



Editorial special issue: plant-soil interactions in the Amazon rainforest

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Introduction

Climate is often considered the main environmental factor driving ecosystem functioning and dynamics at regional to global scales (Hirota et al. 2011; Blois et al. 2013; Wiczyński et al. 2019). Yet, when it comes to landscapes, fine-scale soil gradients play a fundamental role (Baldeck et al. 2013). For instance, soil physical properties influence water availability to plants (Lambers and Oliveira 2019). Soil nutrient availability is another important driver of species distribution and plant community assembly (Quesada et al. 2012; Baldeck et al. 2013; Oliveira et al. 2019). In the case of tropical forest ecosystems, because overall nutrient stocks are often greater in the aboveground biomass than in soils (Paiva et al. 2015), microbial processes are fundamental to maintain ecosystem processes, and they do so by interacting with soils and plants (Moore

et al. 2004; Milton and Kaspari 2007; Camenzind et al. 2018).

The Amazon rainforest biome, including the Amazon basin and Guyana Shield, covers an area of 6.7 million km², and is formed by a complexity of habitats and species that interact in many ways (Fig. 1). Soils exhibit heterogeneities at a continental scale, shaped by long term geological and geomorphological processes (Hoorn et al. 2010). For instance, in the northeast of the Amazon basin and the Guiana Shield, pre-Cambrian rocks have been exposed to weathering and erosion for over 2 billion years, and therefore originate nutrient-poor soils. Much of the central and eastern parts of the Amazon sedimentary basin (i.e. east from Manaus) have received sediments originating from this old region, and therefore have low natural soil fertility. In contrast, across the western Amazon, Andean orogeny has brought to surface fresh sediments that rejuvenate the soils and create highly productive landscapes wherever they are deposited (ter Steege et al. 2006; Quesada et al. 2010, 2012; Tuomisto et al. 2019). Along the floodplains of white-water rivers, Andean eroded sediments that have travelled long distances throughout the Amazon are deposited in layers of up to 80 cm thick during rainy La Niña years (Aalto et al. 2003). With animals moving across the landscape, nutrients are eventually transported from these floodplains into the uplands (Buendía et al. 2018).

The Amazon rainforest harbours huge biodiversity and provides services that affect societies globally, such as carbon storage, climate regulation and cultural values (Levis et al. 2020a). Thus, understanding how this

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system functions and what controls its resilience to environmental change is crucial for preserving it for future generations. Ecosystem resilience is partly shaped by the strength of external stressors, such as climate change or degrading activities caused by humans (Hirota et al. 2011; Barlow et al. 2018). It is also internally shaped by interactions between biodiversity and the environment, implying that changes in the environment may reshape the resilience (Scheffer et al. 2001; Dakos et al. 2019). Particularly important are the interactions that form feedbacks, because when feedbacks change as a result of external stressors or perturbations, they may trigger cascading effects and push the entire ecosystem to an alternative state (Estes et al. 2011). As global changes intensify, extreme weather events are occurring more frequently and intensely (Arneeth et al. 2019), human activities are disrupting plant-soil interactions, and the Amazon rainforest may approach a tipping point (Davidson et al. 2012; Lovejoy and Nobre 2019).

We still know very little about how Amazonian plants interact with the soils beneath them, and even less with soil microorganisms (Ritter et al. 2019). Here we address these interactions in the context of some of the most intriguing features of this system, including the Andes-Guyana soil fertility gradient, islands of particularly low fertility on white-sands, islands of relatively high fertility on anthropogenic dark earth soils, and the hydrological niches associated with topography. This special issue comprises nine articles that address different aspects of plant-soil interactions in the Amazon rainforest. New findings are revealed across multiple spatial scales and in regions with contrasting soil conditions. These findings are multifaceted in nature, covering the effects of soil on plants, and plants on soils, interactions between soils and microorganisms, and the negative and positive effects of human activities on plant-soil interactions. Overall, studies combined into this special issue provide new evidence on some of the most fascinating details about tropical rainforest functioning.

