



# How does biodiversity thrive in phosphorus-limited tropical forests

Ewuketu Linger<sup>1,2</sup> · Richard T. Corlett<sup>3</sup> ·  
J. Aaron Hogan<sup>4,5</sup> · Wenxing Long<sup>1,2,6</sup>

Received: 20 December 2024 / Accepted: 20 May 2025  
© Northeast Forestry University 2026

**Abstract** Tropical forests, renowned for their exceptional biodiversity, often thrive despite inherently low soil phosphorus (P) availability. However, a comprehensive synthesis of the mechanisms that facilitate the coexistence of diverse species, and how these mechanisms respond to P addition, remains poorly understood. This review consolidates research findings on how tropical forest biodiversity is sustained under low P conditions, how P addition influences the overall biodiversity system, identifies research gaps, and suggests future directions. The relationship between P and biodiversity is complex: while P-limited forests support high diversity, P addition may lead to species disappearance, raising the question of why some forests that maintain high species diversity under P limitation continue to do so, while others experience a decline in diversity following P addition. Despite P limitation, forests can support high species diversity through adaptive strategies such as resource partitioning

and P-use efficiency, which enable diverse communities to flourish. In low-P environments, species conserve P through resorption from older tissues and allocation to leaves, promoting photosynthesis and growth. These species exhibit lower specific leaf area and higher leaf dry matter content. While functional diversity is constrained, species diversity remains high as species adopt similar strategies. Specialized root traits, including finer roots and mycorrhizal symbioses, facilitate P uptake in low-P soils. However, P addition may lead to competitive exclusion, with species adapted to P-rich conditions outcompeting low-P specialists. Some species may dominate early successional stages by rapidly utilizing available P, suppressing other species, and reducing biodiversity over time. Anthropogenic P additions, such as agricultural fertilization and erosion, can intensify this effect, further decreasing species diversity and altering community composition, including fauna and microbial components of the forest. Due to the complexity and variability of tropical environments, critical knowledge gaps remain in understanding how diverse forest components, soil organisms, and environmental conditions interact with P addition, particularly at local and regional scales. Long-term studies, especially in less accessible or underfunded tropical regions, are essential

**Project funding:** This study was supported by the Natural National Science Foundations of China (32171772) and National Key R&D Program of China (Grant No.2021 YFD220040304).

The online version is available at <https://link.springer.com/>

Corresponding editor: Shuxuan Li.

✉ Wenxing Long  
oklong@hainanu.edu.cn

<sup>1</sup> College of Ecology, Hainan University, Haikou 570228, People's Republic of China

<sup>2</sup> College of Tropical Agriculture and Forestry, Hainan University, Haikou 570228, People's Republic of China

<sup>3</sup> Center for Integrative Conservation and Yunnan Key Laboratory for the Conservation of Tropical Rainforests and Asian Elephants, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Xishuangbanna 666303, People's Republic of China

<sup>4</sup> USDA Forest Service, International Institute of Tropical Forestry, San Juan, PR 00927, USA

<sup>5</sup> Department of Ecology & Conservation Biology, Texas A&M University, College Station, TX 77843, USA

<sup>6</sup> Wuzhishan Forest Ecosystem Monitoring and Research Station of National Park of Hainan Tropical Rainforest, Hainan University, Haikou 570228, People's Republic of China

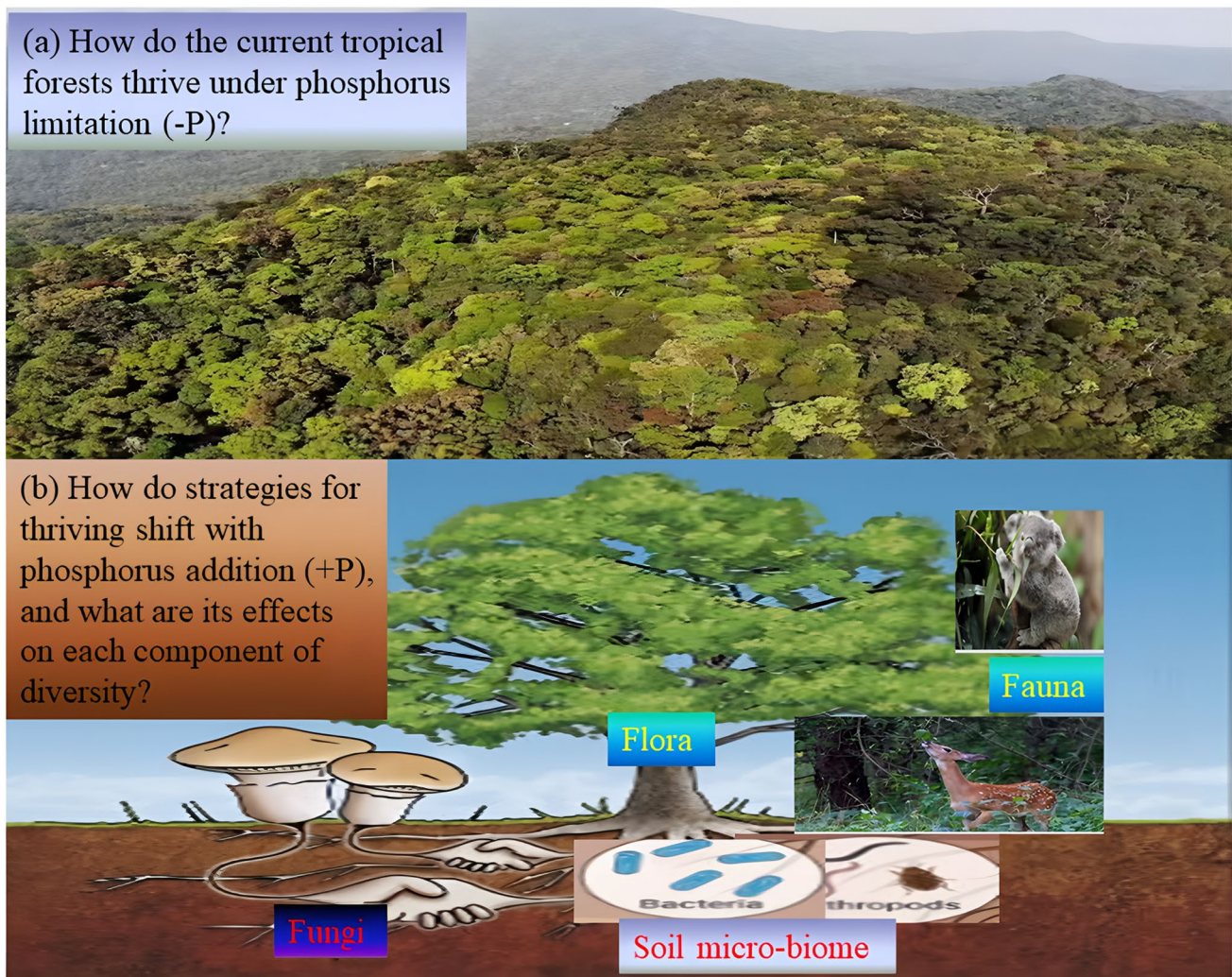
to improve understanding of species interactions, resource partitioning, and biodiversity functioning under P-limitation.

**Keywords** Adaptive strategies · Biodiversity trade-offs · Functional diversity · Nutrient cycling · Nutrient limitation

## Introduction

Tropical forests, recognized globally as the most biodiverse terrestrial ecosystems (Harvey et al. 2020; Raven et al. 2020), play a crucial role in global climate regulation, water cycling, soil protection and in preventing extreme droughts and floods (Bonan 2008; Pan et al. 2011; Ellison et al. 2017). Covering approximately 10% of the Earth's land surface, tropical forests harbor over half of the planet's terrestrial

species, making them one of the most biologically diverse ecosystems on Earth (Lewis 2006; Gibson et al. 2011; Lewis et al. 2015). These forests are primarily distributed across the Amazon Basin in South America, the Congo Basin in Central Africa, in Southeast Asia, and on tropical islands such as Madagascar and Papua New Guinea (Malhi et al. 2008). Despite their vast extent and ecological importance, many of these forests, particularly those in highly weathered regions like the Amazon, face significant challenges due to inherent phosphorus (P) limitation (Sun et al. 2020; Basak et al. 2022; Cunha et al. 2022), which in turn constrains nutrient-use strategies of species (Turner et al. 2018), biodiversity, and ecosystem productivity. Although P is scarce in these forests, they support a remarkable diversity of plants, animals, microbes, and fungi (Fig. 1), illustrating their ecological resilience through intricate nutrient adaptations,



**Fig. 1** Conceptual representation of tropical forest ecosystems in relation to P availability. **a** Depicts the current state of tropical forests functioning under natural P limitation (-P), where biodiversity thrives through long-term adaptations to nutrient-poor conditions. **b**

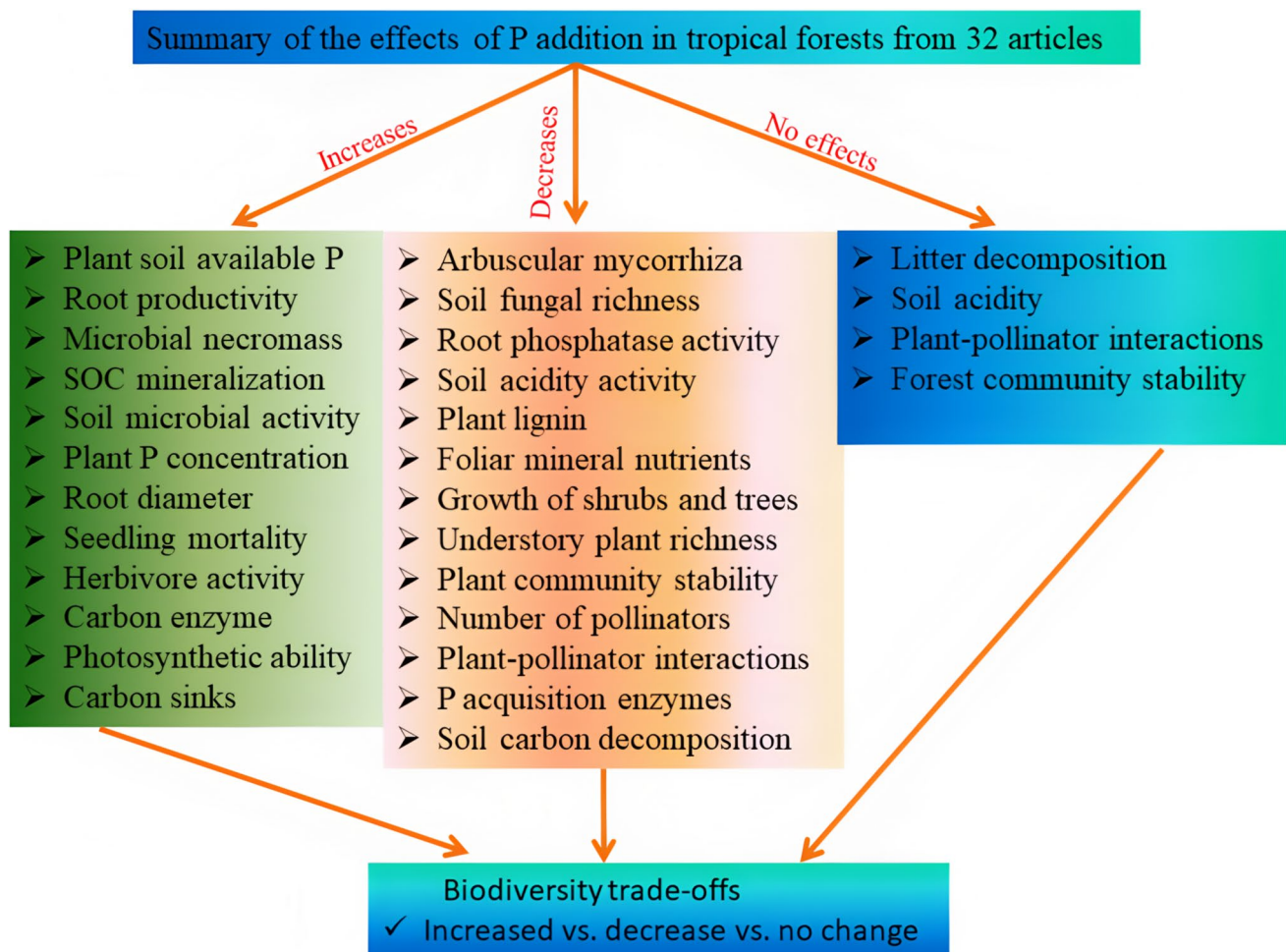
With P addition (+P), how do strategies for thriving shift, and what are the effects on each component (flora, fauna, microorganisms and fungi) of biodiversity? (source: Pixabay and Wenxing Long)

which remain an important subject of exploration (Roberts et al. 2021; Pillay et al. 2022).

