



Impacts of climate variability on tree demography in second growth tropical forests: the importance of regional context for predicting successional trajectories

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ABSTRACT

Naturally regenerating and restored second growth forests account for over 70% of tropical forest cover and provide key ecosystem services. Understanding climate change impacts on successional trajectories of these ecosystems is critical for developing effective large-scale forest landscape restoration (FLR) programs. Differences in environmental conditions, species composition, dynamics, and landscape context from old growth forests may exacerbate climate impacts on second growth stands. We compile data from 112 studies on the effects of natural climate variability, including warming, droughts, fires, and cyclonic storms, on demography and dynamics of second growth forest trees and identify variation in forest responses across biomes, regions, and landscapes. Across studies, drought decreases tree growth, survival, and recruitment, particularly during early succession, but the effects of temperature remain unexplored. Shifts in the frequency and severity of disturbance alter successional trajectories and increase the extent of second growth forests. Vulnerability to climate extremes is generally inversely related to long-term exposure, which varies with historical climate and biogeography. The majority of studies, however, have been conducted in the Neotropics hindering generalization. Effects of fire and cyclonic storms often lead to positive feedbacks, increasing vulnerability to climate extremes and subsequent disturbance. Fragmentation increases forests' vulnerability to fires, wind, and drought, while land use and other human activities influence the frequency and intensity of fire, potentially retarding succession. Comparative studies of climate effects on tropical forest succession across biogeographic regions are required to forecast the response of tropical forest landscapes to future climates and to implement effective FLR policies and programs in these landscapes.

Abstract in Spanish is available with online material.

Key words: Drought; fire; hurricanes; regrowth forests; warming.

MORE THAN 70 PERCENT OF ALL REMAINING TROPICAL FORESTS ARE SECOND GROWTH FORESTS ON FORMER AGRICULTURAL OR LOGGED LANDS (FAO 2010). These forests, which include both unassisted natural regeneration and forests actively planted for initiating natural regeneration, provide a wide range of ecosystem services (e.g., carbon storage, regulation of water flows, biodiversity conservation) on which present and future societies and economies depend. For instance, recent studies have estimated that carbon is accumulating in second growth tropical forests at rates as high as 3 Pg C/yr, accounting for more than 40 percent of the global aboveground carbon sink (Pan *et al.* 2011, Grace *et al.* 2014). Poorter *et al.* (2016) reported an average annual carbon gain of 3.05 Mg/ha for Neotropical secondary forests.

Despite the potential benefits of large-scale Forest Landscape Restoration (FLR) for climate mitigation and adaptation, climate variability and change may also hinder large-scale FLR efforts. Climate change is likely to alter successional trajectories

of forest structure and biomass accumulation, and increase the likelihood of large-scale fires, intense tropical storms, and outbreaks of forest pests and diseases. Yet, our understanding of climate change effects on FLR processes in tropical regions and potential feedbacks to the atmosphere remains limited (Anderson-Teixeira *et al.* 2013). This gap in our knowledge is of paramount importance given that tropical nations have committed more than 45 million ha to FLR by 2030 (<http://www.bonnchallenge.org>) and that climate variability and change may compromise or lessen the benefits of these commitments for climate mitigation and adaptation.

Climate change is expected to cause directional changes and increasing variability in mean annual temperature and precipitation (IPCC 2007, Anderson 2011, Diffenbaugh & Scherer 2011), with some of the fastest changes occurring in the tropics (Christensen *et al.* 2007, Anderson 2011, Mora *et al.* 2013). The tropics are predicted to experience extreme seasonal heat: between 2010 and 2039, up to 70 percent of seasons in the tropics may exceed late 20th century temperature maxima (Diffenbaugh & Scherer 2011). Precipitation patterns are also expected to shift (Neelin

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et al. 2006, Dai 2013, Feng *et al.* 2013, Mora *et al.* 2013). Though models disagree on predictions of drought more so than on tropical temperature extremes (Good *et al.* 2013), most predict stronger droughts in the Amazon (Joetzjer *et al.* 2013), Central America and the Caribbean, (Neelin *et al.* 2006), West Africa, and peninsular Southeast Asia (Zelawski *et al.* 2011), making FLR efforts in these regions particularly vulnerable to climate extremes (Fig. 1). Changes in the timing, magnitude, and duration of seasonality of precipitation are also expected to vary geographically (Feng *et al.* 2013, Mora *et al.* 2013, Greve *et al.* 2014). For example, western Africa and central Brazil have undergone marked reductions in rainfall seasonality due to decreases in their rainfall amounts while Central Africa has experienced a lengthening of the rainy season (Feng *et al.* 2013).

Beyond its effects on temperature and precipitation, climate change is likely to alter disturbance regimes (Dale *et al.* 2001,

DOE 2012). The frequency and/or intensity of disturbances, including fires, cyclonic storms, and floods, are anticipated to rise with climate change. Since cyclonic storms derive their energy from ocean heat, their intensity is forecasted to increase with a warming climate (Emanuel 2005, Webster *et al.* 2005) but predictions differ by ocean basin (Knutson *et al.* 2010). The most significant increase in observed cyclone intensity has occurred in the North Atlantic. By 2100, maximum sustained wind speeds and precipitation associated with storm events are predicted to increase. Fire is also strongly linked to climate variability (Swetnam 1993, Kitzberger *et al.* 2007) with greater fire risk during drought and ENSO events (Fu *et al.* 2013). Climate change is predicted to alter fire regimes, but there is uncertainty and disagreement across models about the extent and direction of these changes in the tropics (Pechony & Shindell 2010, Liu *et al.* 2010, Moritz *et al.* 2012), hindering our ability to identify regions where FLR efforts may be compromised (Fig. 1).

Effects of climate on disturbance may be intensified by shifts in land use throughout the tropics. Disturbance regimes and their interactions with land use also exhibit regional variability and may respond differently to a changing climate. Regional variation in the extent and spatial patterns of road building, land use, and landscape fragmentation leads to added variation in drought-induced fire activity (Nepstad *et al.* 2001, Cochrane & Laurance 2008, Uriarte *et al.* 2012a). For example, distance to forest edge in fragmented forests has been associated with increased fire activity in the Amazon (Alencar *et al.* 2004) but Slik *et al.* (2011) found limited edge effects in a burned forest in Borneo suggesting that the interactive effects of edges and fire may differ across regions. Since second growth and forest restoration plantings are more prevalent in human-modified, fragmented landscapes (Sloan *et al.* 2015), this is a key research gap. Heterogeneity in predicted spatial and temporal scales of climate change, including its effects on disturbance regimes and land use, is one of the challenges in drawing generalizations about the impacts of climate change on FLR in the tropics (Cavaleri *et al.* 2015).

An additional difficulty in assessing the response of tropical second growth forests and forest restoration plantings to climate change is the heterogeneity in their ecological dynamics and environmental context. From a biogeographic perspective, tropical forests can be classified into Neotropical, Afrotropical, and Indo-Malau-Australasian. Differences in the evolutionary history of regional species pools, geology, disturbance regimes, and current and past climates across these broad regions are likely to modulate responses to climate variability and change (Malhi *et al.* 2014). There is evidence that the sensitivity of rain forest trees to climate varies geographically across the tropics, with those in more aseasonal climates (*e.g.*, Southeast Asia) showing substantially larger increases in mortality under drought (Kumagai *et al.* 2008, Phillips *et al.* 2010) than those of Amazonia, for example, although data are extremely limited.

