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Viewpoint

Soil fertility controls on tropical forest productivity and mortality: synthesis and roadmap

Summary

Tropical forests are highly diverse and productive ecosystems and store nearly 60% of vegetation biomass. Across the tropics, forests span large gradients of soil fertility, from vast regions situated on highly weathered, ancient geological formations to others on young, nutrient-rich landscapes. Tropical forest productivity, mortality, and biomass all vary systematically across these gradients in soil fertility. Aboveground forest productivity tends to increase with higher soil fertility, while counterintuitively, aboveground biomass does not increase proportionally. This disconnect is likely due to coinciding increases in mortality with higher soil fertility. However, we know relatively little about the mechanisms underlying how soil fertility regulates productivity or mortality – two critical determinants of forest biomass – and even less about how these relationships will shape tropical forest responses to global change. Here, we present a mechanistic framework for understanding how soil fertility affects productivity through photosynthesis, carbon allocation, and carbon-use efficiency; how it modulates mortality via direct and indirect interactions with various drivers of mortality; and how global change may alter these relationships. Based on this synthesis, we outline a roadmap to advance our understanding of tropical forests and improve predictions of their responses to global change.

Introduction

Tropical forests and their soils play an outsized role in Earth's carbon balance and climate (Luyssaert *et al.*, 2007; Beer *et al.*, 2010; Spawn *et al.*, 2020; Pan *et al.*, 2024). In theory, soil fertility – characterized by a multidimensional set of physical, chemical, and biological properties (Box 1) – is a key driver of variation in forest biomass through its effects on plant functional composition, forest productivity, and biomass turnover rates via tree mortality (Dybzinski *et al.*, 2015; Fig. 1; Box 2). However, there is immense uncertainty about the future of tropical forest carbon stocks and fluxes, in part because of their vast biogeochemical heterogeneity and high species and functional diversity (Townsend *et al.*, 2008). Most tropical forests are situated on highly weathered, ancient geological formations that are low in soil fertility, but a meaningful proportion of tropical forests grow on young, eroding landscapes with high soil fertility. Across tropical forests, plant species composition varies substantially, driving variation in how forest productivity and biomass turnover rates respond to soils (John *et al.*, 2007; Condit *et al.*, 2013; van der Sande *et al.*, 2016; Turner *et al.*, 2018; Peguero *et al.*, 2023). Thus, large uncertainties remain about the mechanisms linking soil fertility to tropical forest carbon storage and its dynamics, particularly under the influence of global change (Cavaleri *et al.*, 2015; Pugh *et al.*, 2019). We must address these uncertainties to predict the future of tropical forest carbon cycling and guide informed policy and management decisions.

Soil fertility remains one of the least understood drivers of forest biomass carbon dynamics. Despite the inconsistencies in how soil fertility is characterized (Box 1), more fertile soils generally support higher aboveground net primary productivity, but may or may not support higher aboveground forest biomass (Vitousek & Sanford, 1986; Quesada *et al.*, 2012; Muller-Landau *et al.*, 2021). Of the 26 studies investigating relationships of soil fertility with aboveground biomass, 13 find increasing aboveground biomass with soil fertility, seven find decreasing aboveground biomass, and six find no relationship (Ding & Zang, 2021; Muller-Landau *et al.*, 2021; Bukombe *et al.*, 2022; Abbasi *et al.*, 2023; Batool *et al.*, 2024; Simmavong *et al.*, 2025; Brunello *et al.*, 2025). When considered experimentally, three studies that report biomass differences with nutrient addition in mature tropical forests found no effect of nutrients (Cusack *et al.*, 2011; Markewitz *et al.*, 2012), while two studies in young tropical forests found positive effects of nitrogen (Davidson *et al.*, 2004; Tang *et al.*, 2026). The variation in both direction and magnitude of the relationship between fertility and biomass stocks suggests that biomass might peak at intermediate soil fertilities (Muller-Landau *et al.*, 2021; Fig. 2a). Such a unimodal pattern would emerge if biomass turnover rates and productivity both increase with soil fertility, resulting in carbon losses from higher mortality rates exceeding carbon gains from higher productivity in the most fertile soils (Fig. 2a). A limited number of studies have found increasing mortality rates with increasing soil fertility (Phillips *et al.*, 2004; Bellingham & Sparrow, 2009; de Toledo *et al.*, 2011; Stephenson *et al.*, 2011; Quesada *et al.*, 2012; Galbraith *et al.*, 2013; Sawada *et al.*, 2015; Soong *et al.*, 2020). However, there is limited empirical evidence for a hump-shaped relationship of biomass with fertility, in part because of the difficulties of aligning different soil fertility metrics across studies, and the large sampling errors inherent to estimates of mortality rates (Muller-Landau *et al.* 2021; see Box 2). Although productivity has been studied more frequently across fertility gradients, the numerous soil fertility and productivity metrics used also hamper a quantitative synthesis. Resolving the underlying relationships between fertility, productivity, and mortality and

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Box 1 Defining and conceptualizing soil fertility

Soil fertility is usually defined as the capacity for soil to sustain plant growth. It is a plant-centric term that encompasses the chemical, physical, and biological properties of soils that determine nutrient availability for plants, as well as a lack of conditions that inhibit plant growth (e.g. toxic metals). Soil fertility is part of the broader concept of soil health (e.g. Lehmann *et al*., 2020).

Because soil fertility is a multidimensional and often ambiguous term, there is no one measurement that can capture a unified axis of fertility. Describing fertility on one axis is further complicated by the possibility that different individuals, species, and communities can experience the same nutrient conditions in different ways, including over ontogeny and time. A fertile environment for one group of species may be poor for another group.

In practice, soil fertility is represented imperfectly by one or more metrics of soil properties thought to capture or correlate with soil fertility. Commonly used metrics include pH, cation exchange capacity, and various nutrient concentrations. Metrics may be selected for ease of use, what matters for the local plant community, or other reasons. Soil fertility measurements frequently focus on nutrients that are expected to be limiting in a given system, such as base cations and phosphorus on heavily weathered soils, or nitrogen in early successional and montane tropical forests (Vitousek & Sanford, 1986; Davidson *et al*., 2007). However, many other elements can also limit plant performance, including via co-limitation (Kaspari & Powers, 2016). Furthermore, many soil physical and chemical properties are correlated because of the transformations that occur during pedogenesis (e.g. Quesada *et al*., 2010), potentially obscuring the independent roles of properties which are measured less frequently. Importantly, the soil properties that regulate productivity may not be those that regulate mortality (Quesada *et al*., 2009; de Toledo *et al*., 2012).

Differences in the properties selected for measurement and variation in sampling and analytical approaches present substantial challenges to cross-site synthesis and comparison across tropical forests. Here, we rely on how individual studies define soil fertility for their given study system.