Understanding the role of P addition in shaping forest biodiversity is essential for predicting ecosystem responses to environmental change and informing conservation strategies. Throughout this paper, P addition refers to the natural and human-induced input of P into the forest ecosystem from sources such as direct P fertilization, agricultural runoff from Diammonium Phosphate (DAP), a widely used fertilizer, atmospheric deposition of phosphorus-rich dust, and hydrological pathways like rainwater, rivers and groundwater transport. P is a crucial macronutrient for plant growth and development, involved in energy transfer, photosynthesis and nucleic acid formation (de Bang et al. 2021;

Freire 2023). In tropical regions, P limitation impacts plant productivity (Cunha et al. 2022; Manu et al. 2022), foliar stoichiometry (Massmann et al. 2022), community composition (Zhang et al. 2021) and competitive dynamics (Liu et al. 2021; Umaña et al. 2021), affecting the entire foodweb of the forest ecosystem (Vitousek et al. 2010; Menge et al. 2012), including its micro and mega-fauna components (Hu et al. 2021; Teste et al. 2021; Cunha et al. 2022; Coleman et al. 2024; Kang et al. 2024). To cope with P deficiency, plants in tropical forests have evolved various adaptive strategies (Fig. 2).

These adaptive strategies include developing specialized root systems for better P absorption, forming symbiotic relationships with mycorrhizal fungi to enhance P uptake,



**Fig. 2** Tropical forests and their adaptive strategies for P limitation. This diagram illustrates the low soil P nature and adaptive strategies of tropical forest trees, along with the overall implication on forest biodiversity components. It shows how low P levels in soil lead to P limitation, which drives trees to adjust to various adaptive strategies. These strategies encompass physiological mechanisms (Woodrow and Berry 1988; Lum and Hirsch 2002; Cope et al. 2021; Lambers 2022), production of defensive compounds (Coley et al. 1985; Mahmoud and Croteau 2002; Iqbal et al. 2021), and morphological

changes (Sarmiento et al. 1985; Baraloto et al. 2006; Løvdaal et al. 2008; Yetgin 2024). While these adaptive strategies support overall ecosystem biodiversity by benefiting flora, microorganisms and fauna, the production of defensive compounds introduces a trade-off. The trade-off arises due to reduced herbivory, which in turn diminishes faunal diversity but maintains high plant diversity. The diagram also raises questions about how P addition might alter these dynamics and influence adaptive strategies and biodiversity in tropical forests in the future

recycling P within their tissues, and minimizing reliance on external P sources (Aoyagi et al. 2022; Pan et al. 2022). This interplay between nutrient limitation and biodiversity highlights the complex nutrient balance that sustains tropical forests. As environments change due to increasing atmospheric CO<sub>2</sub> and nutrient deposition, the resilience of tropical forests under P limitation becomes increasingly critical to understand. Long-term precipitation change and droughts may drive drier tropical forests (Lewis et al. 2004) towards increased functional, taxonomic and phylogenetic homogeneity (Aguirre-Gutiérrez et al. 2020). However, there is limited comprehensive knowledge of how tropical forest biodiversity acclimatizes to nutrient scarcity, which could provide valuable insights for informing conservation strategies and deepening our understanding of these critical ecosystems (Cusack et al. 2021). Therefore, this review investigates how biodiversity has persisted in P-limited tropical forests and explores how adaptive strategies shift with P addition, emphasizing the implications for future biodiversity in the face of environmental change.

### Tropical forests adaptation mechanisms for P-limitation

Tropical forests have unique adaptation mechanisms (Fig. 2). Existing regional- and local-scale literature highlights how species coexist and adjust in P-limited environments, influencing the structure and diversity of tropical forest ecosystems.

At the species level, research by Turner et al. (2018), Wright et al. (2018) and Wright (2019) demonstrates that while P limitation affects plant growth, its impact varies significantly among species. Some species exhibit strong growth constraints at low soil P levels, while others maintain high productivity even under extreme P scarcity. This divergence suggests that tropical tree species have evolved diverse strategies to cope with nutrient limitation. Mechanisms such as efficient P acquisition through mycorrhizal associations, the exudation of root enzymes that enhance P solubilization and internal nutrient recycling through resorption allow species to thrive despite low soil P availability. These adaptations reduce direct competition for P, thereby supporting coexistence and maintaining high biodiversity.

Successional dynamics and nutrient heterogeneity also contribute to maintaining species diversity in P-limited forests. The meta-analyses by Wright (2019) indicated that P limitation interacts with forest age, being more pronounced in early successional forests where biomass accumulation demands high nutrient uptake. In contrast, old-growth forests exhibit slower growth responses to P addition, likely due to the long-term development of internal nutrient cycling mechanisms such as litter decomposition and root turnover. These patterns create opportunities for different functional groups of species to persist, allowing both fast-growing,

P-acquisitive species and slow-growing, P-conservative species to coexist. Traditional ecological models have suggested that P-limitation dominates in tropical lowland forests, while N limitation is more prevalent in tropical montane and temperate ecosystems. However, large-scale meta-analysis challenges this assumption, showing that N and P often co-limit plant growth across various elevations in the tropics (Wright 2019) and across ecosystems worldwide (Du et al. 2020).

Factorial fertilization experiments further reveal that P addition does not always elicit stronger growth responses than N, indicating that nutrient limitation is highly context-dependent. Moreover, interactions between P and other macronutrients such as potassium, calcium, and magnesium influence plant responses. This complexity suggests that biodiversity persists in these forests partly because no single nutrient consistently limits all species, leading to spatial and temporal variation in competitive interactions. Disturbance regimes, functional diversity, and ecosystem resilience further shape species responses to nutrient limitation. Turner et al. (2018) further provides evidence that species-specific growth constraints become pronounced below a critical soil P concentration, yet no universal community-wide growth response to P addition is observed. This suggests that species turnover along P gradients allows forests to maintain productivity, even if individual species experience nutrient constraints (Condit et al. 2013). The ability of species to shift their distribution in response to varying nutrient levels ensures long-term stability and resilience of tropical forests. Wardle and Zackrisson (2005)'s research highlights that the consequences of biotic loss for ecosystem functioning vary greatly among ecosystems and depend on the specific abiotic and biotic attributes of the system; herbivore-plant interactions through browsing animals often significantly shape plant community composition, reducing the abundance of palatable broad-leaved species and disrupting plant interactions (Wardle et al. 2001). These disturbances prevent competitive exclusion by favoring different nutrient-use strategies among species. The persistence of both P-efficient specialists and opportunistic generalists allows ecosystems to maintain productivity under nutrient-poor conditions.

The following four paragraphs outline key strategies that enable tropical forest plants to adjust to and thrive under P limitation:

### Symbiotic relationships

Plants form mutualistic partnerships with mycorrhizal fungi to enhance P uptake from the soil. These fungi extend their hyphae from roots into the soil, increasing the effective surface area for nutrient absorption. By enhancing P acquisition, mycorrhizal fungi support plant health and ecosystem productivity. This symbiosis is particularly vital in tropical forests, where P availability is limited. Fungal efficiency

in accessing P can vary, with some arbuscular mycorrhizae (AM) being highly effective at mobilizing P from the soil solution. Additionally, when mycorrhizal P-scavenging strategies are less effective, carboxylate-releasing P-mining strategies become more effective. Understanding these interactions provides insights into how tropical forests acclimate to nutrient limitation and maintain biodiversity (Buscot et al. 2000; Finlay 2008; Lambers et al. 2018; Usman et al. 2021; Lambers 2022; Yan et al. 2022, 2025).

### Microbial contributions

Microbial communities are essential for nutrient cycling, decomposing organic matter to release P in forms accessible to plants. This decomposition is crucial for recycling nutrients and sustaining plant growth. Microbial diversity also helps adjust to P limitation through processes such as nitrogen fixation and organic P mineralization (Felzenberg et al. 1996; McLaughlin and Wimmer 1999; Aanderud et al. 2008; Dai et al. 2020; Zhang et al. 2024).

### Trait plasticity

Plants in P-limited environments have evolved strategies to enhance P-use. They prioritize leaf P resorption and mining strategies via phosphatases and organic acids (Reichert et al. 2022). Additionally, plants can resorb P from older organs to minimize losses. Root-produced phosphatase enzymes, in conjunction with mycorrhizal fungi, help break down organic P into absorbable forms. To maximize phosphorus use efficiency (PUE), plants may adjust by reallocating P from non-photosynthetic functions and extending its residence time within organs. For example, in six Proteaceae species in south-western Australia, phospholipid levels strongly decreased during leaf development, whereas those of galactolipids and sulfolipids strongly increased (Lambers et al. 2012). In addition, other species found in Australian sclerophyll forest ecosystems (e.g., *Lomandra longifolia* Labill.), can have a lower investment of P into phospholipids in response to P-deficiency (Liang et al. 2024); still, others replace phospholipids with galactolipids in their leaves to maintain growth under low P conditions, which may contribute to species persistence and diversity in P-limited environments (Schmid and Ohlrogge 1996; Hölzl and Dörmann 2007; Siebers et al. 2015; Reichert et al. 2022; Xiao et al. 2022; Yu et al. 2022b; Yang et al. 2024).

### Ecosystem dynamics

The interactions between plants, mycorrhizal fungi, and microbes create a resilient ecosystem capable of sustaining biodiversity and productivity in P-limited soils. These diverse strategies ensure ecosystem functioning despite

nutrient scarcity, highlighting the importance of preserving complex plant-soil interactions to maintain healthy ecosystems and biodiversity (Ouchi et al. 1982; Rapport et al. 1998; Loreau et al. 2001; Gao et al. 2022; Allsup et al. 2023).

The coexistence and adaptation of biodiversity components in P-limited ecosystems reflect the remarkable resilience and efficiency of natural systems. Through mutualistic relationships and adaptive strategies, these ecosystems thrive despite nutrient limitation.

