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# Ecosystem Processes and Biogeochemical Cycles in Secondary Tropical Forest Succession

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## Abstract

Secondary tropical forests that are in a state of regeneration following clearing for agriculture are now more abundant than primary forests. Yet, despite their large spatial extent and important role in the global carbon (C) cycle, secondary tropical forests are understudied, which challenges our ability to predict how tropical landscapes will respond to future disturbance and global change. We summarize research advances on alterations to C and nutrient dynamics during reforestation and how these are influenced by ecosystem state factors. During forest succession, aboveground biomass stocks and litter fluxes increase in a predictable way, but patterns in soil C dynamics are highly variable. The heterogeneous response of nutrients to reforestation is influenced by multiple factors, including losses incurred during prior land use and management. In contrast to primary tropical forests, where productivity is often limited by rock-derived nutrients, secondary forest growth may be more limited by nutrients from the atmosphere. Future research should identify which nutrients constrain forest regrowth.



## 1. INTRODUCTION

By all metrics, tropical forests are one of the most important biomes worldwide. With only ~12% of the global land area, they act as both global warehouses of biodiversity—containing an estimated 50% of species—and of carbon (C), storing 25% of plant biomass (Townsend et al. 2011). Tropical forests also dominate terrestrial C dynamics, with an estimated  $1.2 \pm 0.4$  Pg C/year uptake in intact forest and  $1.6 \pm 0.5$  Pg C/year in regrowth forest, contributing almost 70% of the global gross forest C sink for the time period of 1990–2007 (Pan et al. 2011). Tropical forests are increasingly under threat owing to human activities, such as logging and conversion to pastures and cash crop agriculture, which may compromise their ability to contribute to regulating the climate system and to conserve biodiversity (Lewis et al. 2015). The narrative of tropical land use change has often focused on deforestation and forest loss, as these processes currently are more dynamic in the tropics compared with subtropical, temperate, or boreal latitudes (Hansen et al. 2013). However, forest regrowth is also increasing in tropical latitudes (Chazdon 2014), and now there are more secondary than primary tropical forests globally (FAO 2010).

Even though secondary forests are currently the dominant tropical forest type, they have historically received less study than primary forests, in part owing to traditional research focus on undisturbed ecosystems. That has changed in the last 15 years with the recognition of the importance of tropical secondary forests. A burgeoning literature is providing new data on changes in forest species composition (Chazdon 2014, Dent & Wright 2009, Derroire et al. 2016, Lohbeck et al. 2013) with the aim of determining the extent to which these regrowing forests provide habitat and conditions to conserve biodiversity. In contrast, important gaps in our knowledge of the role of tropical secondary forests in global biogeochemical cycles remain. For example, although secondary forests clearly have the potential to sequester large quantities of atmospheric carbon dioxide (CO<sub>2</sub>) (Chazdon et al. 2016), multiple factors interact to affect the magnitude and direction of C and nutrient trajectories after land use change, with often unpredictable consequences. Many elemental cycles are coupled (Townsend et al. 2011), thus the C sink strength of regrowing forests is likely influenced by the availability of certain nutrients (Wieder et al. 2015, Yang et al. 2010), although the potential magnitude of this effect and identities of the limiting nutrients remain unknown. Moreover, the evidence for directional changes in ecosystem processes and biogeochemical cycling with tropical secondary succession, as seen for temperate ecosystems (Gorham et al. 1979), and how these changes are influenced by past land use and ecosystem state factors, is fragmented and has not been synthesized recently.

In this review, we synthesize the exponentially growing literature to determine successional patterns in tropical forest ecosystem biogeochemistry and rates of ecosystem processes like nutrient cycling. Understanding successional patterns in tropical forests and the mechanisms that underlie them is important because ecosystem processes and biogeochemical cycles both respond to and act as drivers of change in biotic communities during succession. Biogeochemical processes influence nutrient availability, energy transfers, and biomass production, which determine food resources available to primary and secondary consumers and decomposers as well as ecosystem structure and habitat for biodiversity. Furthermore, understanding succession can help us predict how tropical forests respond to future environmental change and disturbance events, which is key for improving climate change projections and for land management and conservation.

Simple conceptual models of succession suggest predictable changes in C stocks and fluxes as forests mature (e.g., Turner 2010), but trends for other elements are less clear. We start by synthesizing patterns of C stocks, allocation, and dynamics, and then we evaluate evidence that nitrogen (N), phosphorus (P), and other element cycles change predictably during tropical succession. Expected patterns and whether empirical data support these predictions are presented



in **Figure 1** for key stocks or fluxes in the C, N, and P cycles for a hypothetical tropical land use trajectory from primary forest through clearing and forest regeneration. Next, we focus on how context-dependent factors including forest age, past land use type and intensity, disturbance regimes, soils, and climate modulate the successional trajectories of forest ecosystem processes. We then review whether existing conceptual models are sufficient to describe ecosystem processes during tropical forest succession or whether these should be revised. Finally, we conclude by highlighting research questions that future studies should prioritize. Although secondary forests can regenerate following a variety of disturbances, including hurricanes, landslides, and fire (Chazdon 2014), our primary focus is on regeneration following human land use, typically for grazing or cropping (**Figure 1**).