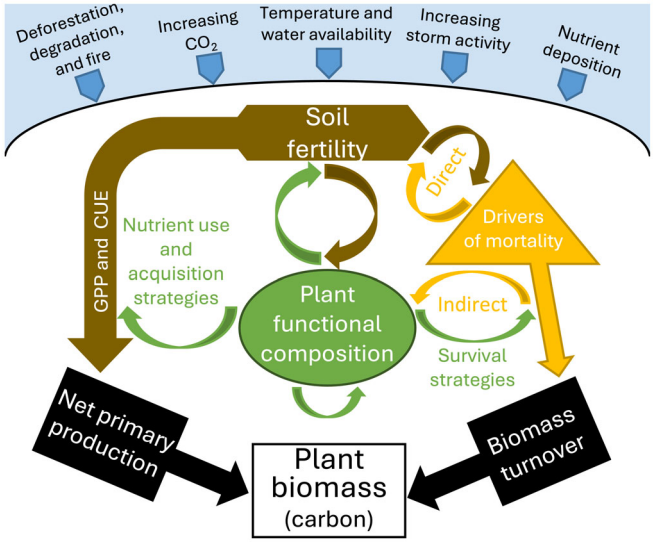

Fig. 1 Conceptual map of links between soil fertility and forest carbon dynamics. Forest carbon cycling (carbon fluxes in black and biomass carbon stocks in white) is regulated by soil fertility (brown) and its interactions with plant functional composition (green) and drivers of plant mortality (yellow, with labels for direct and indirect effects of fertility on mortality), all of which are being altered by global change (blue). Plant functional composition is a property that emerges from variation in the function of individual trees of the same species, shifts in the community composition of individuals of the same species with phenotypic plasticity, shifts in community composition of species with different functions, and/or differences in size structure. Plants and their functional composition in a forest modify the effect of fertility on primary production via shifting nutrient use and acquisition strategies, and on biomass turnover by modifying the survival strategies and therefore susceptibility to a given mortality driver. Plant functional composition can feedback on itself via iterative interactions between plants and between plants and their environment. Arrows indicate directional effects between two components of the system, and paired cyclic arrows indicate potential feedback loops, with the width indicating the strength of the interaction. Key global change drivers that are likely changing these interactions over time and are further discussed in 'Global change impacts on soil fertility–productivity–mortality feedbacks and interactions'.

their emergent effects on forest biomass-fertility relationships is critical for understanding and predicting the impacts of global change on future tropical forest carbon cycling. These limited observations and the clear need for resolution provide strong motivation for additional research around three key areas: (1) quantifying the strength and magnitude of fertility–productivity relationships; (2) determining the mechanisms underlying the potential fertility–mortality relationship; and (3) empirical testing of potential interactions with global change, including land-use change and rising CO_2.

Fundamentally, the effects of fertility on productivity and mortality are mediated by interactions of soil fertility with plant functional composition. Differences in plant functional composition can be shaped by plant strategies and functional traits across several scales. This includes trait plasticity and allocation shifts in response to differing environmental conditions (e.g. shifts in allocation between growth and defense of the same plants). This also includes, at the community level, turnover in individuals of the same species that have different traits because of phenotypic or genetic variation, or turnover of species with different traits. Plant species composition varies with soil fertility, and community-weighted means of plant functional traits have been correlated with soil fertility in multiple studies (Fyllas *et al*., 2009; Quesada *et al*., 2012; Fortunel *et al*., 2014; Libalah *et al*., 2017; Umaña *et al*., 2021; ter Steege *et al*., 2025; Aguirre-Gutiérrez *et al*., 2025; Fig. 2b). Shifts in plant functional composition across fertility gradients could moderate or amplify the direct effects of nutrient limitation on productivity via associated changes in plant nutrient use and acquisition strategies. In addition to increasing productivity, shifts in functional composition on fertile soils may favor species that allocate resources toward rapid growth and reproduction rather than storage or defense, potentially increasing susceptibility to various agents of mortality (e.g. the 'live fast, die young' trade-off; Stephenson *et al*., 2011). These compositional shifts could therefore influence mortality rates and biomass loss (Fig. 2c). Overall, plant communities and their functional traits are key mediators shaping how forest dynamics relate to soil fertility.

Box 2 Definitions of tropical forest soil fertility, dynamics, and biomass

Biomass: the mass of living matter in an ecosystem. Here, we focus on tree biomass, which dominates total biomass in tropical forests. Biomass data in the studies that we discuss are most often aboveground woody biomass estimated from measurements of tree diameter, tree height, and wood density using allometric equations.

Productivity: flux of carbon fixed into organic matter (units of mass per time). Gross primary production (GPP) is carbon fixed by photosynthesis; net primary production (NPP) is the net carbon gained by primary producers (plants) and equals the difference between GPP and autotrophic respiration. Most studies reported here focus on aboveground woody biomass productivity (a subset of total NPP, which also includes production of leaves, roots, and reproductive tissues), although studies that consider other aspects of productivity are also discussed.

Mortality rate: the rate at which individuals die, or biomass is lost in a forest. Mortality rate can be calculated as an instantaneous rate ($time^{-1}$) or a discrete rate for a given time interval (e.g. yr^{-1}; see Kohyama *et al*., 2018). It is sometimes reported as a fraction of individuals or biomass lost per year (% yr^{-1}) or as the amount of biomass or basal area lost per year (e.g. Mg ha^{-1} yr^{-1}). The most commonly reported metric for tropical forests is the mean tree mortality rate, a measure that is dominated by the more abundant smaller trees. The less commonly reported metric is biomass mortality rate (Mg ha^{-1} yr^{-1}) largely determined by the mortality rates of larger trees.

Biomass mortality flux: the flux (units of mass per time) of biomass that dies and is therefore transferred to the necromass pool. The vast majority of necromass will be respired and emitted as carbon to the atmosphere within years to at most decades of death. Most of the studies that report the biomass mortality flux focus on aboveground woody mortality.

Tissue turnover: nonlethal loss of biomass (to necromass), for example leaves, fine roots, and branches.

Projecting future tropical forest structure and dynamics is particularly challenging because rapid climate and land-use change could interact with both soil fertility and tropical forest dynamics (Fig. 1). Global change drivers – such as deforestation and degradation, rising CO_2, changing climate, and nutrient deposition – can alter nutrient supply and demand, potentially influencing productivity and mortality in complex ways. Overall, global change is likely to modulate, and be modulated by, the effects of soil fertility on forest productivity and mortality. Here, we present a framework for understanding how soil fertility influences tropical forest productivity and mortality. We also explore how these relationships could shift under global change.

Soil fertility tends to promote forest productivity, but uncertainty persists

Soil fertility can increase forest productivity by increasing gross primary production (GPP), net primary production (NPP), either directly through enhanced resource availability or indirectly through shifts in plant functional composition. Fertility can enhance GPP by increasing nutrient concentrations in leaves (e.g. Reich *et al*., 1991; Wright *et al*., 2004; Ellsworth *et al*., 2022), leaf area index (Giardina *et al*., 2003), and/or leaf lifespan (Manu *et al*., 2024), thereby improving light capture, photosynthetic efficiency, and carbon assimilation. Fertility also supports greater biomass production efficiency (biomass produced per GPP; by *c*. 16% across sites: Vicca *et al*., 2012) and carbon-use efficiency (NPP per GPP; by *c*. 14% across sites: Doughty *et al*., 2018) by decreasing respiration costs, reducing the need for carbon allocation toward nutrient acquisition (e.g. root exudates, mycorrhizal symbionts, and symbiotic nitrogen fixation; Chapin *et al*., 1986; Davidson *et al*., 2004; Batterman *et al*., 2013; Hawkins *et al*., 2023; Chari *et al*., 2024), increasing water-use efficiency (Wright *et al*., 2004; Osnas *et al*., 2013; Adams *et al*., 2016), and/or increasing allocation to longer-lived tissues (i.e. wood and coarse roots; Vicca *et al*., 2012; Doughty *et al*., 2018).