### Impact of P addition on tropical forests diversity: contrasting response scenarios

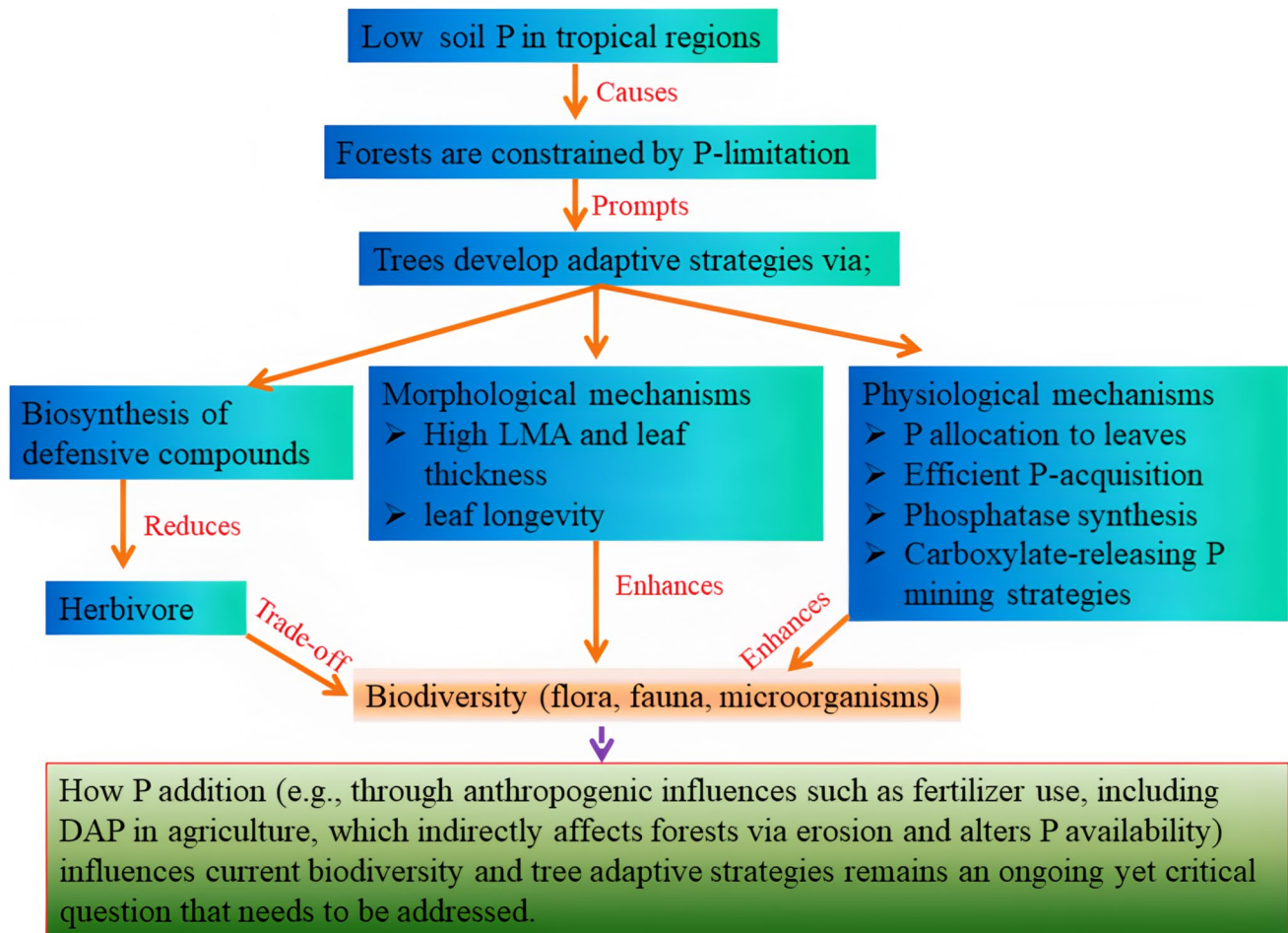
Experimental P addition plays a key role in understanding nutrient dynamics and biodiversity patterns in tropical forest ecosystems, where P is often limiting. The diversity response of various lifeforms to P addition can follow three potential patterns (Fig. 3): an increase, a decrease or no change.

Regardless of how ecosystems respond to P addition, a common management goal is to maintain maximum productivity and long-term ecological health. Understanding these varying responses is essential for predicting the long-term impacts of the addition of P on forest health and for developing sustainable management strategies that maintain species diversity, ecological integrity and plant productivity (Luo et al. 2024).

Expanding on the three distinct scenarios from current nutrient-biodiversity research, here we consider both the direct effects of P addition on plant species diversity and the broader implications for other life-forms of the forest ecosystem. Changes in one life-form, such as tree species diversity, can have cascading effects on other organisms (Pirttilä et al. 2023), including mycorrhizal fungi (Ding et al. 2021), herbivores (Shao et al. 2021; Zaret et al. 2023) and animal communities, ultimately influencing the overall health and functioning of the forest (Hernández-Blanco et al. 2022).

#### Scenario A: decrease in species diversity

The addition of P oftentimes leads to a decrease in species diversity (Huston 1979; Ostertag and Verville 2002; Beaugard et al. 2010; Ma et al. 2021; Seabloom et al. 2021). The augmented P levels can favor fast-growing, competitive species, which outcompete and displace slower-growing species that are crucial for ecosystem functions, such as nutrient cycling, soil stability and habitat provisioning. This shift can reduce overall species diversity, leading to a loss of these key functions. It can also lead to competitive exclusion, where P-efficient species outcompete others, potentially reducing plant species richness, strongly impacting plant communities (Wassen et al. 2021). This reduction in plant diversity can lead to a homogenization of plant communities, affecting ecosystem stability and resilience. A reduction



**Fig. 3** P and species diversity relationships for three life-forms (herbivorous animals, plants and soil microorganisms). The hypothetical impacts of P addition on species diversity in tropical forests showing

**a** decreases, **b** increases, or **c** no change in diversity. The dotted trend line represents the ideal condition of a healthy ecosystem under P addition, serving as a reference for the desired biodiversity outcome

in tree diversity could diminish the variety of habitats and food sources available to herbivores and animals, leading to potential population declines (Fleming et al. 2021). Additionally, certain tree species have symbiotic relationships with mycorrhizal fungi, which are crucial for nutrient uptake. If these trees are outcompeted, the associated fungal communities may suffer; further disrupting nutrient cycling and soil health (Gómez-Aparicio et al. 2022). This interconnectedness underscores the risk of a feedback loop in which the initial loss of plant diversity triggers a cascade of negative effects throughout the ecosystem. The ecosystem may become less resilient to disturbances, such as climate change or invasive species, as the loss of biodiversity weakens the intricate web of interactions that sustain the forest.

### Scenario B: increase in species diversity

In contrast, in the second scenario, where P is added from various sources, it becomes an abundant resource. In the

case, high-available P allows for the accommodation of a diverse range of species (Gough et al. 2000; Benner and Vitousek 2007; Luo et al. 2022), thereby enabling more complex interactions among forest life-forms. An increase in plant diversity could enhance the availability of resources for herbivores and other animals, potentially boosting their populations and promoting greater biodiversity at multiple trophic levels (Wan et al. 2020; Li et al. 2024). Enhanced plant growth might also support a more diverse and robust community of mycorrhizal fungi, improving soil health and nutrient cycling (Ma et al. 2020). However, this positive response may be contingent on the ecosystem's ability to maintain balance among its life-forms. Moreover, changes in plant community composition could alter the types of leaf litter and root exudates entering the soil, affecting decomposer organisms and nutrient cycling dynamics (Yang et al. 2021b). The implications for ecosystem health are therefore mixed, depending on the long-term sustainability of the increased

diversity and the stability of the interactions among different forest life-forms.

### Scenario C: stability in species diversity

The third scenario, where species diversity remains stable despite changes in P levels indicates a highly resilient ecosystem, as synchrony matters more than species diversity (Valencia et al. 2020). The forest might possess mechanisms that buffer against the impacts of nutrient addition (Hong et al. 2022), such as species redundancy or adaptive shifts in community composition that maintain functional diversity. This stability in plant diversity could help preserve the intricate relationships between plants and other forest life-forms. For example, mycorrhizal fungi that depend on a diverse array of tree species might continue to thrive, ensuring efficient nutrient uptake and soil health. Similarly, stable plant diversity can sustain a variety of herbivores and animal species, supporting a balanced food web. This scenario suggests that the ecosystem can absorb the nutrient perturbations caused by P addition without significant disruption to its overall functioning. However, the resilience observed may depend on the scale and duration of P input, as well as the specific characteristics of the ecosystem (Tao et al. 2022).

Across all three scenarios, it is crucial to recognize the interconnectedness of forest life-forms. Changes in one aspect, such as tree species diversity, can reverberate throughout the ecosystem, affecting soil microbes, fungi, herbivores and higher trophic levels. The loss of a keystone species, for example, could lead to the decline of organisms that depend on it, reducing the ecosystem's overall complexity and resilience (Mouquet et al. 2013). Conversely, an increase in diversity enhances ecosystem services like carbon sequestration, water regulation and habitat provision, but only if the balance among species and life-forms is maintained (Isbell et al. 2011).

The implications of these scenarios extend beyond immediate biodiversity outcomes. They highlight the importance of considering nutrient management in a holistic context, where the goal is not just to preserve individual species but to maintain the functional integrity of the entire ecosystem. Effective conservation and restoration strategies should therefore account for the potential cascading effects of nutrient additions on multiple forest life forms, ensuring that interventions do not inadvertently destabilize the complex networks of species interactions that sustain tropical forest health.

### Ecosystem responses to P addition in tropical forests: a synthesis of studies

Numerous studies have highlighted the positive, negative and neutral effects of P addition on one or more components

of tropical forests diversity, emphasizing the complexity of nutrient dynamics in these ecosystems (Fig. 4).

### Positive effects: enhanced ecosystem productivity

P addition has been shown to increase soil and plant P concentrations, plant growth, enhance ecosystem productivity, improve photosynthetic rates, and increase total plant biomass (Yu et al. 2020, 2022a; Li et al. 2024) and carbon sequestration in tropical forests (Wang et al. 2020). P addition stimulates microbial activity, thereby promoting the decomposition of organic matter (Luo et al. 2022), facilitating nutrient cycling and enhancing soil fertility. The enhanced activity of carbon acquisition enzymes and phosphorus utilization by plants further drives productivity gains.