At the landscape and local scales, heterogeneity in soil properties, interactions among species, and disturbance regimes have shaped the life histories of tropical trees in ways that are likely to influence forest responses to climate (DOE 2012). Forests

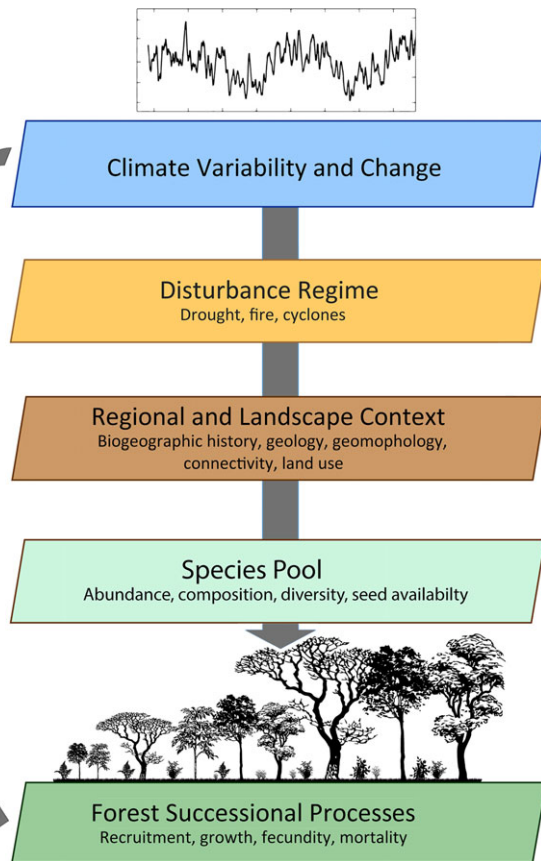


FIGURE 1. Changes in climate and climate variability can affect tree recruitment, growth, and other demographic processes that shape forest succession directly or by altering the frequency and intensity of climatic disturbance events, such as drought, fire, and tropical cyclones. The effects of climate and disturbance events on forest successional trajectories can also be mediated by regional and landscape factors that affect the species pool available for reforestation. For example, geomorphology and human land use can affect species' exposure to fire and continental differences in rainfall seasonality and biogeographic histories can influence species' tolerance to drought.

subjected to frequent, annual tropical storms (*e.g.*, Taiwan), for example, are low statured and more resilient and resistant to wind damage and therefore to increases in storm frequency or intensity, than forests that experience storm damage on decadal scales (Caribbean, South Pacific and Australian forests). Understanding the single or interactive effects of climate variability and change on the structure, composition, and dynamics of naturally regenerating second growth forests and, consequently, on large-scale FLR efforts will require a comprehensive, comparative approach across different patterns of climate variability and change, biogeographic regions and landscapes (Fig. 1).

To date, most research on climate impacts on tropical tree growth and survival has been conducted in old growth forests (*e.g.*, Feeley *et al.* 2007, Phillips *et al.* 2010). For example, several thorough reviews highlight the potential for increased temperatures to negatively affect carbon storage and biodiversity in tropical forests (Wright *et al.* 2009, Corlett 2011, Wood *et al.* 2012). None of these reviews, however, examine climatic impacts on second growth forests and how these may differ from old growth forests. Understanding how tropical second growth forests respond to climate change and variability, including disturbance regimes, is critical for improving predictions of feedbacks between the terrestrial biosphere and climate. Yet, our current understanding does not incorporate potential differences in physiological and ecological response of successional forests to climate and related disturbance events. This knowledge gap is critical because not only are natural and restored second growth forests widespread today, they are increasingly becoming dominant worldwide, particularly in the context of ongoing large-scale FLR efforts (Chazdon 2014).

Second growth forests and assisted regeneration may be more vulnerable to climate variability and change than old growth forests. At the stand scale, early successional forests may be particularly vulnerable to climate extremes due to rapid stem turnover and low basal area, which result in elevated light and temperature in the understory (Fig. 2A) (Nicotra *et al.* 1999, Hasselquist *et al.* 2010, Lebrija-Trejos *et al.* 2011). Competition for soil nutrients and water, which may intensify under drought, may also be more intense in young second growth forests than in old growth as a consequence of fast growth rates of growing vegetation and high stem densities (Fig. 2B). Legacies of previous land use can lead to depleted soil nutrient supply, so that second growth forest productivity can be limited by nitrogen (N) whereas old growth lowland tropical forests can show a surplus of N (Vitousek & Reiners 1975, Davidson *et al.* 2004, Batterman *et al.* 2013).

At the community scale, second growth forests contain a greater proportion of pioneer and fast growing tree species, whose physiological characteristics may make them more vulnerable to drought and temperature increases (Bazzaz & Pickett 1980, Phillips *et al.* 2010, Lohbeck *et al.* 2013, Ouedraogo *et al.* 2013). For example, high rates of hydraulic conductance in early successional trees have been linked to leaf and wood functional traits that confer high rates of photosynthesis and transpiration but increase risk of xylem cavitation under drought conditions (O'Brien *et al.* 2004, Santiago *et al.* 2004, Markesteijn *et al.* 2011,

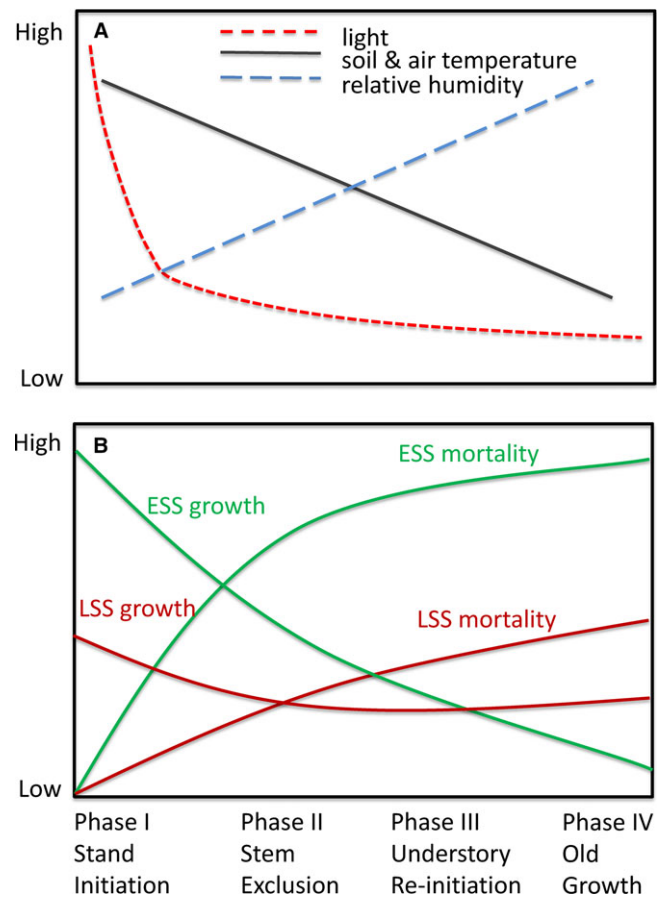


FIGURE 2. (A) Hypothesized changes in environmental conditions and abiotic resources across four stages of succession which may modify tree and forest responses to climatic variability and change. Successional stages are derived from Chazdon (2008). Note that these apply to wet forests and dry forests during the wet season. Hypothesized changes are based on data from Lebrija-Trejos *et al.* 2011, Denslow and Guzman 2000. (B) Hypothesized shifts in tree growth and mortality for early successional (ESS) and late successional specialists (LSS) across the four successional stages.

McCulloh *et al.* 2011). A recent global analyses on the relationship between drought mortality found that low-wood density trees, a trait typically associated with low shade tolerance, were at greater risk of drought-associated mortality (Phillips *et al.* 2010).

At the landscape scale, the location of natural and restored second growth forests is non-random, as agricultural abandonment occurs earlier on less accessible, steeper areas with lower soil fertility and greater hydrological stress (Asner *et al.* 2009). This spatial distribution may magnify the effects of climatic variation on ecological processes. Many tropical second growth and restored forests also exist in landscapes heavily modified by human activities, putting them at risk of drought-induced fires (Gutierrez-Velez *et al.* 2014).

In a recent review of climate effects on global forest recovery, Anderson-Teixeira *et al.* (2013) highlighted large gaps in our understanding of climate change effects on natural second growth tropical forests compared to temperate or boreal forest biomes.

