New Phytologist

Research

Nutrient cycling drives plant community trait assembly and ecosystem functioning in a tropical mountain biodiversity hotspot

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Received: *15 December 2020*
Accepted: *28 June 2021*

New Phytologist (2021)
doi: 10.1111/nph.17600

Key words: dynamic vegetation model, mycorrhiza, nutrient cycling, plant community assembly, plant functional traits, tropical montane forests (TMF).

Summary

- Community trait assembly in highly diverse tropical rainforests is still poorly understood. Based on more than a decade of field measurements in a biodiversity hotspot of southern Ecuador, we implemented plant trait variation and improved soil organic matter dynamics in a widely used dynamic vegetation model (the Lund-Potsdam-Jena General Ecosystem Simulator, LPJ-GUESS) to explore the main drivers of community assembly along an elevational gradient.
- In the model used here (LPJ-GUESS-NTD, where NTD stands for nutrient-trait dynamics), each plant individual can possess different trait combinations, and the community trait composition emerges via ecological sorting. Further model developments include plant growth limitation by phosphorous (P) and mycorrhizal nutrient uptake.
- The new model version reproduced the main observed community trait shift and related vegetation processes along the elevational gradient, but only if nutrient limitations to plant growth were activated. In turn, when traits were fixed, low productivity communities emerged due to reduced nutrient-use efficiency. Mycorrhizal nutrient uptake, when deactivated, reduced net primary production (NPP) by 61–72% along the gradient.
- Our results strongly suggest that the elevational temperature gradient drives community assembly and ecosystem functioning indirectly through its effect on soil nutrient dynamics and vegetation traits. This illustrates the importance of considering these processes to yield realistic model predictions.

Introduction

Predicting the assembly of plant communities from the species pool and their functional traits has been a major aim of community ecology for decades (Keddy, 1992; Fukami *et al.*, 2005; Shipley *et al.*, 2006). Plant community trait composition influences and is influenced by ecosystem processes, such as net primary production (NPP), carbon (C) storage and soil nutrient cycling (Díaz & Cabido, 2001; Eviner, 2004; Bardgett *et al.*, 2014). Plant functional traits determine the competitive performance of species (Díaz *et al.*, 2016; Kunstler *et al.*, 2016), and functional constraints lead to trade-offs. These trade-offs are represented by relationships between traits that can be generalized across species and plant communities (Wright *et al.*, 2004; Díaz *et al.*, 2016; Bruelheide *et al.*, 2018). The analysis of such relationships has been boosted by an increasing aggregation of plant trait data in large databases (Kattge *et al.*, 2020). Furthermore, functional composition is strongly shaped by the abiotic conditions of the environment, although species composition often is largely driven by stochastic processes or dispersal limitation (Fukami *et al.*, 2005; Bruelheide *et al.*, 2018). In spite of these advancements, community assembly in highly diverse tropical ecosystems is still poorly understood (Paine *et al.*, 2011).

Trait research also provides data and theoretical background for the development of process-based dynamic vegetation models (DVMs). These models simulate community assembly and ecosystem functioning, such as biomass growth and carbon cycling; however, community assembly has commonly only been modeled at the level of broadly defined plant functional types (PFTs, e.g. tropical broadleaved evergreen trees) with mostly fixed average parameter values. This approach ignores the vast diversity of plants in tropical ecosystems, which might also have strong functional implications (Tilman *et al.*, 1997; Díaz & Cabido, 2001). Recently, different approaches have been developed to represent trait variability in global DVMs (DGVMs) or more regional DVMs, based on plant trait trade-offs, in particular the leaf and wood economic spectra (Wright *et al.*, 2004; Chave *et al.*, 2009; Baraloto *et al.*, 2010). In these models, woody individuals differ in their trait values, and the community trait composition emerges via ecological sorting (Scheiter *et al.*, 2013; Fyllas *et al.*, 2014; Sakschewski *et al.*, 2015; Maréchaux & Chave, 2017; Fauset *et al.*, 2019; Koven *et al.*, 2019).

Most of these models, however, do not yet include soil organic matter dynamics and/or nutrient supply limitations to photosynthesis and plant growth. These are important regulators of the global carbon cycle (Fernández-Martínez *et al.*, 2014) which have been addressed in recent model developments but not in models accounting for within-PFT trait variability (e.g. Wang *et al.*, 2007; Smith *et al.*, 2014). Including nutrient cycling in models has partly been motivated by the need to predict the potential effects of CO_2 fertilization more realistically (Hickler *et al.*, 2015; Olivares *et al.*, 2015; Sitch *et al.*, 2015; Fleischer *et al.*, 2019b). Model results so far do indeed suggest substantially smaller CO_2 fertilization effects as a result of nitrogen (N) (Wårlind *et al.*, 2014) and more recently phosphorus (P) limitation to plant growth (Wang *et al.*, 2010; Wieder *et al.*, 2015; Fleischer *et al.*, 2019a; Thum *et al.*, 2019). The development of flexible C allocation schemes (i.e. root vs leaf C allocation) is also expected to improve model predictions regarding CO_2 fertilization scenarios (Franklin *et al.*, 2012). Therefore, combining model representations of trait variability and nutrient dynamics is expected to be relevant as community traits affect soil nutrients (Zhu *et al.*, 2016) and *vice versa* (Werner & Homeier, 2015). In addition, it can also be crucial to account for the role of mycorrhiza-mediated nutrient uptake (Kirschbaum & Paul, 2002; Orwin *et al.*, 2011; Hodge & Storer, 2014; Hofhansl *et al.*, 2016; Jansa *et al.*, 2019). Mycorrhiza-mediated nutrient uptake has been estimated to contribute up to 80% of plant N and P uptake (van der Heijden *et al.*, 2008; Nagy *et al.*, 2009). This process is considered to be particularly important for maintaining high N and P uptake by plants in environments where high C : N and C : P ratios of litter limit organic matter decomposition (Hobbie & Chapin, 1998).

The interplay between nutrient availability and plant functional diversity is particularly evident in tropical mountain forests (Homeier *et al.*, 2012, 2013). In these environments, a large diversity of plant species occurs along elevation and topographic gradients, where many plants are endemic to specific elevation ranges along the gradient. Long-term scientific research in tropical mountain forests indicates that, with increasing elevation, reduced temperature limits plant tissue decomposition rates and thus nutrient mineralization rates (Wilcke *et al.*, 2008; Wolf *et al.*, 2011; Marian *et al.*, 2017). Reduced nutrient availability restricts the establishment of plants, with lower nutrient demands and nutrient tissue concentrations thereby producing a strong environmental filter, which in turn exacerbates nutrient limitation as a result of low nutrient concentrations in litter (Wilcke *et al.*, 2011; Werner & Homeier, 2015). However, tropical mountain forests are not only particularly valuable because of their exceptional biodiversity – they can also store as much, or even more, C than lowland tropical forests due to their high soil carbon storage (Wilcke *et al.*, 2002; Leuschner *et al.*, 2013; Duque *et al.*, 2021).

While it has been suggested that nutrient limitation may play an important role for community assembly across elevation gradients in tropical mountain forests (Andersen *et al.*, 2012; Glassman *et al.*, 2017; Xu *et al.*, 2017), the interplay with other factors, such as temperature effects on photosynthesis, is not clear. Also, scaling the effect of environmental changes from the individual to the community level remains a challenge due to the multiple processes and related feedbacks involved, but functional traits are thought to be crucial (Suding *et al.*, 2008). Disentangling confounding factors from *in-situ* experiments is challenging and, at the very least, restricted to short time spans only. In this regard, model-based approaches may provide valuable insights with theoretical experiments, in spite of their inherent process simplifications.

In this study, we used a dynamic vegetation model (the Lund-Potsdam-Jena General Ecosystem Simulator, LPJ-GUESS) to explore how soil organic matter dynamics influence community plant functional trait assembly along an elevational gradient on the humid Amazon-exposed eastern slope of the eastern Andean cordillera in southern Ecuador, located in the Tropical Andes biodiversity hotspot. We implemented trait variability, soil P dynamics, plant uptake and limitation (note that soil N dynamics, plant uptake and limitation was already included in the model) and mycorrhiza-mediated nutrient uptake supported by two decades of trait measurements and ecosystem research at our study sites. The new model version (LPJ-GUESS-NTD, where NTD stands for nutrient-trait dynamics) was tested against field data on community trait gradients and vegetation structure along an elevational gradient from 1000 m to 3000 m above sea level (asl). Our goals were three-fold. Firstly, we wanted to know how well the LPJ-GUESS-NTD model reproduced observed patterns of plant traits and ecosystem processes along the elevation gradient. Secondly, by switching trait variability and nutrient limitation in the model on and off, we aimed to evaluate how both processes affect community plant trait assembly, biomass and net primary production. Thirdly, we additionally addressed the role of mycorrhiza-mediated plant nutrient uptake in overcoming nutrient limitation.