Edaphic conditions and tree community dynamics

Soil conditions interfere with how plants interact with their environment, other organisms and with each other; and as a result, they shape plant species composition and ecosystem functioning (Diaz et al. 2004; ter Steege et al. 2006; Wright et al. 2010; Quesada et al. 2012; Baldeck

et al. 2013). Among the many patterns that emerge in tropical forests, one in particular has attracted the attention of scientists; the dominance of few tree species (Connell 1978; Pitman et al. 2001; ter Steege et al. 2013). Half of all trees in the Amazon belong to a small group of 227 hyperdominant tree species (ter Steege et al. 2013). Some hypotheses to explain this pattern include a high resistance to pathogens and herbivores, and also high dispersal capability related to humans propagation (Levis et al. 2017). In rare cases, however, one single species dominates tree communities, forming monodominant forests (ter Steege et al. 2019). Recent evidence suggests that monodominance is probably a result of metacomunity dynamics in harsh isolated ecosystems, such as white-sand forests (ter Steege et al. 2019). Another widely accepted mechanism is the symbiosis between dominant trees and ectomycorrhizal fungi, which enhances nutrient uptake and defence against pathogens, and gives a competitive advantage to the host tree (Marx 1972; Connell and Lowman 1989; Peh et al. 2011; Corrales et al. 2018; Lambers et al. 2018).

In this special issue, Marimon-Junior et al. (2020) addressed the question of what explains the monodominance of the tree species *Brosimum rubescens* in the Southern Amazon region, where during four months, rainfall is under 100 mm. They tested the role of low soil water retention capacity, as a proxy for drought exposure, and related this soil condition with the minimum water potential (Ψ_{\min}) of *Brosimum rubescens* and six other species common in adjacent mixed-forests. As previously shown, isolated patches of limiting edaphic conditions are potential areas for the development of monodominated forests (ter Steege et al. 2019). Their results, however, indicate that drought exposure is probably not the cause of monodominance in these forests, which opens possibilities for other mechanisms. For instance, *Brosimum rubescens* has a high capacity to acclimate to light variation, which could increase its recruitment rates in both shaded and gap conditions, resulting in a competitive advantage. Moreover, their findings exemplify the complexity of mechanisms that shape tree community dynamics and assembly in tropical forest ecosystems.

In Central Amazonia, the genus *Vismia* dominates forests previously used for slash-and-burn agriculture. Light may not be the limiting factor for young trees in those forests, and competition might happen at the root zone, impeding the recruitment of other species