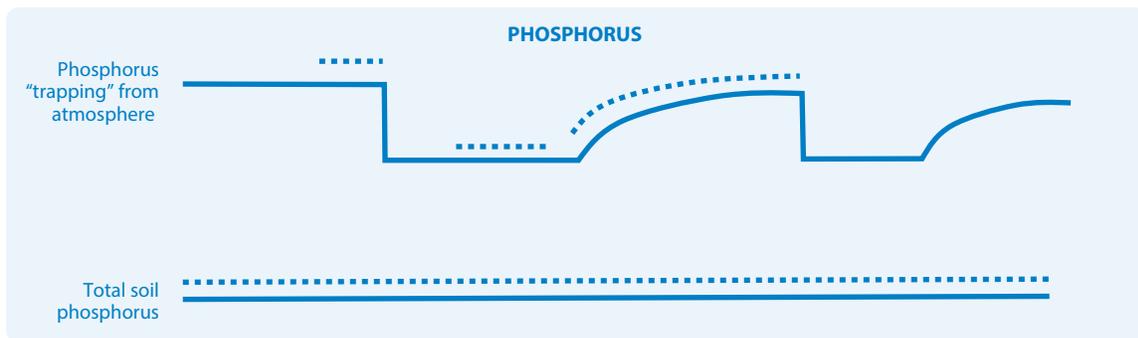
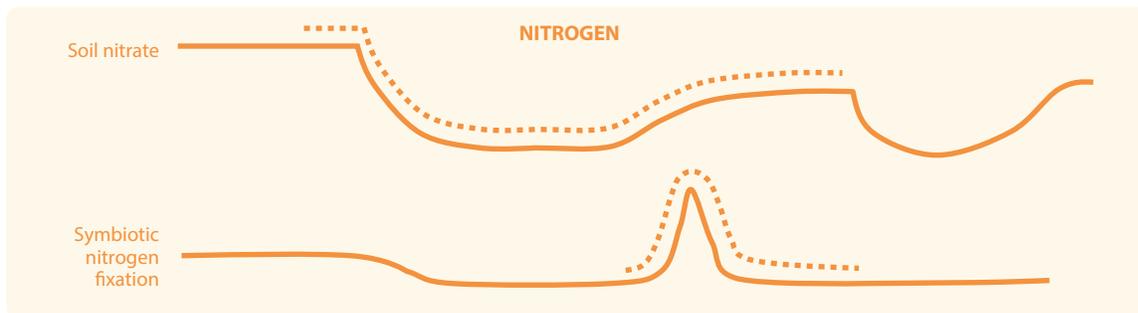
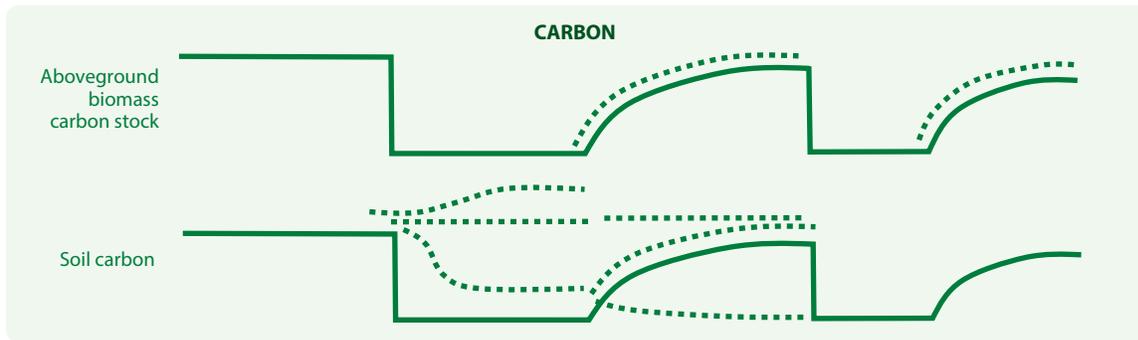
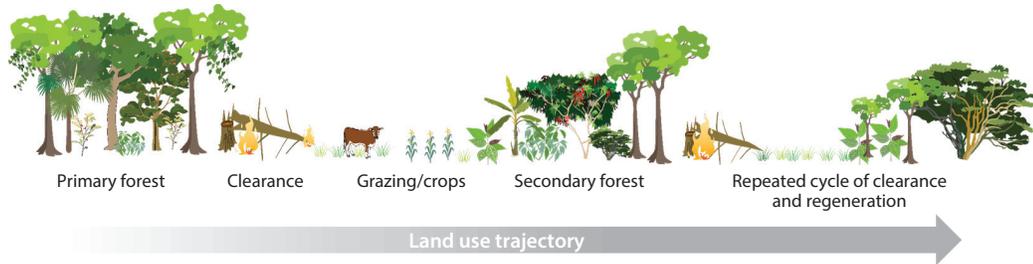
Before proceeding, no discussion of tropical succession and ecosystem processes would be complete without, first, a necessary caveat and, second, an important tip of the hat. Most studies of secondary succession use chronosequences of forests of different ages, or space-for-time substitutions, to make inferences about processes occurring over decadal to centennial timescales. As is the case with many chronosequence studies, those of tropical forest secondary succession have rarely tested the implicit assumptions that all relevant ecological and biophysical conditions are identical in the different plots or sites that make up the chronosequence and that forest age or time since disturbance is the only factor that differs among plots (Johnson & Miyanishi 2008). The second acknowledgment is that much of what we do know about how ecosystem processes change with tropical forest succession comes from studies of shifting cultivation (Ewel 1976). These studies are aimed at understanding to what extent forest succession during fallow periods, when fields are left uncropped, can restore soil fertility to sustain successive cropping (Adedjei 1984, Styger et al. 2007). In now classic articles, Ewel (1976) and Greenland & Nye (1959) concluded that the traditional practice of natural fallowing in shifting cultivation is superior to other types of management for food production in the humid tropics, precisely because of the recovery of soil nutrients during forest succession. Thus, although many studies of shifting cultivation have different goals than understanding forest recovery after grazing or other land uses, they still provide useful insights and are included in this review.

## 2. ELEMENT CYCLING AND ECOSYSTEM PROCESSES THROUGH SECONDARY SUCCESSION IN TROPICAL FORESTS

### 2.1. Patterns of Carbon Accumulation and Fluxes

Element stocks are defined as reservoirs or pools of an element such as C or N; for example, the amount of C stored in a forest as aboveground biomass or belowground in soil organic matter. Fluxes are defined as processes that move elements from one stock to another, such as photosynthesis moving C from the atmosphere or C moving to the forest floor via litterfall. Studies of stocks are more common than studies of fluxes, and trends in C stocks during secondary succession in tropical forests have been much better studied than those for any other element, given widespread interest in climate change mitigation. Increases in aboveground biomass C stocks over succession have been well documented (Becknell et al. 2012, Chazdon et al. 2016, Martin et al. 2013) and are consistent with simple models of monotonic increases that eventually saturate around biomass quantities found in primary forests (**Figure 1**). Biomass accrual to levels seen in primary forest may occur relatively quickly. A recent analysis of 1,500 secondary forest plots found that aboveground biomass may reach values similar to primary forests in 60 years, with faster rates of accumulation in wet compared with dry forests (Poorter et al. 2016).





--- Changes in element dynamics supported by evidence  
 — Hypothesized changes

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In contrast to aboveground biomass C, the response of soil C stocks (excluding roots) to reforestation is less predictable. An early synthesis concluded that soil C in forest fallows requires 35 years to reach full recovery to primary forest levels after agricultural use (Detwiler 1986), assuming that patterns of soil C mimic those in aboveground biomass. Results from individual field studies vary (**Figure 1**), with some studies reporting gains, losses, or no net change in bulk soil C with tropical secondary forest succession (Bautista-Cruz & del Castillo 2005, de Koning et al. 2003, Hughes et al. 1999, Marín-Spiotta et al. 2009, Powers et al. 2011). Prior land use and management may be key in reconciling these contrasting findings. In a global meta-analysis of tropical studies, soil C pools showed a weak positive relationship with forest age only for sites that were cleared and abandoned with no intermediate land use and showed no such relationship for forests regrowing on former pastures or croplands (Marín-Spiotta & Sharma 2013). After multiple cycles of shifting cultivation, forest age was a significant predictor of aboveground biomass but not of belowground C (Eaton & Lawrence 2009).

In addition to differences in the absolute levels of ecosystem C stocks between secondary and primary forests as young forests mature, the relative distribution of C between above- and belowground pools may vary with succession. These differences can provide insight into the processes responsible for observed patterns, such as changing allometry (i.e., root-to-shoot ratios) or C inputs via root production. In tropical secondary forests, the relative contribution of belowground C to total ecosystem C pools can exceed that of primary forests. For example, soil organic C to a 4-m depth represented 84% of total forest C stocks in secondary forests compared with 59% in primary forests, although the latter had greater belowground biomass, dominated by coarse roots (Sierra et al. 2007). In a study on abandoned pastures in Colombia, the sum of C inputs to the soil from litterfall and root mortality in secondary forests averaged 60% that of primary forests after 10 years (Moreno & Oberbauer 2008). In lowland Costa Rica, 15–20-year-old tree plantations with native species allocated more C belowground via root production than primary forests (Raich et al. 2014). This strategy has been proposed to be an important mechanism for C accumulation via enhanced nutrient uptake, as tree growth and aboveground net primary production (NPP) were positively correlated with belowground C allocation. By contrast, a recent review found no difference in root-to-shoot ratios between naturally regenerated tropical forests and tree plantations and instead reported an increase in belowground biomass allocation with forest age (Waring & Powers 2017). Root-to-shoot ratios were negatively correlated with mean annual precipitation (MAP), suggesting important climatic controls on C accumulation. In both tropical dry forests in Costa Rica (Powers & Perez-Aviles 2013) and rainforests in Borneo (Brearley 2011), fine root biomass showed no relationship with forest age and instead correlated negatively to indices of soil fertility.