Materials and Methods

General model description

The Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS) is a dynamic vegetation model for local to global applications (Smith *et al.*, 2001, 2014) (http://web.nateko.lu.se/lpj-guess/). It combines generalized ecophysiological process representations (e.g. photosynthesis, plant and soil respiration, ecosystem carbon, water and nitrogen cycling) as commonly used in DGVMs (Sitch *et al.*, 2003; Prentice *et al.*, 2007), with detailed representations of tree population dynamics (establishment, growth and death of individual trees) and canopy gap dynamics adopted from forest gap models (Botkin *et al.*, 1972; Bugmann, 2001; Shugart *et al.*, 2018). Its modular framework has been designed for flexible adaptation to different research questions and study areas. The main developments of the model version for this study, LPJ-GUESS-NTD (where NTD stands for nutrient-trait dynamics), have been the implementation of variable traits related to the leaf and wood economic spectrum instead of mostly fixed traits per PFT, and improvements of the soil organic matter and nutrient dynamics, in particular an implementation of the phosphorus cycle and plant nutrient uptake via mycorrhizas. In previous versions of LPJ-GUESS, trait values were fixed for given PFTs, based on the average of field observations. In the version here they emerge through environmental filtering and competition between woody individuals for resources (light, water and nutrients). Selection in the models works primarily through variations in mortality, which is a function of plant growth (with higher mortality under low growth) and wood specific gravity (WSG). Growth in the given environment in turn is determined by the plant traits (and competition with other individuals for resources, see also Supporting Information Notes S1). The resource availability may be externally driven – for example by climate, soil type and nutrient deposition – or emerge from plant interactions that influence light, soil water or nutrient availability. Model parameters beyond the adaptations of the model for the study sites are described by Wårlind *et al.* (2014). A detailed description of LPJ-GUESS-NTD is given in the next sections of the methods, and a general diagram of the model is shown in Fig. 1. Further model adaptations to the study sites are described in the Notes S1–S3, such as a flexible leaf and fine root C allocation scheme.

Trait variation

The trait variability module for LPJ-GUESS-NTD followed a similar approach to the Lund-Potsdam-Jena managed land model with flexible individual traits (LPJmL-FIT) and the adaptive dynamic global vegetation model v.2 (aDGVM2), which do not include nutrient cycling (Sakschewski *et al.*, 2015; Langan *et al.*, 2017). These models simulate trait diversity and community trait shifts along two general principles: the values of key traits from plant individuals are randomized at establishment; and other traits are derived by regression of measured trait trade-offs on these key traits (Kattge *et al.*, 2011; Markesteijn *et al.*, 2011; Bendix *et al.*, 2021). Key traits are typically independent from each other and can be related to the leaf economic spectrum (Wright *et al.*, 2004), linked, for example, to photosynthetic capacity, and the wood economic spectrum (Chave *et al.*, 2009), which is related to plant mortality. Once individuals are established, filtering occurs as mortality of less competitive individuals (details in Notes S1). Besides their role in plant physiology, these key traits are crucial for adaptability in changing environments and have been widely measured in the field, both globally (Kattge *et al.*, 2020) and at our study site (Báez & Homeier, 2018). Large observation trait datasets are also crucial for adequately characterizing trait variability in the community. In the implementation of trait variability presented here, trait combinations are produced by drawing random specific leaf area (SLA) and WSG trait values for each established woody individual from a uniform distribution. The range of randomized values is defined by the field-measured data spanning the whole elevational gradient (1000–3000 m asl), assuming therefore that there is no dispersal limitation for trait ranges (Table S1; Fig. 1) across the area. Using data from our field site contrasts with the approach in LPJmL-FIT by Sakschewski *et al.* (2015), who used global values for the corresponding global PFT from the TRY database (Kattge *et al.*, 2020). Other parameters are then calculated using trait–trait correlations from field measurements or data from the TRY database, resulting in a total of six traits which are randomly defined at plant establishment (Fig. 1) and which were previously fixed parameters per PFT. The relationships from field measurements are shown together with the same relationships calculated from the global TRY database in Fig. S1. Details of tradeoff calculations are described in Notes S2.

Soil organic matter (SOM) and nutrient dynamics

The soil organic matter (SOM) module of LPJ-GUESS is based on the CENTURY/DAYCENT/FORCENT soil model group (Parton *et al.*, 1993, 2010; Kirschbaum & Paul, 2002), which includes C, N and P cycles, and is described in detail for N in a study by Smith *et al.* (2014). Recent vegetation model developments (Fisher *et al.*, 2018; Thum *et al.*, 2019) and empirical studies on the P cycle, some of which were conducted in our study area (Wullaert *et al.*, 2010; Báez & Homeier, 2018), have demonstrated the importance of accounting for P limitation for plant growth. From a global perspective, this is especially the case in the tropics, where P availability is frequently the dominant limitation for plant growth (Chadwick *et al.*, 1999; Townsend *et al.*, 2007; Dalling *et al.*, 2016), because in aged soils, which are common in the tropics, most of the P has been leached, sequestered, or occluded (Walker & Syers, 1976; Lambers *et al.*, 2008). However, most tropical mountain forest soils are relatively young and P-rich and therefore more likely to be N-limited, in particular at higher elevations, while N and P co-limitation has been observed at intermediate elevations (Unger *et al.*, 2010; Wullaert *et al.*, 2010; Homeier *et al.*, 2012; Fisher *et al.*, 2013; Velescu *et al.*, 2016).

Here, P cycling was implemented in LPJ-GUESS-NTD following the approach of the initial CENTURY model (Parton *et al.*, 1993) but adopting the implementations of the Carnegie-Ames-Stanford approach carbon-nitrogen-phosphorous (CASA-CNP) model (Wang *et al.*, 2007, 2010). Phosphorus data for model input and evaluation were taken from field study results for our study region (Table S1). Mineral weathering and precipitation/dissolution of P were not considered since they occur in the mineral part of the soil and mineral contributions to the organic layer (where most roots are located) are minor at the 2000 and 3000 m asl elevations. At 1000 m asl, where the thin organic layer plays a smaller role in nutrient supply, mineral weathering is so advanced that the P release can be neglected. However, inclusion of weathering and dissolution/precipitation processes of P might improve future modeling efforts (Wilcke *et*