Together, these findings suggest that fertility influences productivity via both GPP and carbon-use efficiency, but disentangling the relative contributions of these pathways requires explicitly evaluating how fertility affects the capacity for photosynthesis, carbon allocation, and tissue residence time. Complicating interpretation of the congruence between any productivity–fertility relationship and a fertility–biomass relationship is the observation that – of the 37% of GPP that goes to NPP (Doughty *et al*., 2018) – only *c*. 39% is allocated to woody productivity, while *c*. 34% of NPP is allocated to leaves and *c*. 27% to fine roots (n = 35 forest sites primarily in the Americas and a few in Asia; Malhi *et al*., 2011). Thus, the degree to which any fertility–productivity relationship contributes to a positive fertility-aboveground biomass relationship depends on how short-lived leaf or fine root tissues vs long-lived woody tissue, the latter of which dominates the biomass pool, changes across fertility gradients.

Shifts in NPP allocation to different tissues across fertility gradients and nutrient addition experiments are poorly quantified, especially allocation to reproductive tissues and coarse roots (but see Ward *et al*., 2025). Theory predicts that total, leaf, and woody production – in both absolute terms and relative to total production – should increase with higher soil fertility. By contrast, theory predicts that relative allocation to fine root production may increase or decrease depending on how much NPP plants must allocate belowground to acquire nutrients when they are limiting (i.e. potentially more belowground production when fertility is low; Bloom *et al*., 1985; Dybzinski *et al*., 2011, 2015). These theoretical predictions vary in the degree to which they are supported by empirical data across fertility gradients and experiments.

Fertilization experiments, which have the advantage of isolating the effects of nutrient availability, show mixed responses of forest productivity to fertility. Across the tropics, experiments generally find that individual-scale tree growth and/or stand-scale leaf production increases when fertilized with nitrogen, phosphorus, or other cations (Wright, 2019; Cunha *et al*., 2022; Manu *et al*., 2024; Yu *et al*., 2025). By contrast, stand-scale woody production increased in only three of 11 fertilization experiments (Tang *et al*., 2026). Differences across experiments may reflect underlying variation in edaphic characteristics of the sites, while differences between individual and stand-scales may reflect results dominated by small and large trees, respectively. Fine root production either increases or shows no change with fertilization (Yuan & Chen, 2012; Alvarez-Clare *et al*., 2013; Waring *et al*., 2019; Lugli *et al*., 2021; Mosquera & Moreno-Hurtado, 2022; Cunha *et al*., 2022). It is possible that increases in fine roots may reflect

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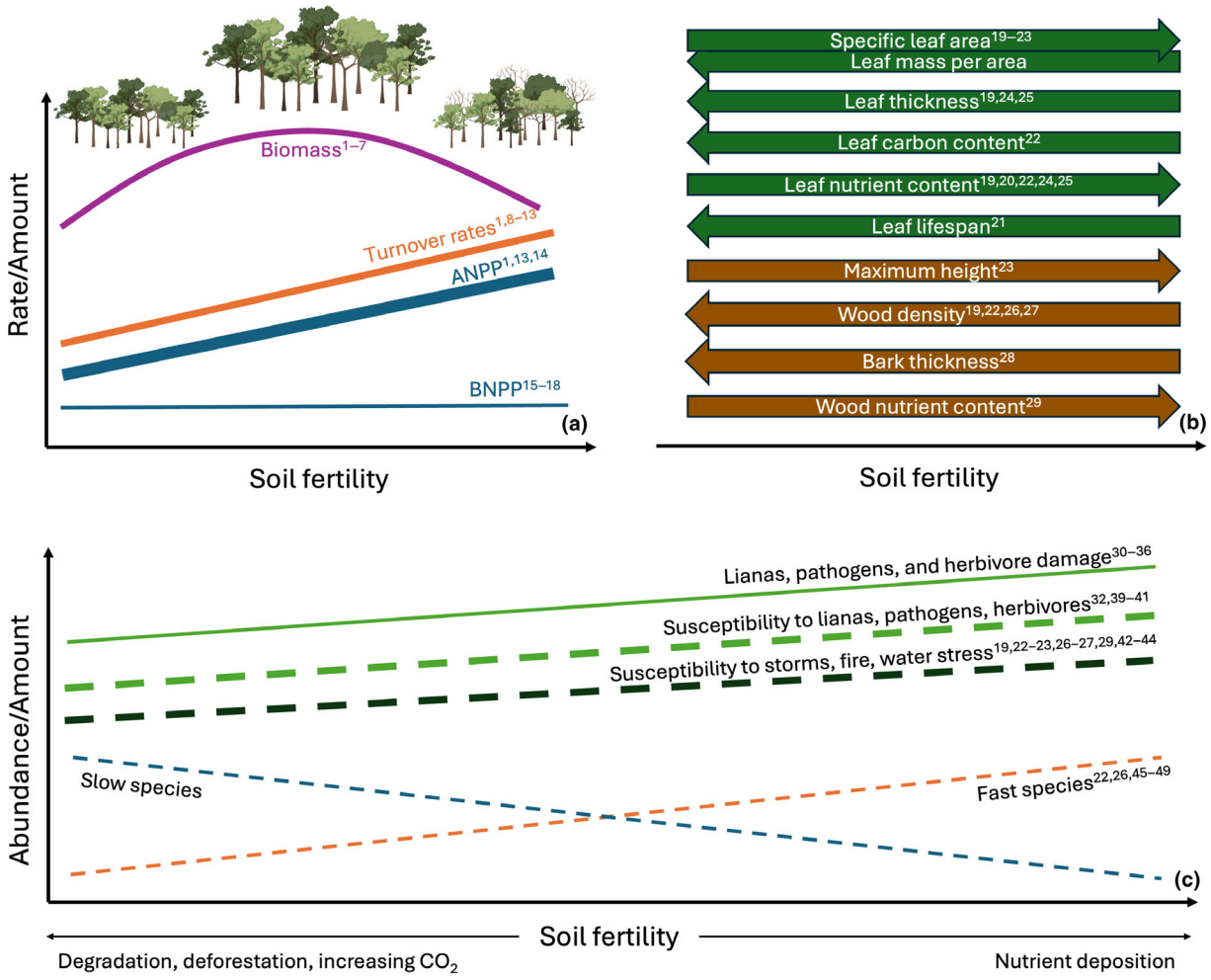