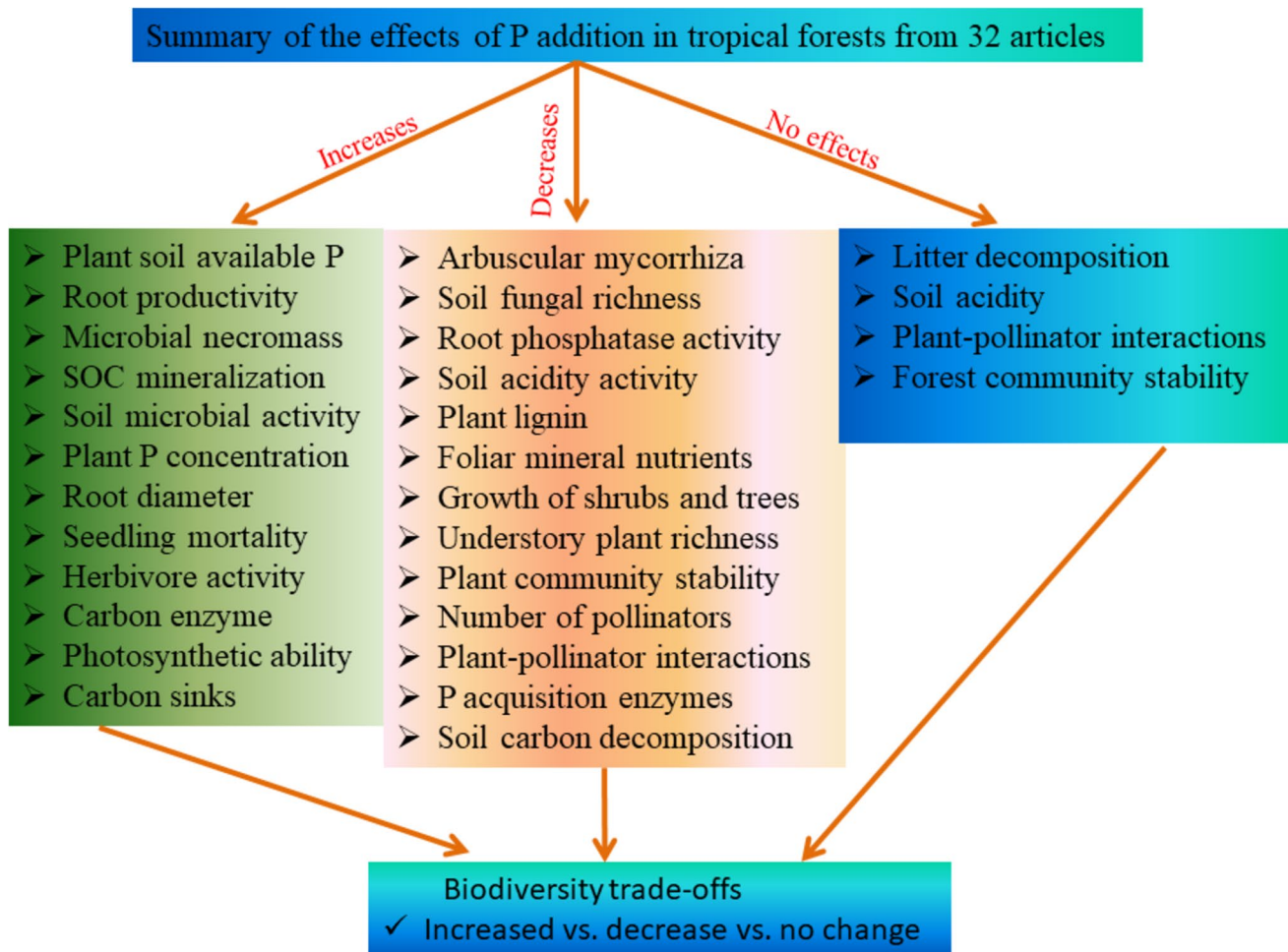
Increased root biomass and shrub growth have also been observed following P addition (Van Langenhove et al. 2020; Poudyal et al. 2021). These changes stabilize soils and enhance nutrient uptake, fostering greater plant growth. However, this growth often benefits fast-growing species, leading to shifts in community composition as nutrient-conserving species are outcompeted (De Britto Costa et al. 2021). Despite these productivity gains, the longer-term implications of these shifts in community structure warrant closer examination (Dueñas et al. 2020).

Nutrient availability controls herbivore activity (Sitters et al. 2020); it may or may not increase as increased plant productivity provides more resources for herbivores (Segar et al. 2022). This can lead to greater herbivore populations but may also alter herbivore dynamics and resource availability, influencing the broader forest community. In sum, P-addition impacts community assembly and carbon sinks (Cui et al. 2022). While there may be initial increases in tree species diversity and carbon sequestration, long-term effects may include shifts in community composition and reduced functional diversity.

### Negative effects: the cost of P-addition

While P-addition boosts productivity, it also disrupts symbiotic relationships, particularly with arbuscular mycorrhizal fungi (AMF) (Ma et al. 2021). AMF play a key role in nutrient uptake in low-P environments, and their presence varies depending on P availability (Treseder and Allen 2002). The reduction in AMF and other soil fungi with P addition can impair nutrient exchange processes, decreasing forest resilience to environmental stresses (Wahab et al. 2023).

The decline in mycorrhizal fungi, coupled with changes in foliar mineral nutrient concentrations, typically reduces plant diversity. For instance, understory plant richness and density decrease with P-addition (Mao et al. 2021), which in turn impacts herbivores (Balandier et al. 2022) and other species dependent on the understory for food and shelter.



**Fig. 4** Summary of P addition effects on tropical forest ecosystems: a synthesis of 32 studies (Elwood et al. 1981; Georg Joergensen and Scheu 1999; Nohrstedt 2001; Davidson et al. 2004; Liu et al. 2012; Santiago et al. 2012; Mayor et al. 2014; Li et al. 2015; Mo et al. 2019, 2021; DeForest and Moorhead 2020; Ma et al. 2020; Wei et al. 2020; Blubaugh et al. 2021; Fortier and Wright 2021; Liu 2021; Maitra et al. 2021; Mao et al. 2021; Yang et al. 2021a; Yuan et al. 2021; Ao

et al. 2022; Cunha et al. 2022; Gu et al. 2022; Luo et al. 2022; Moeneclaey et al. 2022; Wang et al. 2022; Zhang et al. 2022; Fang et al. 2023; Huang et al. 2023; Sengupta and Krishna 2023; Thuma et al. 2023; Xia et al. 2024). The figure categorizes empirically-measured responses to P-addition across studies as either: increased, decreased, or no effect on the response variable (listed), emphasizing biodiversity trade-offs across these response groups

Furthermore, P addition increases competition among established plants by promoting the invasion of exotic species (Fisher et al. 2006; Yang et al. 2023), leading to higher seedling mortality (Mao et al. 2021), thus hindering forest regeneration and further reducing biodiversity (Li et al. 2024). Additionally, P addition suppresses the activity of root and soil phosphatase enzymes and carboxylate release (Ao et al. 2022), further affecting nutrient acquisition.

The ecological consequences of P enrichment extend beyond the plant–soil interface and may influence biotic interactions in ecosystems, including those between plants and pollinators. For example, Wang et al. (2022) found that while nitrogen and phosphorus additions individually had limited direct effects on pollinator richness, abundance, and interaction structure in an alpine grassland system, the

combined N + P treatment increased species and interaction dissimilarity and reduced generality in plant–pollinator networks. These findings indicate that nutrient enrichment, especially when multiple nutrients are added, can disrupt the stability and specificity of mutualistic interactions. Although derived from a grassland context, such patterns raise important considerations for forest ecosystems, where nutrient limitation and complex biodiversity networks are both present. In P-limited tropical forests, shifts in plant community composition resulting from P addition can gradually alter interaction networks and ecological functioning, even if initial effects appear minimal. This underlines the need to examine not just species-level responses, but also the integrity of interaction networks under changing nutrient conditions. Additionally, plant lignin concentrations

are significantly reduced by P addition (Han et al. 2022; Luo et al. 2022), which could influence carbon cycling and decomposition, potentially buffering certain ecosystem functions despite shifts in nutrient availability.

### **No effects: resilience in stability**

Not all ecosystem processes are sensitive to P addition. For instance, some studies highlight that litter decomposition rates remain largely unaffected by changes in soil P levels (Zhang et al. 2020, 2022). This stability in decomposition suggests that microbial communities involved in organic matter breakdown are highly resilient to nutrient enrichment.

### **Biodiversity trade-offs: navigating complex ecosystem responses**

P addition in tropical forests presents notable biodiversity trade-offs. Although in some scenarios P enhances productivity and carbon sequestration, it sometimes comes at the expense of biodiversity. Faster-growing species tend to dominate, while slower-growing, nutrient-conserving species decline, resulting in the homogenization of plant communities. This shift likely reduces forest resilience to disturbances including climate change or invasive species.

These trade-offs extend to trophic interactions. For example, P-enrichment may increase herbivore activity by providing more food resources, but it also alters plant-pollinator dynamics, further destabilizing community interactions. These biodiversity trade-offs illustrate the delicate balance between nutrient availability, species interactions and ecosystem stability, highlighting the potential for short-term productivity gains to come at the cost of long-term ecosystem health. Enhanced root phosphatase activity and phosphorus acquisition enzymes indicate improved phosphorus utilization by plants (Lugli et al. 2021; Guilbeault-Mayers and Laliberté 2024). These changes can affect competitive dynamics among plant species, potentially influencing overall biodiversity and community composition.

### **Conclusion**

Our synthesis of studies on P addition in tropical forests underscores the complexity of nutrient dynamics and their effects on biodiversity and ecosystem functioning. While P addition can enhance productivity and carbon sequestration, it simultaneously introduces significant biodiversity trade-offs and disrupts the symbiotic relationships critical to forest resilience. Understanding these detailed effects is essential for developing conservation strategies that protect the rich biodiversity of tropical forests while accounting for the broader implications of nutrient enrichment.

Furthermore, this review highlights the interconnected dynamics between P-limitation and biodiversity in tropical forests. Despite severe nutrient constraints, these ecosystems demonstrate resilience through adaptive strategies across a broad spectrum of life forms, including plants, fauna, microbes and fungi. These interactions not only sustain species diversity but also emphasize the intricate web of dependencies that characterize tropical forest ecosystems. Adaptive management strategies should employ a holistic strategy that facilitate mycorrhizal fungi, microbial communities and plants working in concert to optimize P acquisition and utilization, ensuring the continued functioning and productivity of these ecosystems despite nutrient scarcity.

As environmental changes and human activities continue to alter nutrient dynamics, it becomes increasingly crucial to understand how these ecosystems might respond. Conservation and management strategies must account for the delicate balance of nutrient availability, species interactions and ecosystem functioning to safeguard the biodiversity and stability of tropical forests. The resilience of these forests under P limitation is a testament to the adaptive capacities of their diverse flora and fauna. However, as global environmental changes intensify, the stability of these adaptive mechanisms may be challenged in unprecedented ways. Despite growing interest in nutrient dynamics, significant research gaps remain in our understanding of how P availability influences biodiversity patterns and ecosystem functioning in tropical forests. Most studies are geographically concentrated, leaving remote or less accessible regions underrepresented. Moreover, few have explored the long-term, multi-taxa impacts of P addition under real-world conditions. The interactions between P enrichment and other global stressors—such as climate change and anthropogenic disturbances—also remain poorly understood.

Therefore, future research should prioritize examining how P addition interacts with these co-occurring stressors across all levels of biodiversity. Moving forward, studies should aim to clarify the long-term impacts of P addition on tropical forests, particularly under the combined pressures of nutrient enrichment and climate change (e.g., warming). It is also essential to investigate how forests with varying degrees of P limitation respond to nutrient inputs, and to assess the role of other potentially limiting nutrients in shaping these responses, especially in underfunded tropical regions such as Africa. Such insights are critical for developing sustainable management strategies that protect the unique biodiversity and ecosystem services of tropical forests.

**Acknowledgement** We extend our gratitude to the authors of the research papers we synthesized, as their work has significantly contributed to the understanding of the topics discussed in this review. We also appreciate the handling editor and two anonymous reviewers for their valuable comments and constructive feedback, which have helped improve the quality of this manuscript. JAH was supported in part by

an appointment to the United States Forest Service (USFS) Research Participation Program administered by the Oak Ridge Institute for Science and Education (ORISE) through an interagency agreement between the U.S. Department of Energy (DOE) and the U.S. Department of Agriculture (USDA). Oak Ridge Associated Universities (ORAU) manages ORISE under DOE contract DE-SC0014664. All opinions expressed in this paper are the author's and do not necessarily reflect the policies and views of USDA, DOE, or ORAU/ORISE.

