and nutrient poor soils found in much of the Amazon region, high aboveground biomass was linked to higher clay contents and low biomass was linked to sand, Zn levels and aluminum saturation; the clay soils were linked to higher levels of total N, organic C, most cations and lower aluminum saturation and less sand. Sotta et al. (2007) suggested greater resilience to drought occurred on clay Oxisols compared to sandy Oxisols. The Laurance et al. (1999) study reported that a third of the variation in aboveground biomass was explained by soil fertility factors for forests growing on clay soil, i.e., clay soils were linked to higher levels of total N, organic C, most cations and lower aluminum saturation. While the Paoli et al. (2008) study identified extractable P and percent sand explaining 31% of the aboveground biomass variance of mature Bornean forests. Their study showed that the abundance of emergent trees that had diameters at breast height greater than 120 cm was positively correlated to soil P and soil exchangeable bases. Paoli et al. (2008) also suggested that a combination of soil factors (texture, P and exchangeable base cations levels) were important drivers of the amount of aboveground biomass and the predominance of emergent trees in Borneo's forests. These results were reported for forests not growing under low precipitation levels where the benefits of the clay textured soils are less relevant.

One could speculate that the forests most at risk to reduced precipitation inputs are those currently growing in areas receiving between 1500 and 2000 mm of precipitation and on silty clay and clay textured soils (Figure 2; see Palmiotto et al. 2004; Quesada et al. 2011). These forests have been able to maintain high NPP ($> 28 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) at these lower precipitation inputs but their production is vulnerable to drought. Other forests located in this same precipitation range grow on sand, loamy sand soil textures which have a low plant available water storage capacity in soils. These forests already have low NPP ($< 10 \text{ Mg ha}^{-1} \text{ yr}^{-1}$) and would face 'carbon starvation' and potentially transition to what Hirota et al. (2011) called 'treeless state'. This needs further research.

Whether NPP thresholds are crossed during a drought cannot be verified using the study database since it is not clear that the lower NPP levels are temporary or long-term reductions in site productivity. The fact that productivity threshold shifts may persist for five years after a drought event does suggest that forest productivity thresholds have been crossed. This is further supported by our research in Indonesia where forests shifted from growing at a high NPP level to medium growth rates. Even though the amount of forest NPP unavailable in 2006 had recovered to 82% of the 2001 NPP value by 2010 (NPP = $23.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$), NPP levels remained at levels found in the Medium NPP grouping (Gmur *unpublished data*). This analysis suggests a productivity threshold may have been crossed since NPP did not recover to pre-drought levels. Further long-term monitoring of these sites is needed to verify whether this trend would be maintained. If NPP levels remain lower for several years after a drought, it suggests a longer term reductions in the available NPP that can be harvested from a forest.

4.4 Heuristic analysis of tropical forest NPP and vulnerability of coupled socio-ecological systems to droughts

Over the past 10 years, large-scale periodic regional droughts and a general drying trend has reduced global terrestrial NPP (Zhao and Running 2010). Under a changing climate, severe regional droughts have become more frequent, a trend expected to continue for the foreseeable future. Therefore assessments of the vulnerability of coupled socio-ecological systems to climate change need to explore drought impacts. Assessing the vulnerability of coupled socio-ecological

systems requires knowledge of two different types of information: (1) During a drought, how much NPP is not produced and therefore how much is not available for humans to harvest; and (2) how much productivity capacity is collected by humans? This study addressed the first question using meta-analysis and a multivariate statistical approach. Data do not exist, however, to answer the second question due to a lack of data on how much productivity capacity is harvested by people from forests where the field plots are located. The second question can be indirectly explored heuristically by estimating how much productivity is no longer available for harvest by local communities due to droughts and where data were aggregated by each of the three soil textures classes that account for 59% of the soils in the humid tropics (Sanchez 1982). It allows us to explore the impact of droughts on productivity level for the most common soil textures found in the tropics.

The results of this paper supports the use of precipitation and productivity relationships to estimate how much NPP levels are reduced by different levels of drought as well as how much precipitation is needed to grow 1 Mg ha⁻¹ yr⁻¹ of biomass. This comparison uses changes in NPP due to drought to explore whether sufficient biomass will remain to meet the needs of a growing and healthy forest ecosystem and for humans to collect forest-based survival resources, such as food, fiber, fuel, etc. Since we do not have data for how much productivity capacity is collected by people from the 96 site database, a conservative 20% estimate of forest productivity was used for all sites. Global estimates of how much productivity is harvested by humans varies from 14.2% to 39% of the total terrestrial NPP (Vitousek et al. 1986; Rojstaczer et al. 2001; Haberl et al. 2007). Human appropriation of forest productivity will be much higher than the 20% used in this analysis but it provides a conservative baseline to make comparisons to demonstrate the influence of soil texture on NPP levels.