Fig. 2 Relationships between soil fertility (*x*-axis) and above and belowground net primary productivity (ANPP and BNPP), turnover rates, and biomass in tropical forests (*y*-axis) (a). The thickness of the line indicates how much relative empirical support exists for each relationship. Current understanding of how functional traits related to nutrient use, growth, and mortality change across fertility gradients (b). Green lines represent leaf traits and brown lines represent wood-related traits. The direction of the arrow indicates increasing values. Panel (c) highlights the hypothesized mechanisms underlying the relationships, such as increasing turnover rates with increasing soil fertility, measured in (a), whereby direct effects are represented by a solid line and indirect effects (susceptibility to mortality drivers) are represented by a dashed line. Light green represents biotic factors, dark green represents abiotic factors, blue represents the abundance of slow (conservative; Reich 2014) species, and orange represents the abundance of fast (acquisitive) species changes across soil fertility. Global change is expected to alter soil fertility, with increasing soil fertility in response to nutrient deposition and declining soil fertility with forest degradation, deforestation, and increasing CO_2 (c). Trees in (a) were created in BioRender (Wong, M. 2026; https://BioRender.com/yalthl2). References: [1]Muller-Landau *et al*. (2021) (and citations within); [2]Ding & Zang (2021); [3]Bukombe *et al*. (2022); [4]Abbasi *et al*. (2023); [5]Batool *et al*. (2024); [6]Simmavong *et al*. (2025); [7]Brunello *et al*. (2025); [8]Dalagnol *et al*. (2021); [9]Reis *et al*. (2022); [10]Sousa *et al*. (2022); [11]Muñoz *et al*. (2023); [12]Zhang *et al*. (2025); [13]Gourlet-Fleury *et al*. (2023); [14]Medina-Vega *et al*. (2025); [15]Aragão *et al*. (2009); [16]Bukombe *et al*. (2022); [17]Huaraca Huasco *et al*. (2021); [18]Yuan & Chen (2012); [19]Fortunel *et al*. (2014); [20]Fyllas *et al*. (2009); [21]Russo & Kitajima (2016); [22]ter Steege *et al*. (2025); [23]Umaña *et al*. (2021); [24]Homeier *et al*. (2021); [25]Libalah *et al*. (2017); [26]Chen *et al*. (2024); [27]Quesada *et al*. (2012); [28]Jones *et al*. (2019); [29]Heineman *et al*. (2016); [30]Buscardo *et al*. (2022); [31]DeWalt *et al*. (2006); [32]Endara & Coley (2011); [33]Landsberg & Gillieson (1995); [34]Laurance *et al*. (2001); [35]Malizia *et al*. (2010); [36]Putz & Chai (1987); [37]Santiago *et al*. (2012); [38]Schappe *et al*. (2020); [39]Fine *et al*. (2006); [40]McKey *et al*. (1978); [41]Reich *et al*. (1991); [42]Oliveira *et al*. (2019); [43]Oliveira *et al*. (2021); [44]Rosell *et al*. (2023); [45]Russo *et al*. (2005); [46]Ferry *et al*. (2010); [47]Viani *et al*. (2011); [48]Sawada *et al*. (2015); [49]Tavares *et al*. (2023).

short-term proliferation in plant species adapted to low nutrient conditions (Sayer *et al*., 2006). Despite the benefits of experiments, extrapolating from their results can be challenging because most experiments are short (<6 yr), small in scale (≤0.25 ha), add rather than remove nutrients, and hamper the capture of long-term and broad-scale responses, such as via changes in community composition (Wright *et al*., 2018).

Observational studies across natural spatial variation find that higher soil fertility is generally associated with higher aboveground productivity, but inconsistently associated with belowground productivity. Whereas experimental studies isolate the effects of nutrient addition, observational studies can have confounding, correlated variation in plant species composition and other soil and environmental variables (e.g. topography and

land-use history). Aboveground productivity increases with fertility in 20 of 21 studies (Muller-Landau *et al.*, 2021; Gourlet-Fleury *et al.*, 2023; Medina-Vega *et al.*, 2025). Leaf production, which is typically characterized by litterfall production, also tends to increase with fertility, with 10 out of 13 studies finding positive relationships between litterfall and soil fertility (Vitousek & Sanford, 1986; Dent *et al.*, 2006; Muller-Landau *et al.*, 2021; Becknell *et al.*, 2021), two showing no relationship (Kitayama & Aiba, 2002; Heineman *et al.*, 2015), and one finding both negative and positive relationships depending on the soil nutrients studied (Bukombe *et al.*, 2022). By contrast, fine root production has been much less studied and shows no consistent pattern across fertility gradients, with studies reporting increases, decreases or no response to fertility (Aragão *et al.*, 2009; Yuan & Chen, 2012; Huaraca Huasco *et al.*, 2021; Bukombe *et al.*, 2022). Testing and interpreting belowground production responses to fertility is challenging because methods to quantify fine root production differ across studies, and because fine root production has substantial spatial and temporal variation that studies may not capture (Cordeiro *et al.*, 2020; Huaraca Huasco *et al.*, 2021). Overall, predicted increases in total aboveground production, wood production, and – to a lesser degree – leaf production with increasing soil fertility are largely supported (Muller-Landau *et al.*, 2021), whereas trends of belowground production across fertility gradients are much less studied and remain unclear.

A further consideration for understanding the fertility–productivity relationship is how fertility affects tissue turnover or residence time in trees, including leaves, branches, fine roots, and reproductive structures, because any such sublethal biomass turnover that changes with fertility could cloud productivity responses. Plants situated on low fertility soils are expected to exhibit more conservative traits, such as high leaf mass per area (LMA) and wood density, and low tissue turnover to increase their nutrient-use efficiency (Chapin, 1980; Fig. 2b). However, directly quantifying turnover rates requires measurements of either tissue production or loss and standing biomass pools, while most studies have only reported litterfall fluxes alone. One fertilization study also finding increased root tissue turnover rates (Yavitt *et al.*, 2011). Consequently, our understanding of tissue turnover rates is strongest for leaves, with much less known about roots, branchfall (Marvin & Asner, 2016; Gora *et al.*, 2019; Zuleta *et al.*, 2023), or reproductive tissues (Vitousek & Sanford, 1986; Ward *et al.*, 2025). Overall, increases in tissue turnover rates could substantially decrease biomass and hinder accurate measurement of productivity, but these processes are infrequently studied and their variation with fertility is unclear.

Despite these overall positive trends between soil fertility and productivity, the magnitude of increases in production are much lower than corresponding changes in soil properties across natural gradients. For example, plots sampled across the Amazon Basin capture a moderate 65% increase in wood production across a two-orders of magnitude increase in extractable soil phosphorus (Quesada *et al.*, 2012). This less-than-proportional increase could be due to: (1) methods of measuring soil phosphorus which may not represent what is available to plants; (2) the contrasting effects on productivity of another factor correlated with fertility (e.g. rainfall); (3) other constraints, such as water, temperature, or other limiting nutrients (Fatichi *et al.*, 2019); (4) plant adaptation and acclimation to low soil fertility through adjustments in strategies of nutrient acquisition, use, and carbon allocation; and/or (5) increased consumption or resource capture by natural enemies (herbivores, pathogens, parasites, and even lianas). Changes in plant strategies include increasing nutrient resorption before litterfall, changing nutrient concentrations of tissue, and adjusting allocation to fine roots, enzymes, organic acids, and symbioses. These changes can occur via flexibility within individuals and/or shifts in species composition (Batterman *et al.*, 2013; Condit *et al.*, 2013; Zalamea *et al.*, 2016; Turner *et al.*, 2018; Reichert *et al.*, 2022; Aoyagi *et al.*, 2022). The maintenance of primary productivity on low fertility soils likely reflects shifts in nutrient strategies, but the contributions of nutrient use and acquisition strategies to forest productivity and the scale at which they change (i.e. individual plasticity or community composition changes in individuals or species) remain underexplored. Resolving the importance and flexibility of nutrient strategies is particularly important to understand how forest productivity will be sustained under global change.