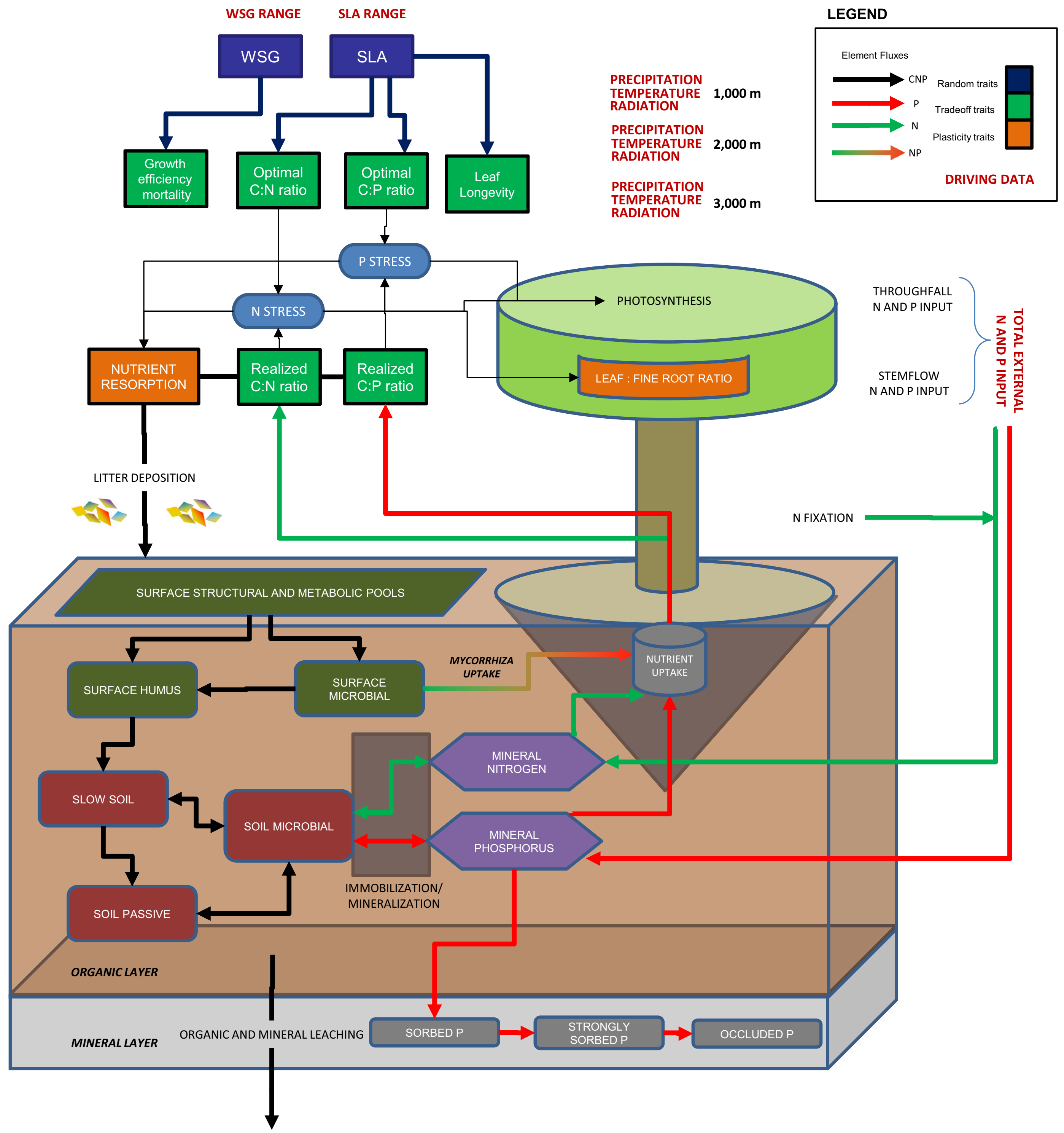

Fig. 1 Trait diversity and soil organic matter scheme of LPJ-GUESS-NTD, an update of the scheme presented by Smith *et al*. (2014) including the phosphorus (P) cycle, based on the CASA-CNP model by Wang *et al*. (2007, 2010) and mycorrhiza-mediated plant nutrient uptake based on Kirschbaum & Paul (2002). As in LPJ-GUESS, matter transfer between pools depends on mass-based carbon to nitrogen (C : N) or C : P ratios, which determine immobilization or mineralization.

al., 2019). Phosphorus is added to the SOM code structure following the N implementation in LPJ-GUESS, which represents SOM in several pools differing in C : N ratios. These pools are now also characterized by C : P ratios. In contrast to the C-N-only model version (Smith *et al*., 2014), LPJ-GUESS-NTD includes a reduction of decomposition rates through low mineral P or low N as implemented by the CASA-CNP model, with the actual decomposition rate being the smallest of both limiting factors (Wang *et al.*, 2010). This effectively provides an implementation of N or P limitation of microbial activity (decomposition) which competes with plants for available mineral nutrients (Zhu *et al.*, 2016). Biological N fixation in the model is independent of deposition, and was unchanged from the global standard version of LPJ-GUESS, which uses a general empirical relationship with annual evapotranspiration and is based on the work of Cleveland *et al.* (1999). Field data show that along the elevational gradient, free living N fixation does not differ significantly between the sites and is of the order of 1.5 kg $\mathrm{ha}^{-1}\ \mathrm{yr}^{-1}$ N (Matson *et al.*, 2015). Symbiotic N_2 fixation is not included in the model. However, the measured abundance of the family Fabaceae (which are potential N-fixers) is decreasing with elevation – for the trees > 10 cm diameter at breast height (DBH) it is 6% at 1000 m, 2% at 2000 m and 0% at 3000 m asl.

In addition, two other important updates were carried out based on the work of Kirschbaum & Paul (2002) in order to improve SOM dynamics for forested environments. First, N and P mineralization is restricted to the soil microbial SOM pool, which results in a more realistic process representation and reduced net mineralization rates in forest ecosystems. Following the approach of Kirschbaum & Paul (2002), this was done mainly to allow a net mineralization under the high soil C : N and C : P ratios of forests, which otherwise would be greatly constrained. Therefore, mineralization or immobilization of N and P were dependent only on the stoichiometry of the microbial SOM pool. Second, we added mycorrhiza-mediated uptake of N and P to the SOM module. According to field data, arbuscular mycorrhizal fungi (AMF) are dominant at the study site, and are associated with virtually all tree species, thus providing nutrient uptake also from organic sources otherwise unavailable to plants (Kottke *et al.*, 2004; Cárate-Tandalla *et al.*, 2018). In LPJ-GUESS-NTD, the implementation of mycorrhiza-mediated N and P plant uptake was adopted from the approach described by Kirschbaum & Paul (2002), with plants allowed to take up a fraction of N directly from the organic microbial pool. Since AMF are predominantly able to take up N from microbial sources and not directly from organic material (Jansa *et al.*, 2019), and at the study sites the rooting of plants is concentrated in the organic layer (Soethe *et al.*, 2006), mycorrhiza-mediated plant nutrient uptake in the model occurs from the surface microbial pool $X_{\mathrm{Surfacemicrobial}}$ (Fig. 1). Our implementation is defined as follows:

$$\frac{\mathrm{d}X_{\mathrm{uptakemycorrhiza}}}{\mathrm{d}t} = \mathrm{c} \cdot X_{\mathrm{Surfacemicrobial}} \cdot M(T_{\mathrm{soil}}) \cdot f_{\mathrm{Xindiv}} \cdot P_{\mathrm{rootindiv}} \qquad \text{Eqn 1}$$

where $M(T_{\mathrm{soil}})$ is the temperature modification scalar, as defined by Kirschbaum & Paul (2002), f_{Xindiv} is the fraction of the plant's X (N or P) demand (simulated by LPJ-GUESS as a function of growth and tissue stoichiometry) not satisfied by mineral sources, and $P_{\mathrm{rootindiv}}$ is the root projective cover (i.e. the fraction of the simulated area covered by roots in $\mathrm{m}^2\ \mathrm{m}^{-2}$ for mineral uptake of N and P). The parameter c is the mycorrhizal root colonization rate, a fraction of the root projective cover available for mycorrhiza-mediated plant nutrient uptake. This equation results in reduced mycorrhizal activity under lower soil temperatures, and, when the plant's demand is satisfied by mineral sources, no mycorrhiza-mediated plant nutrient uptake takes place. This is based on the fact that the fungus–root symbiosis is more active in nutrient-stressed plants, with a decoupling of the interaction as mineral nutrient availability increases (Orwin *et al.*, 2011). Mycorrhiza-mediated plant nutrient uptake occurs directly from the organic N and P pool mass, therefore increasing C : N and C : P ratios of the surface microbial pool (Fig. 1) and effectively reducing decomposition and mineralization rates of SOM, as described by Kirschbaum & Paul (2002). Although root mycorrhizal colonization rates vary widely between species and with elevation, here we kept this value fixed at 0.39, which is the average value per species observed along the three elevational sites (Camenzind *et al.*, 2016).

Study area and data for model input

In this study, we simulated a tropical forest gradient in southern Ecuador that spans edaphic, floristic and climatic changes from 1000 to 3000 m asl.

The Reserva Biológica San Francisco (RBSF) and the adjacent Podocarpus National Park in southern Ecuador have been hosting scientific projects for the last 20 yr and thus there is a rich database of biotic, edaphic and climatological measurements (Bendix *et al.*, 2008; Richter *et al.*, 2013). Field plots have been established from 1000 to 3000 m asl elevation and provide a thermal and precipitation gradient (Table S2).