## References

- Aanderud ZT, Shuldman MI, Drenovsky RE, Richards JH (2008) Shrub-interspace dynamics alter relationships between microbial community composition and belowground ecosystem characteristics. *Soil Biol Biochem* 40(9):2206–2216. <https://doi.org/10.1016/j.soilbio.2008.04.008>
- Aguirre-Gutiérrez J, Malhi Y, Lewis SL, Fauset S, Adu-Bredu S, Affum-Baffoe K, Baker TR, Gvozdevaite A, Hubau W, Moore S, Peprah T, Ziemińska K, Phillips OL, Oliveras I (2020) Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity. *Nat Commun* 11:3346. <https://doi.org/10.1038/s41467-020-16973-4>
- Allsup C, Marquardt S, Lankau R (2023) Mycorrhizal driven positive feedbacks and forest resilience to reduced rainfall. *Fungal Ecol* 65:101280. <https://doi.org/10.1016/j.funeco.2023.101280>
- Ao G, Feng JG, Han MG, Wang XD, Tang M, Ma SH, Zhu B (2022) Responses of root and soil phosphatase activity to nutrient addition differ between primary and secondary tropical montane forests. *Rhizosphere* 24:100610. <https://doi.org/10.1016/j.rhisph.2022.100610>
- Aoyagi R, Kitayama K, Turner BL (2022) How do tropical tree species maintain high growth rates on low-phosphorus soils? *Plant Soil* 480(1–2):31–56. <https://doi.org/10.1007/s11104-022-05602-2>
- Balandier P, Mårell A, Prévosto B, Vincenot L (2022) Tamm review: forest understorey and overstorey interactions: so much more than just light interception by trees. *Ecol Manag* 526:120584. <https://doi.org/10.1016/j.foreco.2022.120584>
- Baraloto C, Bonal D, Goldberg DE (2006) Differential seedling growth response to soil resource availability among nine neotropical tree species. *J Trop Ecol* 22(5):487–497. <https://doi.org/10.1017/s0266467406003439>
- Basak BB, Sarkar B, Saha A, Sarkar A, Mandal S, Biswas JK, Wang HL, Bolan NS (2022) Revamping highly weathered soils in the tropics with biochar application: what we know and what is needed. *Sci Total Environ* 822:153461. <https://doi.org/10.1016/j.scitotenv.2022.153461>
- Beauregard MS, Hamel C, Atul-Nayyar S-A (2010) Long-term phosphorus fertilization impacts soil fungal and bacterial diversity but not AM fungal community in alfalfa. *Microb Ecol* 59(2):379–389. <https://doi.org/10.1007/s00248-009-9583-z>
- Benner JW, Vitousek PM (2007) Development of a diverse epiphyte community in response to phosphorus fertilization. *Ecol Lett* 10(7):628–636. <https://doi.org/10.1111/j.1461-0248.2007.01054.x>
- Blubaugh CK, Carpenter-Boggs L, Reganold JP, Snyder WE (2021) Herbivore-herbivore interactions complicate links between soil fertility and pest resistance. *Basic Appl Ecol* 52:57–67. <https://doi.org/10.1016/j.baae.2021.02.002>
- Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Sci* 320(5882):1444–1449. <https://doi.org/10.1126/science.1155121>
- Buscot F, Munch JC, Charcosset JY, Gardes M, Nehls U, Hampp R (2000) Recent advances in exploring physiology and biodiversity of ectomycorrhizas highlight the functioning of these symbioses in ecosystems. *FEMS Microbiol Rev* 24(5):601–614. <https://doi.org/10.1111/j.1574-6976.2000.tb00561.x>
- Coleman DC, Geisen S, Wall DH (2024) Soil fauna: occurrence biodiversity and roles in ecosystem function. In: Eldor A, Paul I, Serita D (eds) *Frey soil microbiology ecology and biochemistry*. Elsevier, Amsterdam, pp 131–159
- Coley PD, Bryant JP, Chapin FS III (1985) Resource availability and plant antiherbivore defense. *Sci* 230(4728):895–899. <https://doi.org/10.1126/science.230.4728.895>
- Condit R, Engelbrecht BMJ, Pino D, Pérez R, Turner BL (2013) Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proc Natl Acad Sci* 110(13):5064–5068. <https://doi.org/10.1073/pnas.1218042110>
- Cope OL, Lindroth RL, Helm A, Keefover-Ring K, Kruger EL (2021) Trait plasticity and trade-offs shape intra-specific variation in competitive response in a foundation tree species. *New Phytol* 230(2):710–719. <https://doi.org/10.1111/nph.17166>
- Cui EQ, Lu RL, Xu XN, Sun HF, Qiao Y, Ping JY, Qiu SY, Lin YH, Bao JH, Yong YT, Zheng ZM, Yan ER, Xia JY (2022) Soil phosphorus drives plant trait variations in a mature subtropical forest. *Glob Change Biol* 28(10):3310–3320. <https://doi.org/10.1111/gcb.16148>
- Cunha HFV, Andersen KM, Lugli LF, Santana FD, Aleixo IF, Moraes AM, Garcia S, Di Ponzio R, Mendoza EO, Brum B, Rosa JS, Cordeiro AL, Portela BTT, Ribeiro G, Coelho SD, de Souza ST, Silva LS, Antonieto F, Pires M, Salomão AC, Miron AC, de Assis RL, Domingues TF, Araújo LEOC, Meir P, Camargo JL, Manzi AO, Nagy L, Mercado LM, Hartley IP, Quesada CA (2022) Direct evidence for phosphorus limitation on amazon forest productivity. *Nat* 608(7923):558–562. <https://doi.org/10.1038/s41586-022-05085-2>
- Cusack DF, Addo-Danso SD, Agee EA, Andersen KM, Arnaud M, Batterman SA, Brearley FQ, Ciochina MI, Cordeiro AL, Dallstream C, Diaz-Toribio MH, Dietterich LH, Fisher JB, Fleischer K, Fortunel C, Fuchslueger L, Guerrero-Ramírez NR, Kotowska MM, Lugli LF, Marín C, McCulloch LA, Maeght JL, Metcalfe D, Norby RJ, Oliveira RS, Powers JS, Reichert T, Smith SW, Smith-Martin CM, Soper FM, Toro L, Umaña MN, Valverde-Barrantes O, Weemstra M, Werden LK, Wong M, Wright CL, Wright SJ, Yaffar D (2021) Tradeoffs and synergies in tropical forest root traits and dynamics for nutrient and water acquisition: field and modeling advances. *Front Glob Change* 4:704469. <https://doi.org/10.3389/ffgc.2021.704469>
- Dai ZM, Liu GF, Chen HH, Chen CR, Wang JK, Ai SY, Wei D, Li DM, Ma B, Tang CX, Brookes PC, Xu JM (2020) Long-term nutrient inputs shift soil microbial functional profiles of phosphorus cycling in diverse agroecosystems. *ISME J* 14(3):757–770. <https://doi.org/10.1038/s41396-019-0567-9>
- Davidson EA, de Reis Carvalho CJ, Vieira ICG, de O Figueiredo R, Moutinho P, Yoko Ishida F, dos Primo Santos MT, Benito Guerrero J, Kalif K, Tuma Sabá R (2004) Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. *Ecol Appl* 14(4):150–163. <https://doi.org/10.1890/01-6006>
- de Bang TC, Husted S, Laursen KH, Persson DP, Schjoerring JK (2021) The molecular-physiological functions of mineral macronutrients and their consequences for deficiency symptoms in plants. *New Phytol* 229(5):2446–2469. <https://doi.org/10.1111/nph.17074>
- de Britto Costa P, Staudinger C, Veneklaas EJ, Oliveira RS, Lambers H (2021) Root positioning and trait shifts in *hibbertia racemosa* as dependent on its neighbour's nutrient-acquisition strategy. *Plant Cell Environ* 44(4):1257–1267. <https://doi.org/10.1111/pce.13991>
- DeForest JL, Moorhead DL (2020) Effects of elevated pH and phosphorus fertilizer on soil C, N and P enzyme stoichiometry in an

- acidic mixed mesophytic deciduous forest. *Soil Biol Biochem* 150:107996. <https://doi.org/10.1016/j.soilbio.2020.107996>
- Ding XX, Liu GL, Fu SL, Chen HYH (2021) Tree species composition and nutrient availability affect soil microbial diversity and composition across forest types in subtropical China. *CATENA* 201:105224. <https://doi.org/10.1016/j.catena.2021.105224>
- Du EZ, Terrer C, Pellegrini AFA, Ahlström A, van Lissa CJ, Zhao X, Xia N, Wu XH, Jackson RB (2020) Global patterns of terrestrial nitrogen and phosphorus limitation. *Nat Geosci* 13(3):221–226. <https://doi.org/10.1038/s41561-019-0530-4>
- Dueñas JF, Camenzind T, Roy J, Hempel S, Homeier J, Suárez JP, Rillig MC (2020) Moderate phosphorus additions consistently affect community composition of arbuscular mycorrhizal fungi in tropical montane forests in southern Ecuador. *New Phytol* 227(5):1505–1518. <https://doi.org/10.1111/nph.16641>
- Ellison D, Morris CE, Locatelli B, Sheil D, Cohen J, Murdiyarto D, Gutierrez V, van Noordwijk M, Creed IF, Pokorny J, Gaveau D, Spracklen DV, Tobella AB, Ilstedt U, Teuling AJ, Gebrehiwot SG, Sands DC, Muys B, Verbist B, Springgay E, Sugandi Y, Sullivan CA (2017) Trees, forests and water: cool insights for a hot world. *Glob Environ Change* 43:51–61. <https://doi.org/10.1016/j.gloenvcha.2017.01.002>
- Elwood JW, Newbold JD, Trimble AF, Stark RW (1981) The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. *Ecol* 62(1):146–158. <https://doi.org/10.2307/1936678>
- Fang Z, Yu HL, Li CH, Wang B, Jiao F, Huang JY (2023) Long-term phosphorus addition alters plant community composition but not ecosystem stability of a nitrogen-enriched desert steppe. *Sci Total Environ* 879:163033. <https://doi.org/10.1016/j.scitotenv.2023.163033>
- Felzenberg ER, Yang GA, Hagenzieker JG, Poindexter JS (1996) Physiologic, morphologic and behavioral responses of perpetual cultures of *Caulobacter crescentus* to carbon, nitrogen and phosphorus limitations. *J Ind Microbiol Biotechnol* 17(3–4):235–252. <https://doi.org/10.1007/bf01574698>
- Finlay RD (2008) Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical *mycelium*. *J Exp Bot* 59(5):1115–1126. <https://doi.org/10.1093/jxb/ern059>
- Fisher JL, Veneklaas EJ, Lambers H, Loneragan WA (2006) Enhanced soil and leaf nutrient status of a Western Australian *Banksia* woodland community invaded by *Ehrharta calycina* and *Pelargonium capitatum*. *Plant Soil* 284(1–2):253–264. <https://doi.org/10.1007/s1104-006-0042-z>
- Fleming PA, Wentzel JJ, Dundas SJ, Kreplins TL, Craig MD, Hardy GE (2021) Global meta-analysis of tree decline impacts on fauna. *Biol Rev* 96(5):1744–1768. <https://doi.org/10.1111/brv.12725>
- Fortier R, Wright SJ (2021) Nutrient limitation of plant reproduction in a tropical moist forest. *Ecol* 102(10):e03469. <https://doi.org/10.1002/ecy.3469>
- Freire MÁ (2023) The origins of photosynthetic systems: clues from the phosphorus and sulphur chemical scenarios. *Biosyst* 226:104873. <https://doi.org/10.1016/j.biosystems.2023.104873>
- Gao C, Xu L, Montoya L, Madera M, Hollingsworth J, Chen L, Purdom E, Singan V, Vogel J, Huttmacher RB, Dahlberg JA, Coleman-Derr D, Lemaux PG, Taylor JW (2022) Co-occurrence networks reveal more complexity than community composition in resistance and resilience of microbial communities. *Nat Commun* 13:3867. <https://doi.org/10.1038/s41467-022-31343-y>
- Georg Joergensen R, Scheu S (1999) Response of soil microorganisms to the addition of carbon, nitrogen and phosphorus in a forest Rendzina. *Soil Biol Biochem* 31(6):859–866. [https://doi.org/10.1016/S0038-0717\(98\)00185-0](https://doi.org/10.1016/S0038-0717(98)00185-0)
- Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF, Lovejoy TE, Sodhi NS (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nat* 478(7369):378–381. <https://doi.org/10.1038/nature10425>
- Gómez-Aparicio L, Domínguez-Begines J, Villa-Sanabria E, García LV, Muñoz-Pajares AJ (2022) Tree decline and mortality following pathogen invasion alters the diversity, composition and network structure of the soil microbiome. *Soil Biol Biochem* 166:108560. <https://doi.org/10.1016/j.soilbio.2022.108560>
- Gough L, Osenberg CW, Gross KL, Collins SL (2000) Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos* 89(3):428–439. <https://doi.org/10.1034/j.1600-0706.2000.890302.x>
- Gu HJ, Wang H, Liu M, Shangguan ZJ, Shi HJ, Xu W, Ren F, Zhu JX, He JS (2022) Leaf N: P stoichiometry overrides the effect of individual nutrient content on insect herbivore population dynamics in a Tibetan Alpine grassland. *Agric Ecosyst Environ* 336:108032. <https://doi.org/10.1016/j.agee.2022.108032>
- Guilbeault-Mayers X, Laliberté E (2024) Root phosphatase activity is coordinated with the root conservation gradient across a phosphorus gradient in a lowland tropical forest. *New Phytol* 243(2):636–647. <https://doi.org/10.1111/nph.19567>
- Han XJ, Zhao YQ, Chen YJ, Xu J, Jiang C, Wang XQ, Zhuo RY, Lu MZ, Zhang J (2022) Lignin biosynthesis and accumulation in response to abiotic stresses in woody plants. *Res* 2:9. <https://doi.org/10.48130/FR-2022-0009>
- Harvey MG, Bravo GA, Claramunt S, Cuervo AM, Derryberry GE, Battilana J, Seeholzer GF, McKay JS, O'Meara BC, Faircloth BC, Edwards SV, Pérez-Emán J, Moyle RG, Sheldon FH, Aleixo A, Smith BT, Chesser RT, Silveira LF, Cracraft J, Brumfield RT, Derryberry EP (2020) The evolution of a tropical biodiversity hotspot. *Sci* 370(6522):1343–1348. <https://doi.org/10.1126/science.aaz6970>
- Hernández-Blanco M, Costanza R, Chen HJ, de Groot D, Jarvis D, Kubiszewski I, Montoya J, Sangha K, Stoeckl N, Turner K, van 't Hoff V (2022) Ecosystem health, ecosystem services, and the well-being of humans and the rest of nature. *Glob Change Biol* 28(17):5027–5040. <https://doi.org/10.1111/gcb.16281>
- Hölzl G, Dörmann P (2007) Structure and function of glycolipid-erolipids in plants and bacteria. *Prog Lipid Res* 46(5):225–243. <https://doi.org/10.1016/j.plipres.2007.05.001>
- Hong PB, Schmid B, De Laender F, Eisenhauer N, Zhang XW, Chen HZ, Craven D, De Boeck HJ, Hautier Y, Petchey OL, Reich PB, Steudel B, Striebel M, Thakur MP, Wang SP (2022) Biodiversity promotes ecosystem functioning despite environmental change. *Ecol Lett* 25(2):555–569. <https://doi.org/10.1111/ele.13936>
- Hu DD, Wang MT, Zheng Y, Lv M, Zhu GJ, Zhong QL, Cheng DL (2021) Leaf litter phosphorus regulates the soil meso- and microfaunal contribution to home-field advantage effects on litter decomposition along elevation gradients. *CATENA* 207:105673. <https://doi.org/10.1016/j.catena.2021.105673>
- Huang J, Liu L, Liu JX, Zhang W, Wang SH, Ye Q, Mo JM, Zheng MH (2023) Seven years phosphorus addition has no effect on soil acidity in two tropical plantations. *Ecol Manag* 532:120822. <https://doi.org/10.1016/j.foreco.2023.120822>
- Huston M (1979) A general hypothesis of species diversity. *Am Nat* 113(1):81–101. <https://doi.org/10.1086/283366>
- Iqbal Z, Iqbal MS, Hashem A, AbdAllah EF, Ansari MI (2021) Plant defense responses to biotic stress and its interplay with fluctuating dark/light conditions. *Front Plant Sci* 12:631810. <https://doi.org/10.3389/fpls.2021.631810>
- Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M (2011) High plant diversity is needed to maintain ecosystem services. *Nat* 477(7363):199–202. <https://doi.org/10.1038/nature10282>

