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Key Points:

- Negative effects of all global change factors were found for humid tropical forest biogeochemical processes
- All global change factors except carbon dioxide fertilization are likely to promote warming and/or greenhouse gas emissions
- Effects of drying and deforestation are relatively clear; effects of CO₂ fertilization and N deposition are less certain

Supporting Information:

- Supporting Information S1
- Table S1

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Global change effects on humid tropical forests: Evidence for biogeochemical and biodiversity shifts at an ecosystem scale

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Abstract Government and international agencies have highlighted the need to focus global change research efforts on tropical ecosystems. However, no recent comprehensive review exists synthesizing humid tropical forest responses across global change factors, including warming, decreased precipitation, carbon dioxide fertilization, nitrogen deposition, and land use/land cover changes. This paper assesses research across spatial and temporal scales for the tropics, including modeling, field, and controlled laboratory studies. The review aims to (1) provide a broad understanding of how a suite of global change factors are altering humid tropical forest ecosystem properties and biogeochemical processes; (2) assess spatial variability in responses to global change factors among humid tropical regions; (3) synthesize results from across humid tropical regions to identify emergent trends in ecosystem responses; (4) identify research and management priorities for the humid tropics in the context of global change. Ecosystem responses covered here include plant growth, carbon storage, nutrient cycling, biodiversity, and disturbance regime shifts. The review demonstrates overall negative effects of global change on all ecosystem properties, with the greatest uncertainty and variability in nutrient cycling responses. Generally, all global change factors reviewed, except for carbon dioxide fertilization, demonstrate great potential to trigger positive feedbacks to global warming via greenhouse gas emissions and biogeophysical changes that cause regional warming. This assessment demonstrates that effects of decreased rainfall and deforestation on tropical forests are relatively well understood, whereas the potential effects of warming, carbon dioxide fertilization, nitrogen deposition, and plant species invasions require more cross-site, mechanistic research to predict tropical forest responses at regional and global scales.

1. Introduction

Humid tropical forests are one of the planet's greatest natural resources, serving as a terrestrial warehouse for organic carbon (C), protecting nearby communities from runoff and soil erosion, and providing habitat for a spectacular diversity of living organisms. The potential for anthropogenic climate change to disrupt ecosystem processes has long been recognized [Vitousek, 1994], but the effects of individual and interacting global change factors have not been comprehensively reviewed. The need for such a review is particularly urgent. Human populations and the extraction of resources continue to increase [Lutz et al., 2001; Watson et al., 2001], and a suite of global-scale consequences are rapidly unfolding on ecosystems across the globe.

While climate change is broadly recognized as the most important global change that humans and natural ecosystems face, other factors are also likely to have important effects on all ecosystems, with unique and potentially more accelerated effects on tropical ecosystems. This paper is organized around different aspects of global change that are impacting humid tropical ecosystems. The global change factors are presented in two broad groups that each includes several specific aspects of change. Within (2.1) Changing Cycles we include (2.1.1) Climate Change, (2.1.2) CO₂ Fertilization, and (2.1.3) Nitrogen (N) Deposition. Within (2.2) Land Use/Land Cover Change we include (2.2.1) Deforestation and (2.2.2) Unmanaged Land Cover Change, which explore successional trajectories of lands abandoned postdeforestation. A brief introduction to each of these global change factors is provided at the beginning of each section.

Within each of these five sections, we synthesize how a particular global change factor is currently altering key ecosystem processes and properties. We focus on five ecosystem properties that are crucial for ecosystem function and which will determine whether tropical humid forests of the future will resemble those of the past

and present. The ecosystem properties we review for each global change factor are (i) plant growth, including rates of photosynthesis, plant respiration, growth of individual plants, and ecosystem rates of net primary productivity (NPP); (ii) carbon storage at an ecosystem scale in standing plant biomass and in soils, with attention also to changes in ecosystem-scale C loss (e.g., plant mortality, net ecosystem respiration, and/or soil respiration); (iii) nutrient availability, including discussions of plant nutrition, soil nutrient levels, and nutrient recycling; (iv) plant and animal biodiversity, particularly in relation to ecosystem function; and (v) disturbance regimes, with attention to how each global change factor may alter or create new disturbance regimes in tropical forests. Below, the importance of these five ecosystem processes and properties is described, followed by a comprehensive review of how different global change factors are altering humid tropical ecosystems.

The first and second ecosystem properties, tropical plant growth and ecosystem C storage, are closely intertwined. Plant growth removes CO₂ from the atmosphere via photosynthesis and provides the basis of ecosystem food webs. Plant growth is discussed with reference to changes in photosynthetic uptake of C and changes in plant respiration of CO₂ back to the atmosphere. Much of the available data focuses on responses by individual plants. Where possible, we also review how the different global change factors alter ecosystem-scale rates of NPP. For C storage, we focus on global change effects on standing stocks of plant biomass aboveground and in roots, as well as detrital plant material stored as soil organic matter (SOM). In our discussion of C storage, we review how global change may alter ecosystem-scale C losses (e.g., via plant mortality, net ecosystem respiration, and/or soil respiration). In contrast to plant growth, which focuses on plant physiology and the flux of C into ecosystems, C storage focuses on the net effect to carbon pools.

Carbon storage is particularly important in tropical forests at a global scale. They are among the most C dense ecosystems, storing up to 55% of the planet's total aboveground C, and act as a major C sink worldwide [Pan *et al.*, 2011]. Canopy trees comprise the greatest portion of living biomass [Slik *et al.*, 2013], holding an estimated 247 Pg of C in aboveground and belowground biomass [Saatchi *et al.*, 2011]. Tropical forests also appear to act as an ongoing C sink, taking up more C on an annual basis than is lost via respiration. Using forest inventory data, tropical forests have been estimated to take up 1.2 Pg C/yr during the 1990–2007 period [Pan *et al.*, 2011], although this is an upper estimate, since it assumes that tropical forest cover is consistently comprised of tall, closed canopy forests, which is not the case worldwide [Wright, 2013]. In addition, approximately 30% of global soil C stocks (totaling >2000 Pg-C in the top three meters) is stored in tropical forests as dead organic matter (i.e., plant and microbial tissues that have been incorporated into soils) [Jobbagy and Jackson, 2000], with soils storing more C globally than plants and the atmosphere combined [Post *et al.*, 1982; Tamocai *et al.*, 2009]. Soil C storage is generally a longer-term global C sink than C storage in living aboveground plant biomass because of its slower overall turnover time [Mayer, 1994; Torn *et al.*, 1997; von Lutzow *et al.*, 2006]. After aboveground biomass and soils, roots are the third greatest C pool and account for an estimated 21% of total forest biomass in tropical ecosystems [Cairns *et al.*, 1997]. Thus, biome-scale changes in plant growth and C storage in tropical forests are of broad concern. The ability of tropical ecosystems to continue functioning as C repositories depends greatly on how they will respond to global change.

The third ecosystem function we assess is nutrient availability. Available nutrients for plant and microbial uptake are generally found as simple inorganic compounds in soils. Inorganic nutrients are also termed “mineral” nutrients, meaning that they are not bound in organic C-containing tissues produced by living organisms. Soil and nutrient characteristics of humid and wet tropical forests make them somewhat unique among forested ecosystems and necessitate biome-specific components in ecosystem models. In most high latitude ecosystems on less weathered soils, plant growth is most often limited by N [Churkina *et al.*, 2010; Nadelhoffer *et al.*, 1999; Townsend *et al.*, 1996]. In contrast, the highly weathered status of many tropical soils means that they are relatively poor in the availability of rock-derived nutrients like phosphorus (P) and base cations (e.g., potassium [K⁺]), which have leached out over geological timescales [Vitousek and Sanford, 1986; Walker and Syers, 1976], and are often rich in N, with high N availability and rapid rates of internal N cycling [Chestnut *et al.*, 1999; Hedin *et al.*, 2009; Martinelli *et al.*, 1999; Templer *et al.*, 2008]. Therefore, P and base cations are often the most limiting nutrients to plant growth and decomposition in these tropical forests [Allison and Vitousek, 2005; Cleveland *et al.*, 2006; Harrington *et al.*, 2001]. While soil N is relatively abundant in highly weathered soils, global change effects like CO₂ fertilization and deforestation can reduce soil N levels, changing the relative availability of N versus P. Because N, P, base cations, and other nutrients must be available in a narrow range of relative abundances for biological function (i.e., stoichiometric nutrient ratios)

[Cleveland and Liptzin, 2007; McGroddy *et al.*, 2004; Redfield, 1934], we discuss how global change may alter the availability of each.

Although the majority of rainforests across the Neotropics, Africa, and the Asian-Pacific region grow on the two most highly weathered soil orders, ultisols and oxisols [Holzman, 2008], it should be noted that rainforests also occur across a broad range of soil orders that are less weathered and thus have higher P availability. For example, there are broad geological gradients that create landscape-scale shifts in soil P and N availability across the Amazon [Quesada *et al.*, 2010, 2011] and across the Isthmus of Panama [Turner and Engelbrecht, 2011]. Also, long-distance transport of dust with P-rich minerals has been shown to support plant growth in some tropical forests on highly weathered soils, such as wind inputs of dust to the Amazon from the Sahara and to the Pacific islands from Asia [Chadwick *et al.*, 2009; Koren *et al.*, 2006]. Therefore, while most rainforests tend to have high soil N and low soil P and cation availability, significant variability exists within the biome.

Standing stocks of available mineral nutrients are the easiest to measure and most often reported, but understanding how the broader processes of nutrient recycling are being altered by global change is also important for predicting ongoing and future shifts in ecosystem function. In highly weathered soils, ecosystem recycling of P and cations via litterfall, decomposition, and plant/microbial uptake is particularly important for maintaining soil nutrient availability tropical forest plant productivity [Vincent *et al.*, 2010]. Decomposition of litter biomass has long been recognized as a key process for releasing essential nutrients from plant organic matter and making them available in soils as inorganic (i.e., mineral) nutrients [Tiessen *et al.*, 1994]. The main ecosystem processes responsible for maintaining nutrient availability over annual cycles are (1) plant and microbial uptake of inorganic nutrients, (2) plant and microbial incorporation of nutrients back into organic (i.e., C containing) biological tissues, (3) plant litterfall production (i.e., senescence of leaves, branches, and root tissues) and microbial biomass turnover (i.e., death), which transfer organic-bound nutrients to soils as detrital material, and (4) microbial decomposition, which releases inorganic nutrients from organic compounds and makes them available for uptake again. In addition to these four basic steps in nutrient cycling, other processes like herbivory and abiotic reactions can contribute to nutrient cycling rates and nutrient availability. For example, the cycling of P in acidic and redox fluctuating moist soils is quite complex, with changes in soil chemistry driving P in and out of unavailable mineral precipitates and protected organic P over relatively short time periods [Chacon *et al.*, 2006; Olander and Vitousek, 2005]. Here we review the available literature on the effects of global change on nutrient recycling, in addition to our review of observed changes in the standing stocks of available nutrients with global change.

Fourth, biodiversity of plant, animal, and microbial species is a key ecosystem property in tropical forests, which contain the majority of the Earth's terrestrial biodiversity [Mittermeier *et al.*, 1998]. Comprising only 7% of total landmass, tropical forests are estimated to contain over 50% of the world's terrestrial species [Dirzo and Raven, 2003] and have the highest rates of endemism. Biodiversity is not typically thought of as an ecosystem process in quite the same way as C cycling or nutrient cycling, since biodiversity is usually considered the outcome of many long-term interacting ecological, geological, and biological processes, rather than the driver behind those processes. However, many of the essential ecosystem services provided by tropical forests are underpinned by plant and animal biodiversity. As the biodiversity of an ecosystem declines, so too does the efficiency by which ecological communities capture essential resources, produce biomass, decompose organic material, and recycle nutrients [Cardinale *et al.*, 2012]. The link between biodiversity and biomass, in particular, was recently highlighted in a study across 59 sites in the lowland Neotropics, which found that species richness had an independent, positive effect on aboveground biomass [Poorter *et al.*, 2015]. The direct effect of biodiversity on ecosystem processes depends upon the functional capabilities of the particular species present. Functional redundancy across multiple species is one general ecosystem property that biodiversity generally increases and which improves ecosystem resilience and recovery from disturbances like those presented by global change [Tilman, 1999]. Nonetheless, a recent review also demonstrated that rare species in highly diverse ecosystems often possess distinct combinations of traits that are not replicated by more common species [Mouillot *et al.*, 2013]. Thus, assessing global change effects on biodiversity in humid tropical forests is of paramount importance for maintaining ecosystem properties in the face of global change.

Fifth, disturbance regimes are considered due to their importance in long-term maintenance of ecosystem processes and species diversity. A disturbance regime is a natural recurrence of events that remove biomass

and/or nutrients from an ecosystem. Common natural disturbances in tropical forests vary in scale, ranging from tree falls that kill surrounding vegetation and create large gaps, which then undergo forest succession [Brokaw, 1985], to category 4–5 hurricanes which can remove >50% of foliage in entire rainforests [Walker, 1991]. In tropical forests, in particular, natural disturbance regimes have been credited with maintaining high levels of biodiversity, in part because of the range of successional stages present across landscapes with intermediate levels of disturbance [Connell, 1978]. However, recent data suggest that low levels of disturbance may be less important in rainforests than in other tropical forest types (e.g., dry tropical forests) [Bongers *et al.*, 2009]. Nonetheless, disturbances are important because they affect ecosystem processes on various temporal and spatial scales, and changes to natural disturbance regimes may drive major changes in biogeochemistry and biodiversity of tropical forests. Different global change factors have varying likelihood of drastically altering disturbance regimes, as described within each section.

Below we assess the effect of different global change factors on each of these five ecosystem processes and properties. We include a summary graphic for each global change factor, showing positive, negative, and mixed effects on each ecosystem property, as well as the scientific certainty of each of those effects (Figures 3–9). The scientific certainty is qualitatively assigned (i.e., certain, not certain but likely) by the authors based on the depth and breadth of convincing scientific research demonstrating an effect of a specific global change factor on a specific ecosystem property in tropical forests. To convey the broad significance of these ecosystem changes, we also show feedbacks to climate change in the figures. In general, assigning feedbacks relied on strong scientific support from globally reputable sources (e.g., Intergovernmental Panel on Climate Change (IPCC) reports) that a given ecosystem shift (e.g., reduced C storage and increased greenhouse gas emissions) either exacerbates or mitigates climate change. Feedbacks are assigned for individual global change factors, and we do not attempt to assess the relative magnitudes of all the different feedbacks to climate change, although this review aims to help modelers do just this. For the feedbacks, the negative or positive arrow represents the net effect of the featured global change factor back to itself (or to another global change factor), via changes in a given ecosystem process (e.g., changes in C storage and nutrient availability). For example, if warming decreases tropical ecosystem C storage, this relationship is assigned a negative arrow. This decrease in C storage in turn promotes additional warming because more C is returned to the atmosphere as CO₂, so this relationship is assigned a positive arrow. Thus, the sign of the arrows entering a box give the net effect on that factor. We also provide two summary figures: (1) a compilation of the effects of climate change, CO₂ fertilization, and N deposition on ecosystem properties (Figure 1) and (2) alternative successional pathways following tropical deforestation, including agropastoral management, land abandonment, and subsequent land cover change (Figure 2). Over 600 studies across tropical regions were included in this synthesis (Table 1 and supporting information Table S1), and glossary terms are provided (Table 2).

2. Review of Global Change Effects on Tropical Ecosystems

2.1. Changing Cycles

Climate change, CO₂ fertilization, and deposition of biologically available N to natural ecosystems are considered together as “Changing Cycles” because of their global scale effects and interconnectivity. For example, warming and drying may reduce forest uptake of CO₂ via decreased plant growth. If the rate of C uptake by plants declines, then atmospheric CO₂ concentrations will increase even faster. Atmospheric CO₂ concentrations, in turn, have the potential to increase plant growth via accelerated photosynthetic activity and may represent a negative feedback to climate change by promoting CO₂ removal from the atmosphere. However, the extent to which CO₂ fertilization may occur is intimately linked to the availability of essential soil nutrients like N, P, and base cations. Nitrogen deposition, in turn, has the potential to alter the availability of all of these nutrients in tropical soils via a suite of effects on soil microbial and chemical processes. Thus, N deposition has the potential to increase or suppress the CO₂ fertilization effect on plant growth, even in N-rich tropical forests. Also, N deposition could stimulate or suppress CO₂ losses from soils via effects on microbial activity and heterotrophic respiration. Hence, climate change, CO₂ fertilization, and N deposition are connected through a myriad of linked effects and potential feedbacks.

A novel contribution of this section is a synthesis of how changing climate, CO₂ fertilization, and N deposition are altering tropical forest ecosystem processes (i–v above). We include discussion of interactions and

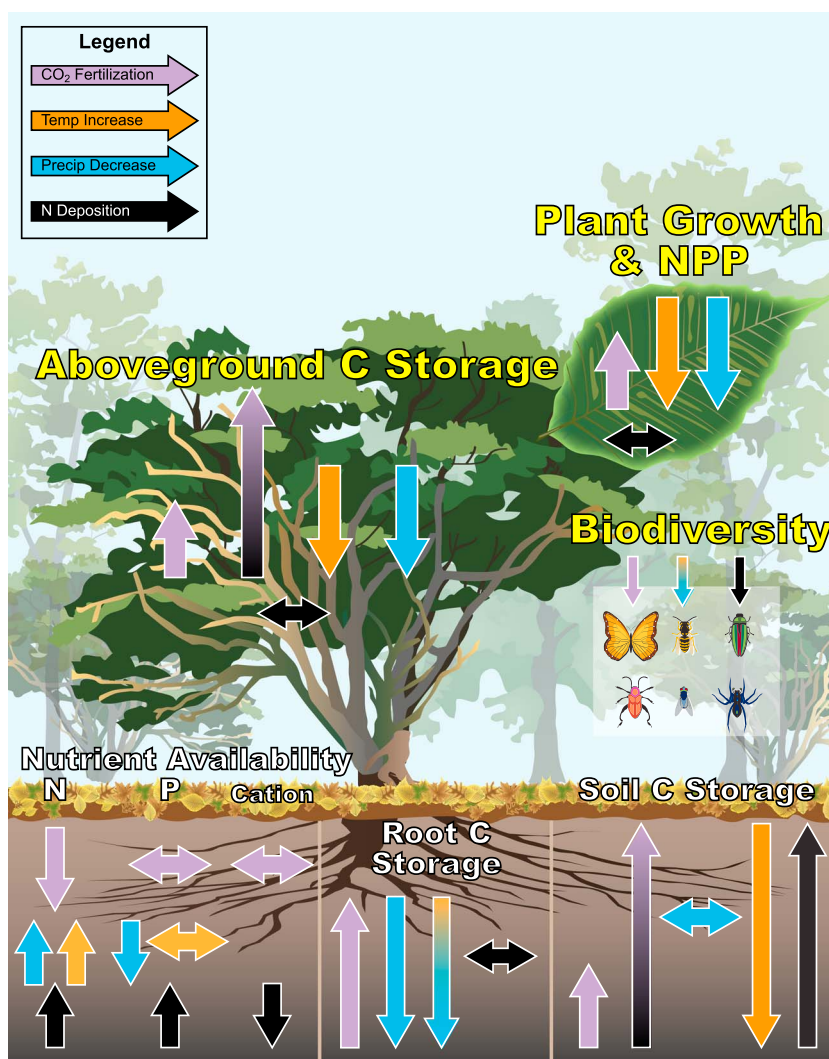


Figure 1. The relative magnitude and direction of the effect of four large-scale global change factors on biogeochemical processes and ecosystem properties are shown. Upward arrows show a positive effect, sideways arrows show inconclusive or conflicting evidence, and downward arrows show negative effects. Arrows of two colors indicate an interacting effect of two or more global change factors on a given ecosystem property. Arrow colors correspond to the different global change factors. Clip art courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

feedbacks among these three global-scale factors wherever possible and summarize the effects of these global change factors on ecosystem processes (Figure 1).

2.1.1. Climate Change in the Humid Tropics

Both temperature and precipitation regimes will shift significantly with climate change in tropical regions in the coming decades. Mean global temperatures are expected to increase by 1°C by 2030 and 2.5–5°C by the end of the 21st century [IPCC, 2013]. Tropical mean annual temperatures (MAT) have followed an increasing trend for the past 130 years, with a modeled rate of increase of 0.1°C per decade between 1900 and 1950 [IPCC, 2013], an observed average increase of 0.26°C per decade since the mid 1970s [Malhi *et al.*, 2009], and MAT in tropical regions reaching peaks of 28°C in the 2000s [Corlett, 2011]. This overall increase in temperature represents an enormous change on a global scale. The warming may have particularly large effects on humid tropical forests, which are adapted to relatively constant year round temperatures and have potentially little capacity to adapt to shifts in temperature compared with temperate ecosystems [Feeley and Silman, 2010].

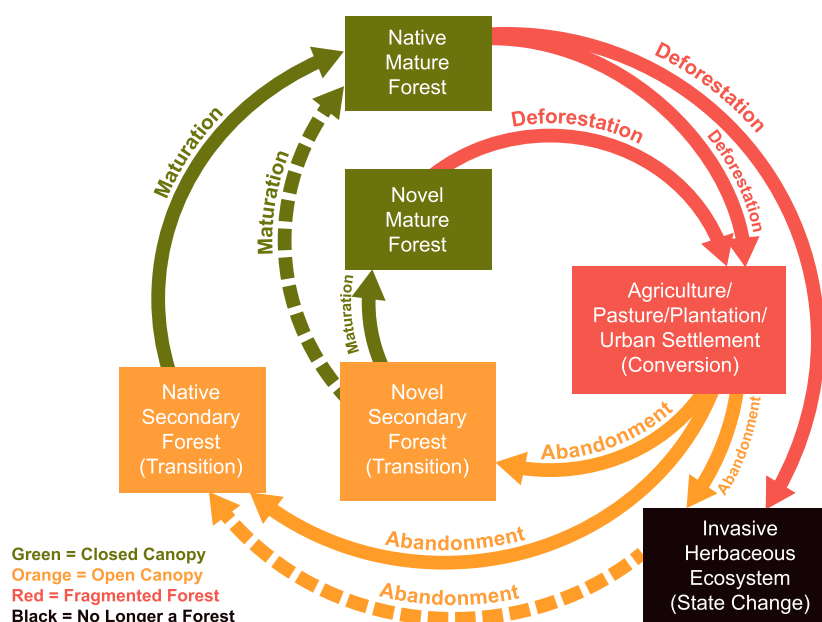


Figure 2. Alternate ecosystem trajectories following deforestation in humid tropical regions are shown. Shifts in ecosystem properties and biogeochemical processes following deforestation are strongly influenced by the subsequent land use and successional pathway. Dashed lines show transitions that may require active management strategies to restore native forest processes. Green boxes indicate mature forests with closed canopies, orange boxes indicate forests in secondary succession with more open canopies, the red box indicates lands that have been converted from forest but which may still have interspersed or fragmented forest cover, and the black box indicates deforested lands that have been invaded by herbaceous vegetation cover.

Extreme temperature events will also likely become more frequent in the coming decades over tropical land-masses [IPCC, 2013]. An analysis of projected changes in extreme weather events from the CORDEX RegCM hyper-Matrix (CREMA) ensemble model predicted that the intensity, frequency, and duration of heat waves will increase in tropical regions [Giorgi et al., 2014]. An increase in tropical heat waves is likely to have significant consequences for ecosystem dynamics, such as rapid heat-induced tree mortality of mature individuals [Allen et al., 2015a]. Despite projected warming for the tropics, which are the most consistently warm ecosystems on Earth, there have been relatively few studies focusing on tropical ecosystem responses to rising temperatures and heat waves.

The global hydrological cycle will be directly affected by rising temperatures, with tropical precipitation expected to become increasingly variable, and more extreme rainfall events expected by the late 21st century. Many humid tropical forests are adapted to high and relatively constant levels of rainfall, with some experiencing a short dry season (<3 months), so these forests are likely to be negatively affected by drying, drought, and changes in seasonality [Gatti et al., 2014]. Simulations using 13 global climate models (GCMs)

Table 1. The Number of Studies Reviewed Here From Different Tropical Regions for Each Global Change Factor Is Shown^a

Global Change Factor	Africa and Madagascar	Asian Tropics	Australia, NZ, and Hawaii	Neotropics	Pantropical	Global	High Latitude Comparisons
Climate change	10	11	1	87	17	27	5
CO ₂ fertilization	2	2	1	25	16	53	30
N deposition	3	28	15	46	2	46	18
Deforestation	3	11	1	38	2	31	0
ULCC invasions	1	3	9	16	3	12	2
ULCC secondary forests	1	4	2	41	10	8	1
Total	20	59	29	253	50	177	56

^aGlobal-scale studies with particular reference to the tropics were included, plus studies from high latitude regions with particular relevance to the discussion on the tropics. In total over 600 studies were reviewed. Details of the studies are provided in Table S1. ULCC = unmanaged land cover change. Studies cited only in section 1 are not included in this table.

Table 2. Glossary Terms Used in the Text Are Defined

Term	Definition
Acclimation	The process in which an individual organism adjusts to a change in the environment, such as warming, to maintain performance (also acclimatization)
Anaerobic	Lacking oxygen
Autotrophic respiration/heterotrophic respiration	The proportion of ecosystem CO ₂ losses attributable to plant metabolism
Bioclimatic niche	Environmental conditions to which plants are best adapted, or can survive in
Biological nitrogen fixation	The conversion by microbes of inert dinitrogen gas (N ₂) to biologically available forms of mineral N
Carbon allocation	The distribution of carbon acquired through photosynthesis to various parts of a plant
Carbon dioxide (CO ₂) fertilization	Enhancement of photosynthetic rates and/or plant growth by CO ₂ enrichment in the atmosphere
Cation availability	Generally refers to the abundance of charged nutrient cations (e.g., Ca ₂ ⁺ , Mg ₂ ⁺ , and K ⁺) in soils for plant and microbial uptake
Deforestation	The complete removal of tree cover from a previously forested area, usually followed by a change in land use
Denitrification	A microbially mediated process by which available soil nitrate is lost from soils as gaseous N oxides or N ₂ gas
Diameter at breast height (DBH)	A standard method of measuring the diameter of the stem of a standing tree. In the US, DBH is measured at a height of 1.37 m
Disturbance regime	A natural recurrence of events that causes a pronounced change in an ecosystem, such as remove biomass and/or nutrients
Dynamic Global Vegetation Model (DGVM)	A computer program that simulates shifts in the potential vegetation and its associated biogeochemical and hydrological cycles as a response to climate change
Endemism	The ecological state of a species being unique to a defined geographic location
Evapotranspiration (ET)	The sum of evaporation and plant transpiration from the Earth surface, accounting for movement of water to the air from soils and canopies
Fine roots	Generally classified as roots < 2 mm in diameter
Forest degradation	The reduction in the capacity of a forest to produce ecosystem services such as carbon storage and wood products, as a result of human activity like selective logging or road construction
Forest succession	The observed process of change in the species composition and structure of a forest over time following a severe disturbance
Functional diversity	The variety of biological processes or characteristics that occur in a particular ecosystem
Herbaceous	Plants that have no persistent woody stem aboveground
Herbivory	The eating of living plants, typically by insects
Heterotrophic respiration	The proportion of ecosystem CO ₂ losses attributable to microbial metabolism
Invasive species	A plant, fungus or animal species that is not native to a specific location, and which has a tendency to spread and displace native species (aka introduced or exotic species)
Leaching	The loss of soil nutrient that drain away in rainwater (e.g., via runoff)
Litterfall productivity	The quantity of plant biomass that falls from trees as senesced tissues (e.g., leaves, and twigs), generally reported as a dry weight per area per year
Mature forest	A forest that has reached an equilibrium in species composition, and in which biomass accumulation (i.e., plant growth) is roughly balanced with biomass loss (i.e., plant decay)
Methanotrophy	The uptake and metabolism of methane by a group of prokaryotes, resulting in reduced methane production from soils
Microbial biomass	A measure of the living proportion of bacteria and fungi in soil organic matter
Mineralization	The decomposition or oxidation of organic compounds into inorganic forms available for plant and microbial uptake
Mycorrhizae	A group of fungi that grow in association with the roots of plants, generally in a symbiotic relationship in which fungi exchange nutrients for carbon (i.e., photosynthate sugars)
Net primary production (NPP)	The amount of carbon taken up and stored by plants, generally reported on an annual basis
Nitrification	A microbially mediated process by which soil ammonium is oxidized to form soil nitrate; both forms of N are available for uptake by plants and microbes, but nitrate is more mobile and easily lost from soils
Nitrogen deposition	Generally the input of biologically available and reactive nitrogen from the atmosphere to the biosphere as gasses, dry deposition, and in precipitation; may also refer to reactive forms of nitrogen transported from fertilized areas via runoff to natural ecosystems
Nitrogen emissions	The production of nitrogen oxides (NO _x) in the atmosphere from inert N ₂ gas as a byproduct of fossil fuel combustion

Table 2. (continued)

Term	Definition
Nitrogen oxides	Any of several oxides of nitrogen, most of which are produced in combustion and are considered atmospheric pollutants, such as nitric oxide, nitrogen dioxide, and nitrous oxide.
Nitrogen saturation	The point at which an ecosystem cannot store any more nitrogen, such that nitrogen losses via leaching and off gassing increase
Novel forest	A forest that includes a mix of native and non-native tree species
Nutrient limitation	An organism is limited when it is not growing as fast as it is theoretically able to. In ecosystems, a nutrient is considered limiting when increasing its availability increases plant or microbial growth; nutrients are often colimiting, such that addition of multiple nutrients increases growth more than addition of a single nutrient.
Priming effect	The stimulation of microbial decomposition of existing soil organic matter by inputs of new, often chemically simple, organic compounds (e.g., root exudates)
Redox	Chemical reduction-oxidation reactions, which occur together.
Resilience	The amount of disturbance that an ecosystem could withstand without changing ecological processes and structures
Secondary forest	A forest in a state of succession that has regrown after a major disturbance
Seed bank	The plant seeds present in soils. After a major disturbance, these seeds germinate and grow rapidly, generally establishing faster than seeds brought to the site via dispersal (wind, animal transport, etc.)
Soil organic matter	The organic component of soil, consisting of plant and animal residues at various stages of decomposition, cells of soil organisms, and substances synthesized by soil organisms
Soil redox dynamics	A sequence of chemical reactions that change the chemical character of many nutrients, and occurs when oxygen becomes depleted
Soil respiration	Losses of C as CO ₂ from soils; when measured in the field this typically includes both microbial and root respiration
Species evenness	The relative abundance of different species within a community
Species richness	The number of species present in a community
Stemflow	Precipitation that gathers in the canopy and runs down tree stems to reach the ground, generally becoming nutrient enriched by this contact with plants
Stoichiometry	The relative quantities of different substances, such as nutrients, present in tissues, typically expressed as ratios (e.g., C:N ratio)
Sunfleck	Brief increases in solar irradiance that occur in forest understories when sunlight directly reaches the ground.
Taxonomic diversity	The number and relative abundance of different species in a community
Thermal optimum	The optimal temperature range for a species' niche, or the optimum range for a biological process
Thermal tolerance	The temperature limits before molecular functions become disturbed
Throughfall	Precipitation that passes through the forest canopy before reaching the ground, generally becoming nutrient enriched by contact with plants
Tropospheric ozone	Ozone (O ₃) that forms in the boundary layer of the Earth surface (typically lower than 12 km); human activities increase its concentrations, and it is a greenhouse gas and a constituent of smog

from the Coupled Model Intercomparison Project 5 (CMIP 5) predicted increased dry season intensity and duration for seasonal tropical regions [Joetzjer *et al.*, 2013]. This prediction reached further consensus in a more recent ensemble of 36 GCMs constrained with historic precipitation data for the Amazon [Boisier *et al.*, 2015]. Together with drying, seasonality indices created using pantropical precipitation data sets showed increased variability in seasonal rainfall across the tropics, with spatial differences among tropical regions [Feng *et al.*, 2013]. In this study, the wet season was projected to get wetter for parts of the Amazon, whereas wet season rainfall was predicted to decline in drier parts of the African tropics. These predictions for the Amazon are supported by recent data showing greater river discharge for the Amazon basin during the rainy season [Gloor *et al.*, 2013]. These recent studies predict greater variability and intensity in tropical precipitation changes relative to older models [Allan and Soden, 2008]. Incorporating the correct mechanisms into models to accurately predict the large changes in tropical precipitation has proven challenging. For example, simulations of eight GCMs underpredicted actual observed increases in dry season length for the southern Amazon from 1979 to 2005 [Fu *et al.*, 2013]. Effects of decreased rainfall on tropical forests

have generally received more attention than effects of warming, but this biome is generally understudied for both aspects of climate change relative to temperate ecosystems.

In summary, tropical rainforests are expected to experience warming and drying, with more extreme heat, drought, and heavy rainfall events in the coming century. These changes in climate are likely to alter every aspect of ecosystem function. The below section reviews the potential effects of climate change on humid tropical forests, assessing lab, field, and modeling studies. The following synthesis strongly suggests that both warming and drying are likely to negatively affect humid tropical forests.

2.1.1.1. Climate Change and Tropical Plant Growth

Climate change may affect plant growth by altering photosynthetic uptake of C, plant respiration, and allocation of C to new leaf, wood, and root growth. The potential effects of climate change on individual plant growth and on ecosystem rates of NPP are reviewed below.

2.1.1.1.1. Climate Change and Tropical Plant Growth: Warming Effects

The most studied potential effect of warming on plant growth for tropical species has been changed in photosynthesis and related physiology. Rising temperatures can reduce photosynthesis by reducing the efficiency of enzyme activity and electron transportation capacity within cells, as well as by influencing evapotranspiration [Lloyd and Farquhar, 2008]. A meta-analysis indicated that the tropics are likely already near optimal temperatures thresholds for plant metabolism [Way and Oren, 2010], and a further increase in temperatures will reduce photosynthetic rates by creating supraoptimal temperatures [Yamori et al., 2014]. Leaf level observations from a montane tropical forest in Indonesia and an aseasonal wet forest in the Congo Basin found that leaf net photosynthetic rates declined during the warmest times of day because of increased photorespiration [Ishida et al., 1999; Koch et al., 1994], suggesting that the hottest part of the day is already supraoptimal for C assimilation. A leaf level warming experiment in a seasonal tropical forest of Brazil over 2 years also found leaf photosynthesis rates decreased when leaves were warmed from 30°C to 35°C due to stomatal closure to conserve water [Doughty, 2011; Doughty and Goulden, 2008]. Similarly, a chamber warming experiment of tropical saplings from an aseasonal wet forest in Guyana found declines in photosynthesis at 5–10°C warming due to increased moisture demands [Pons and Welschen, 2003]. Illustrating the interacting effects of warming and moisture availability, chamber warming experiments of seedlings from a lowland Panamanian tropical forest showed that higher nighttime temperatures led to increased growth if moisture availability was also increased [Cheesman and Winter, 2013; Krause et al., 2013]. These manipulative studies used large increases in air temperature relative to predictions for the coming century. Nonetheless, these data suggest that individual tropical trees will have declines in photosynthetic rates with warming, which may then lead to reduced plant growth (Figure 3).

Even relatively modest increases in air temperature have the potential to greatly increase leaf temperature. Leaf temperature can greatly exceed ambient air temperatures under certain wind, radiation, and moisture conditions. For example, canopy leaf temperatures in a tropical forest in Indonesia were found to exceed ambient air temperature by 7°C [Ishida et al., 1999], which is typical under conditions of low wind and high solar irradiance [Harrison et al., 2010; Krause et al., 2010]. Similarly, leaf temperatures of seedlings in understories of Malaysia increased up to 8°C higher than ambient air temperatures in response to direct radiation from sunflecks [Leakey et al., 2003]. Decreased photosynthesis during periods of high canopy air temperatures can lead to a reduction in evaporative cooling if stomata close, further increasing canopy leaf temperatures, according to a recent review on tropical lowland rainforests [Corlett, 2011]. Thus, if leaf temperatures respond significantly to shifts in air temperature, even modest gains in air temperature may strongly negatively affect photosynthesis.

Large increases in leaf temperature can cause permanent heat damage, irreversibly decreasing photosynthesis. Photosynthesis rates can become unstable after just a few minutes above threshold temperatures, and recovery when temperatures decline again is strongly variable [Huve et al., 2011]. For example, leaf level warming experiments of trees from tropical forests in Brazil found that leaf temperatures, which ranged from 28°C to 37°C during midday, could go up to 45°C with just a 2°C increase in air temperature, resulting in permanent heat damage and sustained declines in photosynthesis [Doughty, 2011; Doughty and Goulden, 2008]. Warming of tropical tree seedlings from Panama cultivated at ambient temperatures showed similar results, with heat stress decreasing plant growth due to irreversible leaf damage when leaf temperature was over 51°C [Krause et al., 2010]. Similarly, a warming experiment on canopy sun leaves collected from mature trees in Panama found that heat damage started at 48°C leaf temperature [Krause et al., 2015]. The possibility of

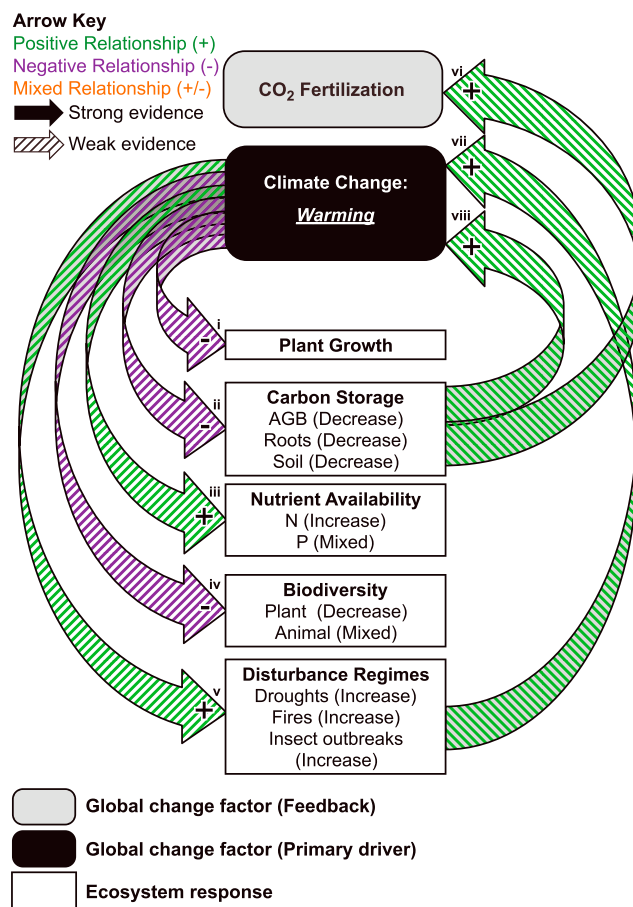


Figure 3. A synthesis of the effects of warming on plant growth, carbon storage, nutrient availability, biodiversity, and disturbance regimes is shown. We include arrows showing feedbacks and effects on other global change factors. For the feedbacks, the negative or positive arrow represents the net effect of the featured global change factor back to itself (or to another global change factor), via changes in the given ecosystem process. Roman numerals refer to citations in Table S1 that support the direction and certainty of each arrow.

ologies in a seasonal tropical forest in the Congo Basin showed a decline in growth rates over the past century for three tree species, which was best explained by increased local temperatures [Battipaglia *et al.*, 2015]. Increased nighttime temperatures in particular appear to suppress tree growth because of elevated CO₂ losses via respiration and moisture losses via transpiration. Plot level inventories of canopy tree growth in a Costa Rican forests showed that increased nighttime minimum temperatures corresponded to decreased stem growth [Clark *et al.*, 2010], with wood production rates decreasing 22% in response to a 1°C increase in minimum nighttime temperatures over 12 years [Clark *et al.*, 2013]. Similarly, a study of 50 ha plots in Panama, Thailand, and Malaysia over 10 years found that tree growth rates were negatively related to nighttime temperatures [Dong *et al.*, 2012]. While these large-scale observational studies are correlative and do not provide direct evidence, they strongly suggest a negative effect of warming on tropical forest plant growth. More long-term large-scale studies monitoring tropical tree growth in relation to temperature anomalies are needed.