Here, we synthesize existing literature on second growth forest demographic responses to natural climate variability as manifested by extreme rainfall events and disturbances such as cyclones and fire. We aim to identify the intrinsic (i.e., age and composition), and extrinsic factors (i.e., landscape and regional context), that mediate vulnerability of tropical second growth forests to climate change and to identify gaps and geographic biases in current knowledge. We hope that filling these gaps will enhance the success of FLR in tropical regions. Our review builds on that of Anderson-Teixeira *et al.* (2013) by linking species successional and life history stages to climate drivers and examining the effects of climate variability, not just climate trajectories, and climate-driven disturbance events. We include individual species responses as well as consequences for successional dynamics (i.e.,

effects on forest structure and composition). Finally, given the large climatic and biogeographic diversity of natural and restored second growth tropical forests worldwide, we assess how regional and landscape context mediate impacts of climate variability (Fig. 1). The latter is of paramount importance for understanding the present and future persistence (and the role they will play in biodiversity maintenance, and supply of ecosystem functions and services) of second growth forests in human-modified landscapes.

Tropical climates vary across multiple temporal scales: seasonal, inter-annual, and multi-annual (e.g., ENSO) (Fig. 3). The range of historical conditions experienced in any one location often includes that of near-term forecasts of climate change (~20–40 years), making extrapolation of future responses feasible.

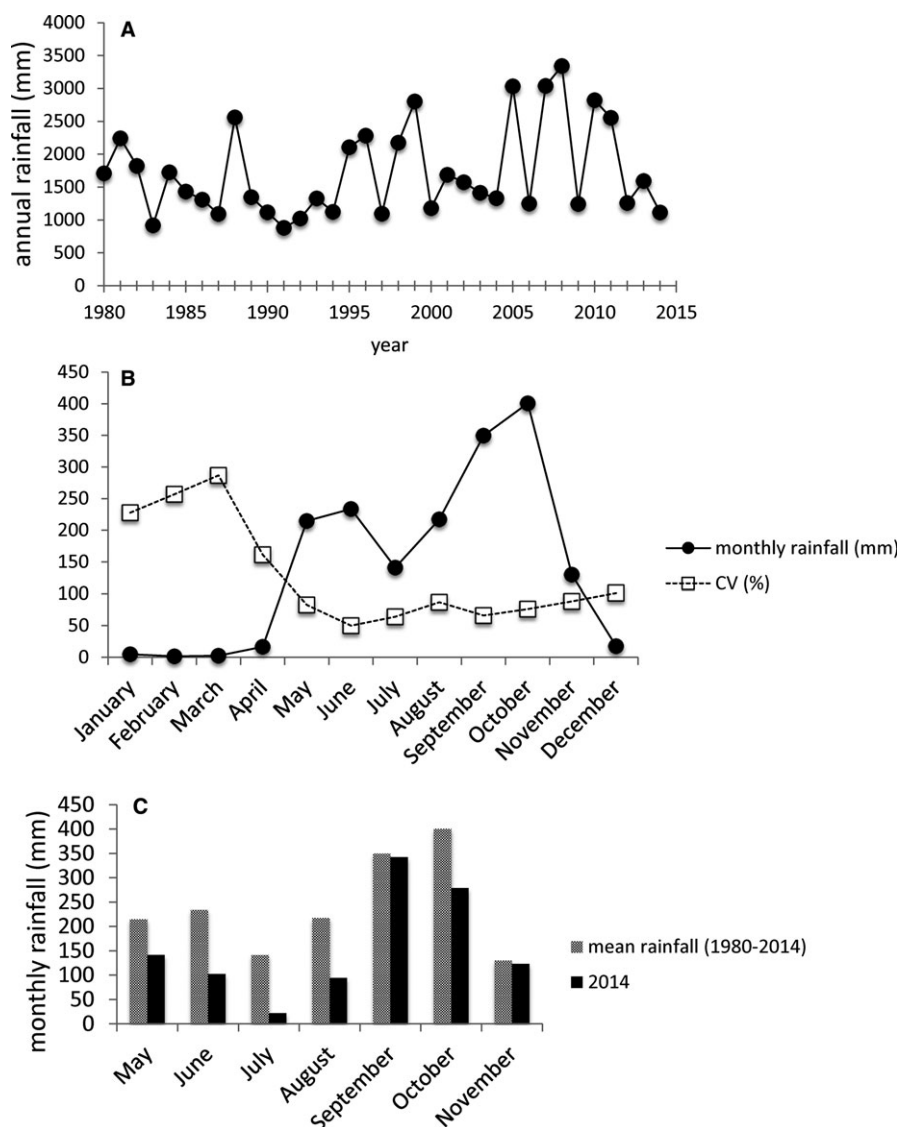


FIGURE 3. Multiple scales and aspects of climate variability in a tropical dry forest. (A) Annual precipitation in Santa Rosa, Costa Rica between 1980 and 2015, (B) Mean and CV of monthly precipitation in Santa Rosa, Costa Rica between 1980 and 2015 (C) Comparison of average and 2014 monthly precipitation data during the rainy season. Data are from the Área de Conservación Guanacaste (<http://www.acguanacaste.ac.cr/>).

We include experimental and observational studies of tree demographic responses to climate change, climate variability, or disturbance at single or multiple stages of forest development, and attempt to identify the most vulnerable life history or successional stages (Table 1; Fig. 2). Where research on second growth forests is lacking, we refer to literature on old growth forests and hypothesize how the response may differ, based on what we know about successional processes. In the discussion, we focus on synthesizing results from our literature search to address the following questions: (1) which life history stages and successional groups are particularly vulnerable to climate variability and to related disturbance events and what are the consequences for succession? (2) How do regional and landscape context mediate second growth forest responses to climate variability and altered disturbance regimes?

METHODS

To identify relevant literature, we searched the ISI Web of Science using the following key words: (climate OR precipitation OR temperature OR enso OR drought OR fire OR tropical storm\$) AND tropical forest AND (mortality OR recruitment OR species turnover OR growth OR species loss) AND (succession OR logged OR regrowth OR recovery OR secondary forest). To

expand our literature search, we also included studies cited in the papers identified by our ISI search and other studies contributed by experts on the subject. From these results, we selected papers that met the following criteria: (1) directly considered at least one climate factor as a predictor variable; (2) considered some aspect of forest stand dynamics (growth, mortality, recruitment, fecundity, species composition, forest structure) as a response variable; and (3) was conducted in a tropical second growth forest. This ultimately resulted in a total of 110 studies, which we classified according to location of study, climate factors considered, forest type (wet or dry), response variables, and tree size classes measured (Appendix S1).

RESULTS AND DISCUSSION

WHICH LIFE HISTORY STAGES AND SUCCESSIONAL GROUPS ARE PARTICULARLY VULNERABLE TO CLIMATE VARIABILITY AND TO RELATED DISTURBANCE EVENTS?—Mortality was by far the most common demographic process studied across all climate factors (Table 2). Growth, recruitment, and re-sprouting were far less frequently studied, despite being key successional processes. This discrepancy may be because mortality is easier to measure than growth or recruitment, especially if measurements occur immediately after a disturbance event. Forest structure and composition

TABLE 1. Hypothesized effects of climate variability and change at multiple temporal scales on the demography of different tropical forest trees at different life history stages. Based on these effects, we predict the successional stage likely to be most affected. Successional stages: stand initiation (I), stem exclusion (II), understory re-initiation (III), old-growth (IV) derived from Chazdon (2007). We expect that short-term drought and extreme precipitation events will primarily influence seedling recruitment and mortality and these effects will be most marked in the early stages of succession. Effects of annual droughts will be most marked in the stem-exclusion stage when canopy transpiration rapidly increases and competition for water peaks (Fig. 1).

Driver	Temporal scope	Demographic Process	Succession	Life History Stage
Drought/ Extreme	Short-term	Recruitment, mortality	I, II	Seedlings
Precipitation	Annual scale	Fecundity, growth, mortality	II	Adults, saplings, seedlings
	Periodic: ENSO, ASST	All processes	I – IV	All stages
Temperature	Daily, annual, and long-term	Unknown	Unknown	Unknown
Fire	Frequency	Mortality	I – IV	Sapling, seedlings
	Intensity	“+ recruitment	I – IV	All stages
Hurricanes	Frequency	“	I – IV	All stages
	Intensity	“	III, IV	Adults

TABLE 2. Number of studies focused on specific response variables by primary climatic driver considered. We examine demographic rates as well as vulnerability to drivers, that is, damage from cyclones and flammability during fires. We also summarize the number of studies that examined effects of climate drivers on forest structure and composition. Some studies examined multiple response variables, so the sum of the column totals is greater than the total number of studies reviewed ($n = 110$). For growth, mortality, recruitment, and resprouting, we show in parentheses the direction of response to climate-mediated effect relative to undisturbed controls (+, –, 0). The symbol + indicates that the response variable was higher in ‘treatment’ (effect of climate extreme or disturbance) forest relative to control, – indicates a decrease in the response, and 0 indicates no change was detected. The numbers in the parenthesis only include studies that compared the response to either an undisturbed or pre-disturbance control. Data were not sufficient to evaluate directionality of the response for other demographic processes.