For this assessment, a 30% precipitation deficit was assumed to be a realistic level of precipitation reduction for our calculations since reported precipitation deficits range from 20 to 50% during a drought year (Table 3). When Nepstad et al. (2007) implemented their precipitation exclusion study in the Amazon, they reduced precipitation levels by 60% or excluded 620 to 890 mm of throughfall each year. The 30% calculated precipitation deficit (426-821 mm yr⁻¹) for this study (Table 4) is very similar to the levels used by Nepstad et al. (2007). Since precipitation-exclusion studies test the worst case scenario, e.g., drought durations that are not commonly found during non-experimental conditions, these results explore reductions in NPP due to extreme drought events. Nepstad et al. (2007) set up their precipitation exclusion experiment in a forest that typically receives ~2000 mm yr⁻¹ of precipitation but where the forests are deep rooted and acquire water from depths of 11 m (Nepstad et al. 2007). In the Nepstad et al. study, forests were resilient during the first two years of the experiment but began to have significantly higher mortality rates starting in the third year, i.e., 38% increased mortality rate of trees, especially large trees.

Also, the reduction in the amount of NPP produced due to a drought estimated by this study, i.e., 4.3 – 9.1 Mg ha⁻¹ yr⁻¹ of unavailable NPP (Table 4), are comparable to values reported by other studies (e.g., Tan et al. 2010). In fact for a seasonal dry tropical forest in China, Tan et al. (2010) reported a 38% reduction in NPP (i.e., 4.5 Mg biomass carbon ha⁻¹ yr⁻¹ lost) due to a drought. Fisher et al. (2007) reported a similar reduction in gross primary production when they experimentally tested the response of an Amazonian rain forest to induced drought stress using a throughfall exclusion experiment. This experiment showed that two years of continuous rainfall exclusion (50% reduction in throughfall reaching the soil) resulted in a modeled prediction of an average decrease of 13-14% in GPP and 40-45% decrease in GPP during the dry period of the year. In Indonesia, six months of drought resulted in 660 mm of less rain during 2006 and NPP levels decreased by 8.4 Mg ha⁻¹ yr⁻¹, a 30% reduction in NPP levels from 2001 to 2006 (Gmur *unpublished data*).

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Table 4. Estimates of how much net primary productivity (NPP) of tropical forests growing on different soil textures could be lost due to droughts and subsistence harvesting by the local population. This heuristic exercise assumed 20% appropriation or extraction of NPP by forest dependent people from forests growing on sand [n = 6], sandy loam [n = 9] and clay [n = 8] textured soils.

Soil Texture Class	Prec non-drought years ^a (mm yr ⁻¹)	Prec deficit ^b (mm yr ⁻¹)	Prec levels for 1 Mg biomass ^c (mm yr ⁻¹)	Avg NPP ^d (Mg ha ⁻¹ yr ⁻¹)	NPP lost with 30% prec deficit ^e (Mg ha ⁻¹ yr ⁻¹)	NPP harvest by people ^f (Mg ha ⁻¹ yr ⁻¹)	Total NPP unavailable due to drought + harvest by people ^g (Mg ha ⁻¹ yr ⁻¹)	Available NPP ^h (%)
sand	2729	819	180	28.5	4.5	5.7	10.2	64
sandy loam	1421	426	100	20.9	4.3	4.2	8.4	60
clay	2736	821	90	17.8	9.1	3.6	12.7	29

- 488 ^a Average annual precipitation occurring in these tropical forests found on different soil textures during none drought years.
489 Prec = precipitation.
- 490 ^b Precipitation deficit is how much less annual precipitation input occurs if a drought decreases the average annual precipitation by 30%.
- 491 ^c Precipitation amounts needed to produce on average 1 Mg ha⁻¹ yr⁻¹ of tropical forest biomass by the three soil texture classes.
- 492 ^d Average net primary productivity (in Mg ha⁻¹ yr⁻¹) found on each soil texture class when no droughts or subsistence harvesting have
493 occurred.
- 494 ^e The amount of NPP not produced with a 30% precipitation deficit.
- 495 ^f The amount of NPP harvested by subsistence harvesters which was assumed to be 20% for this exercise.
- 496 ^g Total amount of NPP not available for a growing forest due to drought and harvest.
- 497 ^h Percent of NPP available after subtracting unavailable NPP due to the drought and human harvesting.

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499 Compared to clay textured soils, forests growing on sand and sandy loam textured soils (which
500 account for about 14% of the humid tropical region, Sanchez et al. 1982), and experiencing a 30%
501 precipitation deficit, would be able to maintain annual forest growth rates at levels sufficient to
502 maintain ecosystem functions while producing harvestable NPP by local communities. A 30%
503 precipitation deficit would result in 4.5 and 4.3 Mg ha⁻¹ yr⁻¹ of NPP, respectively, becoming
504 unavailable to support ecosystem functions or to be harvested by local communities (Table 4).
505 Despite this loss of productivity, the calculations suggest that almost 60-64% of the site NPP would
506 still be available for maintaining ecosystems functions of forests growing on sand and sandy loam
507 textured soils.

508
509 In contrast, forests growing on clay textured soils (which accounts for 45% of the total terrestrial
510 area of humid tropics; Sanchez et al. 1982) were at risk to lose NPP if precipitation increased
511 (perhaps the clays become waterlogged) (see Figure 3). For the clay textured soils, no data points
512 were available for forests growing below 2000 mm yr⁻¹ in our database to determine how
513 productivity levels would respond to lower precipitation levels. Of course if annual precipitation is
514 normally lower than about 2000 mm yr⁻¹, then one should expect NPP to also decrease on clay soils
515 if a drought were to occur (see the curvilinear curve in Figure 3). For the data assumptions used in
516 this study, imposing a 30% precipitation deficit for forests growing on clay textured soils resulted in
517 NPP levels decreasing to 9.1 Mg ha⁻¹ yr⁻¹ from a pre-drought NPP of 17.8 Mg ha⁻¹ yr⁻¹. If forests
518 growing on clay textured sites were located in areas of forest-savanna transitions, this level of
519 reduction in productivity levels should increase the risk of loss of forests and the ability of local
520 communities to harvest forest NPP.