Modeling studies also generally predict that increased temperatures will decrease tropical plant growth, with most models using observed changes in photosynthesis in response to warming to predict changes in growth. A leaf level photosynthesis model for the Amazon predicted that photosynthetic rates decrease at leaf temperatures above 30°C, with subsequent declines in plant growth when leaf temperatures reach 38°C to 40°C [Lloyd and Farquhar, 2008]. In this study, declines in growth were mitigated under scenarios

widespread heat damage to rainforest canopy leaves particularly likely if extreme heat anomalies become more frequent in tropical areas, as predicted by the CMIP5 (Coupled Model Intercomparison Project) global climate models [Coudou and Robinson, 2013]. Even with just a 2°C increase in air temperature, which is predicted by many climate models, could thus lead to permanent heat damage and declines in photosynthesis if leaf temperatures rise over 45°C in warm tropical canopies.

Despite these negative effects of warming on photosynthesis, it is possible that plants exposed to slow and steady warming would adapt over time. A meta-analysis across temperate and tropical sites found that leaves that developed at warmer temperatures had elevated capacity for acclimation to heat and reduced nighttime respiration than plants grown at lower temperatures [Slot and Kitajima, 2015]. However, the rate of metabolic acclimation among tropical plant species relative to the current rate of warming is largely unknown.

Linking the above experimental observations of decreased photosynthesis to broader trends, data from larger-scale studies show negative effects of increased temperature on rainforest plant growth. For example, a 75 ha study of tree-ring chron-

of elevated atmospheric CO₂. Similarly, a canopy tree growth model for Thailand over a 30 year period showed a negative effect of increased maximum temperatures on plant growth because of increased respiration [Schippers *et al.*, 2015]. In this study, acclimation only led to <1% improvement in plant growth. In contrast, a global model parameterized with thermal acclimation data for five tree species from Panama showed a 21% greater increase in NPP with acclimation versus without over 100 years [Slot *et al.*, 2014]. The difference in the magnitude of the effects of acclimation on plant growth among modeling studies is likely the result of variation in assumptions about how thermal tolerances affect rainforest tree growth [Corlett, 2011]. Thus, while most models are in agreement that rising temperatures will suppress plant growth in humid tropical forests, more extensive data on tropical plant thermal tolerances and acclimation over the longer term is needed to adequately parameterize these models.

2.1.1.1.2. Climate Change and Tropical Plant Growth: Drying Effects

Projected changes in precipitation for humid tropical forests are likely to alter plant growth, as shown by a number of field experiments that manipulated soil moisture. A 2 year precipitation exclusion experiment in Indonesian forests resulted in a 30% decrease in annual stem diameter growth [Schuldt *et al.*, 2011]. Similarly, a 4 year 40% rainfall reduction experiment in 1 ha plot in lowland Amazonian forests showed a 41% reduction in total plant growth (wood, root, and litter production) [Brando *et al.*, 2008]. In this study, wood production decreased 13% in the first year and 63% thereafter. Rainfall reductions of 50–60% in 1 ha plots in the Amazon also showed strong declines in tree stem growth and wood production at 2, 4, and 7 years [da Costa *et al.*, 2010; Nepstad *et al.*, 2002, 2007]. These Amazon growth declines were linked to reduced photosynthetic capacity with drying for some tree species [Nepstad *et al.*, 2002]. A 12 year soil moisture reduction experiment in 1 ha plots in the eastern Amazon found that plant respiration increased on average by 28% in dried sites, whereas leaf photosynthetic capacity did not change [Rowland *et al.*, 2015a], suggesting that drying may suppress plant growth by affecting respiration and/or photosynthetic potential. These plot-scale drying experiments show that drying is likely to lead to substantial negative effects on tropical forest plant growth on decadal timescales (Figure 4), while longer-term effects on plant mortality and forest species composition require further investigation.

Large-scale observational studies also provide strong support for decreased tropical plant growth with drying. A West African seasonal rainforest study using tree rings showed that the stem growth rates of six tree species were positively correlated to precipitation over a 300 year period, with slower growth during dry periods [Schongart *et al.*, 2006]. Similar results were obtained from a 10 year observational study of a seasonal tropical forest in China, where stem growth rates were positively correlated with soil moisture availability [Tan *et al.*, 2013]. A 10 year study of 165 1 ha plots across Bolivian lowland rainforest also showed that moisture availability was the strongest positive driver of tree growth rates [Toledo *et al.*, 2011]. Belowground, a 2 year observation study on root growth in Brazil showed that fine root growth, length, and surface area were all reduced when soils dried [Metcalfe *et al.*, 2008]. Overall, drying generally appears to reduce woody plant growth in tropical forests (Figure 4), whereas effects on leaf and root growth require more study.

Drought events in particular appear to suppress plant growth. A 7 year study in a Peruvian lowland rainforest found that stem biomass increment decreased 40–55% when rainfall during the dry season was below average [Rowland *et al.*, 2014]. Similarly, remote sensing of solar-induced fluorescence, a measure of total forest C uptake (gross primary productivity), showed a 15% decrease during the 2010 Amazon drought compared to the previous year [Lee *et al.*, 2013]. Comparing drying with warming effects, a study in Costa Rica over 12 years after severe droughts associated with El Niño–Southern Oscillation (ENSO) events showed that tropical rainforest canopy height growth was more sensitive to moisture deficits than to high temperature, particularly on slopes and plateaus [Silva *et al.*, 2013]. Thus, drought events are particularly likely to suppress plant growth in tropical forests (Figure 4).

Model projections generally reflect experimental and observational data that tropical plant growth will decline with reductions in precipitation. A tree diameter growth model for >50 species of tropical trees in French Guiana predicted that stem growth would respond positively to seasonal rainfall and annual soil moisture availability [Wagner *et al.*, 2012]. A model for Amazon forests over a 7 year period found that plant growth rates were driven by annual precipitation more strongly than temperature [Fyllas *et al.*, 2014]. And, five global ensemble models simulating Amazonian forest productivity predicted reduced forest growth in

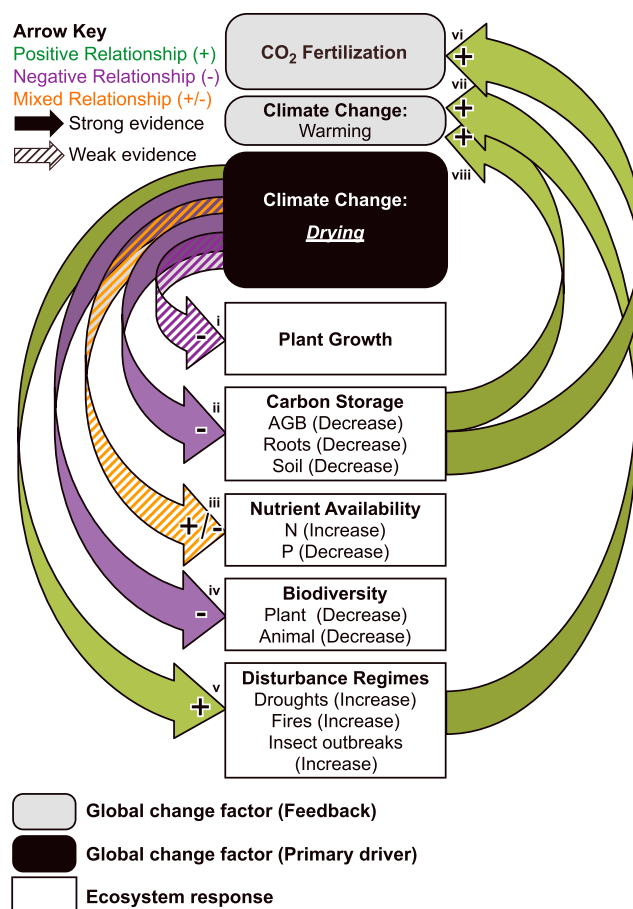


Figure 4. A synthesis of the effects of drying on plant growth, carbon storage, nutrient availability, biodiversity, and disturbance regimes is shown. We include arrows showing feedbacks and effects on other global change factors. For the feedbacks, the negative or positive arrow represents the net effect of the featured global change factor back to itself (or to another global change factor), via changes in the given ecosystem process. Roman numerals refer to citations in Table S1 that support the direction and certainty of each arrow.

drier and warmer climates [Rowland *et al.*, 2015b]. These modeling studies suggest that drying is likely to have stronger negative effect on tropical plant growth than is warming.

It is important to note that most models of tropical plant growth responses to drying are based on observed photosynthetic and respiration responses. However, plant growth in tropical forests is driven largely by growth of plant tissues, particularly wood, which may not reflect changes in photosynthesis [Fatichi *et al.*, 2014]. For example, a 4 year observation study in two 1 ha Bolivian plots found that photosynthesis decreased during a strong drought, but plant NPP remained unchanged, and canopy and fine root growth actually increased during the 6 months following the drought [Doughty *et al.*, 2014]. An analysis of 14 1 ha plots in tropical humid lowlands, humid highlands, and dry lowlands showed a negative effect of dry season on wood growth, but root and leaf growth were sustained during the dry season and total NPP was unchanged [Doughty *et al.*, 2015a]. In this study, nonstructural carbohydrates stored in plants were used for growth when dry periods reduced photosynthetic activity. And, during the 2005 and 2010 Amazonia droughts plant photosynthesis

decreased, but so did plant respiration, such that total NPP remained unchanged in thirteen 1 ha rainforest plots [Doughty *et al.*, 2015b]. These studies highlight the complexity of using only photosynthesis and/or stem growth measures to predict changes in total NPP with drying. A better understanding of root and canopy growth in response to drying is needed for a broader range of tropical sites and plant species.

There is some evidence for long-term adaptation and resilience of tropical plant growth in response to drying. In particular, remote sensing analyses of African rainforest after short-term droughts during a decade showed greater resilience in plant growth rates than had been observed in Amazonian lowland forests during the same period, potentially resulting from longer-term gradual drying trends in the African region [Asefi-Najafabady and Saatchi, 2013]. Within the Amazon, trees that survived droughts subsequently had more resilient growth under repeated cycles of drying in 1 ha plots over >3 year moisture reduction studies, although large trees had high initial mortality rates [Brando *et al.*, 2008; da Costa *et al.*, 2010]. Thus, historic and ongoing trends of drying in the tropics may result in more resilient forests over the longer term, although effects on tree mortality may lead to long-term shifts in species composition and C storage (see below).

In summary, observational, experimental, and modeling studies agree that climate change will lead to declines in tropical plant photosynthesis and woody growth. Increased temperatures may decrease plant growth by both suppressing photosynthesis and increasing respiration. However, the link between warming and changes in woody growth requires further investigation. Plant growth is most clearly negatively affected

by drying, especially drought events. Even with drying though, care must be taken to consider changes in total NPP, not just woody growth. Despite the potential for long-term adaptation and/or acclimation of tropical plants to gradual shifts in climate, plant growth is likely to decrease in response to rapid climate change (Figures 3 and 4).

2.1.1.2. Climate Change and Topical Carbon Storage

Climate change can affect long-term C storage in tropical forests by changing standing stocks of C in plant biomass both aboveground and belowground (i.e., in roots), C stocks in soil organic matter, and/or by altering ecosystem-scale C losses (e.g., via tree mortality and/or soil respiration losses of CO₂). The below section reviews the evidence for how the C sink in tropical forests has and will respond to climate change.

2.1.1.2.1. Climate Change and Tropical Carbon Storage: Plant Biomass

Changes in plant biomass C stocks have been observed particularly in response to drought, which commonly includes warming and drying effects. Thus, because warming and drying are difficult to disentangle when assessing ecosystem-scale plant biomass, consequences of rising temperature and decreased precipitation for C storage are discussed together in this section.

Aboveground C stocks in tree biomass have generally declined with drought. In the Amazon, for example, drought has had a long-term negative effect on C storage. Data from 321 plots in the Amazon basin over 30 years showed a net decrease in aboveground plant C stocks of 0.033 mg C ha⁻¹ yr⁻¹, primarily because of increased tree mortality during the 2005 and 2010 droughts [Brienen *et al.*, 2015]. Similarly, a study across 55 long-term monitoring plots showed that the 2005 Amazon drought decreased aboveground plant biomass because of small decreases in wood growth and large increases in tree mortality [Phillips *et al.*, 2009]. Remote sensing over the Amazon basin between the 2005 and 2010 droughts also showed a persistent negative effect of the drought, with ongoing plant mortality even after precipitation returned to normal [Anderson *et al.*, 2010; Saatchi *et al.*, 2013]. Moderate Resolution Imaging Spectroradiometer (MODIS) remote sensing measurements during the 2005 and 2010 Amazonian droughts showed that drought-affected areas with particularly high temperatures had the largest negative effects on aboveground plant biomass [Toomey *et al.*, 2011]. A global analysis of plot surveys and remote sensing data found that tree mortality has increased since 1970 in both African and Amazonian humid tropical forests, likely because of extreme droughts and heat stress [Allen *et al.*, 2010]. These data suggest that extreme drought events are likely to have strong negative effects on C storage in aboveground plant biomass across tropical forests (Figures 3 and 4), particularly due to plant mortality.

Aboveground forest C storage in tropical forests is also likely to shift if plant life forms change toward structures that hold less woody biomass. For example, liana abundance throughout the Amazon has increased at a rate of 1.5–4.5% per year over the past two decades, likely related to climate change [Phillips *et al.*, 2009]. Lianas store much less C than trees. As lianas spread they outcompete trees by increasing shade in the canopy and can reduce tree growth and increase tree mortality, removing woody tree biomass and reducing aboveground C storage [Duran and Gianoli, 2013; Duran and Sanchez-Azofeifa, 2015]. A 3 year liana removal experiment in a humid lowland Panamanian forest found an overall increase in woody biomass following liana removal, with woody stems going from 29% to 44% of aboveground biomass when lianas were absent [van der Heijden *et al.*, 2015]. A recent model simulation also indicated that rising temperatures and increased dryness favored liana growth, with an overall negative effect on aboveground forest C storage [Duran *et al.*, 2015]. Thus, reductions in tree biomass in favor of other life forms may reduce aboveground C storage in tropical forests with climate change.

Belowground, available research suggests that reduced precipitation in particular is likely to suppress C storage in live root biomass, with little research on warming effects. Fine root biomass in three 1 ha plots was positively correlated with soil water content of the preceding 30 days in Malaysian seasonal forests and reduced root biomass during the dry season [Green *et al.*, 2005], showing relatively rapid effects of changing moisture on fine root C stocks. Similarly, in a 7 year Costa Rican study root biomass responded to monthly and annual shifts in soil moisture, with spatial and temporal variation in responses related to shifts in soil fertility levels [Espeleta and Clark, 2007]. Whereas seasonal forests show rapid declines in root biomass with drying and rapid recovery, wet forests may be less resilient to ongoing drying trends. For example, a survey of root biomass for 62 tropical tree seedlings showed shallower, more lateral rooting structures in wetter versus more seasonal forests [Markestijn and Poorter, 2009], likely making root biomass in wetter forests more vulnerable to drying in surface soils. This will be particularly if tropical rooting depths do not adapt

to changes in moisture, as shown by the lack of an effect of moisture manipulation on rooting depths for seedlings in Panama [Yavitt and Wright, 2001]. Despite the limited number of studies on root responses to climate change, it appears that drying in particular may lead to rapid declines in C storage in tropical root biomass (Figure 4), with decreased belowground C storage most likely to be sustained in wet aseasonal forests if shallow roots die off.

Modeling simulations similarly predict declines in tropical plant biomass with climate change. An integrated vegetation, land use, and C cycle model of pantropical ecosystems found that a temperature increase of 3°C by 2100 would transform 10% of tropical forests into less C-rich ecosystem types, primarily due to increased moisture deficits [Leemans and Eickhout, 2004]. Barring complete losses of tropical forests, vegetation models also predict decreases in aboveground and live-root biomass C stocks across Neotropical lowland rainforests in response to drying over the coming century [Huntingford et al., 2013; Zelazowski et al., 2011]. In three dynamic global vegetation models, temperature was found to be a more important driver than drying of biomass loss in the Amazon, largely because of decreased photosynthesis and increased respiration at high temperatures [Galbraith et al., 2010]. While climate change is broadly expected to reduce C storage in tropical plant biomass, more work must be done to tease apart warming versus drying effects.

In summary, reduced C storage in tropical plant biomass with ongoing drying trends appears very likely. The available data also indicate that combined warming and drying, as during drought, are particularly likely to reduce C storage in tropical plant biomass (Figures 3 and 4). The direct effects of warming on C storage in tropical plant biomass, both aboveground and belowground, require much more research.

2.1.1.2.2. Climate Change and Tropical Carbon Storage: Soil Organic Matter

2.1.1.2.2.1. Climate Change and Tropical Carbon Storage: Warming Effects on Soil Organic Matter

Elevated soil CO₂ fluxes from microbial respiration represent the main way that tropical soil C stocks may decline with climate change. In particular, increased temperature has long been recognized as a driver of increased soil respiration [Raich and Schlesinger, 1992], but the great majority of studies on soil respiration have taken place in temperate or boreal soils [Wood et al., 2012]. Laboratory and field studies indicate that tropical soil C respiration is very likely to increase to some extent with warming, albeit not as much as in cooler biomes. Observational measurements from three 20 × 20 m plots in a southern China tropical montane forest found that soil temperatures accounted for 60% of the annual variability in soil C losses [Zhou et al., 2013]. Another study tested the temperature sensitivity of soil respiration during 1 h incubations for five soils ranging from Alaskan boreal forests to Costa Rican tropical forests and found that soils from colder climates were more sensitive to increases in temperature, although tropical soils also showed increased respiration [German et al., 2012]. Similarly, a soil incubation using Puerto Rican rainforest soils from two tropical forest types showed greater temperature sensitivity for an upper elevation, cooler rainforest versus a lower elevation warmer forest [Cusack et al., 2010]. Thus, increased tropical soil C losses with global warming are likely to be greatest in cooler and more mountainous tropical regions, although losses are also likely for lowland forests.

Interestingly, an analysis of the effects of temperature on C stocks in mature tropical forests with dry seasons under 3 months found greater aboveground C storage in areas with higher mean annual temperature but greater soil C storage in areas with at lower mean annual temperature [Raich et al., 2006]. The differences in aboveground and belowground C storage balanced each other out, such that there was no trend in total ecosystem C storage across the forest sites with temperature. Thus, if soil respiration responds to warming more strongly than plant growth, warming could lead to elevated overall C losses in the tropics (Figure 3).

2.1.1.2.2.2. Climate Change and Tropical Carbon Storage: Drying Effects on Soil Organic Matter

Declines in precipitation appear to negatively affect tropical soil C storage. A number of small-scale field studies have excluded rainfall from reaching soils, thus performing soil drying experiments without effecting trees. A small-scale 3 month rainfall exclusion experiment in Puerto Rico using 1.5 m² plots found that soil respiration increased 35% in response to a 29% reduction in soil moisture, which was attributed to the alleviation of anaerobic conditions at high soil moisture that suppress microbial respiration [Wood et al., 2013]. This study suggests that declines in tropical precipitation may increase soil respiration in very wet soils as they become more aerobic, thus driving down soil C stocks. Another small-scale field experiment in a Costa Rican rainforest used 20 partially covered 2.5 m² plots and found that a 25% reduction in rain inputs led to a 13% increase in soil C loss via respiration, and a 50% reduction in rain inputs led to a 25% increase in soil respiration [Cleveland et al., 2010]. Similarly, a 3 year soil moisture exclusion that reduced rainfall by 50% in five 100 m² plots in a tropical forest in Southwestern China showed soil moisture declined by

4–5.5% during the wet season, and 1–5% during the dry season, with no effect on soil temperature. In this study, soil respiration increased by 30% during the rainy season over 3 years, with no effect during the dry season [Zhang *et al.*, 2015], again suggesting that C stocks in wetter soils are more vulnerable to drying. In a 100% precipitation exclusion experiment in 0.5 m² plots in Costa Rican forests and in lab incubations using a range of soil moistures, soil respiration increased following intense short-term reductions in precipitation [Waring and Hawkes, 2015]. A review of rainfall reduction experiments showed that CO₂ efflux from soils appears to have a threshold response to drying, with large increases in C loss after 50% reductions in extractable soil water [Meir *et al.*, 2015]. In this study, soil respiration responses to soil drying occurred more rapidly (i.e., at higher moisture levels) for clay-rich soils versus clay-poor soils, so the increase in soil respiration achieved by a given level of rainfall reduction will vary across sites depending on soil texture. These small-scale experiments suggest that declines in precipitation in tropical rainforests are highly likely to stimulate soil respiration and C losses (Figure 4), at least in the short term.

Larger-scale drying experiments that include dominant canopy trees do not show clear changes in soil C storage compared with the small-scale studies above. A drying experiment in the eastern Amazon basin, which reduced precipitation to entire forest, stands by 50% in 1 ha for 7 years found no consistent changes in soil respiration rates [Brando *et al.*, 2008]. Similarly, a drying experiment in six 20 m diameter plots around dominant trees in a seasonal Bornean lowland forests found no effect of a 30% decline in soil moisture on soil respiration over 1 year [Ohashi *et al.*, 2015]. This discrepancy with the smaller-scale studies could be the result of soil textures, or the starting level of soil moisture. Overall, the above experiments demonstrate that tropical soil C storage is likely to be sensitive to short-term drying because of CO₂ losses. Large increases in soil respiration and losses of soil C should be expected primarily for very wet, anaerobic, and high-clay tropical soils. Given the amount of C stored in tropical soils, further examination of the relationship between warming, precipitation, and soil C losses should be a high priority for future tropical research.

The heavy focus on drying effects on C storage in tropical forests, rather warming effects, reflects predictions that tropical forests are particularly moisture sensitive. A comparison of 10 global biosphere models run for 100-year simulations found that soil C losses in tropical regions showed greater sensitivity to precipitation than to temperature, opposite of trends in most other biomes where warming drove increased soil respiration [Tian *et al.*, 2015]. In this study, the greatest intermodel uncertainty in soil respiration was also for the tropics, highlighting that we still need a better mechanistic understanding of how tropical soil C stocks are likely to respond to both warming and drying.

2.1.1.3. Climate Change and Tropical Nutrient Availability

Rising temperatures and altered precipitation are certain to affect tropical forest nutrient cycling, including plant nutrition, soil nutrient availability, and nutrient recycling via changes in litterfall chemistry, microbial decomposition rates, nutrient leaching, and soil redox reactions.

2.1.1.3.1. Climate Change and Tropical Nutrients: Plant Nutrition

2.1.1.3.1.1. Climate Change and Tropical Nutrients: Warming Effects on Plant Nutrition

Plant nutrient content appears to be negatively affected by warming. For example, leaf concentrations of N, P, and potassium (K) were lower at relatively warming sites across 62 plots in the Amazon [Fyllas *et al.*, 2009]. Similarly, a 7 year study in Costa Rica found that plant litter N concentrations declined with elevated temperatures over time [Tully and Lawrence, 2010]. These studies show broad-scale negative relationships between temperature and foliar nutrient concentrations, which could reflect shifts in plant nutrient allocation, stoichiometry, nutrient use efficiency, and/or nutrient availability. More research on how warming will alter plant nutrition for mature rainforest trees is needed.

2.1.1.3.1.2. Climate Change and Tropical Nutrients: Drying Effects on Plant Nutrition

The effects of drying on tropical plant nutrition appear to be mixed. A study of nine Costa Rican forests across a rainfall gradient found that foliar N concentrations did not change, even though production of soil nitrate (NO₃[−]) via nitrification was lower at higher rainfall, suggesting changes in soil N availability [Alvarez-Clare and Mack, 2011]. Similarly, foliar N concentrations did not respond to seasonal changes in precipitation across three Costa Rican lowland forests, but foliar P concentrations increased 25% during the dry season [Townsend *et al.*, 2007]. A similar trend of increased foliar P at drier sites was observed across a rainfall gradient of 1800–3500 mm mean annual precipitation (MAP) in Panama [Santiago *et al.*, 2005]. Similar to these studies on green foliage, litterfall N and P show different trends with drying. For example, rainfall was not related to seasonal changes in litterfall N concentrations across 18 plots in a lowland wet forest in Costa Rica, whereas

litterfall P was positively correlated with cumulative rainfall over 2 week periods during a 4 year study [Wood *et al.*, 2005]. Thus, plant foliar and litter N content do not appear sensitive to changes in rainfall in tropical forests. In contrast, P in foliage has shown an increase during the dry season, and P in litterfall has shown an increase in relatively wetter sites. Because of the scarcity of large-scale data on how tropical plant nutrition responds to drying, it is difficult to draw substantive conclusions, making this an area for further research. Nonetheless, from the available data it appears that plant N status is less sensitive than plant P to changes in tropical rainfall.

2.1.1.3.2. Climate Change and Tropical Nutrients: Soil Nutrient Availability

2.1.1.3.2.1. Climate Change and Tropical Nutrients: Warming Effects on Soil Nutrient Availability

Increased temperatures have been shown to generally increase soil N availability, although reports on warming effects on tropical forest soils are rare. One laboratory warming experiment with soils from two Puerto Rican montane tropical forests found that 10°C increases in temperatures significantly increased total dissolved N in soils by >18% after 245 days, which appeared to result from elevated microbial decomposition activity [Cusack *et al.*, 2010]. Soil warming experiments across nontropical regions have also found increases in soil ammonium (NH_4^+) production related to elevated microbial activity. For example, a meta-analysis of experiments in temperate and high-latitude ecosystems found that net NH_4^+ production rates of the upper organic soil horizon increased by 46% with warming across 12 field sites [Rustad *et al.*, 2001]. Given the limited data available for tropical forests, plus the more extensive data from other biomes, it seems likely that warming in tropical forests will increase soil N availability and N cycling rates because of increased microbial decomposer activity (Figure 3).

Effects of warming on soil P availability have been more variable, and data from tropical forests are also generally lacking. In the Puerto Rican soil incubation above, warming suppressed the activity of microbial decomposer enzymes the release available forms of P from organic tissues [Cusack *et al.*, 2010], suggesting that soil P availability likely declined. Results from high-latitude ecosystems give mixed results for the effects of warming on soil P. A 2 year warming experiment in Alaskan spruce forest showed that extractable mineral P concentrations increased in the forest floor due to higher decomposition rates [Van Cleve *et al.*, 1990]. In contrast, a 3 year warming experiment in a boreal forest in central Alaska found that soil extractable mineral P declined with warming, possibly due to lower P mineralization or increased P uptake by roots and microbes [Allison and Treseder, 2008]. The effect of warming on soil P availability in tropical forests is of particular importance, given the scarcity of this nutrient in highly weathered soils, and thus should be a future research priority. Given the generally smaller P pools in tropical forests versus northern sites, we might expect even greater sensitivity of soil P availability to warming, but it is unclear what the overall direction of change will be (Figure 3).

2.1.1.3.2.2. Climate Change and Tropical Nutrients: Drying Effects on Soil Nutrient Availability

Changes in soil moisture have been linked to shifts in soil nutrient availability, with different results for short-term manipulations versus long-term observational trends. For soil N availability, changes in moisture appear to have a small effect. A 10 month rainfall exclusion experiment in Puerto Rico showed no significant effect on soil inorganic N (NO_3^- and NH_4^+) [Bouskill *et al.*, 2013]. Similarly, a small-scale experimental drought in Puerto Rico on 30 1.5 m² plots showed no significant change in NO_3^- , but NH_4^+ increased with drying 65% for wetter valley sites, with no changes on ridges and slopes [Wood and Silver, 2012]. This Puerto Rico study suggests that drying may increase soil NH_4^+ availability on wetter, more anaerobic soils. At a broader scale, a study of seven tropical lowland forests with similar soils in Panama, Colombia, and Costa Rica across a rainfall gradient of 2650–9510 mm MAP found no significant relationship between rainfall and total soil N, although isotopic $\delta^{15}\text{N}$ data suggested greater overall N availability in dryer sites [Posada and Schuur, 2011]. Thus, the little evidence available suggests that drying may increase soil N availability, particularly for very wet sites (Figure 4).

Phosphorus availability appears more sensitive than N to drying in tropical forests. Drying was linked to lower available soil PO_4^{3-} after a 10 month throughfall exclusion experiment in Puerto Rico, which was explained by sorption of P to oxidized iron in drier soils [Bouskill *et al.*, 2013]. Similarly, a small-scale experimental drought in Puerto Rico found a 10% reduction in extractable soil P after 12 weeks, with the greatest reductions in P on slopes and ridges as opposed to wetter valleys [Wood and Silver, 2012]. From these data, it appears that decreased precipitation in wet tropical forests may decrease soil P availability, particularly after some threshold level of drying. In contrast with these experiments, observational data from the 2650–9510 mm MAP gradient in seven tropical lowland forests showed that live root P, total soil P, and leaf litter P were greater in relatively

drier sites [Posada and Schuur, 2011]. These results likely reflect longer-term soil development processes, in which rainfall leaches P from soils over geological timescales [Walker and Syers, 1976]. In the shorter term, the experimental studies suggest that drying may remove soil P from readily plant-available pools, exacerbating conditions of P scarcity (Figure 4).

2.1.1.3.3. Climate Change and Tropical Nutrients: Nutrient Recycling

2.1.1.3.3.1. Climate Change and Tropical Nutrients: Warming Effects on Nutrient Recycling

Positive relationships between temperatures and microbial decomposition rates have been observed across a wide range of field studies. A leaf litter decomposition experiment across five 1 ha plots on a 2500 m elevational gradient in Peru found that leaves from all plant species decomposed faster at higher temperatures [Salinas *et al.*, 2011]. Similarly, a field experiment across five distinct Neotropical forest sites found that sites with greater ambient temperatures had elevated root decomposition rates within soils [Cusack *et al.*, 2009b]. Warmer temperature has also been linked to increased nutrient recycling via insect activity. An observational study of insect herbivory along a tropical temperature gradient in Peru found that soil N and P availability increased in warmer areas because of elevated herbivory and herbivore excretions [Metcalfe *et al.*, 2014]. Thus, warmer temperatures may promote greater activity of organisms responsible for converting organic-bound nutrients into plant-available mineral nutrients, accelerating nutrient cycling rates, and likely linked to the increased soil N availability observed with warming above.

2.1.1.3.3.2. Climate Change and Tropical Nutrients: Drying Effects on Nutrient Recycling

Drying has also been linked to changes in decomposition rates at some tropical sites, but the effect appears to depend on starting moisture conditions. A rainfall exclusion in Costa Rica found that drying reduced decomposition rates across leaf litters of different chemistry [Wieder *et al.*, 2009]. Similarly, seasonal drought in dry and mesic tropical forests has been shown to slow decomposition rates [Goulden *et al.*, 2004]. A study across five lowland Neotropical sites with 508–4100 mm MAP showed a relatively linear increase in decomposition rates of standard leaf tissues with moisture and increased decomposition rates of native leaf litters up to 5500 mm MAP [Cusack *et al.*, 2009b]. In contrast to these studies, a relatively constrained Panamanian rainfall gradient of 1900 to 2700 mm MAP in seasonal forests showed no relationship between rainfall and leaf litter decomposition rates during the wet season [Dale *et al.*, 2015]. At the very wet end of the rainfall spectrum decomposition may be inhibited by low oxygen availability [McGroddy and Silver, 2000], such that drying could actually increase decomposition rates. For example, a Hawaiian study across a montane rainfall gradient of 2000–5000 mm MAP showed a linear decline in decomposition rates with rainfall [Schuur, 2001]. In the Hawaiian montane forest study, high rainfall combined with lower temperatures likely led to greater soil saturation, lower oxygen diffusion and anaerobic conditions, inhibiting decomposer organisms [Bloomfield *et al.*, 1993; McGroddy and Silver, 2000; Schuur, 2001]. Thus, decreased rainfall in very wet and cool tropical sites may increase decomposition rates if soils become more aerobic, whereas decreased rainfall in warmer lowland tropical sites may decrease decomposition rates. These different patterns in decomposition rate could also explain why the availability of soil N (i.e., mineral N released from leaves via decomposition) increased with drying in wetter sites (section 2.1.1.3.2.2).

2.1.1.4. Climate Change and Tropical Biodiversity

Under rapid climate change, tropical communities may be expected to show declines in biodiversity, particularly for species with narrow temperature ranges. However, studies of the fossil record during periods of rapid climate change suggest that there is also the potential for adaptation by some species and even increases in biodiversity for some areas due to range shifts and community turnover [Willis and MacDonald, 2011]. Thus, local effects on biodiversity may differ from regional or biome-scale shifts.

Past extreme changes in climate have led to drastic shifts in the locations and ranges of tropical forest ecosystems. A paleoclimatic study of West African vegetation over the past 25,000 years found that warmer and drier climates corresponded to shifts from rainforest species compositions to semideciduous dry forests, and then to present day grassland, with overall declines in biodiversity [Willis *et al.*, 2013]. Similarly, a modeling study on Amazonian plant distributions predicted that 24% of Amazon forests would become savannas by 2070 with projected temperature and precipitation changes [Anadon *et al.*, 2014]. Current trends in warming and drying seem very likely to force a complete loss of humid tropical forest cover in parts of this ecosystem's current range. In addition to complete loss of rainforests from large land areas, it is likely that biodiversity within tropical forests will change. Below we review the evidence for how biodiversity may respond to warming and drying.

2.1.1.4.1. Climate Change and Tropical Biodiversity: Warming Effects

Despite uncertainty about the overall effects of warming on future tropical biodiversity, research suggests that significant community turnover is likely to occur, and some studies predict greater declines in biodiversity for tropical rainforests relative to other biomes. For example, species distribution models for Madagascar plants found that the largest declines in biodiversity with warming were for humid forests that had particularly high rates of endemism and biodiversity, compared to other ecoregions such as deciduous forest or woodlands [Brown *et al.*, 2015]. A model of African responses to climate change predicted a 25–42% decrease in tropical plant species numbers by 2085 due to loss of suitable habitat [McClean *et al.*, 2005]. Plant biodiversity may be particularly susceptible to climate change because migration into new areas is slow and depends on seed dispersal to favorable climates. Even with eventual range shifts, plant biodiversity may decline since coevolved pollinators and seed dispersers can shift their ranges relatively quickly, moving them away from plants which may rely on them for reproductive success [Olivares *et al.*, 2015].

Because plant species can only shift range on generational time scales, the effects of climate change on biodiversity will largely depend on plants' thermal tolerance levels and capacities for adaptation, which are unknown for most tropical species. A species distribution model using herbarium collections for 3000 Amazonian plant species compared the potential effects of warming, drying, and deforestation on future biodiversity. This study found that the future of Amazonian plant biodiversity depended primarily on the ability of species to tolerate or adapt to warming, which had a greater effect on biodiversity than either drying or deforestation [Feeley *et al.*, 2012]. Similarly, a bioclimatic niche modeling study for South America estimated loss of plant species ranging anywhere from 30 to 50% with a 5°C temperature increase, with the large level of variation reflecting different assigned thermal tolerance niches [Feeley and Silman, 2010]. While adaptation to future warming is unknown for the majority of tropical plants, there are indications from the fossil record that some tropical species will adapt. A comparative phylogeographic model of 12 widespread Amazonian tree species suggested that nine species had lineages dating 2.6–8 million years ago (Ma), indicating that these species withstood the Pliocene (2.6–5 Ma) and/or late Miocene (8–10 Ma) when air temperatures were similar to warming projections for the year 2100 [Dick *et al.*, 2013]. Thus, while it appears that plant biodiversity in tropical forests is likely to decline with future warming, spatial variation and net effects on plant biodiversity are likely to depend on the thermal tolerance levels and adaptation capacities of individual species and communities (Figure 3).

Tropical insect and animal biodiversity also seem likely to respond negatively to warming. A bioclimatic niche model using data collected from 2001 to 2008 along an elevational gradient in Costa Rica suggested that an increase of 3.2°C would correspond to an 80% decline in ant species [Colwell *et al.*, 2008]. Ecological niche models for Puerto Rico indicated that greater climatic variation over time corresponded to reduced frog genetic diversity [Barker *et al.*, 2015], suggesting that current climate change may also reduce from biodiversity. For insect and animal species that are sensitive to temperature variation, the ability to migrate will affect future biodiversity in tropical regions. A statistical modeling study of African mammals predicted anywhere from 10 to 40% reduction in biodiversity by 2080 with warming, depending on how well species could migrate to and colonize new suitable habitat [Thuiller *et al.*, 2006]. Organisms with ranges that already cover greater variation in temperature are likely to better withstand future warming. For example, a global model assessment of tropical insects found that species with ranges that covered greater temperature variation also had greater tolerance to warming [Bonebrake and Deutsch, 2012]. These studies show a great variability in the potential effects of warming on insect and animal biodiversity. While future changes in insect and animal species numbers with warming are difficult to predict, the studies available strongly indicate that the insect and animal community composition in rainforests is almost certain to change with warming (Figure 3).