Summary of fertility–productivity knowledge gaps

Many aspects of the fertility–productivity relationship remain unknown. First, despite relatively widespread monitoring of aboveground biomass dynamics across fertility gradients, we know relatively little about how carbon is allocated and retained across tissues and functions. Unknowns include fertility effects on how efficiently GPP is converted to NPP, on allocation of NPP to aboveground competition for light, belowground resource acquisition, or reproduction, and on tissue turnover times for leaves, roots and branches. Second, we have yet to resolve the degree to which changes in productivity, carbon allocation and nutrient strategies across fertility gradients are due to flexibility within individual plants (i.e. trait plasticity) or changes in community composition and life-history strategies. Determining the level of organization at which these characteristics change is critical for understanding and predicting the resilience and vulnerability of tropical forests and the fertility–productivity relationship to global change. Because much of the research on tropical forests stems from the Americas, substantial geographic gaps in our understanding remain, including across forest ecotypes and in Asian and African tropical forests.

Developing a mechanistic understanding of how soil fertility influences tree mortality

Soil fertility tends to be positively associated with tree mortality rates (Phillips *et al.*, 2004; Bellingham & Sparrow, 2009; de Toledo *et al.*, 2011; Stephenson *et al.*, 2011; Quesada *et al.*, 2012; Galbraith *et al.*, 2013; Sawada *et al.*, 2015; Soong *et al.*, 2020) although there have been fewer analyses of this relationship compared with aboveground productivity. Of 14 studies investigating relationships of soil fertility with tree mortality or woody biomass turnover rates, four studies found no relationship, and 10

studies reported a positive relationship (Dalagnol *et al.*, 2021; Muller-Landau *et al.*, 2021; Sousa *et al.*, 2022; Reis *et al.*, 2022; Muñoz *et al.*, 2023; Zhang *et al.*, 2025). Observed positive relationships are moderately strong, with nearly a doubling of turnover and mortality rates with increasing fertility, based on categorical soil fertility groupings across the Amazon Basin (Phillips *et al.*, 2004; Galbraith *et al.*, 2013) and spanning *c.* 1.5 orders of magnitude increase in total soil phosphorus in French Guiana (Soong *et al.*, 2020). However, across some sites it remains unclear whether increased nutrient availability drives mortality rates or whether observed patterns instead arise from correlated soil properties. Along the well-studied fertility gradient in the Amazon Basin – from the nutrient-rich western and southwestern Amazon to the relatively infertile central and eastern Amazon – higher mortality rates in the west coincide with greater nutrient availability as well as shallow rooting depth, poor soil structure, and low water-holding capacity (Phillips *et al.*, 2004; Quesada *et al.*, 2012), as well as climatic effects which can be challenging to disentangle (Wu *et al.*, 2026). Two experimental fertilization studies have also found an increase of mortality in response to nutrient addition under certain conditions (Waring *et al.*, 2019; Tang *et al.*, 2026). Overall, these limited data suggest that tree mortality rates increase with soil fertility, but spatiotemporal variability and underlying covariation in this relationship need further investigation.

The mechanisms underlying the fertility–mortality relationship are unclear. The higher growth rates of trees, either within or across species, in more fertile soils are hypothesized to cause higher mortality – the 'live fast, die young' paradigm (Stephenson *et al.*, 2011; Brienen *et al.*, 2020). Importantly, trees do not die directly from growing faster; the growth–survival trade-off likely occurs because allocation to faster growth comes at the cost of allocation to traits that reduce susceptibility to one or more agents of mortality. However, we know little about how agents of mortality or susceptibility to agents of mortality change with soil fertility (Table 1). This is a critical knowledge gap because global change is intensifying the effects of multiple agents of tree mortality (McDowell *et al.*, 2018), each with distinct spatiotemporal patterns and consequences for forest dynamics (McDowell *et al.*, 2020; Gora & Esquivel-Muelbert, 2021). Given that tree mortality shapes patterns of tropical forest biomass (Galbraith *et al.*, 2013; Johnson *et al.*, 2016), the unknown contributions of soil fertility to patterns of tree mortality are a major source of uncertainty for the future of tropical forest carbon storage (Friend *et al.*, 2014; Hubau *et al.*, 2020).

Soil fertility–mortality framework

There are two nonexclusive pathways by which higher fertility could increase mortality. First, fertility could directly affect the prevalence or strength of an agent of mortality, thereby altering its contributions to tree death and biomass mortality (*direct* effects; Fig. 2c). Second, soil fertility could alter individual plant function or plant community composition such that the survival strategies make trees more or less susceptible to a given agent of mortality (*indirect* effects; e.g. fast-growing taxa may devote less to defense and are therefore vulnerable to pathogens; Fig. 2c). In the context of these two pathways, we synthesize the literature and evaluate the evidence for relationships between soil fertility and the primary agents of tropical tree mortality – pathogens, herbivores, competition, lianas, drought, fire, wind, and lightning – so that soil fertility can be explicitly linked to associated changes in tree mortality and ultimately to patterns of global change (McDowell *et al.*, 2020; Gora & Esquivel-Muelbert, 2021; Supporting Information Notes S1). The extent to which a mortality agent influences fertility–mortality relationships depends on both the sensitivity of the mortality agent to fertility, as well as its overall contribution to total biomass mortality. This reframing in the context of specific agents of mortality is important because it will allow us to interpret patterns and make predictions about the independent and interactive effects of both changing soil fertility and changes in each driver of mortality.

The direct effects of fertility on mortality are generally associated with biotic agents of tree death (Table 1). There are three potential mechanisms for this relationship. First, fertility increases aboveground productivity, and in principle, individual trees grow and reach larger tree sizes at faster rates, thereby increasing plant competition and competition-associated mortality (McDowell *et al.* 2018). Second, fertility could directly increase herbivore and pathogen abundance, thereby increasing herbivore and pathogen-induced mortality (i.e. the 'natural enemies' hypothesis; Stephenson *et al.* 2011). This would occur if higher fertility soils alleviate nutrient limitation of higher trophic levels via either the consumption of more nutrient-rich plant tissues or nonbiotic sources (e.g. geophagy, 'salt licks', supplements in water). Third, liana abundance and biomass could increase with soil fertility (Proctor *et al.*, 1983; Putz & Chai, 1987; Gentry, 1992; Laurance *et al.*, 2001; DeWalt *et al.*, 2006; Malizia *et al.*, 2010), but see (Ibarra-Manríquez & Martínez-Ramos, 2002; Dalling *et al.*, 2012; Schnitzer *et al.*, 2020; Liu *et al.*, 2021), and liana infestations can increase tree mortality rates (Schnitzer & Carson, 2010; Visser *et al.*, 2018; Estrada-Villegas *et al.*, 2022). Apart from relationships with biotic agents, it is possible that higher soil fertility is confounded with lower stability, increasing rates of windthrow and treefall in more fertile places (Phillips *et al.*, 2004; Quesada *et al.*, 2012). However, empirical investigation into these relationships is extremely limited, and the contributions of these direct effects to fertility–mortality relationships are unclear because this relationship is largely unexplored (Table 1).