521
522 The results of this study suggest that forests with low NPP levels are frequently located in transition
523 areas (e.g., transitioning from a tropical forest regime to a savanna regime) and are therefore
524 especially vulnerable to changes in precipitation levels (see Figure 2). Model predictions by
525 Anadón et al. (2014) suggested that droughts in transition areas would cause a shift from forests to
526 savannas resulting in a significant decrease in forested areas. This study suggests that their model
527 prediction would be especially relevant for forests growing on sandy loam soils or sand and clay
528 textured soils that have normal annual precipitation rates of less than 2000 mm yr⁻¹. Forests
529 growing in the clay textured soils, that have low NPP levels (e.g., in the Low NPP grouping before
530 the occurrence of a drought), would certainly be at risk of transitioning to a savanna.

531
532 If people harvest from these transition zone forests during droughts, it may decrease the ability of
533 the forest to maintain its functions during and following a drought or even future disturbances. It is
534 likely that a drought would trigger a regime or biome shift with the forests being converted to
535 savannas. People dependent upon these forests for harvesting its productivity capacity would find it
536 more difficult to survive following a drought. Forests growing on clay textured soils appear to be
537 especially vulnerable to drought since only 29% of the NPP would be available to continue to
538 maintain ecosystem functions if local communities continue to harvest forest materials (Table 4).
539 These study results need to be further explored to determine whether forests growing on clay
540 textured soils are at a higher risk to climate change. Since people living in savannas are still
541 dependent on acquiring fuelwood from trees to provide from 60-90% of their cooking and heating
542 needs (WRI 1998), knowledge of the relationships between soil texture classes and forest
543 productivity levels may be useful to determine the risk of forest loss due to prolonged droughts.
544 Savannas provide different ecosystem services compared to forests and would be unable to provide
545 the water and soil benefits commonly delivered by forest ecosystems.

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5.0 Conclusion

Research on understanding the outcomes of common pool resources has contributed significantly to linking processes occurring in socio-economic-ecological systems, e.g., cultural, historical, political, demographic and/or social, and ecological resources held in common by a group of people (Laerhoven and Ostrom 2007; Agrawal 2014). This body of research has used quantitative and qualitative approaches to demonstrate the links between social and ecological systems, e.g., fishery, forestry, irrigation, water management and animal husbandry by focusing on institutions and the economics of these resources. Despite an abundant literature base, Agrawal (2014) suggests that there is a need to expand on what has already been done by using tools designed to causally explain the complex and multiple outcomes found in coupled social and ecological systems. Using the definition published by Mumby et al. (2014), this study supports the use of variations in productivity capacity linked to edaphic factors to detect social and ecological system vulnerability to droughts in tropical forests. Since productivity capacity determines how much biomass can be collected by humans to survive, it will indicate whether sufficient productivity is available. Further, since drought decreases NPP levels, less productivity capacity becomes available for humans to collect as well as for forests to maintain a positive carbon balance to recover following a disturbance. Therefore, the assessment conducted for this study suggests that productivity capacity connects both parts of the coupled socio-ecological system and can be used to explore where thresholds will be reached in both systems.

This study further suggests that NPP can be used to explore the vulnerability of both the social and ecological system to drought. By focusing on changes in productivity levels (NPP), it is possible to explore the vulnerability of tropical forests for crossing a threshold of productivity and whether it will result in less productivity for human harvest. Productivity thresholds occur when droughts cause an irreversible shift in productivity: such as, (i) from the medium NPP grouping to rates typically found in the low NPP grouping, or, (ii) from the low NPP level to savannas as result of negative carbon balance. The frequency of droughts in the tropics attests to its importance as a driver of landscape change in vegetation dominance that results in humans being able to appropriate fewer ecosystem services from the land.

Our approach of using NPP, given certain soil textures and precipitation, to assess its potential response to a disturbance, such as a drought, would mechanistically link both the social and ecological system since productivity is used as the common metric that links the vulnerability of each system. It also provides a process to determine where forests and people may be less vulnerable to drought as well as where drought dramatically increases the vulnerability of the coupled socio-ecological system. There are many examples of human-induced changes in landscapes or management activities that affect how ecological systems respond to climate change. For example, research has documented how indigenous peoples in Australia altered the climate vulnerability of their environment using cultural and management practices based on their locally developed knowledge (Leonard et al. 2013). These examples have causally linked the coupled socio-ecological systems.

Despite the fact that plants or trees are highly adapted to the site growing conditions, thresholds are often crossed as demonstrated by the high mortality rates of trees following a drought in tropical forests. The use of NPP as a tool or framework for detecting changes at the site level, where social and ecological system functions intersect, demarcate areas more vulnerable to drought. Using a robust database, this study suggests that the vulnerability of forests to the loss of NPP can be detected for over half of the global tropical forests. Other tropical forest sites would require further research to identify alternative site factors influencing NPP levels due to drought.