As model input (i.e. driving data) we used climatic, plant trait, and nutrient deposition data from three sites along the elevation gradient: 1000 m ('Bombuscaro'), 2000 m ('ECSF') and 3000 m asl ('Cajanuma'). Climatic data for the elevation gradient was taken from weather stations (temperature, radiation and precipitation; e.g. Bendix, 2020). Trait data for the gradient concerning possible values of SLA and WSG were defined by maxima and minima observed along the elevation gradient and taken from studies by Homeier & Leuschner (2021), Báez & Homeier (2018) and Homeier (2017a,b).

Inorganic nutrient forms in the model were ammonium (NH_4^+) and nitrate (NO_3^-) for inorganic N (N_i, assumed to form the same nutrient pool) and phosphate (PO_4^{3-}) for inorganic P (P_i), and were considered as the external inputs to the soil (deposition, same for all elevation sites). Mineral weathering for input in the mineral P_i pool was considered to be insignificant for plant growth at our study sites. In tropical forested environments, throughfall and stemflow are important sources of nutrients. Dissolved nutrients in throughfall and stemflow originate from plant leaching and wash-off of dry deposition to the canopy surface. Epiphytes and bryophytes located in stems and the canopy can retain a considerable part of the total deposited N (Clark *et al.*, 2005; Wullaert *et al.*, 2010; Schwarz *et al.*, 2011; Wilcke *et al.*, 2013), and can also fix N_2 (Stanton *et al.*, 2019) providing in practical terms a 'canopy organic matter pool' (Vance & Nadkarni, 1990). Therefore, as external inputs of N and P to the SOM module of LPJ-GUESS-NTD we did not consider the values of dry and wet deposition but the measured values of throughfall and stemflow N_i and P_i going directly into the mineral pools available for plant uptake. These were taken from Wilcke *et al.* (2013, 2019), Velescu & Wilcke (2020a,b) and Velescu *et al.* (2020a).

Data for model evaluation

In order to test this model, we used field data measured at the same study sites. This validation dataset is based on measurements of 282 tree species for SLA and 347 tree species for WSG. At least ten individual trees (DBH ≥ 10 cm) have been sampled in each of 54 permanent old-growth forest plots (plots were 20 × 20 m in size, were equally distributed among the three study sites and cover the topographic gradient within each site). Trait data can be accessed at http://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?citid=1835; detailed methods for SLA and WSG determination are as described previously by Báez & Homeier (2018). Simulated data were compared to observations (SLA, WSG, C : N and C : P) using pairwise Wilcoxon tests. Forest structure properties such as biomass and NPP (from data measured at the same 54 plots for individuals > 5 cm DBH), as well as organic matter stocks and litterfall were compared to the averages and confidence intervals (CI) measured in the field (Wilcke *et al.*, 2002; Wolf *et al.*, 2011; Leuschner *et al.*, 2013; Velescu & Wilcke, 2017a,b; Velescu *et al.*, 2020b; Homeier & Leuschner, 2021). Additionally, we collected soil samples and determined the 1 M KCl-extractable mineral N concentrations of ammonium (NH_4–N) and nitrate (NO_3–N) for three soil profiles in Oi, Oe and Oa horizons on each of the permanent 1 ha old-growth forest plots, which we used for model evaluation of plant-available soil N stocks (Table S2). The data are available from the FOR2730 data warehouse (Velescu *et al.*, 2020a,b,c), and details of the sampling and chemical analysis are included in Notes S3.

Modeling protocol

Except for the climatic driving variables, LPJ-GUESS-NTD was applied with the same parameters for all three elevations (Table S1), meaning differences in emerging ecosystem properties in the model results were exclusively attributable to the climatic gradient. The full range of observed SLA and WSG values (SLA = 15.5–273.5 $cm^2\ g^{-1}$; WSG = 0.158–1.02 $g\ cm^{-3}$, Table S1) were also the same for all elevations, as we assume that dispersal limitation or differential recruitment are not relevant here, and the elevational gradient in community traits should emerge in the model via competition between plant individuals for resources. Thus, in our model mortality is the main selection mechanism for community assembly. The mean soil texture is predominantly a silty loam across the study area and is therefore fixed across all elevations, having sand and clay fraction contributions of 28% and 12% respectively (Wolf *et al.*, 2011).

The Lund-Potsdam-Jena General Ecosystem Simulator was simulated for 700 yr, with the first 500 yr as spinup from bare ground and the last 200 yr being used for the analysis of results.

The trait-based approach reduces the need for a detailed local calibration since many parameter values which were previously fixed and could be candidates for calibration are now varying and defined by ecological filtering (through competition for resources). We chose not to carry out additional local calibration of the remaining fixed parameters for multiple reasons: we want to keep the model as broadly applicable as possible so that in future it can be applied on a larger spatial scale; we wanted to test the validity of this potential future application by observing how well the generalized parameters fare at the local scale; and our focus here is not on achieving the best fit but rather on evaluating the effect of nutrient limitation on community assembly within a general and robust modeling framework.

The model was set up in three different configurations in order to test the effect of trait diversity and nutrient limitation on community trait assembly: NTD, nutrient limitations on and trait variation on (with different traits for each woody individual; see 'Trait variation' in Material and Methods section); Nlim-OFF, N and P limitations off but with trait variability on; and TraitVar-OFF, trait variability deactivated but with nutrient limitations on. In this last scenario, SLA and WSG were fixed to the average values observed in the field (SLA = 82.5 $cm^2\ g^{-1}$, WSG = 0.56 $g\ cm^{-3}$). Nutrient limitations were de-activated by using photosynthesis equations in the model which did not depend on leaf N or P concentrations. For the NTD and the Nlim-OFF scenario, 30 replicate runs were executed, changing the sequence of randomly drawn values of SLA and WSG. In order to test the model's power to filter and predict SLA and WSG distributions, we also conducted an additional simulation set in which SLA and WSG min–max ranges were expanded to SLA = 5.0–350 $cm^2\ g^{-1}$; WSG = 0.1–1.6 $g\ cm^{-3}$. To test the role of mycorrhiza-mediated plant nutrient uptake in model performance, we compared NTD model runs with deactivated mycorrhiza-mediated plant nutrient uptake (AMF-OFF). Finally, to evaluate the impact of individual climatic drivers in driving trait shifts, we ran a climatic sensitivity analysis on the three elevation sites with the whole gradient of average temperature, precipitation and radiation values, and then compared this average simulation to additional runs in which only one of each driver was allowed to vary (single run per site and driving factor).

Results

Model predictions along the elevational gradient

Although all three simulated sites were initialized with the same range of SLA and WSG values, the simulated trait frequency distributions with nutrient limitation diverged across the elevation gradient after 700 simulated years and averages corresponded well to the observed SLA and WSG community trait values (Fig. 2a,b). Means of SLA only differed between the NTD simulations and observations for the 3000 m asl site, and not for the others (1000 m asl: Wilcoxon test, $W = 83\ 867\ 874$, P-value = 0.07; 2000 m asl: $W = 213\ 175\ 160$, P-value = 0.11). Simulated WSG differed for all observations except the 1000 m asl site ($W = 143\ 291\ 518$, P-value = 0.076), but like the field data increased with elevation. The shape of the distributions for SLA and WSG were similar to – but for most elevation ranges, wider