Many studies have demonstrated clear links between C stocks and fluxes during tropical forest succession, finding that changes in aboveground biomass are the most important driver of many

### Figure 1

A generalized land use trajectory in the tropics starting with primary forest that is cleared for crops or grazing, after which time secondary forest regenerates. The cycle of agricultural use and secondary forest regeneration or forest fallow may be repeated a number of times but is shown here once. Hypothesized changes in key pools and fluxes of the carbon, nitrogen, and phosphorus cycles are depicted as solid lines corresponding to different stages in the land use trajectory. Changes in element dynamics that are supported by evidence from field studies are depicted as hashed lines immediately above hypothesized patterns (Eaton & Lawrence 2009, Keller & Reiners 1994, Lawrence & Schlesinger 2001, Lawrence et al. 2007, Marín-Spiotta & Sharma 2013, Poorter et al. 2016, Powers et al. 2011). Artwork used to construct the land use trajectory figure is courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (<http://ian.umces.edu/symbols/>).



ecosystem processes in secondary forests, despite observed differences in species functional traits during postagricultural succession (Lohbeck et al. 2015b). Litterfall rates typically return to those of primary forests quickly, within 10–20 years, with the recovery of tree biomass (Barlow et al. 2007, Brown & Lugo, 1990b, Ewel 1976). In some cases, litterfall rates can surpass those of reference primary forests (Aryal et al. 2015, Ostertag et al. 2008), owing to differences in tree species composition.

Patterns in decomposition during succession seem to follow those of litterfall. In tropical dry forests in Costa Rica, both litter decay and turnover rates, measured via litterbag decomposition of standard substrates and as litter standing stock divided by litter inputs, increased with forest age (Schilling et al. 2016). In wet and moist tropical forests, once the canopy closes, which can occur in less than two decades, litter decomposition rates do not appear to be influenced by forest age (Barlow et al. 2007, Ewel 1976). The explanation for the positive correlation between forest biomass and decomposition may be through indirect effects, as soil moisture typically increases and soil temperature decreases during succession, compared with open pastures or crops with low canopy cover (Lebrija-Trejos et al. 2011). However, these effects are most pronounced in early stages of succession. In subtropical wet secondary forests aged 10–80 years on former pastures, no predictable effect of forest age on litter and root decomposition rates and generally no consistent differences in belowground C cycling between primary and secondary forests were observed (Ostertag et al. 2008). A study in secondary tropical wet forests aged <1–29 years in Mexico identified the mechanisms responsible for patterns between decomposition and forest biomass during succession (Lohbeck et al. 2015b). In situ litter decomposition rates (litter decomposed in its native site) were positively correlated with aboveground biomass along the chronosequence. Species functional differences in litter quality became important only when litter from all secondary forests was decomposed at the same site, controlling for differences in abiotic conditions among the sites. These results suggest that the accumulation of plant biomass is an important determinant of ecosystem process rates, presumably through effects on microclimatic conditions (Lohbeck et al. 2015b).

Soil respiration is an important flux in the C cycle that encompasses both root and soil microbial respiration, but few studies have measured it in tropical secondary forests. Salimon and colleagues (2004) reported strong seasonal effects of rainfall on soil CO<sub>2</sub> fluxes but no effects of forest age or biomass. Overall, rates of soil respiration were comparable between secondary and primary forests and lower than rates under pastures on the same soil type. In forests aged 50–400 years in China, soil respiration did appear to increase with successional stage (Yan et al. 2009). Soil respiration is affected by multiple factors, which may vary differentially with succession: above- and belowground C inputs; microbial communities; and microclimate, especially soil moisture in tropical forests. Research on tropical forests following hurricane disturbance suggests that rates of CO<sub>2</sub> production can be altered by litter inputs and changes in soil temperature with forest canopy changes (Vargas 2012).

In summary, C is the most studied element during tropical forest secondary succession. Aboveground biomass shows predictable gains over time, approaching and sometimes surpassing C stocks in primary forests. The rate of increase varies with environmental factors such as climate, disturbance regime, and historical land use and is discussed in more detail below (Kauffman et al. 2009, Poorter et al. 2016, Silver et al. 2000). Species replacement after pasture or agriculture use can also influence the accumulation of C in secondary forest stands, as tree species with conservative trait syndromes *sensu* Reich (2014) are replaced by species with acquisitive traits in dry forest successions, with the opposite trend for wet forests (Lohbeck et al. 2013). For most secondary forests, rates of aboveground biomass C accumulation decrease as forests age. Moreover, the number of times that a patch of land undergoes cycles of clearing and fallow can affect biomass



C accumulation, with declining rates each successive cycle (Eaton & Lawrence 2009), especially when fallow lengths are not sufficient to restore soil fertility (Styger et al. 2007) (see **Figure 1**). Belowground, successional patterns for soil C and root biomass are less predictable, with some studies showing gains or no net change and fewer studies showing initial losses early in succession. These conclusions are tempered by the strong bias in the literature toward young successional stages, with the majority of data coming from forests aged  $\leq 20$  years (Marín-Spiotta & Sharma 2013, Martin et al. 2013).

## 2.2. Nutrient Cycling and Soil Biogeochemistry

C is not the only element that changes with succession, as at least 25 elements are required for life and are linked to C through stoichiometry (Kaspari & Powers 2016). During primary succession, rock-derived nutrients like P and major cations, such as calcium (Ca) and potassium (K), enter ecosystems through rock weathering and dust deposition, whereas nutrients primarily derived from the atmosphere, such as N, enter the biosphere through processes such as biological N fixation (N also can weather from sedimentary rocks) (Chadwick et al. 1999, Morford et al. 2016, Walker & Syers 1976). Nutrients are removed from ecosystems via vertical and horizontal fluxes, or are rendered inaccessible to plants through strong sorption to soil minerals. When mature forests are cleared for cropping or grazing, nutrients are lost through plant harvest, fire, trace gas emissions, volatilization, hydrologic losses, and/or soil erosion (Davidson & Martinelli 2009, Holscher et al. 1997, McDonald et al. 2002). Fires may also redistribute nonvolatile nutrients, such as P and Ca, from biomass to the soil surface; indeed, this pulse of nutrients supports the cropping phase of shifting cultivation or so-called slash-and-burn agricultural systems (Adedeji 1984). Large litter production in tropical secondary forests contributes to nutrient returns to the soil, at rates greater than for many temperate forests (Ewel 1976). Thus, regulation of nutrient cycles may differ between primary and secondary succession (Gorham et al. 1979). Moreover, secondary succession in the tropics may differ from that in temperate and boreal forests because of differences in where soils fall along weathering gradients—in other words, the geologically older age of many tropical soils contributes to P limitation of NPP (Cleveland et al. 2011). Here, we focus on noncarbon elements and address evidence for directional changes in the patterns of nutrient availability and nutrient cycling (i.e., processes that cycle nutrients among vegetation, microbial communities, and soils), the mechanisms that underlie these patterns, the sources of nutrients to support regrowing forests, and consequences of nutrient limitation for biomass accumulation.