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615 **References**

- 616
- 617 Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., 2009. Temperature sensitivity of
618 drought-induced tree mortality portends increased regional die-off under global-change-type
619 drought. *Proc. Natl. Acad. Sci.* 106, 7063-7066.
- 620 Agrawal, A., 2014. Studying the commons, governing common-pool resource outcomes: Some
621 concluding thoughts. *Environ. Sci. Policy* 36, 86-91.
- 622 Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., et al.,
623 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate
624 change risks for forests. *Forest Ecol. Manage.* 259, 660-684.
- 625 Anadón, J.D., Sala, O.E., Maestre, F.T., 2014. Climate change will increase savannas at the expense
626 of forests and treeless vegetation in tropical and subtropical Americas. *J. Ecol.* 102, 1363-1373.
- 627 Baldos, A.P., Corre, M.D., Veldkamp, E., 2015. Response of N cycling to nutrient inputs in forest
628 soils across a 1000-3000 m elevation gradient in the Ecuadorian Andes. *Ecology* 96, 749-761.
- 629 Barbosa, H.A., Huete, A.R., Baethgen, W.E., 2006. A 20-year study of NDVI variability over the
630 Northeast Region of Brazil. *J. Arid Environ.* 67, 288-307.
- 631 Bartlett, M.K., Scoffoni, C., Sack, L., 2012. The determinants of leaf turgor loss point and
632 prediction of drought tolerance of species and biomes: a global meta-analysis. *Ecol. Lett.* 15,
633 393-405.
- 634 Beard, K.H., Vogt K.A., Vogt D.J., Scatena, F.N., Covich, A., Sigurðardóttir, R., et al., 2005.
635 Structural and functional responses of a subtropical forest to 10 years of hurricanes and
636 droughts. *Ecol. Monogr.* 75, 345-361.
- 637 Becker, P., Ong, C.H., Goh, F., 1998. Selective drought mortality of dipterocarp trees: No
638 correlation with timber group distribution in Borneo. *Biotropica* 30, 666-671.
- 639 Brown, S., Lugo, A.E., 1982. The storage and production of organic matter in tropical forests and
640 their role in the global carbon cycle. *Biotrop* 14:161-187.
- 641 Castilho, C.V. de, Magnusson, W.E., Araújo, R.N.O. de, Luizao, R.C.C., Luizao, F.J., Lima, A.P.,
642 et al., 2006. Variation in aboveground tree live biomass in a central Amazonian forest: Effects
643 of soil and topography. *Forest Ecol. Manage.* 234, 85-96.
- 644 Caviedes, C.N., 1984. El Niño 1982-83. *Geo. Rev.* 74, 267-290.
- 645 Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., et al., 2005. Tree
646 allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecol*
647 145:87-99.
- 648 Chuvieco, E., Martínez, S., Román, M.V., Hantson, S., Pettinari, M.L., 2014. Integration of
649 ecological and socio-economic factors to assess global vulnerability to wildfire. *Global Ecol.*
650 *Biogeogr.* 23, 245-258.
- 651 Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J, et al., 2001.
652 Net primary production in tropical forests: An evaluation and synthesis of existing field data.
653 *Ecol Appl* 11:371-384.
- 654 Clark, D.A., Piper, S.C., Keeling, C.D., Clark, D.B., 2003. Tropical rain forest tree growth and
655 atmospheric carbon dynamics linked to interannual temperature variation during 1984-2000.
656 *Proc. Natl. Acad. Sci.* 100, 5852-5857.
- 657 Condit, R., Hubbell, S.P., Foster, R.B., 1995. Mortality rates of 205 neotropical tree and shrub
658 species and the impact of a severe drought. *Ecol. Monogr.* 65, 419-439.
- 659 Cukjati, D., Robnik-Sikonja, M., Rebersek, S., Kononenko, I., Miklavcic, D., 2001. Prognostic
660 factors in the prediction of chronic wound healing by electrical stimulation. *Medical & Biol.*
661 *Eng. Comp.* 395:542-550.
- 662 Davies, S.J., Tan, S., LaFrankie, J.V., Potts, M.D., 2005. Soil-Related Floristic Variation in a
663 Hyperdiverse Dipterocarp Forest. In: Roubik, D.W., Sakai, S., Hamid, K., Abang, A. (Eds.),
664 *Pollination ecology and the rain forest: Sarawak studies.* Springer, New York, pp.22-34.

665 DeWalt, S.J., Chave, J., 2004. Structure and biomass of four lowland neotropical forests.
666 *Biotropica*, 36, 7-19.

667 Donatuto, J., Grossman, E.E., Konovsky, J., Grossman, S., Campbell, L.W., 2014. Indigenous
668 Community Health and Climate Change: Integrating Biophysical and Social Science Indicators.
669 *Coastal Manag.* 42, 355-373

670 Downing, A.S., van Nes, E.H., Balirwa, J.S., Beuving, J., Bwathondi, P.O.J., Chapman, L.J., et al.,
671 2014. Coupled human and natural system dynamics as key to the sustainability of Lake
672 Victoria's ecosystem services. *Ecol. Soc.* 19, article 31.

673 Erasmi, S., Propastin, P., Kappas, M., 2009. Spatial patterns of NDVI variation over Indonesia and
674 their relationship to ENSO warm events during the period 1982–2006. *J. Clim.* 22, 6612-6623.