The indirect effects of fertility on mortality could be associated with any abiotic or biotic driver of tree death. The 'fast–slow' continuum of plant life-history traits across species is characterized by a trade-off between investment in growth vs investment in more expensive and long-lived tissues (Stearns, 1992; Reich, 2014), including defenses against pathogens or herbivores (Janzen, 1974; Coley *et al.*, 1985; Coley, 1987). However, there is limited evidence that trees on more fertile soils invest less in defense (Landsberg & Gillieson, 1995; Fine *et al.*, 2004, 2006; Endara & Coley, 2011), and no evidence that there are greater herbivore effects on more fertile soils (Lamarre *et al.*, 2012; Fortunel *et al.*, 2016). It is also possible that traits facilitating fast growth on high fertility soils exhibit a trade-off with traits that make trees susceptible to other drivers of tree death, including abiotic drivers of mortality that are

Table 1 Summary of the literature investigating potential relationships between tropical soil fertility or fertilization and agents of tree mortality in tropical forests.

	Direct evidence of fertility–mortality associations		Circumstantial evidence of fertility–mortality associations		
Agents	Direct pathway	Susceptibility pathway	Increased damage with fertility or fertilization	Fertility or fertilization associations with hypothesized mortality agent	Fertility or fertilization associations with hypothesized susceptibility trait
Herbivores	Seedling mortality (Fortunel *et al*., 2016)	None	**Herbivory damage** (Landsberg & Gillieson, 1995; Endara & Coley 2011; Santiago *et al*., 2012) Herbivore damage probability (Fine *et al*., 2006) Herbivory damage (Lamarre *et al*. 2012)	Invertebrate abundance and richness (Kaspari *et al*., 2017)	**Herbivore defenses** (McKey *et al*., 1978, Reich *et al*., 1991; Fine *et al*., 2006, Endara & Coley 2011)
Pathogens	None	None	None	**Pathogen richness** (Schappe *et al*., 2020) **Pathogen abundance** (Buscardo *et al*., 2022) Pathogen abundance (Schappe *et al*., 2020)	None
Competition	Tree mortality (Rozendaal *et al*., 2020)	None	None	None	None
Lianas	None	None	None	**Liana abundance and/or biomass** (Putz & Chai 1987; Laurance *et al*., 2001; DeWalt *et al*., 2006; Malizia *et al*., 2010) Liana abundance (Ibarra-Manríquez & Martínez-Ramos, 2002; Dalling *et al*., 2012; Schnitzer *et al*., 2020; Liu *et al*., 2021)	None
Water stress	None	None	None	None	**Vessel diameter** (Li *et al*., 2022) **Hydraulic safety margin and P50** (Oliveira *et al*., 2019, 2021) *Vessel density* (Li *et al*., 2022)
Wind	None	None	**Litterfall during hurricanes** (Bomfim *et al*., 2022)	None	**Wood density and soil P** (Quesada *et al*., 2012; Heineman *et al*., 2016; Umaña *et al*., 2021; Rosell *et al*., 2023); **Wood density and many nutrients** (Fortunel *et al*., 2014; Chen *et al*., 2024; ter Steege *et al*., 2025) Wood density and other nutrients (Heineman *et al*., 2016; Bauters *et al*., 2022) *Wood density and wood N* (Martin *et al*., 2014)
Lightning	None	None	None	None	None
Fire	None	None	None	None	None

Evidence is separated into two broad categories, either direct evidence or tests of fertility–mortality associations for a given driver, or circumstantial evidence of fertility–mortality associations. Direct evidence is broken into two categories, either fertility directly changing a mortality agent (direct pathway) or fertility altering plant functional composition to produce greater susceptibility to a driver of mortality. The circumstantial evidence is broken into three categories: (1) evidence of increased tree damage by a given agent with fertilization or a gradient of fertility, but without evidence of increased mortality, (2) evidence of associations between fertility or fertilization and a hypothesized agent of mortality, but without evidence that this agent is causing more damage or mortality, and (3) evidence of associations between fertility or fertilization and a trait associated with greater susceptibility to a mortality agent, but without evidence that this susceptibility causes increased mortality. For all types of evidence, we list the measured response variable and citation in different colors to indicate trends that support a positive soil fertility–mortality, mortality agent, or susceptibility to mortality relationship (bold), negative trends (italicized), or either no effect or mixed effects (regular). We note that this is not a systematic review, but a summary of the literature as known.

not directly tied to fertility. Importantly, because larger trees dominate trends in biomass carbon cycling and the dominant drivers of tree death appear to shift from biotic to abiotic drivers with increasing tree size, even a weak relationship between fertility and traits that make trees susceptible to abiotic drivers of mortality could cause a large increase in biomass carbon mortality (Gora & Esquivel-Muelbert, 2021). Moreover, there are logical reasons to expect associations between fertility and susceptibility to abiotic agents of mortality. For example, fast-growing taxa with lower wood density tend to be more abundant on more fertile soils (Quesada *et al.*, 2012; Chen *et al.*, 2024; ter Steege *et al.*, 2025; Fig. 2b), and all else equal, low wood density taxa are expected to be less resistant to wind damage (Jackson *et al.*, 2024) and less conservative in their hydraulic traits, making them less resistant to drought (Gessler *et al.*, 2017; Oliveira *et al.*, 2019, 2021; Tavares *et al.*, 2023). Accordingly, trees on more fertile soils could therefore be more susceptible to both drought and wind, although empirical links remain untested. However, we are unable to test for an indirect effect of fertility on mortality, much less its association with a specific driver of tree death, because of the dearth of empirical studies (Table 1).

These potential relationships are further complicated by potential feedbacks between fertility on mortality and productivity. Separate from any potential direct effects of fertility on mortality, higher mortality rates could alternatively affect soil fertility via several mechanisms. First, increases in mortality could also increase soil fertility by altering plant community function. For example, after a disturbance event, the abundance of nitrogen-fixing trees can increase and drive higher nitrogen fixation rates (Barron *et al.*, 2011; Wurzburger & Hedin, 2016; McCulloch & Porder, 2021). Second, a positive feedback could occur as increasing mortality increases plant necromass – and therefore nutrient – inputs to the soil, increasing soil fertility. However, inputs of carbon-rich necromass could also decrease soil fertility by inducing competition with microbial decomposers for nutrients, leading to immobilization (Zimmerman *et al.*, 1995). Finally, increases in tree mortality can lead to greater physical erosion which displaces nutrients (Veldkamp *et al.*, 2020) or via nutrient losses due to increased leaching or gaseous emissions following disturbance. Although these feedbacks may exert relatively modest effects on soil fertility, over longer timescales they could reshape fertility–productivity–mortality relationships.