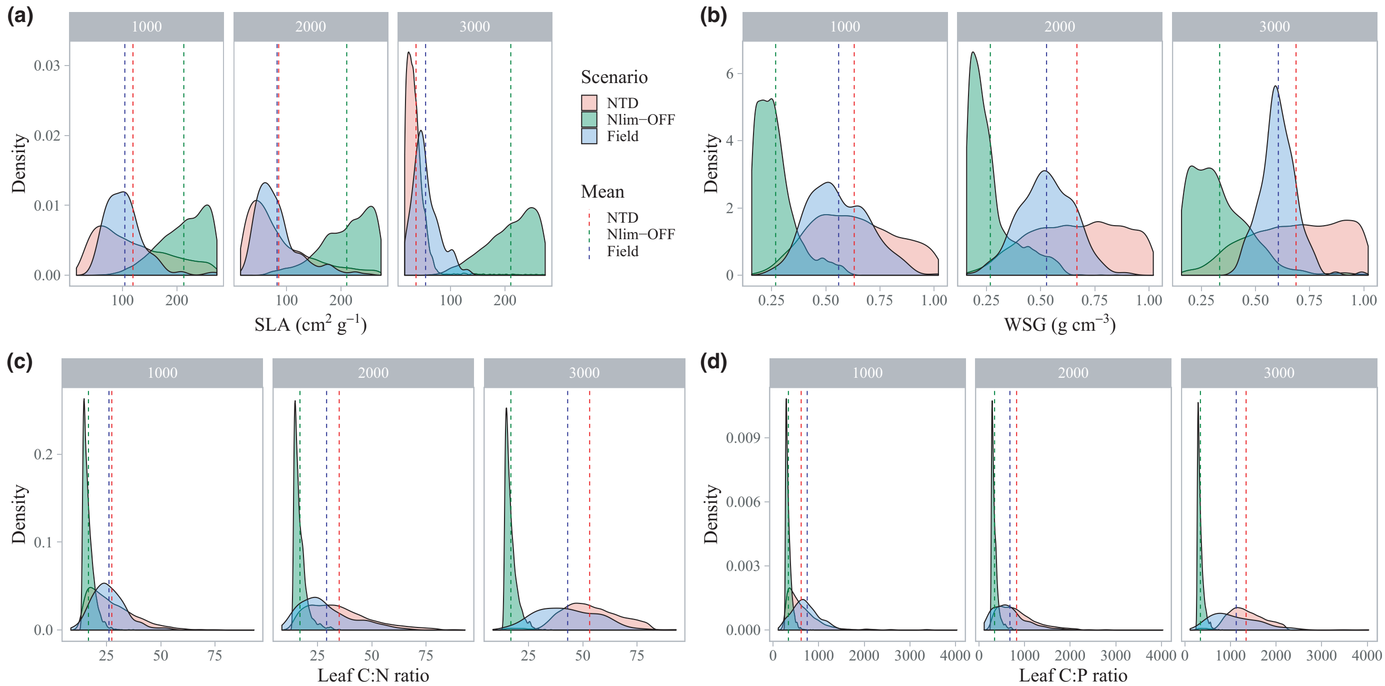

Fig. 2 Simulated and observed community trait frequencies for (a) specific leaf area (SLA), (b) wood specific gravity (WSG), (c) mass-based carbon to nitrogen concentration ratio (C : N) and (d) carbon to phosphorus (C : P) concentration ratio in leaves along the elevational gradient (1000, 2000 and 3000 m asl). Scenarios refer to the Nutrient-Trait-Dynamics mode (NTD); nutrient limitation off, trait variation on (Nlim-OFF) and field observations.

than – those of the field data, as inferred from the inter-quartile range values (Table S3). Accordingly, leaf C : N and C : P ratios, which were related to SLA based on field observations, also exhibited good agreement to field data (Fig. 2c,d). The C : N ratios in leaves at 1000 m asl did not differ significantly between the NTD scenario and field data (W = 123 792 496, P-value = 0.705). Increasing the range of randomized SLA and WSG values did not produce different results, with the exception of the WSG values for the 3000 m asl site, which filtered towards even higher values (Fig. S2). The increased range also did not affect biomass or productivity (Fig. S3). The results from the climatic sensitivity simulations show clearly that the runs with varying temperature have by far the greatest effect on shifting SLA and other traits from the average. Precipitation simulations have little or no effect on traits or productivity, and radiation has an effect on productivity, but not on traits (Fig. S4).

Model results with nutrient limitation fit in the observed confidence interval for vegetation C mass at 1000 m asl, though the model overestimated the vegetation C stock at 2000 m asl and underestimated it at 3000 m asl (Fig. 3a). Net primary production fitted best for the 2000 and 3000 m asl sites (Fig. 3b). In particular, the new implementation of the leaf/fine root allocation improved the fit to field measurements of leaf/fine root ratios (Fig. S5). The average number of simulated individuals with DBH > 5 cm ranged from 544 (± 23 SD) per hectare at the lowest 1000 m asl site to 1121 (± 33 SD) per hectare at the highest 3000 m asl site.

Simulated soil inorganic N stocks fell within the observed confidence intervals for the 1000 m asl and 2000 m asl sites, decreasing with elevation and indicating that the soil organic matter dynamics simulated correctly the nutrient limited environment (Fig. S6a). This is also confirmed by the results on nutrient return to the soil through litter fall, for which N and P fell within the confidence intervals for all sites (Fig. S6b,c). Modeled nutrient-use efficiency increased with elevation, which is consistent with observations, but declined with elevation when trait variability was deactivated in the TraitVar-OFF scenario (Fig. 4). This suggests, unsurprisingly, that fixing the traits results in communities less adapted to the nutrient-limited environments. Nitrogen fixation was higher than the observations, at *c.* 6 kg $\mathrm{ha^{-1}\ yr^{-1}}$ N. However, using prescribed field measured N_2-fixation values for the simulations had no significant impact on the results (Fig. S7).

Role of nutrient limitation, trait diversity and mycorrhizas for model results

The model only reproduced the elevational gradient of trait distributions well when nutrient limitations were switched on (Fig. 2). The deactivation of nutrient limitation in the Nlim-OFF scenario had a strong effect on SLA and WSG distributions along the elevation gradient, eliminating the distinction between the communities among the three elevations and resulting in SLA and WSG values generally indicative of high productivity (high SLA and low WSG) and high mortality (low WSG). A similar pattern was observed for leaf stoichiometry (C : N and C : P ratios), driven by the tradeoffs with SLA in the model (Fig. 2c,d).

As expected, NPP was consistently higher in the Nlim-OFF scenario compared to the simulations with nutrient limitation

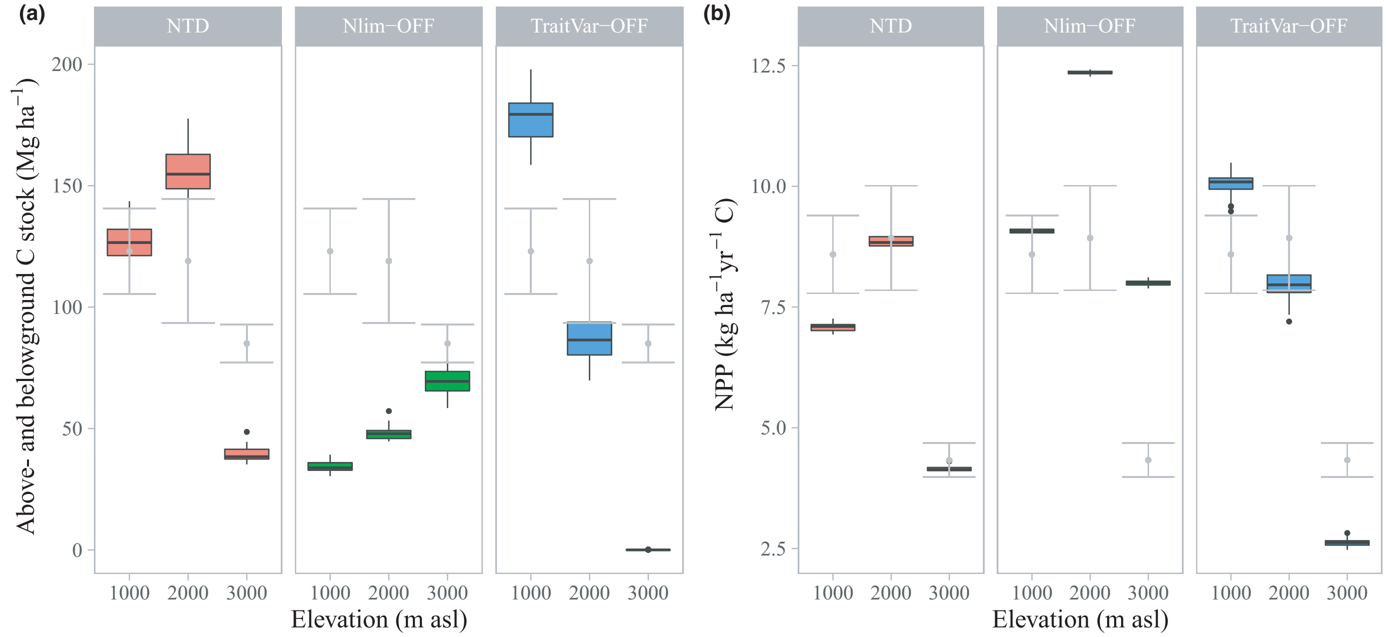

Fig. 3 Processes related to the carbon (C) cycle along the elevational gradient, (a) Above- and below-ground stocks and (b) net primary production (NPP). Grey lines indicate means and confidence intervals (n = 18 for each site) from field data (Leuschner *et al*., 2013). Scenarios refer to the Nutrient-Trait-Dynamics mode (NTD), nutrient limitation off, trait variation on (Nlim-OFF) and nutrient limitation on, trait variation off (TraitVar-OFF).