675 Espinoza, J.C., Ronchail, J., Guyot, J.L., Junquas, C., Drapeau, G., Martinez, J.M., et al., 2012.
676 From drought to flooding: understanding the abrupt 2010–11 hydrological annual cycle in the
677 Amazonas River and tributaries. *Environ. Res. Lett.* 7, 024008.

678 Everitt, B., Torsten, H., 2010. *A Handbook of Statistical Analyses Using R*. CRC Press, Boca
679 Raton.

680 Fisher, R.A., Williams, M., Costa, A.L. da, Malhi, Y., Costa, R.F. da, Almedia, S., et al., 2007. The
681 response of an eastern Amazonian rain forest to drought stress: results and modeling analyses
682 from a throughfall exclusion experiment. *Global Change Biol.* 13, 2361-2378.

683 Gentry, A.H., Terborgh, J., 1990. Composition and dynamics of the Cocha-Cashu “mature”
684 floodplain forest. In: Gentry, A.H. (Ed.), *Four Neotropical Rainforests*. Yale University Press,
685 New Haven, CT, USA, pp 542-564.

686 Gereta, E., Mwangomo, E., Wolanski, E., 2009. Ecohydrology as a tool for the survival of the
687 threatened Serengeti ecosystem. *Ecohydrol. Hydrobiol.* 9, 115-124.

688 Gmur, S.J., Vogt, D.J., Vogt, K.A., Suntana, A.S., 2013. Effects of different sampling scales and
689 selection criteria on modelling net primary productivity of Indonesian tropical forests. *Environ.*
690 *Conserv.* 41, 187-197.

691 Görg, C., Spangenberg, J.H., Tekken, V., Burkhard, B., Truong, D.T., Escalada, M., Heong, K.L.,
692 et al., 2014. Engaging local knowledge in biodiversity research: Experiences from large inter-
693 and transdisciplinary projects. *Interdiscip. Sci. Rev.* 39, 323-341.

694 Gutman, G., Csiszar, I., Romanov, P., 2000. Using NOAA/AVHRR products to monitor El Niño
695 impacts: focus on Indonesia in 1997–1998. *B. Am. Meteorol. Soc.* 81, 1189–1205.

696 Haberl, H., Erb, K.H., Krausmann, F., Gaube, V., Bondeau, A., Plutzer, C., et al., 2007.
697 Quantifying and mapping the human appropriation of net primary production in earth's
698 terrestrial ecosystems. *Proc. Natl. Acad. Sci.* 104, 12942-12947.

699 Hastenrath, S., Polzin, D., 2007. Diagnosing the 2005 drought in equatorial East Africa. *J. Clim.* 20,
700 4628- 4637.

701 Hertel, D., Moser, G., Culmsee, H., Erasmi, S., Horna, V., Schuldt, B., et al., 2009. Below- and
702 above-ground biomass and net primary production in a paleotropical natural forest (Sulawesi,
703 Indonesia) as compared to neotropical forests. *For. Ecol. Manage.* 258:1904–1912.

704 Hirota, M., Holmgren, M., Van Nes, E.G., Scheffer, M., 2011. Global resilience of tropical forest
705 and savanna to critical transitions. *Science*, 334, 232-235.

706 Holdridge, L.R., 1947. Determination of world plant formations from simple climatic data. *Science*
707 105:367-368.

708 IPCC, 2012. *Managing the Risks of Extreme Events and Disasters to Advance Climate Change*
709 *Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on*
710 *Climate Change*. Field, C.B., Barros, V., Stocker, T.F., Qin, D., Dokken, D.J., Ebi, K.L., et al.
711 (Eds.), Cambridge University Press, Cambridge, UK; New York, NY, USA, 582 pp.

712 Jha, C.S., Singh, J.S., 1990. Composition and dynamics of dry tropical forest in relation to soil
713 texture. *J. Veg. Sci.* 1,609-614.

714 Jiménez, E.M., Peñuela-Mora, M.C., Sierra, C.A., Lloyd, J., Oliver, L., Phillips, O.L., et al., 2014.
715 Edaphic controls on ecosystem-level carbon allocation in two contrasting Amazon forests. *J.*
716 *Geophys. Res. Biogeosci.*, 119, 1-11.

717 Kane, R.P., 2000. El Niño/La Niña relationship with rainfall at Huancayo, in the Peruvian Andes.
718 *Int. J. Clim.* 20, 63-72.

719 Kenzo, T., Ichie, T., Hattori, D., Itioka, T., Handa, C., Ohkubo, T., et al., 2009. Development of
720 allometric relationships for accurate estimation of above- and below-ground biomass in tropical
721 secondary forests in Sarawak, Malaysia. *J. Trop. Eco.* 25:371-386.

722 Kijazi, A.L., Reason, C.J.C., 2009. Analysis of the 1998 to 2005 drought over the northeastern
723 highlands of Tanzania. *Clim. Res.* 38, 209–223.

724 Laerhoven, F.V., Ostrom, E., 2007. Traditions and trends in the study of the commons. *Int. J.*
725 *Common.* 1, 3–28.

726 Lambers, H., Poorter, H., 1992. Inherent variation in growth rate between higher plants: A search
727 for physiological causes and ecological consequences. *Adv. Ecol. Res.* 23, 187–261.