2.1.1.4.2. Climate Change and Tropical Biodiversity: Drying Effects

A number of observational studies have linked tropical plant biodiversity to rainfall and seasonality, with relatively clear implications for how drying may alter biodiversity. A meta-analysis in Neotropical forests found that biodiversity was positively correlated with annual rainfall until reaching saturation in species numbers at 4000 mm MAP [Gentry, 1988]. An observational study of 62 sites with rainfall ranging from 400 to 9000 mm MAP across the Amazon also found that tree and liana biodiversity was positively correlated with increased annual rainfall, with very little effect of soil fertility [Clinebell *et al.*, 1995]. In this study, tropical forests with little or no seasonality had much greater plant biodiversity overall, suggesting that predicted changes in dry season length and intensity may be of particular concern. Another study in the Amazon

and Guiana Shield also found a positive correlation between biodiversity and precipitation over a range of 1000–4000 mm MAP, which was driven by a particularly steep increase in species numbers at sites with <2000 mm MAP [Ter Steege *et al.*, 2000], suggesting greater vulnerability of biodiversity to drying in drier tropical forests. Along this line, a Panama study of 550 tree species also found that areas with higher levels of rainfall during the dry-season had greater biodiversity [Condit *et al.*, 2013], and a longer dry season was related to lower biodiversity of plants for two Amazon sites [Vieira *et al.*, 2004]. Thus, greater overall rainfall is correlated with greater plant biodiversity across tropical forests, whereas greater seasonality and more severe dry seasons correspond to decreased plant biodiversity, suggesting that drying is likely to result in reduced biodiverse tropical forests in the future (Figure 4).

Repeated or prolonged droughts in particular appear to shift the functional composition of tropical forests, potentially changing overall biodiversity and species composition. Repeated drought shifted forest composition from larger tree species toward smaller, denser-wooded species on a decadal timescale, according to a study of 119 monitoring plots from 10 countries in the Amazon and Borneo [Phillips *et al.*, 2010]. Similarly, two decades of long-term reductions in rainfall in Ghana shifted the plant community composition to more drought tolerant species, although there was no change in species number [Fauset *et al.*, 2012]. Based on these large-scale observational studies, both declines in tropical biodiversity and a change in the overall structure and function of rainforest may be expected in response to drying (Figure 4).

In the geological record, there is also evidence for long-term positive relationships between plant biodiversity and rainfall. African palm species richness from 0.021 to 10 Ma ago was modeled using geographical records, showing historical declines in palm biodiversity during periods with low rainfall [Blach-Overgaard *et al.*, 2013]. Similarly, droughts have significantly decreased biodiversity in the eastern Amazon over the past 250 and 20 thousand years, while biodiversity increased in the western Amazon as precipitation increased, as shown by a study using oxygen isotopes in cave rock formations to reconstruct historic precipitation [Cheng *et al.*, 2013]. These data support the shorter-term observational studies above and indicate a negative effect of drying, drought, and increased dry season severity on tropical plant biodiversity.

Similar to the potential for some species to adapt to warmer temperatures, it is also possible to some tropical tree species will be able to adapt to drying to some extent. With decreased moisture, tree mortality generally occurs because of hydraulic failure or insufficient photosynthesis to support maintenance and growth. Tropical trees can adapt to drying and drought by developing or increasing deciduousness, resistant xylem, high sapwood capacitance, deep roots, and greater regulation of gas exchange [Santiago *et al.*, 2016]. The potential for plant species to adapt to novel precipitation regimes produced by climate change is one of the great uncertainties in projecting future changes in tropical biodiversity.

2.1.1.5. Climate Change and Tropical Disturbance Regimes

Increased drought intensity and duration are probably the main disturbance expected to increase with climate change [IPCC, 2013]. Since droughts generally include more warming and drying, these two aspects of climate change will be considered together in this section. Climate records from the Amazon basin in particular show that climate anomalies in general have become more frequent and intense over the past 40 years, with notable increases in drought [Marengo *et al.*, 2011]. Observational data indicate that drought is becoming more frequent and affecting larger areas, with a 2010 drought in the Amazon affecting 20% more land area than a 2005 Amazon drought [Lewis *et al.*, 2011]. The main disturbance effect of increased droughts on tropical forests is large increases in tree mortality. A pantropical meta-analysis of 113 plots over 4–30 year periods found that strong droughts, such as those observed in Indonesia (1982–1983 and 1997–1998) and the Amazon (2005), significantly increased mortality rates of large trees more than smaller trees [Phillips *et al.*, 2010]. This positive effect of climate change on drought occurrence is likely to create a positive feedback, further exacerbating climate change, because tree mortality will lead to C losses from tropical forests as CO₂ (Figures 3 and 4).

Drought not only increases tree mortality but also promotes fire within tropical forests, intensifying another disturbance regime. Increased dry season length and reduced precipitation have been found to co-occur with greater fire activity and longer fire seasons in Amazonian forests [Fu *et al.*, 2013]. In addition to the direct effects of climate change on fire, increased human activity in tropical forests during dry periods can also promote more fire [Corlett, 2011]. Also, every 1°C increase in temperature is projected to increase lightning activity by 10%, which can ignite and increase tropical forest fires [Price, 2013]. Highly productive forests are particularly vulnerable to wildfire during dry periods because of high fuel loadings, leading to more

intense and severe wildfires [Pausas and Ribeiro, 2013]. Thus, climate change-induced warming, drying, and lightning are all likely to promote more active fire regimes in tropical regions. As with increased tree mortality, increased wildfire activity will release more C from tropical ecosystems as CO₂ and thus create a positive feedback to climate change (Figures 3 and 4).

Savannization, or permanent transition of rainforest areas to savanna cover, is of concern with increased drought and fire in tropical forests. The transition from forest to savanna generally occurs via effects of fire, which are more frequent with drought [Hoffmann *et al.*, 2012; Malhi *et al.*, 2009; Murphy and Bowman, 2012]. A comparison of three Dynamic Global Vegetation Models for tropical and subtropical regions suggested that decreased rainfall will interact with fire to promote the expansion of savannas into areas currently covered by rainforest [Baudena *et al.*, 2015]. Data from 98 plots across a forest-savanna transition in Brazil showed that savannization generally includes major changes in soil nutrients, soil C, and plant traits, such that a natural recovery of forest cover is unlikely [Dantas *et al.*, 2013]. Savannization has also been associated with large C losses from ecosystems, such as in southern Venezuela where conversion from primary forest to savanna with fires led to 98% reductions in aboveground C stocks [Dezzeo and Chacon, 2005], representing a major flux of CO₂ to the atmosphere. Thus, drought and fire in humid tropical forests may mean not only C losses and forest degradation but complete losses of tropical forest cover and reduced C storage.

Finally, insect outbreaks in tropical forests also appear to respond positively to climate change, representing another potential change in tropical forest disturbance regimes. Insect outbreaks are part of the normal disturbance regime in many tropical forests, with moth outbreaks (*Eulepidotis* spp.) recorded in normal rainfall years in seasonal Panamanian forests [Barone, 2000]. However, insect outbreaks in tropical forests are more common after extreme weather events. Outbreaks of at least 12 moth species in seasonal Panamanian forests followed the 1997–1998 ENSO event, with leaf damage levels 250% higher than in normal years [Van Bael *et al.*, 2004]. In this study, a subset of trees suffered the greatest herbivory levels, with leaf damage reaching 100% on some individuals. El Niño–Southern Oscillation events are expected to increase with climate change [Timmermann *et al.*, 1999], so these types of insect outbreaks are likely to increase. Other aspects of climate change can also promote tropical insect outbreaks. For example, moth outbreaks in Puerto Rican montane wet forests were observed following Hurricane Hugo (1989) [Torres, 1992], with hurricane activity projected to increase across the Caribbean because of climate change [Goldenberg *et al.*, 2001]. And, a large moth outbreak occurred in Bornean rainforests after the severe drought of 1998 [Itioka and Yamauti, 2004]. Insect outbreaks can greatly disturb ecosystem function by reducing foliar biomass, with potential negative effects on plant growth and mortality, which could again create feedback to climate change if C is lost from the ecosystems.

In summary, climate change is likely increase a number of related disturbances in tropical forests, including drought, fire, and insect outbreaks, which in turn are all likely to create positive feedbacks to climate change because of C released as CO₂ from tropical forests (Figures 3 and 4).

2.1.2. Carbon Dioxide Fertilization in the Humid Tropics

Atmospheric CO₂ has been steadily increasing since the mideighteenth century following the industrial revolution [Schlesinger, 1993; Taub, 2010], due primarily to the burning of fossil fuels and land cover change (e.g., deforestation) [IPCC, 2013; Oreskes, 2004; Vitousek, 1994]. At present, atmospheric CO₂ concentrations have passed 400 ppm, higher than they have been in millions of years [Scripps, 2015]. Without a binding international agreement on stringent emissions reductions targets, atmospheric CO₂ concentrations are on track to reach 900 ppm by 2100 [van Vuuren and Riahi, 2011]. Even with an immediate and complete elimination of anthropogenic CO₂ emissions, mean temperatures are still projected to rise according to simulations using the UVic Earth System Climate Model [Matthews and Weaver, 2010].

In addition to climate change, increased atmospheric CO₂ concentrations can affect terrestrial systems directly via CO₂ fertilization (see section 2.1.1) [Curtis and Wang, 1998]. Carbon dioxide fertilization refers to the potential for higher CO₂ concentrations to facilitate increased plant photosynthetic activity and growth [Srivastava *et al.*, 2012], which has already affected terrestrial ecosystems globally [Chen *et al.*, 2011a; Sala *et al.*, 2000; Tans *et al.*, 1990]. According to modifications of the Coupled Climate–Carbon Cycle Model Intercomparison Project (C4MIP), increased atmospheric CO₂ concentrations globally promote terrestrial C storage via increased plant growth, leading to a negative feedback on global warming (Figure 5) [Jones *et al.*, 2009]. This study also indicated greater uncertainty in the magnitude of CO₂ effect on plant growth versus the warming effect

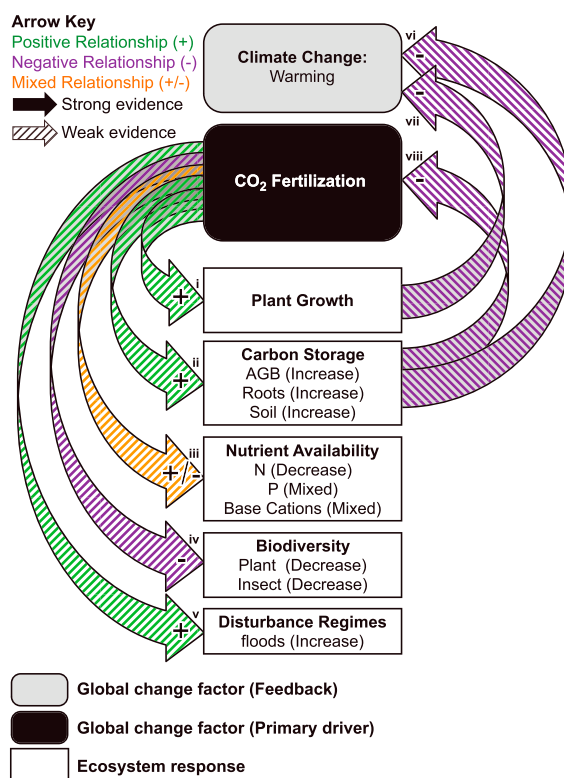


Figure 5. A synthesis of the effects of CO₂ fertilization on plant growth, carbon storage, nutrient availability, biodiversity, and disturbance regimes is shown. We include arrows showing feedbacks and effects on other global change factors. For the feedbacks, the negative or positive arrow represents the net effect of the featured global change factor back to itself (or to another global change factor), via changes in the given ecosystem process. Roman numerals refer to citations in Table S1 that support the direction and certainty of each arrow.

apart these two global change factors. For example, CO₂ fertilization effects may be intensified at higher temperatures, because of accelerated rates of photosynthetic enzyme activities and electron transport with warming, according to a review of several laboratory and field experiments [Mooney *et al.*, 1991]. To disentangle climate effects from CO₂ fertilization effects, a variety of techniques can be used at multiple scales, including (1) single-plant open-top chambers (OTC) that are placed in situ over plants. The chambers supply plants with CO₂, for months to years, which is free to diffuse out of the open top, retaining ambient weather conditions [Drake *et al.*, 1985]; (2) closed growth chamber or greenhouse experiments using potted plants; (3) ecosystem-scale Free-Air CO₂ Enrichment (FACE) experiment, which typically include 10 to 15 towers that circle a forest stand and reach to top of the canopy, supplying CO₂ while allowing for ambient climatic and soil conditions. Currently, the first FACE experiment in the tropics is being planned for an entire forest stand in the Amazon [Lapola and Norby, 2014]. The new experiment builds on a number of prior or ongoing temperate site FACE experiments.

Below, we review the relevant literature across scales from individual-plant fertilizations to regional and global-scale modeling studies, incorporating results from other nontropical sites where information for the humid tropics is not yet available. Based on our review, we make specific recommendations for the new tropical FACE, focusing on the need to assess effects across the range of soil conditions found in humid tropical forests. Overall, our review suggests that the unique nature of N and P availability in highly weathered tropical soils may lead to distinct ecosystem responses compared with temperate sites on less weathered soils.

2.1.2.1. CO₂ Fertilization and Tropical Plant Growth

Carbon dioxide fertilization may affect plant growth by altering photosynthetic uptake of C, plant respiration, and/or allocation of C to new leaf, wood, and root growth. The potential effects of CO₂ fertilization on individual plant growth and on ecosystem rates of NPP are reviewed below.

because the two factors are often grouped in coupled model experiments. More recently, results from the National Center for Atmospheric Research (NCAR) Community Earth System Model (CESM1.0.4) experiment suggest that CO₂ fertilization at a global scale since 1850 has been responsible for a 2.3 Pg C/yr removal of CO₂ from the atmosphere via increased NPP, with N deposition also promoting 2.0 Pg C/yr increase in NPP, such that these two factors appear to be responsible for a net terrestrial C sink in recent decades despite global warming [Devaraju *et al.*, 2015c]. Effects of CO₂ fertilization are of particular concern in humid tropical forests, since these ecosystems dominate land-atmosphere CO₂ exchange [Townsend *et al.*, 2011], yet there is little experimental data assessing how these ecosystems might respond differently to CO₂ fertilization compared with more extensively studied temperate sites. Below we assess relevant experimental and modeling data for CO₂ fertilization effects on tropical forests specifically.

Certainly, CO₂ fertilization is likely to have interacting effects with climate change, making it difficult to tease

Increased atmospheric CO₂ is likely to increase plant photosynthesis because in the current climate photosynthetic processes are not yet C saturated [Long *et al.*, 2004]. Accordingly, a review of observational and modeling studies concluded that increased atmospheric CO₂ concentrations will increase tropical tree photosynthetic rates, with CO₂ fertilization more than compensating for declines in plant growth due to increased temperatures [Lloyd and Farquhar, 2008]. It should be noted that large-scale, long-term CO₂ fertilization studies have focused on crops and temperate forests or grasslands, while data for tropical species responses generally come from smaller-scale open-top chamber (OTC) and growth chamber studies. For example, an OTC experiment with one Neotropical tropical tree species, *Hymenaea courbaril*, resulted in doubling of photosynthetic rates after 98 days at 2 times ambient CO₂ [Aidar *et al.*, 2002]. Similarly, OTCs at 2 times ambient CO₂ significantly increased photosynthetic activity for six Panamanian C3 plants after 3 months, including herb, crop, woody hemiepiphytic species, forest shrub, and canopy tree species [Ziska *et al.*, 1991]. A tropical Brazilian bamboo species, *Aulonemia aristulata*, nearly doubled photosynthetic rates with elevated CO₂ [Grombone-Guaratini *et al.*, 2013]. Certainly, great variation in photosynthetic response to elevated CO₂ has been shown across tropical forest species. Comparing tree species from different forest successional stages, photosynthetic rates increased the most for early successional (i.e., pioneer) species in an OTC experiment at 2 times ambient CO₂ after 6 months in Panama [Lovelock *et al.*, 1998]. Thus, at least in the short term, it appears likely that large increases in CO₂ will promote greater photosynthetic rates for many tropical plant species, although the extent of variation among species is largely unknown.

If CO₂ fertilization alters photosynthetic properties of tropical plants, the overall reflectance (i.e., albedo) of tropical forest canopies may change, create a feedback to climate change. With increased CO₂, plants may not need to invest in as many chlorophyll pigments to support photosynthesis. For example, a growth chamber experiment with three leguminous Southeast Asian tropical trees (*Intsia palembanica*, *Sindora echinocalyx*, and *Adenanthera pavonina*) showed decreased leaf chlorophyll at 2 times ambient CO₂ concentrations, which resulted in a lighter color of the leaves, significantly increasing canopy albedo [Thomas, 2005]. Increased albedo creates a cooling effect, since less solar radiation is absorbed by ecosystem surfaces and transferred into heat [IPCC, 2013]. Thus, changes in leaf photosynthetic properties with elevated CO₂ may provide a negative feedback to mitigate global warming (Figure 5).

In general, plant growth responses to elevated CO₂ are more variable and of smaller magnitude than photosynthetic responses. A global review of 156 plant species found that growth increased by an average of 37% with CO₂ fertilization, which was much smaller than expected from ideal photosynthesis CO₂-response curves [Poorter, 1993]. In this review, there was great variation in the growth responses across plant groups. For example, plants with C3 photosynthesis had greater growth responses than did other photosynthetic pathways, fast-growing species responded more than slow-growing species, plants with N-fixing symbionts responded more than non-N-fixing plants, and herbaceous dicots had larger growth responses to elevated CO₂ than did monocots. In general, because tropical forests have the greatest plant biodiversity on Earth [Richkles, 2004], strong variability in species-level growth responses to CO₂ may be particularly important for this biome.

Nonetheless, the few small-scale studies available suggest that tropical plant growth will respond positively to short-term increases in CO₂ for many species. For example, 2 times ambient CO₂ increased plant height and photosynthetic rates after 4 months for tropical herbaceous *Vernonia herbacea* [Oliveira *et al.*, 2009] and 60 days at 1.5 times ambient CO₂ increased growth for the Paleotropical perennial herbaceous species, *Commelina benghalensis* [Price *et al.*, 2009]. A growth chamber study with six epiphyte species from the Neotropics and southern Asia (*Aechmea fasciata*, *Tillandsia fasciculata*, *Catopsis juncifolia*, *Vriesea Splenriet*, *Bulbophyllum longissimum*, and *Oncidium enderianum*) showed a 5.5% growth increase after 3 months of 1.4 times ambient CO₂ [Monteiro *et al.*, 2009]. Similar to the variation observed in photosynthetic responses to elevated CO₂ across successional stages (above), a growth chamber study with two Costa Rican tree species found greater increases in seedling growth for early versus late successional species at 2 times ambient CO₂ after 3 months [Oberbauer *et al.*, 1985]. In a Panamanian experiment that grew two tree species together, only the fast-growing early successional species (*Ficus insipida*) increased in growth rate at elevated CO₂, whereas a shade-tolerant late successional species (*Virola surinamensis*) actually declined in growth rate because it was shaded by the faster-growing species [Winter *et al.*, 2000]. This suggests that slower-growing mature forest trees may not benefit as much from CO₂ fertilization in diverse stands relative to faster-growing

pioneer species. In contrast, another Panamanian OTC experiment with ten species of tree seedlings from three successional classes found no increases in plant growth for the whole community or for individual species after 6 months at 2 times ambient CO₂, despite increases in photosynthetic rates for some species [Lovelock *et al.*, 1998]. The limited data available thus suggest that at least some tropical herbaceous species and certain groups of trees are likely to increase in growth under elevated CO₂ (Figure 5).

Tropical grasses have also shown positive short-term growth responses to elevated CO₂. Plant height increased by 32% and 49% in two tropical grasses native to Africa, *Panicum maximum* and *Stylosanthes hamata*, under 2 times ambient CO₂ over 3 years, reflecting increased rates of photosynthesis and stomatal conductance [Bhatt *et al.*, 2010]. The tropical Indian Cajanus cajan, a common pigeon pea crop, also had increased photosynthetic rates and a 29% increase in biomass at 1.4 times ambient CO₂ after 120 days [Sreeharsha *et al.*, 2015]. These experiments strongly indicate that on a short-term basis, large increases in ambient CO₂ levels are likely to have a positive effect on tropical grass species photosynthetic rates and growth. More research on the relative competitiveness of tropical tree versus grass growth under elevated CO₂ could provide some insight to the future of herbaceous invasions in tropical regions (see section 2.2.2).

The positive growth response of tropical plants to CO₂ fertilization will likely depend on the availability of soil nutrients to support increased growth. A study of two Panamanian tree seedlings showed that biomass accumulation increased by 52% at 2 times ambient CO₂ in OTCs when soils were also fertilized, with greater biomass accumulating in leaves, resulting in higher leaf area ratios and lower root:shoot ratios [Winter *et al.*, 2001]. Similarly, root biomass of Costa Rican tree seedlings *Cedrela odorata* increased by 23% after 119 days of 2 times ambient CO₂ in growth chambers only at a high nutrient treatment. Soil nutrient availability is thus likely to limit the positive growth response to CO₂ fertilization in tropical forests (see section 2.1.2.3).

At an ecosystem scale, the CO₂ fertilization effect on plant growth has been studied extensively in temperate and northern sites using FACE experiments [Filion *et al.*, 2000; Nowak *et al.*, 2004], but none have been conducted in the tropics to date. Still, results from temperate FACE sites provide some indication of what might happen in the tropics. A review of 12 FACE experiments established between 1989 and 2000 with exposures to 1.4–1.7 times ambient CO₂ showed overall positive effects on plant growth, with an observed average 28% increase in growth across temperate pastures, plantations, desert, forest, and grassland sites, and greater responses in trees versus herbaceous species [Ainsworth and Long, 2005]. Similarly, a review of 16 FACE experiments in bogs, forests, grasslands, and deserts found that woody species had greater CO₂ growth responses than herbaceous species [Nowak *et al.*, 2004]. Temperate FACE data also indicate that there is likely to be a declining effect of CO₂ fertilization over time in natural ecosystems. For example, NPP increased 24% during years 3–5 of 1.5 times ambient CO₂ but was only 9% above background by year 10 at a forest FACE site in Oak Ridge, TN [Norby *et al.*, 2010]. This shift likely reflected diminishing soil N availability over time. In tropical sites, we may expect a similar reduction in the positive growth effect of CO₂ fertilization over time because of declines in soil P or cation availability (see 2.1.2.3 below). These temperate FACE experiments, together with the overall positive effects of CO₂ fertilization on tropical plant photosynthesis and growth in smaller-scale experiments (above), suggest that tropical ecosystem plant growth will respond positively to elevated CO₂, at least for some time period.

In lieu of tropical FACE experiments, there are a number of recent regional- and decadal-scale observational studies assessing tropical forest growth with increased atmospheric CO₂. An inventory of 50 South American long-term plots from 1971 to 2002 showed accelerated tree stem growth rates in tropical sites, which the authors attributed primarily to CO₂ fertilization, increased solar radiation, and warming [Lewis *et al.*, 2004]. Similarly, data from a 10 country network of 79 long-term monitoring plots across African lowland tropics showed increased C storage in trees from 1968 to 2007 of 0.63 Mg C/ha/yr, similar to increases in the Amazon per unit area, which was attributed to CO₂ fertilization [Lewis *et al.*, 2009b]. A review of 72 studies on tropical forest plant physiology, long-term growth, and C fluxes also showed an overall increase in recent decades in tree growth and productivity across the tropics, which the authors tentatively attributed to CO₂ fertilization [Lewis *et al.*, 2009a]. In contrast to these indications of a broad-scale positive effect of CO₂ fertilization, a study comparing seasonal tree growth and with atmospheric CO₂ concentrations in Central Africa since 1850 also found no evidence for CO₂ fertilization effects but did show negative effects of warming on growth [Battipaglia *et al.*, 2015]. Also, a study examining stable C isotope ratios ($\delta^{13}\text{C}$) in wood cellulose of tree rings for three seasonal tropical forests in Bolivia, Cameroon and Thailand found no effect of elevated

CO₂ on growth over the past 150 years but did link CO₂ fertilization to increased water-use efficiency [van der Sleen *et al.*, 2015]. A study in an old growth tropical wet forest of Costa Rica also found no correlation of CO₂ concentrations and tree growth from 1983 to 2006, despite significant changes in tree growth over the period [Clark *et al.*, 2010]. Thus, broad-scale observational studies do not agree on whether there has already been a positive CO₂ fertilization effect on tropical plant growth at large scales. The variation among these studies is likely due to the many different factors affecting plant growth at large scales and over longer time periods, such as interacting global change factors and local natural disturbances. The direct effect of CO₂ fertilization on tropical forest plant growth will most easily be disentangled with ecosystem-scale FACE experiments in a variety of humid tropical forests, such as the new one planned for the Amazon [Lapola and Norby, 2014].

Modeling studies have generally predicted increases in global NPP with CO₂ fertilization, with increased plant growth in the tropics a substantial component of the global response. The Dynamic Land Ecosystem Model (DLEM) predicts that CO₂ fertilization will result in a 14% increase in global NPP, with a plateau occurring near the end of the 21st century due to CO₂ saturation of plant growth and nutrient limitation [Pan *et al.*, 2014]. This study predicted substantial increases in NPP in the tropics but even larger effects in tundra and boreal forests. In tropical Africa specifically, this model suggested that increased NPP was due to a combination of elevated CO₂, warmer and wetter conditions, and N deposition from 1980 to 2009 [Pan *et al.*, 2015a]. Thus, regional responses of NPP to CO₂ fertilization are likely to depend on the simultaneous influence of other global change factors.

In summary, it seems likely that CO₂ fertilization will have a generally positive effect on tropical plant growth at least in the short term (Figure 5), as has been broadly observed in other ecosystems. Long-term growth responses, however, are likely to depend on local ecosystem conditions like soil nutrient availability and interacting effects with other global change factors like warming.

2.1.2.2. CO₂ Fertilization and Tropical Carbon Storage

Carbon dioxide fertilization may affect long-term C storage in tropical forests by altering the amount of C held in plant biomass both aboveground and belowground (i.e., in roots), changing tree mortality, and/or via changes in net ecosystem respiration, decomposition, and soil respiration losses of CO₂. The below section reviews the evidence for how the C sink in tropical forests may respond to CO₂ fertilization.

If C storage does increase in tropical forests with CO₂ fertilization, this could create a significant negative feedback to climate change and to CO₂ fertilization. Increased C storage would effectively remove CO₂ from the atmosphere [IPCC, 2013]. This could both mitigate the negative effects of climate change but may also slow the CO₂ fertilization effect itself (Figure 5).

2.1.2.2.1. CO₂ Fertilization and Tropical Carbon Storage: Plant Biomass

Very little experimental data exist for changes in tropical forest aboveground C storage with CO₂ fertilization. Carbon dioxide fertilization of an enclosed artificial rainforest in Biosphere 2 showed that exposing the plant community to varying levels of CO₂ up to 3 times ambient significantly increased net canopy C uptake without changing soil respiration, suggesting a net accumulation of C over short time periods (2–7 weeks) [Lin *et al.*, 1998]. In this study, net C uptake increased nonlinearly in response to incremental increases in ambient CO₂ concentrations, with large initial increases eventually plateauing around 800 ppm CO₂. While this study suggests a community-wide short-term increase in plant C storage with CO₂ fertilization, much more research is required to determine longer-term effects on natural tropical forests.

Belowground, there is indication from temperate FACE studies that elevated CO₂ may increase C storage in tropical live root biomass. A meta-analysis of 104 FACE, OTC, and growth chamber studies in temperate forest, grassland, and tundra species showed that elevated CO₂ had a larger effect on root growth and biomass than aboveground effects, with overall increases in root:shoot ratios and the largest increases in plant C storage belowground [Luo *et al.*, 2006]. For example, live fine root biomass increased 86% at a loblolly pine *Pinus taeda* FACE experiment after two years of 1.5 times ambient CO₂ [Matamala and Schlesinger, 2000], and fine root production doubled after 6 years of 2 times ambient CO₂ at the same site [Norby *et al.*, 2004]. Because tropical rainforests contain some of the largest pools of fine root biomass among ecosystems [Jackson *et al.*, 1997], a similar effect of CO₂ fertilization in these ecosystems would represent a substantial increase in belowground C storage globally.

In the absence of on-the-ground experimental data, regional and global models have generally predicted positive effects of CO₂ fertilization on C storage in tropical forests. Results from 12 atmospheric inverse and transport models suggested that tropical ecosystems have dominated the net terrestrial C sink over the past decades, potentially related to CO₂ fertilization and increased C storage [Stephens *et al.*, 2007]. A recent integration of terrestrial C models in the Trends in Net Land Atmosphere Carbon Exchanges (TRENDY) concluded that for 1990–2007, 60% of the terrestrial C sink was explained by increasing atmospheric CO₂ concentrations, with this effect dominated by elevated C storage in the tropics in particular [Schimel *et al.*, 2015]. Another recent analysis using seven global vegetation models (HYBRID4, JeDi, JULES, LPJmL, Organizing Carbon and Hydrology in Dynamic Ecosystems (ORCHIDEE), SDGVM, and VISIT) predicted that the CO₂ fertilization effect will increase terrestrial vegetation C stocks by 52–477 Pg C by the year 2100, with increases especially large in Southeast Asian, tropical Africa, and boreal regions [Friend *et al.*, 2014].

While the above results suggest substantial increases in C storage in tropical forests with CO₂ fertilization, global-scale models may not be parameterized to accurately predict tropical forest responses to CO₂ fertilization. Notably, a recent review of process-based models suggested that the production of wood with CO₂ fertilization, and thus C storage in plants, is generally overestimated in tropical ecosystems when compared to observational and experimental data [Hickler *et al.*, 2015]. This overestimation for the tropics occurs because nutrient dynamics in models like the Lund-Potsdam-Jena Dynamic Global Vegetation Model with General Ecosystem Simulator (LPJ-GUESS DVM) are parameterized using temperate forest FACE results, where nutrient availability and limitation to plant growth poorly represent tropical forest dynamics [Hickler *et al.*, 2008]. A smaller-scale individual-tree-based model for the Central Amazon was parameterized using experimentally measured 25% increases in tree growth over 40 years and predicted a modest C sequestration rate for these forests (0.05–0.2 Mg C/ha/yr) [Chambers and Silver, 2004]. The relatively small increases in C storage in this study were attributed to slow growth rates in mature tropical forests. The authors concluded that regional changes in disturbance and rainfall are more likely than CO₂ fertilization to cause large changes in tropical C storage. These two studies indicate that the positive effect of CO₂ fertilization on tropical forest C storage in plants is likely smaller than currently suggested by most global models.

In summary, the scarce experimental and modeling data available suggest that CO₂ fertilization may increase C storage in plant biomass in the tropics somewhat (Figure 5), but much more experimental research and biome-appropriate model parameterization are needed.

2.1.2.2.2. CO₂ Fertilization and Tropical Carbon Storage: Soil Organic Matter

There is virtually no data on how soil C storage may respond to CO₂ fertilization in tropical ecosystems, but temperate experiments may provide some insight. Changes in soil C storage, which result from the balance between increased inputs of organic matter to soils versus increased soil respiration, have been variable across sites. A meta-analysis of 53 CO₂ fertilization experiments in high-latitude forests showed that transfer of plant detritus to soils increased by 23%, but soil respiration rates also increased, such that soil C stocks only gained +3.3% [van Groenigen *et al.*, 2014]. This small overall increase reflects substantial variability among sites. An Italian FACE experiment at 1.5 times ambient CO₂ concentrations in a Poplar forest showed increased soil C stocks related to elevated litterfall and root exudation after 5 years [Hoosbeek *et al.*, 2006]. Also, 9 years of 1.5 times ambient CO₂ at a FACE experiment in Oak Ridge, TN, resulted in a doubling of fine root turnover (i.e., mortality and regrowth) [Iversen *et al.*, 2008, 2012], which was linked to increased soil C storage in the top 5 cm of soil [Jastrow *et al.*, 2005]. However, increased litterfall and root inputs to soils have not led to increased soil C storage across sites. For example, C inputs to soils from fine root turnover increased 68% after 2 years of 1.5 times ambient CO₂ at a loblolly pine FACE experiment at the Duke forest, but this did not result in increased soil C storage [Matamala and Schlesinger, 2000], likely because of increased decomposition and/or microbial priming [Hoosbeek *et al.*, 2004]. Thus, increased plant growth, root turnover, and litterfall with CO₂ fertilization may not lead to proportionally large increases in long-term soil C stocks in tropical ecosystems and will depend on both plant growth responses and microbial decomposer responses. Nonetheless, given the limited evidence for increased plant growth with CO₂ fertilization, it is certainly possible that some new organic C will be transferred to long-term soil C stocks in tropical forests (Figure 5).

2.1.2.3. CO₂ Fertilization and Tropical Nutrient Availability

Elevated CO₂ concentrations may affect soil nutrient availability through a suite of biotic and abiotic mechanisms, including changes in plant nutrient uptake, litter chemistry, decomposition rates, and via

changes in soil biogeochemical properties like soil pH which can alter weathering processes and release of nutrients from minerals.

2.1.2.3.1. CO₂ Fertilization and Tropical Nutrients: Plant Nutrition

With CO₂ fertilization, increased C assimilation is likely to increase demand for nutrients by plants and at the same time dilute nutrients in leaves and drive up foliar C:nutrient ratios. For example, an OTC experiment in Panama using 10 species of tree seedlings from three successional classes measured decreased foliar N for all species, with the greatest increases in leaf C:N for late successional species at 2 times ambient CO₂ after 6 months [Lovelock *et al.*, 1998]. Similarly, two Panamanian tree seedlings, *Ficus insipida* and *Virola surinamensis*, had elevated foliar C:N at 2 times ambient CO₂ in OTCs in native soils, but when soil nutrients were applied with CO₂ fertilization, growth increased while foliar C:N remained unchanged over 30 weeks [Winter *et al.*, 2000, 2001], suggesting increased uptake of N. These two studies suggest that additional C can be assimilated from CO₂ without additional nutrients, but additional nutrients will be utilized if available.

Examples from temperate CO₂ fertilization studies provide some insight to how plant uptake of other nutrients may change. For example, white oak trees seedlings had increased growth in 2 times ambient CO₂ with commensurate increased uptake of P and K but no change in uptake of N, sulfur (S), or boron (B) [Norby *et al.*, 1986]. Similar results were obtained for birch trees grown at 1.7 times ambient CO₂, with decreased leaf litter N concentrations, increased C concentrations, but no change in P concentrations [Cotrufo and Ineson, 1996]. The steady uptake of P with CO₂ fertilization in these temperate studies may just reflect the greater relative abundance of P and K versus N in these younger soils, or these could be indicative of less flexibility in P requirements relative to N requirements at elevated CO₂. The second scenario would severely limit the capacity of tropical plants to increase growth with CO₂ fertilization on P-poor soils.

Over the long term, it is possible that plants in elevated ambient CO₂ could increase nutrient uptake via belowground changes in root and microbial growth and activity. For example, simulation of hundreds of years at 2 times ambient CO₂ with a Multi-Element Limitation (MEL) model predicted enhanced nutrient uptake due to larger root systems could eventually diminish initial nutrient limitations to growth [Rastetter *et al.*, 1997]. Indeed, across three temperate forest FACE sites elevated CO₂ increased N uptake due to increased fine root growth, increased allocation of C to mycorrhizal fungi, and increased decomposition rates of soil organic matter [Finzi *et al.*, 2007]. At the Duke loblolly pine FACE experiment, root exudates, which may be a nutrient acquisition strategy, had positive effects on microbial decomposition and release of N after 11 years at 1.5 times ambient CO₂ [Phillips *et al.*, 2011]. Whether tropical forests would be able to similarly overcome P or cation limitation at elevated CO₂ by expanding root systems, increasing associations with mycorrhizal fungi, or promoting faster decomposition via root exudates is unknown. Certainly, increased exploitation of soil nutrients would drive down the pool sizes of available nutrients in soils, tying up more nutrients in plant tissues (Figure 5).

2.1.2.3.2. CO₂ Fertilization and Tropical Nutrients: Soil Nutrient Availability

As plant growth increases with CO₂ fertilization, plants require greater quantities of soil nutrients to maintain growth. This increased nutrient uptake can in turn lead to reductions in soil nutrient availability, such that soil nutrients may eventually limit the responsiveness of plant growth to elevated CO₂. Across many temperate forests FACE experiments, N has been identified as the main nutrient that limits plant growth, and which eventually limits plant responsiveness to elevated CO₂, which has been termed “progressive N limitation” [Luo *et al.*, 2004]. Because of the progressive increase in nutrient limitation, plant growth often increases during initial stages CO₂ fertilization (<6 years across temperate FACE sites), with some increases in N use efficiency, but then accelerated growth plateaus [Johnson, 2006]. Among 16 temperate FACE experiments, growth responses varied in parallel with site-level differences in nutrient availability, with greater growth on more fertile soils [Nowak *et al.*, 2004]. A synthesis of 19 CO₂ fertilization experiments in temperate sites showed that the production of plant-available NH₄⁺ via mineralization of organic matter increased only at particularly N-poor soils [Rütting and Andresen, 2015]. Because tropical forests on highly weathered soils are generally N-rich compared to temperate sites like those above [Post *et al.*, 1985], these data suggest that NH₄⁺ levels may not be affected by elevated CO₂ at these sites. Since tropical forests on highly weathered soils are typically rich in N relative to temperate sites but poor in P and base cations [Vitousek and Sanford, 1986; Walker and Syers, 1976], progressive nutrient limitation is more likely to occur with P. Thus, CO₂ fertilization is likely to decrease soil P and base cations, although soil N may also decrease in the long term.