Response	Drought	Fire	Cyclone	Temperature	Total
Growth	6 (0, 3, 3)	2 (1, 0, 0)	15 (0, 5, 0)	0	23
Mortality	8 (5, 0, 2)	21 (17, 0, 0)	23 (8, 0, 0)	0	52
Fecundity	2	1	3	1	8
Germination	1	3	0	0	5
Recruitment	4 (0, 2, 1)	6 (1, 2, 0)	10 (3, 0, 0)	0	20
Resprouting	0	8 (4, 0, 0)	5 (1, 0, 0)	0	13
Damage	0	0	19	0	23
Flammability	0	3	0	0	3
Structure	4	18	19	0	57
Composition	2	12	16	0	40
Total studies	17	37	55	1	

were also commonly studied. Reproduction received scant attention with only eight studies on fecundity and five on germination, primarily in wet forests (Table 3). Most studies focused on large size classes (adult trees >10 cm dbh), rather than seedlings or saplings, though small trees may be more vulnerable to some climate extremes and disturbances and are key to regeneration processes (Table 4). Here, we focus on what is known about how intra- and inter-annual variability in temperature, precipitation, tropical cyclones, and fire affects successional processes, drawing from the 112 studies mentioned above and from the richer literature of climate impacts on old growth tropical forests.

Impacts of Temperature and Precipitation Variability.—Temperature.—Our understanding of temperature effects on second growth forest is extremely limited (Table 2). Because the light environment in the understory of second growth forests can be far different from that of old growth forests (Nicotra *et al.* 1999, Hasselquist *et al.* 2010, Lebrija-Trejos *et al.* 2011), temperature changes are likely to have strong impacts, particularly in early successional stages, through effects on seed germination. For example Aud and Ferraz (2012) examined the effects of temperature fluctuations on seed germination of seven species and found positive, negative and non-significant responses. On the other hand, early successional species in tropical forests may be adapted to cope

with extreme temperatures and/or dissipate increased heat loads of early successional environments, as has been shown for seasonally dry tropical forest in Mexico (Lebrija-Trejos *et al.* 2010). However, effects of high temperatures on regeneration may differ between wet and dry forests. Resolving whether and which tropical tree species are uniquely adapted or alarmingly vulnerable to predicted temperature change should be a priority for the global change community.

Large-scale warming experiments are currently underway in one tropical forest in Puerto Rico but to date, the only published studies of physiological and growth responses of tropical tree species to altered temperature come from diurnal temperature gradients (Slot *et al.* 2013), growth chamber experiments (Cunningham & Reed 2003, Cheesman & Winter 2013), cut leaves in warmed chambers (Doughty & Goulden 2008), or branch warming experiments (Slot *et al.* 2014). Relative growth rates of seedlings grown at a range of temperatures showed that pioneer species performed better than late successional species at higher temperatures (Cheesman & Winter 2013). This trend persisted at the highest temperature (35°C), at which growth rates for old growth species were severely depressed. In a field study canopy whole leaf respiration for early successional species responded more to elevated temperature than mid- or late-successional species (Slot *et al.* 2013). Both of these studies suggest that the physiological and growth responses of species to elevated temperature vary by successional status, but the implications of this variation for successional dynamics are not clear.

Long-term datasets that span a broad range of temperatures are useful for making inferences about tropical forest processes under a warming climate. High temperatures reduced growth rates in old growth forests (Clark *et al.* 2003, 2010). By using long-term records of reproduction that spanned a 1–4°C gradient in temperature, Pau *et al.* (2013) showed increased flower production with increasing temperatures in an ever-wet second growth forest in Puerto Rico. Changes in flower production and seed availability that may accompany climate change can alter successional pathways by affecting the distribution of propagules and seedling recruitment. However, higher flower production may not

TABLE 3. Number of studies focused on each response variables by biome (wet or dry forest). Total studies do not always add up to totals in table 2 because there was one study that compared across wet and dry forest. For growth, mortality, recruitment, and resprouting, we show in parentheses the direction of response to climate-mediated effect relative to undisturbed controls (+, –, 0). The symbol + indicates that the response variable was higher in 'treatment' (effect of climate extreme or disturbance) forest relative to control, – indicates a decrease in the response, and 0 indicates no change was detected. The numbers in the parenthesis only include studies which compared the response to either an undisturbed or pre-disturbance control. Data were not sufficient to evaluate directionality of the response for other demographic processes.

	Dry	Wet
Growth	6 (0, 3, 1)	18 (1, 5, 3)
Mortality	10 (4, 0, 1)	42 (25, 0, 2)
Fecundity	1	6
Germination	2	1
Recruitment	4 (0, 2, 0)	15 (4, 2, 1)
Resprouting	6 (1, 0, 0)	6 (3, 0, 0)
Damage	1	18
Flammability	0	3
Composition	3	27
Structure	2	39
Drought	3	13
Fire	5	31
Cyclone	5	50
Temperature	0	1
Total studies	14	96

TABLE 4. Number of studies that have examined impacts of drought, extreme temperatures, fire, and tropical cyclones on growth and mortality of tropical forest trees in secondary forests by life history stage. We show in parentheses the direction of response to climate-mediated effect relative to undisturbed controls (+, –, 0). The symbol + indicates that the response variable was higher in 'treatment' (effect of climate extreme or disturbance) forest relative to control, – indicates a decrease in the response, and 0 indicates no change was detected. The numbers in the parentheses only include studies which compared the response to either an undisturbed or pre-disturbance control.

	Adults (>10 cm dbh)	Saplings (<10 cm dbh)	Seedlings	All sizes
Growth	14 (0, 7, 0)	10 (1, 4, 1)	7 (0, 0, 2)	0
Mortality	32 (21, 0, 1)	14 (7, 0, 1)	11 (1, 0, 0)	8 (6, 0, 0)

necessarily result in higher seed production if rates of ovule abortion or pollination visitation are affected by high temperatures. Clearly, the most salient conclusion from the limited data base we were able to compile on how temperature variability affects tropical tree species in second growth forests is that much remains to be learned. More studies are needed to determine the consequences of species' variation in physiological responses to temperature for tree demography and forest dynamics. Since the potential for latitudinal shifts toward cooler climates is limited in tropical regions, studies should focus in regions where the absence of mountains precludes elevational range shifts (Colwell *et al.* 2008).

Drought.—Annual rainfall totals and rainfall seasonality in tropical forests can be quite variable (Fig. 3). Some of this variability may be attributed to cyclical or multi-annual processes, such as the Atlantic Multi-decadal Oscillation or El Niño/La Niña while short-term drought spells are also a common phenomenon. In contrast with our limited understanding of the potential effects of changing temperatures on tropical forest dynamics, phenology, and successional processes, the role of water availability has received more attention (Table 2). Drought affects many aspects of second growth dynamics, including growth and mortality of trees, seed quality, and/or fecundity, and these responses may occur during drought or following a time lag (Maza-Villalobos *et al.* 2013).