728 Larsen, M.C., 2000. Analysis of the 20th century rainfall and streamflow to characterize drought
729 and water resources in Puerto Rico. *Phys. Geog.* 21, 494-521.

730 Laurance, W.F., Fearnside, P.M., Laurance, S.G., Delamonica, P., Lovejoy, T.E., Rankin de
731 Merona, J.M., et al., 1999. Relationship between soils and Amazon forest biomass: a landscape-
732 scale study. *Forest Ecol. Manage.* 118, 127-138.

733 Lemon, S.C., Roy, J., Clark, M.A., Friedmann, P.D., Rakowski, W., 2003. Classification and
734 regression tree analysis in public health: Methodological review and comparison with logistic
735 regression. *Annals Behavioral Medicine* 26.3:172-81.

736 Leonard. S., Parsons, M., Olawsky, K., Kofod, F., 2013. The role of culture and traditional
737 knowledge in climate change adaptation: Insights from East Kimberley, Australia. *Global*
738 *Environ. Change* 23, 623-632.

739 Levine, J.S., 1999. The 1997 fires in Kalimantan and Sumatra, Indonesia: Gaseous and particulate
740 emissions. *Geophys. Res. Lett.* 26, 815-818.

741 Lewis, R.J., 2000. An introduction to classification and regression tree (CART) analysis. In: 2000
742 Annual Meeting of the Society for Academic Emergency Medicine, pp. 14.

743 Li, W., Zhang, P., Ye, J., Li, L., Baker, P.A., 2011. Impact of two different types of El Niño events
744 on the Amazon climate and ecosystem productivity. *J. Plant Ecol.* 4, 91-99.

745 Liu, J., Dietz, T., Carpenter, S.R., Alberti, M., Folke, C., Moran, E., 2007. Complexity of coupled
746 human and natural systems. *Science* 317, 1513-1516.

747 Liu, J., Mooney, H., Hull, V., Davis, S.J., Gaskell, J., Hertel, T., 2015. Systems integration for
748 global sustainability. *Science* 347, 964-978.

749 Loh, W.-Y., 2006. Logistic regression tree analysis. In: Pham, H. (Ed.), *Springer handbook of*
750 *engineering statistics*, Springer, London, pp. 537-49.

751 Lugo, A.E., Scatena, F.N., Waide, R.B., Pringle, C.M., Willig, M.R., Vogt, K.A. et al., 2012.
752 Management implications and applications of long-term ecological research. In: Brokaw, N.,
753 Crawl, T.A., Lugo, A.E., McDowell, W.H., Scatena, F.N., Waide, R.B., Willig, M.R. (Eds.), *A*
754 *Caribbean Forest Tapestry: The Multidimensional Nature of Disturbance and Response*. Oxford
755 University Press, Oxford, UK, pp. 305-360.

756 Lugo, A.E., Waide, R.B., 1993. Catastrophic and background disturbance of tropical ecosystems at
757 the Luquillo Experimental Forest. *J. Biosci.* 18, 475-481.

758 Malhi, Y., Doughty, C., Galbraith, D., 2011. The allocation of ecosystem net primary productivity
759 in tropical forests. *Phil. Trans. R. Soc. B.: Biol. Sci.* 366:3225-3245.

760 Marengo, J.A., Nobre, C.A., Tomasella, J., De Oliveira, G.S., De Oliveira, R., Camargo, H., 2008.
761 The drought of Amazonia in 2005. *J. Clim.* 21, 495-516.

762 Marengo, J.A., Tomasella, J., Alves, L.M., Soares, W.R., Rodriguez, D.A., 2011. The drought of
763 2010 in the context of historical droughts in the Amazon region. *Geophys. Res. Lett.* 38,
764 L12703, doi:10.1029/2011GL047436.

765 Maxwell, K.B., 2014. Commentary: Getting there from here. Institutions need to adapt to ensure
766 coequal social and biophysical global change science. *Nat. Clim. Change* 4, 936-937.

767 Mumby, P.J., Chollett, I., Bozec, Y.M., Wolff, N.H., 2014. Ecological resilience, robustness and
768 vulnerability: how do these concepts benefit ecosystem management? *Curr. Opin. Environ.*
769 *Sustain.* 7, 22-27.

770 NASA, 2013. Study finds severe climate jeopardizing Amazon Forest. 01.17.13.
771 <http://www.nasa.gov/topics/earth/features/earth20130117.html>, accessed 17 January 2013.

772 Nepstad, D.C., Tohver, I.M., Ray, D., Moutinho, P., Cardinot, G., 2007. Mortality of large trees and
773 lianas following experimental drought in an Amazon forest. *Ecology*, 88, 2259-2269.

774 Newbery, D.M., Lingenfelder, M., 2004. Resistance of a lowland rain forest to increasing drought
775 intensity in Sabah, Borneo. *J. Trop. Ecol.* 20, 613-624.

776 Ogutu, J.O., Piepho, H.P., Dublin, H.T., Bhola, N., Reid, R.S., 2007. El Niño-Southern Oscillation,
777 rainfall, temperature and Normalized Difference Vegetation Index fluctuations in the Mara-
778 Serengeti ecosystem. *Afr. J. Ecol.* 46, 132-143.

