Community dynamics of soil-borne fungal communities alongelevation gradients in neotropical and palaeotropical forests

József Geml, Anne Elizabeth Arnold, Tatiana A. Semenova-Nelsen, Eduardo R. Nouhra, Elisandro R. Drechsler-Santos, Aristóteles Góes-Neto, Luis N. Morgado, Péter Ódor, Balázs Hegyi, Grau Oriol, Alicia Ibáñez, Leho Tedersoo, François Lutzoni

DOI:
https://doi.org/10.1111/mec.16368

Received: 4 March 2020 | Revised: 28 December 2021 | Accepted: 18 January 2022

DOI: 10.1111/mec.16368

ORIGINAL ARTICLE

MOLECULAR ECOLOGY WILEY

Community dynamics of soil-borne fungal communities along elevation gradients in neotropical and palaeotropical forests

József Geml[1,2] | Anne Elizabeth Arnold[3] | Tatiana A. Semenova-Nelsen[2] | Eduardo R. Nouhra[4] | Elisandro R. Drechsler-Santos[5] | Aristóteles Góes-Neto[6] | Luis N. Morgado[2,7] | Péter Ódor[8] | Balázs Hegyi[9,10] | Grau Oriol[11,12,13] | Alicia Ibáñez[3] | Leho Tedersoo[14] | François Lutzoni[15]

[1]ELKH-EKKE Lendület Environmental Microbiome Research Group, Eszterházy Károly Catholic University, Eger, Hungary

[2]Biodiversity Dynamics Research Group, Naturalis Biodiversity Center, Leiden, The Netherlands

[3]School of Plant Sciences and Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA

[4]Multidisciplinary Institute of Plant Biology (IMBIV), CONICET, FCEFyN, National University of Córdoba, Córdoba, Argentina

[5]Laboratory of Mycology, Federal University of Santa Catarina, Florianópolis, Brazil

[6]Department of Microbiology, Federal University of Minas Gerais, Belo Horizonte, Brazil

[7]Department of Biosciences, Faculty of Mathematics and Natural Sciences, University of Oslo, Oslo, Norway

[8]Centre for Ecological Research, Institute of Ecology and Botany, Vácrátót, Hungary

[9]Research and Development Centre, Eszterházy Károly Catholic University, Eger, Hungary

[10]Doctoral School of Earth Science and Department for Landscape Protection and Environmental Geography, University of Debrecen, Debrecen, Hungary

[11]CREAF, Global Ecology Unit, Cerdanyola del Vallès, Spain

[12]Cirad, UMR EcoFoG (AgroParisTech, CNRS, Inra, Univ. Antilles, Univ. Guyane), Kourou, French Guiana

[13]Spanish National Research Council (CSIC), Global Ecology Unit, CREAF-CSIC-UAB, Cerdanyola del Vallès, Spain

[14]Mycology and Microbiology Center, University of Tartu, Tartu, Estonia

[15]Department of Biology, Duke University, Durham, North Carolina, USA

Correspondence
József Geml, ELKH-EKKE Lendület Environmental Microbiome Research Group, Eszterházy Károly Catholic University, Leányka u. 6, H-3300 Eger, Hungary.
Emails: jozsef.geml@gmail.com; geml.jozsef@uni-eszterhazy.hu

Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 311158/2018-8; SECYT Universidad Nacional de Córdoba, Grant/Award Number: 124/13, 162/12 and 26/11; National Science Foundation, Grant/Award Number: DEB 1541548 and DEB-1541496; Fundação de Amparo à Pesquisa e Inovação do Estado de Santa Catarina, Grant/Award Number: 2018TR0928; Magyar Tudományos Akadémia, Grant/Award Number: Lendület 96049; CNPq/Capes/FAPs/BC-Fundo Newton/PELD, Grant/Award Number: 15/2016