Nonetheless, other biogeochemical processes may also increase the transfer of soil P from unavailable pools into plant available pools. In general, total mineral P in tropical soils is greater than plant-available orthophosphate (PO_4^{3-}), with much of the unavailable P occluded in Fe and Al oxides or Ca compounds. The release of this recalcitrant P into plant available pools has been observed with decadal-scale changes in soil biogeochemistry [Richter *et al.*, 2006] and with fungal activity [Barroso and Nahas, 2005]. In particular, root-associated mycorrhizal fungi can mobilize occluded P from soil minerals or organic matter [Smith *et al.*, 2011]. Thus, if CO_2 fertilization promotes the release of P from unavailable pools, there may be some increases in soil P availability even as plant uptake of P also increases, resulting in a mixed effect on P availability (Figure 5).

Indeed, CO_2 fertilization has been shown affect soil biogeochemistry and microbial activity in ways that promote release of unavailable P. First, increased atmospheric CO_2 drives dissolution of CO_2 into soil water, producing weak carbonic acids that can promote weathering and release of P and cations from minerals [Berner, 1992]. For example, an experiment from the temperate Duke FACE site leached soil columns with carbonic acid, resulting in increased acidity of the naturally acidic and highly weathered ultisols [Oh and Richter, 2004]. At the Duke FACE site, 1.5 times ambient CO_2 led to increases in dissolved CO_2 concentrations in soils, increased soil acidity, and up to 271% increase in base cations after 3 years, presumably because of increased rock weathering [Andrews and Schlesinger, 2001; Oh *et al.*, 2007], with the effect falling slightly to 175% increase in cations by year 12 at this site [Jackson *et al.*, 2009]. Results from the highly weathered soils at the Duke FACE site may be particularly applicable to predicting how tropical soil P will respond to elevated CO_2 , because most tropical soils are also highly acidic, weathered, and poorly buffered [Sanchez, 1976]. Other temperate FACE sites have also shown increases in soil carbonic acids [Karberg *et al.*, 2005]. In line with these studies, a southern China CO_2 fertilization combined with N addition resulted in decreased pools of recalcitrant organic and occluded inorganic forms of P and overall greater P availability in soils [Huang *et al.*, 2014]. Still, it is unclear how much weathering of primary and secondary minerals may occur with CO_2 fertilization in tropical sites, even with increased acidity (Figure 5).

Limited evidence exists from temperate FACE sites that mycorrhizal fungal activity can change with CO_2 fertilization, with potential effects of P uptake by plants. For example, temperate sites in Missouri had increased mycorrhizal colonization of roots, which was related to the release of P into available pools and increased P uptake at elevated CO_2 [Norby *et al.*, 1986], whereas CO_2 enrichment combined with N fertilization reduced mycorrhizal colonization of plant roots with declines in soil P availability at an Italian Poplar FACE site [Lagomarsino *et al.*, 2008]. This would be particularly relevant to tropical forests and merits further investigation. How mycorrhizal fungi and related P availability will respond in tropical sites is still an open question. If P limitation can be overcome by increased root and mycorrhizal growth, more rapid and efficient cycling, and release of P occluded in precipitates, then it is possible that over long periods of elevated CO_2 nutrient limitation effects on tropical trees will be minimal, with other factors like light and space playing a more important role in limiting plant growth.

2.1.2.3.3. CO_2 Fertilization and Tropical Nutrients: Nutrient Recycling

Decomposition is the main way that nutrients bound in organic plant litterfall and roots are returned to soil mineral nutrient pools, so effects of CO_2 fertilization on decomposition rates and litter chemistry can directly lead to changes in soil nutrient availability. Rates of decomposition under elevated CO_2 may decline if plant litter chemistry becomes more C rich and nutrient poor, with a greater concentration of antiherbivore compounds (i.e., phenols and tannins) which may also impede decomposition. For example, an OTC experiment in Brazil using guava plants (*Psidium guajava*) at 2 times ambient CO_2 showed that foliar production of antiherbivore compounds increased significantly [de Rezende *et al.*, 2015]. Changes in antiherbivore compound concentrations in litterfall may in turn affect decomposition. However, a positive effect of herbivory on foliar defense compound production was observed for 17 Amazonian tree species exposed to varying levels of herbivory, but this increase in defense compounds did not subsequently alter decomposition rates [Cardenas *et al.*, 2015]. In model tropical plant communities that were housed in greenhouses, there was no significant change in leaf tissue chemistry of species exposed to 1.8 times ambient CO_2 concentrations for 1.5 years [Arnone *et al.*, 1995]. In a lowland seasonal Panamanian forest, 1.5 times ambient CO_2 also had no effect on decomposition rate for litter from two tropical tree species, a pioneer species (*Cecropia peltata*) and a fig tree (*Ficus benjamina*) [Hirschel *et al.*, 1997]. This handful of tropical studies suggests that CO_2 effects on decomposition rates via changes in litterfall chemistry may not be large.

These tropical results are in contrast with temperate and high latitude studies that have showed large changes in litterfall chemistry and decomposition rates. A review of temperate and high latitude ecosystems showed that CO₂ fertilization resulted in increased secondary C compounds and reduced N in plant litterfall and that these changes in chemistry were related to decreased decomposition rates across studies [Mcguire *et al.*, 1995]. Similarly, a meta-analysis of CO₂ enrichment studies across high-latitude ecosystem types found a 7% decline in N concentration of leaf litter with CO₂ fertilization [Norby *et al.*, 2001]. Reduced litter N concentrations and elevated C:N can negatively affect decomposition and soil N availability, because immobilization of inorganic N in litter occurs when tissue C:N ratios are much higher than the C:N ratios required by microbial decomposers [Booth *et al.*, 2005]. A feedback can occur when N immobilization in litter in turn can lead to lower soil N availability, which reduces plant uptake of N, and then drives litter C:N ratios even lower, as demonstrated by experiments with the General Ecosystem Model created by the Marine Biological Lab (MBL-GEM) parameterized for arctic and temperate forests [Rastetter and Houghton, 1992]. In tropical sites, we may see similar responses in nutrient recycling for P and base cations if these become progressively scarcer in soils due to CO₂ fertilization. However, it is unclear to what extent progressive P limitation may be mediated by the release of additional P from occluded pools via acidification and mycorrhizal activity.

2.1.2.4. CO₂ Fertilization and Tropical Biodiversity

2.1.2.4.1. CO₂ Fertilization and Tropical Biodiversity: Effects on Plant Communities

Elevated CO₂ is likely to promote the competitive advantage of some species over others in tropical plant communities. In particular, CO₂ fertilization appears to increase plant tolerance to stress, including low water availability, shifts in temperature, and low light, with different responses among species [Hogan *et al.*, 1991]. So, some species may increase their advantage within existing ranges and/or expand their ranges into previously unfavorable sites, which may be particularly important for tropical species adapted to narrow temperature and moisture regimes. Species-specific responses to CO₂ fertilization are likely to lead to new community structures, changes in biological interactions among plants, animals, insects and microbes, and shifts in phenology [Korner, 1998].

Experiments with tropical tree seedlings have shown that CO₂ fertilization can confer a particular advantage to fast-growing, high-light, early successional species. For example, an experiment with five tropical Mexican seedling species showed that CO₂ fertilization promoted height growth among some species, which then shaded out less responsive species at 1.5 times and 2 times ambient CO₂ for 111 days, with eventual changes in species composition [Reekie and Bazzaz, 1989]. Interestingly, the performance of the five species when grown alone at elevated CO₂ in this experiment was not a good predictor of how they performed when grown together in direct competition. Similarly, a study of two Panamanian tree seedlings grown together, fast-growing *Ficus insipida* and slow-growing shade-tolerant *Virola surinamensis*, showed greater biomass and height growth for *F. insipida*, such that *V. surinamensis* was heavily shaded and grew more slowly at 2 times ambient CO₂ in OTCs over 30 weeks [Winter *et al.*, 2000]. A similar study with nine Panamanian seedling species grown together also showed that fast-growing pioneer species responded to 2 times ambient CO₂ with a 74% increase in growth relative to ambient conditions after 39 days when water and soil nutrients were plentiful, whereas slow-growing late successional species had very small or no response to elevated CO₂ [Winter and Lovelock, 1999]. These studies suggest that CO₂ fertilization may give a competitive advantage for light resources to fast-growing tree species over slow-growing species, with the potential to shift community composition over time.

Shade species can also respond positively to CO₂ fertilization. A Panamanian study comparing five understory species grown together (seedlings *Beilschmiedia pendula* and *Tachigalia versicolor*, shrubs *Piper cordulatum* and *Psychotria limonensis*, and grass *Pharus latifolius*) in deep shade at 2 times ambient CO₂ found that stimulation of plant growth for woody species increased as light decreased, but not for the grass [Wurth *et al.*, 1998]. In this study, it took a year for any positive growth effect to be detected on understory species, which is much slower than the fast-growing species in the studies on light-loving species, and seedlings responded to CO₂ fertilization faster than did shrubs. Contrary to predictions that fast-growing, light-loving lianas are favored by CO₂ fertilization [Laurance *et al.*, 2014], a comparison of Panamanian liana versus tree seedlings grown at 2 times ambient CO₂ for 3–6 months found no difference in responses for the two life forms, with increased growth for both [Marvin *et al.*, 2015]. Thus, there is evidence for some species-specific differences in growth responses to elevated CO₂ across successional groups and species. From the limited data available, it seems that CO₂ fertilization may have the potential to decrease woody plant biodiversity in tropical forests (Figure 5).

Plants with different photosynthetic pathways are also likely to respond differently to rising CO₂ concentrations. Plants with C₃ photosynthetic pathways are likely to gain the greatest advantage, since they typically have lower photosynthetic efficiency than C₄ or Crassulacean acid metabolism (CAM) photosynthetic pathways [Bowes, 1993; Ghannoum *et al.*, 2000; Welkie and Caldwell, 1970]. While most tree species have C₃ photosynthesis, there are numerous unique C₄ and CAM tree species throughout tropical forests, many of which are important canopy or emergent species that contribute to overall biodiversity [Ball *et al.*, 1991; Holtum *et al.*, 2004; Luttge, 2008]. An OTC experiment using nine Panamanian seedling species showed greater photosynthetic responses for C₃ versus C₄ or CAM plants at 2 times ambient CO₂ levels over 3 months [Ziska *et al.*, 1991]. Similarly, C₃ epiphytes from Central and South America grew 60% faster than CAM epiphytes at 2 times ambient CO₂ over 6 months [Monteiro *et al.*, 2009]. Also, a meta-analysis of 12 temperate FACE experiments showed that plant growth responses were 3 times greater for plants with C₃ photosynthesis versus C₄ photosynthesis [Ainsworth and Long, 2005]. One leaf-scale model showed that C₃ plant growth was indeed favored at elevated CO₂ and elevated temperatures [Ehleringer *et al.*, 1997]. Similarly, a simulation using the adaptive Dynamic Global Vegetation Model (aDGVM) showed a shift from C₄ grass cover to C₃ woody-plant cover at a global scale, with C₃-dominated areas increasing from 31% to 47% by 2100 with 2 times ambient CO₂ concentrations [Higgins and Scheiter, 2012]. However, C₄ or CAM tend to be more competitive in very hot or dry conditions [Webster *et al.*, 1975], and it is not clear how CO₂ fertilization concurrent with climate change will shift the dominance of different photosynthetic pathways in the tropics. Also, fire promotion of C₄ grasses in the short term will likely outweigh the longer-term promotion of C₃ species by CO₂ fertilization in fire-vulnerable tropical areas. It does seem that CO₂ fertilization alone may favor C₃, diminishing overall plant biodiversity (Figure 5).

2.1.2.4.2. CO₂ Fertilization and Tropical Biodiversity: Effects on Insect Communities

Elevated CO₂ also has the potential to alter insect biodiversity via changes in foliar chemistry. Classic reviews show that herbivores play a much larger role in humid tropical ecosystem dynamics relative to other biomes, due to higher rates of herbivory, greater plant production of antiherbivory compounds, and tight coevolution of herbivores and plants [Coley, 1998; Coley and Barone, 1996]. Particularly because of the tight coevolution of herbivores and plants, changes in foliar tissue chemistry of even a subset of plant species could dramatically affect certain insect populations.

Commonly, the relative availability of N is low compared to insect requirements (i.e., C:N ratios of leaves are high), and elevated CO₂ has broadly been shown to decrease foliar N contents and increase foliar C:N ratios (see above section 2.1.2.3). When foliar N declines, herbivore growth and reproduction are likely to respond negatively [Mattson, 1980]. There is evidence for decreased herbivory and mortality when foliar C:N ratios increase with CO₂ fertilization from some temperate forest experiments [Fajer, 1989; Hall *et al.*, 2005], but there is very little similar data for tropical forests. If there is no change in foliar chemistry with CO₂ fertilization, an effect on herbivory is unlikely, as was observed in model tropical plant communities in greenhouses exposed to 1.8 times ambient CO₂ concentrations for 1.5 years [Arnold *et al.*, 1995]. Thus, changes in foliar N and C:N with elevated atmospheric CO₂ have great potential to affect herbivory, with possible negative effects on insect biomass and biodiversity, depending on the species' stoichiometric flexibility (Figure 5).

2.1.2.5. CO₂ Fertilization and Tropical Disturbance Regimes

The main effect of increased atmospheric CO₂ concentrations on humid tropical forest disturbance regimes is likely to be through changes in hydrological processes, with potential effects on landslides and flooding. In particular, reduced stomatal conductance in leaves is linked to improved plant water use efficiency [Drake *et al.*, 1997], such that CO₂ fertilization has the potential to positively affect soil moisture and ecosystem runoff, and negatively affect evapotranspiration and local rainfall in the tropics [Field *et al.*, 1995; Holtum and Winter, 2010]. The C and water cycles are biologically linked in ecosystems via evapotranspiration, but this coupling is underrepresented in ecosystem model development [Wang and Dickinson, 2012]. Particular attention should be given to how CO₂ fertilization is likely to alter tropical forest hydrology via changes in evapotranspiration.

Small-scale studies with tropical plants suggest that CO₂ fertilization can decrease water loss at the leaf scale. For two tropical tree seedlings, *Maranthes corymbosa* and *Eucalyptus tetrodonta*, stomatal conductance declined in both species at 2 times ambient CO₂ treatment [Berryman *et al.*, 1994]. For *M. corymbosa*, stomatal conductance was also more sensitive to leaf water status under CO₂ enrichment, and for *E. tetrodonta* stomatal conductance was less sensitive to temperature at elevated CO₂. Another study using two Costa Rican seedling species, fast-growing *Ochroma lagopus* and slow-growing *Pentaclethra macroloba*, also showed

decreased stomatal conductance and increased water use efficiency for both species at 2 times ambient CO₂ after ~4 months [Oberbauer *et al.*, 1985]. These results point to possible interacting effects of CO₂ fertilization and climate change, with some species more sensitive to climate change under elevated CO₂, and other species less sensitive to climate change under elevated CO₂.

Larger-scale studies at temperate sites provide additional evidence that CO₂ fertilization can increase soil moisture and decrease water transfer to the atmosphere via evapotranspiration. A review of FACE experiments across higher-latitude ecosystems showed broad ecosystem-scale reductions in evapotranspiration with plants grown under elevated CO₂ concentrations [Bernacchi and VanLoocke, 2015]. A reduction in evapotranspiration was also shown in model simulation of elevated CO₂ concentrations over the next century using the Dynamic Land Ecosystem Model [Pan *et al.*, 2015b]. Increases in soil moisture with CO₂ fertilization were observed for a soybean FACE experiment in central Illinois over four growing seasons at 1.5 times ambient CO₂ [Bernacchi *et al.*, 2007]. These results for ecosystem-scale temperate CO₂ fertilization studies, together with the above studies showing that elevated CO₂ can improve tropical plant water use efficiency, suggest that similar effects on soil moisture and evapotranspiration may occur in tropical forests as atmospheric CO₂ continues to increase.

Increased soil moisture is particularly liable to increase disturbances in wet high-clay tropical forest soils. First, tropical sites on slopes are very susceptible to landslide disturbance. For example, the frequency and severity of landslides is directly related to soil moisture levels for montane forests in Puerto Rico [Lepore *et al.*, 2013]. Also, increased soil moisture is positively linked to the occurrence of floods [Bronstert *et al.*, 2012]. In addition to the obvious large-scale effects of landslides and flooding on soils and tree mortality, smaller-scale landslides and floods can also have negative consequences for tropical forest function. For example, a Panamanian experiment showed that flooding manipulations decreased photosynthetic activity of tropical tree species [Lopez and Kursar, 1999], and persistent seasonal flooding was linked to lower tree species diversity in the Panamanian forests [Lopez and Kursar, 2003]. Landslides can also change forest biodiversity, with severe landslides completely changing forest composition from mature forest species to palm forests in Puerto Rico [Guariguata, 1990]. Thus, there is a potential for increased floods and landslides in humid tropical forests under elevated CO₂ concentrations because of soil saturation (Figure 5). Although, to our knowledge, there is no current literature exploring the link between elevated atmospheric CO₂ and flooding or landslides in the tropics.

2.1.3. Nitrogen Deposition in the Humid Tropics

Nitrogen deposition spreads biologically available N from urban and agricultural centers onto surrounding ecosystems. Nitrogen is an essential nutrient for life, and although it constitutes 78% of the Earth's atmosphere, it must be converted into a biologically available form of inorganic N in soils for most plants and microbes uptake. Human activities have more than doubled biologically available N on Earth [Fowler *et al.*, 2013; Smil, 1990; Vitousek *et al.*, 1997a]. For example, fossil fuel combustion, industry, cultivation of N fixing crops, and application of N fertilizers produce acidic N oxides (NO_x) and ammonia (NH₃), which are then transported through the atmosphere and deposited on natural ecosystems via rainfall and dust [Krusche *et al.*, 2003; Lara *et al.*, 2001; Martinelli *et al.*, 2006]. Agricultural N fertilizer can be transported to natural ecosystems via runoff as mineral N, or can be off gassed from soils, generally as ammonia (NH₃), and transported via atmospheric N deposition. Fossil fuel combustion generally creates atmospheric N oxides which can then be transported to natural ecosystems. Unlike CO₂, N related emissions are regionally concentrated and are generally deposited within kilometers from the original source of pollution [Baron *et al.*, 2014; Sutton *et al.*, 2011]. In both temperate and tropical sites, urban-proximate forests can have higher soil mineral N levels, mineralization rates, and N leaching relative to rural reference sites [Cusack, 2013; Groffman *et al.*, 2009; Lara *et al.*, 2001; McDonnell *et al.*, 1997; Pouyat *et al.*, 1995]. Once deposited, excess N can acidify soils, stimulate leaching of base cations, and negatively affect water quality [Matson *et al.*, 1999]. Nitrogen deposition is increasing particularly rapidly in tropical regions, and annual tropical N deposition rates are expected to be among the highest globally in the coming decades [Galloway *et al.*, 2004]. This century, 40% of all N fertilizers produced industrially are used in the tropics and subtropics, and this figure is projected to grow to 60% by 2020, which would lead to a doubling of N deposition rates in the tropics in 2050 compared to levels in the 1990s [Galloway *et al.*, 2003]. The ecological consequences of these projected increases in N deposition on tropical sites are of broad concern.

Unlike most temperate sites, tropical forests on highly weathered soils tend to have relatively high background N availability [Chestnut *et al.*, 1999; Hedin *et al.*, 2009; Martinelli *et al.*, 1999; Walker and Syers, 1976],

so it was posited over a decade ago that the negative effects of N deposition would be more rapid and occur at lower N deposition rates in tropical forests compared to temperate forests [Matson *et al.*, 1999]. In temperate sites, N deposition rates of just 8–10 kg ha^{−1} year^{−1} can result in N saturation, or the point at which ecosystems no longer retain added N, resulting in N leaching, and altering ecosystem functioning [MacDonald *et al.*, 2002]. The N saturation point is likely to be much lower in N-rich tropical versus temperate forests because of high background levels of soil N. Rates of N deposition in many urban-proximate tropical regions are in fact already far above 10 kg N/ha/yr. For example, N deposition in 14 tropical forests along an urban-to-rural gradient around the Guangzhou metropolitan area in southern China showed that N deposition ranged from 11.7 to 65.1 kg N ha^{−1} year^{−1} [Fang *et al.*, 2011]. Although N deposition studies in tropical forests have increased in recent years, there are still relatively few long-term N deposition monitoring sites. Most research on N deposition in the tropics currently relies on experiments that directly apply N fertilizer to the forest floor, which imperfectly replicates atmospheric N deposition to the forest canopy. Here we review the mounting evidence that the rapidly growing problem of tropical N deposition alters ecosystem processes and properties in humid tropical forests.

2.1.3.1. Nitrogen Deposition and Tropical Plant Growth

Nitrogen deposition may affect plant growth by altering photosynthetic uptake of C, plant respiration, and/or allocation of C to new leaf, wood, and root growth. The potential effects of N deposition on individual plant growth and on ecosystem rates of NPP are reviewed below.

There is some evidence that atmospheric N deposition may have a direct negative effect on photosynthetic processes in tropical forests. A study using a global eddy covariance data set for 80 Flux Network forest sites showed that photosynthetic capacity of 13 evergreen broadleaf forests, including nine pantropical forests, was negatively related to N deposition rates [Fleischer *et al.*, 2013], potentially because of acid damage to leaves. Similarly, acidic N deposition has been shown to damage foliage and epiphytes across a variety of high latitude ecosystems, which could reduce photosynthetic rates [Cape, 1993; Farmer *et al.*, 1991; Leith *et al.*, 1989]. Thus, elevated rates of acidic atmospheric N deposition in tropical regions could negatively affect plant photosynthesis (Figure 6), although subsequent effects on plant growth require further investigation.

Despite the potentially negative effects of acid N deposition on leaf tissues, N is an essential nutrient, so where N is scarce N deposition also has the potential to increase plant growth, as has been seen in a number of northern latitude sites [Bedison and McNeil, 2009; Hogberg *et al.*, 2006; Solberg *et al.*, 2009]. However, humid forests on highly weathered soils have high levels of available soil N relative to rock-derived nutrients like P and cations. A seminal study directly assessed N availability and plant N uptake using 15 N stable isotopes in plant tissues across eight broad tropical regions and showed a general abundance of N and lack of N limitation to plant growth in tropical forests [Martinelli *et al.*, 1999], suggesting that N deposition is not likely to stimulate plant growth for large expanses of the tropics.

A growing number of N fertilization experiments in humid forests on highly weathered soils show no increase in plant growth or NPP at ecosystem scales, supporting the hypothesis that plant growth in these ecosystems is not limited by N alone. For example, no significant response of tree stem growth was observed after 4 years of N fertilization (225 kg N/ha/yr) nor of fine litterfall productivity after 1 year, in a lowland mature tropical dipterocarp forest on highly weathered soil in Indonesia [Mirmanto *et al.*, 1999]. Similarly, experimental N addition for 6 years (125 kg N/ha/yr) in a lowland mature seasonal forest in Panama on highly weathered soil did not increase leaf or twig litterfall productivity [Kaspari *et al.*, 2008]. In the same site, stem diameter growth rate of trees, fine litterfall, and fine-root biomass production in the top 10 cm soil also did not change after 11 years of N fertilization [Wright *et al.*, 2011]. An N fertilization experiment in lower and upper montane rainforests in Puerto Rico on highly weathered soils also showed no response of tree stem growth or litterfall productivity during years 3–6 of N addition (50 kg N/ha/yr) [Cusack *et al.*, 2011a]. A Hawaiian N fertilization experiment on highly weathered montane tropical soils similarly showed no change in leaf area index or stem growth with N fertilization after 1 year (100 kg N/ha/yr) [Herbert and Fownes, 1995] nor after 11 years [Harrington *et al.*, 2001]. In a Costa Rican lowland tropical wet forest there was no change in basal area, root growth, or litterfall productivity after 3 years of N fertilization (125 kg N/ha/yr) [Alvarez-Clare *et al.*, 2013]. In southern China, N addition for 8 years in a subtropical monsoon forest on highly weathered soils did not increase plant growth across a range of N addition rates (60, 120, and 240 kg N/ha/yr) [Fan *et al.*, 2014]. An observational study in Costa Rica also showed no relationship between forest stand stem growth rates and total soil N across five wet tropical forest sites on soils ranging from young entisols to highly weathered

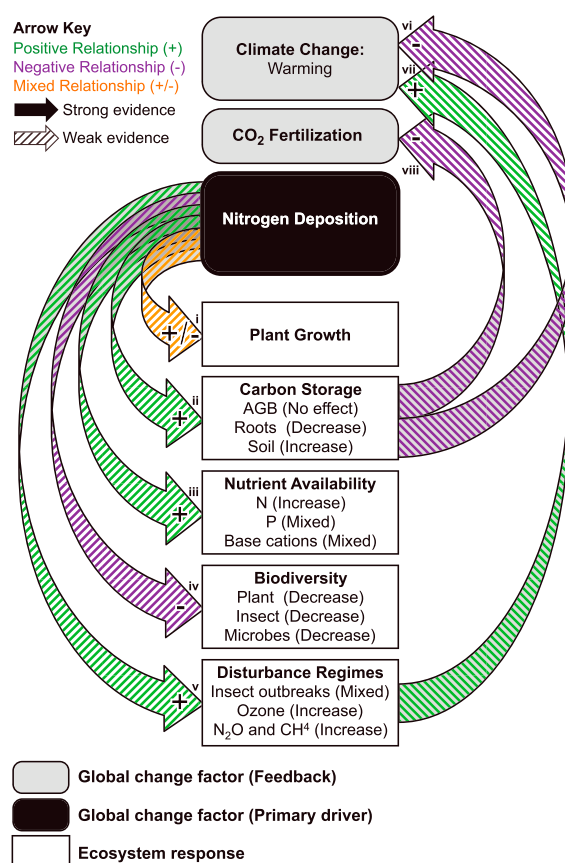


Figure 6. A synthesis of the effects of N deposition on plant growth, carbon storage, nutrient availability, biodiversity, and disturbance regimes is shown. We include arrows showing feedbacks and effects on other global change factors. For the feedbacks, the negative or positive arrow represents the net effect of the featured global change factor back to itself (or to another global change factor), via changes in the given ecosystem process. Roman numerals refer to citations in Table S1 that support the direction and certainty of each arrow.

oxisols in southern China seedling growth rates generally responded positively to lower rates of N addition (5–15 kg N/ha/yr) but negatively to a higher rate of N addition (30 g N m⁻² years⁻¹) [Mo *et al.*, 2008a]. Thus, N deposition may improve access to N for some seedlings species, or seedlings may require more N than mature trees. These studies suggest that seedling photosynthesis and growth may respond positively to N deposition in some tropical forests, even on N-rich highly weathered soils (Figure 6).

While NPP on highly weathered tropical soils is unlikely to respond to N deposition, growth effects can be expected to vary spatially within tropical regions depending on soil types and disturbance history. For example, cooler tropical montane forests are often found on relatively N-poor soils, and regenerating secondary forests may occur on disturbed soils where N has been leached out after previous deforestation (see section 2.2.1). Nitrogen fertilization experiments in tropical montane rainforests on less weathered soils have increased tree stem growth after just 1–2 years in Panama (125 kg N/ha/yr), Ecuador (50 kg N/ha/yr), and Hawaii (25 kg N/ha/yr) [Adamek *et al.*, 2009; Homeier *et al.*, 2012; Vitousek and Farrington, 1997; Vitousek *et al.*, 1993]. Similarly, N fertilization increased trunk growth and litterfall productivity in a montane rainforest on poorly weathered Inceptisols in Venezuela after 4.5 years (150 kg N/ha/yr) [Tanner *et al.*, 1992]. Nitrogen fertilization also increased the photosynthetic rates of seven out of nine palm species seedlings in N-poor lower montane tropical forests in western Panama [Andersen *et al.*, 2010]. In 6 year old secondary forests in the Amazon, N fertilization (100 kg N/ha/yr) increased tree growth on highly weathered soils [Davidson *et al.*, 2004b]. Subhumid secondary forests in the Yucatan also had increased trunk growth after 3 years of

ultisols, although the distributions of four plant species in these highly diverse ecosystems were correlated to soil mineral N levels [Baribault *et al.*, 2012]. While fertilization studies certainly do not replicate atmospheric N deposition perfectly, these studies do show that relatively high rates of N addition on decadal time scales generally do not affect tree growth in these ecosystems. These data suggest that NPP in tropical forests on highly weathered soils is unlikely to respond positively to atmospheric N deposition (Figure 6).

In contrast to mature trees, some understory vegetation and seedlings may be more likely to have positive photosynthetic and growth responses to N additions on highly weathered soils, since small plants have small root systems that may be limited by localized soil N availability. For example, one pioneer tree seedling species (*Alseis blackiana*) in low-land seasonal Panamanian forests on highly weathered soils showed a 9% increase in maximum photosynthetic capacity after 10 years of fertilization (125 kg N/ha/yr) [Pasquini and Santiago, 2012], while there was no growth response among seedlings of the five most common woody species [Santiago *et al.*, 2012]. In a tropical forest on highly weathered

N fertilization (220 kg N/ha/yr) in 10 and 60 year old forests [Campo and Vazquez-Yanes, 2004]. This type of spatial variability in tropical forest responses to N fertilization led one global meta-analysis to conclude that tropical forest growth is N limited [LeBauer and Treseder, 2008], but this result relied heavily on fertilization experiments in secondary forests [Davidson *et al.*, 2004a], montane tropical forests on young soils [Tanner *et al.*, 1992], dry tropical forests [Campo and Vazquez-Yanes, 2004], and on poorly weathered Hawaiian soils, which are not representative of the majority of lowland tropical forests on high-weathered soils. Still, N deposition has the potential to increase tropical plant growth and NPP in forests where soil N is relatively scarce (Figure 6).

It is important to note that while N alone has not been shown to stimulate NPP in tropical forests on highly weathered soils, N may stimulate plant growth if the availability of other nutrients also increases, in what has been termed “colimitation.” For example, a meta-analysis using 173 terrestrial sites across latitudes showed that neither N nor P alone broadly increased plant growth, but N and P together generally stimulated growth, providing evidence for broad-scale colimitation of NPP by N [Elser *et al.*, 2007]. In this study, the tropical forests included still showed stronger growth responses to P addition alone than to N addition alone, supporting that N deposition alone is unlikely to generally increase tropical NPP. Another analysis of 641 freshwater, marine, and terrestrial sites also found that 28% of fertilized sites showed plant growth colimitation by N and P, although few tropical forests were included [Harpole *et al.*, 2011]. A factorial fertilization study in lowland Panamanian forests on highly weathered soils showed that addition of N and K together stimulated mature tree growth, N, P, and K added together stimulated seedling growth, and N, P, and K added together suppressed fine root growth [Santiago *et al.*, 2012; Wright *et al.*, 2011; Wurzbarger and Wright, 2015], indicating colimitation of plant growth by N in this forest where N alone did not have an effect. Also, in a lowland Indonesian forest, N and P together increased litterfall productivity, but there was no significant effect on stem growth after 5 years [Mirmanto *et al.*, 1999]. Understanding how global change will alter the relative availability of N, P, and other nutrients in tropical soils is essential for understanding potential future changes in forest structure [Townsend *et al.*, 2007] and plant growth [Cleveland *et al.*, 2011]. While N appears to be an important colimiting nutrient for plant growth in some tropical forests, whether or how N deposition might occur at the same time as increased availability of rock-derived nutrient like P or K is uncertain. Possibly, N deposition will have secondary effects on decomposition that may increase P availability (see section 2.1.3.3.3), or increases in global dust production and transfer due to drought and land use change may deliver more rock-derived nutrients to humid tropical forests from arid regions [Mulitza *et al.*, 2010; Prospero and Lamb, 2003]. These scenarios could lead to a more generalized positive effect of N deposition on tropical plant growth if N is broadly colimiting NPP, even on highly weathered tropical soils.

Rather, it seems more likely that N deposition could have long-term negative effects on plant growth because of related declines in the availability of other nutrients. For example, an integrated terrestrial biophysics-biogeochemical process model, TerraFlux, projected that an N deposition rate of $>10 \text{ kg N}^- \text{ ha}^{-1}$ per year in N-rich tropical sites could reduce plant productivity by 12–25% in 50 years [Asner *et al.*, 2001], largely because N deposition is likely to lead to losses of base cation nutrients, which are readily leached out of soils together with excess NO_3^- [Gundersen *et al.*, 2006; Johnson and Reuss, 1984] (see section 2.1.3.3.2). Thus, despite the fact that N may be an important colimiting nutrient in some tropical forests on highly weathered soils, N deposition alone is still not expected to increase plant growth in these ecosystems, and indirect effects on other nutrients may even suppress plant growth (Figure 6).

It is possible that N limitation to tropical plant growth will become more important in the context of other simultaneous global change factors like increased atmospheric CO_2 . For example, an OTC experiment in southern China on highly weathered ultisols exposed seedlings of five tree species to 2 times ambient CO_2 and/or N fertilization (100 kg N/ha/yr). This experiment showed that average seedling growth showed no response to CO_2 alone, but increased 64% with both N addition plus elevated CO_2 , and increased by 56% with N alone. Responses varied among species, with plant growth increasing for a pioneer species (*Schima superba*) with N addition alone and plant growth increasing only with N addition plus elevated CO_2 for an N-fixing species (*Ormosia pinnata*) [Yan *et al.*, 2014]. These results suggest that N limitation to plant growth may become more important as atmospheric CO_2 concentrations continue to increase (see section 2.1.2.3.2), making N deposition more likely to positively affect tropical NPP in the future.

In summary, mature tropical forest growth on highly weathered soils is not likely to increase with N deposition. These forests may even show negative growth responses if soil base cations are progressively leached

out of soils with added NO_3^- or if acidic forms of atmospheric N deposition damage foliage and reduce photosynthetic capacity. In contrast with the null or negative growth responses of mature forests on highly weathered soils, N deposition may increase plant growth for some tropical forests that occur on N-poor soils, such as wet montane forests on less weathered soils or young secondary forests on disturbed soils. Seedlings may also show more positive growth responses than mature trees to N deposition, particularly for fast-growing pioneer seedling species. Finally, other global change factors, such as CO_2 fertilization or dust deposition, may generally increase tropical plant growth limitation or colimitation by N eventually. Overall, the available data suggest that N deposition will have mixed effects on plant growth in the tropics, with variation across space and among plant cohorts (Figure 6).

2.1.3.2. Nitrogen Deposition and Tropical Carbon Storage

Nitrogen deposition may affect long-term C storage in tropical forests by altering the amount of C held in plant biomass both aboveground and belowground (i.e., in roots), changing tree mortality, and/or via changes in net ecosystem respiration, decomposition, and soil respiration losses of CO_2 . The below section reviews the evidence for how the C sink in tropical forests may respond to N deposition.

2.1.3.2.1. Nitrogen Deposition and Tropical Carbon Storage: Plant Biomass

Because N deposition alone is unlikely to increase mature tree growth in tropical forests on highly weathered soils (see above), it follows that N deposition is also unlikely to increase C storage in plant biomass. Overall, most tropical N fertilization studies have focused on measuring plant growth rather than C stocks. One N fertilization study in lower and upper montane rainforests in Puerto Rico that found no effect on plant growth also found no effect on aboveground biomass after 5 years [Cusack *et al.*, 2011a]. While few studies have quantified responses of aboveground biomass to N deposition in the tropics, meta-analyses and reviews have attempted to predict N deposition effects on tropical C storage using global data sets. One study using global stoichiometric relationships concluded that tropical trees on N-rich, highly weathered soils are unlikely to accumulate N, and since plant tissue C:N ratios are relatively constrained, so there is also low likelihood of increased C storage with N deposition [Townsend *et al.*, 1996]. A more recent review also concluded that N deposition is not likely to contribute sizeable quantities of new plant biomass in tropical forests [Cleveland *et al.*, 2013]. Some meta-analyses and reviews, however, have attempted to predict N deposition effects on tropical C storage using data sets from other biomes, giving likely erroneous predictions of increased C storage in plant biomass. For example, a meta-analysis of 257 N fertilization studies across ecosystem types globally concluded that N addition increased aboveground C pools by 36% on average [Lu *et al.*, 2011]. However, of the 13 tropical forest studies cited by the study, not a single study examined carbon storage in tropical tree woody tissues, so this increase in C storage does not apply to tropical forests. In another cross-site review, forest retention rates of added N were gathered from N fertilization studies and then used with common C:N ratios of plant tissues to scale up and estimate C storage in woody biomass [de Vries *et al.*, 2014]. The authors estimated that current N deposition rates of $\sim 7 \text{ Tg N/yr}$ would lead to an additional C sequestration of $\sim 40 \text{ Tg C/yr}$ in evergreen broadleaf forests, mainly in the tropics. However, actual observations of the quantities of N retained in plant tissues in mature tropical rainforests are extremely scarce, and there are no ecosystem-scale studies specifically tracing retention of added N, as there have been in temperate sites [e.g., Nadelhoffer *et al.*, 2004]. Thus, when humid tropical forests are lumped together with other forest types in meta-analyses, the effects of N deposition on tropical forest plant biomass are misleading. This highlights the small number of N fertilization studies in humid tropical forests on highly weathered soils relative to other ecosystem types and cautions against using global trends to predict tropical forest responses to N deposition. Overall, the available data indicate that increased aboveground C storage with N deposition is unlikely for mature tropical forests on highly weathered soils (Figure 6).