- Kang HB, Xue Y, Cui YX, Moorhead DL, Lambers H, Wang DX (2024) Nutrient limitation mediates soil microbial community structure and stability in forest restoration. *Sci Total Environ* 935:173266. <https://doi.org/10.1016/j.scitotenv.2024.173266>
- Lambers H (2022) Phosphorus acquisition and utilization in plants. *Annu Rev Plant Biol* 73:17–42. <https://doi.org/10.1146/annurev-arplant-102720-125738>
- Lambers H, Cawthray GR, Giavalisco P, Kuo J, Laliberté E, Pearse SJ, Scheible WR, Stitt M, Teste F, Turner BL (2012) *Proteaceae* from severely phosphorus-impooverished soils extensively replace phospholipids with galactolipids and sulfolipids during leaf development to achieve a high photosynthetic phosphorus-use efficiency. *New Phytol* 196(4):1098–1108. <https://doi.org/10.1111/j.1469-8137.2012.04285.x>
- Lambers H, Albornoz F, Kotula L, Laliberté E, Ranathunge K, Teste FP, Zemunik G (2018) How belowground interactions contribute to the coexistence of mycorrhizal and non-mycorrhizal species in severely phosphorus-impooverished hyperdiverse ecosystems. *Plant Soil* 424(1–2):11–33. <https://doi.org/10.1007/s11104-017-3427-2>
- Lewis SL (2006) Tropical forests and the changing earth system. *Philos Trans R Soc Lond B Biol Sci* 361(1465):195–210. <https://doi.org/10.1098/rstb.2005.1711>
- Lewis SL, Malhi Y, Phillips OL (2004) Fingerprinting the impacts of global change on tropical forests. *Philos Trans R Soc Lond B Biol Sci* 359(1443):437–462. <https://doi.org/10.1098/rstb.2003.1432>
- Lewis SL, Edwards DP, Galbraith D (2015) Increasing human dominance of tropical forests. *Sci* 349(6250):827–832. <https://doi.org/10.1126/science.aaa9932>
- Li J, Li ZA, Wang FM, Zou B, Chen Y, Zhao J, Mo QF, Li YW, Li XB, Xia HP (2015) Effects of nitrogen and phosphorus addition on soil microbial community in a secondary tropical forest of China. *Biol Fertil Soils* 51(2):207–215. <https://doi.org/10.1007/s00374-014-0964-1>
- Li Y, Schuldt A, Ebeling A, Eisenhauer N, Huang YY, Albert G, Albracht A, Amyntas A, Bonkowski M, Bruehlheide H, Bröcher M, Chesters D, Chen J, Chen YN, Chen JT, Ciobanu M, Deng XL, Fornoff F, Gleixner G, Guo LD, Guo PF, Heintz-Buschart A, Klein AM, Lange M, Li S, Li Q, Li YB, Luo AR, Meyer ST, von Oheimb G, Rütten G, Scholten T, Solbach MD, Staab M, Wang MQ, Zhang NL, Zhu CD, Schmid B, Ma KP, Liu XJ (2024) Plant diversity enhances ecosystem multifunctionality *via* multitrophic diversity. *Nat Ecol Evol* 8(11):2037–2047. <https://doi.org/10.1038/s41559-024-02517-2>
- Liang GH, Butler OM, Warren CR (2024) Lipid profiles of plants and soil microbial communities are shaped by soil parent material in Australian sclerophyll forests. *Plant Soil* 498(1–2):39–55. <https://doi.org/10.1007/s11104-023-06075-7>
- Liu D (2021) Root developmental responses to phosphorus nutrition. *J Integr Plant Biol* 63(6):1065–1090. <https://doi.org/10.1111/jipb.13090>
- Liu L, Gundersen P, Zhang T, Mo JM (2012) Effects of phosphorus addition on soil microbial biomass and community composition in three forest types in tropical China. *Soil Biol Biochem* 44(1):31–38. <https://doi.org/10.1016/j.soilbio.2011.08.017>
- Liu XJ, Tan ND, Zhou GY, Zhang DQ, Zhang QM, Liu SZ, Chu GW, Liu JX (2021) Plant diversity and species turnover co-regulate soil nitrogen and phosphorus availability in Dinghushan forests, Southern China. *Plant Soil* 464(1–2):257–272. <https://doi.org/10.1007/s11104-021-04940-x>
- Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Sci* 294(5543):804–808. <https://doi.org/10.1126/science.1064088>
- Løvdaal T, Skjoldal EF, Heldal M, Norland S, Thingstad TF (2008) Changes in morphology and elemental composition of *Vibrio splendidus* along a gradient from carbon-limited to phosphate-limited growth. *Microb Ecol* 55(1):152–161. <https://doi.org/10.1007/s00248-007-9262-x>
- Lugli LF, Rosa JS, Andersen KM, Di Ponzio R, Almeida RV, Pires M, Cordeiro AL, Cunha HFV, Martins NP, Assis RL, Moraes ACM, Souza ST, Aragão LEOC, Camargo JL, Fuchslueger L, Schaap KJ, Valverde-Barrantes OJ, Meir P, Quesada CA, Mercado LM, Hartley IP (2021) Rapid responses of root traits and productivity to phosphorus and cation additions in a tropical lowland forest in Amazonia. *New Phytol* 230(1):116–128. <https://doi.org/10.1111/nph.17154>
- Lum MR, Hirsch AM (2002) Roots and their symbiotic microbes: strategies to obtain nitrogen and phosphorus in a nutrient-limiting environment. *J Plant Growth Regul* 21(4):368–382. <https://doi.org/10.1007/s00344-003-0003-1>
- Luo RY, Kuzyakov Y, Zhu B, Qiang W, Zhang Y, Pang XY (2022) Phosphorus addition decreases plant lignin but increases microbial necromass contribution to soil organic carbon in a subalpine forest. *Glob Change Biol* 28(13):4194–4210. <https://doi.org/10.1111/gcb.16205>
- Luo XZ, Elrys AS, Zhang LL, Ibrahim MM, Liu Y, Fu SL, Yan JH, Ye Q, Wen DZ, Hou EQ (2024) The global fate of inorganic phosphorus fertilizers added to terrestrial ecosystems. *One Earth* 7(8):1402–1413. <https://doi.org/10.1016/j.oneear.2024.07.002>
- Ma SH, Chen GP, Tian D, Du EZ, Xiao W, Jiang L, Zhou Z, Zhu JL, He HB, Zhu B, Fang JY (2020) Effects of seven-year nitrogen and phosphorus additions on soil microbial community structures and residues in a tropical forest in Hainan Island, China. *Geoderma* 361:114034. <https://doi.org/10.1016/j.geoderma.2019.114034>
- Ma XC, Geng QH, Zhang HG, Bian CY, Chen HYH, Jiang DL, Xu X (2021) Global negative effects of nutrient enrichment on arbuscular mycorrhizal fungi, plant diversity and ecosystem multifunctionality. *New Phytol* 229(5):2957–2969. <https://doi.org/10.1111/nph.17077>
- Mahmoud SS, Croteau RB (2002) Strategies for transgenic manipulation of monoterpene biosynthesis in plants. *Trends Plant Sci* 7(8):366–373. [https://doi.org/10.1016/S1360-1385\(02\)02303-8](https://doi.org/10.1016/S1360-1385(02)02303-8)
- Maitra P, Zheng Y, Wang YL, Mandal D, Lü PP, Gao C, Babalola BJ, Ji NN, Li XC, Guo LD (2021) Phosphorus fertilization rather than nitrogen fertilization, growing season and plant successional stage structures arbuscular mycorrhizal fungal community in a subtropical forest. *Biol Fertil Soils* 57(5):685–697. <https://doi.org/10.1007/s00374-021-01554-4>
- Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li WH, Nobre CA (2008) Climate change, deforestation, and the fate of the Amazon. *Sci* 319(5860):169–172. <https://doi.org/10.1126/science.1146961>
- Manu R, Corre MD, Aleee A, Mwanjalolo MJG, Babweteera F, Veldkamp E, van Straaten O (2022) Responses of tree growth and biomass production to nutrient addition in a semi-deciduous tropical forest in Africa. *Ecol* 103(6):e3659. <https://doi.org/10.1002/ecy.3659>
- Mao QG, Chen H, Gurmesa GA, Gundersen P, Ellsworth DS, Gilliam FS, Wang C, Zhu F, Ye Q, Mo JM, Lu XK (2021) Negative effects of long-term phosphorus additions on understory plants in a primary tropical forest. *Sci Total Environ* 798:149306. <https://doi.org/10.1016/j.scitotenv.2021.149306>
- Massmann A, Cavaleri MA, Oberbauer SF, Olivás PC, Porder S (2022) Foliar stoichiometry is marginally sensitive to soil phosphorus across a lowland tropical rainforest. *Ecosyst* 25(1):61–74. <https://doi.org/10.1007/s10021-021-00640-w>
- Mayor JR, Wright SJ, Turner BL (2014) Species-specific responses of foliar nutrients to long-term nitrogen and phosphorus additions in a lowland tropical forest. *J Ecol* 102(1):36–44. <https://doi.org/10.1111/1365-2745.12190>