Abstract

Because of their steep gradients in abiotic and biotic factors, mountains offer an ideal setting to illuminate the mechanisms that underlie patterns of species distributions and community assembly. We compared the composition of taxonomically and functionally diverse fungal communities in soils along five elevational gradients in mountains of the Neo- and Palaeotropics (northern Argentina, southern Brazil, Panama, Malaysian Borneo and Papua New Guinea). Both the richness and composition of soil fungal communities reflect environmental factors, particularly temperature and soil pH, with some shared patterns among neotropical and palaeotropical regions. Community dynamics are characterized by replacement of species along elevation gradients, implying a relatively narrow elevation range for most fungi, which appears to be driven by contrasting environmental preferences among both functional and taxonomic groups. For functional groups dependent on symbioses with plants (especially ectomycorrhizal fungi), the distribution of host plants drives richness and community composition, resulting in important differences in elevational patterns between neotropical and palaeotropical montane communities. The pronounced

compositional and functional turnover along elevation gradients implies that tropical montane forest fungi will be sensitive to climate change, resulting in shifts in composition and functionality over time.

KEYWORDS
altitudinal zonation, cloud forests, DNA metabarcoding, ITS, soil microbiome

1 | INTRODUCTION

Montane ecosystems generally are recognized as biodiversity hotspots as well as areas of high endemism (Lomolino, 2001). Despite representing about one-eighth of the world's land area outside Antarctica, mountains harbour about one-third of all terrestrial species (Antonelli, 2015; Spehn et al., 2012). Since the early scientific studies of Darwin, Wallace and von Humboldt on mountain biota, documentation of changes in species richness and community composition have been central to ecological and biogeographical studies (Lomolino, 2001; McCain & Grytnes, 2010). Mountains provide unique opportunities to test various ecological hypotheses, such as those relevant to climate change, as they are characterized by gradients of abiotic factors such as temperature and available moisture (Guo et al., 2013). However, in most organismal groups, we lack answers to fundamental questions regarding diversity, distributional patterns and community composition in montane systems (Guo et al., 2013; Lomolino, 2001; Perrigo et al., 2020).

Numerous abiotic factors that shape biological communities change more or less predictably with increasing elevation. Among these, temperature is the most predictable, with an average decrease of ~0.6°C per 100 m increase in elevation (Barry, 2008). In contrast, changes in precipitation along elevation gradients generally are less predictable due to complex relationships of regional climate and topography (Barry, 2008). In mid- and high latitudes, precipitation tends to increase with elevation, whereas tropical mountains typically show little variation in rainfall along an elevation gradient or exhibit a moderate midelevation peak (McCain & Grytnes, 2010). Related environmental factors vary with temperature and precipitation to determine biological productivity, including solar radiation, cloud cover, edaphic properties, as well as habitat surface area due to geometric constraints (Rosenzweig, 1995; Stevens, 1992). Because organisms occupy niches along elevation gradients according to their physiological requirements and their interactions with other species, changes in community composition with increasing elevation have been a focal point for ecological and evolutionary research, providing insight into spatial patterns of biodiversity and their underlying mechanisms.

On a global scale, most studies of species richness along elevation gradients have focused on vascular plants and animals (e.gCardelús et al., 2006; Ghalambor et al., 2006; Grau et al., 2007; Grytnes et al., 2008; Liew et al., 2010; Nor, 2001; Parris et al., 1992; Wood et al., 1993). Fungi represent one of the largest groups of living organisms with key roles in the functioning of ecosystems. Several studies have been conducted in mountains in temperate regions on the distribution of specific fungal functional groups along elevation gradients: phyllosphere fungi (Coince et al., 2014; Cordier et al., 2012), bryophyte-associated fungi (Davey et al., 2013), wood-inhabiting fungi (Meier et al., 2010), arbuscular mycorrhizal (AM) fungi (Gai et al., 2012), foliar endophytes (Bowman & Arnold, 2018; Siddique & Unterseher, 2016) and ectomycorrhizal (ECM) and other root-associated fungi (Bahram et al., 2012; Bowman & Arnold, 2018; Bueno et al., 2021; Coince et al., 2014; Javis et al., 2015; Miyamoto et al., 2014; Nouhra et al., 2012; Rincón et al., 2015; Schön et al., 2018; Truong et al., 2019). On the other hand, species richness and composition of fungal communities in tropical mountains remain scarcely known. There have been a few studies on fungi along tropical elevational gradients based on sporocarps (Gómez-Hernández et al., 2012; Rojas-Jimenez et al., 2016; Shearer et al., 2015) or environmental DNA (Geml, 2017; Geml et al., 2014, 2017; Merckx et al., 2015; Oita et al., 2021), each mostly limited to one region of interest. Despite these important advances, we still lack a synthetic view of the ways in which species richness and composition of fungal communities shift with elevation: are similar factors important for different functional guilds and for montane systems in neotropical and palaeotropical forests? This gap in our knowledge seems particularly concerning because fungi are major drivers of the diversity and composition of plant communities in tropical forests (e.g., Bagchi et al., 2014) and because fungi, through their interactions with plants, contribute to ecosystem services such as the provision of clean water, food and air (Bakker et al., 2019).