Unlike aboveground biomass, some N fertilization studies suggest that root biomass may respond to N fertilization in tropical forests, although the general trend seems to be toward a decline in roots. In fact, studies in both tropical and temperate forests have reported negative response of root biomass to N addition but likely for different reasons. In general, plants invest less in root production when limiting nutrients are more available. In N-poor temperate forest soils, N addition can directly increase the availability of scarce N, resulting in trends toward less root biomass [Nadelhoffer, 2000]. Tropical forests on N-poor soils, such as in montane settings, may be expected to respond similarly to the temperate forests. For example, N fertilization ($50 \text{ kg N ha}^{-1} \text{ year}^{-1}$) in a mature tropical montane moist forest in Ecuador on nutrient poor soils also showed a 15% decline in fine root biomass after 1 year [Homeier *et al.*, 2012]. In highly weathered tropical

soils, a similar end result is likely to be caused indirectly, with N fertilization altering other aspects of soil biogeochemistry like base cation mobilization (see section 2.1.3.3.2), which in turn may alter root biomass. For example, an N fertilization experiment (50 kg N ha⁻¹ year⁻¹) in a lower and an upper montane humid tropical forest in Puerto Rico on N-rich highly weathered soil found that fine root biomass declined in fertilized plots after 5 years [Cusack *et al.*, 2011a], which was likely related to the increased mobility and availability of scarce base cations in soil water [Cusack *et al.*, 2016]. Thus, increased availability of nutrient cations with N deposition could also result in reduced root biomass because plants do not need to invest in seeking out these additional nutrients. In the Puerto Rico study, however, it was unclear whether relatively short-term base cation mobilization with N additions would eventually lead to leaching losses and subsequent cation scarcity, which could change the effect on root biomass over time. Another N fertilization study (150 kg N/ha/yr) in mature forests on highly weathered soils in China also found a decline in fine root biomass with N fertilization after 2–3 years [Mo *et al.*, 2008b], which may also have been related to increased base cation mobility. In Hawaii and Panama, studies on highly weathered soils showed no responses of fine root biomass or root N concentrations to N fertilization after 5 and 14 years, respectively [Ostertag, 2001; Wurzbarger and Wright, 2015]. In contrast with these studies, a Costa Rican study of mature forests on highly weathered soils found an opposite response, with N fertilization increasing fine root biomass after 3 years in small plots [Cleveland and Townsend, 2006], potentially because of “root baiting” in the relatively small plots used, which could have created hot spots of N availability. Thus, responses of root biomass to N deposition in highly weathered tropical soils are likely to depend on secondary effects of the mobilization or leaching of base cations.

In summary, field studies suggest that aboveground C storage will not respond positively to N addition in tropical forests on highly weathered soils, and belowground C storage in roots is likely to have a mixed response across sites, with declines or no change most likely in the short to midterm (Figure 6). Longer-term studies (e.g., > 10 years) on the effects of N additions on tropical root biomass are needed. Longer term studies may show that root biomass in highly weathered soils eventually increases with N deposition if substantial base cations are leached and lost from soils, exacerbating nutrient scarcity and promoting belowground C allocation by plants.

2.1.3.2.2. Nitrogen Deposition and Tropical Carbon Storage: Soil Organic Matter

A number of recent studies have shown that increased N availability in humid tropical forests on highly weathered soils has the ability to increase C storage in SOM, despite a lack of N limitation to plant growth. In an experimental N fertilization experiment in lower and upper montane rainforests in Puerto Rico, N fertilization significantly increased soil C concentrations after 5 years of N fertilization because of decreased microbial decomposer activity and an apparent transfer of SOM into long-lived mineral-associated soil fractions [Cusack *et al.*, 2011a]. Similarly, N fertilization decreased soil microbial respiration and increased soil C storage after 8 years on highly weathered soils in south China [Fan *et al.*, 2014]. A 7 year fertilization experiment in a mature tropical forest in southern China also caused a 14% decline in soil respiration, which was attributed to a reduced litter decomposition rate [Mo *et al.*, 2008b], suggesting an accumulation of soil C. Thus, N addition has been shown to reduce rates of litter decomposition and microbial respiration, thus reducing C losses and increasing soil C storage in highly weathered tropical soils. While ecosystem-scale studies like these are still relatively scarce for the humid tropics, the results available suggest that increased soil C storage with N fertilization is likely for at least some forests on highly weathered soils in the humid tropics (Figure 6).

In contrast to the above studies, other tropical sites have no response of soil C storage to N fertilization. Nitrogen fertilization (150 kg N/ha/yr) in N-rich mature tropical forests in southern China showed no effect on bulk soil C storage, although more labile fractions of SOM declined with N fertilization after 4.5 years [Liu *et al.*, 2013], suggesting stimulation of microbial decomposition rates for some portion of SOM. In contrast, another study on highly weathered soils in southern China observed no effect of N fertilization (150 kg N/ha/yr) on decomposition of woody SOM after 3 years [Chen *et al.*, 2015]. These two Chinese studies suggest that decomposition rates of labile versus woody fractions of SOM may respond differently to N additions, with net changes in soil C storage apparent only if the relative magnitudes of the effects are not in balance. A meta-analysis which included 12 tropical forest studies among 247 total studies found no overall change in soil C storage with N fertilization across a global set of sites [Lu *et al.*, 2011], although the results are clearly driven by nontropical ecosystem types. Since soils hold large stocks of C, changes in this stock

can be difficult to detect over the relatively short time periods of these studies. A broader set of tropical N fertilization studies over longer time periods would help clarify why certain sites appear to increase soil C storage with N addition, while others show no net effects.

Smaller-scale laboratory studies have provided additional mechanistic insight to how N additions may alter soil C storage in highly weathered tropical soils. One lab study added N to highly weathered soils from subtropical China, leading to reduced soil microbial respiration and reduced soil C losses [Ouyang *et al.*, 2008]. Similarly, N fertilization plus litter addition in a laboratory incubation with Costa Rican soils suppressed soil microbial respiration [Cleveland *et al.*, 2006]. A lab incubation using soils from lower and upper elevation Puerto Rican montane forests also found that N fertilization decreased overall microbial respiration, which was related to increased soil C storage in slowly cycling pools [Cusack *et al.*, 2010]. Nitrogen deposition may also increase soil C storage indirectly by suppressing what has been called the “priming effect” of microbial decomposition, in which new inputs of C from root exudates can stimulate microbial decomposition of older SOM. For example, Panamanian forest soils from 11 lowland sites showed that addition of N (NH_4NO_3) suppressed the effect of new C (sucrose) in “priming” losses of extant soil C [Nottingham *et al.*, 2015], suggesting that N deposition may increase overall soil C retention and reduce decomposition. Also, lab additions of + nitrogen, phosphorus and potassium with sucrose to three of the Panama soils confirmed that priming-related losses of soil C were reduced at greater nutrient availability [Nottingham *et al.*, 2011], indicating that nutrients limit microbial utilization of new C, and that the priming effect is driven by a quest for nutrients. Together, these laboratory studies provide evidence that microbial respiration and decomposition may decline with N deposition in highly weathered tropical soils, thus reducing C losses and potentially increasing soil C storage in the longer term (Figure 6).

In addition to altering soil C losses via changes in decomposition, N deposition has the potential to alter soil C storage via physiochemical mechanisms that may alter the recalcitrance or sorption of C into long-term pools. First, N can directly interact with organic compounds released from plant tissues to produce humic materials, which may be recalcitrant to decomposition and stored in soil for long time periods [Moran *et al.*, 2005]. Second, a broad-scale study across a set of European watersheds suggested the extent of acidification created by N deposition was directly related to storage or loss of soil C [Evans *et al.*, 2008], with sorption of dissolved organic C onto soil minerals greatest at acidic pH [Jardine *et al.*, 1989]. In the tropics, change in soil acidity due to N deposition could change the overall charge density and sorption potential of tropical clays [Chorover and Spósito, 1995], potentially altering the amount of charged dissolved organic C stored in mineral soils. For example, increased sorption of dissolved organic C to soil minerals, resulting from a shift in soil acid neutralizing capacity with N deposition, was one apparent driver of increased soil C storage in Puerto Rican field N fertilization experiments [Cusack *et al.*, 2011a]. Also, increased acidity can promote leaching and transfer of dissolved organic C from the forest floor into mineral soils, where it can then be sorbed and stored for long time periods, as was observed with varying N fertilization rates (50, 100, and 150 kg N/ha/yr) over 7 years in a mature south China forest on highly weathered soils [Lu *et al.*, 2013]. Thus, abiotic chemical reactions and acidification that can be caused by N deposition both have the potential to increase soil C storage in highly weathered tropical soils (Figure 6), although these effects require more investigation.

In summary, the above studies indicate that N deposition may have varying effects on different C pools in tropical forests. The empirical evidence suggests that N deposition in tropical forests on highly weathered soils is (1) not likely to have a significant effect on aboveground C storage in plant biomass, (2) likely to decrease root C storage in sites where N addition increases mobility and availability of base cations, although longer-term leaching losses of mobilized cations may reverse this effect, and (3) likely to increase soil C storage in some highly weathered N-rich soils, potentially promoting sorption of C into relatively stable mineral-associated SOM pools (Figure 6). The net effect of N deposition on humid tropical forest C storage may be driven by the magnitude of the soil C response, rather than by biomass accumulation, since soils appear to be most responsive to changes in N availability in N-rich soils.

2.1.3.3. Nitrogen Deposition and Tropical Nutrient Availability

Although N is often relatively available in highly weathered soils, there are unique aspects of the N cycle that may shift with N deposition. For example, despite higher levels of soil N in wet tropical forests on highly weathered soils relative to northern ecosystems [Post *et al.*, 1985], biological N fixation rates in root nodules and by free-living microbes is often unexpectedly high given the high energetic costs of this microbial process. This apparent discrepancy in tropical forests has been termed the “N paradox” [Hedin *et al.*, 2009].

Several hypotheses have been explored to better understand why substantial energy would be expended in N-rich tropical forests to acquire more N.

One explanation is that N remains an important limiting or colimiting nutrient for microbial growth and activity in tropical forest microsites, especially in C/energy-rich, N-poor microsites like on decomposing leaf litter. For example, heterotrophic N fixation activity can be high in decomposing soil organic matter even when soil N levels are relatively high, as well as on leaf litter, in arboreal mosses and lichens, and on leaf epiphylls, contributing substantially to overall fluxes of N into tropical forests [Carpenter, 1992; Cusack *et al.*, 2009a; Forman, 1975; Goosem and Lamb, 1986; Reed *et al.*, 2007, 2008]. This N limitation for heterotrophic microbes is further confirmed by the downregulation of N fixation when N is added to these ecosystem compartments [Cusack *et al.*, 2009a]. Nitrogen limitation to some microbial processes, particularly decomposition, has been demonstrated across ecosystems at a global scale [Parton *et al.*, 2007]. The N cycle in wet tropical forests is thus often characterized by N abundance in general, but N can be scarce in some microsites. Thus, although energetically costly, it appears that different groups of microbes benefit from fixing their own N rather than acquiring it from soils.

Another explanation for the N paradox is that excess N can increase plant access to soil P. Active N fixation by root nodules in N-rich tropical forests also appears to promote plant P acquisition [Houlton *et al.*, 2008], both via increased production of N-rich enzymes that acquire mineral P from organic P compounds and via increased colonization by arbuscular mycorrhizal fungi, which also acquire P for plants [Nasto *et al.*, 2014]. Thus, N fixation by plants appears to support various mechanisms for acquiring scarce P from soils. So, even though atmospheric N deposition in tropical regions is often delivering more N to already N-rich ecosystems, N deposition has the potential to suppress or alter the natural inputs of N to tropical ecosystems via biological N fixation. The downstream ecological consequences of suppressing biological N fixation are virtually unknown. More research is required to understand the extent to which N deposition may replace biological N fixation as the main N input to tropical ecosystems.

2.1.3.3.1. Nitrogen Deposition and Tropical Nutrients: Plant Nutrition

If plants take up additional N with N deposition, then we would expect to see increased N concentrations in plant tissues. It should be noted that foliar and litter nutrient concentrations are not definitive measures of plant nutrition, but because actual nutrient uptake rates are lacking for most mature forests, these data can be used to indicate plant nutritional responses to N fertilization. Generally, tropical N fertilization studies have not shown an increase in plant N concentrations. In Puerto Rico, N fertilization studies did not alter foliar N or litterfall N concentrations, even though soil N increased [Cusack *et al.*, 2009a, 2011a]. Similarly, N fertilization ($100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) in mature and secondary rainforests in Costa Rican montane moist forests on relatively nutrient rich inceptisol and ultisol soils showed no changes in community-wide foliar N concentration after 2 years of fertilization [Alvarez-Clare and Mack, 2015]. Also, N fertilization on highly weathered N-rich Hawaiian soils led to no change in foliar N [Ostertag, 2010]. These results of no change in foliar N are in line with expectations that plant uptake of N will not increase with N deposition on N-rich tropical soils.

In contrast, some tropical fertilization studies do show responses of plant tissue N concentrations, typically for on N-poor soils, suggesting changes in plant nutrition. For example, foliar N concentrations increased with N fertilization in a relatively N-poor Ecuadorian montane moist forest [Homeier *et al.*, 2012] and in relatively N-poor secondary forests in the Yucatan Peninsula [Campo and Vazquez-Yanes, 2004]. Interestingly, foliar N concentrations also increased in N-rich Panama forests with N fertilization, even when plant growth did not change [Kaspari *et al.*, 2008]. Also, N fertilization ($150 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) in a relatively N-rich south China forest had increased foliar N concentration in one dominant understory species (*Randia canthioides*) after 3 years, but not in the other dominant understory species (*Cryptocarya concinna*) [Zhu *et al.*, 2014]. Thus, while N deposition may not increase overall plant biomass in tropical forests with highly weathered soils (see section 2.1.3.1), the additional N may still be taken up and incorporated into foliar content, even on some N-rich soils, potentially via what has been termed “luxury consumption” (i.e., storage of additional nutrients beyond requirements).

2.1.3.3.2. Nitrogen Deposition and Tropical Nutrients: Soil Nutrient Availability

Given the limited uptake of additional N by plants in N-rich tropical soils, it is expected that N deposition will lead to increases in soil N availability. A Puerto Rican N fertilization experiment in two humid forests found that soil total N and mineral N concentrations increased with fertilization after 6 years of adding 50 kg N/ha/yr [Cusack, 2013; Cusack *et al.*, 2011a], indicating that a significant proportion of added N was

retained in soils. Similarly 125 kg N/ha/yr fertilization per year for 4 years increased concentrations of mineral N in a lowland moist forest in Panama [Yavitt *et al.*, 2011]. Nitrogen fertilization also increased total inorganic N in three types of subtropical forest on highly weathered soils in southern China after 2 and 6 years at three application rates (50, 100, and 150 kg N/ha/yr) [Lu *et al.*, 2009, 2014]. In this study, extractable NO_3^- concentrations increased at all levels of fertilization, while NH_4^+ increased only at high N addition levels. In an observational study, measures of the stable ^{15}N isotope in plant tissues in a moist tropical forest in Panama for 1968 and 2007 indicated an overall increase in soil N availability for the ecosystem, likely due to atmospheric N deposition, and similar longer-term trends were shown for a Thailand seasonal forest over the last century using tree rings [Hietz *et al.*, 2011]. Thus, even in N-rich tropical forests where plant uptake of additional N is minimal, added N can be retained in soils in significant quantities (Figure 6).

In addition to increased soil N availability in tropical forests, studies suggest that N deposition is likely to alter the forms of N available to plants and microbes. In soils, NH_4^+ is generally considered the most available form of N for plant and microbial uptake, while NO_3^- , which can also be utilized by plant and microbes, is more energetically costly to assimilate. A landscape-scale study of urban-proximate and remote forests in Puerto Rico showed that urban-proximate tropical forests had higher NO_3^- and lower NH_4^+ compared with remote forests [Cusack, 2013], indicating a shift in the nature of N available in soils. Similarly, in a seasonal lowland Panamanian forest, 7 years of N fertilization increased soil NO_3^- by 25%, whereas NH_4^+ declined, and total available N did not change [Sayer *et al.*, 2012]. Nitrogen fertilization in a Hawaiian N fertilization experiment on highly weathered N-rich soils also resulted in increased soil NO_3^- pools relative to NH_4^+ , with no change in total soil N [Lohse and Matson, 2005]. Thus, N additions to highly weathered N-rich soils appear to shift mineral N pools toward NO_3^- , which may have farther-reaching consequences on the environment.

In particular, NO_3^- is more likely than NH_4^+ to leach out of soils and contaminate groundwater and to be lost from soils via denitrification to greenhouse gases [Gundersen *et al.*, 2006; Johnson and Reuss, 1984]. Detrimental N losses from tropical forests have indeed been observed with N fertilization in a number of tropical studies. For example, in a southern China study where soil N increased with fertilization, 25–66% of added N leached out of soils over the 3 year experiment [Fang *et al.*, 2009]. The extent of N retention versus loss with N additions depends in part on preexisting N levels. For example, Hawaiian N fertilization experiments increased soil N availability in one rainforest that had N-poor young soils, but not in a rainforest on highly weathered N-rich soils [Hall and Matson, 2003]. Rather, in the N-rich forest there were rapid and large increases in denitrification, leading to nitrous oxide (N_2O) and nitric oxide (NO) off-gassing (further discussion on N_2O production and other greenhouse gases in section 2.1.3.5). Soil moisture can also play an important role in site-level differences in N losses, particularly because both leaching and off gassing are greater in wet, anaerobic soils. In Panama, N fertilization was slower to alter N losses in a lowland forest with N-rich soils, compared with rapid losses in N-poor soils in a montane forest site. In this case, N fertilization in the wetter montane site resulted in rapid increases in NO_3^- leaching, and N oxide emissions after 1 year, whereas similar changes were only observed after 9 years in the drier lowland forest soils [Corre *et al.*, 2010]. Thus, we can expect N deposition to result in detrimental losses of excess N from N-rich tropical sites and also from very wet tropical soils. Spatial variability in N losses with N deposition is therefore likely to reflect soil weathering status, as well as soil saturation levels across tropical landscapes.

Nitrogen deposition may also alter the availability of other mineral nutrients like P and base cations via a suite of biogeochemical mechanisms. First, elevated concentrations of NH_4^+ in soil solution can directly exchange for positively charged base cations on soil surfaces, bringing cations into solution and potentially making them more available. However, because excess NO_3^- is highly mobile in soils and readily leaches out, it can sorb and remove positively charged ions like base cations [Gundersen *et al.*, 2006; Johnson and Reuss, 1984]. Thus, mobilization of cations from soil surfaces into solution may increase their availability to plants in the short term, but chronic N additions are likely to lead to cation leaching losses in the longer term [Mitchell and Smethurst, 2008]. Second, increased NH_4^+ can lead to elevated nitrification to NO_3^- , and/or plant uptake of NH_4^+ , both of which release protons into soil solution and can increase acidity [Van Miegroet and Cole, 1984]. Added protons can also exchange for and displace positively charged cations on soil surfaces, again bringing more cations into soil solution and potentially increasing their availability and/or leaching. Also, with increased acidity labile forms of inorganic P (e.g., H_2PO_4^-) can react with or become adsorbed to the surfaces of oxides of aluminum, iron, or manganese, thus becoming unavailable for plants [Brady and Weil,

2008]. These effects of N deposition-related soil acidification are likely to be especially important in highly weathered tropical soils, which are already acidic and poorly buffered [Sanchez and Logan, 1992]. In summary, N deposition and related increases in acidity can have a progressive effect on base cation losses, as well as decrease soil P availability (although see positive effects of N addition on P availability via changes in microbial activity in section 2.1.3.3.3).

Several tropical field studies demonstrate that the processes described above are prevalent in highly weathered tropical soils when N is added. For example, an N fertilization study in two tropical forests in Puerto Rico showed significant mobilization of base cations over 5 years, with an increasing effect over time [Cusack *et al.*, 2016]. Similarly, increased acidity with N fertilization was related to increased mobility of base cations in a humid tropical Panamanian forest on highly weathered soils [Turner *et al.*, 2013]. Nitrogen fertilization in forests of southern China also significantly increased soil acidification after 2 years, with elevated leaching of base cations and Al mobilization [Lu *et al.*, 2009]. Longer-term N fertilization (6 years) in the same Chinese site further increased soil acidification, leading to declines in soil extractable nutrient base cations [Lu *et al.*, 2014]. More broadly, a meta-analysis of 106 experimental N fertilization studies globally, including 11 tropical studies with 34 separate sites, showed overall significant increases in soil acidity with N fertilization. The average pH decrease across the sites globally was 0.26 units, with similar declines in the tropical forest sites [Tian and Niu, 2015]. Across these studies, it is clear that N deposition has significant potential to increase soil acidity, mobilize base cations into solution, and potential promote leaching losses of base cations in tropical forests. More research on pH-related declines in available P with N additions in tropical soils is needed. In summary, the effects of N deposition on base cation availability are likely to shift over time, with increased availability followed by declines (Figure 6).

2.1.3.3.3. Nitrogen Deposition and Tropical Nutrients: Nutrient Recycling

Nitrogen deposition is also likely to alter patterns of nutrient recycling in tropical forests via changes in microbial decomposition and litterfall chemistry. In particular, added N may promote the production of some decomposer enzymes, which are made by microbes and by plant roots and require high levels of N to produce. A meta-analysis across temperate and tropical sites showed that added N generally increased the activity of enzymes that release available forms of inorganic P from organic matter (i.e., phosphatase enzymes), thus increasing soil P availability [Marklein and Houlton, 2012]. Similarly, N addition increased phosphatase enzyme activity in highly weathered soils in southern Chinese forests, showing that even in N-rich soils additional N can promote enzyme production to acquire scarcer nutrients [Zhu *et al.*, 2013]. Also in the southern China site, N fertilization increased pools of available inorganic P and decreased P in organic compounds, indicating elevated microbial decomposition [Huang *et al.*, 2014]. P acquisition enzyme activities similarly increased with N fertilization in one N-rich upper montane Puerto Rican forest, with no change in a lower elevation forest [Cusack *et al.*, 2010]. The net effect of N fertilization on decomposition may vary across tropical sites depending on background N availability. In Hawaii, N fertilization increased P acquisition enzyme activities in bulk soils at a younger N-poor forest, but not in N-rich forests on highly weathered soils [Olander and Vitousek, 2000]. In this study, it seems that microbial enzyme production in the highly weathered soils did not benefit from additional N, unlike the other studies reviewed above for N-rich sites. Also in Hawaii, however, N fertilization increased the production of P acquisition enzymes by roots specifically (as opposed to the bulk soils above, which include microbial enzymes), across a range of soil types with different background N levels [Treseder and Vitousek, 2001]. These changes improved plant acquisition of P, although the increases were not likely enough to completely alleviate P limitation to plant growth on highly weathered soils [Vitousek *et al.*, 2010]. Thus, most of the research to date suggests that N deposition may promote the recycling of P from organic plant tissue back into available inorganic soil pools. However, more studies are required to assess what site conditions determine the net effect of N additions on soil P availability, including the potentially negative abiotic effects of increased soil acidity (see above section 2.1.3.3.2).

In addition to decomposition, N deposition can also affect the recycling of P via plant uptake and return of P to soils via litterfall. For example, a southern China study that compared different forest types found that N fertilization increased litterfall P concentrations, resulting in increased available soil P in one site, but suppressed decomposition rates and thus decreased available soil P in another site [Lu *et al.*, 2012]. These results illustrate that plant release of P in litterfall and microbial release of P from litter via decomposition are both central to maintaining soil P availability, and the relative shifts in these processes will be important drivers of variation across sites. The net effect of N deposition on available soil P will depend both on abiotic effects of

increased acidity and on the biological effects of decomposition and plant nutrition, giving mixed results across studies (Figure 6).

In summary, N deposition in tropical forests on highly weathered soils can increase soil N availability and shift the composition of soil mineral N pools toward NO_3^- , potentially leading to N losses in groundwater and off gassing, detrimental to the broader environment. Nitrogen deposition may also alter P and base cation availability via abiotic soil processes like acidification, sorption/desorption, and leaching, as well as via biological nutrient recycling by microbial decomposers and plant litterfall. The net effects on P and base cation availability appear to vary across sites but may be predictable based on the soil and microbial characteristics.

2.1.3.4. Nitrogen Deposition and Tropical Biodiversity

Nitrogen deposition is affecting the most biodiverse places on Earth, termed “hot spots” by Conservation International, which contain very high vascular plant biodiversity. Two out of nine tropical forest biodiversity hot spots already have N deposition rates $>15 \text{ kg N ha}^{-1} \text{ year}^{-1}$, and five have rates $>10 \text{ kg N ha}^{-1} \text{ year}^{-1}$, with rates overall expected to continue growing [Phoenix *et al.*, 2006]. Nitrogen deposition has the potential to decrease tropical biodiversity via changes in competitive advantage among species, promotion of invasive species (see section 2.2.2.3), nutrient imbalances across trophic levels, and deterioration of soil quality through acidification [Hicks *et al.*, 2014]. Although little is known about the effect of N deposition on tropical forest biodiversity [Baron *et al.*, 2014], evidence is accumulating that elevated N can have direct and significant negative effects on the diversity of tropical plants, animals, and microorganisms.

In terms of plant biodiversity, most empirical evidence suggests that N deposition has the greatest negative effect on N-poor tropical forests, in secondary forests, and on understory woody and herbaceous species. In Hawaii, N fertilization led to declines in understory plant species richness (herbaceous plants and tree seedlings) in forests on N-poor soils, whereas plant biodiversity was not altered by N fertilization at a site with N-rich soils [Ostertag and Verville, 2002]. In contrast, in N-rich sites in southern China, N fertilization decreased understory plant species richness by 74% [Lu *et al.*, 2010], which was attributed to increased soil acidity, decreased base cation availability, and Al mobilization. A different southern China study in urban-proximate forests near Guangzhou city also found that understory herbaceous diversity was negatively correlated with N deposition, again related to increased acidity and decreased base cation availability [Huang *et al.*, 2012]. In a secondary forest in the Amazon, N fertilization also decreased plant biodiversity, promoting growth of just three tree species and reducing the abundance of other plant species after 6 years [Siddique *et al.*, 2010]. Thus, N deposition appears most likely to negatively affect understory plant biodiversity, both in N-poor sites and in N-rich sites that experience increased soil acidity or losses of other nutrients because of N deposition. These changes in understory biodiversity may alter the trajectory of forest succession by giving certain species a competitive advantage. Overall, these studies suggest a likely negative effect of N deposition on tropical forest plant biodiversity (Figure 6).

There is also some indication that N deposition may have a negative effect on soil invertebrate biodiversity. In mature forests on highly weathered soils in southern China, high N fertilization levels (100 kg N/ha/yr) caused declines in the density, group abundance, and overall diversity of soil macroinvertebrates, most likely related to soil acidification, while a lower N fertilization level (50 kg N/ha/yr) had no effect [Xu *et al.*, 2006]. Similarly, 2 years of N fertilization on highly weathered soils showed a negative effect on soil nematode species diversity in forests in southern China, which was attributed to declines in bacterial food sources and increased dominance by fungi [Zhao *et al.*, 2014]. Thus, the limited research available suggests that N deposition on highly weathered N-rich tropical soils is likely to negatively affect the soil invertebrate community (Figure 6), particularly if acidification occurs. These results have implications for soil food webs and decomposition processes.

Nitrogen deposition also can alter microbial biodiversity in tropical forests. A global meta-analysis, which included three tropical montane forests from Hawaii, showed that the abundance of mycorrhizal fungi decreased by 15% with N fertilization, with no difference between ectomycorrhizal and arbuscular mycorrhizal responses [Treseder, 2004]. In accordance with the broader results, the Hawaiian studies included in the meta-analyses found that N fertilization on highly weathered, N-rich soils decreased arbuscular mycorrhizal colonization of roots, but there was no significant effect in N-poor soils [Treseder and Vitousek, 2001]. The authors suggest that N fertilization in the N-rich sites shifted plant investment for P acquisition away from mycorrhizal symbionts, possibly favoring root production of P acquisition enzymes and thus decreasing the

abundance of mycorrhizae. Similarly, N fertilization on highly weathered soils in a seasonal forest in Panama resulted in decreased arbuscular mycorrhizal colonization of roots after 14 years [Wurzburger and Wright, 2015]. Like these results for these N-rich soils, N additions in tropical montane Ecuadorian rainforests on relatively N-poor inceptisols also showed decreased arbuscular mycorrhizal species diversity and root colonization rates after 2 years of N additions, apparently because of increased dominance by a few taxonomic groups of mycorrhizae [Camenzind *et al.*, 2014]. Thus, a handful of studies suggest that the biodiversity and abundance of mycorrhizal fungi may decline with N deposition in tropical forests, even when background N is high (Figure 6).

The community composition of other soil microbes also appears to shift in response to N fertilization in tropical forests, although detailed studies of bacterial and fungal genetic biodiversity are scarce. In Puerto Rico, experimental N fertilization increased soil microbial biomass after 6 years of fertilization in both upper and lower elevation N-rich forests, but community composition shifted differently in each site, with increased bacterial dominance in the lower elevation forest, and increased fungal dominance in the upper elevation montane forest [Cusack *et al.*, 2011b]. Nitrogen fertilization in a southern China forest also reduced the relative abundance of bacterial groups in the microbial community after 3 years [Li *et al.*, 2014]. Similarly, in another southern China study, N fertilization reduced bacterial dominance and increased fungal dominance in the microbial community, with notable declines in nitrifying bacteria [Liu *et al.*, 2013]. Whether N fertilization will favor fungal dominance over bacteria across a broader range of tropical forest sites remains to be seen. In contrast with these broad changes in microbial community characteristics, a genetic study of the diversity of N-fixing bacteria in Costa Rica on highly weathered ultisols found no response to N fertilization [Reed *et al.*, 2010]. These studies show that increased soil N availability is likely to alter the relative abundance of broad groups of microorganisms like fungi versus bacteria, but the nature of these shifts may be site specific. More research on detailed shifts in finer-scale genetic biodiversity within microbial clades is needed.

In summary, the above research demonstrates that N deposition in N-rich tropical forests can significantly reduce the biodiversity of understory plants and soil fauna and shift the character of the microbial community (Figure 6). The most negative impacts of N addition on tropical biodiversity are apparently related to secondary changes in the environment, like soil acidification and leaching of base cations.

2.1.3.5. Nitrogen Deposition and Tropical Disturbance Regimes

Nitrogen deposition has the potential to alter disturbance regimes in tropical forests on multiple scales. Most directly, increased foliar N with N deposition, which has been observed in some tropical sites on more N-poor soils (see section 2.1.3.3.1), may increase herbivory. Second, N deposition may increase tropospheric ozone in tropical forests via increased production of the ozone precursor gaseous nitric oxide (NO) from soils, causing potential leaf damage and declines in plant growth [Seinfeld and Pandis, 2006]. Finally, at the broadest scale, N deposition to wet, N-rich tropical soils can lead to increased production of the important greenhouse gases nitrous oxide (N₂O), and methane (CH₄), exacerbating the largest-scale disturbance, global warming [Tian *et al.*, 2015].

In areas where N deposition alters foliar chemistry, herbivore abundance and potential insect outbreaks may increase. A strong positive relationship between foliar N concentration and insect survivorship, growth and reproductive success has been demonstrated for many insect species at a global scale, including tropical sites [Lu *et al.*, 2008; Mattson, 1980; Scriber and Slansky, 1981]. However, the positive effect of increased foliar N on herbivory has not been consistently observed across tropical sites. In a lower montane Panamanian forests on N-poor soils, N fertilization increased foliar N concentrations for seedlings of nine palm species, with positive effects on herbivory [Andersen *et al.*, 2010]. Nitrogen fertilization for 3 years in a humid forest on nutrient poor soils in the Yucatan led to increased foliar N for one nonleguminous tree species (*Bursera simaruba*), but there were no effects on herbivory [Campo and Dirzo, 2003]. In this same study, foliar N concentrations were positively related to herbivory only in younger secondary forests (10 year old) for two N-fixing tree species (*Leucaena leucocephala* and *Lysiloma latisiliquum*). Finally, in lowland N-rich Panama forests, N fertilization increased foliar N concentrations by 11%, but there was no related effect on herbivory [Santiago *et al.*, 2012]. Rather, in this Panama study, herbivory responded positively to fertilization with P and K. From these few tropical studies, it seems that N deposition effects on herbivory and insect outbreaks are likely to be greatest in secondary and low-N tropical forests or via indirect effects on foliar content of other nutrients like P and cations (see section 2.1.3.3). These data indicate mixed effects of N deposition on herbivory (Figure 6).

Nitrogen deposition to tropical forests can also damage foliage via changes in tropospheric ozone levels. In particular, production of gaseous N oxides (NO_x) from soils can increase with added N, and these are important precursors to tropospheric ozone production. A review of 60 papers found that the largest N oxide emissions globally are in tropical forests, largely because of their high background levels of soil N and high soil moisture [Davidson and Kinglerlee, 1997]. With N deposition, these high background N oxide fluxes will only increase. Elevated N oxide emissions were observed from soils in N fertilized plots for a lowland and a montane forest in Panama over a 2–11 year period, with greater increases in emissions from the wetter soils the montane forest versus drier lowland soils [Corre et al., 2014]. Nitrogen fertilization also quadrupled soil N oxide emissions in a lower montane mid successional forest in Puerto Rico after 7 years [Erickson et al., 2001]. Given the increases in N oxide emissions expected for tropical forests with N deposition, and subsequent increases in ozone production, a global chemical transport model predicted that 48% of humid tropical forests will reach critical levels of tropospheric ozone (60 ppb) by 2100 [Fowler et al., 1999].

Leaf exposure to chronic ozone above this critical level can decrease photosynthetic rates and ultimately reduce plant growth, as has been observed in a large number of northern temperate forests [Ashmore, 2005; Wittig et al., 2007, 2009]. To date, this effect has not yet been well documented for tropical forests. The most extensively studied ozone effects on tropical forests have been in subtropical mountains outside Mexico City, where ozone has been linked to foliar damage and chlorotic mottling on broadleaved species, premature defoliation on pines, and a general decline in the abundance of sacred fir [de Bauer and Hernandez-Tejeda, 2007]. In summary, increased N deposition is highly likely to elevate tropospheric ozone levels within humid tropical forests (Figure 6), but the effects of elevated ozone on foliar tissue damage and plant growth in tropical forests merit further investigation.

Nitrogen deposition is also highly likely to increase greenhouse gas emission from tropical soils. Nitrogen in excess of plant demand in humid soils can increase off gassing of nitrous oxide (N_2O) via microbial denitrification. In particular, the high levels of soil moisture, soil N availability, soil microbial activity, and fluctuating soil redox common in many tropical forests make them dominant contributors to N_2O fluxes on a global scale [Breuer et al., 2000; Crill et al., 2000; Davidson et al., 2000]. Using a neural network approach and field observation data, one study showed that tropical forests are a major global contributor to N_2O emissions globally, contributing 1.0 Tg N yr^{-1} , out of a total of 3.4 Tg N yr^{-1} emitted from all natural terrestrial ecosystems globally [Zhuang et al., 2012]. Nitrous oxide is a much more potent greenhouse gas on a per molecule basis than CO_2 (i.e., traps more heat), and it currently contributes ~6% of observed global warming, with major fluxes coming from N-rich tropical rainforests [Werner et al., 2007]. Thus, if N deposition increases N_2O fluxes even more from tropical forests, this could have significant positive effects on global warming (Figure 6).

Nitrogen fertilization studies indicated that added N will indeed increase N_2O emissions from tropical soils, particularly in N-rich forests. Nitrogen fertilization in a Hawaiian forest on N-rich, highly weathered soils led to a 4% loss of added N as N_2O emissions, while losses from N-poor soils were <0.6% of added N [Hall and Matson, 1999]. Similarly, over an elevation gradient in montane Ecuadorian forests, N fertilization resulted in more rapid increases in N_2O emissions at lower elevation soils that were richer in N [Martinson et al., 2013]. Nitrogen fertilization also increased N_2O emission by 39% in a tropical secondary forest on highly weathered soils in China over 3 years [Wang et al., 2014], and N fertilization doubled soil N_2O emissions in a lower montane secondary forest in Puerto Rico over 7 years [Erickson et al., 2001]. Nitrogen fertilization in tropical agricultural soils confirms the positive effects of soil moisture and high soil N levels on N_2O emissions [Matson et al., 1996; Veldkamp et al., 1998; Weitz et al., 2001]. Some of this agricultural work has also indicated that N_2O emissions can be extremely variable temporally, with the highest emissions immediately following N additions [Brumme and Beese, 1992; Crill et al., 2000]. This is relevant to predicting how N deposition will increase N_2O emissions from tropical forests, because atmospheric N deposition varies temporally according to rainfall, dust production, and industrial or agricultural activity nearby. Clearly, N deposition has great potential to increase tropical forest N_2O emissions (Figure 6), with spatial variability likely predictable to some extent based on soil moisture and N status, and temporal variability requiring further investigation.

A second greenhouse gas likely to increase from tropical forests with N deposition is methane (CH_4). Nitrogen deposition has the potential to increase CH_4 fluxes from tropical soils because NH_4^+ is chemically very similar to CH_4 and can displace it during soil microbial processes that would otherwise consume CH_4 (i.e., methanotrophy) and convert it to the less potent greenhouse gas, CO_2 [Konda et al., 2010; Zhang

et al., 2008, 2011]. Methane, like N_2O , is a much more potent greenhouse gas than CO_2 on a per molecule bases and currently contributes about 25–35% of the climate forcing represented by CO_2 [Hansen *et al.*, 2000]. Tropical forests have been identified as important sources of CH_4 in atmosphere, emitting between 4 and 38 Tg CH_4/yr [do Carmo *et al.*, 2006; Sinha *et al.*, 2007]. Nitrogen fertilization experiments indicate that N deposition is likely to increase CH_4 production from tropical forests because of reduced methanotrophy. For example, in southern China, N fertilization at 50, 100, and 150 $\text{N ha}^{-1} \text{yr}^{-1}$ for 16 months increased CH_4 emissions by 6, 14, and 32%, respectively [Zhang *et al.*, 2008]. In another study at the same site, CH_4 emissions were 24% higher after 33 months of N fertilization at 150 $\text{N ha}^{-1} \text{yr}^{-1}$ [Zhang *et al.*, 2011]. The form of N added appears to have a large effect on the greenhouse gas emitted. A study on Acacia mangium plantations in Sumatra showing that N fertilizer that included NO_3^- significantly increased N_2O fluxes, whereas N fertilization that included NH_4^+ significantly increased CH_4 emissions [Konda *et al.*, 2010]. Across all of these studies, N fertilization promoted increased greenhouse gas emissions from tropical soils, representing a potentially large feedback to climate change (Figure 6).

In summary, N deposition has the potential to alter various aspects of tropical forest disturbance regimes. First, if N deposition alters foliar N, P or K concentrations, increased herbivory and even insect outbreaks may occur. Second, N deposition is likely to increase soil emissions of N oxide gases, which promote tropospheric ozone production, which in turn causes foliar tissue damage and may decrease plant growth. These first two effects of N deposition on tropical disturbance regimes are the least certain and merit increased research. Finally, N deposition is almost certain to increase emissions of the potent greenhouse gases, N_2O and CH_4 , from tropical soils. Tropical forests already produce globally significant quantities of these gases, and further increases could have severe negative effects on global warming.