**2.2.1. Directional changes in nutrient availability, cycling, and soil biogeochemistry.** As forests regrow, nutrient demand by plants increases (Hughes et al. 1999) and the abiotic environment changes, with soil temperature and light decreasing and soil moisture increasing (Lebrija-Trejos et al. 2011). As a result, directional patterns in nutrient cycling may reveal either causes or consequences of successional changes in plant communities. The variety of processes that affect soil nutrient concentrations and dynamics leads to contrasting predictions about changes through succession. On the one hand, concentrations of rock-derived nutrients in the soil may decrease as forests regrow and nutrients are incorporated into biomass. On the other hand, nutrients with soil dynamics closely linked to litterfall, or that are redistributed by fine roots from deep to shallow soil layers, may increase in availability through succession. The dynamics of individual nutrient elements through the soil and hydrologic system (i.e., input, retention, and loss) may vary as a function of the degree to which those nutrients limit NPP (Vitousek & Reiners 1975). Gorham and colleagues (1979) contrasted processes affecting elemental budgets (e.g., weathering, atmospheric



inputs, decomposition, biomass accumulation, plant nutrient use efficiency) during primary and secondary succession. They proposed that net ecosystem production (NEP) played an important role in driving biogeochemical cycling and that the predictive power of NEP on any elemental budget was proportional to the accumulation of said element in plant biomass. What evidence is there for directional changes in soil biogeochemistry and nutrients through secondary tropical succession?

Studies that have measured multiple elements in soil, such as P and cations, find contrasting patterns among elements and between organic and mineral soil horizons. For example, in three chronosequences of more than 100 years of montane cloud forest in Mexico, directional changes in soil properties were most apparent during the first 15 to 45 years of regeneration following maize cropping, but dynamics of soil acidity and cations differed among chronosequences (Bautista-Cruz & del Castillo 2005). In these forests where pines are the dominant early successional trees, exchangeable soil cations declined through succession—presumably because they were being redistributed from the soil to plant biomass—but there were concomitant increases in extractable-Bray P (a potential measure of plant available P) and no changes in total soil N over that timescale. In wet tropical forests on former pastures in Puerto Rico on highly weathered soils, the activity of extracellular enzymes produced by microorganisms and involved in C, N, and P cycling did not show predictable trends with secondary forest age, despite successional patterns in microbial and plant community composition (Smith et al. 2015). Enzyme activity varied more between seasons than among pastures and forest cover types, with greatest sustained activities for phosphatase, which is used by microbes for P acquisition, across all sites. In a 50-year chronosequence on low-fertility soils in Mexico from a slash-and-burn pineapple cultivation system, very few changes in extractable-Bray P or exchangeable cations with forest fallow were seen through succession (Wadsworth et al. 1990). By contrast, in the Blue Mountains of Jamaica, secondary forests after slash-and-burn land use recovered plant-available soil nutrient concentrations comparable with those of primary forests in 20 years (McDonald & Healey 2000). Lower nutrient values in runoff than in throughfall suggest nutrient conservation in these forests. At a longer timeframe, total P in the top 30 cm of soil did not change in a study of multiple cycles of long-fallow shifting cultivation in Indonesia (Lawrence & Schlesinger 2001). However, P was redistributed among chemically defined fractions that vary in bioavailability, with relative decreases in available and recalcitrant inorganic fractions and corresponding increases in organic and occluded P forms, in part because forest fallow trees had deep roots and moved P from lower to more surficial soil layers. Collectively, these studies suggest an overriding influence of initial conditions and context dependencies in determining trajectories of nutrient availability during succession, and they also underscore the utility of sampling multiple soil horizons to account for depth-dependent redistribution of nutrients.

In addition to studies of soils, nutrient concentrations and quantities in litterfall may also suggest limitation or conservation, but again, results differ among studies. In forest fallow sites ranging from 1 to 14 years after shifting cultivation in Guatemala, litterfall nutrient fluxes did not vary with forest age; instead, N and P return to the soil via litterfall was consistently high (Ewel 1976). By contrast, litter production increased during succession in subhumid tropical forests in Mexico, leading to C, N, P, and K accumulation in the organic horizon of the soil but not in the mineral soil (Aryal et al. 2015). In an ~60-year-old chronosequence in seasonally dry tropical forest in Mexico, litter P concentrations increased from young successional forests to primary forests, despite lower  $\text{NaHCO}_3$ -extractable P and no change in total soil P (Valdespino et al. 2009). These data suggest more conservative P cycling early in succession and that the redistribution of P from less biologically available soil pools to more labile pools was sufficient to meet P demand of the growing forest.



Because of its important role in photosynthesis and the C cycle, many studies have focused exclusively on N dynamics during succession. Work on a variety of different types of successions in the temperate zone has shown that N availability is low during initial stages of primary succession but may vary widely thereafter, from large initial pulses of N, followed by rapid declines during the early stages of secondary succession after large disturbances, to no clear trends in early forest development following periods of prolonged agriculture (Vitousek et al. 1989). Studies conducted in the tropics show a similar range of low or high rates of N mineralization following deforestation and during early regeneration. After the removal of vegetation during land clearing on tropical soils, high rates of nitrification and denitrification can lead to large N losses from the soil (Robertson 1989). High loss rates are often sustained in the earliest stages of forest succession, before decreasing to lower levels in old secondary forests and primary forests, consistent with the model of Gorham et al. (1979), in which nutrient dynamics are influenced by NEP. Robertson & Tiedje (1988) measured large denitrification rates in early successional stages after clearing. Rates decreased in older secondary forests and increased again in primary forests. Soil nitrification rates measured in a laboratory incubation increased in soil samples from sites up to approximately 16 years after abandonment from agricultural use and remained elevated in samples collected from stands more than 60 years old on high-fertility soils in a high-rainfall zone (Robertson 1984). By contrast, soil N availability and potential transformations were greatest in early stage (10–15 years) and midstage (20–30 years) seasonally dry tropical forest compared with late stage (60 years) and primary forest sites (Saynes et al. 2005). The authors attributed these patterns in N cycling to the dominance of N-fixing legumes in early succession. In replicated chronosequences in Puerto Rico, soil N availability and nitrous oxide (N<sub>2</sub>O) fluxes were greatest in midsuccession forest in one set of sites but not in the other (Erickson et al. 2001), which the authors also related to differences in the abundance of N-fixing legumes. This contrasts with studies in Brazil and Costa Rica that have shown steady increases in soil nitrate concentrations as forests regenerate (Davidson et al. 2007, Keller & Reiners 1994). These studies underscore the conclusion that both initial conditions and prior land use history as well as differences among sites in the functional composition of the plant communities hinder broad generalizations about N dynamics during secondary succession in the tropics.