Forest inventory and dynamics plot studies and the dendroecological literature offer insights into demographic responses to short-term or multi-annual variability. It is well known that radial growth in tropical trees is positively correlated with precipitation (*e.g.*, Brien *et al.* 2005, Zuidema 2010, Zuidema *et al.* 2012, Paredes-Villanueva *et al.* 2013) and that reduced precipitation during ENSO events can lead to declines in tree growth (Brien *et al.* 2010, Paredes-Villanueva *et al.* 2013). ENSO events in second growth tropical forests increased stem mortality and recruitment (Slik 2004, Chazdon *et al.* 2005, Ouedraogo *et al.* 2013). In wet forests, mortality can be dependent on tree size but is highly site specific, as both trees in small size classes (Chazdon *et al.* 2005) and large trees (>20 cm DBH) (Slik 2004) experience increased mortality in drought years (Bennett *et al.* 2015). Drought also increases seedling mortality (Engelbrecht *et al.* 2006). Moderate ENSO events have been found to favor seed production for masting (Curran *et al.* 1999) and non-masting trees (Wright & Calderon 2006). Extreme precipitation events that affect all recruits equally might result in pulsed or synchronized recruitment, such that there are 'good years', punctuated by 'bad years' with little to no recruitment (Castilleja 1991, Zimmer & Baker 2009, Vlam *et al.* 2014, Maza-Villalobos *et al.* 2013). These findings reveal that predicted increases in the frequency of severe ENSO events (Federov & Philander 2000, Yeh *et al.* 2009) have the potential to lead to large-scale reductions in tree growth, recruitment, and seed production, along with increases in stem mortality.

Guild-specific responses to drought, such as differential growth, survivorship, or recruitment may also alter successional

dynamics. Studies in second growth forests found drought led to greater recruitment (Slik 2004) and higher mortality for pioneer trees (Ouedraogo *et al.* 2013, Uriarte *et al.* 2016). Short-term droughts can also influence the seed and seedling life history stages, which may be particularly vulnerable, and consequently, community composition (Engelbrecht & Kursar 2003, Engelbrecht *et al.* 2006, 2007). Engelbrecht *et al.* (2006), for example, found that short dry spells in the wet season increased mortality of pioneer seedlings in Panama. This effect may be more important in seasonally dry forests where pioneer species are more vulnerable to xylem cavitation than late successional species (Markestijn *et al.* 2011). Recent studies of functional traits suggested that early successional species were more water limited than late-successional trees in tropical second growth forests (Lohbeck *et al.* 2015, Uriarte *et al.* 2016a, b).

Differential vulnerability to drought between regenerative guilds, however, might not always result in clear outcomes for succession. For example, in a pot experiment from a dry forest in Mexico where drought was imposed on 1 year-old seedlings, tree species exhibited a continuum of mechanisms to tolerate or avoid drought (Pineda-Garcia *et al.* 2013). This resulted in no clear differences in physiological performance among early and late successional species. Similarly, a 13-year record of tree mortality from forest inventory plots in Trinidad showed no differences in response to drought between pioneer and old growth forest tree species (Oatham & Ramnarine 2006). By contrast, Schönbeck *et al.* (2015) found that later successional species were actually more sensitive to drought, and speculated that early successional species may have belowground adaptations to cope with water deficits.

Comparing the direct and lagged effects of rainfall variability on forest dynamic processes in stands ranging from very young second growth forests to old growth forests should be a priority for future studies. Experimental approaches such as large-scale irrigation or drought manipulations may reveal causal links between climate variability and successional processes that observational approaches cannot, because of the co-variation between climatic variables such as rainfall, temperature, and solar radiation (Pau *et al.* 2013). Large-scale throughfall exclusion studies in an old growth forest in Brazil revealed tree responses to reduced soil moisture (Nepstad *et al.* 2007, Brando *et al.* 2008, Da Costa *et al.* 2010), demonstrating the feasibility of this approach for understanding drought in second growth forests. Identification of the physiological mechanisms that underlie differential vulnerability to drought will be the key in predicting the effects of increased drought on tropical forest succession.

Impacts of Altered Fire Regimes.—Most studies of impacts of fire on second growth tropical forests have focused on post-fire mortality and forest structure, perhaps because mortality and its effects on structure are easily measured immediately after fire (Table 2). Post-fire sapling and tree mortality can reach 75–100 percent in some tropical forests (Woods 1989, Flores *et al.* 2014), but tree species and size classes differ in their vulnerability. Mortality is highest in smaller size classes (Van Nieuwstadt *et al.* 2001, Van

Nieuwstadt & Sheil 2005, Brando *et al.* 2012), though larger trees can experience delayed mortality (Barlow *et al.* 2003). Fire tolerance varies with functional and life history traits. Early successional species and deciduous species suffer greater mortality (Santiago-Garcia *et al.* 2008, Balch *et al.* 2011). Mortality is negatively correlated with bark thickness and wood density (Uhl & Kauffman 1990, Slik *et al.* 2010, Brando *et al.* 2012). Since community mean wood density generally increases with forest age (Bazzaz & Pickett 1980, Plourde *et al.* 2015, but see Craven *et al.* 2015), we may expect fire-induced mortality to decrease over succession. Though an important trait for fire tolerance, relatively few studies have examined how bark thickness varies with successional status or life history strategy. These studies have found mixed results: in some ecosystems, bark thickness is linked to fire regime (Pausas 2014), though studies in tropical forests have shown no pattern in relation to fire and instead find that bark thickness is linked to adult stature, defense, and stem water content (Paine *et al.* 2010, Ibanez *et al.* 2013, Poorter *et al.* 2013, Rosell *et al.* 2013). Flammability may also vary with forest age: mature stands with tall canopies and high leaf area index maintain more humid microclimates than younger stands (Ray *et al.* 2005, 2010). However, few studies have linked forest age and structure or forest type to flammability (Table 2).

Following fire, plants can regenerate via two main strategies: reseedling and resprouting. High intensity fire that causes adult mortality favors reseedling (Pausas & Keeley 2014). Resprouting is more common after low intensity fire and when post-fire conditions are favorable because sprouts can quickly fill in gaps and limit seedling recruitment (Kauffman 1991, Vesik & Westoby 2004, Pausas & Keeley 2014). In an experiment in a Bolivian dry forest that had previously been selectively harvested, sprouts dominated post-fire regeneration over seedlings, but this trend reversed after a high-intensity fire (Kennard *et al.* 2002). Observational studies in burned old growth forests and experimental studies have shown sapling and seedling growth are either increased by fire or not significantly altered (Fredericksen *et al.* 2000, Cleary & Priadhati 2005).

Differences in post-fire mortality, growth, and regeneration success across species lead to declines in species richness and compositional changes in burned forests (Cleary & Priadhati 2005, Slik *et al.* 2008, Balch *et al.* 2013), and return to pre-fire conditions is slow (Cleary & Priadhati 2005). For example, in Amazonian floodplain forests, burned forests still resembled first-year post-fire sites 13 years after fire (Flores *et al.* 2014). Still, the combined effects of selective pressure on vegetation composition and direct mortality can lead to prolonged changes in community assembly, altering ecosystem development (Barlow *et al.* 2008, Gerwing 2002, Van Nieuwstadt & Sheil 2005).

Changing fire regimes could ultimately limit tropical forest regrowth. In Australia, fire is an important factor in determining tropical rain forest boundaries (Ash 1988, Bowman 2000). Globally, fire limits the occurrence of forest and maintains savanna vegetation in areas with intermediate rainfall (Staver *et al.* 2011). Shifts in fire frequency could reduce favorable conditions for forest, which may be particularly important for young second

growth forests as they are more exposed to anthropogenic fire. Whether this occurs will depend on the resilience of the forest biota to fire, and how climate change ultimately ends up changing fire regimes. Identification of thresholds for forest regeneration and resilience will require coordinated studies across gradients of fire occurrence and climate conditions. Effective FLR in fire-prone landscapes may include fire suppression, planting of fire-resistant species, or inclusion of fire breaks. Through forest management will not prevent fire impacts altogether, doing so can at least minimize vulnerability to fire for FLR in fire-prone landscapes.