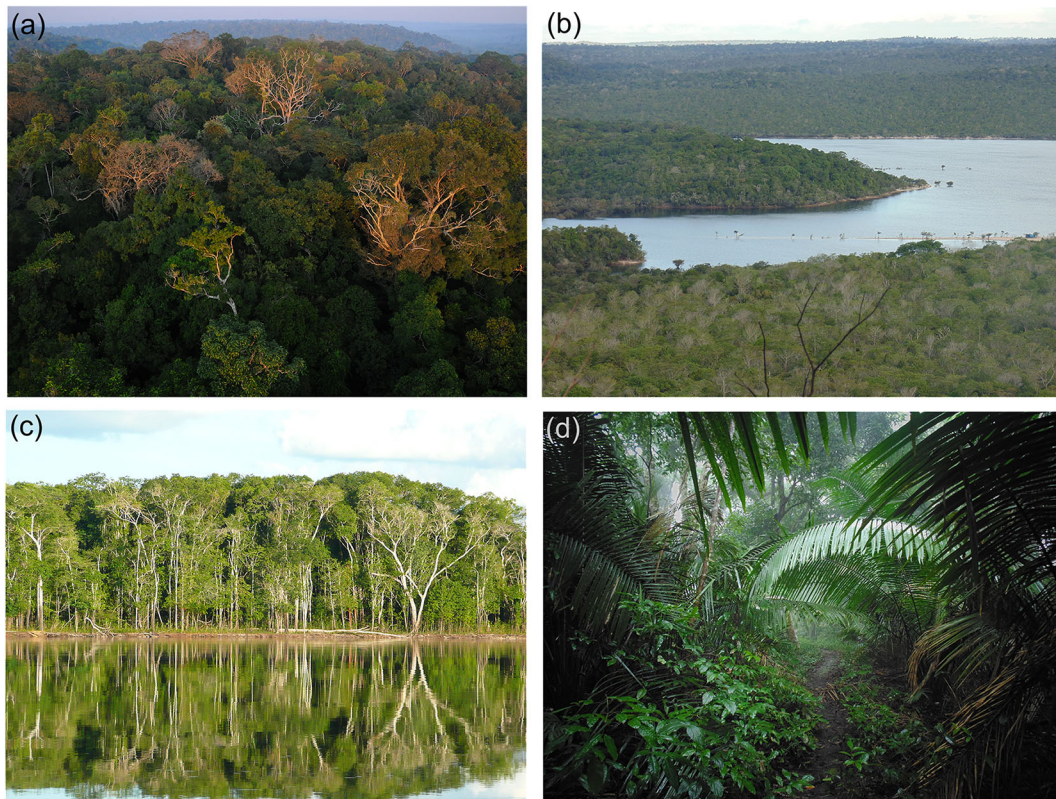


Fig. 1 Examples of Amazonian habitats with contrasting plant-soil interactions. (a) Central Amazonian forests on clay-rich soil. (b) Forest-savanna mosaics on sandy soils at Alter do Chão, Lower Tapajós. (c) Floodplain forests on silty soils at Barcelos, Middle Rio Negro. (d) Managed forests on anthropogenic dark soils at the Lower Tapajós. Plants and soils interact in multiple ways, with nutrient-poor soils often selecting for plant species with

conservative strategies, and rich soils selecting for plants with acquisitive strategies (Díaz et al. 2004). Two-way interactions can form feedbacks that influence ecosystem dynamics, for instance, when forest litter transfers nutrients to soils and those soils influence forest growth (e.g., Paiva et al. 2015). Photo credits: Rafael Oliveira (a), Bernardo Flores (b, c), Carolina Levis (d)

(Jakovac et al. 2014). Inspired by classical theory of forest succession (Connell and Slatyer 1977), Mazzochini and Camargo (2020) hypothesised that self-perpetuating mechanisms related to competition may contribute to maintain *Vismia* dominance in the system (Mesquita et al. 2001). They experimentally quantified competition and facilitation among understory woody plants, both below- and aboveground. They planted seedlings of three local tree species, with contrasting seed masses, and manipulated their interactions over a chronosequence of secondary succession. Their findings indicate that young trees compete with the resident vegetation across all stages of forest succession. Although it was not possible to disentangle the roles of light and nutrients, their results highlight the importance of strong competition between young trees and the understory vegetation as a cause of *Vismia* monodominance.

Edaphic conditions and plant-soil-microbial interactions

The Amazon rainforest hosts a large fraction of the world's biodiversity, and yet, we know very little about the microorganisms, which probably are the most diverse and abundant group (Ritter et al. 2019). Microorganisms play essential roles in ecosystem functioning, regulating most of the nutrient cycling processes (Lambers and Oliveira 2019). For instance, in the nutrient-poor tropical forests of the Guyana Shield, McGuire et al. (2010) found evidence that ectomycorrhizal (EM) fungi associated with a dominant tree species was slowing-down tree litter decomposition, and affecting nutrient availability for other microorganisms and plants. Microbial processes are often regulated by edaphic conditions, in particular, phosphorus (P) availability (Camenzind et al. 2018), and as a

result, plant-microbial interactions vary with soil conditions.

Vasco-Palacios et al. (2020) studied different forest ecosystems of the Colombian Amazon to explore how edaphic conditions shape fungal communities. They assessed three distinct forest types in detail: (1) *terra firme* forests with trees known to host arbuscular mycorrhizal (AM) fungi, (2) *terra firme* forests dominated by the Dipterocarpaceae species *Pseudomonotes tropenbosii*, known to host EM fungi, and (3) white-sand forests dominated by trees of the genera *Dicymbe* and *Aldina*, known to host EM fungi. They found 2507 fungal operational taxonomic units (OTUs), of which 59% belonged to saprotrophs, 9% to plant-pathogens, 6% to EM fungi, 5% to AM fungi, lichens and mycoparasites together, and 22% were unknown. The proportions of these functional groups did not vary across forest types. Unexpectedly, *terra firme* forests dominated by AM host trees had high EM fungal diversities, possibly because of scattered EM host trees of the genera *Coccoloba*, *Guapira* and *Neea*. White-sand forests had a contrasting fungal composition due to their relatively lower soil carbon content, shown to be the most important factor structuring fungal communities. The study reveals the interplay between edaphic conditions and tree species composition in shaping fungal communities, and draws attention to the enormous knowledge gap regarding fungal diversity in these rainforests.