779 Olson, R.J., Johnson, K.R., Zheng, D.L., Scurlock, J.M.O., 2001. Global and Regional Ecosystem
780 Modeling: Databases of Model Drivers and Validation Measurements. ORNL/TM-2001/196.
781 [Olson, et al., 2001, 2013; Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q.,
782 Thomlinson, J.R., Ni, J. & Holland E.A., 2001. NPP Tropical Forest: Consistent Worldwide
783 Data, 1967-1999. [<http://www.daac.ornl.gov/>] from the Oak Ridge National Laboratory
784 Distributed Active Archive Center, Oak Ridge, Tennessee, U.S.A.

785 Palmiotto, P.A., Davies, S.J., Vogt, K.A., Ashton, M.S., Vogt, D.J., Ashton, P.S., 2004. Soil-related
786 habitat specialization in dipterocarp rain forest tree species in Borneo. *J. Ecol.* 92,609-623.

787 Paoli, G.D., Curran, L.M., Slik, J.W.F., 2008. Soil nutrients affect spatial patterns of aboveground
788 biomass and emergent tree density in southwestern Borneo. *Oecologia* 155, 287-299.

789 Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nunez, P.V., Vasquez, R.M., et al., 1998.
790 Changes in the carbon balance of tropical forests: Evidence from long-term plots. *Science*
791 282:439-442.

792 Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lyod, J., López-González, G., et al.,
793 2009. Drought sensitivity of the Amazon rainforest. *Science* 323, 1344-1347.

794 Potts, M.D., 2003. Drought in a Bornean everwet rain forest. *J. Ecol.* 91, 467-474.

795 Quesada, C.A., Lloyd, J., Anderson, L.O., Fyllas, N.M., Schwarz, M., Czimczik, C.I., 2011. Soils
796 of Amazonia with particular reference to the RAINFOR sites. *Biogeosci.* 8, 1415-1440.

797 Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patiño, S., et al., 2012.
798 Basin-wide variations in Amazon forest structure and function are mediated by both soils and
799 climate. *Biogeosci.* 9,2203-2246.

800 Rojstaczer, S., Sterling, S. M., Moore, N., 2001. Human appropriation of photosynthesis products.
801 *Science* 294, 2549-2552.

802 Running, S.W., Nemani, R., Glassy, J.M., Thornton, P.E., 1999. MODIS daily photosynthesis
803 (PSN) and annual net primary production (NPP) product (MOD17) Algorithm Theoretical Basis
804 Document. SCF At-Launch Algorithm ATBD Documents, University of Montana, USA.
805 http://modis.gsfc.nasa.gov/data/atbd/atbd_mod16.pdf, accessed 23 January 2015.

806 Russo, S.E., Davies, S.J., King, D.A., Tan, S., 2005. Soil-related performance variation and
807 distributions of tree species in a Bornean rain forest. *J. Ecol.* 93, 879-889.

808 Salafsky, N., 1994. Drought in the rainforest: Effects of the 1991 El Niño Southern Oscillation
809 event on a rural economy in West Kalimantan, Indonesia. *Clim. Change* 27, 373-396.

810 Sanchez, P.A., Couto, W., Buol, S.W., 1982. The fertility capability soil classification system:
811 Interpretation, applicability and modification. *Geoderma* 27, 283-309.

812 Sanchez, P.A., Palm, C.A., Buol, S.W., 2003. Fertility capability soil classification: a tool to help
813 assess soil quality in the tropics. *Geoderma* 114:157-185.

814 Sanford, R.L., Saldarriaga, J., Clark, K.E., Uhl, C., Herrera, R., 1985. Amazon rain-forest fires.
815 *Science* 227, 53-55.

816 Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to
817 observation. *Trends Ecol. Evol.*, 18(12), 648-656.

818 Scheffer, M., Barrett, S., Carpenter, S.R., Folke, C., Green, A.J., Holmgren, M. et al., 2015.
819 Creating a safe operating space for iconic ecosystems. *Science* 347, 1317-1319.

820 Scullion, J., Vogt, K., Sienkiewicz, A., Gmur, S., Trujillo, C., 2014. Assessing the influence of land
821 cover change and conflicting land-use authorizations on ecosystem conversion on the forest
822 frontier of Madre de Dios, Peru. *Biol. Conserv.* 171, 247-258.

823 Seastedt, T.R., Hobbs, R.J., Suding, K.N., 2008. Management of novel ecosystems: are novel
824 approaches required? *Front. Ecol. Environ.* 6, doi:10.1890/070046.

825 Siebert, F., Ruecker, G., Hinrichs, A., Hoffmann, A.A., 2001. Increased damage from fires in
826 logged forests during droughts caused by El Niño. *Nature* 414, 437-440.

827 Silva, L.C.R., 2014. Importance of climate-driven forest-savanna biome shifts in anthropological
828 and ecological research. *Proc. Natl. Acad. Sci.* 37, E3831-E3832.

829 Slik, J.W.F., 2004. El Niño droughts and their effects on tree species composition and diversity in
830 tropical rain forests. *Oecologia* 141, 114–120

831 Smith, K.T., 2015. Compartmentalization, resource allocation, and wood quality. *Curr. Forest. Rep.*
832 1, 8-15.

833 Soil Survey Staff, 1999. Soil taxonomy: A basic system of soil classification for making and
834 interpreting soil surveys. 2nd Edition. United States Department of Agriculture. pp. 436.