In this study, we compared the community composition and richness of diverse functional groups of fungi in forest soils along elevation gradients in five tropical mountain areas: Andean Yungas in northwestern Argentina, Atlantic Forests in southern Brazil, Central American forests in western Panama, Bornean forests in Sabah, Malaysia, and Oceanian forests in Papua New Guinea. The aims of this work were to (i) assess the compositional dynamics of soil fungal communities along elevational gradients in neotropical and palaeotropical mountains; (ii) compare elevation patterns of richness in taxonomic and functional groups of fungi in tropical montane systems; and (iii) evaluate the possible influence of climatic and edaphic factors on fungal community composition in tropical mountains.

We hypothesized that elevation gradients would primarily structure fungal communities through changes in temperature and to a smaller extent in precipitation and via their effects on soil edaphic variables and plant community composition. Fungal richness and distribution on a global scale are strongly influenced by mean annual

temperature (MAT), mean annual precipitation (MAP), soil pH and, in the case of ECM fungi, by the diversity and abundance of host plants (Tedersoo et al., 2014; Větrovský et al., 2019). Therefore, we expected MAT, MAP and soil pH to be the strongest drivers of fungal community composition along the sampled elevation gradients irrespective of geographical region (Hypothesis 1). We also hypothesized that elevational patterns of composition would differ among functional groups, reflecting different environmental optima corresponding to distinct life strategies and resulting in proportional differences of functional groups in the community among elevation zones (Hypothesis 2). For example, given the high turnover of plant community with increasing elevation in tropical mountains (McCain & Grytnes, 2010), we expected that fungi intimately associated with plants, such as ECM, plant pathogens, root-associated fungi and wood decomposers, would be affected more strongly by elevation than those with indirect associations with plants (i.e., animal pathogens, mycoparasites and generalist saprotrophs). As a result, we predicted greater changes in richness and community composition for plant-associated fungi along the elevation gradients (Hypothesis 2a). Finally, we expected negative relationships between elevation and species richness of animal pathogens, plant pathogens, wood decomposers and generalist saprotrophs due to higher host and substrate richness at low to midelevations (McCain & Grytnes, 2010; Nouhra et al., 2018; Rahbek, 2005) and more energy available for decomposition (Hypothesis 2b).

2 | MATERIALS AND METHODS

We analysed data from five data sets corresponding to three Neotropical and two Palaeotropical regions. Elevation, localities, geographical coordinates and environmental variables of the sampling sites are shown in Table S1 and on maps corresponding to the five sampling regions (Figures S1–S5). Three of these are new data sets prepared for this paper, i.e., data from Brazil, Panama and Malaysian Borneo, except for a small subset of the data representing ECM fungi from Malaysian Borneo published by Geml et al. (2017). These were combined with the Yungas data set from northwestern Argentina from Geml et al. (2014), which is re-analysed here. In addition, from the global study of Tedersoo et al. (2014), we extracted sequences and distribution data of fungal operational taxonomic units (OTUs) from selected Papua New Guinea sites representing lowland, lower montane and upper montane forest. For these, we provide an updated functional assignment and novel analyses as detailed below.