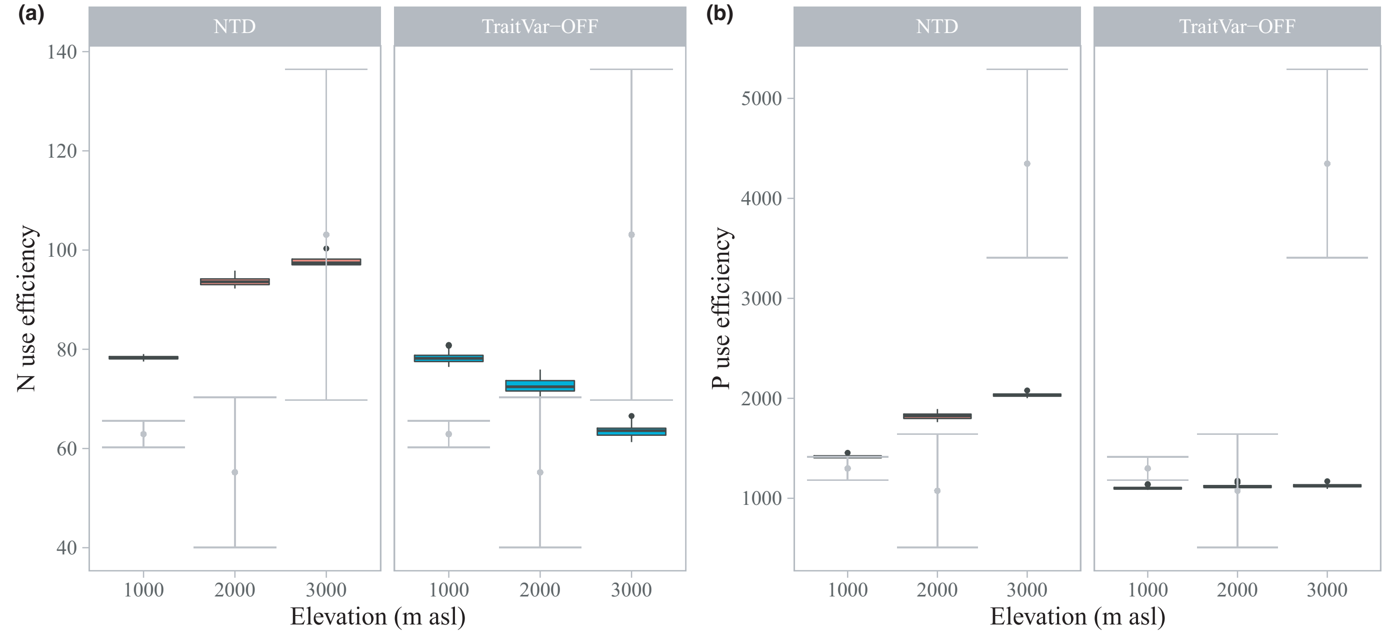

Fig. 4 Simulated (a) nitrogen (N) and (b) phosphorus (P) use efficiency (i.e. the ratio of leaf to litter nutrient concentration per total dry mass) along the elevation gradient. Scenarios refer to the Nutrient-Trait-Dynamics mode (NTD), nutrient limitation off, trait variation on (Nlim-OFF) and nutrient limitation on, trait variation off (TraitVar-OFF). A more rigorous definition of nitrogen use efficiency is net primary production (NPP) per nutrient uptake (e.g. Zaehle *et al*., 2014). However, measuring all components of NPP is challenging, and stem growth and litterfall are often used as proxies for important components of NPP (Chapin *et al*., 2011). Grey error bars indicate field measured averages and confidence intervals (n = 18 for each site); references are given in Supporting Information Table S2.

(Fig. 3b). By contrast, biomass for the Nlim-OFF scenario showed for most sites much lower values than the NTD (Fig. 3a). The low diversity scenario (TraitVar-OFF) on the other hand showed higher values of biomass and NPP than the NTD scenario at 1000 m asl, but lower values of biomass and NPP at 2000 m asl and particularly 3000 m asl. At 3000 m asl, fixing the traits to mean values drove the community to biomass values close to zero (0.035 Mg ha^{-1} C, Fig. 3a). When considering the

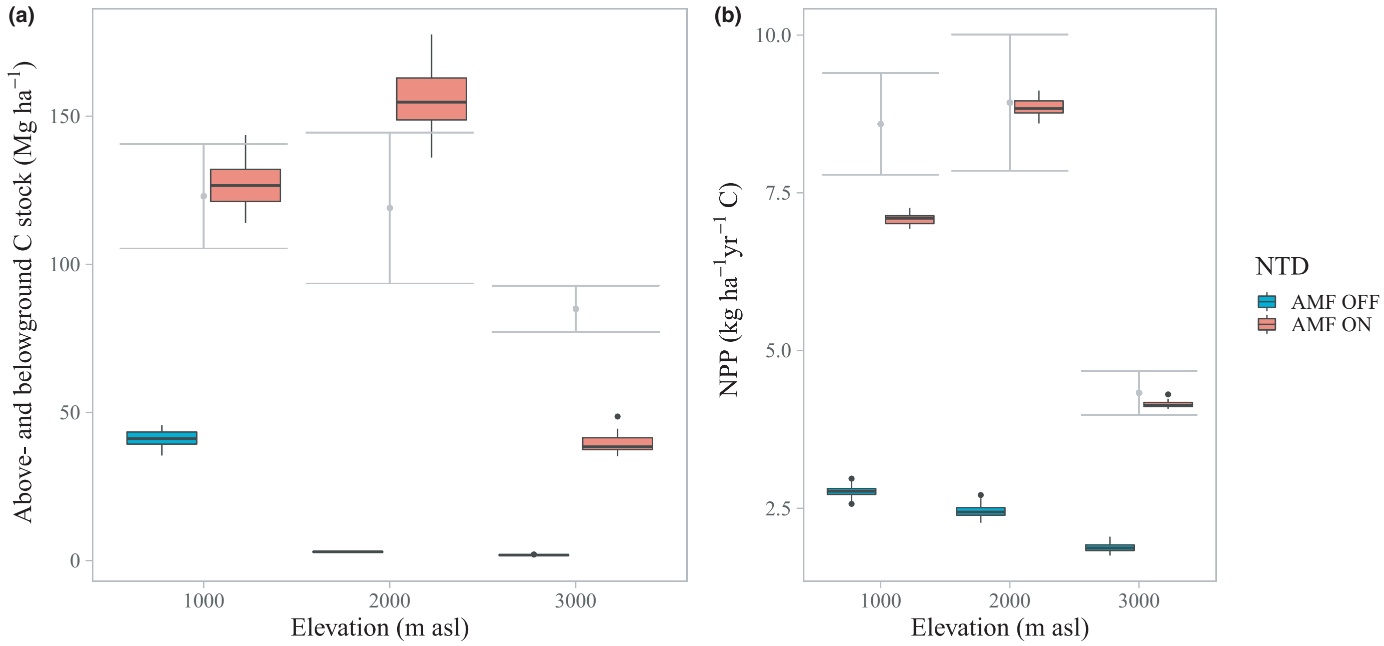

Fig. 5 Comparison of plant nutrient uptake mediated by arbuscular mycorrhizal fungi (AMF) ON and OFF in the model (Nutrient-Trait Dynamics (NTD) mode), and its effects on (a) tree biomass and (b) net primary production for the three study sites. Grey error bars indicate field measured averages and confidence intervals (n = 18 for each site); references are given in Supporting Information Table S2.

whole gradient range (1000–3000 m asl), we observed that average biomass in the NTD scenario was significantly higher than in the low diversity scenario (NTD: 108 Mg ha^{-1} C, TraitVar-OFF: 88 Mg ha^{-1} C, $W = 30\,333$, P-value = 0.02938). Net primary production on the other hand showed no significant differences between NTD and TraitVar-OFF averages for the whole range.