835 Sotta, E.D., Veldkamp, E., Schwendenmann, L., Guimaraes, B.R., Paixao, R.K., Ruvio, M.L.P., et
836 al., 2007. Effects of an induced drought on soil carbon dioxide (CO₂) efflux and soil CO₂
837 production in an eastern Amazonian rainforest, Brazil. *Global Change Biol.* 13, 2218-2229.

838 Staver, C.A., Archibald, S., Levin, S.A., 2011. The global extent and determinants of savanna and
839 forest as alternative biome states. *Science* 334, 230-232.

840 Swaine, M.D., Lieberman, D., Putz, F.E., 1987. The dynamics of tree populations in tropical
841 forests: a review. *J. Trop. Ecol.* 3, 359-366.

842 Tan, Z., Zhang, Y., Yu, G., Sha, L., Tang, J., Deng, X. et al., 2010. Carbon balance of a primary
843 tropical seasonal rain forest. *J. Geophys. Res.* 115, 1-17.

844 Tanaka, S., Sugimura, T., Mishima, S., 2000. Monitoring of vegetation extent around Kitui Pilot
845 Forest (Afforestation test site) in Kenya with rainfall with satellite data. *Adv. Res. Space* 26,
846 1039-1042.

847 Therneau, T.M., Atkinson, E.J., 2011. An introduction to recursive partitioning using the RPART
848 routines. Mayo Foundation, January 11, 2011.

849 Therneau, T.M., Atkinson, B., Ripley, B., 2011. Rpart: Recursive Partitioning. [online] URL:
850 //CRAN.R-project.org/package=rpart, accessed November 1, 2012.

851 Tittonell, P., Vanlauwe, B., Shepherd, K.D., Giller, K.E., 2008. Unravelling the effects of soil and
852 crop management on maize productivity in smallholder agricultural systems of western Kenya -
853 An application of classification and regression tree analysis. *Agric. Ecosyst. Environ.* 123,137-
854 150.

855 Vitousek, P. M., Ehrlich, P. R., Ehrlich, A. H., Matson, P. A., 1986. Human appropriation of the
856 products of photosynthesis. *Biosci.* 36, 363-373.

857 Vogt, K.A., Grier, C.C., Vogt, D.J., 1986. Production, turnover, and nutrient dynamics of above-
858 and belowground detritus of world forests. *Adv. Ecol. Res.* 15:303-377.

859 Vogt, K., Vogt, D., Brown, S., Tilley, J., Edmonds, R., Silver, W., et al., 1995. Forest floor and soil
860 organic matter contents and factors controlling their accumulation in boreal, temperate and
861 tropical forests. In: Lal, R., Kimble, J., Levine, E, Stewards, B.A. (Eds.), *Advances in soil
862 science, soil management and greenhouse effect*, CRC Press, Boca Raton, Florida, pp. 159-178.

863 Vogt, K.A., Vogt, D.J., Palmiotto, P., Boon, P., O'Hara, J., Asbjornsen, H., 1996. Review of root
864 dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil*
865 187, 159-219.

- 866 Vogt K.A., Grove, M., Asbjornsen, H., Maxwell, K., Vogt, D.J., Sigurðardóttir, R., Larson, B.C.,
867 Schibli, L., Dove, M., 2002. Linking social and natural science spatial scales. In: Jianguo, L.,
868 Taylor, W.M. (Eds.) Integrating Landscape Ecology into Natural Resource Management.
869 Cambridge University Press, pp. 143-175.
- 870 Waring, R.H., Franklin, J.F., 1979. Evergreen coniferous forests of the Pacific Northwest. *Science*
871 204, 1380-1386
- 872 Waring, R.H., 1991. Response of evergreen trees to multiple stresses. In: Mooney, H.A., Winner,
873 W.E., Pell, E.J., Chu, E. (Eds), *Response of Plants to Multiple Stresses*. Academic Press, Inc.,
874 San Diego, New York, Boston, USA, pp. 371-390.
- 875 Williams, E., Dall'Antonia, A., Dall'Antonia, V., de Almeida, J.M., Suarez, F., Liebmann, B., et
876 al., 2005. The Drought of the Century in the Amazon Basin: An Analysis of the Regional
877 Variation of Rainfall in South America in 1926. *Acta Amaz.* 35, 231-238.
- 878 Wooster, M.J., Perry, G.L.W., Zoumas, A., 2012. Fire, drought and El Niño relationships on
879 Borneo (Southeast Asia) in the pre-MODIS era (1980–2000). *Biogeosci.* 9, 317-340.
- 880 WRI, 1998. *World Resources Report 1998–99. Environmental Change and Human Health*. World
881 Resources Institute, Oxford University Press, Oxford, United Kingdom, 384 pp.
- 882 Xu, L., Samanta, A., Costa, M.H., Ganguly, S., Nemani, R.R., Myneni, R.B., 2011. Widespread
883 decline in greenness of Amazonian vegetation due to the 2010 drought. *Geophys. Res. Lett.* 38,
884 940-943.
- 885 Zhao, M., Running, S.W., 2010. Drought-induced reduction in global terrestrial net primary
886 production from 2000 through 2009. *Science* 329, 940-943.