In Argentina, the Yungas comprise tropical and subtropical humid montane forests on the eastern slopes of the Andes, which are influenced by orographic rains. The flora and fauna of the Yungas have been relatively well studied and are very diverse and rich in endemics (e.g., Blake & Rougés, 1997; Brown et al., 2001; Lavilla & Manzano, 1995; Ojeda & Mares, 1989). Together with adjacent, seasonally dry piedmont forests, the Yungas constitute the southern limit of the Amazonian biogeographical domain (Cabrera, 1976; Prado, 2000). Forests in this region are classified into three major elevational types: piedmont forest, montane forest and montane cloud forest (Brown et al., 2001, 2005). In Brazil, we focused on the Atlantic Forest biome, a world-renowned biodiversity hotspot. We sampled the southern Atlantic Forest, where at least two recognized biogeographical subregions can be found: wet coastal forests and high-elevation mixed temperate forests characterized by *Araucaria angustifolia* (Neves et al., 2017; Ribeiro et al., 2011; Veloso, 1992). Panama and neighbouring countries in Central and South America represent a biodiversity hotspot that is one of the richest in the world. With respect to trees alone, at least 2300 species are known to occur in Panama (Condit et al., 2011). The Caribbean side of the isthmus and the central mountains receive more than 3000 mm precipitation per year. The Pacific side tends to be somewhat drier, but there is greater regional variation in rainfall, resulting in a mosaic of wet (>3000 mm per year), moist (1500–3000 mm per year) and dry (<1500 mm per year) forests (Condit et al., 2011). From Southeast Asia to Oceania, the tallest mountains are found in Borneo and Papua New Guinea: Mt Kinabalu (4095 m asl) in Malaysian Borneo and Mt Wilhelm (4509 m) in Papua New Guinea. These reach above the tree line, encompassing a full elevation gradient of forests. The vegetation of Borneo and Papua New Guinea generally is described as lowland forests, lower montane forests and upper montane forests (Beaman & Anderson, 2004; Beaman & Beaman, 1990; Hope, 1976; Kitayama, 1992).

2.1 | Sample collection and molecular analyses

Soil samples were collected in 2011 and 2013 in Jujuy, Salta and Tucumán provinces of Argentina; in 2016 in Santa Catarina, Brazil, and in Bocas del Toro, Chiriquí, Colón and Panamá provinces of Panama; in 2012 in Sabah, Malaysian Borneo; and in 2011 in the Eastern Highlands and Morobe provinces of Papua New Guinea. The sampling sites represent the entire elevation range of forests in the respective regions.

In Argentina, Brazil and Borneo, 40 soil cores, 2 cm in diameter and ~20 cm deep, were taken at each sampling site (~10 × 25 m) after carefully removing the litter layer. Cores were collected ~2 m from each other to minimize the probability of sampling the same genet repeatedly. In Panama, 10 soil cores of the above dimensions were collected in each site (~4 × 5 m). In Papua New Guinea, 40 soil samples were taken from a circular area of ~2500 m^2 (for details, see Tedersoo et al., 2014). Soil cores taken at a given site were pooled, resulting in a composite soil sample for each site. For samples collected in Argentina, Brazil and Panama, ~20 g of each sample was kept frozen until lyophilization ~2 weeks later. For samples collected in Borneo, and Papua New Guinea, the more remote location and lack of laboratory equipment in the field led us to air-dry samples immediately at 25–35°C. Because differences in field preservation of soils is expected to have limited effect on the fungal community composition (Castaño et al., 2016; Delavaux et al., 2020), we regard the data set as being representative for each sampled area. However, because of the differences in sampling design and field

preservation, we conservatively chose to conduct statistical analyses for each region separately. We consider the total number of OTUs to be of relatively marginal importance, as our main goal was to observe and compare trends in richness and community composition among elevation zones and regions.

For the newly generated data from Brazil, Panama and Borneo, we used the same protocol used previously for the Argentinian samples, which are described in detail in Geml et al. (2014). Namely, genomic DNA was extracted from 0.5 g of dry soil from each sample with the NucleoSpin soil kit (Macherey-Nagel Gmbh & Co., Düren, Germany) according to manufacturer's protocol. For each sample, two independent DNA extractions were carried out and the extracts were pooled. We used 1 μl of DNA template with DNA concentration normalized for all samples from that region and followed the PCR (polymerase chain reaction) and sequencing methodology in Geml et al. (2014). The ITS2 region (~250 bp) of the nuclear ribosomal DNA repeat was amplified via PCR with primers fITS7 (Ihrmark et al., 2012) and ITS4 (White et al., 1990). The ITS4 primer was labelled with sample-specific Multiplex Identification DNA-tags (MIDs). The amplicon libraries were normalized for the quantity of DNA and were sequenced at Naturalis Biodiversity Center (Naturalis) with an Ion 318 Chip and an Ion Torrent Personal Genome Machine (Life Technologies). Chemical analyses of soil samples from Argentina, Borneo and Papua New Guinea were carried out as described in Geml et al. (2014), Geml et al. (2017), and Tedersoo et al. (2014), respectively. Samples from Brazil and Panama were analysed by the Empresa de Pesquisa Agropecuária e Extensão Rural de Santa Catarina and the Instituto de Investigación Agropecuaria de Panamá, respectively. Climate data were obtained from the WorldClim database (www.worldclim.org) based on the geographical coordinates of the sampling sites.