Impacts of Tropical Cyclone Activity.—The most widely studied impacts are tree mortality and stand structural changes (Table 2; Tanner *et al.* 1991, Walker *et al.* 1992, Boucher *et al.* 1994, Imbert *et al.* 1996, Uriarte *et al.* 2004a, Pascarella *et al.* 2004a, Franklin 2007, Ostertag *et al.* 2005, Van Bloem *et al.* 2005, 2006, Walker 1995). Generally, tall forests with denser canopies are more susceptible to wind damage (Everham & Brokaw 1996, Walker 1991), suggesting increased vulnerability of older second growth forest stands (Flynn *et al.* 2010 but see Franklin *et al.* 2005). On the other hand, a dense, well-developed canopy may reduce tree mortality from tip-ups in waterlogged soil (Arriaga 2000, Lugo 2008). Rapid forest structure and biomass recovery have led researchers to conclude that storm effects on tropical forests are short-lived (Boucher *et al.* 1994, Scatena *et al.* 1996, Beard *et al.* 2005). A focus on community dynamics offers a more nuanced picture of the potential effects of tropical storms on the composition and successional dynamics of second growth tropical forests (*e.g.*, Crow 1980, Lugo 2008, Uriarte *et al.* 2009, Heartsill Scalley *et al.* 2010).

Tree species differ in their susceptibility to wind disturbance, the nature of the damage they sustain, and their ability to recover, at the individual plant and population levels. Fast growing tree species with low wood density and high specific leaf area are particularly vulnerable to trunk damage and defoliation (Zimmerman *et al.* 1994, Vandermeer *et al.* 1997, Ross *et al.* 2001, Franklin *et al.* 2004, Ostertag *et al.* 2005, Curran *et al.* 2008, Pohlman *et al.* 2008, Canham *et al.* 2010). The high resource conditions that typically follow storms result in large but short-lived increases in seedling establishment and tree growth and decreases in understory tree mortality, particularly for light-demanding species (Guzman-Grajales & Walker 1991, Burslem *et al.* 2000, Uriarte *et al.* 2004a,b, 2009, Comita *et al.* 2009, 2010, Shiels *et al.* 2010, Uriarte *et al.* 2005, Walker *et al.* 2003). Second growth forest specialists often produce new sprouts and branches in response to wind damage and higher resource availability (Bellingham *et al.* 1994, Zimmerman *et al.* 1994, Uriarte *et al.* 2012b). This strategy is expected to affect long-term growth and survival. Sprouting responses to hurricanes are particularly important in slow-growing dry forests where water, rather than light, limits tree growth and seedling recruitment is low (Castilleja 1991, Van Bloem *et al.* 2006). Fecundity of reproductive trees may also be affected by individual tree damage and subsequent changes in resources (Wunderle 1999, Uriarte *et al.* 2012b). Depending on the availability of seeds from different successional stages, both within the

stand and in the surrounding landscapes, wind damage may retard or accelerate succession (Flynn *et al.* 2010). Fast growing pioneer species that can reach reproductive size quickly under the increased light conditions that follow a storm may benefit the most (Uriarte *et al.* 2009, 2012b) but the implications for successional dynamics is unclear.

Expected increases in the intensity of tropical storms should have a significant effect on the demography, successional dynamics, and community composition of second growth tropical forests (Lugo 2008). Greater storm severity may cause an increase in tree mortality rates and high sapling recruitment, particularly for pioneer and second growth forest species, retarding succession. It may also lead to an increase in the extent of second growth forests naturally regenerating after storm passage. In the absence of posthurricane salvage operations, a portion of the carbon in timber downed during a hurricane may return to the atmosphere through accelerated decomposition, or through heightened susceptibility to fire, potentially increasing greenhouse gas emissions (Miranda 1996, Foster *et al.* 1997). The potential for synergistic effects of wind damage and fires remains unexplored in tropical landscapes and is critical for understanding the effects of climate variability and change on FLR.

HOW DO REGIONAL AND LANDSCAPE CONTEXTS MEDIATE SECOND GROWTH FOREST RESPONSES TO CLIMATE VARIABILITY AND ALTERED DISTURBANCE REGIMES?—Predictions of the response of second growth and restored tropical forests to changes in climate and climate-driven disturbances are challenged by the diversity of biogeographic histories and environmental conditions at continental, regional, and landscape scales that will undoubtedly influence successional trajectories and their sensitivity to external factors (Fig. 1). Climate impacts will vary geographically, but so do historical climate and exposure to variability. The causes and consequences of environmental change in future tropical forests will manifest in different ways across geographic regions and regional differences in ecological histories will affect the resilience of tropical forests (Malhi *et al.* 2014). This heterogeneity must be considered when planning FLR activities.

At the global scale, tropical second growth forests are shaped by different biogeographic histories (Chazdon 2014). Within biogeographic regions, natural selection and other evolutionary forces, as well as human movement, affect the species pool available for reforestation. Depending on historical exposure to climate stressors and associated selective pressure, these species can have different life history traits that shape their responses to climate and disturbance. At regional to landscape scales, physical factors such as geologic substrates and topography create heterogeneous environments (Townsend *et al.* 2008), which can influence resource availability for forest regrowth and species distributions (Fortunel *et al.* 2014), and exposure to climate extremes.

Human factors, such as land use practices and exploitation of forest resources, can affect the rate of reforestation as well as species establishment in second growth forests (Crk *et al.* 2009, Atkinson & Marín-Spiotta 2015). Given that most second growth

forests are fragments in human-modified landscape mosaics, factors such as fragment size, connectivity, edge-to-area ratios, and surrounding land use can affect species dispersal and recruitment (Galanes & Thomlinson 2008, Ramjohn *et al.* 2012) and exposure to disturbance (Laurance & Curran 2008). Disturbance history and previous land-use type, intensity, and duration can also leave long-lasting legacies on soil resources and species composition that can influence the future trajectory of second growth forests. Hence, not only are tropical forests diverse, second growth forests are embedded in landscapes made more heterogeneous by past and current human activities.

Our review uncovered strong biome-specific and regional biases in research of climate impacts on successional forests. Among the 112 studies, only 14 were conducted in dry forests (Table 3). The majority of studies was located in the Neotropics and Africa had the fewest studies (Fig. 4). Research focus varies according to regional climatic stressors: studies on hurricanes dominated in the Caribbean and Central America, droughts in Central Africa, and drought-induced fire in South America and Southeast Asia. Below we discuss context-specific factors that may modify the responses of second growth forests to climate variability and changing disturbance regimes. These factors may not only modify the responses of second growth forest to climate variability and change but also determine the potential for natural regeneration in the landscape (*e.g.*, when forest remnants in the landscape are scarce or when agricultural land uses dominate the landscape, Chazdon & Guariguata 2016).

Impacts of Life Zone, Biogeography, and Historic Climate Regime.—Different biogeographic and climatic histories can lead to regional differences in how species respond to climate. At coarse continental scales, floras from different regions vary in traits. For example, mast flowering is more common in Asian Dipterocarp forests than in the Neotropics. In regions where mast flowering appears to be triggered by ENSO-linked droughts (Sakai *et al.* 2006), the consequences of climate change for regeneration may be very different. High densities of large mammalian herbivores in Afrotropical forests can suppress small tree growth and favor large trees that accumulate more carbon (Slik *et al.* 2013), which in turn can be more vulnerable to climate extremes (*e.g.*, drought in old growth stands, Phillips *et al.* 2010).