2.2. Land Use/Land Cover Change

In this section we review different phases of land use/land cover change, and how these alter ecosystem properties and biogeochemical processes. Pressures such as export-oriented agricultural, urbanization, and natural resource extraction have converted large swathes of native, mature forests into cultivated land. In place of dense forest, many tropical regions are now characterized by a mosaic of agricultural fields, pastures, plantations, roads, and urban settlements. The ecosystem responses following these conversions are discussed in the deforestation section (section 2.2.1).

In some cases, agricultural and pastoral lands are eventually abandoned, allowing plants to regrow in what is generally unmanaged succession. When these abandoned sites are reclaimed by trees that resemble historical assemblages, they form a native secondary forest. If the trees are nonnative, they form a novel secondary forest. Both native and novel secondary forests are distinct from mature forests in that they are still in a phase of transition. Once a secondary forest achieves maximal biomass accumulation, it returns to the state of a mature forest, either native or novel, depending on the final species assemblage. Mature forests remain in this state until the next external disturbance, whether it is anthropogenic or environmentally induced. Trees, however, do not always regrow. In some instances, invasive herbaceous species take over an ecosystem. This transformation can occur either directly after a mature forest has been deforested, or after intermediate land uses have been abandoned. Herbaceous species can be so successful in establishing themselves that they completely displace native and nonnative trees, constituting a permanent state change. Three pathways are compared: (1) return to mature native forest, (2) alternate successional pathways to mature forest with novel species composition (i.e., including naturalized exotic species), and (3) permanent state change to invasive herbaceous cover. The relative ecosystem effects of forest regeneration versus invasion by herbaceous species in humid tropical environments are assessed in the unmanaged land cover change section (section 2.2.2).

A novel contribution for the land use/land cover section is a synthesis showing these potential trajectories of humid tropical forests after deforestation (Figure 2), with discussion of how these different trajectories alter ecosystem properties and feedback to climate change.

2.2.1. Deforestation in the Humid Tropics

Of the predominant global change factors assessed in this review, deforestation may pose the most immediate threat to humid tropical forests. Cities are rapidly expanding across the globe, placing greater pressure on tropical forests to meet global demands for export-oriented agriculture, timber products, mined materials,

and developable land [DeFries *et al.*, 2010; Hosonuma *et al.*, 2012; Seto *et al.*, 2012]. In the Brazilian Amazon, for example, the population increased from 6 million in 1960 to 25 million in 2010, and forest cover declined about 80% [Davidson *et al.*, 2012]. Although the net rate of deforestation is slowing down across the tropics, decreasing from a loss of 11.55 million hectares per year between 1990 and 2000 to a loss of 8.62 million hectares per year between 2000 and 2010 [Houghton, 2012], the overall magnitude of forest loss is still considerable and poses serious consequences for ecosystem processes and properties.

Many studies have documented agricultural expansion as the main driver of tropical deforestation [Food and Agriculture Organization (FAO), 2010; Geist and Lambin, 2001; Gibbs *et al.*, 2010; Houghton, 2012], but there are a number of other factors that also contribute to forest loss. Using data collected from 46 tropical and subtropical countries, one study estimated that commercial agriculture accounted for 40% of total deforestation, local/subsistence agriculture accounted for 33%, infrastructure and urban expansion each accounted for 10%, and mining accounted for the remaining 7% of forest loss [Hosonuma *et al.*, 2012]. In addition to deforestation, which here we use in reference to the complete removal of forests, tropical ecosystems are also greatly damaged by forest degradation resulting primarily from selective logging of mature, valuable individual trees (i.e., high grading). In some cases, partial logging and understory fires have damaged more forest area than clear-cutting, such as in the Brazilian Amazon during the late 1990s [Nepstad *et al.*, 1999]. Since there are less accurate baselines with which to measure the progress of forest degradation as a unique global change factor, this review focuses primarily on the ecosystem consequences of complete deforestation.

Using historical patterns of deforestation to make predictions about future changes in forest cover, it is likely that tropical deforestation will continue over the coming decades. Worldwide demand for agricultural products is expected to increase 50% from 2010 to 2050, which will require an estimated 10 billion new hectares of agricultural land [Tilman *et al.*, 2001]. Given the limited availability of undeveloped arable land in temperate areas, tropical regions are most likely to be impacted by increased demand [Gibbs *et al.*, 2010]. Additionally, if current trends in population density and urban expansion continue, then by 2030 urban land cover will increase by 120 million hectares, nearly tripling the global urban land area since 2000 [Seto *et al.*, 2012]. Although urbanization itself is a relatively small driver of forest loss, urban population growth is strongly correlated with demands for agricultural product exports from developing countries, further exacerbating the pressure on tropical forests [DeFries *et al.*, 2010]. Thus, the global demand for commercial agricultural commodities is growing, promising to make deforestation an ongoing and large-scale global change problem.

2.2.1.1. Deforestation and Tropical Plant Growth

It is clear from multiple assessments over the past decades that deforestation has caused substantial declines in NPP globally and in tropical ecosystems specifically. A seminal study on the human appropriation of NPP estimated that anthropogenic deforestation and degradation over the course of human history had reduced annual global forest NPP by 28% [Vitousek *et al.*, 1986]. A model of the global C cycle using satellite-derived maps of vegetation showed that continents with significant tropical forest cover (South America, Asia, and Africa) had net losses of NPP due to forest conversion to cropland, whereas the opposite was true for North America and Europe where fertilizer and irrigation had boosted agricultural productivity to NPP rates above preexisting vegetation (which in many cases was not forest) [DeFries *et al.*, 1999]. A recent biogeochemical process model of global vegetation concluded that land use changes had reduced historical NPP 7% in Latin America and the Caribbean, 12% in Sub-Saharan Africa, and 15–17% in South and Southeast Asia in the year 2000 [Haberl *et al.*, 2007]. The reduction in NPP represented by forest conversion is very slightly offset by aerosol production during forest burning, which increased Amazon NPP rates by 0.6% from 1998 to 2007 because of positive effects of aerosol production on diffuse radiation, light scattering, and illumination of parts of the canopy that would otherwise be shaded [Rap *et al.*, 2015]. Nonetheless, across these large-scale assessments, mature tropical forests consistently have greater plant growth than other land uses (Figure 7).

Recent research has provided more detailed estimates for comparing NPP in tropical forests to subsequent land uses after deforestation. A global model indicated that the conversion of tropical forest to cropland could result in a significant decline in NPP from 7.8 tC/ha/yr to 4.3 tC/ha/yr [Devaraju *et al.*, 2015a]. The conversion of forests into tree-based plantations has shown more mixed results than conversion to agriculture with respect to NPP. A pantropical study comparing NPP for forests versus oil palm, rubber, and cacao plantations in Indonesia, Cameroon, and Peru showed that rubber and cacao plantations had lower NPP versus

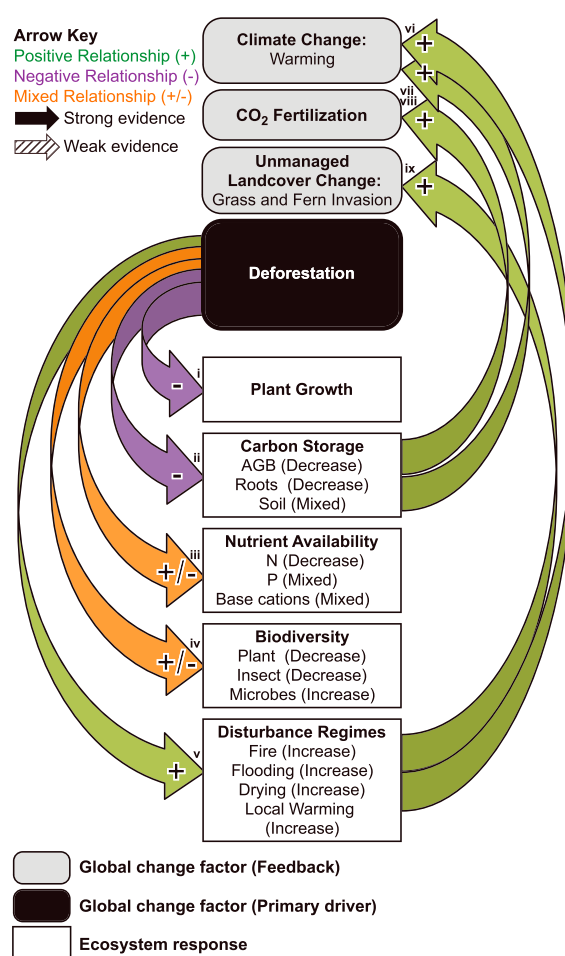


Figure 7. A synthesis of the effects of deforestation on plant growth, carbon storage, nutrient availability, biodiversity, and disturbance regimes is shown. Effects of deforestation are in comparison with subsequent agropastoral land uses. We include arrows showing feedbacks and effects on other global change factors. For the feedbacks, the negative or positive arrow represents the net effect of the featured global change factor back to itself (or to another global change factor), via changes in the given ecosystem process. Roman numerals refer to citations in Table S1 that support the direction and certainty of each arrow.

coarse roots), and soil (i.e., dead organic material) is removed or released to the atmosphere through fire and decomposition. Summed globally, deforestation and forest degradation is estimated to have contributed between 6 and 17% of anthropogenic CO₂ emissions between 2000 and 2005 [van der Werf et al., 2009], representing losses of C previously stored in tropical forests. Separating the relative contributions of tropical forest degradation versus complete deforestation in tropical ecosystems, one study found that degradation accounted for 10–40% of CO₂ emissions from tropical forests and deforestation accounted for 60–90% [Houghton, 2012]. Assessing the effect of deforestation on long-term C storage in tropical forests requires careful estimation of losses across the three main pools of C in forest ecosystems (aboveground biomass, belowground biomass, and soils). The below section reviews the evidence for how the C sink in tropical forest plant biomass and soils has changed with large-scale deforestation. This section reviews total C losses from tropical regions due to deforestation and compares C stocks in mature forests with those in subsequent agropastoral land uses.

2.2.1.2.1. Deforestation and Tropical Carbon Storage: Plant Biomass

Loss of aboveground plant biomass with deforestation represents by far the most certain decline in tropical C storage with deforestation. Using published data on forest C stocks in undisturbed forests versus cultivated lands, one study estimated that total C losses via CO₂ emissions from land use change in the tropics, including

natural forests (15–20 MgC/ha/yr, 10 MgC/ha/yr, and 23–26 MgC/ha/yr, respectively) but that oil palm plantations had the highest rates of NPP among land use types (30–33 MgC/ha/yr) [van Straaten *et al.*, 2015]. However, 50–60% of the biomass production in the palm plantations was removed through harvest of oil palm fruit, showing that rapid plant growth does not necessarily translate into C storage on managed lands (see section 2.2.1.2 below). Similar results were found in another study on conversion of mature tropical forests to rubber and oil palm monocultures in Sumatra, where NPP was smallest in rubber plantations (20.1 Mg/ha/yr) and greatest in oil palm monocultures (31.7 Mg/ha/yr), with intermediate NPP in mature tropical forests (24.1 Mg/ha/yr) [Kotowska *et al.*, 2015]. Again, more than half (54%) of the NPP in oil palm plantations was in fruit production and therefore harvested. Thus, when harvested biomass is excluded from the estimation of onsite NPP, mature forests have much greater NPP than dominant types of tropical plantations.

2.2.1.2. Deforestation and Tropical Carbon Storage

There is clear evidence that deforestation has greatly reduced the amount of C stored in tropical ecosystems. When forests are cleared or degraded, C stored in aboveground biomass (i.e., stems, branches, and leaves), belowground biomass (fine and

deforestation, forest degradation, and wildfires, was 1.1 PgC/yr between 1990 and 2000 [Achard *et al.*, 2004]. In this study, deforestation alone accounted for 91% of total CO₂ emission during the period (1.0 PgC/yr), with lost plant biomass contributing 78% of emissions from deforestation (0.78 PgC/yr), and the rest coming from soil C losses (0.22 PgC/yr). Based on this estimate and assuming that aboveground biomass accounts for 76% of live forest biomass in humid tropical forests [Mokany *et al.*, 2006], then somewhere between 0.59 and 0.78 PgC/yr of deforestation CO₂ emissions could have come from aboveground pools specifically, depending on the contribution of root death and decomposition to plant CO₂ emissions. More recent data suggest even greater C losses from aboveground pools with tropical deforestation. A combination of remote sensing and field data from 283 plots across tropical Africa, America, and Asia estimated that tropical deforestation resulted in CO₂ emissions of 1.0 PgC/yr between 2000 and 2010 due solely to losses of aboveground live biomass [Baccini *et al.*, 2012]. Thus, the emissions from aboveground biomass loss reported by Baccini *et al.* [2012] are nearly as high as the total deforestation emissions reported 8 years earlier by Achard *et al.* [2004]. In fact, deforestation rates actually declined from 1990 to 2010 [Houghton, 2012], so true emissions over the time period should have decreased. It is likely that the estimate from Baccini *et al.* [2012] is the most accurate assessment of C losses from aboveground biomass due to tropical deforestation, since it relied on newer and improved methods for estimating tropical C stocks. To put these emissions into context, annual CO₂ emissions from fossil fuel consumption were 7.2 PgC/yr between 2000 and 2005 [IPCC, 2013]. Thus, while not the lead cause of global CO₂ emissions, the loss of aboveground biomass in tropical ecosystems is still a key contributor elevated atmospheric CO₂ concentrations globally. In summary, deforestation in tropical forests has clearly led to a substantial decline in aboveground plant C storage (Figure 7).

Losses of belowground root biomass likely contribute a relatively small proportion of deforestation related emissions, although these estimates are much less certain because of the difficulties in measuring root biomass across large spatial scales [Cairns *et al.*, 1997] and the even greater difficulty of tracking the fate of dead root biomass to CO₂ emissions versus long-term storage of dead root biomass in soils after deforestation. Only a few studies have estimated biome-scale averages of root biomass as a proportion of total forest biomass in tropical ecosystems. Available estimates of root:shoot ratios range from 0.19 in a review of nine tropical evergreen forests [Jackson *et al.*, 1996], to 0.21 in a review of 39 studies in tropical upland forests [Cairns *et al.*, 1997], to 0.24 in a critical review that identified only 10 tropical moist forests with reliable data [Mokany *et al.*, 2006]. These estimates were made using field studies that reported root biomass from standard spatially distributed soil cores or pits (generally to depths of 40 to 100 cm) for fine to medium roots, and partial to complete excavation and/or allometry for coarser roots. Applying this proportion to reported 1.0 PgC/yr C emissions coming just from aboveground biomass for 2000–2010 [Baccini *et al.*, 2012], losses of root biomass could represent an additional maximum of 0.32 Pg C/yr if all root biomass were lost from soils after deforestation. It is unlikely that complete losses of dead root biomass would occur for several reasons. First, emissions from root decay are likely to occur with a lag, since the decomposition of root biomass is a slower process than the burning or clearing of aboveground biomass. Second, some unknown proportion of dead root biomass is most certainly retained in soil organic matter (SOM) pools over indefinite time periods, representing C storage [Rasse *et al.*, 2005]. Thus, while root death is likely to be 100% with forest clearance, this does not necessarily mean that all or even most of the forest root biomass C is lost as CO₂ emissions.

Furthermore, new land cover types like cropland, pasture, and plantations replace some live root biomass lost during deforestation. However, croplands and tropical grasslands typically contain less biomass in their root systems than tropical forests, with global averages of 0.15 kg biomass/m² and 1.4 kg biomass/m² in roots, respectively, compared to 4.9 kg biomass/m² in tropical evergreen forest roots [Jackson *et al.*, 1996]. Recent research suggests that even tree-based plantations do not completely replace the live root biomass found in mature forests. In Sumatra, Indonesia, for example, a study that used field measurements of aboveground biomass and fine roots to 50 cm depths, as well as estimates of coarse roots using allometric equations, found that mature tropical forests contained the greatest stocks of C in root systems (34 MgC/ha), followed by rubber plantations (8–20 MgC/ha) and oil palm plantations (6–9 MgC/ha) [Kotowska *et al.*, 2015]. Similar results were found in Sulawesi, Indonesia, where a study that sampled fine and coarse roots to 300 cm found that mature forests contained 31 MgC/ha within root systems, while cacao plantations contained only 4 MgC/ha [Leuschner *et al.*, 2013]. Overall, losses of live root biomass C stocks due to tropical deforestation are not

completely replaced by root systems in managed land uses, resulting in an overall decline in root C storage with tropical deforestation (Figure 7).

2.2.1.2.2. Deforestation and Tropical Carbon Storage: Soil Carbon

More C is generally contained in soils than in plant biomass in tropical forests, and soils contribute relatively less emissions following deforestation. Compared with plant biomass, soils are a relatively stable C stock because of the slower overall turnover time of SOM [Mayer, 1994; Torn *et al.*, 1997; von Lutzow *et al.*, 2006]. Also unlike biomass, soils are not directly targeted for removal during the deforestation process. Still, deforestation disrupts inputs of new C to soils because of reduced plant growth, litterfall, and root inputs. Also, disturbance to soil during deforestation can lead to C losses. For example, a pantropical review showed that forest disturbances removed soil C via increased erosion, and more aerated soils after disturbances had faster microbial decomposition and related CO₂ losses [Lugo and Brown, 1993]. Between 1990 and 2000, losses of soil C following deforestation were estimated to contribute 20% of net emissions from land use change in the tropics (0.22 PgC/yr), based on a review of soil C emissions data following land use change in the humid and dry tropics [Achard *et al.*, 2004]. In general, soil C losses vary spatially and are very field work intensive to measure, so this must be taken as a rough estimate of soil emissions due to deforestation. Nonetheless, the available data indicate sizeable proportions of soil C stocks are lost during tropical deforestation (Figure 7). Improved large-scale estimates of soil C losses for tropical forests should be an ongoing research focus.

The magnitude of losses of soil C with deforestation also varies greatly depending on subsequent land use. A global meta-analysis of 385 studies on land use change in the wet and dry tropics showed that conversion of mature forest into cropland (i.e., perennial and annual crops) reduced soil C storage by 25–30%, and conversion of mature forest into grassland (i.e., pasture) reduced soil C storage by 12% [Don *et al.*, 2011]. The magnitude of soil C change with deforestation varies considerable across sites. Some of the most dramatic losses of soil C have been documented for conversion of forest to tree plantations (palm oil, rubber, and cacao) in Indonesia, Cameroon, and Peru, where soils lost up to 50% of soil C under planted trees [van Straaten *et al.*, 2015]. On highly weathered ultisols and oxisols in southern Costa Rica, conversion of forest to pasture led to moderate losses of soil C (16 mgC/ha to 30 cm depth) [Krishnaswamy and Richter, 2002]. In this study, site-specific changes in soil physical properties like bulk density (i.e., compaction), acidification, and soil aggregate stability after clearing and burning led to variation among sites. In contrast with the above studies, a meta-analysis of soil C losses in the Amazon indicated that conversion of forest to pastureland increased soil C stocks by 4–10%, because of the large root systems of pasture grasses and retention of extant soil C accumulated under forest cover [Fujisaki *et al.*, 2015]. Thus, there is great variability in soil C losses after deforestation depending on subsequent land use and site characteristics, with studies giving mixed results (Figure 7). There are also far fewer studies documenting these changes than for changes in plant biomass C stocks, partly because soil C cannot be assessed quickly with remotely sensed images at a large scale like aboveground biomass. More extensive measures of where and how soil C stocks change in postdeforestation land uses would be extremely useful for understanding changes to the global C budget.

In summary, losses of aboveground plant biomass represent the greatest regional-scale reductions in C storage with deforestation in the humid tropics. Losses of belowground C storage in live plant roots may also be sizeable after trees are removed, but the proportion of dead root biomass that is lost from the ecosystem versus converted into long-term soil C is unknown. Finally, most studies show overall losses of soil C after deforestation, but there have been mixed results. Despite uncertainties in the absolute quantity of emissions, the overall trend that deforestation causes a net loss in terrestrial C stocks is clear (Figure 7), with these emissions contributing to elevated atmospheric CO₂ and global warming [IPCC, 2013].

2.2.1.3. Deforestation and Tropical Nutrient Availability

2.2.1.3.1. Deforestation and Tropical Nutrients: Soil Nutrient Availability

Research suggests that significant losses of N can occur from soils over time after deforestation, despite short-term spikes in N availability. In the short term, slash-and-burn forest clearance is widely practiced because it can improve soil fertility by adding nutrients mineralized from combusted forest biomass [Nye and Greenland, 1964]; however, retention of this N is often low and losses can lead to long-term declines in N availability. Deforestation and conversion to cultivation can reduce net nutrient use by plants. Aboveground, experimental slash-and-burn clearance for converting mature forest to pasture has also caused reductions of biomass N by as much as 68%, which is N that is ultimately lost from the ecosystem and will not replenish soil N stocks

[Kauffman *et al.*, 1995]. In a study comparing undisturbed tropical rainforests to 6 month old and 3 year old slash-and-burn sites in Venezuela, NH_4^+ and NO_3^- productions were higher in the slash-and-burn soils at both ages, but leaching of NO_3^- was also 3.6 times greater in burned sites than in forests, likely because new crop plants could not take up as much mineral N as was produced [Montagnini and Buschbacher, 1989]. Thus, increased levels of soil N were highly susceptible to rapid loss. In the Brazilian Amazon, losses of mineral N were also measured after forest slash-and-burn clearance, with 1 year old pastures containing an average of 48% less mineral N in forest topsoil compared to forested soils [Luizao *et al.*, 1992]. Over the longer-term data suggest that deforestation decreases soil N availability. For example, slash-and-burn conversion of tropical forests to rubber plantations in Indonesia led to significantly reduced N availability, even 12–17 years after land conversion [Allen *et al.*, 2015b]. Similarly, 30 year old tropical pastures in Southeast Mexico had only 5% of the N levels found in nearby mature forests [Roa-Fuentes *et al.*, 2015]. These studies show that deforestation and conversion to managed land uses has great potential to diminish soil N availability in humid tropical forests (Figure 7).

In comparison with N, phosphorus (P) is relatively less affected by slash-and-burn practices over the long term [Kauffman *et al.*, 1995]. Shortly after forest clearance, organic inputs from burnt biomass generally enhance soil available mineral P, similar to patterns for N. In Brazil, for example, soil available P increased during the first 3–5 years after conversion of forest to pasture, with proportionally more P held in forms that cycle quickly in burned sites, versus proportionally more P in occluded unavailable forms in forests [Garcia-Montiel *et al.*, 2000]. However, after 5 years available soil P levels declined in the pastures and unavailable P in occluded pools increased, suggesting only a short-term spike in available P following deforestation and burning. A meta-analysis of over 100 studies in the Amazon examining the conversion of forest to pasture over 5–20 years showed no difference in P availability for pastures of any age versus forests [McGrath *et al.*, 2001]. Conversion of forests to rubber plantations in Indonesia, in contrast, showed a decline in available soil P during 12–17 years after forest clearance, which was attributed to high acidity and the low acid-buffering capacity of soils [Allen *et al.*, 2015b]. Unlike soil N, which shows fairly clear trends of long-term decline after forest conversion, trends for P are more variable and appear to depend more on environmental conditions and subsequent land use (Figure 7).

Similar to N and P, soil base cations can increase for short time periods following deforestation. An experimental slash-and-burn study in Sri Lanka, Malaysia, and Thailand found that forest clearance resulted in considerable increases in base cation availability in the top 25 cm of soil within 4 months after burning, including a 10–100% increase in calcium (Ca), 15–45% increase in magnesium (Mg), and 6–80% increase in potassium (K) [Andriess and Schelhaas, 1987]. Clearing without burning has also shown a similar increase in soil base cations. Experimental clear-cutting in Costa Rica resulted in temporary increases in the availability of exchangeable Ca and Mg in the soil, but base cation pools had generally returned to preharvest values after 9 weeks [Silver *et al.*, 1996]. Increased mobility of base cations after deforestation can also be linked to increased leaching losses. For example, in a Puerto Rico experimental clear-cut, soil Ca and Mg levels decreased during the first year after clearing, likely due to leaching [Teh *et al.*, 2009]. This effect, however, was relatively short-lived, and soil pools returned to baseline levels by the second year after clearing in unmanaged sites. When conversion of forest to pasture leads to large changes in hydrology, however, persistent losses of nutrients may occur. In southwest Brazil, for example, increased storm flow discharge from sites converted to pasture led to ongoing leaching of K and Mg, with essentially no leaching from nearby forested sites [Germer *et al.*, 2009]. These findings suggest that initial increases in base cation levels can occur immediately after deforestation, but the long-term effect of subsequent leaching losses are not well documented.

In summary, deforestation, particularly with burning, increases soil nutrient availability in the short term. In the midterm to long term, however, N leaching losses are pervasive, whereas P availability appears to depend more on subsequent land use and factors like soil acidity. Thus, the net effect of deforestation on soil nutrient availability is variable across nutrients and over time (Figure 7).

2.2.1.3.2. Deforestation and Tropical Nutrients: Nutrient Recycling

In general, nutrient recycling rates decline when tropical forests are converted to alternative land uses (in the absence of fertilizer application). Since nutrients in tropical forests are largely bound in tree biomass, the removal of that biomass often corresponds to a decline in ecosystem nutrient levels. In a litterfall trap experiment in southwest China, for example, there was a marked decline in litterfall biomass in open land (3.3 ± 1.5 Mg/ha in grasslands and terraced tea fields), compared to nearby mature tropical forest

(11.1 ± 1.3 Mg/ha) [Paudel *et al.*, 2015a]. Similarly, in southeast Mexico, pastures had only 20% of the litterfall biomass present in nearby mature forests [Roa-Fuentes *et al.*, 2015]. In Puerto Rico a rainforest clear-cutting experiment also led to a 78–85% reduction in daily litterfall compared to intact forest [Silver *et al.*, 1996]. Decreased litterfall can have significant long-term consequences for soil fertility. In Venezuela, for example, agricultural crop production on highly weathered soils could only be sustained for three years without fertilization, pointing to declines in soil fertility following slash-and-burn forest clearance [Tiessen *et al.*, 1994]. Thus, reduced litterfall with deforestation is likely to both decrease nutrient recycling rates and decrease soil nutrient availability.

Deforestation can also alter nutrient recycling by slowing microbial decomposition of senesced plant tissues, which releases available nutrients into soils. For example, increased canopy openness leads to higher day-time temperatures and drying of plant tissues on the ground [Zhang and Zak, 1995]. Drying in particular can slow rates of litter decomposition in wet tropical forest ecosystems [Cuke and Srivastava, 2016; Paudel *et al.*, 2015b]. For example, in southwest China, a 1 year litter decomposition experiment showed faster decomposition rates in mature forests compared to open land (i.e., grasslands and terraced tea fields), with 7–10% greater mass loss at the beginning of the dry season in forests versus open land, followed by 25–44% greater mass loss at the beginning of the wet season, showing an increased difference between the two land covers as decomposition progressed [Paudel *et al.*, 2015b]. Similar results occurred in a litter bag experiment in western Kenya, where decomposition rates over a 5 week period were greater in mature tropical forest than in nearby farmlands and grasslands [Kagezi *et al.*, 2016]. Tree-based agricultural systems can also show declines in decomposition rates relative to mature tropical forests. In the Brazilian Amazon, for example, decomposition rates in polyculture rubber tree plantations were 60% slower than in mature forest [Hofer *et al.*, 2001]. In contrast, when fertilizers were applied in orange fields in northwestern Costa Rica, decomposition rates did not differ from those in nearby mature forests [Cuke and Srivastava, 2016], suggesting that progressive nutrient losses after deforestation may also contribute to slowed decomposition rates. In summary, deforestation appears to lead to decreased overall rates of nutrient recycling, both in terms of reduced litterfall returning nutrients in organic plant tissues to soils and reduced rates of microbial decomposition that release nutrients from organic tissues. These reductions in nutrient recycling rates are most certainly linked to reduced soil nutrient availability after deforestation (Figure 7).

2.2.1.4. Deforestation and Tropical Biodiversity

Deforestation is a major threat to plant biodiversity because it directly alters ecosystems and fragments undisturbed habitats. Much of the research looking at deforestation effects on biodiversity focuses on forest fragmentation and changes in biodiversity in remnant fragments. As forest fragments decrease in size so too does the species richness of leaf bryophytes, trees seedlings, and palms [Laurance *et al.*, 2011]. Subcanopy trees that are physiologically specialized for growing and reproducing in dark forest-interior conditions are especially vulnerable to increased light and drying that occurs with increased fragmentation and forest edge area (i.e., “edge effect”) [Laurance *et al.*, 2006]. In a 6.5 year long experiment in Amazonian forest fragments, increased edge exposure reduced the number of species in understory seedlings by 40% [Benitez-Malvido and Martinez-Ramos, 2003]. Forest fragmentation has also been documented as a key driver of plant species losses in Singapore, where nearly a quarter of all vascular plant species disappeared from 1819 to 2002 [Brook *et al.*, 2003]. Thus, in addition to complete removal of tropical forest biodiversity due to clear-cutting, remnant forests can also have reduced plant biodiversity because of changing abiotic conditions related to the edge effect (Figure 7).

Similar to effects on plant species, deforestation and forest fragmentation can have rapid and severe negative effects on animal biodiversity. In particular, decreased plant biodiversity within remnant forests can have a cascading effect through food webs, decreasing the diversity of higher life forms [Hutchinson, 1959]. In a 22 year study in the Amazon, there was a positive relationship between forest fragment size and animal biodiversity, with smaller forest fragments corresponding to a decrease in the species richness of primates, understory birds, beetles, and butterflies [Laurance *et al.*, 2002]. In a follow up study 10 years later, highly mobile species such as ant-loving birds, also disappeared from smaller forest fragments [Laurance *et al.*, 2011]. Research in Thailand found similar results, with near-total losses of native small mammals within 5 years of severe habitat reduction and fragmentation and within 25 years of moderate habitat reduction [Gibson *et al.*, 2013]. The positive relationship between fragment size and biodiversity provides ample evidence that small patches of tropical forest cannot maintain the biome’s high levels of biodiversity.

In addition to size, the proximity and connectivity of forest fragments with areas of continuous forest also impact biodiversity. In the Brazilian Amazon, negative relationships were shown between distance to large forest area and multiple biodiversity indicators, including endemic species richness, endemic species abundance, and endangered species (i.e., International Union for Conservation of Nature red listed) abundance [Magnago *et al.*, 2015]. In a pantropical study, the number of species guilds within 60 nature reserves dropped within 20–30 years after losses of nearby forest cover outside of the reserve boundaries occurred Laurance *et al.* [2012]. These findings confirm that effects of deforestation on biodiversity occur at a landscape scale, with negative effects extending beyond cleared areas into surrounding forest.

The diversity of soil microorganisms is also affected by deforestation, with an increase in functional diversity after disturbance, but a potential decrease in the extent of the gene pool for performing key functions like nutrient cycling. In the Brazilian Amazon, sites that were converted to pasture and cropland via slash-and-burn clearance showed greater functional diversity of microbes in agricultural versus forest soils [Mendes *et al.*, 2015]. However, in this study the abundance of genes related to key ecosystem functions (e.g., C, N, and sulfur cycling) was twofold to fourfold higher in forests, suggesting greater redundancy in the number of genera fulfilling these important ecosystem functions. Similarly, a history of slash-and-burn forest clearance in the Amazon corresponded to greater diversity of bacterial genera, with greater prevalence of certain functions (DNA repair, protein modification, and degradation) in cleared areas, likely related to adaptations of soil microbial communities to major changes in the soil environment with deforestation [Navarrete *et al.*, 2015]. Similarly, the abundance and taxonomic diversity of Verrucomicrobia, a recently described and very common phylum of bacteria, were higher in pasture soils with a history of slash-and-burn compared to mature or secondary forests, but the ecological function of this group is still unknown [Ranjan *et al.*, 2015]. Thus, fire and agricultural activities can increase the diversity of soil microbiota (Figure 7), yet this may represent a loss of redundancy in key functions, such that microbial communities in cleared lands may be less resistant to future disturbance.

In summary, deforestation, fragmentation, and losses of connectivity very clearly drive losses of plant and animal biodiversity (Figure 7). Changes in microbial diversity are more complex, with genetic diversity often increasing, but functional redundancy decreasing. The effects of changing microbial biodiversity in tropical soils with deforestation should continue to be a focus of ongoing research, since these changes may ultimately drive ecosystem functions like C and nutrient cycling.

2.2.1.5. Deforestation and Tropical Disturbance Regimes

Deforestation in the humid tropics has high potential to increase subsequent disturbances, including fire, drying, and flooding.

In particular, deforestation in humid tropical forests promotes wildfire associated clearing, which can be particularly severe during times of drought. In Peru, the fire return interval (i.e., the average period between fires) between 2000 and 2011 in humid montane forests was shorter than that of more fire-prone lowland Amazonian forest, most likely related to forest clearing and burning practices in the high-altitude region [Oliveras *et al.*, 2014]. In the Brazilian Amazon, fires intended to burn felled trees in preparation for crops or pasture, or to improve pasture forage, often spread as wildfire into undisturbed forests [Nepstad *et al.*, 1999, 2008]. The escape of fire beyond its intended boundaries is particularly pronounced during times of extended drought. In the Amazon, for example, the area burned by understory fire during the severe drought of 1998 was twice the area of annual deforestation, with 91% of the burned area occurring within 4 km of cleared areas [Alencar *et al.*, 2006]. Similarly, in Southeast Asia, the annual forest loss during the 1990s (1.5–1.7%) was significantly higher than in the 2000s (1.0%), likely due to widespread fire in Indonesia during the 1997–1998 drought [Miettinen *et al.*, 2011]. In the Amazon, the synergistic effects of deforestation and drought on fire are estimated to trigger up to 6.6 times more areas that undergo a permanent shift from rainforest cover to savannah (savannization) compared with either deforestation or drought alone [Staal *et al.*, 2015]. Deforestation therefore can greatly increase fire disturbance in a much broader area than is targeted for clearing (Figure 7), particularly during times of drought, suggesting a positive interaction with climate change as droughts become more common in this biome.

Forest fire can also increase susceptibility to subsequent wildfires, setting of a set of feedbacks that can create a wildfire disturbance regime in areas where fire was previously rare. First, fires create increased edges and openings in the forest canopy, which increase solar inputs to the forest floor, leading to drying and increased

fuel production both within cleared areas and in nearby forest areas [Nepstad *et al.*, 2001]. Second, edge effects in fragmented areas can also increase tree mortality in remnant forests due to drying [Laurance *et al.*, 1997], with the drying impact of edge effects (e.g., increased evaporative drying rates) shown to reach the center of 100 ha forest fragments in the Amazon [Didham and Lawton, 1999]. Third, tree cover loss reduces evapotranspiration over surface land, thereby reducing cloud formation, rainfall, and soil moisture, further increasing drying [Nepstad *et al.*, 1994]. Finally, fire and forest degradation can promote invasion by exotic species like fast-growing grasses that provide more fuel for fires [Silverio *et al.*, 2013] and may result in permanent land cover change (see section 2.2.2 and Figure 7). The recent increase in tropical forest fires release significant amounts of C to the atmosphere, with this biome contributing around 20% of global fire C emissions between 2001 and 2009 [Nepstad *et al.*, 2004; van der Werf *et al.*, 2010]. The CO₂ emissions from increased tropical wildfires create a positive feedback to climate change, further intensifying global warming [IPCC, 2013] (Figure 7).

Deforestation also impacts the hydrological cycles of tropical ecosystems by decreasing evapotranspiration. Since cleared areas have less leaf area and shallower rooting depths, less water is transferred from soils into the atmosphere via evapotranspiration [Laurance *et al.*, 2011]. A dynamic global vegetation and water balance model estimated that global land cover change from 1961 to 1990 reduced the flow of water from the soil to the atmosphere by approximately 7%, with the most substantial decreases in tropical southeastern Asia where forest transpiration has declined >100 mm per year [Gerten *et al.*, 2005]. This phenomenon has also been documented in field studies, such as in the Amazon Basin, where the daily average evapotranspiration from an evergreen forest was significantly greater than from a pasture during the dry season of 1992 (3.6 and 3.0 mm, respectively) [Nepstad *et al.*, 1994]. Thus, deforestation can drive a major shift in tropical forest hydrological cycles, which can both increase soil saturation and runoff and decrease local rainfall.

Because of increased soil moisture, deforestation has long been linked to increased flooding in tropical rainforest regions like the Amazon [Gentry and Lopezparodi, 1980]. With less transfer of moisture out of soils, deforestation can lead to increased river discharge, erosion, and sediment flows. These effects on rainforest hydrology have been documented to impact broad regions in the Amazon. In the Tocantins watershed of the Amazon basin, a 25% increase in watershed discharge between 1949 and 1988 was attributable primarily to deforestation [Costa *et al.*, 2003]. Similarly, in the Araguaia watershed in the Amazon basin, deforestation increased discharge by 16% in the 1990s compared to the 1970s [Coe *et al.*, 2011]. The increase in discharge from deforestation along the Araguaia River has been so great that 37% of small river islands disappeared between the 1960s and 1990s [Latrubesse *et al.*, 2009]. Increased erosion and flooding are thus likely outcomes of the large-scale changes in the hydrological cycle in tropical forests resulting from deforestation (Figure 7).

In addition to increased flooding, decreased evapotranspiration with deforestation has been linked to regional drying and reduced rainfall. Warm, dry air over clearings create a gradient in humidity that draws water vapor away from nearby intact forests, thereby reducing convection and rainfall over forested areas [Laurance *et al.*, 2011]. If complete tropical deforestation were to occur, annual rainfall would drop drastically across tropical regions, with the most severe effects predicted in the Amazon (−375 mm MAP decline), followed by Southeast Asia (−179 mm MAP decline) and Central Africa (−88 mm MAP decline) [Lawrence and Vandecar, 2015]. Drying and decreased rainfall have serious consequences for tropical forest ecosystem function (see section 2.1.1), including suppressed tree growth and increased tree mortality [Nepstad *et al.*, 2004]. Thus, somewhat paradoxically, deforestation can lead to both increased flooding and decreased rainfall in humid forest regions, shifting the hydrological cycle toward net losses from these moisture-dependent ecosystems.