2.2 | Bioinformatics

Sequences were sorted according to samples, and adapters (identification tags) were removed in GALAXY (https://main.g2.bx.psu.edu/root). Primer sequences were removed and poor-quality ends were trimmed based on a 0.02 error probability limit in GENEIOUS PRO 5.6.1 (BioMatters). Sequences were filtered with USEARCH version 8.0 (Edgar, 2010) with the following settings: all sequences were truncated to 200 bp and sequences with expected error >1 were discarded. For each sample, identical sequences were collapsed into unique sequence types while preserving their counts. The quality-filtered sequences from all samples were grouped into OTUs at 97% sequence similarity in USEARCH, and global singletons and putative chimeric sequences were removed. We assigned sequences to taxonomic groups based on pairwise similarity searches against the curated UNITE + INSD fungal ITS sequence database (version August 22, 2016), containing identified fungal sequences with assignments to Species Hypothesis groups based on dynamic similarity thresholds (Kõljalg et al., 2013). We excluded OTUs with <80% similarity or <150-bp pairwise alignment length to a fungal reference sequence. To minimize artefactual OTUs that may have been generated during the molecular work, in subsequent analyses we only included OTUs that occurred in at least two samples.

We assigned fungal OTUs to putative functional guilds using the curated FungalTraits database (Põlme et al., 2020). We recognize the limitations of functional inference based on partial ITS sequences, and here use these guilds as hypothetical functional groups. For the statistical analyses, we focused only on the functional groups with a relatively high number of OTUs. Although AM fungi are ecologically important in tropical forests as symbiotic partners of most trees as well as diverse nonwoody plants, we were only able to analyse their composition in three regions, because their number of OTUs were too low for comparison in data from Brazil and Papua New Guinea. This may partly be caused by primer bias or by the above-mentioned sampling differences among regions. Overall, functional assignments were made for 66.76% ± 6.2% of fungal OTUs obtained in our study. The quality-filtered data set contained 8720, 2828, 4498, 7829 and 4305 fungal OTUs in the samples from Argentina, Brazil, Panama, Borneo and Papua New Guinea, of which 5917, 1698, 2896, 5078 and 3301 OTUs were assigned to functional groups, respectively. Sequence data corresponding to the study regions have been deposited at DDBJ/EMBL/GenBank as Targeted Locus Study projects under accessions KDPX00000000 (Argentina), KEXW00000000 (Brazil), KDPY00000000 (Borneo) and KDPZ00000000 (Panama). The versions described in this paper are the first versions, namely KDPX01000000, KEXW01000000, KDPY01000000 and KDPZ01000000, respectively. The OTU sequences for the Papua New Guinea samples can be downloaded from Tedersoo et al. (2014).

2.3 | Statistical analyses

All analyses were done in the R 3.6.3 statistical environment (R Core Team, 2020). For each biogeographical region, we normalized the OTU table for subsequent analyses by rarefying the number of high-quality fungal sequences per sample to the smallest library size in that region (14,241 reads for the Argentinian Yungas, 7442 for Brazil, 2000 for Panama, 24,812 for Borneo and 1441 for Papua New Guinea). Rarefying data, while sometimes problematic in microbial surveys (e.g., McMurdle & Holmes, 2014), was appropriate in this case because our analyses do not centre on comparing relative abundance of OTUs among regions. In each geographical region, OTU richness, proportional richness and proportional abundance of functional groups were tested for correlation with elevation using quadratic regressions.