In summary, four trends from the literature emerge: (a) most changes in soil nutrient availability and biogeochemical processes happen within 10–15 years of forest regrowth, although this conclusion is tempered by the caveat that some studies compare secondary forests with pastures and some compare secondary forests with primary forests, limiting our ability to make inferences across land use trajectories that include stages of primary or reference forest, managed agricultural lands, and regenerated forest; (b) changes in rock-derived nutrients involve redistribution from lower to more superficial soil layers (Lawrence & Schlesinger 2001) or from soils to plant biomass (Bautista-Cruz & del Castillo 2005), which may result in apparent increases or decreases in soil nutrient availability depending on the soil depth examined; (c) directional shifts in N availability and transformations are more difficult to discern from chronosequence sites, in part because they are strongly coupled to changes in plant community composition (especially the abundance of legumes), which is not always predictable on the basis of forest age, plant traits, or regional species pools (Norden et al. 2015); and (d) studies of hydrologic losses of nutrients are conspicuously lacking from research that addresses changes in patterns of soil nutrients during secondary succession in the tropics.

**2.2.2. Sources of nutrients to support regrowing forests.** What are the element requirements for regenerating forests, and where do these elements come from? The answer depends, in part, on nutrient losses during deforestation and land use prior to forest regeneration. Wood harvest can



lead to substantial removal of carbon and nutrient reserves from a site after conversion (Kauffman et al. 2009). As above- and belowground biomass stocks vary greatly within and among primary tropical forests (influenced by climate, soil type, and biogeographic species pools), absolute losses of nutrients from burning during forest clearance also vary widely. For example, Kauffman et al. (2009) reported losses ranging from 673 to 1,218 kg N ha<sup>-1</sup> and from 67 to 444 kg Ca ha<sup>-1</sup> for a variety of Neotropical forest types. Subsequent land use such as grazing and cropping can lead to further increases or decreases in remaining soil nutrient stocks, depending on crop or pasture species traits, such as rooting depth, and management practices, including fertilization and the use of fire to clear and maintain pasture grasses. For example, long-term and intensive grazing can result in reductions in standing organic matter and associated nutrient stocks with decreased plant inputs, as reported for pastures in the tropical dry forest life zone of Hawai'i (Elmore & Asner 2006). Similarly, repeated cycles of burning during slash-and-burn cultivation or pasture management can exhaust readily available N pools (Davidson et al. 2007). Thus, secondary forests that regenerate after land is taken out of agricultural production may start with vastly different amounts of nutrient capital depending on macroclimate, soil parent material, and inherent site fertility and depending on the type, intensity, and duration of prior land use (Feldpausch et al. 2004, Kauffman et al. 2009).

Several studies have determined the importance of recycled N from soil organic N stocks versus new inputs from N fixation to support secondary forest or tree plantation regrowth, with the expectation that N fixation would be the dominant N source due to the large abundance of N-fixing trees in tropical forests. Russell & Raich (2012) constructed detailed N mass-balance budgets to track stocks and fluxes in 16-year-old monospecific plantations of four native tree species growing on former pastureland in a high-rainfall lowland region in Costa Rica. Surprisingly, the high rates of biomass accumulation were supported by mobilization of soil organic N for three of the four species, even for a N-fixing legume, suggesting that the presence of N-fixing tree species does not imply that symbiotic N fixation is the primary mechanism for N availability. N requirements for a fourth species were met by high rates of asymbiotic N fixation (Russell & Raich 2012). Similarly, in West Africa, young successional forests (0–20 years) removed an average 229 kg ha<sup>-1</sup> year<sup>-1</sup> N from the soil solution, incorporating approximately half of it in accumulating biomass (Robertson & Rosswall 1986). By contrast, other studies have stressed the important role of legumes with the potential to fix N in early tropical succession. In second-growth forest in Amazonia, isotopic evidence and the high abundance of legumes that potentially fix N throughout 25 years of regrowth suggest that symbiotic N fixation was an important source of N throughout early succession and midsuccession forests, whereas legume abundance was low in mature forests (Gehring et al. 2005). More quantitative estimates of symbiotic N fixation were generated by coupling successional stage- and species-specific measurements of nodule biomass and N fixation rates for a long chronosequence in Panama (Batterman et al. 2013). These data suggest that > 50% of the N requirement of rapidly growing forest was supplied by N fixation for the first 12 years of regrowth (Batterman et al. 2013). In a continental-scale study in the Neotropics, the abundances of legume trees with the ability to fix N varied systematically over gradients of succession and MAP, with greatest values in early successional and drier forests compared with rainforests (M.G. Gei, A. Rozendaal, L. Poorter, F. Bongers, J.I. Sprent, et al., unpublished manuscript). In conclusion, the role of N fixation versus other sources such as soil organic matter in meeting the N demands of regenerating forests appears more complicated than previously thought, and continental-scale data are required to resolve the magnitude and distribution of different N cycling processes.

Although symbiotic N fixation provides a clear mechanism to increase N supply as forests regenerate and accumulate biomass (Batterman et al. 2013, Gehring et al. 2005), no analogous processes occur in the P cycle that couple biological demand and supply so closely. Although



tropical tree species do vary in their ability to access different P forms (Steidinger et al. 2015), whether predictable associations exist between successional status and preferred forms of P is unknown, likely because of limited research on mycorrhizae during tropical succession. By contrast, strong evidence has been found that vegetation structure mediates P inputs from atmospheric deposition and acts as a positive feedback to deforestation that diminishes ecosystem resilience to land use (Lawrence et al. 2007). In a shifting cultivation system in dry forest in the Yucatan, patches that had undergone repeated cycles of deforestation, cultivation, and forest fallow showed declining productivity. By quantifying P inputs, internal recycling via litterfall, and outputs via leaching in forests that had undergone one, two, or three cultivation cycles, Lawrence and colleagues (2007) showed that P trapping from dry atmospheric deposition and rainfall on foliar surfaces was a critical input (**Figure 1**). Fallow lengths were not sufficient to develop the canopy structure and P trapping capacity necessary to offset P losses through harvest and leaching, compromising productivity after multiple cultivation cycles (Lawrence et al. 2007). Collectively, these studies illustrate that N and P cycles are strongly affected by regenerating forests through a variety of mechanisms, and they also underscore that the painstaking approach of quantifying nutrient budgets by measuring inputs, internal transformations, and outputs (*sensu* Gorham et al. 1979) is one of the best ways to identify mechanisms of biogeochemical changes during ecosystem succession.

**2.2.3. Evidence for nutrient limitation of forest regrowth.** What evidence do we have that nutrients limit C accumulation during secondary succession? Do patterns of nutrient limitation of secondary forest regrowth differ from those of mature forests, and does the identity of the most limiting nutrient shift over succession (Davidson & Martinelli 2009, Davidson et al. 2007, Nagy et al. 2017)? Understanding the nature of nutrient limitation of secondary forest regrowth is important in the context of understanding the C sink strength of the terrestrial biosphere and effects on the climate system (Wang et al. 2015).