Tropical deforestation also alters Earth surface properties in ways that feedback to climate change at broad scales. The decrease in cloud cover that results from declines in evapotranspiration makes the Earth surface darker and decreases albedo (i.e., the reflectiveness of Earth's surface), allowing more solar radiation to be absorbed by exposed dark canopies (i.e., warming effect). At the same time, however, the replacement of dark tree cover with lighter pastures or agricultural fields can increase surface albedo, reducing absorption of solar radiation (i.e., cooling effect). The net effect of these changes in albedo on climate will depend on the relative changes in cloud cover versus forest conversion. Also, deforestation causes a decline in surface roughness, suppressing vertical wind velocities, and reducing the transport of heat from the surface to the atmosphere (i.e., warming effect). At a global scale, the biophysical effects of large-scale tropical

deforestation are predicted to cause 0.1–0.7°C warming, effectively doubling the observed temperature increases since 1850 due to fossil fuel burning [Lawrence and Vandecar, 2015]. Within the tropics alone, large-scale deforestation has been predicted to cause warming of 0.2°C [Devaraju et al., 2015b]. Looking at tropical regions separately, total deforestation of the Amazon could increase regional temperatures by 0.8°C [Lejeune et al., 2015], and complete deforestation of the Congo basin could cause an even stronger warming response, raising local temperatures 2–3°C [Bell et al., 2015]. Clearly these numbers are upper estimates, since complete deforestation is unlikely. However, extensive deforestation across the tropics currently seems unavoidable, so a significant contribution of changes Earth surface properties to global warming is expected (Figure 7).

In summary, deforestation in humid tropical regions will and already has greatly increased regional disturbances like fire, flooding, and drying. At a global scale, the combined biogeochemical effects of deforestation are already contributing to greater temperatures.

2.2.2. Unmanaged Land Cover Change in the Humid Tropics

In the early 1990s, the total area of deforested and degraded tropical land worldwide (approximately 2 billion ha) surpassed the area of mature tropical forests (1.8 billion ha) [Lugo, 1997]. Despite this overall trend toward deforestation, abandonment of agricultural land is a growing phenomenon in some tropical regions, especially where economic development and urban expansion is occurring rapidly [Franco et al., 1997; Grau et al., 2003; Lambin et al., 2003; Rudel et al., 2000]. Once abandoned, there is a trend toward unmanaged forest regrowth (afforestation) on former agricultural land, particularly in Latin America [Grau and Aide, 2008; Lugo, 2004]. Thus, at regional scales, human migration to urban centers due to urbanization and economic development can directly promote forest regeneration and C storage in deforested lands [Ausubel, 1996]. While the afforestation process may return native tropical forest cover to some areas, the spread of exotic tree or herbaceous plants into these lands is a growing concern. Biological invasions are a major driver of global environmental change, endangering native species populations and potentially altering ecosystem structure and function [Vitousek et al., 1996, 1997b]. Thus, after deforestation there are different successional pathways that can occur (Figure 2), with very different implications for ecosystem characteristics. Comparison of the ecosystem-scale effects of secondary forest regeneration versus invasion by herbaceous land cover has received little attention, despite widespread concern about C storage and biodiversity maintenance in tropical forests.

Regeneration of native forests without active management (i.e., afforestation) can be particularly rapid in humid tropical regions because of high plant growth rates. Humid forest cover in Puerto Rico, for example, had been 90% converted to agriculture during the 1930s [Dietz, 1986], yet by 1991 humid forest cover had regained ~42% of its native area because of agricultural abandonment with economic development [Helmer, 2004]. While deforestation remains the dominant trend across the tropics, land use changes that restore native tropical forest cover without management or infrastructure costs have significant and positive implications for plant growth and terrestrial C storage at a global scale [Grau and Aide, 2008; Grau et al., 2003].

However, not all cleared and abandoned lands return to native rainforest cover. Abandoned areas in humid tropical forests can also undergo alternative successional pathways, with a high likelihood for the establishment and spread of exotic tree and/herbaceous species. Urban centers are a major source of entry for exotic plants species to degraded or deforested areas [Chytry et al., 2008; Cowie and Werner, 1993; McKinney, 2002, 2008]. In particular, the loss of forest canopy has been linked to the subsequent spread of shade intolerant exotic grasses, especially in tropical sites like where mature forest canopies are dense and native plants are adapted to low light for germination, as has been observed in northern Australia [Murphy et al., 2008] and southeastern Brazil [Siddique et al., 2008]. Alternatively, there has been an argument that tropical forests should be less susceptible to plant invasion than temperate sites because high species and functional diversity leaves little niche space for competitors [Fine, 2002]. However, there is no observational research to support a particular resistance of tropical forests to invasions following clearance.

Colonization of disturbed urban-proximate forests by introduced species could drastically alter successional pathways. First, if exotic trees successfully establish themselves and grow to reach the canopy, they may persist and dominate species assemblages in the long-term, especially if they are shade tolerant with high survival and growth under the canopy [Murphy et al., 2008]. Alternately, initial cohorts of exotic trees may facilitate the regeneration of native species if they improve site conditions, resulting in novel species

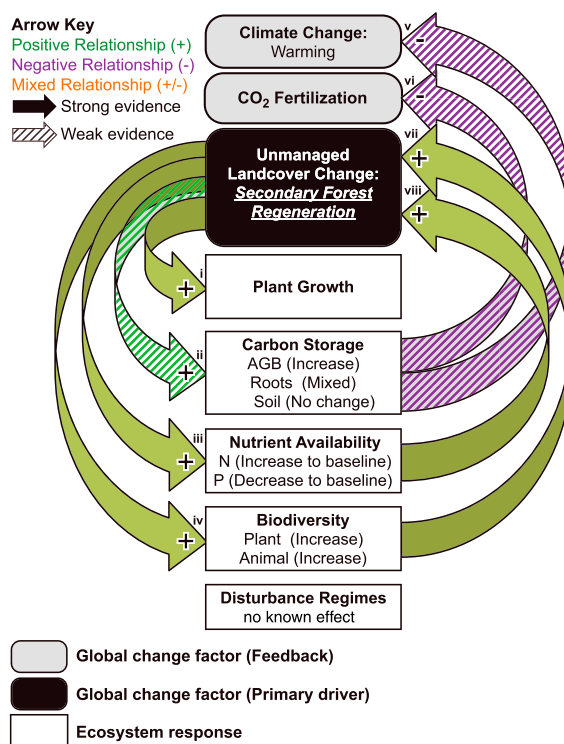


Figure 8. A synthesis of the effects of unmanaged secondary forest regeneration on plant growth, carbon storage, nutrient availability, biodiversity, and disturbance regimes is shown. Effects of secondary forest regeneration are in comparison with prior agropastoral land uses. We include arrows showing feedbacks and effects on other global change factors. For nutrient availability, the effect of secondary regeneration relative to agropastoral land uses is to restore “baseline” nutrient levels found in mature tropical forests. Because nutrient levels are restored overall, this arrow is assigned a positive sign. For the feedbacks, the negative or positive arrow represents the net effect of the featured global change factor back to itself (or to another global change factor), via changes in the given ecosystem process. Roman numerals refer to citations in Table S1 that support the direction and certainty of each arrow.

trajectory restores ecosystem properties found in mature secondary forests. Second, we compare ecosystem properties under these alternate successional pathways with the most prevalent prior land uses (agriculture and pasture). Our review suggests that if abandoned lands return to forest cover, either with native tree cover or novel species assemblages, there can be a general restoration of ecosystem properties and biogeochemical processes without any active management strategy (Figure 2). However, restoration of ecosystem function, even with afforestation, is likely to be unequal across ecosystem properties. For example, aboveground C storage may recover much faster than biodiversity. In contrast to secondary forest regeneration, invasive herbaceous species are likely to cause more extreme changes in ecosystem properties and may cause a permanent state change, with no return to natural forest absent active management strategies. Thus, for forest regeneration, we focus our assessment primarily on the comparison of ecosystem properties of secondary forests with prior land uses (Figure 8), since regeneration eventually restores most properties of mature forests. For invasion by herbaceous species, we focus our assessment primarily on the comparison of ecosystem properties in invaded lands with secondary and mature forests (Figure 9), since herbaceous invasions can represent a permanent alternative successional pathway.

2.2.2.1. Unmanaged Land Cover Change and Tropical Plant Growth

Unmanaged land cover change may affect plant growth by altering photosynthetic uptake of C, plant respiration, and/or allocation of C to new leaf, wood, and root growth. These effects on plant growth are likely to vary depending on whether regenerating plants are trees, shrubs, or herbaceous life forms and depending

assemblages [Lugo and Helmer, 2004], or could lead to complete restoration of native species compositions eventually. Alternately, exotic grasses or other herbaceous species may invade cleared sites, and if successful they can persist indefinitely and interrupt successional trajectories [Cusack and Montagnini, 2004; Kuusipalo et al., 1995; Parrotta et al., 1997; Powers et al., 1997], effectively converting tropical forests to exotic grasslands. Investigation of the landscape-scale effects of exotic herbaceous cover on soil C storage in humid tropical forests has received little attention, despite widespread concern about the long-term stability of tropical C stocks.

In this section, we assess the potential fates of abandoned lands in the humid tropics, highlighting the different ecosystem effects of (1) return of native forest cover via unmanaged afforestation; (2) exotic tree species establishment, either in monocultures or interspersed with native tree species to create “novel” ecosystems; and (3) exotic herbaceous species cover, which completely and often permanently converts forest area to grass or fernlands. There are two points of reference for these alternative successional trajectories. First, we assess the extent to which each

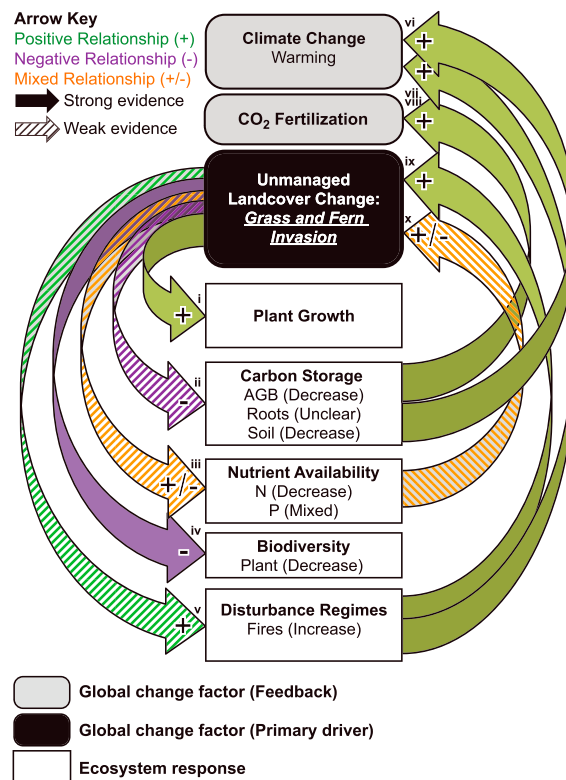


Figure 9. A synthesis of the effects of herbaceous plant invasions on plant growth, carbon storage, nutrient availability, biodiversity, and disturbance regimes is shown. Effects of herbaceous invasions are in comparison with the alternate successional pathway of forest regeneration. We include arrows showing feedbacks and effects on other global change factors. For the feedbacks, the negative or positive arrow represents the net effect of the featured global change factor back to itself (or to another global change factor), via changes in the given ecosystem process. Roman numerals refer to citations in Table S1 that support the direction and certainty of each arrow.

was faster biomass accumulation in rainforests and montane forests versus tropical deciduous forests [Anderson-Teixeira *et al.*, 2016]. Similarly, a review of 44 tropical studies showed that regrowth of native forests after land abandonment was faster in wet versus seasonal tropical forests during the first 20 years, with C accumulation on average $2\text{--}3.5\text{ Mg C ha}^{-1}$ per year during the initial stages of regrowth [Silver *et al.*, 2000]. Secondary forest regeneration also tends to be faster for lands that were used less intensively. For example, a review of 134 studies showed that tropical forest regeneration and plant growth in the Neotropics was faster on old pastures versus on previously cultivated land [Marin-Spiotta *et al.*, 2008]. Also, a study in the Amazon also showed that the number of trees in secondary forests, tree growth, and seedling growth were all faster on abandoned clear-cuts versus abandoned pastures that had a history of burning [Jakovac *et al.*, 2014; Williamson *et al.*, 2014]. Thus, plant growth rates in secondary forests are high overall, particularly during early successional phases when plant growth rates are much higher than in previous land uses or in mature forests (Figure 8).

Plant growth rates of invasive plant species are also likely to be high initially. Broadly speaking, invasive plants have physiological attributes that give them a competitive advantage to native species. First among these advantages, invasive species generally have higher relative growth rates than noninvasive species, which allows them to outcompete slower growing native species and reproduce more quickly [Pattison *et al.*, 1998; Rejmanek and Richardson, 1996]. For example, a global review of 79 studies comparing invasive plant species traits to resident native species found that invaders always had faster growth rates than native species [Ehrenfeld, 2003]. Another meta-analysis of temperate forest and grassland ecosystems assessed 199 studies and found that exotic tree and herbaceous species generally increased

on the new species composition. The potential effects of land cover change on plant growth and on ecosystem rates of NPP are reviewed below.

Potential plant growth rates in humid tropical regions are generally high, so forest regeneration after land abandonment can be rapid if trees are able to establish. Plant growth generally occurs most rapidly during the initial stages of forest recovery, eventually slowing as early successional species mature, die, and are later replaced by slower-growing species [Bonner *et al.*, 2013]. The rate at which plant growth and successional processes occur on abandoned lands is greatly dependent upon what types of plants colonize (e.g., trees versus grasses), as well as other local factors like climate, nutrient availability, and land use history. A recent data synthesis of 845 plots across the tropics showed that aboveground biomass in regenerating forests accumulated most rapidly during the first 20 years following clearing, with slower but positive biomass accumulation occurring up to 100 years, at which point regenerating forest biomass was similar to that in mature forests. In this study there

ecosystem NPP of invaded communities [Vila *et al.*, 2011]. Almost by definition, invasive species have inherently high growth rates, since this property is a necessary condition for their high competitiveness in new environments.

The broadly observed growth advantage of invasive species over resident native species has been observed in humid tropical sites, although the number of field studies is relatively low. A global meta-analysis of 125 invasive and 196 noninvasive plants in field studies and experimental gardens, including nine studies comparing growth rates for invasive species versus resident native species in tropical sites, found that invaders in tropical sites had particularly fast growth rates versus native species compared with other biomes, indicating the particular importance of fast growth as a characteristic of invasive species in the humid tropics [van Kleunen *et al.*, 2010]. A Hawaiian study comparing 34 native versus 30 invasive tree species also found that the invasive trees had leaf traits indicative of rapid growth [Baruch and Goldstein, 1999]. The invasive species in the Hawaiian study had 22.5% greater (leaf area):(leaf mass) ratios (i.e., specific leaf area), which is indicative of lower resource investment into leaf structures, shorter leaf life spans, and faster growth. Although we know of no tropical studies specifically comparing growth rates of invasive herbaceous species versus native plants, it seems likely that successful invasive herbaceous species also have a growth advantage. Thus, available data for invasive tree species suggest a competitive growth advantage against native humid tropical forest trees on unmanaged lands (Figure 9).

2.2.2.2. Unmanaged Land Cover Change and Tropical Carbon Storage

Unmanaged land cover change from agropastoral uses to secondary forests or invasive herbaceous cover may affect long-term C storage in humid tropical regions by altering the amount of C held in plant biomass both aboveground and belowground (i.e., in roots), and/or via changes in net ecosystem respiration, decomposition, and soil respiration losses of CO₂. The below section reviews the evidence for how the C sink in tropical forests has responded to large-scale land cover change. In general, secondary forest regeneration is compared with prior agropastoral land uses, whereas invasive herbaceous cover is compared with the alternative successional pathway of forest regeneration (Figure 2). Carbon stocks in mature humid tropical forests are also used for reference.

2.2.2.2.1. Unmanaged Land Cover Change and Tropical Carbon Storage: Plant Biomass

In terms of providing a C sink, secondary forests contain significant amounts of aboveground biomass compared with prior agropastoral plant cover. However, secondary forests generally do not acquire aboveground biomass levels comparable to mature tropical forests during the first decades of growth. In a data synthesis of 845 plots across the tropics, both aboveground and root biomass were greater for mature forests (>100 years old) versus young (<20 years old) and intermediate-aged (20–100 years old) forests [Anderson-Teixeira *et al.*, 2016]. For example, study in the eastern Amazon compared mature forests with secondary forest stands at 10, 20, and 40 years after agricultural abandonment and showed that mature forests had greater aboveground biomass and C storage than secondary forests because of more woody tissue, even though secondary forests had greater foliar biomass [Johnson *et al.*, 2001]. Similarly, 12–14 year old secondary forests on former pastureland in Amazonia contained only 25–50% of the biomass in nearby mature forests [Feldpausch *et al.*, 2004]. A recent study examining 4, 10, 20, and 35 year old stands in southern Mexico showed aboveground C storage to be 12, 29, 41, and 56 MgC/ha, respectively, whereas mature forests contained 100 MgC/ha [Aryal *et al.*, 2014]. Similar numbers were documented in the western Amazon Basin of Peru, where aboveground C storage was 40 ± 10 MgC/ha for secondary forests from 10 to 42 years old, versus 93 ± 39 MgC/ha in nearby mature forests [Gonzalez *et al.*, 2014]. For comparison with prior land uses, cultivated lands in the Amazon, for example, contained approximately 4 MgC/ha in aboveground plant biomass, and pastures without remnant trees had approximately 2 MgC/ha [Costa *et al.*, 2012]. Thus, while secondary forests generally contain < 50% of the aboveground biomass in mature forests during the first 40 years of regeneration, they still have sizeable C stocks in plant biomass relative to cleared lands or prior agropastoral vegetation cover (Figure 8).

Over the longer-term, reviews suggest that secondary tropical forests can accumulate aboveground plant biomass similar to mature forests within 60–80 years [Marin-Spiotta *et al.*, 2008; Silver *et al.*, 2000]. A number of field studies across the tropics confirm the potential for older secondary forests (>50 years) to achieve similar aboveground C stocks as nearby mature forests, including studies in southern Mexico, Peru, Brazil, and Puerto Rico [Aryal *et al.*, 2014; Gonzalez *et al.*, 2014; Hughes *et al.*, 1999; Marin-Spiotta *et al.*, 2007; Shimamoto *et al.*, 2014; Silver *et al.*, 2000]. The presence of particular tree species in older secondary forests

may even lead to aboveground C stocks that are greater than in mature forests. One chronosequence study of secondary forests of different ages in Puerto Rico found that 80 year old secondary forests had greater aboveground biomass than mature forests, because of elevated abundance of palms in the secondary forest [Marin-Spiotta *et al.*, 2007]. Also, in a 300 year forest regeneration chronosequence in Panama, native N-fixing tree species in secondary forests sequestered C nine times faster than native non-N-fixing trees [Batterman *et al.*, 2013], illustrating the potential importance of particular secondary forest species for C storage in secondary forests. Thus, secondary forests, if maintained and protected, hold great potential for recovering the large stocks of aboveground C storage in mature tropical forest ecosystems.

Belowground, live root biomass appears to increase during secondary forest succession, although studies assessing changes over time in tropical forests are scarce. Including dead and live root biomass, one review found that total root biomass across 21 tropical secondary forest studies did not change over time and was not different from mature forests [Hertel *et al.*, 2007]. In this study, however, the dead roots probably represented root biomass from prior agropastoral land uses. Looking only at live roots, one study in Costa Rica comparing secondary forests of 10–15 years and 40 years with mature forests found that live fine root biomass was greater in mature forests than in secondary forests [Hertel *et al.*, 2003]. Similarly, a forest secondary regeneration study in southwest China also found greater live fine root biomass in mature forests relative to 40 year old secondary forests [Muthukumar *et al.*, 2003]. Another study in Costa Rica also found that root biomass increased during the first 20 years of regeneration [Fonseca *et al.*, 2011]. Thus, while live tree fine root biomass may tend to increase during secondary succession, it seems that total fine root biomass (including dead fine roots) may not be different from root biomass in prior agropastoral land uses, providing somewhat mixed results (Figure 8).

In contrast with secondary forest regeneration, invasive herbaceous species in tropical forest regions clearly reduce aboveground C storage relative to secondary regeneration or mature forest cover [Ehrenfeld 2003; Lucas *et al.*, 1996; Williams and Baruch, 2000]. For example, in Puerto Rican humid forest areas, invasive grassland sites contained 15 MgC/ha in aboveground biomass [Cusack *et al.*, 2015], compared with 120–160 Mg C/ha aboveground in mature Puerto Rican forests with similar climates [Cusack *et al.*, 2011a; Marin-Spiotta *et al.*, 2007]. The aboveground biomass in the Puerto Rican invasive grasslands was also substantially lower than the range of 12–50 Mg C/ha in aboveground biomass found in the secondary tropical forests reviewed above. Even shrubby sites, like in tropical Argentina Gran Chaco, contain significantly less aboveground biomass than nearby mature forests (14 Mg C/ha versus 300 Mg C/ha, respectively) [Bonino, 2006]. While more studies are needed on this topic, it seems clear that invasive grasslands, fernlands, or even shrublands in humid tropical regions are certain to contain smaller C stocks in aboveground plant biomass than if tree cover were restored (Figure 9). The effects of these invasive herbaceous plants on C stocks belowground in live root also require further investigation.

It should be noted that more broadly, invasive plants do not always lead to reduced C stocks in biomass, with the ultimate effect strongly influenced by species traits and life form (e.g., tree versus herbaceous). In fact, a meta-analysis across ecosystem types showed that invaded ecosystems on average had 11.6% larger C stocks than native ecosystems, including plant and soil components [Vila *et al.*, 2011]. Another global meta-analysis also showed that aboveground C stocks in invaded ecosystems increased 177% relative to paired sites with native plants, root biomass C stocks increased 5%, and soil C stocks increased 7% [Liao *et al.*, 2008]. However, these two meta-analyses included few tropical forests, and most sites were invaded by species of similar life form (e.g., exotic grasses invading a native grassland). For the tropics, an analogous comparison would be for plant biomass in forest stands dominated by invasive trees versus native trees. In a Puerto Rican study, secondary forests with substantial numbers of exotic trees in the canopy (i.e., novel species composition) had less aboveground biomass than native secondary forests of similar age, although much of the difference was attributed to past land use [Lugo and Helmer, 2004]. Another Puerto Rican study found no significant relationship between stem biomass and the proportion of exotic tree species in the canopy [Cusack and McCleery, 2014]. Because of the limited number of studies on biomass in exotic-dominated versus native-dominated secondary forests on abandoned lands, and because of the many site and land use history factors affecting rates of plant growth and biomass accumulation, it is difficult to generalize whether invasive tropical trees generally decrease C stocks in novel secondary forests relative to native secondary forests.

2.2.2.2.2. Unmanaged Land Cover Change and Tropical Carbon Storage: Soil Carbon

In contrast with trends for plant C storage, there is a notable lack of difference for soil C stocks in secondary tropical forests versus mature forest sites. One review of studies in the Neotropics found no overall difference in

soil C stocks for secondary forests relative to mature forests, active pastures, or agricultural sites [Marin-Spiotta *et al.*, 2008]. Similarly, a chronosequence of secondary forests in Costa Rica during 15–60 years of regeneration showed no pattern of change in soil C stocks with forest age, and most differences among sites were related to soil characteristics [Jimenez *et al.*, 2008]. A comparison of soil C across a chronosequence of native species secondary forests in Puerto Rico also showed no difference in soil C stocks across secondary forest ages or pastures [Marin-Spiotta *et al.*, 2009]. Even in sites where soil C has been observed to increase relative to prior land use, additional C storage is often modest. For example, secondary rainforests of different ages in northeast Costa Rica had 80–87 Mg C/ha in soils, whereas nearby pastures had 77 Mg C/ha [Powers, 2004; Powers and Veldkamp, 2005]. One explanation for the general lack of soil C accumulation with forest regeneration is that pastures and agricultural sites also have significant stocks of soil C because of extensive root systems and rapid root turnover of herbaceous plants [Jackson *et al.*, 1997]. Also, older soil C from previous forest inputs is not all lost after deforestation and conversion to agropastoral land uses [Marin-Spiotta *et al.*, 2009]. Thus, soil C stocks show no clear pattern of change with secondary forest regeneration on abandoned lands (Figure 8), in part because there is not a clear pattern of soil C loss after deforestation (Figure 7).

In contrast to the generally null effect of secondary forest growth on soil C storage, invasion by herbaceous species after land abandonment appears to be associated with sustained reduction in soil C storage relative to forested sites. For example, soil C stocks in exotic grasslands in Puerto Rico contained only 70% of the soil C in nearby secondary forests for 0–10 cm depths, regardless of whether comparison forests were dominated by native or exotic tree species [Cusack *et al.*, 2015]. Similarly, areas invaded by exotic grasses, shrubs, and vines contained only 77% of the soil C found in mature semievergreen forests in Bangladesh for 0–60 cm depths [Islam *et al.*, 2001]. We know of no studies comparing soil C storage in tropical invasive grass or fernlands versus land uses prior to abandonment (e.g., pastures). From the few available studies, it is difficult to conclude whether exotic herbaceous invasions actually cause declines in soil C relative to secondary forest growth or whether these herbaceous species are just more competitive on degraded sites that already had reduced soil C. Nonetheless, there appears to be a trend of lower soil C storage in invaded grasslands compared to secondary or mature tropical forests (Figure 9).

In summary, secondary forest regeneration clearly has a net positive effect on tropical C storage relative to prior land uses and may lead to aboveground C storage similar to mature tropical forests over 60–80 years. This increase in C storage relative to prior land use in turn creates a negative feedback to atmospheric CO₂ and warming (Figure 8) [IPCC, 2013]. In contrast with secondary forests, the effect of invasive herbaceous species on ecosystem C storage is clearly negative relative to secondary or mature tropical forests, creating a positive feedback to climate change because of reduced C storage (Figure 9) [IPCC, 2013]. Comparing invasive herbaceous plant cover versus secondary forests, the former clearly have less aboveground biomass and also appear to have less soil C storage, although the mechanisms for reduced soil C storage in invasive herbaceous lands merit further investigation.

2.2.2.3. Unmanaged Land Cover Change and Tropical Nutrient Availability

2.2.2.3.1. Unmanaged Land Cover Change and Tropical Nutrients: Soil Nutrient Availability

Abandoned agropastoral lands commonly have depleted soil N pools relative to native forests. Depleted soil nutrients appear to either recover to baseline levels with forest regeneration or promote invasion by exotic species, which in turn appear to maintain low soil nutrient levels. In particular, soil compaction and topsoil removal (e.g., erosion) associated with agricultural land uses can decrease the availability of N and other nutrients in surface soils [Woodward, 1996]. A forest chronosequence study in the Amazon showed that younger secondary forests were characterized by low soil N availability, presumably because of losses after deforestation [Davidson *et al.*, 2007]. In this study, older secondary forests promoted high soil N levels similar to mature forests, indicating that soil N levels can recover with afforestation on decadal timescales. Similarly, land cleared for roads in Puerto Rican montane rainforests had lower total soil N levels than mature forest 6 months after clearing but recovered to high background levels of soil N found in mature forests after 35 years of unmanaged forest regeneration [Olander *et al.*, 1998]. Many tropical forests have native N-fixing trees, which can serve as early successional species that ameliorate soil conditions and increase soil N levels. For example, a 300 year chronosequence study in Panama also showed that the number of native N-fixing trees and soil N levels peaked in 12 year old secondary forests (71% of trees), suggesting that N fixers played a crucial role in restoring soil N levels [Batterman *et al.*, 2013]. Similarly, a forest regeneration chronosequence in the Amazon showed that younger and intermediate-aged secondary forests (2–4 and 12–25 years old,

respectively) had higher proportions of native N-fixing trees in the canopy (91% and 88%, respectively), compared to older secondary forests (>25 years old, 57% N fixers), with native N fixers playing a central role in restoring soil N levels [Gehring *et al.*, 2005]. Thus, forest regeneration appears to increase soil N availability from depleted levels back to the relatively high levels found in mature tropical forests (Figure 8).

However, the relatively low soil N levels found in abandoned lands may promote species invasions. In particular, N depletion in humid tropical soils can have a negative effect on the establishment of native tropical forest plants [Reiners *et al.*, 1994], since native plants are adapted to the high background N availability in highly weathered tropical soils. Thus, for humid tropical sites, soil disturbances that deplete naturally high N pools have been shown to favor introduced species adapted to low soil N, as has been observed in Hawai'i [Funk and Vitousek, 2007]. Species invasions in N-poor soils in the tropics exhibit opposite patterns from those observed in high latitude sites, where increased N availability in N-poor soils (e.g., from N deposition) favors the spread of exotic N-loving plants [Howard *et al.*, 2004]. In both tropical and temperate sites, a change to the natural N status therefore can give a competitive advantage to exotic species better adapted to the new conditions.

In the event that exotic species establish in abandoned lands, the characteristics of the particular establishing species will have a large effect on subsequent N availability. For example, plants with N-fixing capabilities in the Fabaceae family are highly likely to successfully establish in N-poor soils, subsequently increasing soil N levels [Binggeli, 1996; Pysek, 1998]. Although many tropical forests do have native N-fixing plants, there are tropical areas where native N-fixing plants are rare or absent [Allen and Allen, 1981]. In areas with degraded soils and no native N fixers, exotic N fixers can be particularly successful invaders. For example, exotic N-fixing plants have been very successful invaders in Hawaiian montane tropical forests and have been shown to increase soil N availability over time [Vitousek *et al.*, 1987]. Unlike native N-fixing trees, however, invasive N fixers like those in this Hawaiian study increase soil N to levels greater than under native forest and maintain dominance over a site rather than diminishing like native early successional N-fixing plants would. Similarly, a study in Puerto Rico compared two sets of forest chronosequences: one with all native, non-N-fixing trees, and one that included an exotic N-fixing tree in older secondary forests [Erickson *et al.*, 2001]. In this study, soil N levels in late successional forests were higher than in pastures, as expected. However, in the chronosequence with the exotic N fixer, midsuccessional secondary forests (25–45 years old) with the N-fixing species had higher soil N availability than mature native forests, and the highest N₂O gas emissions. These studies show that native N-fixing species during secondary forest regeneration can help restore high soil N availability levels typical of mature tropical forests on highly weathered soils (Figure 8). At the same time, however, establishment of exotic N fixing trees may lead to even more elevated soil N levels compared with mature forests, potentially leading to elevated gaseous N losses.

Ultimately, soil N availability across abandoned sites is generally spatially variable, even across nearby areas. The spatial variability is due both to past land use intensity and the species composition of regenerating ecosystems. For example, secondary forests along an urban-rural gradient in Puerto Rico showed very high variability in soil N levels among nearby secondary forest stands [Cusack, 2013]. In these sites, some of the spatial variability in soil N was related to varying abundances of exotic N-fixing trees across secondary forests [Cusack and McCleery, 2014], with additional variability likely caused by differences in land use history.

In contrast to the trends with forest regeneration, colonization of abandoned lands by herbaceous species may cause soil N availability to remain low or even diminish. For example, invasive species like grasses often have greater resource use efficiency than native species, thus requiring less nutrients for equal growth, which confers them a competitive advantage against native species in nutrient-poor sites [Baruch and Goldstein, 1999; Ehrenfeld, 2003]. Invasive plants with low N requirements and high nutrient use efficiency may even exacerbate declines in soil N if root uptake is lower than availability, which could lead to off gassing or leaching losses of excess N. For example, exotic ferns in Hawaiian wet forests led to decreases in available soil N because of reduced N uptake relative to forests and subsequent leaching of mobile mineral N [Allison and Vitousek, 2004]. Similarly, sites under invasive herbaceous cover had 82% less soil N relative to nearby forests in Bangladesh [Islam *et al.*, 2001]. Also, there was a trend of decreased soil N availability in exotic grasslands versus secondary forests in Puerto Rico [Cusack *et al.*, 2015]. In addition to nutrient losses due to reduced nutrient uptake by herbaceous species, the complete replacement of a forest structure with herbaceous plants can reduce inputs of nutrients to soils. First, large forest canopies

are no longer present to “scrub” mineral forms of N from the atmosphere and deliver these to soils [Clark *et al.*, 1998; Schulze, 1989]. Second, loss of trees signifies a loss of stemflow, by which rainfall is delivered to soil down tree trunks, and stemflow tends to enrich precipitation inputs to soils with nutrients like N by 10–50% [Levia and Germer, 2015]. Thus, N depleted soils in abandoned tropical lands are very likely to remain N depleted or become even poorer in N if there is invasion by herbaceous non-N-fixing species (Figure 9).

Soil available P has shown somewhat different trends than soil N during forest regeneration. While N generally shows a gradual accumulation during tropical forest succession, P availability can spike and then decline over time, eventually reaching the low levels typical in mature tropical forests on highly weathered soils. In a chronosequence in the Amazon, younger secondary forests were characterized by relatively high P, and P became scarcer over longer term succession, reaching typically low levels in mature forests [Davidson *et al.*, 2007]. Similarly, after experimental clear-cutting in Puerto Rico, soils had elevated soil P availability during the first 2 years, but P levels then returned back to lower baseline levels after 5 years of forest regeneration [Teh *et al.*, 2009]. Soils on former roads in Puerto Rico also confirmed these trends, with 6 month old clearings showing an increase in soil P concentrations, but P availability then decreased to levels in mature forest after 35 years of natural forest regeneration [Olander *et al.*, 1998]. Thus, after an initial spike in P, forest regeneration appears to restore naturally low levels of soil P, indicating that P availability changes over the successional process in tropical forests (Figure 8).

In contrast with the trends of diminishing P with secondary forest regeneration, some exotic plants may have the capacity to increase soil P availability. For example, N-fixing plant establishment in abandoned lands may increase P availability, both because N-fixing plants can elevate available soil P by producing more N-rich phosphatase enzymes and because N fixers can have greater colonization by mycorrhizal fungi that acquire P relative to other plants [Nasto *et al.*, 2014]. For example, invasion of abandoned lands by N-fixing herbaceous species in southeast Brazil led to elevated P content of tissues in other (non-N fixing) plants [Siddique *et al.*, 2008], indicating that the N fixers elevated soil P availability for the plant community in general. More research is needed on the potential for N-fixing species to ameliorate soil P availability on abandoned lands.

In summary, forest regeneration on abandoned lands, with or without native N-fixing trees, is likely to have a positive effect on soil N availability, and return soil P availability to naturally low levels. Establishment of exotic N-fixing species during secondary regeneration may actually elevate soil N availability above naturally high N levels found in mature forests, and may also increase soil P availability (Figure 8). In contrast, invasion by non-N-fixing herbaceous species, like exotic grasses, can maintain low N availability on abandoned sites, which in turn may favor continued dominance of species that are competitive at low N availability, resulting in a positive feedback loop that sustains exotic herbaceous cover (Figure 9). The direction of causality between low soil N levels and grass invasion in humid tropical sites merits further investigation.

2.2.2.3.2. Unmanaged Land Cover Change and Tropical Nutrients: Nutrient Recycling

Even in secondary forests that do not contain N-fixing species, soil nutrient availability can improve relative to prior land uses because of accelerated nutrient recycling. Trees, in general, can increase the nutrient status of topsoils via litterfall, and by promoting more rapid decomposition processes, thus accelerating nutrient cycling overall, and increasing soil mineral nutrient availability in particular [Grubb, 1995]. Secondary forests may restore litterfall production on abandoned lands relatively rapidly. In a Puerto Rican chronosequence study, secondary forests achieved litterfall production and decomposition rates similar to mature forests after just 10 years [Ostertag *et al.*, 2008], showing much faster recovery for nutrient recycling than was observed for aboveground biomass [Marin-Spiotta *et al.*, 2007] (and see section 2.2.2.2.1). In fact, secondary forests may have more rapid nutrient recycling than mature forests. A 10 year study in Xishuangbanna, China, found that litterfall production and decomposition rates were greater in a secondary forest versus a mature seasonal tropical forest, indicating more rapid N cycling and greater soil N availability in the secondary forest [Tang *et al.*, 2010]. Exotic herbaceous species may also accelerate nutrient recycling if litter production is high. For example, exotic ferns in Hawaiian wet forests increased nutrient cycling rates because of increased litterfall production, although increased N availability ultimately led to N leaching [Allison and Vitousek, 2004]. In general, nutrient recycling rates are likely to increase with either herbaceous invasions or forest regeneration relative to prior agropastoral uses, during which plant biomass was likely removed from sites.

2.2.2.4. Unmanaged Land Cover Change and Tropical Biodiversity

While there is great potential for forest recovery on abandoned lands in humid tropical forests, secondary forests on abandoned lands often have decreased biodiversity or altered species composition relative to mature tropical forests, particularly during early stages of succession [Chazdon, 2003]. Nonetheless, fast-growing tree seedlings can establish in abandoned lands, start forest successional processes, and promote regeneration of native tree biodiversity. If successfully established, native or exotic trees may promote understory regeneration by shading out grasses and facilitating the influx of slower-growing mature forest species that germinate in diffuse light [Grubb, 1995]. For example, secondary monodominant stands of exotic African tulip tree (*Spathodea campanulata*) in Puerto Rico had diverse native seedling communities growing in the understory and no germination of the exotic species [Cusack and McCleery, 2014], indicating that these exotic trees require high light levels to germinate and that sites initially colonized by this tree are likely to restore native plant biodiversity in the long term. Among secondary forests, the amount of shade produced by the canopy species can have a significant effect on restoration of understory biodiversity, with high sun and extreme shade limiting understory seedling establishment, as has been observed across humid tropical sites in Southeast Asia and Central America [Cusack and Montagnini, 2004; Kuusipalo et al., 1995; Parrotta et al., 1997; Powers et al., 1997]. Thus, early successional trees that create intermediate shade in the understory are likely to promote native species biodiversity in secondary forests (Figure 8).