At coarse spatial and temporal scales, climate history may affect responses of contemporary forests to climate variability. For example, rain forest trees in more aseasonal climates (*e.g.*, Southeast Asia) may be more vulnerable to drought through reduced stomatal control of leaf water potential (Kumagai *et al.* 2008) than those of regions with more seasonality. At the same time, severe droughts in 2005 and 2010 caused significant reductions in forest growth and elevated tree mortality in Amazonia that persisted through time (Phillips *et al.* 2010) but extreme water deficits over this same period in West and Central Africa showed little effect on canopy processes (Asefi-Najafabady & Saatchi 2013). These different responses may be due to long-term precipitation reductions in West and Central Africa that shifted forest community composition toward more drought-tolerant

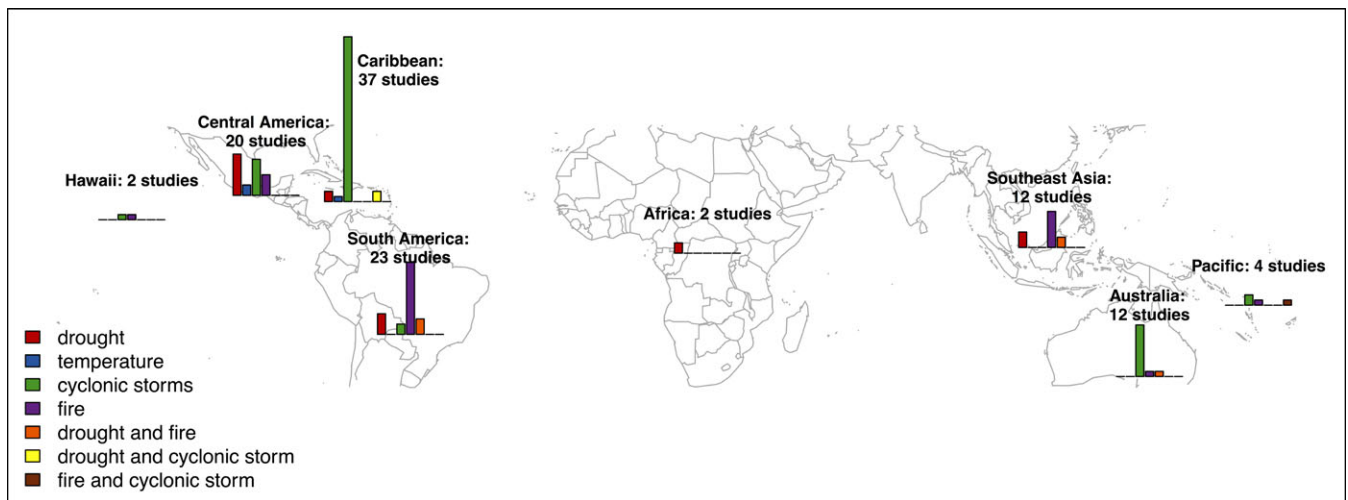


FIGURE 4. Geographic distribution of studies of climate effects on demography of tropical forest trees, including incidence of droughts, fires, and cyclonic storms, conducted in secondary forest stands.

species (Fauset *et al.* 2012). Variation in responses may also reflect species adaptations to the historical seasonality in precipitation with species growing with more seasonal environments (*e.g.*, Africa and Amazonas) exhibiting weaker responses to drought than those in aseasonal climates (Southeast Asia). Because of different baseline precipitation regimes, climate variability may also have different effects on successional processes in tropical dry forests compared to wet forests (Ewel 1977, Marod *et al.* 2002). Dry forests exhibit more rapid responses to short-term precipitation than rain forests, which may make these ecosystems particularly vulnerable to sustained declines in precipitation over longer time scales (Vicente-Serrano *et al.* 2013).

Exposure and vulnerability to disturbance also vary across biogeographic regions (Fig. 2). Fire has been an important evolutionary force shaping species and ecosystems (Bond & Keeley 2005), and variation in traits like resprouting and bark thickness have been linked to fire regimes (Pausas 2014, Pausas & Keeley 2014). However, the distribution of traits associated with adaptations or vulnerability to fire across biogeographic regions is not known for many tropical forests. Wet second growth forests may be more significantly altered by fire relative to dry forests since species are not pre-adapted to withstand fire (Gerwing 2002, Barlow *et al.* 2003, Van Nieuwstadt & Sheil 2005). Very high mortality has been documented in some wet tropical forest sites—for example 75–100 percent in the Rio Negro floodplain (Flores *et al.* 2014)—compared to as low as 12 percent in Nicaraguan dry forests (Otterstrom *et al.* 2006). However, resilience to fire varies across rain forest biomes. For example, rain forests in Australia are remarkably resilient to a single low-intensity fire: though less resilient than savanna species, many rain forest species survive and resprout vigorously after fire, and for some species, fire actually enhances germination (Stocker 1981, Williams 2000, Fensham *et al.* 2003). Mortality, however, greatly increases with repeated fires (Fensham *et al.* 2003).

Across the tropics, the frequency of cyclonic storms ranges from annual in the northwest Pacific (*e.g.*, Taiwan) (Lin *et al.*

2010) to decadal in many parts of the Caribbean (Pielke *et al.* 2003, Boose *et al.* 2004) and multi-decadal in Queensland, Australia (Turton 2008). Life histories of tree species reflect responses to the frequency and intensity of selective pressures from tropical storm regimes (Webb 1958, Zimmerman *et al.* 1994, Curran *et al.* 2008, Lin *et al.* 2010, Uriarte *et al.* 2012b). Generally, forests subjected to frequent, annual tropical storms are low statured and more resilient and resistant to wind damage than forests that experience storm damage on decadal scales. This variation may make Caribbean, South Pacific and Australian forests, for example, more susceptible to storm intensity increases.

Despite evidence that the effects of climate variability on tropical second growth forests vary across biogeographic regions, there is strong geographic bias in where studies are conducted, though biases do reflect regional stressors (Fig. 4). The vast majority of studies on tropical storm impacts have been conducted in the Caribbean (see review in Tanner *et al.* 1991, Fig. 4), with some work in Australia (Turton 2008, SI 1) and far fewer studies in Asia and the Pacific (Burslem *et al.* 2000, Franklin *et al.* 2004, Lin *et al.* 2010), despite the high frequency of cyclones there. Though fire is a global phenomenon, most studies of fire effects on tropical secondary forests are from South America, with several from Southeast Asia. We identified few studies from Africa related to effects of climate variability on second growth forest. There is also a strong bias toward wet forests (Table 3) although there is strong evidence that vegetation in many dryland ecosystems is very sensitive to inter-annual and intra-annual changes in rainfall (Gibbes *et al.* 2014) and interactions with land use (Serneels *et al.* 2007). These biases make prediction of climate impacts on tropical second growth forests difficult given the strong regional variation in these processes, and reducing these biases should be a priority for future research.

Impacts of Local Topography, Geologic Substrate, and Soil Properties.—Precipitation, insolation, drainage, and substrate conditions all

vary with topography (elevation, slope, aspect). These abiotic gradients can underlie variation in forest species composition, structure, and function, and can lead to differences in exposure to climate extremes and disturbance. Landscape position and other geomorphic factors that influence soil moisture and nutrient availability may differentially affect species' responses to climate variability, with cascading effects on community composition. For example, a forest restoration study in a dry forest in northwest Peru found a threshold response of vegetation cover to topographic wetness index, and increased success of tree recruitment when planting was timed with ENSO events (Sitters *et al.* 2012). In an eroded pasture in Mexico, soil depth was found to mediate the differential response of early and late-successional species to drought, with reduced mortality of the smallest seedlings on deeper soils (Martínez-Garza *et al.* 2013).

A large body of literature exists on topographic controls on fire activity in higher latitudes (*e.g.*, Taylor & Skinner 1998, Cary *et al.* 2006, Flatley *et al.* 2011) yet far less is known for tropical forests in general and for second growth forests in particular. However, fire activity is linked to annual precipitation and drought across tropical forests (Van Der Werf *et al.* 2008), and moisture gradients associated with topography likely underlie landscape-scale heterogeneity in fire activity and fire effects. For example, in old growth gallery forests of Belize, wetter sites along rivers and swamps were less likely to burn (Kellman & Meave 1997). In a rain forest in Kalimantan, multiple fires greatly reduced the density of late-successional species, but this effect was weaker in swamps, river valleys and lower slopes relative to drier upland areas (Slik *et al.* 2010), likely due to differences in fire intensity. Second growth forests tend to occur non-randomly with regards to topography and soils; regrowth happens most frequently on lands marginal for agriculture (Asner *et al.* 2009, Aide *et al.* 2013). Where these sites are drier than average, exposure to fire could be particularly high, leading to severe fire effects.

Modeling and observational studies suggest that old growth and second growth forests growing at high elevation or on windward slopes are more exposed to wind damage, and may experience greater mortality from storm events (III Everham & Brokaw 1996, Arriaga 2000, Bellingham & Tanner 2000, Boose *et al.* 2004). The relationship between tree damage and topography is not always clear, however, possibly because species themselves are distributed in a non-random fashion with respect to topography (*e.g.*, Basnet 1992). For example, in Puerto Rico, exposed hillslopes at high elevation are dominated by palm forests, which recover quickly from hurricanes and may be maintained by frequent disturbance (Zimmerman & Covich 2007). Due to effects of terrain on wind dynamics, the relationship between topographic location and wind exposure become less clear at finer spatial resolutions.