- McLaughlin SB, Wimmer R (1999) Tansley review no. 104: calcium physiology and terrestrial ecosystem processes. *New Phytol* 142(3):373–417. <https://doi.org/10.1046/j.1469-8137.1999.00420.x>
- Menge DNL, Hedin LO, Pacala SW (2012) Nitrogen and phosphorus limitation over long-term ecosystem development in terrestrial ecosystems. *PLoS ONE* 7(8):e42045. <https://doi.org/10.1371/journal.pone.0042045>
- Mo QF, Li ZA, Sayer EJ, Lambers H, Li YW, Zou B, Tang JW, Heskell M, Ding YZ, Wang FM (2019) Foliar phosphorus fractions reveal how tropical plants maintain photosynthetic rates despite low soil phosphorus availability. *Funct Ecol* 33(3):503–513. <https://doi.org/10.1111/1365-2435.13252>
- Mo QF, Wang WJ, Lambers H, Chen YQ, Yu SQ, Wu CS, Fan YX, Zhou Q, Li ZA, Wang FM (2021) Response of foliar mineral nutrients to long-term nitrogen and phosphorus addition in a tropical forest. *Funct Ecol* 35(10):2329–2341. <https://doi.org/10.1111/1365-2435.13896>
- Moeneclaey I, Schelfhout S, Vanhellemont M, DeCock E, Van Coillie F, Verheyen K, Baeten L (2022) Species ecological strategy and soil phosphorus supply interactively affect plant biomass and phosphorus concentration. *Basic Appl Ecol* 62:1–11. <https://doi.org/10.1016/j.baec.2022.03.013>
- Mouquet N, Gravel D, Massol F, Calcagno V (2013) Extending the concept of keystone species to communities and ecosystems. *Ecol Lett* 16(1):1–8. <https://doi.org/10.1111/ele.12014>
- Nohrstedt HÖ (2001) Response of coniferous forest ecosystems on mineral soils to nutrient additions: a review of Swedish experiences. *Scand J Res* 16(6):555–573. <https://doi.org/10.1080/02827580152699385>
- Ostertag R, Verville JH (2002) Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests. *Plant Ecol* 162(1):77–90. <https://doi.org/10.1023/a:1020332824836>
- Ouchi T, Ibrahim AK, Latham GV (1982) Seismicity and crustal structure in the orozco fracture zone: project rose phase II. *J Geophys Res* 87(B10):8501–8507. <https://doi.org/10.1029/jb087ib10p08501>
- Pan YD, Birdsey RA, Fang JY, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao SL, Rautiainen A, Sitch S, Hayes D (2011) A large and persistent carbon sink in the world's forests. *Sci* 333(6045):988–993. <https://doi.org/10.1126/science.1201609>
- Pan YJ, Song YP, Zhao L, Chen PF, Bu CH, Liu P, Zhang DQ (2022) The genetic basis of phosphorus utilization efficiency in plants provide new insight into woody perennial plants improvement. *Int J Mol Sci* 23(4):2353. <https://doi.org/10.3390/ijms23042353>
- Pillay R, Venter M, Aragon-Osejo J, González-del-Pliego P, Hansen AJ, Watson JE, Venter O (2022) Tropical forests are home to over half of the world's vertebrate species. *Front Ecol Environ* 20(1):10–15. <https://doi.org/10.1002/fee.2420>
- Pirttilä AM, Brusila V, Koskimäki JJ, Wäli PR, Ruotsalainen AL, Mutanen M, Markkola AM (2023) Exchange of microbiomes in plant-insect herbivore interactions. *Mbio* 14(2):e03210–e03222. <https://doi.org/10.1128/mbio.03210-22>
- Poudyal S, Owen JS, Sharkey TD, Fernandez RT, Cregg B (2021) Phosphorus requirement for biomass accumulation is higher compared to photosynthetic biochemistry for three ornamental shrubs. *Sci Hortic* 275:109719. <https://doi.org/10.1016/j.scienta.2020.109719>
- Rapport DJ, Costanza R, McMichael AJ (1998) Assessing ecosystem health. *Trends Ecol Evol* 13(10):397–402. [https://doi.org/10.1016/S0169-5347\(98\)01449-9](https://doi.org/10.1016/S0169-5347(98)01449-9)
- Raven PH, Gereau RE, Phillipson PB, Chatelain C, Jenkins CN, Ulloa Ulloa C (2020) The distribution of biodiversity richness in the tropics. *Sci Adv* 6(37):eabc6228. <https://doi.org/10.1126/sciadv.abc6228>
- Reichert T, Rammig A, Fuchslueger L, Lugli LF, Quesada CA, Fleischer K (2022) Plant phosphorus-use and-acquisition strategies in *Amazonia*. *New Phytol* 234(4):1126–1143. <https://doi.org/10.1111/nph.17985>
- Roberts P, Hamilton R, Piperno DR (2021) Tropical forests as key sites of the “Anthropocene”: past and present perspectives. *Proc Natl Acad Sci* 118(40):e21109243118. <https://doi.org/10.1073/pnas.2109243118>
- Santiago LS, Wright SJ, Harms KE, Yavitt JB, Korine C, Garcia MN, Turner BL (2012) Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition. *J Ecol* 100(2):309–316. <https://doi.org/10.1111/j.1365-2745.2011.01904.x>
- Sarmiento G, Goldstein G, Meinzer F (1985) Adaptive strategies of woody species in neotropical savannas. *Biol Rev* 60(3):315–355. <https://doi.org/10.1111/j.1469-185x.1985.tb00420.x>
- Schmid KM, Ohlrogge JB (1996) Chapter 14 lipid metabolism in plants. In: Vance DE, Vance JE (eds) *New compr biochem*. Elsevier, Amsterdam, pp 363–389
- Seabloom EW, Adler PB, Alberti J, Biederman L, Buckley YM, Cadotte MW, Collins SL, Dee L, Fay PA, Firn J, Hagenah N, Harpole WS, Hautier Y, Hector A, Hobbie SE, Isbell F, Knops JMH, Komatsu KJ, Laungani R, MacDougall A, McCulley RL, Moore JL, Morgan JW, Ohlert T, Prober SM, Risch AC, Schuetz M, Stevens CJ, Borer ET (2021) Increasing effects of chronic nutrient enrichment on plant diversity loss and ecosystem productivity over time. *Ecol* 102(2):e03218. <https://doi.org/10.1002/ecs.3218>
- Segar J, Pereira HM, Baeten L, Bernhardt-Römermann M, De Frenne P, Fernández N, Gilliam FS, Lenoir J, Ortmann-Ajkai A, Verheyen K, Waller D, Teleki B, Brunet J, Chudomelová M, Decocq G, Dirnböck T, Hédl R, Heinken T, Jaroszewicz B, Kopecký M, Macek M, Máliš F, Naaf T, Orczewska A, Reczynska K, Schmidt W, Šebesta J, Stachurska-Swakoń A, Standovář T, Swierkosz K, Vild O, Wulf M, Staude IR (2022) Divergent roles of herbivory in eutrophying forests. *Nat Commun* 13:7837. <https://doi.org/10.1038/s41467-022-35282-6>
- Sengupta U, Krishna S (2023) More is not always better: impact of nutrient-addition on floral traits important for buzz pollination. *Acta Oecol* 121:103957. <https://doi.org/10.1016/j.actao.2023.103957>
- Shao XL, Zhang Q, Yang XT (2021) Spatial patterns of insect herbivory within a forest landscape: the role of soil type and forest stratum. *Ecosyst* 8:69. <https://doi.org/10.1186/s40663-021-00347-3>
- Siebers M, Dörmann P, Hölzl G (2015) Membrane remodelling in phosphorus-deficient plants. *Phosphorus Metab Plants* 48:237–264. <https://doi.org/10.1002/9781118958841.ch9>
- Sitters J, Wubs ERJ, Bakker ES, Crowther TW, Adler PB, Bagchi S, Bakker JD, Biederman L, Borer ET, Cleland EE, Eisenhauer N, Firn J, Gherardi L, Hagenah N, Hautier Y, Hobbie SE, Knops JMH, MacDougall AS, McCulley RL, Moore JL, Mortensen B, Peri PL, Prober SM, Riggs C, Risch AC, Schütz M, Seabloom EW, Siebert J, Stevens CJ, Veen GFC (2020) Nutrient availability controls the impact of mammalian herbivores on soil carbon and nitrogen pools in grasslands. *Glob Change Biol* 26(4):2060–2071. <https://doi.org/10.1111/gcb.15023>
- Sun F, Song CJ, Wang M, Lai DYF, Tariq A, Zeng FJ, Zhong QP, Wang FM, Li ZA, Peng CL (2020) Long-term increase in rainfall decreases soil organic phosphorus decomposition in tropical forests. *Soil Biol Biochem* 151:108056. <https://doi.org/10.1016/j.soilbio.2020.108056>
- Tao Y, Zhou XB, Li YG, Liu HL, Zhang YM (2022) Short-term N and P additions differentially alter the multiple functional traits and trait associations of a desert ephemeral plant in China. *Environ Exp Bot* 200:104932. <https://doi.org/10.1016/j.envexpbot.2022.104932>