To compare community composition along the sampled elevation gradients, we used the *vegan* package (Oksanen et al., 2015) to run global nonmetric multidimensional scaling (GNMDS) ordinations on the Hellinger-transformed abundance table and a secondary matrix containing environmental variables mentioned above. Ordinations were run separately for functional groups as well as for all fungi in each geographical region with the *metaMDS* function,

which uses several random starts to find a stable solution. Data were subjected to 999 iterations per run with the Bray–Curtis distance measure. Pearson correlation coefficient (*r*) values and statistical significance between environmental variables and fungal community composition were calculated with the *envfit* function, and vectors of variables with statistically significant correlations were plotted in ordinations. Environmental variables included were MAT, MAP, soil pH, soil organic matter content (OM), soil nitrogen content (N), soil carbon to nitrogen ratio (C/N) and soil phosphorus content (P). We plotted isolines of elevation on the GNMDS ordinations with the *ordisurf* function.

We estimated the relative importance of environmental (continuous) variables as sources of variation in fungal community composition by permutational multivariate analysis of variance (PERMANOVA) for all fungi and each functional group with the *adonis* function in *vegan*. Statistical tests of the equality variances via the *betadisper* function indicated no significant difference in multivariate homogeneity of group dispersions in any region. To account for correlations among environmental variables, we performed a forward selection of parameters, including only significant environmental variables in the final model. In addition, we used partial Mantel tests in *vegan* to differentiate the effects of spatial distance and abiotic environmental variables, standardized with the *scale* function, on community composition.

To better understand the roles of replacement (i.e., the substitution of a species by a different one) and nestedness (where a poor community is the strict subset of a richer one) in community dynamics along the elevation gradients, we used Sørensen dissimilarity as total beta diversity and estimated the replacement (Simpson dissimilarity) and nestedness components based on presence/absence data using the *betapart* R package (Baselga & Orme, 2012). Relationships between replacement, nestedness and total beta diversity and pairwise differences in elevation were explored with quadratic regressions.

To identify pantropical trends shared among neotropical and palaeotropical montane regions, relationships between the richness of the main fungal groups (all fungi, ECM fungi, plant pathogens, saprotrophs and wood decomposers; treated as response variables) and environmental variables were explored by general linear mixed models (GLMMs; Zuur et al., 2009). The explanatory variables available for all sites were MAT, MAP, pH, OM, N and C/N. In all models, Gaussian error structure was assumed for the response variables. To fulfil the normality condition of the model residuals, some response variables were transformed (logarithmic for ECM fungi, square-root for saprotrophs and wood decomposers). All environmental variables were standardized for zero mean and variance before the analysis. Elevation was excluded from the environmental variables because it was correlated strongly with MAT ($r = -.88$). For all other environmental variables, the absolute values of the intercorrelations were lower than 0.6 (Table S2). Because the main purpose was to identify common trends among regions, we treated region as a random factor. Scatterplots between the response and environmental variables were checked before model selection. In the full model, all environmental variables, their second-order component (if the scatterplots showed unimodal response) and first-order interactions were included. Model selection was based on backward elimination using deviance analysis (Faraway, 2005, 2006). The importance of variables was analysed by type-II analysis of variance using Wald's Chi^2 test of the *Anova* function of the *car* package (Fox & Weisberg, 2019). All models were implemented in the *lme4* package (Bates et al., 2015). Pseudocoefficients of determination of the fixed effects (marginal effects) were calculated with the *MuMIn* package (Bartoń, 2019). Normality and homoscedasticity of the model residuals were verified visually.

3 | RESULTS

3.1 | Environmental drivers

Abiotic environmental variables were correlated with elevation to a varying degree in the sampled regions. As expected, MAT was correlated negatively with elevation in all regions. In addition to MAT, soil pH and soil OM showed consistent elevational trends across biogeographical regions: with increasing elevation, soil pH tended to decrease and OM tended to increase (Figure S6). The other measures considered here (soil N content and C/N) did not vary consistently with elevation across the regions studied here (data not shown).