Summary of fertility–mortality knowledge gaps

In summary, many aspects of the fertility–mortality relationship remain unknown. First, while there is some empirical evidence for a positive fertility–mortality relationship, fertility-associated trends in mortality are almost never connected to a given driver of mortality, as most studies have not explicitly examined these connections (Table 1). Second, despite changes in forest composition across fertility gradients, we have limited empirical support for consistent directional shifts in species that are more or less vulnerable to mortality agents. Most of the theory for the higher mortality rates on more fertile soils has been associated with the growth–survival trade-off, whereby fast-growing, short-lived species are more abundant on more fertile soils, and slow-growing, more persistent species are more abundant on less fertile soils (Russo *et al.*, 2005; Chao *et al.*, 2008; Ferry *et al.*, 2010; Viani *et al.*, 2011; Quesada *et al.*, 2012; Sawada *et al.*, 2015; Russo & Kitajima, 2016; Tavares *et al.*, 2023) (but see Bruelheide *et al.*, 2018; Aoyagi *et al.*, 2023; Bialic-Murphy *et al.*, 2024). However, all moist tropical forests exhibit a broad range of life-history strategies (Rüger *et al.*, 2020; Kambach *et al.*, 2022), likely due to the effects of canopy gaps and disturbance in generating heterogeneous regeneration environments (Terborgh *et al.*, 2020; Detto *et al.*, 2022). Overall, the positive fertility–mortality relationship appears to play a major role in regulating forest biomass carbon dynamics, and the near-absence of data directly exploring this topic suggests that there are opportunities for very rapid advancement (Table 1).

Global change impacts on soil fertility–productivity–mortality feedbacks and interactions

Global change can influence fertility–productivity–mortality relationships through three pathways. First, global change may influence soil fertility directly. This would result from global change effects on nutrient inputs, outputs, pools, and transformation rates. Second, global change could modify the relationships between fertility and productivity or mortality. Third, global change could alter the relationship between fertility and mortality, with associated feedbacks on productivity. We review these potential effects and then discuss potential emergent interactions with global change drivers (Fig. 1; Notes S2).

Direct effects on soil fertility

Human activities are directly and strongly altering soil fertility in many places. Nutrient deposition typically increases the availability of soil nutrients (especially nitrogen) and thereby increases soil fertility (Van Langenhove *et al.*, 2020; Galloway & Cowling, 2021; Goll *et al.*, 2023). By contrast, nutrients are often lost from ecosystems following physical disturbances, including deforestation, degradation, fire, and storms, all common and increasing threats to tropical forests, either directly caused by human activities or increasing due to human-caused climate change (Maxwell *et al.*, 2019; Matricardi *et al.*, 2020; Gora *et al.*, 2025). Deforestation, degradation, and fire lead to nutrient losses during biomass removal and combustion, and all disturbances increase nutrient losses through subsequent leaching, runoff, erosion, and/or gaseous losses (the latter of nitrogen) due to the lack of plant nutrient uptake and soil stabilization during the early stages of forest recovery (Robertson & Tiedje, 1988; Robertson, 1989; Neill *et al.*, 1997, 2006). Depending on the size and intensity of fire, nutrients that are lost through combustion can be returned to surface soil through ash (Nardoto & Bustamante, 2003; Verma *et al.*, 2019) or redistributed to other regions via atmospheric deposition (Mahowald *et al.*, 2005; Bauters *et al.*, 2018, 2021a). These disturbance-induced nutrient losses can be particularly impactful when disturbances are repeated (Herbert *et al.*, 2003; Bauters *et al.*, 2021b) and in regions where the majority of ecosystem

nutrients are stored in biomass (Bauters *et al.*, 2022; Dalling *et al.*, 2024). Although lost nitrogen may eventually be replaced during recovery via biological nitrogen fixation (Batterman *et al.*, 2013; Sullivan *et al.*, 2014; Bauters *et al.*, 2016), rock-derived nutrients typically cannot recover following severe disturbances on highly weathered soils without external inputs (Bauters *et al.*, 2022; Dalling *et al.*, 2024).

Other agents of global change, such as rising CO_2 (Fleischer & Terrer, 2022; Cui *et al.*, 2024), warming (Nottingham *et al.*, 2020), and changing water availability, including drought frequency and intensity (Phillips *et al.*, 2010; Gloor *et al.*, 2013), could also impact nutrient cycling processes by altering the quantity and quality of litter, the rates of nutrient fluxes and transformations, and the distribution of nutrients across soils and biomass pools (see Notes S2 for expanded discussion). Global change can also alter nutrient cycling in opposing ways: warming or moderate drying may increase nutrient availability by accelerating litter inputs and decomposition, while extreme drought or excess moisture can suppress decomposition, reduce mobilization, and increase nitrogen losses. Because these drivers can push nutrient cycling in different directions, the net effect of global change on soil fertility remains highly uncertain.

Altering the soil fertility–productivity relationship

Widespread increases in tropical forest productivity over recent decades (Hubau *et al.*, 2020; Pan *et al.*, 2024) have major implications for the fertility–productivity relationship. Regardless of whether increased productivity is due to CO_2 fertilization (Walker *et al.*, 2021) or one of many debated alternatives (Wright, 2005; Raich *et al.*, 2006; Phillips *et al.*, 2009; Muller-Landau, 2009; Zhan *et al.*, 2025), increasing productivity leads to greater nutrient demand. Increased plant nutrient uptake may decrease nutrient availability in the soil and limit further increases in productivity (Fleischer *et al.*, 2019; Fleischer & Terrer, 2022). However, the degree to which forests can adjust to local changes in nutrient demand and/or availability and thereby maintain increased productivity remains unclear. Extant tropical forest communities have had millennia to adapt to their local fertility conditions, and it is possible that they may not be able to adjust rapidly enough to keep up with changing nutrient demand. The capacity of forest ecosystems to meet productivity-associated changes in nutrient demand will likely be determined by the size of the soil nutrient pools and the ability of trees to adjust nutrient use (e.g. lower nutrient content in tissues; Ellsworth *et al.*, 2004) or acquisition strategies (e.g. priming microbial communities, investing in mycorrhizal fungi, or fixing nitrogen; Sayer *et al.*, 2011; Trierweiler *et al.*, 2018; Nasto *et al.*, 2019; Terrer *et al.*, 2021; Reichert *et al.*, 2022). Furthermore, global change is likely to shift plant functional composition, and these compositional shifts in turn may alter forest productivity in ways that vary with soil fertility. Global change could thus alter the intercept or slope of the fertility–productivity relationship relative to the currently observed trend, potentially with major consequences for the forest carbon sink and its saturation.

Altering the soil fertility–mortality relationship

Global change is rapidly shifting plant functional composition and patterns of mortality, with potential effects on the fertility–mortality relationship. Insofar as global change is modifying fertility, we would expect associated shifts in biotic-driven mortality as changes in fertility cascade to tree vital rates as well as abundances of pathogens, herbivores, competing trees, and lianas. Conversely, if higher mortality in more fertile places is due to fertility-driven differences in greater susceptibility via plant functional traits, then global change could modify the fertility–mortality relationship via shifts in community composition. For example, if increasing disturbances due to global change create more forest gaps and shift plant composition toward higher abundances of fast-growing and less resilient taxa (e.g. poor defenses, drought intolerant, and wind infirm), then we could see a flattening of the fertility–mortality relationship as all sites become more similarly susceptible to mortality. Lastly, we might observe fertility–mortality agent relationships limit the effects of global change if separate increases in certain agents of death, such as possible CO_2-driven increases in liana abundance (Phillips *et al.*, 2002; Schnitzer, 2015), are ultimately modulated by nutrient limitation. Given evidence that forest composition is actively changing, it is very likely that compositional effects of fertility on mortality are changing, but quantifying these effects or their trajectories will require new analyses relating tree mortality, soil fertility, and forest composition.