A handful of studies have directly tested the hypothesis that nutrients limit secondary forest regrowth by fertilizing young forest plots (Campo et al. 2012, Davidson et al. 2004, Gehring et al. 2005, Harcombe 1977, Markewitz et al. 2012). Davidson and colleagues (2004) applied N and/or P fertilizer to 6-year-old secondary forest plots regrowing on an Oxisol following grazing and burning. Grass growth was limited by both N and P, whereas growth of young trees responded positively to N addition only (Davidson et al. 2004). N limitation of early secondary succession forest in Amazonia was further corroborated by an observational study along a chronosequence of more than 100 years, in which patterns of N cycling, including depleted foliar N isotopic composition (suggestive of symbiotic N fixation), low litterfall N/P ratios, and low soil nitrate concentrations, indicated conservative N cycling early in succession (Davidson et al. 2007). This contrasts with the view that in tropical forests on highly weathered soils, NPP is primarily limited by P or cations, not by N (Cleveland et al. 2011, Vitousek & Farrington 1997). After several decades of succession, data from Davidson and colleagues (2007) suggested a more leaky N cycling associated with a presumed shift to P limitation. The authors suggested that prolonged grazing accompanied by repeated cycles of pasture burning, which volatilizes N but not P, essentially depleted soils of N capital. Thus, regenerating secondary forests may function more like young primary successional sites in being limited by atmospherically derived N (Davidson & Martinelli 2009; Davidson et al. 2004, 2007).

Results from the moist evergreen forests in Amazonia described above contrast with data from a seasonally dry tropical forest in Mexico. Campo and colleagues (2012) established a factorial N and P fertilization experiment in 10- and 60-year-old secondary forests on limestone soils in the Yucatan and found that responses to fertilization depended on tree species and forest age. In the youngest site, two of the three dominant tree species did not respond to fertilization with increased



stem growth, and one species responded positively to all treatments. By contrast, two of the three dominant species in the older forest responded to added P or N + P, including one that appeared in both forests and did not respond in the younger stand. Some species responded to fertilization through altered foliar nutrients, whereas others responded with stem growth, depending on site soil fertility (Campo et al. 2012).

Globally, nutrient limitation of forest regeneration has consequences for the C cycle and climate (Yang et al. 2010). Using an earth system model with C-N-P coupling, Wang and colleagues (2015) estimated that nutrient limitation could reduce the C sink of regrowing forests by up to 50% compared with model runs that excluded N and P. Given this strong feedback to the global C cycle and the limited empirical data to understand the magnitude and distribution of nutrient limitation to secondary forest regrowth, fertilization experiments across gradients of ecosystem state factors should be a high priority.

### 3. CONTEXT DEPENDENCIES AND STATE FACTORS

Research on disturbance and recovery in temperate ecosystems has shown that a host of biotic and abiotic factors affect rates and trajectories of ecosystem recovery, such that for any given stage of succession, there may be large variation in processes such as rates of aboveground C accumulation or N mineralization across the landscape (see Meiners et al. 2015, Turner 2010). In addition, tropical forests are heterogeneous in terms of ecosystem state factors, *sensu* Jenny (1941): climate, parent material, age, topography, and biota. Thus, many factors may modulate how ecosystem processes and biogeochemical cycles change during secondary succession, and whether and where we should expect to see nutrient limitation of forest regrowth. These include physical factors such as soil parent material and climate, biotic factors such as community composition and historical biogeography, as well as management-related variables such as type and duration of prior land use, as we describe below.

#### 3.1. Soil and Landscape Heterogeneity

The myth that soils in the tropics are uniformly low in soil fertility was put to rest decades ago (Richter & Babbar 1991, Sanchez & Logan 1992), and it is widely acknowledged that ecosystem state factors such as parent material, weathering ages, topography, and landscape dynamics are as varied in the tropics as in the temperate and boreal zones, if not more so (Townsend et al. 2008). This variation can affect the magnitude—and in some cases even the direction—of changes in ecosystem processes and properties with land use change. Soil C stocks are a prime example of an ecosystem property for which land use change interacts strongly with soil mineralogy and other chemical and physical properties that control soil C dynamics, to produce a bewildering range of responses (López-Ulloa et al. 2005, Powers et al. 2011), including gains, losses, or no change in soil C stocks with large reductions in aboveground biomass and shifts in plant species diversity.

Although some aspects of nutrient availability and cycling change as a result of plant processes during secondary succession (Batterman et al. 2013), soil fertility and total element concentrations are also products of soil parent material and weathering age, and as such the soil template may affect succession. For example, the pace of old field succession in the temperate zone is thought to be controlled by soil fertility in somewhat counterintuitive ways (Meiners et al. 2015). On high-fertility soils, luxuriant growth of grass and herbaceous species can slow the growth of woody vegetation, whereas on low-fertility soils, woody species face reduced competition and thus greater rates of biomass growth (Meiners et al. 2015). Whether similar feedbacks between soil fertility and succession hold for the tropics is not known, although data from Brazil suggest greater rates of



tree growth in secondary forests on higher-nutrient Alfisols compared with Oxisols and Ultisols (Lu et al. 2002). Soil mineralogy can also have strong bottom-up controls on the response of belowground C and nutrient pools to changes in aboveground biomass and land use by influencing the sensitivity of soils to disturbance (Hughes et al. 1999). There are other ways that the soil template may affect succession in addition to effects on tree growth rates. In a large data set from the Central African Republic, tree species and functional traits sorted over soil gradients during community assembly, but these initial differences diminished as forest succession proceeded (Rejou-Mechain et al. 2014). Thus, soil properties can act as environmental filters, favoring or disfavoring species with certain functional trait values.

Differences in soil resources can also be influenced by disturbance regime and land use history. Fire can deplete soil nutrients during multiple cycles of slash-and-burn agriculture, and forest recovery rates can be negatively affected by the number of fires (Zarin et al. 2005). Past land use intensity and soil properties can affect biomass C pools and accumulation rates. In a study of 87 plots in Chiapas, Mexico, representing a range of soil parent materials, total ecosystem C pools in secondary forests increased with forest age, but soil organic C pools alone did not (Orihuela-Belmonte et al. 2013). Instead, soil organic C pools were positively correlated with a site quality index of soil physical properties, related to topography, rockiness, and fire disturbance, and negatively correlated with land use intensity. In Ecuador, the length of former pasture duration explained the direction of soil C changes during forest succession (de Koning et al. 2003), reflecting decreases in soil C with increasing pasture use. Secondary forests on pastures >20 years old accumulated C, whereas those on pastures <10 years old lost C with reforestation. Information on the duration and type of former land use is not always available, which could contribute to the large variability of responses observed both above and below ground (Nagy et al. 2017).

### 3.2. Climate

Climate can exert a strong control on biogeochemical cycling during secondary succession through its influence on soil resources, NPP, pests and pathogens, and disturbances such as fire, drought, and tropical cyclones. Globally, aboveground biomass accumulation rates in successional forests increase with decreasing latitude (Anderson et al. 2006) and at faster rates in tropical than temperate secondary forests (Brown & Lugo 1990b). This strong latitudinal relationship is highly predicted by average growing season temperature (Anderson et al. 2006). During primary succession along an elevational gradient in Hawai'i, the accumulation of soil P, N, and C stocks and of plant biomass increased with mean annual temperature (MAT) at typically faster rates on the wet side of the mountain than on the leeward side (Anderson-Teixeira et al. 2008).