Invasion by herbaceous species is particularly likely in abandoned lands with rapidly growing grass seeds in the soils. The seed bank in soils of abandoned lands is likely to reflect prior land use, and this will drive initial successional stages after abandonment. For example, the soil seed bank in an abandoned pasture in Chiapas, Mexico, contained 99% nonnative herbaceous seeds [Lopez-Toledo and Martinez-Ramos, 2011]. Rapid germination of herbaceous species from the seed bank can limit the success of woody species germination, because fast-growing grasses or ferns can quickly create too much shade at ground level for tree species to germinate. This extreme shading effect, in combination with degraded soils and lack of nutrients, has prevented the germination and initiation of tree seedlings in invaded grasslands across sites from Southeast Asia and Central America [Kuusipalo et al., 1995; Parrotta, 1992]. In these cases where invasive herbaceous species completely convert a forest to grassland, recovery of biodiversity is stalled indefinitely and may even be lower than the plant communities present during prior agricultural or pastoral activity (Figure 9).

While high light requirement is often a common trait of invasive plants, they are not necessarily shade intolerant and thus can persist as part of the biodiversity in secondary forests. A greenhouse experiment with seven Hawaiian woody species (three exotic and four native) and two herbaceous species (exotic *Bidens pilosa* and native *Bidens sandwicensis*) found that although exotic species of both life forms had significantly higher growth rates in sun versus natives, exotic species also had higher growth than native species in partial and full shade [Pattison et al., 1998]. The capacity for exotic species to regenerate in shady conditions will determine their persistence in ecosystems beyond early successional stages. Persistence of exotic species is not necessarily detrimental to biodiversity. If exotic trees do not subside, they may become integrated into diverse forest ecosystems with native species (i.e., become “naturalized”). For example, secondary forests on old coffee plantations in Puerto Rico contained highly diverse mixtures of native and exotic tree species in what has been termed “novel ecosystem” composition, although these sites still had diminished native tree diversity compared to undisturbed native forest stands after 60–80 years [Lugo and Helmer, 2004]. Thus, if tree species are able to establish on abandoned lands and shade out herbaceous plants, then it is highly likely that successional processes will restore biodiversity well above levels found in prior land uses, even if exotic tree species remain present (Figure 8).

Over the long term, whether secondary forests on abandoned lands fully recover plant biodiversity varies greatly across sites. In southern Brazil, 10 and 25 year old secondary forests also had ~50% of the species present in nearby mature forests [Piotto et al., 2009]. Similarly, in the Dominican Republic secondary forests contained 40% of species in adjacent mature forests, with a particularly high occurrence of native drought tolerant species in the secondary forest [Martin et al., 2004], indicating that soil conditions on the secondary sites were likely still degraded and held less soil moisture (e.g., due to compaction or reduced organic matter) relative to undisturbed sites. In a Brazilian study, 19 year old secondary forests also had just 59% of mature forest species [Barlow et al., 2007]. On the slower side, a Jamaican 150 year old secondary forest on old coffee plantations contained only 54% of the species occurring in a nearby mature forest [Chai and Tanner, 2011]. Similarly, even after 50–150 years of recovery following a logging disturbance, secondary forests in

Madagascar still had less overall species richness than mature forests and were dominated by exotic fruit trees [Brown and Gurevitch, 2004]. There are also examples of more rapid recovery of biodiversity, such as 19 year old forests on abandoned agricultural lands in wet tropical forest of Kenya, which had species diversity similar to nearby mature forests [Mullah *et al.*, 2012], and Chinese secondary forests that had nearly the same diversity index as nearby mature forest [Bu *et al.*, 2014]. Thus, secondary forests across a range of sites can recover ~50% of native biodiversity in the first few decades of growth, but recovery of biodiversity can occur much faster or slower, depending on site conditions like soils and proximity to mature forests. Nonetheless, these studies demonstrate that secondary forests do restore a large proportion of native forest plants diversity compared with prior land uses (Figure 8).

The effects of past land use on soil conditions in particular can influence the restoration of biodiversity in secondary forests. First, the level of soil degradation caused by past land use can severely limit tree growth. One study comparing recovery of native species biodiversity in the Amazon across different land uses found greater native biodiversity on abandoned clear-cuts versus abandoned pastures with a history of burning, with ~2.5 times more native plant species returning on abandoned clear-cuts than on abandoned pastures over 25 years [Williamson *et al.*, 2014]. In this study, the abandoned pastures were dominated by a single fire-adapted tree species that sprouted quickly on the pastures, outcompeting species growing from seed [Wieland *et al.*, 2011]. Similarly, abandoned pasturelands in advanced stages of degradation in Sri Lanka showed minimal recovery of native forests [Ashton *et al.*, 2001]. Likewise, secondary forests on lands that had previously been bulldozed for agriculture in Puerto Rico had only half the diversity of sites that were not bulldozed [Chinea 2002]. And, secondary forests in the Western Ghats of India on relatively more degraded soils had greater abundance of exotic trees versus native trees on less disturbed soils [Joshi *et al.*, 2015]. In contrast, sites with relatively little tilling and fertilizing may recover biodiversity more quickly, as evidenced by 30 year old secondary tropical forests where biodiversity already resembled mature forest stands [Chazdon *et al.*, 2009]. It seems that when soils are extremely degraded at the time of abandonment, and therefore very different from native soils, it is more difficult for native biodiversity to be restored via secondary successional pathways. These sites may also be more susceptible to invasion by herbaceous plants, with low resulting plant biodiversity.

Tree species dispersal into abandoned lands is also highly dependent on the landscape-scale biogeography of nearby forests. The distance to a diverse mature tropical forest is likely one of the main factors determining the eventual plant biodiversity in secondary forests. For example, one of the strongest predictors of understory woody plant diversity on three distant, unmanaged plantations in Costa Rica was proximity to mature forests with native species diversity [Cusack and Montagnini, 2004]. Similarly, abandoned agricultural sites closer to remnant native trees had seedling and sapling diversity more similar to mature forests compared to more isolated sites in northeastern Costa Rica [Norden *et al.*, 2009]. Thus, the proximity of native forests will strongly affect the extent of native biodiversity that can recover on abandoned lands, with invasion by one or two exotic herbaceous species more likely to occur far from native seed sources.

In summary, growth of secondary forests on abandoned lands is likely to restore native plant biodiversity, at least to some extent, whereas herbaceous invasion is likely to inhibit biodiversity recovery. Even when exotic tree species establish quickly after land abandonment, there is the potential for native species to establish in the understory and eventually shift forest species composition toward native biodiversity, creating a positive feedback loop between forest regeneration and biodiversity restoration (Figure 8). In contrast, early dominance of abandoned sites by fast-growing herbaceous species is likely to inhibit native woody species from growing, potentially indefinitely, resulting in low plant biodiversity (Figure 9).

2.2.2.5. Unmanaged Land Cover Change and Tropical Disturbance Regimes

The most likely effect of unmanaged land cover change on disturbance regimes is wildfire if fire-prone grasses invade sites that were previously humid forests. Newly created wildfire regimes can then burn adjacent areas of forest, eventually expanding grasslands farther into forest. A seminal Hawaiian study showed that invasive African grasses create new wildfire cycles in humid forest areas, with grass establishment depleting soil N availability, potentially promoting even more grass establishment [D'Antonio and Meyerson, 2002; D'Antonio *et al.*, 1998; Freifelder *et al.*, 1998; Hughes *et al.*, 1991]. A review of South American humid and subhumid forest research also showed that the frequency, intensity, and range of fires has increased greatly in areas where C4 African grasses are invasive, promoting the creation of savannas at a large scale [Williams and Baruch, 2000]. Similarly, a remote sensing study showed that invasive grasses are leading to savanna expansion in eastern lowlands of Bolivia [Veldman and Putz, 2011]. A controlled study in the Amazon Basin compared the effects

of annual fires, intermittent fire, and no fire using three 50 ha plots and found that burning promoted expansion of exotic African C4 grass (*Brachiaria decumbens*) into adjacent forest, showing 20 times faster invasions with burning versus without [Silverio *et al.*, 2013]. Thus, invasive herbaceous plants can promote wildfire, which in turn promotes more invasions, creating a positive feedback loop (Figure 9).

New wildfire regimes caused by invasive grasses also have a positive effect on climate change via release of CO₂. Net emissions of CO₂ from exotic grassland fires in tropical regions are difficult to calculate, since emissions from any individual fire depend on combustion temperatures and fuel loads. Still, one study estimated that annual CO₂ emissions from grassland fires may be anywhere from 7.5 to 70 Mg C/yr [Cochrane, 2009]. Thus, C emissions related to increased fire, if large enough in scale, are likely to increase atmospheric CO₂ concentrations and temperature increases (Figure 9).

3. Recommendations

This review demonstrates the negative impacts of global change on all tropical ecosystem properties, with the overall greatest uncertainty and variability in nutrient cycling responses. All global change factors except CO₂ fertilization demonstrated great potential to feedback and exacerbate global warming, primarily via increased greenhouse gas emissions from tropical forests. This assessment demonstrates that effects of decreased rainfall and deforestation on tropical forests are relatively well understood (Figures 4 and 7), whereas potential effects of warming, CO₂ fertilization, nitrogen deposition, and species invasions require more cross-site, mechanistic research to predict tropical forest responses at regional and global scales.

Here we suggest priorities for future scientific research on global change in humid tropics and provide recommendations for local- and regional-scale management. The aim is to increase both understanding and effective conservation of these unique ecosystems. We first give general recommendations, followed by specific research and management goals related to each global change factor.

In general, science goals should focus on more large-scale manipulations in the tropics, on understanding interacting effects among global change factors, and on understudied regions of the humid tropics. In this review we have highlighted potential interactions among global change factors where data exist, with most of these predictions supported by modeling studies. Interactions between warming and drying and between CO₂ fertilization and N deposition have been given the most attention generally, although research is still sorely lacking in tropical forests. A greater effort to disentangle the independent and combined effects of these global change factors is needed. More factorial designs for field research assessing individual and combined global change factors would go a long way toward parameterizing models and validating predictions. Modeling efforts, in turn, must assess combined effect of feedbacks from different global change factors to global warming specifically and climate change in general. Also, scientific research in the humid tropics must increase investigations of less studied regions to better understand the effects of global change on the biome globally. From this review, it is clear that the scientific research on global change effects has been focused primarily in Asia and the Neotropics (Table 1). Far fewer studies are available for African humid tropics, so this should be a research priority going forward.

At a broad scale, effective mitigation of climate change impacts on tropical forests clearly must be achieved by international cooperative efforts to curtail CO₂ emissions globally [Climate Institute, 2010; Government Accountability Office, 2011; Keith, 2000; Shepherd *et al.*, 2009; Vaughan and Lenton, 2011]. To date, a large amount of policy and scholarly examination of different international plans has occurred, with no global solution currently in place. Below we briefly summarize some of the major international efforts and then focus recommendations for each global change factor on more locally and regionally focused strategies.

Recently, at the 2015 UN Framework Convention on Climate Change Council of Parties (COP21) in Paris, an unprecedented 195 nations signed a nonbinding agreement to cut greenhouse gas emissions to levels that will limit global warming to below 2°C, with a specific target of 1.5°C. In this agreement, emissions targets are nonbinding and determined by each nation, although commitments to periodic submission and review of emission reduction targets are binding, as is a commitment of a \$100 billion fund to help developing countries move away from fossil fuels [British Broadcasting Corporation, 2015]. The two largest CO₂ emitters globally, USA and China, have national plans to achieve the COP21 commitment. Obama's Climate Action Plan (CAP) and Clean Power Plan (CPP) for the USA aims to reduce CO₂ emissions to 32% below 2005 levels by 2030

[United States Executive Office of the President (*USEOP*), 2013], and China also has a recent initiative to reduce CO₂ emissions [National People's Congress (*NPC*), 2011]. Both of these initiatives rely on self-regulation of CO₂ emissions, building from the structure of the 1997 Kyoto protocol [*UNFCCC*, 1998]. The voluntary country pledges of the Paris COP21 Agreement, which are ultimately nonbinding, still fall short in achieving the warming limits that the agreement defines [*Clemencon*, 2016]. If all of the pledges are actually implemented, global emissions would still put the world on track to a temperature rise of around 2.7–3°C by 2100 [*Jeffery et al.*, 2015]. Given the marginal impact of voluntary agreements, economic approaches like C taxes [*Courchene and Allan*, 2008], and cap and trade programs [*Stavins*, 2008], have many proponents. However, implementing such strategies at a global scale, such as via regulation by the World Trade Organization (WTO), has been opposed broadly for violating international trade rules [*Veel*, 2009] and penalizing developing countries [*Zhang*, 2010]. At a national scale, there is concern that such “command and control” policies would lead to outsourcing of industrial production and CO₂ emissions to countries without these rules.

Regional efforts have also been made to control N deposition. Countries in Europe, North America, and Central Asia participated in the 1979 Convention on Long-range Transboundary Air Pollution (CLRTAP). However, few of the countries have actually achieved significant reductions in N deposition to date [*Spranger et al.*, 2014]. CLRTAP was designed to address major environmental problems caused by transboundary air pollution in North America, Europe, and Asian regions. The most recent implementation of this plan is the Gothenburg Protocol, which aims to reduce the negative ecosystem effects of N deposition, including water contamination, rain and soil acidification, and tropospheric ozone production. There are no similar attempts to control regional N deposition among tropical countries. There have been some national-scale attempts to improve N fertilizer use, however, with one goal of reducing N deposition. One successful case of innovative model-driven integrated soil-crop system management approaches is in China, where across 44 sites maize yield almost doubled with no increase in N fertilizer [*Chen et al.*, 2011b]. This program continues to focus on achieving increased efficiency of fertilizer use on agricultural lands at large scales. Similar programs have not been implemented broadly in tropical countries.

Broader international efforts to stop tropical deforestation have met with relative levels of support and success. Within the broader context of mitigating climate change, forest and soil management in tropical regions are among the most promising of the strategies available for combating climate change [*Cusack et al.*, 2014]. Reforestation programs, such as those funded through the United Nation's Reducing Emissions from Deforestation and Forest Degradation (REDD+) program, could accomplish both mitigation and adaptation goals, sequestering C in forests and providing valuable ecosystem services [*FAO et al.*, 2008]. The establishment of REDD+ demonstrates growing recognition amongst world leaders of the ecosystem services provided by forests. However, there is no long-term financial structure for REDD+, and existing projects are run on a voluntary basis, so tropical forests are far from permanently safeguarded.

Given the limited success in the international political arena, a combination of mitigation and adaptation approaches must be implemented at local and regional scales in order to minimize the extent of global change. Below, our management recommendations generally promote strategies of adaptation, assuming that global change factors will continue or worsen. We support identifying and prioritizing tropical species, communities, and geographic areas that are most likely to withstand global change via tolerance or adaptation. Forest management efforts could target native rainforest species that are particularly tolerant of wider temperature and rainfall ranges than are found in their habitats today. Also, species that can maintain rapid growth under elevated CO₂ conditions without requiring large increases in nutrient availability may be promising for conservation efforts. Our approach does not seek to undermine the valiant efforts underway to conserve nearly extinct humid tropical habitats (e.g., Conservation International's biodiversity hot spots), which are critically important for preserving the magnificent array of life on Earth. Nonetheless, we feel that hedging management approaches with strategically selected species and habitats that are likely to be resistant to global change is the most promising approach for mitigation and the long-term survival of humid tropical forest ecosystems.

3.1. Climate Change Recommendations

Our review of the ecosystem responses to climate change shows that changes in both temperature and rainfall are having strong effects on ecosystem processes and properties in humid tropical forests. The main areas that we recommend expanded research and management efforts on tropical forests and climate change are as follows.

Temperature effects on tropical ecosystem dynamics: The effects of rising temperatures on tropical ecosystems, particularly on soil nutrient availability and belowground C cycling, require more study in tropical forests. In particular, changes in root growth, soil respiration, and nutrient availability are all likely to respond to warming at an ecosystem scale.

This review emphasizes that even small increases in temperature in humid tropical forests are likely already having significant effects on key biogeochemical processes, including C and nutrient cycling. This result is novel in that changes in temperature are often not considered important in humid tropical forests, while much more emphasis has been given to the ecosystem effects of drying. From a science research perspective, large-scale tropical forest warming projects should be given priority as a research goal across a variety of humid tropical forest sites (e.g., lowland wet, lowland seasonal, and montane). The scientific community is coalescing behind the importance of warming in tropical forests [Cavaleri *et al.*, 2015], with some large-scale warming projects forthcoming.

One of the largest planned warming projects nearing implementation is the Tropical Responses to Altered Climate Experiment (TRACE) experiment in Puerto Rican montane forests. The project is sponsored by the U.S. Forest Service and the Department of Energy and will warm soils and individual branches and leaves in canopy plants [TRACE, 2015]. The project is planned to begin warming in 2016. A belowground warming experiment is also in the planning stages for lowland seasonal forests on Barro Colorado Island in Panama, which is being managed by the Smithsonian Tropical Research Institute. Development of additional ecosystem-scale warming experiments should be funded, such that a pantropical network of warming studies can fill knowledge gaps about how belowground and aboveground dynamics across microbial, plant, and forest scales will respond to warming [Reed *et al.*, 2012].

Drying effects on tropical soil C losses across geological gradients: Future research should focus on disentangling the effects of drying on microbial versus root respiration across different tropical soil types in order to (1) better quantify plant belowground C allocation with drying and (2) provide data for future model development to capture physiological responses to drying.

Soil respiration responses to drought across sites and soil types remain uncertain, and results from small scale experiments have not been well replicated in large-scale drying studies.

Identifying tropical plant adaptation to warming and drying for forest management: Large-scale in situ warming and drying experiments should also assess plant thermal and desiccation tolerances, resilience, and adaptation for different plant functional groups.

These results should be incorporated into modeling efforts for long-term predictions of how plant growth and C storage will change with tropical warming. From a management perspective, in situ warming experiments can also be used to assess which tropical trees are most resistant to climate change. These species could then be targeted for reforestation, using resilient and C dense trees to mitigate climate change.

3.2. CO₂ Fertilization Recommendations

Small-scale CO₂ fertilization experiments suggest that plant growth responses among tropical species are likely to vary by successional stage and that soil nutrient availability is likely to have a large effect on how tropical ecosystems respond to this global change factor. As with warming, the most needed research on CO₂ fertilization is at the ecosystem scale in the field. The first forest-scale FACE experiment is currently being planned for the Amazon [Lapola and Norby, 2014], and this should go a long way in improving our understanding of how humid tropical forests will respond to CO₂ fertilization. The main areas that we recommend expanded research and management efforts on tropical forests and CO₂ fertilization are as follows.

Network of tropical FACE experiments: We are in dire need of multiple tropical FACE experiments, which could be supplemented by more extensive studies using open top chambers (OTCs) and growth chambers.

It is clear from the temperate FACE sites that there is high variability in effects across different ecosystem types within a given biome. Like temperate forests, different tropical forests are highly variable in climate, diversity, topography, soils, and successional stage, with these factors ultimately likely to drive spatial variability in humid forest ecosystem responses to elevated CO₂.

Nutrient limitations on tropical plant growth at elevated CO₂: Scarce rock-derived soil nutrients like P may ultimately limit tropical ecosystem responses to elevated atmospheric CO₂, but more field research is needed to confirm variability among regions and species, especially at ecosystem scales using technologies like FACE.

Whether scarce rock-derived soil nutrients like P or base cations will ultimately limit tropical ecosystem responses to elevated atmospheric CO₂ is virtually unknown and cannot be deduced from the dozens of temperate FACE studies. CO₂ effects on soil nutrient availability, via changes in soil chemistry, decomposition, and plant nutrient uptake dynamics, should be emphasized in large-scale tropical FACE experiments.

Biodiversity implications of elevated CO₂: Elevated CO₂ levels can cause changes in foliar chemistry, which in turn could alter herbivory, and thus insect biodiversity. Yet these biodiversity implications have received little attention and warrant further investigation.

Effects of CO₂ fertilization on herbivory and insect biodiversity via changes in foliar chemistry, and potential feedbacks that may occur to plant growth and plant biodiversity if herbivory patterns change, should be a research focus. Currently, this area of investigation is apparently receiving little attention in Amazon FACE research plans relative to goals focusing on nutrient cycling [Lapola and Norby, 2014].

CO₂ effects on hydrological disturbances to tropical forests: The potential effects of reduced evapotranspiration at elevated CO₂ on flooding and landslides have received almost no research attention, despite the obvious importance for human settlements and water quality. This is a question that could likely best be addressed with modeling efforts, using tropical FACE soil moisture responses for parameterization.

At a regional scale, the potential effects of reduced evapotranspiration at elevated CO₂ on flooding and landslides have received almost no research attention, despite the obvious importance for ecosystem disturbance, human settlements, and water quality. This is a question that could likely best be addressed with modeling efforts, using tropical FACE soil moisture responses for parameterization.

Managing reforestation for projected rises in atmospheric CO₂: For the most part, reforestation efforts do not consider the potential future effects of CO₂ on replanted or regrown forests. Thus, CO₂ fertilization studies should focus on finding tropical tree species that will be most able to maintain high growth under elevated CO₂, with minimal requirements for additional nutrients.

Reforestation and afforestation in tropical forests are receiving much attention and funding at a global scale to combat climate change. For the most part, these reforestation efforts do not consider the potential future effects of CO₂ on replanted or regrown forests. Finding species that can sustain increased growth at higher CO₂ levels, and using these in reforestation, could increase the intended negative feedback to climate change.

3.3. Nitrogen Deposition Recommendations

This review shows that although N deposition is unlikely to directly alter plant growth in tropical forests on highly weathered soils, although indirect effects of added N, like changes in soil chemistry and microbial activity, may increase overall C storage. The main areas that we recommend expanded research and management efforts on tropical forests and N deposition are as follows.

Nitrogen deposition effects on soil C and P cycling: Nitrogen deposition may change soil C and P dynamics even in the absence of N limitation to plant growth, via changes in soil biogeochemistry, plant litterfall, and microbial decomposition. The net effect of these processes on soil C and P availability, and on forest growth, requires greater investigation across tropical sites with varying soil N and moisture status.

Notably, soil C storage appears to respond positively to added N even in N-rich humid tropical forests via a suite of biotic and abiotic soil responses. Whether this increase in soil C leads to a net gain in forest C, including changes in aboveground and root biomass, it is important for assessing the fate of global C stocks in the face of environmental change. This review also shows that N deposition may change the availability and cycling rate of P in tropical soils via changes in microbial decomposition, which could create an indirect positive effect on plant growth and decomposition rates, with net effects on C storage likely to vary according to unknown local conditions. Research on the effects of N deposition in the humid tropics should thus continue to pursue effects on soil P and cation availability and long-term cumulative effects on soil C dynamics using long-term N fertilization experiments.

Interactions of N deposition with other global change factors: Nitrogen deposition appears to have great potential to interact with other global change factors. While treatments like warming and CO₂ fertilization are logistically complex and expensive, N fertilization is relatively cheap and easy and should be added as a treatment wherever feasible.

For example, N deposition effects on P cycling are likely to interact with drying effects, which appear to decrease P availability (Figure 4). Similarly, N deposition effects on P cycling may interact with CO₂ fertilization, which can decrease soil P availability via plant uptake, but may also increase P availability via soil acidification (Figure 5). These interactions could feasibly lead to colimitation of plant growth by N and P.

Measuring tropical N deposition rates and studying N deposition gradients: There is still a lack of data on N deposition rates for large areas of the tropics. Improved data on N deposition across regions will particularly improve model predictions of N deposition effects by allowing model intercomparison using alternative data sets [Aas *et al.*, 2014]. Research in existing N pollution gradients could also allow for improved understanding of N deposition interactions with other global change factors, such as unmanaged land cover change [Hicks *et al.*, 2014].

Our knowledge of spatial and temporal variability in N deposition rates and ecosystem consequences across tropical regions is very poor. We still do not have basic data on N deposition rates for large areas of the tropics including South America, Africa, Australia, and Oceania [Dentener *et al.*, 2014]. Long-term monitoring of rainfall chemistry requires some commitment to equipment maintenance and chemical analyses, and there are several successful examples of regional coordinated efforts to do this. For example, the Acid Deposition Monitoring Network in East Asia (EANET), and the European Monitoring and Evaluation Program (EMEP) could provide good guidance on how N deposition monitoring networks can be established and maintained in these areas. In addition, more detailed N chemistry in rainfall, including organic N, ammonium, ammonia, nitrate, nitrite, and nitric acid should be routinely monitored to close the information gaps in global N deposition rates and chemistry [Hicks *et al.*, 2014]. Improved regional values for N deposition could greatly improve models assessing combined effects of N deposition, climate change and land use change [Baron *et al.*, 2014]. Also, ecosystem-scale studies of actual N deposition gradients outside of tropical urban centers are still extremely scarce in the humid tropics, although these may provide some of the most realistic insights to how N deposition will alter ecosystem processes [Cusack, 2013; Huang *et al.*, 2012]. Thus, improved monitoring of N deposition rates and use of existing N deposition gradients for research should be emphasized in the humid tropics.

Identifying “critical load” (CL) N thresholds for tropical watersheds: In order to properly control emissions, policymakers need better information on the CL of N that local tropical forested watersheds can sustain prior to significant changes in ecosystem processes and water contamination.

From a management perspective, N deposition is largely a regional problem with a regional impact, unlike the more far-reaching effects of climate change and CO₂ fertilization. N deposition produced in urban centers is transported in air and waterways but typically is deposited relatively close to pollution centers. About half of the NH₃ emitted to the atmosphere is typically deposited within 50 km of its source, whereas most NO_x is deposited within 800 km [Ferm, 1998]. Use of a critical load (CL) approach to quantify acceptable levels of N deposition could be used more in tropical regions. This data can inform emission control measures such as efficient and cleaner combustion, exhaust catalysts in vehicles, and better management of fertilizer, which have all proved successful at reducing N deposition in Europe [Hicks *et al.*, 2014]. Implementation of similar policies in N management by tropical countries is crucial for controlling a transboundary problem like N deposition [Austin *et al.*, 2013].

Nitrogen fertilizer best practices research and implementation: Adjusting N fertilizer management practices in the humid tropics to account for ambient levels of soil N, and to improve chemical forms, timing and placement of fertilizer could greatly improve the N uptake efficiency in agriculture, thereby reducing N loss and leaching from agricultural areas [Vitousek *et al.*, 1997c]. Future research should test new management practices for tropical forests, like innovative model-driven integrated soil-crop system management approaches [Chen *et al.*, 2011b].

Improved fertilizer use could be a particularly important and relatively easy target for tropical countries aiming to reduce N deposition. Agricultural activity is responsible for the majority of biologically available N globally [Fowler *et al.*, 2013] and is of particular importance in tropical regions [Martinelli *et al.*, 2006]. Particularly in

tropical areas with highly weathered, naturally N-rich soils, N could be greatly reduced or even eliminated from combo fertilizers (e.g., NPK). Best management practices can ultimately end up costing farmers less because of reduced purchases of fertilizers, use of slow-release fertilizers, and spatial and temporal optimization of fertilizer application that balance productivity with soil conservation [Kanter *et al.*, 2015]. One issue is a need for improved agricultural extension efforts that transfer best management practices on fertilizer use to farmers in tropical regions [Shrestha *et al.*, 2014]. Thus, research and management could come together in a more effective way at local scales to improve fertilizer use, reduce N deposition, and increase crop yields. These efforts could be made in tandem with strategies to reduce deforestation (see below).

3.4. Deforestation Recommendations

In contrast to many of the global change factors discussed in this review, the large-scale monitoring and aboveground effects of deforestation in tropical ecosystems are relatively well studied. However, areas like forest degradation and forest management to reduce deforestation require ongoing efforts. The main areas that we recommend expanded research and management efforts on tropical forests and deforestation are as follows.

Soil carbon dynamics following tropical deforestation: The International Soil Carbon Network (ISCN) has made significant headway coordinating independent soil research and monitoring efforts in the USA and internationally, compiling soil C databases from individual researchers (<http://iscn.fluxdata.org/>). However, a coordinated effort using standardized methods across tropical countries is needed to understand the spatial variability and large scale and effects of deforestation on soil C storage and cycling in the tropics.

Unlike aboveground plant biomass, soil carbon pools cannot be measured quickly with remotely sensed images, making large-scale assessment of changes in soil C with deforestation difficult. A more refined understanding of soil carbon dynamics following deforestation is important, especially for developing accurate global carbon models and emissions budgets.

Deforestation effects on soil microbial diversity and ecosystem function: The effects of shifts in microbial community biodiversity and function, as well as the capacity for forest microbial communities to recover with reforestation, should be a priority for future research.

Deforestation appears to greatly alter soil microbial diversity (see section 2.2.1.4); however, the specific ways in which communities and community function are changing have just recently begun to be understood using advanced molecular techniques. In particular, the long-term consequences of changing microbial biodiversity for ecosystem function are unknown. Resilience of microbial communities over the subsequent land use and possible reforestation of deforested lands should also be explored.

Forest degradation detection and monitoring: Like deforestation, degradation of remnant forests is a major driver of environmental change within the tropics. Establishing standards for accurately measuring the extent and severity of forest degradation, both remotely and in the field, will be essential for controlling harmful logging practices that often go undetected.

Unlike forest clearing, forest degradation has received less large-scale research attention, even though degradation is also a major driver of environmental change within the tropics [Nepstad *et al.*, 1999]. Forest degradation is more difficult to document than deforestation, as it usually requires on-the-ground site-specific investigations to verify damages that may not be observable using remote sensing technologies [Saatchi *et al.*, 2011]. Forest degradation can also greatly increase the risk of exotic species invasions into tropical forests [Catford *et al.*, 2012; Padmanaba and Corlett, 2014]. A top priority for humid tropical forest conservation is to use expanded knowledge about forest degradation to limit land use practices that fragment, open, and disturb forests.

Sustainable commercial forestry practices: More research is needed to guide tropical counties in meeting their timber needs without compromising the environmental services provided by forests.

For example, studies that compare the tradeoffs of selective logging, native tree plantations, and conventional tree plantations will help policymakers develop natural resource management strategies that maximize the economic and environmental benefits from tropical forests.

Sustainable agricultural intensification: Since agricultural expansion is a major driver of forest loss, data-driven crop management solutions that balance food security (both local and global) with forest conservation are urgently needed.

From a management perspective, slowing tropical deforestation remains an enormous challenge, especially as developing tropical nations continue to urbanize and expand commercial agricultural production [DeFries *et al.*, 2010; Seto *et al.*, 2012]. Additional research on intensive farming practices that increase food yields and maintain the long-term productivity of tropical agricultural lands, without degrading other ecosystem services, is critical for preserving tropical forests. This area of research could dovetail with the recommendations for improved N fertilizer use in crop systems (above).

Agroforestry implementation: Improving the productivity of agroforestry systems, and identifying the challenges that impede widespread adoption of agroforestry practices, could reduce forest clearing and augment tree cover in tropical regions.

Agroforestry practices, which incorporate trees and crops into a single farming system, can serve as an alternative to complete forest clearance for agricultural land uses. Agroforestry practices have been well documented to offer many of the same environmental services provided by natural forests [Jose, 2009] and can act as important corridors connecting area of intact forest. Nonetheless, agroforestry is not the dominant mode of agricultural production for many shade tolerant crops (e.g., coffee, cacao, and yams).

Community-based tropical forest management models: More research is needed on the kinds of local governance models that have been particularly successful in community managed forests, as well as the barriers for implementing these models in tropical forests managed by government entities.

In the tropics, community managed forests have resulted in lower deforestation rates than federally managed protected areas [Porter-Bolland *et al.*, 2012], in part because communities manage lands for multiple goods and services that can enhance ecological, economic, and social functions of tropical forests [Panayotou and Ashton, 1992]. For example, annual deforestation rates were compared among 40 protected areas and 33 community managed forests and community managed forests resulted in lower and less variable annual deforestation rates than government-protected forests [Porter-Bolland *et al.*, 2012]. Community managed forests require clear and secure tenure arrangements for successful implementation. Research that evaluates the effectiveness of various stakeholder engagement methods, such as participatory land use mapping [Barry and Meinzen-Dick, 2014] and social role play games [Villamor and van Noordwijk, 2011], is effective in the context of tenure negotiation. Given these findings, nations adopting REDD+ policies should secure tenure rights for local communities and engage them in the development of forest management strategies.

Local economic incentives for forest protection: Economic strategies that reward local communities for protecting forests should be studied and implemented across tropical regions.

Access to credit and small loans may provide incentives for local communities to protect forests. For example, in Brazil the deforestation rate dramatically declined by 70% from 2005 to 2013, partly due to economic policies that rewarded farmers in counties with low deforestation rates with access to agricultural credit [Nepstad *et al.*, 2014]. These types of microeconomic solutions could be implemented at a broader scale and at low cost.

3.5. Unmanaged Land Cover Change Recommendations

Secondary forest growth in the humid tropics has been studied extensively over the past decades compared to some of the other global change factors in this review. Still, there is significant uncertainty about how ecosystem properties will respond to different successional trajectories following land abandonment. The main areas that we recommend expanded research efforts on tropical forests and unmanaged land cover change are as follows.

Managing abandoned lands to promote forest regeneration: Abandoned deforested and agriculture sites should be identified as soon as possible, and rather than remaining “unmanaged,” management efforts should be undertaken to prevent herbaceous invasions and promote forest growth. Identification and monitoring of abandoned lands should rely on large scale and nearly real-time remote sensing technologies.

From a policy and management perspective, abandoned lands present a great opportunity to restore lost forest cover in humid tropical regions. Secondary forest growth can greatly restore forest ecosystem processes and biodiversity [Chazdon *et al.*, 2009]. It is important to ensure that all abandoned lands in the humid tropics return to forest cover rather than exotic grass cover. Once identified, abandoned lands should be monitored and managed if necessary to promote forest regeneration rather than allowing invasion by herbaceous species. Prevention of species invasions is much less costly than trying to remove exotic species post-facto [Padmanaba and Corlett, 2014; Vitousek *et al.*, 1997b]. In the case that forest regeneration does not occur spontaneously, the most straightforward management strategy for preventing colonization by invasive herbaceous species is to plant trees and ensure that they pass the seedling stage so that they cannot be shaded out. Studies across tropical sites show that plantations of native or exotic timber species promote woody understory regeneration and biodiversity [Ashton *et al.*, 2001; Carnevale and Montagnini, 2002; Guariguata *et al.*, 1995; Haggard *et al.*, 1997; Keenan *et al.*, 1997, 1999; Kuusipalo *et al.*, 1995; Parrotta *et al.*, 1997; Powers *et al.*, 1997], in addition to restoring soil fertility, reducing erosion, and reducing fire hazard [Parrotta, 1992]. Based on this review, use of certain exotic tree species in reforestation efforts should not be ruled out, particularly in regions where there are no native N-fixing trees, since these can have been shown to particularly improve soil conditions.

Effects of soil biogeochemistry on biodiversity restoration in abandoned lands: Linkages between soil biogeochemical function and biodiversity restoration in abandoned lands require more attention. In particular, the role that native or exotic N-fixing trees play in restoring soil N and P availability, and the effect of this on subsequent forest biodiversity, should be investigated.

Biogeochemical effects on the long-term trajectory of secondary forest succession remain to be explored. In particular, the potential for secondary forests to restore mature forests dominated by native species, versus stands dominated by exotic tree species, deserves further investigation. The effect of initial cohorts of trees on soil biogeochemistry may have a large effect on how effectively native tree species are able to establish and grow into the canopy [Cusack and McCleery, 2014]. Results from this research can be used to identify tree species, native or exotic, that improve site conditions with the long-term goal of biodiversity restoration.

Understanding factors that promote herbaceous invasions: First, broader-scale monitoring is required to assess the spatial extent of herbaceous invasions in the tropics following land abandonment. Then more research is needed to understand the ecosystem factors that promote these invasions and inhibit subsequent successional processes from returning these lands to forest cover.

Very little attention has been given to the prevalence of herbaceous plant invasions on abandoned tropical lands and to the potential for these lands to undergo subsequent forest succession. This review suggests that abandoned lands invaded by exotic herbaceous plants often have lower soil N and C relative to sites with secondary or mature forests. However, the causal link between site conditions and herbaceous invasions is not clear. That is, do herbaceous species preferentially invade sites with more depleted soil nutrients, or do herbaceous species promote nutrient losses and lower soil C, thus perpetuating herbaceous cover? It is likely that both causal directions occur, but more research across a suite of tropical sites should focus on identifying mechanisms that promote successful herbaceous invasions.

Fire vulnerability and resilience in abandoned lands: Given the positive feedback between invasive grassland expansion and wildfire on many abandoned lands, research should focus on developing fire models that incorporate ecosystem predictors of herbaceous invasions in the tropics, such as land use history, soil degradation, and proximity to native forest.

Regional management policies should emphasize ongoing updates to fire management policies. Local and regional management policies for forests should also be expanded to include updated fire management policies [Guariguata *et al.*, 2008], given the growing importance of fire in humid tropical forests.

4. Conclusion

In conclusion, all of the global change factors reviewed here will result in significant negative effects on biogeochemical processes and biodiversity in humid tropical forests, many of which are already occurring. Most of the global change factors are also highly likely to create positive feedbacks to climate change because of C losses from tropical forests. The different global change factors will most certainly cause extreme changes in

tropical forests and Earth systems if unchecked. In the extreme: climate change and associated drought and fire are likely to cause widespread tree mortality and conversion of tropical forests to savanna; CO₂ fertilization has the potential to exacerbate scarcity of nutrients like phosphorus and increase floods in tropical forests; nitrogen deposition will increase greenhouse gas emissions from tropical forests, accelerating climate change; deforestation will continue to decrease tropical biodiversity and release large fluxes of CO₂ from forests converted to agropastoral uses; unmanaged lands following agricultural abandonment are increasingly vulnerable to species invasions with the spread of urbanization, likely resulting in permanent conversion of historical forests to exotic grasslands. Going forward, more experimental work is needed to understand the relative strengths and interacting effects of these global change factors, which we now understand through often conflicting model projections. In particular, we know very little about thermal tolerance and adaptation potential of tropical tree species; large-scale effects of CO₂ fertilization on tropical forest dynamics; interactions of N deposition with other global change factors in the tropics; and long-term resilience of soil carbon storage in deforested lands in the face of climate change and N deposition. From a management perspective, coordinated regional and local initiatives must accompany global-scale efforts to mitigate climate change and reduce CO₂ emissions. In particular, regional controls on N emissions and deposition, community-based forest management practices, and managed succession on abandoned lands to restore forest cover are achievable ways to combat global change, with successful models for implementation. The immediate urgency of protecting, preserving, and restoring humid tropical forests for the well-being of humans, biodiversity, and Earth processes cannot be overstated.

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