The observed associations between topography and tree damage may also be mediated by soil characteristics. Trees growing in shallow soils on ridges or hilltops, on steeper slopes, or on soils with poor drainage have more restricted root growth, and as a result may be more vulnerable to wind-throw and stem break (III Everham & Brokaw 1996, Arriaga 2000, Bellingham &

Tanner 2000). Some species may be particularly adapted to survive these conditions. Basnet (1992) found that *Dacryodes excelsa*, a species growing in shallow soils along ridges in Puerto Rican wet forest, was very resistant to damage, presumably because root grafts among individuals provided structural stability. This species is less abundant or absent from the canopy of early successional forests after land use (Marín-Spiotta *et al.* 2007), which could increase their vulnerability to wind damage with increasing storm intensity. Soil nutrients may also mediate species' ability to recover after a storm, particularly in dry forests where light is not the limiting factor (Lin *et al.* 2003, Van Bloem *et al.* 2006). Soil pH has also been positively associated with posthurricane tree growth in a wet forest in Jamaica (Bellingham & Tanner 2000). Local topography and soil resource availability may have an important effect not only on tropical second growth forest ability to withstand storm damage but also on rates of recovery and succession. To the degree that wind exposure is greater on slopes and at high elevation, increased storm intensity may make secondary forests particularly vulnerable to damage and slow their recovery, as nearly 70 percent of second growth forest regrowth occurs in hilly, upland, and mountainous terrain (Asner *et al.* 2009).

Impacts of Land Use, Fragmentation, and Other Human Activities.—Second growth forests, by definition, exist in areas subject to human influences. Legacies of human activities, along with current land-use and land-management activities, affect forest regeneration processes in these landscapes (Jakovac *et al.* 2015, Martínez-Ramos *et al.* 2016). Specifically, second growth forests are often highly exposed to edge effects, impacts of fragmentation, and anthropogenic disturbances, because regrowth tends to happen along existing forest margins (Asner *et al.* 2009, Sloan *et al.* 2015), and in small fragments surrounded by non-forest land use (Helmer 2000). Forest fragmentation affects microclimates and suitability of microsites for regeneration; these effects are dynamic and may be exacerbated by drought (Asbjornsen *et al.* 2004). A number of studies have demonstrated that high light availability and temperature near edges of fragments reduce tree growth and recruitment, suggesting that warming and drying might exacerbate these effects and reduce persistence of drought-susceptible tree species in fragmented landscapes (Laurance *et al.* 2006).

Fire regimes are closely linked with human activities and landscape context. Land use and the presence of roads, by increasing forests' exposure to anthropogenic fires, can mediate climate variability impacts on fire activity, and subsequent effects on second growth forests. In the Amazon, fires are concentrated along forest edges (Alencar *et al.* 2004) and near roads (Nepstad *et al.* 2001, Cochrane & Barber 2009), and fire occurrence increases with fragmentation (Soares-Filho *et al.* 2012, Armenteras *et al.* 2013). In Southeast Asia, fires are associated with deforestation and human activity (Aiken 2004, Field *et al.* 2009), but there have been few studies examining the effects of fragmentation on fire occurrence. The type of land cover in the matrix surrounding fragmented forests will also affect the degree

to which forests are exposed to fire, because fires are often associated with particular land cover types, such as pasture and fallow (Gutierrez-Velez *et al.* 2014). The concentration of second growth forests in areas with high levels of human impact and the strong links between fire and human activity increase the risk of exposure to fire. Further research is needed to determine the extent to which second growth forests in tropical landscapes are subject to burning and how fire affects tropical forest development (Barlow & Peres 2008).

Invasive species, another important consequence of human activities, can also influence exposure to fire in tropical forests. Grass invasions can initiate a grass-fire cycle, in which flammable, non-native grass species provide a continuous fine fuel layer conducive to fire (D'Antonio & Vitousek 1992). The invasive *Lantana camara* initiates a similar cycle in Australian and Indian forests, where it proliferates under high light conditions and creates a continuous fuel layer in the understory of rain forests (Fensham & Fairfax 1994, Hiremath & Sundaram 2005, Berry *et al.* 2011, Catterall 2016). Invasive species could thus exacerbate impacts of climate change on fire regimes in tropical second growth forests, especially because invasive species are often more abundant in second growth forests.

Landscape heterogeneity in the patterns and legacies of human land use can influence how second growth tropical forest communities respond to tropical storms (Zimmerman *et al.* 1994, Ostertag *et al.* 2005, Uriarte *et al.* 2009, McGroddy *et al.* 2013). Land use increases the regional abundance of second growth forest species, which are often less resistant to storm disturbance than old growth forest species (Thompson *et al.* 2002). By opening up the canopy, storm disturbance may be important in maintaining second growth species in tropical forest stands with a history of human use, thereby providing a positive feedback between human and natural disturbance (Boucher *et al.* 2001, Flynn *et al.* 2010, Comita *et al.* 2010). On the other hand, storm damage may foster establishment of primary forest species already present in the understory, accelerating succession (Lomascolo & Aide 2001). Finally, human-induced landscape fragmentation may influence storm damage. Fragmented forests and trees near edges may be more vulnerable to wind disturbance (Laurence & Curran 2008), although high spatial heterogeneity in wind damage appears to obscure detection of this effect (Catterall *et al.* 2008, Grimbacher *et al.* 2008). Since second growth forests tend to dominate fragmented landscapes, synergies between disturbance and fragmentation may play a key role in the dynamics and persistence of second growth and restored tropical forests.

CONCLUSIONS

The number of studies of climate impacts on second growth and restored tropical forests is increasing, yet our understanding remains rudimentary and regionally biased. Climate models pre-empt increasing warming and drying, more intense cyclonic storms, and altered fire regimes. Our review highlights the following research gaps in our understanding of second growth tropical forests to future climates with implications for FLR.

- The glaring absence of studies on the effects of increasing temperature on second growth forest trees highlights the urgency of developing a coordinated approach to resolve this critical research question. Such approach should combine experimental manipulations, *in situ* physiological measurements, and models that can be benchmarked against longitudinal tree demographic data spanning a range of temperature and precipitation regimes.
- Experimental and observational data illustrate that physiological and growth responses of species to warming, drying, and disturbance vary by successional status, but the implications of this variation for successional dynamics and forest restoration trajectories are not clear.
- Since greenhouse warming is expected to result in simultaneous changes in multiple aspects of climate, a focus on identification of key tradeoffs in species responses to different climate stressors is key for the development of well-parameterized models of forest dynamics.
- Most studies to date have been conducted in Neotropical wet forests, hindering generalization across the diverse tropics. Given the context dependencies of tropical second growth forest responses to climate, our results highlight the need for comparative studies across biogeographic regions and biomes that could lead to generalization and prediction.
- A number of studies suggest that regional variation in species vulnerability to climate stressors reflects exposure to those stressors in the past. However, whether the ability of species to respond to new stressors may exhibit thresholds or biome-specific responses requires further research.
- Globally, the combined effects of human land use and novel climate and disturbance regimes are likely to alter successional trajectories and increase the extent of second growth forests. Identification of thresholds for forest regeneration and resilience will require coordinated, sustained and interdisciplinary research efforts across gradients of disturbance and climate conditions.
- Knowledge on how climate variability and change will influence FLR outcomes should be incorporated into FLR policies (*e.g.*, prioritizing spatial targets for restoration) and programs (*e.g.*, active vs. passive restoration). A number of studies have identified tree species and afforestation practices that can ameliorate effects of climate on plantations and regrowth forests (*e.g.*, adaptation, Stanturf *et al.* 2014). For instance, managers may choose to plant tree species that have been historically absent from a site but can withstand predicted future climate conditions (*e.g.*, species with high resistance to drought stress or fire). Incorporating considerations of the likely effects of climate variability and change on FLR outcomes will lower costs and improve the persistence of FLR outcomes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. List of the papers used in this review.

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