Emergent global change interactions

Global change-driven shifts in fertility and its relationships with productivity and mortality are occurring concurrently and could produce complex feedbacks and interactions. Increases in mortality could shift plant functional composition in a manner that also alters the fertility–productivity relationship. For example, an increase in wind-caused disturbance could increase the prevalence of nitrogen-limited forest gaps, leading to the upregulation of biological nitrogen fixation (e.g. Barron *et al.*, 2011; Wurzburger & Hedin, 2016) and increased abundance of symbiotic nitrogen-fixing species. Over time, increased biological nitrogen fixation could reduce the effects of nitrogen limitation on forest productivity (Levy-Varon *et al.*, 2019). However, there are innumerable ways in which global change, fertility, productivity, and mortality could interact, making it challenging to predict interactions and feedbacks. Fundamentally, we first need to better resolve the basic mechanisms connecting fertility with forest dynamics so that we can begin exploring these higher-level interactions.

The future of soil fertility effects on forest biomass carbon: recommendations

This synthesis identifies four major themes that highlight key knowledge gaps in how soil fertility shapes forest carbon dynamics. First, fertility enhances productivity by influencing both carbon-use efficiency and allocation in individual plants and also via shifts

Box 3 Pathways forward for improving our understanding of soil fertility and tropical forest biomass relationships

(1) **Standardize and contextualize soil fertility measurements**. To resolve how fertility shapes forest carbon dynamics, we need widespread soil measurements that are comparable across sites. We recommend that soil analyses prioritize quantifying the pools and cycling of bioavailable nutrients (e.g. extractable ammonium and nitrate, resin and extractable phosphorus, and exchangeable cations) measured across the full rooting zone to better represent nutrient access and availability. We also recommend prioritizing comparable measurements, as standardized protocols across RAINFOR plots and ForestGEO networks have facilitated multisite analyses across larger regions of the tropics (e.g. Quesada *et al*., 2012; Medina-Vega *et al*., 2025). Identifying which dimensions of fertility become limiting under different environmental contexts will enable clearer cross-site comparisons and improve prediction of productivity and mortality responses. Contextualizing soil characteristics with plant biomass, tissue nutrient concentrations, and belowground dynamics may aid in the standardization of fertility metrics. Integrating these measurements with existing networks of fertilization experiments, forest plots, and flux towers will also generate fertility metrics that reflect ecological function and enable robust cross-site comparisons.

(2) **Resolve how carbon allocation, nutrient strategies, and belowground processes shift across fertility gradients**. Understanding why fertility influences productivity requires coordinated measurements of the pathways that control carbon use and nutrient acquisition. Simultaneous quantification of carbon-use efficiency, NPP allocation (particularly belowground production), and nutrient acquisition and use traits (e.g. root morphology, symbioses, exudation, tissue nutrient concentrations, and stoichiometry) will reveal how trees adjust carbon and nutrient strategies across fertility gradients. For example, measurements that are readily accessible, such as quantifying fine root biomass, fine root productivity, and tissue concentrations across fertility gradients would address key knowledge gaps on the flexibility of nutrient-use and acquisition. Integrating these field measurements with flux tower or remote-sensing-derived GPP measurements will help close the carbon budget and identify which processes drive differences in NPP and carbon-use efficiency.

(3) **Resolve the scale of plant functional composition shifts with fertility**. To understand how fertility-based shifts in plant functional composition modify productivity and mortality, we must determine the scale at which functional traits for nutrient use and survival change. At individual scales, this includes flexibility in traits of individual plants in response to a changing environment, and at community scales, turnover in individuals or species with different traits across environments. Additionally, we must determine the magnitude of flexibility and the degree to which these strategies affect performance (e.g. growth and mortality). For example, quantifying the extent to which increasing soil fertility favors the distribution and growth of fast-growing species (that have 'intrinsically' higher growth rates) vs trees of the same species growing faster would address this critical knowledge gap.

(4) **Quantify how drivers of mortality vary across fertility gradients**. Measuring how the presence, abundance, or intensity of various agents of tree death correlate with biomass mortality across fertility gradients would begin to reveal which agents could be responsible for fertility-associated variation in both mortality and biomass. This could be explored either via proxies (e.g. drought indices, thunderstorm activity, pathogen pressure, and liana abundance) or direct measurements of mortality agents and risk factors (Fontes *et al*., 2018; Arellano *et al*., 2021). Quantifying the contributions of these agents to biomass mortality is challenging, but advances in field ecology and remote sensing could soon make these measurements more feasible (Simonetti *et al*., 2023; Gora *et al*., 2025).

(5) **Test how global change is altering carbon and nutrient pools, stoichiometry and fluxes in plants and soils**. Measuring how soil fertility and plant nutrient content respond to global change, including both long-term monitoring (e.g. utilizing archived plant tissue and soil samples and site remeasurements) and in response to manipulation (e.g. global change experiments or deforestation/reforestation events) would be a critical step at understanding how global change drivers are modifying soil fertility directly.

in species composition, yet the relative importance of these pathways remains unclear. Second, the modest variation in productivity across steep fertility gradients suggests potentially strong compensatory mechanisms through physiological plasticity, nutrient-use efficiency, shifts in plant functional composition, feedbacks from higher trophic levels, or challenges in how we measure fertility from the plant perspective. Third, higher fertility often coincides with elevated mortality, but the mechanisms underlying this relationship remain unclear. And finally, global change is likely to modify nutrient availability and plant demand, creating feedbacks among fertility, productivity, and mortality that remain poorly constrained. We provide key recommendations (Box 3), which represent next steps for addressing these gaps and advancing predictive understanding of tropical forest dynamics.

Importantly, but outside of the scope of this paper, we emphasize that in order to fully understand how soil fertility regulates forest dynamics, we must collect more high-quality soil fertility data using consistent methods. Advancing this field requires coordinated measurements that capture nutrient availability and cycling rates, physical properties (e.g. structure, depth, and water-holding capacity), and site context (e.g. parent material, land-use history, and climate). Existing global soil datasets are too coarse in resolution and inconsistent in coverage to support this effort, and tropical regions remain underrepresented in their underlying data (Batjes, 2016; Hengl *et al*., 2017). Addressing these limitations is essential to produce the *in situ* soil data needed to link fertility, productivity, and mortality across spatial scales, including by taking advantage of increasing satellite data on forest dynamics and structure.

Achieving the coordinated measurements, mechanistic experiments, and integrative approaches outlined in our recommendations will provide the foundation for resolving key uncertainties in forest productivity, mortality, and carbon dynamics. Ultimately, this knowledge will allow more accurate predictions and guide effective restoration, conservation, and management strategies for tropical forests under global change.

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Competing interests

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 Summary of empirical and conceptual basis for mortality agent-specific relationships with fertility.

Notes S2 Summary of empirical and conceptual basis for global change effects on how fertility influences productivity and mortality.

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