Within the tropics, rainfall is a strong predictor of aboveground biomass and C accumulation rates in secondary forests. A recent analysis of 1,500 plots in the Neotropics found larger biomass gains in forests with greater MAP and other measures of water availability, such as reduced evapotranspiration (Poorter et al. 2016). Rates of C accumulation were greater in moist (1,000–2,500 mm MAP) and wet (>2,500 mm MAP) forests compared with dry forests (<1,000 mm MAP) in a pantropical review (Marín-Spiotta et al. 2008). In the first 20 years of succession, moist forests accumulated biomass C faster than wet forests.

Climate can also influence belowground C trajectories, although less predictably than for aboveground biomass. Absolute rates of soil C recovery during succession in a Caribbean study were greater in the moist and wet life zones than in dry forests (Brown & Lugo 1990a). A pantropical synthesis of >500 sites revealed that MAT was the most significant predictor of soil C stocks in tropical successional and plantation forests (Marín-Spiotta & Sharma 2013). The relative importance and interactions among other factors, such as MAP, current forest cover type, soil type,



and previous land use, differed with soil depth. Forest age was a poor predictor of soil C stocks, suggesting that information about individual site conditions is more important than time since forest growth began for estimating belowground C.

At the site level, successional variations in resources and microclimate conditions, such as light, water, temperature, and humidity, are influenced by seasonality, resulting in potentially harsher conditions for tree growth in seasonally dry versus wet tropical forests, which may select for species with different traits by influencing seedling survival (Lebrija-Trejos et al. 2011; Lohbeck et al. 2013, 2015a). Ultimately, resulting differences in species composition driven by environmental resource availability during succession may have consequences for biomass accumulation and nutrient cycling.

How tropical secondary forest ecosystem processes will respond to global change, including warming, elevated CO<sub>2</sub>, changes in rainfall and temperature, and N deposition, is highly uncertain. Cusack and colleagues (2016) identified multiple global change effects on humid tropical forest ecosystem processes, with greatest uncertainty for nutrient cycling. Anderson-Teixeira and colleagues (2013) reviewed available data from experiments and historical records and highlighted gaps in our knowledge of climate change effects on forest growth in tropical forests compared with temperate or boreal forest biomes. They found strong reductions in tree growth, and hence biomass C accumulation, with drought in forests of all ages and found differential response of trees to climate by species and forest age. In a review of climate variability effects on tree demography in tropical secondary forest, Uriarte and colleagues (2016) found that young forests were more vulnerable to drought and had a greater risk of fire and other disturbances with increasing fragmentation. Rising atmospheric CO<sub>2</sub> levels may exert differential effects on tropical trees in secondary versus primary forests owing to differences in growth rates of individual trees with age and with changing species composition during succession (Anderson-Teixeira et al. 2013). However, empirical data are too scarce for robust conclusions (Cusack et al. 2016). Shifts in recruitment, survival, and growth of different tree species in response to changes in climate or CO<sub>2</sub> can affect C and nutrient cycling, especially given the strong effect of biomass on important ecosystem processes, such as litter production and decomposition.

### 3.3. Biogeography

Tropical forests are rich in species, and this biodiversity has a geographic structure and an evolutionary history (Corlett & Primack 2006), such that regional variations are seen in species distributions and their traits, and these differences may affect recovery from disturbance and land use (Cole et al. 2014). A meta-analysis of paleoecological studies showed that Central American and African tropical forests had greater rates of recovery from a range of disturbances compared with Asia and South America, and the authors suggested that exposure to disturbances over millennia might have favored species with traits that confer resilience (Cole et al. 2014). For example, the role of N-fixing Fabaceae in facilitating early succession in Neotropical forests, particularly dry forests, is now firmly established (Batterman et al. 2013, Bhaskar et al. 2016). However, it is not known whether legumes play the same role in Asian tropical forests, where legumes appear to be similarly speciose, but not as abundant, compared with South American and African flora (Yahara et al. 2013). Similarly, many Asian rainforests are dominated by Dipterocarpaceae, which support ectomycorrhizal fungal symbioses, whereas the majority of other tropical tree lineages support arbuscular mycorrhizal fungi (Peay et al. 2010). These fungal types differ in the forms of N they can access, with many ectomycorrhizae being able to use organic N sources (Read & Perez-Moreno 2003), but few studies have examined whether mycorrhizal type is a trait that varies systematically during tropical secondary succession. Incorporating both phylogenetic diversity and



biogeography of plants, microbial symbionts, and animal dispersers into conceptual frameworks of succession may help elucidate variation within and among sites over time and space (Meiners et al. 2015).

#### 4. ARE CLASSIC CONCEPTUAL FRAMEWORKS OF ECOSYSTEM PROCESSES RELEVANT TO TROPICAL SECONDARY FOREST SUCCESSION?

Now that we have reviewed what is known about how biogeochemistry and ecosystem processes change during secondary succession, we can ask whether these systems fit classical notions of nutrient cycling during succession or whether new models are needed to describe tropical secondary forests. Succession has been studied for more than a century (Clements 1916). Many of the model frameworks first developed for primary succession (i.e., ecosystem development on a new substrate or after a catastrophic disturbance) have been modified for secondary succession.

In a classic article, Odum (1969) hypothesized that an ecosystem's ability to conserve nutrients increased as it matures and suggested that, early on during succession, ecosystems lost or leaked nutrients until vegetation biomass was established, and then nutrient accumulation occurred. This model proposed that as long as biomass continued to grow, inputs would exceed outputs. At some point, ecosystems were hypothesized to reach a point of zero NEP, or steady state, at which inputs via production equaled losses from respiration/decomposition and nutrients are conserved or internally recycled in what are considered closed cycles. Vitousek & Reiners (1975) proposed an alternative model, in which nutrient losses are initially high following disturbance, decrease during midsuccession, and increase in late succession. During secondary succession, ecosystems start with an initial nutrient capital in the soil. This nutrient capital can be rapidly depleted temporarily during the disturbance event that initiates succession—for example, during the removal of aboveground biomass during deforestation for pasture or agriculture. As succession proceeds, limiting nutrients and those essential to NPP are predicted to accumulate in regrowing plant biomass, whereas nonessential nutrients are lost from the ecosystem. Where net biomass increment, or growth, is zero or negative, overall nutrient losses increase again, reflecting availability in excess of plant demand. Vitousek & Reiners (1975) thus proposed that mature ecosystems have a leaky or open cycle compared with intermediate-staged successional systems. Stream flux data from the Hubbard Brook Experimental Forest in New Hampshire supported this hypothesis, with greater elemental losses in mature than in successional watersheds (Vitousek & Reiners 1975).

Although these models have been useful for guiding research, especially in temperate areas (e.g., Hedin et al. 1995), some important differences exist between secondary forest succession following land abandonment and the classic situation invoked by these models of forest regeneration immediately following a disturbance. The rich diversity of soil templates (Townsend et al. 2008) and great heterogeneity in land use and management in tropical regions lead to wide variability in starting points for secondary forests in the tropics (a fact that may be overlooked but is likely also true for temperate zone ecosystems). Thus, a variety of starting points exist for secondary forests in the tropics, ranging from sites that have been disturbed by strong storms that kill trees but leave detritus intact to sites that have experienced centuries of agricultural use (Chazdon 2014). Recently cleared lands may lose nutrients quickly (Herrera et al. 1981), but lands that have been under pasture or cropping for years may have reached some sort of steady state, albeit different from the initial forest. For example, deep-rooted grasses introduced to many tropical pastures facilitate soil organic matter accumulation (Fisher et al. 1994) and presumably buffer sites from nutrient loss, despite removal of plant biomass during grazing and animal harvest.