Arbuscular mycorrhiza fungi (AMF)-mediated plant nutrient uptake had a substantial impact on biomass and NPP. Deactivation of AMF uptake resulted in a reduction in average biomass of 68% (1000 m asl), 98% (2000 m asl) and 95% (3000 m asl) (Fig. 5a). Likewise, NPP was also reduced on average by 61% (1000 m asl), 72% (2000 m asl) and 55% (3000 m asl), as seen in Fig. 5(b). This makes sense since simulated total mycorrhiza-mediated plant uptake of nutrients (Fig. S8) accounted for up to 45% of the total N uptake and 57% of the total P uptake of plants.

Discussion

Importance of model implementations for the representation of plant traits and ecosystem processes

Plant trait diversity and nutrient limitation to growth are important drivers of ecosystem functioning and our implementation of these processes in new modules, which also considered the role of mycorrhizas for plant nutrition represents an important advance in our understanding of plant community assembly and in the development of DVMs. The scenario with trait variability and N and P cycling and limitations to plant growth (NTD) broadly reproduced the elevational gradient in plant community traits and ecosystem processes, such as NPP.

The good agreement with observations for the simulated SLA trait distribution (Fig. 2a), suggests that both habitat filtering (shift of the curve mean) and trait divergence due to competition (curve width) were realistically captured by the model. The increased curve width of the simulations may be caused by the large trait space from which the individuals are being recruited. More importantly, the reduction of variance with elevation in the nutrient-limited simulations is a sign of trait filtering, which is also observed in the field data, but was found not to be so relevant in the Nlim-OFF scenario (Table S3). Specific leaf area and traits related to it (Fig. 1) influence competition in particular for light and nutrients in the model. This result is consistent with an analysis of tree species' functional traits and co-occurrence in an Amazon forest. The results of this study suggested that SLA values and leaf N concentrations of co-occurring tree species differ more than expected without competition, exhibiting coexistence patterns observed in the field (Kraft *et al.*, 2008). For WSG, however, only the simulated trait means matched the observed shift across the elevational gradient, since the modeled spread was much wider than in the field data (Fig. 2b). This suggests that competition processes related to WSG and tree mortality are not yet adequately captured by LPJ-GUESS-NTD. This result is not surprising as WSG is strongly related to tree mortality in the model (as detailed in Notes S2), using an empirical relationship from two rainforest sites in Malaysia (King *et al.*, 2006), which might not apply to our study sites. Furthermore, WSG also often correlates with hydraulic traits (Poorter *et al.*, 2010; Langan *et al.*, 2017), which have not been accounted for in the present study.

The scenario without trait variability (TraitVar-OFF) was not able to reproduce field data as well as the high diversity version, since a single trait combination will invariably be more successful in a particular environment but become inefficient in others. According to the model, trait variation is particularly important for biomass and NPP at higher elevations (2000 and 3000 m asl). Substantial biomass at the 3000 m asl site was only simulated with trait variation (Fig. 3a). The nutrient uptake demand of individuals in the TraitVar-OFF scenario was simply too high at the 3000 m asl site, causing severe limitations to photosynthesis. This was not the case for the lowermost site (1000 m asl); conversely, however, the choice of more conservative fixed traits (i.e. lower SLA and higher WSG) would not be as productive as more acquisitive trait combinations in this less nutrient-limited environment. In any case, it is clear that an increase in nutrient use efficiency is a key factor behind improved vegetation productivity along the elevational gradient, a pattern which is observable in the field and in the NTD scenario. This pattern was not produced by the TraitVar-OFF setup which in fact showed a decrease in N use efficiency (Fig. 4).

It might seem counter-intuitive that the nutrient limited NTD scenario gave higher biomass values than the unlimited Nlim-OFF (Fig. 3a). However, this makes sense for multiple reasons: first, trees have higher WSG in the NTD scenario (Fig. 2) and trees with higher wood density will have more biomass than trees of the same size but with lower WSG (aboveground allometry relationships in the model are not affected by WSG); second, the higher WSG reduces growth-efficiency-related mortality and so allows trees to survive better under suboptimal conditions, reducing biomass turnover. A general feature of DVMs appears to be a simulated linear relationship between NPP and biomass, a feature at odds with globally derived empirical analyses which predict nonlinear relationships between the two (Keeling & Phillips, 2007). Potential explanations for this nonlinear relationship commonly involve the increasing dominance of light-demanding, fast-growing species (low wood density) as productivity increases (Baker *et al.*, 2004; Keeling & Phillips, 2007; Quesada *et al.*, 2012), whereby lower community-level wood density limits potential biomass storage (Keeling & Phillips, 2007). In a basin-wide study of Amazonian forest structure, Quesada *et al.* (2012) highlighted the role that nutrient availability may play in mediating growth rates and altering the balance of dominance between fast growing, low wood density species, and slow growing, high wood density species. Here the authors showed that as nutrient availability increased, so too did wood production and that, coincident with these increases, there were decreases in wood density, increases in tree turnover rates, and reductions in forest biomass. Indeed, field data from our study site also agrees with this pattern: a 7-yr fertilization experiment at the 2000 m asl elevation site showed no increase in tree aboveground biomass, because nutrient addition was more beneficial for low WSG species than for the high WSG species (Báez & Homeier, 2018). Our simulation results are in general agreement with the proposed mechanisms leading to the decoupling of NPP and biomass storage as well as with the empirical evidence presented by Quesada *et al.* (2012). In our simulated forest communities we show that the removal of nutrient limitation generally results in higher NPP, lower average wood densities, and higher mortality rates via the trade-off between wood density and growth mortality. These effects would not emerge without trait dynamics, and neatly illustrate that including trait diversity and filtering allows models to capture important but nonobvious controls of crucial properties such as the mechanisms leading to the decoupling of NPP and C in ways which fixed-trait models simply cannot (Sakschewski *et al.*, 2016).

Investigating the factors influencing community assembly and ecosystem processes

Including nutrient limitation in our simulations drove the filtered traits towards more conservative strategies with lower SLA and higher WSG at higher elevational sites. Lower SLA reduces leaf turnover and allows the plants to retain their limiting nutrients for longer, and higher WSG values decrease the mortality risk. This is consistent with the principles underpinning the leaf economic spectrum and wood economic spectrum (Wright *et al.*, 2004; Chave *et al.*, 2009). The activation of nutrient limitation to growth resulted in a change of the distribution of assembled plant community trait values (Fig. 2), confirming from a dynamic modelling perspective that such limitations play a crucial, and often overlooked, role in shaping highly diverse tropical mountain ecosystems (Kottke *et al.*, 2004; Homeier *et al.*, 2012; Werner & Homeier, 2015). This is in agreement with evidence from field research (Homeier *et al.*, 2012; Werner & Homeier, 2015), but the finding that the role of nutrient dynamics in the model is so strong was unexpected.

The much better model fit of the nutrient limitation ON scenario (NTD) suggests that community assembly is driven in our study area through nutrient cycling and soil processes and not vegetation processes. This has important implications for both future modeling and empirical studies, as the soil microbiome may be even more important for biodiversity and the carbon cycle than previously thought (van der Heijden *et al.*, 2008). Other trait-based modeling studies include SLA and WSG linked via trade-offs with other traits, but not detailed nutrient dynamics. Drivers such as precipitation, CO_2, soil depth and fire have been shown to affect community assembly (Scheiter *et al.*, 2013; Langan *et al.*, 2017). Trait data alone offer few clues as to what selection mechanisms affect community assembly and ecosystem properties. Here we have found that nutrient dynamics is the most important driving factor that has not been considered in similar trait-based DVM studies.

The changes in community trait distribution, especially for SLA, were ultimately driven by abiotic changes across the gradient, in particular temperature, as can be observed in the results from the climatic sensitivity (Fig. S4). Besides temperature, WSG was affected by radiation – this is not surprising since radiation has a strong effect on NPP, which in turn has an impact on growth efficiency mortality and the correlated WSG values. The lack of precipitation effects on community assembly is sensible since rainfall is not strongly growth-limiting at our study sites, as suggested by field measurements (Strobl *et al.*, 2017).

Waterlogging, however, which is known to restrict nutrient availability in tropical montane forests (Schuur & Matson, 2001; Roman *et al.*, 2011), may play an increasing role in nutrient dynamics with increasing elevation, due to reduced temperature and evapotranspiration.