As most of the soils in the Amazon basin are ancient and highly weathered, Lugli et al. (2020) hypothesised that trees would develop alternative fine-root strategies for P uptake. Plants and microbes in tropical forests commonly use phosphatase enzymes to degrade organic P compounds (Kitayama 2013). This mechanism is particularly efficient when plants have fine, well-distributed roots to forage P in the soil. In contrast, plants with thicker root systems are not so efficient at P foraging, and are expected to depend more on AM fungi, which have hyphal networks that increase P uptake. In the Central Amazon forest, Lugli et al. (2020) tested whether trees with finer root systems would invest more in phosphatase activity, whereas trees with relatively thicker roots would invest more in the association with AM fungi. Interestingly, they found that, although finer roots exhibited greater phosphatase activity, as predicted, the association with AM was not related to root morphology. One explanation is that both strategies could, in fact, be complementary, allowing

plants to access organic and inorganic P more efficiently in the soil (Nasto et al. 2014; Wen et al. 2019). The study demonstrates how trees can develop multiple strategies for P uptake, particularly in tropical rainforests with P-limiting soils.

Another important limiting factor in terrestrial ecosystems is the availability of nitrogen (N), which strongly influences species interactions and vegetation dynamics (LeBauer and Treseder 2008; Vitousek et al. 2013). The main mechanism by which N enters natural ecosystems is via fixation of atmospheric dinitrogen (N_2) by symbiotic and free-living diazotrophic microorganisms (Vitousek et al. 2013). Van Langenhove et al. (2020) studied the mechanisms that control N_2 fixation by free-living diazotrophic organisms in both sandy and clayey forests of French Guiana, a region with some of the most weathered soils in the Amazon. They studied the soil and litter layers of both forests, which are common habitats of free-living diazotrophs, and found that N_2 -fixation rates were among the lowest ever recorded for tropical forests worldwide. Phosphorus availability has been suggested as a strong limiting factor for N-fixing organisms (Raven 2012), which was confirmed by their findings. They also found that seasonal variation in water availability determined N_2 -fixation rates within the forest litter, with the highest rates observed during the wet season. During the dry season, fixation rates were much lower in the litter layer, but highly heterogeneous, allowing N_2 fixation to persist in few edaphic microsites. The study of Van Langenhove et al. (2020) confirms previous evidence showing that P and water are strong limiting factors of N_2 -fixation rates in tropical forests. With global changes, deforestation may intensify soil erosion (Borrelli et al. 2017), and extreme drought events may happen more often, potentially reducing N inputs into tropical forests and affecting ecosystem dynamics.

Human activities reshaping plant-soil interactions

The evolutionary history of plant-soil interactions in the Amazon has contributed to shape how current ecosystems function (de Souza et al. 2019). This process has been affected by human activities in multiple ways, particularly during the Late Holocene. For instance, before the European conquest of the Americas, indigenous peoples had already changed vast portions of the Amazon forest, locally enhancing soil fertility and the

abundance of domesticated tree species (Levis et al. 2017). More recently, activities of the globalised industrial society, such as land-use change and logging are reducing biodiversity and ecosystem resilience (Barlow et al. 2018). Losses of species and habitats are disrupting interactions that may be structural for ecosystem resilience (Estes et al. 2011). Human activities may have positive or negative effects on plant-soil interactions, and these effects need to be well understood if we intend to manage Amazonian resilience (Scheffer et al. 2015).