- Teste FP, Lambers H, Enowashu EE, Laliberté E, Marhan S, Kandeler E (2021) Soil microbial communities are driven by the declining availability of cations and phosphorus during ecosystem retrogression. *Soil Biol Biochem* 163:108430. <https://doi.org/10.1016/j.soilbio.2021.108430>
- Thuma JA, Duff C, Pitera M, Januario N, Orians CM, Starks PT (2023) Nutrient enrichment and rainfall affect plant phenology and floral resource availability for pollinators. *Front Ecol Evol* 11:1150736. <https://doi.org/10.3389/fevo.2023.1150736>
- Treseder KK, Allen MF (2002) Direct nitrogen and phosphorus limitation of arbuscular mycorrhizal fungi: a model and field test. *New Phytol* 155(3):507–515. <https://doi.org/10.1046/j.1469-8137.2002.00470.x>
- Turner BL, Brenes-Arguedas T, Condit R (2018) Pervasive phosphorus limitation of tree species but not communities in tropical forests. *Nat* 555(7696):367–370. <https://doi.org/10.1038/nature25789>
- Umaña MN, Condit R, Pérez R, Turner BL, Wright SJ, Comita LS (2021) Shifts in taxonomic and functional composition of trees along rainfall and phosphorus gradients in central Panama. *J Ecol* 109(1):51–61. <https://doi.org/10.1111/1365-2745.13442>
- Usman M, Ho-Plágaro T, Frank HER, Calvo-Polanco M, Gaillard I, Garcia K, Zimmermann SD (2021) Mycorrhizal symbiosis for better adaptation of trees to abiotic stress caused by climate change in temperate and boreal forests. *Front Glob Change* 4:742392. <https://doi.org/10.3389/ffgc.2021.742392>
- Valencia E, de Bello F, Galland T, Adler PB, Lepš J, E-Vojtkó A, van Klink R, Carmona CP, Danihelka J, Dengler J, Eldridge DJ, Estiarte M, García-González R, Garnier E, Gómez-García D, Harrison SP, Herben T, Ibáñez R, Jentsch A, Juergens N, Kertész M, Klumpp K, Louault F, Marrs RH, Ogaya R, Onodi G, Pake-man RJ, Pardo I, Pärtel M, Peco B, Peñuelas J, Pywell RF, Rueda M, Schmidt W, Schmiedel U, Schuetz M, Skálová H, Šmilauer P, Šmilauerová M, Smit C, Song MH, Stock M, Val J, Vandvik V, Ward D, Wesche K, Wiser SK, Woodcock BA, Young TP, Yu FH, Zobel M, Götzenberger L (2020) Synchrony matters more than species richness in plant community stability at a global scale. *Proc Natl Acad Sci* 117(39):24345–24351. <https://doi.org/10.1073/pnas.1920405117>
- Van Langenhove L, Janssens IA, Verryckt L, Brechet L, Hartley IP, Stahl C, Courtois E, Urbina I, Grau O, Sardans J, Peguero G, Gargallo-Garriga A, Peñuelas J, Vicca S (2020) Rapid root assimilation of added phosphorus in a lowland tropical rainforest of French Guiana. *Soil Biol Biochem* 140:107646. <https://doi.org/10.1016/j.soilbio.2019.107646>
- Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. *Ecol Appl* 20(1):5–15. <https://doi.org/10.1890/08-0127.1>
- Wahab A, Muhammad M, Munir A, Abdi G, Zaman W, Ayaz A, Khizar C, Reddy SPP (2023) Role of arbuscular mycorrhizal fungi in regulating growth, enhancing productivity, and potentially influencing ecosystems under abiotic and biotic stresses. *Plants* 12(17):3102. <https://doi.org/10.3390/plants12173102>
- Wan NF, Zheng XR, Fu LW, Kiær LP, Zhang ZJ, Chaplin-Kramer R, Dainese M, Tan JQ, Qiu SY, Hu YQ, Tian WD, Nie M, Ju RT, Deng JY, Jiang JX, Cai YM, Li B (2020) Global synthesis of effects of plant species diversity on trophic groups and interactions. *Nat Plants* 6(5):503–510. <https://doi.org/10.1038/s41477-020-0654-y>
- Wang C, Mori T, Mao QG, Zhou KJ, Wang ZH, Zhang YQ, Mo H, Lu XK, Mo JM (2020) Long-term phosphorus addition downregulates microbial investments on enzyme productions in a mature tropical forest. *J Soils Sediments* 20(2):921–930. <https://doi.org/10.1007/s11368-019-02450-z>
- Wang LL, Ren F, Zhang C, Huang XJ, Zhang ZH, He JS, Yang YP, Duan YW (2022) The effects of changes in flowering plant composition caused by nitrogen and phosphorus enrichment on plant–pollinator interactions in a Tibetan Alpine grassland. *Front Plant Sci* 13:964109. <https://doi.org/10.3389/fpls.2022.964109>
- Wardle DA, Zackrisson O (2005) Effects of species and functional group loss on island ecosystem properties. *Nature* 435:806–810. <https://doi.org/10.1038/nature03611>
- Wardle DA, Barker GM, Yeates GW, Bonner KI, Ghani A (2001) Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecol Monogr* 71(4):587–614. [https://doi.org/10.1890/0012-9615\(2001\)071\[0587:ibminz\]2.0.co;2](https://doi.org/10.1890/0012-9615(2001)071[0587:ibminz]2.0.co;2)
- Wassen MJ, Schrader J, van Dijk J, Eppinga MB (2021) Phosphorus fertilization is eradicating the niche of northern Eurasia's threatened plant species. *Nat Ecol Evol* 5(1):67–73. <https://doi.org/10.1038/s41559-020-01323-w>
- Wei SZ, Tie LH, Liao J, Liu X, Du ML, Lan SX, Li XR, Li CS, Zhan HC, Huang CD (2020) Nitrogen and phosphorus co-addition stimulates soil respiration in a subtropical evergreen broad-leaved forest. *Plant Soil* 450(1–2):171–182. <https://doi.org/10.1007/s11104-020-04498-0>
- Woodrow IE, Berry JA (1988) Enzymatic regulation of photosynthetic CO<sub>2</sub> fixation in C<sub>3</sub> plants. *Annu Rev Plant Physiol Plant Mol Biol* 39:533–594. <https://doi.org/10.1146/annurev.pp.39.060188.002533>
- Wright SJ (2019) Plant responses to nutrient addition experiments conducted in tropical forests. *Ecol Monogr* 89:e01382. <https://doi.org/10.1002/ecm.1382>
- Wright SJ, Turner BL, Yavitt JB et al (2018) Plant responses to fertilization experiments in lowland, species-rich, tropical forests. *Ecology* 99:1129–1138. <https://doi.org/10.1002/ecy.2193>
- Xia Y, Peñuelas J, Sardans J, Zhong XJ, Xu LL, Yang ZJ, Yang YS, Yang LM, Yue K, Fan YX (2024) Phosphorus addition accelerates soil organic carbon mineralization by desorbing organic carbon and increasing microbial activity in subtropical forest soils. *Appl Soil Ecol* 193:105166. <https://doi.org/10.1016/j.apsoil.2023.105166>
- Xiao RX, Zou YR, Guo XR, Li H, Lu H (2022) Fatty acid desaturases (FADs) modulate multiple lipid metabolism pathways to improve plant resistance. *Mol Biol Rep* 49(10):9997–10011. <https://doi.org/10.1007/s11033-022-07568-x>
- Yan H, Freschet GT, Wang HM, Hogan JA, Li SG, Valverde-Barrantes OJ, Fu XL, Wang RL, Dai XQ, Jiang L, Meng SW, Yang FT, Zhang MM, Kou L (2022) Mycorrhizal symbiosis pathway and edaphic fertility frame root economics space among tree species. *New Phytol* 234(5):1639–1653. <https://doi.org/10.1111/nph.18066>
- Yan L, Tang D, Pang JY, Lambers H (2025) Root carboxylate release is common in phosphorus-limited forest ecosystems in China: using leaf manganese concentration as a proxy. *Plant Soil* 508(1–2):143–158. <https://doi.org/10.1007/s11104-024-06791-8>
- Yang LM, Yang ZJ, Zhong XJ, Xu C, Lin YY, Fan YX, Wang MH, Chen GS, Yang YS (2021a) Decreases in soil P availability are associated with soil organic P declines following forest conversion in subtropical China. *CATENA* 205:105459. <https://doi.org/10.1016/j.catena.2021.105459>
- Yang XL, Wang XT, Xiao S, Liu ZY, Zhou XH, Du GZ, Liu K, Wang YJ, Chen SY, Nielsen UN (2021b) Dominant plants affect litter decomposition mainly through modifications of the soil microbial community. *Soil Biol Biochem* 161:108399. <https://doi.org/10.1016/j.soilbio.2021.108399>
- Yang XG, Shen KP, Xia TT, He YJ, Guo Y, Wu BL, Han X, Yan JW, Jiao M (2023) Invasive and native plants differentially respond to exogenous phosphorus addition in root growth and nutrition regulated by arbuscular mycorrhizal fungi. *Plants* 12(11):2195. <https://doi.org/10.3390/plants12112195>

- Yang SY, Lin WY, Hsiao YM, Chiou TJ (2024) Milestones in understanding transport, sensing, and signaling of the plant nutrient phosphorus. *Plant Cell* 36(5):1504–1523. <https://doi.org/10.1093/plcell/koad326>
- Yetgin A (2024) Exploring the dynamic nature of root plasticity and morphology in the face of changing environments. *Ecol Front* 44(1):112–119. <https://doi.org/10.1016/j.chnaes.2023.07.008>
- Yu RP, Li XX, Xiao ZH, Lambers H, Li L (2020) Phosphorus facilitation and covariation of root traits in steppe species. *New Phytol* 226(5):1285–1298. <https://doi.org/10.1111/nph.16499>
- Yu QS, Ma SH, Ni XF, Ni XL, Guo ZM, Tan XP, Zhong MY, Abu Hanif M, Zhu JL, Ji CJ, Zhu B, Fang JY (2022a) Long-term phosphorus addition inhibits phosphorus transformations involved in soil arbuscular mycorrhizal fungi and acid phosphatase in two tropical rainforests. *Geoderma* 425:116076. <https://doi.org/10.1016/j.geoderma.2022.116076>
- Yu QS, Ni XF, Cheng XL, Ma SH, Tian D, Zhu B, Zhu JL, Ji CJ, Tang ZY, Fang JY (2022b) Foliar phosphorus allocation and photosynthesis reveal plants' adaptative strategies to phosphorus limitation in tropical forests at different successional stages. *Sci Total Environ* 846:157456. <https://doi.org/10.1016/j.scitotenv.2022.157456>
- Yuan Y, Li Y, Mou ZJ, Kuang LH, Wu WJ, Zhang J, Wang FM, Hui DF, Peñuelas J, Sardans J, Lambers H, Wang J, Kuang YW, Li ZA, Liu ZF (2021) Phosphorus addition decreases microbial residual contribution to soil organic carbon pool in a tropical coastal forest. *Glob Change Biol* 27(2):454–466. <https://doi.org/10.1111/gcb.15407>
- Zaret M, Kinkel L, Borer ET, Seabloom EW (2023) Soil nutrients cause threefold increase in pathogen and herbivore impacts on grassland plant biomass. *J Ecol* 111(8):1629–1640. <https://doi.org/10.1111/1365-2745.14111>
- Zhang JF, Li J, Fan YX, Mo QF, Li YW, Li YX, Li ZA, Wang FM (2020) Effect of nitrogen and phosphorus addition on litter decomposition and nutrients release in a tropical forest. *Plant Soil* 454(1–2):139–153. <https://doi.org/10.1007/s11104-020-04643-9>
- Zhang J, Zheng MH, Zhang YJ, Wang J, Shen H, Lin YB, Tang XL, Hui DF, Lambers H, Sardans J, Peñuelas J, Liu ZF (2021) Soil phosphorus availability affects diazotroph communities during vegetation succession in lowland subtropical forests. *Appl Soil Ecol* 166:104009. <https://doi.org/10.1016/j.apsoil.2021.104009>
- Zhang JF, Zhou JG, Lambers H, Li YW, Li YX, Qin GM, Wang M, Wang J, Li ZA, Wang FM (2022) Nitrogen and phosphorus addition exerted different influences on litter and soil carbon release in a tropical forest. *Sci Total Environ* 832:155049. <https://doi.org/10.1016/j.scitotenv.2022.155049>
- Zhang GL, Bai JH, Zhai YJ, Jia J, Zhao QQ, Wang W, Hu XY (2024) Microbial diversity and functions in saline soils: a review from a biogeochemical perspective. *J Adv Res* 59:129–140. <https://doi.org/10.1016/j.jare.2023.06.015>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.