Conversely, trait variation may also affect the environmental conditions which drive it. The implementation of trait diversity drives changes in litterfall stoichiometry (higher leaf C : N and C : P ratios, Fig. 3d,e), which otherwise would be fixed or highly invariant. The increased C and lower nutrient concentration of litterfall in turn reduces modeled decomposition further if immobilization of nutrients becomes larger than available N_i or P_i. This implies that our model may reproduce the positive feedbacks known to promote the spatial heterogeneity (i.e. increasing soil organic matter stocks with elevation) of tropical montane forests and, thereby, biodiversity (Werner & Homeier, 2015).

Role of mycorrhiza-mediated plant nutrient uptake

The importance of plant nutrient uptake via mycorrhizas in simulations is consistent with field observations for our study site in which fungal inoculation increased biomass of tree seedlings and reduced mortality rates even when compared to mineral fertilization (Urgiles *et al.*, 2009, 2014). Our implementation of mycorrhiza-mediated plant nutrient uptake is relatively simple compared to the multitude of associated processes occurring in the field, and compared to other modeling approaches (Orwin *et al.*, 2011; Allen *et al.*, 2020) which include the costs of root C exchange with the fungal symbionts and soil biota represented at the population level. However, our approach provides a simple mechanism for the coupling/uncoupling of roots and fungi since nutrient uptake by roots from mycorrhizas is increased when mineral sources are not sufficient (van der Heijden *et al.*, 2008).

Differences in AMF colonization rates might also be an important variation across the elevational gradient. In our simulations, the colonization rate was fixed at 39%. Local measurements indicate that average AMF colonization rates range from 22% at 1000 m asl to 49% at 3000 m asl (Camenzind, 2012), with even higher interspecific variability. This suggests that we underestimated the colonization rates for the highest site, which might explain why the model underestimated biomass stocks there due to excessive nutrient limitation. Future model developments in plant nutrient–trait dynamics should therefore account for root traits (e.g. specific root length and diameter) and a variable collaboration gradient with mycorrhizas (Bergmann *et al.*, 2020), which depending on environmental conditions may or not offer competitive advantages.

Therefore, our results highlight the important role that the collaboration of plants with microbes and fungi plays in tropical vegetation dynamics and the community assembly of highly diverse tropical mountain forests (Camenzind & Rillig, 2013; Camenzind *et al.*, 2018; Bergmann *et al.*, 2020). Accounting for these ‘hidden’ below-ground processes and interactions could greatly improve our understanding and predictions of current and future vegetation states.

Conclusions

Individually, both trait variation (Sakschewski *et al.*, 2016) and nutrient limitation (Wang *et al.*, 2010; Thum *et al.*, 2019) were already known to influence ecosystem processes, in particular biomass stocks and NPP. In this study however, the best simulation agreements with field data occurred when the implementations of both ecosystem properties were active, showing that the interaction between diversity and nutrient limitation is important for both the improved simulation of community trait compositions and ecosystem energy flows.

Elevation is generally thought to be the most important predictor of trait community assembly in mountain areas, in particular through the associated changes in temperature (Andersen *et al.*, 2012; Xu *et al.*, 2017). Our simulation results suggest that, at least in the tropical mountains of southern Ecuador, the main temperature effects occur through impacts on soil nutrient dynamics, since when plants are no longer limited by nutrient availability (Nlim-OFF scenario), trait filtering does not occur. This implies that increasing temperatures due to climate change have great potential to affect biodiversity and carbon storage (both in soil and vegetation) along the elevation gradient.

We have shown that the implementation of plant nutrient uptake via AMF crucially mediates simulated patterns of vegetation structure and trait distributions and improves agreement with observations. Removal of AMF uptake in the model resulted in a significant suppression of productivity in relation to field observations (Fig. 5). In agreement with empirical observations (Hodge & Storer, 2014), the plants satisfied a large part of their nutrient demand via mycorrhiza-mediated uptake, in particular of P (Fig. S8). Our representation of nutrient supply via mineralization of SOM and release from the microbial pool might be further improved by taking into account the diverse elements of the soil microbiome. A useful template for incorporating these elements into vegetation models is the MySCaN model by Orwin *et al.* (2011), which is also based on the CENTURY model but distinguishes between bacteria, fungi, mycorrhizal fungi, grazer and predator microbial pools. Decomposition rates of SOM may be strongly altered due to shifts in microbial community structure (McGuire & Treseder, 2010).

The results also have important implications for the development of dynamic vegetation models. While it is widely acknowledged that the representation of trait variability is crucial to addressing the role of biodiversity for ecosystem functioning in such models (Scheiter *et al.*, 2013; Fyllas *et al.*, 2017), realistic predictions might only be possible if interactions with nutrient dynamics are also accounted for (Hofhansl *et al.*, 2016; Zhu *et al.*, 2016; Camenzind *et al.*, 2018; Fleischer *et al.*, 2019a). Such developments become feasible as plant trait databases (Kattge *et al.*, 2020) increasingly include information on traits that are strongly linked with SOM dynamics, such as data on global patterns of leaf N and P concentrations (Walker *et al.*, 2014), half-saturation constants for nutrient uptake (Mulder & Hendriks, 2014), root related processes (Bergmann *et al.*, 2020; Guerrero-Ramírez *et al.*, 2020) and trait data (Pierick *et al.*, 2021).

A fourth axis of plant trait variation, which was not included here, is related to reproduction. This axis represents varying traits related to seed dispersal, establishment and mortality, such as diaspore size and number, light for germination and maximum attainable height (Díaz *et al.*, 2016). Including this axis could have important implications for our results, since changes in seed size distributions can, for example, have large impacts on forest biomass (Bello *et al.*, 2015; Donoso *et al.*, 2017). Representing all four axes (leaf, root, wood and reproductive economic spectrum) will be an important step towards finally achieving a better representation of functional biodiversity in DVMs.

Acknowledgements

We are grateful to the DFG (German Research Foundation) for funding this study in the scope of the Research Unit FOR2730 RESPECT, as well as the previous research units FOR 402 and 816 which contributed long-term data. We thank the Ecuadorian Ministry of Water and the Environment (MAAE) for the permission to conduct research, and to the foundation Nature and Culture International (NCI) for logistical support.

Author contributions

MDdP: design of the research; performance of the research; data analysis and interpretation; writing the manuscript. MF: design of the research; performance of the research; data analysis and interpretation; writing the manuscript. LL: design of the research; data analysis and interpretation; writing the manuscript. JB: performance of the research; data analysis and interpretation; writing the manuscript. JH: performance of the research; data analysis and interpretation; writing the manuscript. AV: data analysis, collection, and interpretation; writing the manuscript. WW: data analysis, collection, and interpretation; writing the manuscript. TH: design of the research; performance of the research; data analysis and interpretation; writing the manuscript.

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Data availability

All field data referenced and collected for this work are available for download at the FOR2730 data warehouse, which is accessible at http://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?cmd=showall.

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Supporting Information

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

Fig. S1 Trait–trait relationships used in the Lund-Potsdam-Jena General Ecosystem Simulator with nutrient-trait dynamics (LPJ-GUESS-NTD) trait variability module, fitted using power laws.

Fig. S2 Expanded trait range simulated and observed community trait frequencies.

Fig. S3 Expanded trait range results for processes related to carbon (C).

Fig. S4 Climatic sensitivity analysis varying, in turn, temperature, precipitation and radiation.

Fig. S5 Modeled results of the leaf : fine root biomass ratio.

Fig. S6. Simulation results of the soil inorganic nitrogen (N) stocks and litter nutrient returns of N and phosphorus (P).

Fig. S7 Simulated trait distributions comparing the standard LPJ-GUESS N-fixing approach to the prescribed N-fixation approach.

Fig. S8 Proportional mycorrhiza-mediated plant nutrient uptake in relation to direct plant nutrient uptake.

Notes S1 Competition and selection mechanisms of LPJ-GUESS and LPJ-GUESS-NTD.

Notes S2 Further modifications of LPJ-GUESS.

Notes S3 Soil sampling and chemical analyses.

Table S1 New parameters implemented into LPJ-GUESS-NTD.

Table S2 Reference values taken from field and laboratory measurements.

Table S3 Summary statistics of the simulated and observed trait distributions.

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