Across most of the tropics, including the Amazon, human and natural disturbances are becoming more frequent in well-preserved ecosystems (Barlow et al. 2018). Flores et al. (2020) addressed the impacts of such disturbances on the plant-soil interactions of tropical forests worldwide. First, they reviewed the literature to understand how the loss of tropical forest cover may increase soil-erosion rates. Then, they compared global spatial data on rainfall erosivity, a measure of soil exposure to water erosion, with data on tree and bare soil cover change. They found that particularly in South America, tropical forests are becoming increasingly exposed to erosion. Based on what is known about the effects of erosion on ecosystems, they propose a feedback mechanism between forest cover and soil erosion that may increase the risk of ecosystem shifts. When a tropical forest is disturbed, for instance by fire or logging, tree cover is reduced, exposing the soil to erosion during rain events. While the forest remains open, erosion reduces soil fertility and the capacity of trees to recruit, until the ecosystem becomes trapped in an open degraded state. Field data from two Amazonian forest types support the proposed feedback, which implies that to restore degraded forests may depend on actively intervening to prevent this feedback.

From another perspective on the effects of humans in Amazonian forests, Levis et al. (2020b) studied how local societies have altered the soils and tree species composition. They investigated in detail the Tapajós and Madeira regions to compare how people of the past (pre-Columbian indigenous societies) and people of the present (current indigenous and traditional societies) have managed ecosystems to increase their productivity. Strikingly, they found a positive effect of past indigenous management in P and calcium (Ca) concentrations in the soils of forests surrounding ancient settlements, which persists even after centuries or millennia since their abandonment. Because these ancient settlements were widespread in the landscape, the observed P and

Ca enrichment effect applies to vast areas of old-growth forest. Forests enriched with P also had higher densities of domesticated trees, currently used as food resources. In contrast, present local societies are mostly settled near the main rivers, and their management practices did not contribute to enrich soils with P. The findings of Levis et al. (2020b) reveal how entire Amazonian landscapes are rich in food resources due to significant soil fertilisation by past indigenous peoples.

Including edaphic conditions in plant species distribution models

With global changes, tropical forest species will have to migrate or adapt, as their habitat distributions shift (Feeley et al. 2012). Even if a plant species is able to persist within its climatic niche, it will still have to deal with potential changes in local soil conditions. Most studies that model future habitat suitability across broad scales use climate data only. Yet, this approach results in large uncertainties about the effects of other important factors at the landscape scale. Zuquim et al. (2020) investigated how predictions of future habitat suitability for Amazonian plants can be improved by including data on exchangeable base cation concentration (K, Mg, Ca) in soil and cation exchange capacity. They modelled present and future habitat suitability for 35 Amazonian plant species, including herbs, lianas, trees and palms, using species distribution models based on climate and soil data. They found that 44% of the species had soil variables as the most important factor. Using future climatic scenarios corresponding to “business-as-usual” and “with governance”, relative to carbon emissions, and assuming that soil conditions did not change, they show that plant habitat suitability may be completely different by 2050. For almost half of the species, future habitats were projected to be smaller when soil conditions were considered, under the business-as-usual scenario. Their findings imply that species adapted to certain soil conditions may go extinct if their habitats disappear or become too sparse for individuals to migrate. The study of Zuquim et al. (2020) shows how including the soil factor in plant species distribution models may reveal a more realistic picture of future habitats, increasing our capacity to predict and manage biodiversity responses to climate change.

Soil conditions become even more relevant at the landscape scale, where edaphic conditions can be very heterogeneous. For instance, fine scale changes in soil conditions along hydro-topographic gradients shape tree communities (Tuomisto et al. 2003; Baldeck et al. 2013; Condit et al. 2013; Schiatti et al. 2014). Topography is often assumed to be a proxy for hydrological drought exposure, with trees on the plateaus being more frequently exposed to drought events, and trees in the valleys having constant access to water. Recent evidence suggests that this hydro-topographic gradient may have selected for tree species with particular hydraulic traits in each habitat (Oliveira et al. 2019). To assess the relative importance of topography versus soil nutrient availability in shaping tree communities in the Colombian Amazon, Zuleta et al. (2020) analysed field data from a 25-ha plot, including detailed information about the distributions of 612 woody species across *terra firme* forest habitats. Statistical methods that simulate null expectations of species habitats allowed them to assess patterns of habitat-association, helping to disentangle the roles of both edaphic filters. Their findings reveal that topography plays a stronger role than nutrient availability in filtering woody plant species distributions in this western Amazonian landscape. The results of Zuleta et al. (2020) confirm previous patterns from the central Amazon (Schiatti et al. 2014; Oliveira et al. 2019), and other tropical forests (Baldeck et al. 2013), and reveal how trees can be limited by water, even in the wettest rainforests, implying that changes in rainfall variability will likely rearrange tree communities.