Not surprisingly, conceptual models developed from data collected in the tropics stress different aspects of biogeochemical change during succession, such as shifts in the identity of the limiting nutrient, compared with temperate-zone literature (Herrera et al. 1981). Building upon data from forests regrowing on abandoned pastures in Amazonia, Davidson & Martinelli (2009) proposed a model that describes changes in N and P cycling during tropical forest secondary succession that parallel patterns observed during ecosystem development and that match expectations from Walker & Syers' (1976) classical work. The Walker–Syers model posited that vegetation growth on primary successions will be limited during early stages by the availability of nutrients derived from the atmosphere, like N, but limited by rock-derived nutrients, such as P, after these are depleted during soil weathering and over geologic time spans. Drawing from field observations, Davidson & Martinelli (2009) proposed that repeated cycles of burning and agricultural use reduce soil N stocks to quantities that limit forest regrowth. During secondary succession, N accumulates in recovering biomass (e.g., via fixation by legumes), alleviating potential N limitation (Davidson et al. 2007). Secondary forests on highly weathered soils are thus predicted to move from a state of N limitation and a closed N cycle to a leaky N cycle and conservative P cycle as they regenerate (Davidson et al. 2007).

## 5. KNOWLEDGE GAPS AND FUTURE DIRECTIONS

Despite significant progress in our understanding of tropical secondary forests, significant gaps still exist in our ability to predict rates of ecosystem process change during postagricultural abandonment and forest regrowth across the tropics and the response of secondary forests to future environmental change. In particular, future studies should consider approaches used to study succession, what measurements are made, how these data inform conceptual models, and how to place site-specific results into the broader context of secondary succession across the tropics.

Forest succession typically occurs over decades to centuries, time spans that far exceed the life span of most research studies. The chronosequence approach is an imperfect tool for a number of reasons (described in Johnson & Miyanishi 2008) but is unlikely to be abandoned anytime soon. Certain aspects of study design can greatly increase the utility of this approach. First, chronosequences must be replicated to detect variation across the landscape at any given successional stage (Bautista-Cruz & del Castillo 2005, Erickson et al. 2001). Second, combining chronosequences with longitudinal data (i.e., repeated measurements over time) is a powerful approach to quantify dynamic processes across different timescales (Chazdon et al. 2007, Mora et al. 2015, Norden et al. 2015). Last, studies should span multiple land use transitions (**Figure 1**) given the heterogeneity in primary forests before conversion and variable effects of land use on soil resources prior to regeneration. For instance, studies of secondary forests include comparisons with primary forest, plantation forest, pastures, or cropped fields, but few studies attempt to reconstruct the entire land use/disturbance sequence (**Figure 1**). Even rarer are studies that examine how multiple cycles of clearance and succession affect ecosystem processes (but see Eaton & Lawrence 2009, Lawrence 2005, Lawrence et al. 2007).

Equally important as the approach and site selection used to study succession are the questions being asked. Identifying which nutrients limit NPP throughout succession and whether the identities of limiting nutrients vary geographically and with land use history is a high priority (Davidson & Martinelli 2009). Such knowledge directly informs understanding of the potential of regrowing forests to sequester C and affects predictions of the future strength of the terrestrial C sink in the context of climate change (Wang et al. 2015). Few studies simultaneously consider how the availability of multiple elements, including and beyond N and P, changes during succession, despite recent evidence for the importance of colimitation on NPP (Kaspari & Powers 2016). Although



nutrient addition experiments are considered the gold standard to identify nutrient limitation, a host of other approaches exist (Sullivan et al. 2014), and proxy measurements have been deployed effectively in successional studies in the Amazon (see Davidson et al. 2007).

A second high-priority knowledge gap is identifying the sources of nutrients that sustain regrowing forests and the biogeochemical mechanisms that underpin these processes. Constructing ecosystem budgets of inputs, internal transformations, and outputs is one of the best ways to accomplish this, as exemplified by studies that revealed soil organic matter as the dominant N source for regrowing plantations (Russell & Raich 2012) and that atmospheric inputs of P were critical to the long-term sustainability of shifting cultivation in dry tropical forests (Lawrence et al. 2007). Quantifying hydrologic losses of nutrients from tropical forests is infrequently done, yet these data form the cornerstone for testing biogeochemical theory (Hedin et al. 1995, Vitousek & Reiners 1975). Unlike in temperate regions, where successional models based on nutrient budgets were first developed, few studies report stream nutrient data at the catchment scale in tropical landscapes dominated by secondary forests. Challenges to implementing catchment-scale studies of the effects of land use change on nutrient export include the large heterogeneity and small scale of landscape change in tropical watersheds (Ponette-González et al. 2014), which may make it difficult to identify effects of individual land cover types. Lysimeters in forest patches could help alleviate this problem in certain regions where conditions are favorable for this type of sampling.

Increasing knowledge of legacy effects of prior land use is key to improving predictions of how secondary forests and land under remaining primary forest will respond to climate change, further conversion, and other global change factors. Land use and disturbance history can modulate the effect of time on recovery rates for aboveground biomass and affect patterns in other ecosystem stocks and fluxes (Nagy et al. 2017). Similarly important is understanding whether successional trajectories in community dynamics and ecosystem processes are deterministic or probabilistic (Lebrija-Trejos et al. 2010, Norden et al. 2015). Most studies do not compare processes under broad land cover types with research on the effects of management, despite findings that different practices (e.g., fertilization, tillage, rotation cycles, grazing intensity) can alter biogeochemical and biophysical forcings on climate (Erb et al. 2017).

## 6. SUMMARY AND CONCLUSION

Secondary forests are a dominant forest cover type globally and in the tropics. Understanding ecosystem processes and biogeochemical cycles in tropical secondary forests is critical for improving our knowledge of their role in the global C cycle and assessing the recovery of habitat for biodiversity conservation, forest ecosystem goods and services, and climate change mitigation and adaptation (Locatelli et al. 2015). We highlighted advances in understanding of how C and nutrient stocks and dynamics are altered during the regrowth of tropical forest cover. The majority of studies on tropical forest secondary succession focus on aboveground biomass, with more recent interest in bulk soil C stocks for a more complete assessment of ecosystem C response to reforestation. Less work has been done on C and nutrient fluxes beyond litterfall studies, on the sensitivity of different soil organic matter pools to disturbance, or on the effects of succession on microbial communities as drivers of biogeochemical cycles. Also poorly represented in the tropical forest literature are studies of nutrient budgets during different stages of forest succession, with quantification of elemental inputs, internal transformation processes and rates, and losses. This lack of data makes it difficult to compare secondary tropical forests with biogeochemical models of ecosystem succession developed from classical temperate watershed studies. Biases in the geographic representation and temporal resolution of tropical forest successional studies hinder our ability to make predictions about long-term trajectories and recovery rates across different tropical



environments, especially beyond the first two decades of succession. We underscore the importance of accounting for coupling between biogeochemical cycles of C and other elements essential for forest growth and the importance of considering how spatial and temporal heterogeneity in ecosystem state factors and biogeographic histories of species can mediate the magnitude and direction of elemental cycling during tropical forest secondary succession.

## DISCLOSURE STATEMENT

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