Conclusions and future prospects

With this special issue, we have collated new insights about plant-soil interactions in the Amazon rainforest. Studies addressed the effects of soil conditions on plant-plant interactions, and how particular mechanisms may lead to hyperdominant or monodominant forests. Marimon-Junior et al. (2020) revealed how the monodominance of *Brosimum rubescens* in seasonal forests of Southern Amazonia is not related to drought stress, but possibly to factors such as acclimation to light intensity. Mazzochini and Camargo (2020) experimentally demonstrated that young trees of varying species compete with the understory vegetation in *Vismia* dominated forests, and that these interactions may contribute to arrest secondary succession. Other studies have

unveiled new insights on how edaphic conditions shape symbiotic and free-living microorganisms. Vasco-Palacios et al. (2020) assessed how edaphic conditions shape fungal communities in the Colombian Amazon, causing white-sand forest communities to largely differ from those of *terra firme* forests. Lugli et al. (2020) showed that in Central Amazonian forests, trees can combine two different root strategies, use of phosphatase enzymes and AM fungal association, to increase P uptake. Van Langenhove et al. (2020) revealed that N_2 -fixation rates in the soil and litter of French Guyanan forests were among the lowest in all tropical forests, likely due to strong P limitation. The consequences of global changes have also been addressed, revealing important risks, and potential solutions for Amazonian societies. Flores et al. (2020) propose a soil-erosion feedback that may contribute to arrest disturbed tropical forests in a persistently-degraded state. Levis et al. (2020b) showed how past indigenous management enriched the soils of old-growth Amazonian forests, allowing edible tree species to persist in high abundances. Finally, two studies assessed the effects of including the soil factor in plant species distribution models. Zuquim et al. (2020) tested the importance of soil conditions for Amazonian plant species distributions, and found that nearly half of the species had their models improved; projecting habitat reductions with climate change. Zuleta et al. (2020) analysed woody plant species distributions in a Colombian Amazon landscape, and found that topography was the most important factor, revealing a strong drought sensitivity of many species even in wettest rainforests.

A series of important new studies assembled in this special issue provide novel insights into plant-soil processes in the Amazon rainforest. However, how general these processes may be outside the Amazon remains uncertain. There are many well-known generalities across the tropics. For instance, on a global scale, P limitation is pervasive (Hou et al. 2020), and tropical forest tree communities are strongly shaped by soil conditions (Baldeck et al. 2013); patterns that were confirmed by Zuquim et al. (2020) and Zuleta et al. (2020) with species distribution models. Soil microbial processes are strongly limited by P availability in tropical forests (Camenzind et al. 2018), which explains why Van Langenhove et al. (2020) found the lowest ever recorded N_2 -fixation rates in the Guiana Shield. We also know that increasing aridity can cause tropical forests to shift into a savanna state (Hirota et al. 2011);

however, we lack mechanistic understanding of the roles played by edaphic conditions. New evidence by Flores et al. (2020) suggests that soil erosion may play a role in reducing the resilience of disturbed tropical forests. Nonetheless, extrapolations from the Amazon may not necessarily apply. Forests like the Kerangas in Asia are largely aseasonal, and although they may share similar climatic conditions with the western Amazonian forests, both are formed by completely different phylogenies (Slik et al. 2018), and likely have unique interactions. For example, the composition of EM fungal communities varies across continents, because host trees belong to different families (Corrales et al. 2018), yet the same process was observed in the Colombian Amazon region (Vasco-Palacios et al. 2020). As a result of contrasting evolutionary histories, ecosystems differ in the way they function and respond to perturbations (Dakos et al. 2019). Although evolution followed different paths across the world, most ecosystems are prone to collapse when interaction chains are broken (Estes et al. 2011). Understanding those interactions and their vulnerabilities is a key step in enhancing our capacity to manage ecosystem responses to global changes.

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