GNMDS ordinations revealed strong structuring of fungal communities according to elevation in all regions, with Pearson's correlations values (all $p < .001$) of $r^2 = .8633$ in Argentina, $r^2 = .94130$ in Brazil, $r^2 = .9661$ in Panama, $r^2 = .9406$ in Borneo and $r^2 = .7851$ in Papua New Guinea (Figure 1). With respect to abiotic variables, MAT and soil pH were correlated strongly with fungal community composition in all cases (all $p < .005$), whereas other climatic and edaphic variables differed in their importance among regions. Partial Mantel tests showed strong correlations among fungal community composition and environmental variables when spatial proximity was controlled: $r = .636$ in Argentina, $r = .706$ in Brazil, $r = .576$ in Panama, $r = .444$ in Borneo and $r = .261$ in Papua New Guinea (all $p < .001$). When abiotic variables were accounted for in partial Mantel tests, fungal communities only showed significant spatial autocorrelation in Brazil ($r = .301$, $p = .025$) and Papua New Guinea ($r = .293$, $p < .001$).

In PERMANOVAs, MAT and pH tended to explain the greatest variation in the total fungal community composition and remained significant contributors in the combined model in all regions when correlation among parameters was accounted for (Table 1). In addition, MAP, C/N, OM and P explained significant proportions of variation of fungal community composition in the combined models in at least two regions, although the contributions differed among geographical regions and functional groups (Table 1). These results are consistent with Hypothesis 1, particularly with respect to MAT, pH and to a lesser extent MAP, as drivers of soil fungal community composition. MAT always and pH mostly correlated with elevation, yet both remained significant in the combined model in four of the

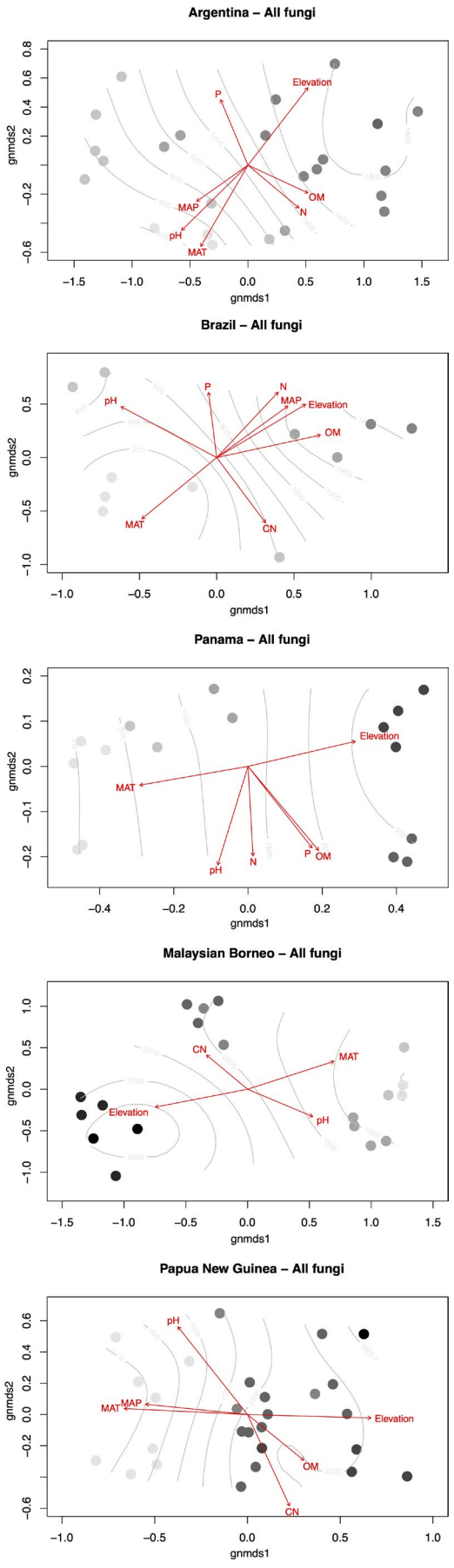

FIGURE 1 Global nonmetric multidimensional scaling (GNMDS) ordination plots of fungal communities in the sampled regions based on Hellinger-transformed data, with elevation displayed as isolines. Localities and descriptions of the sampling sites are given in Table S1. Vectors of environmental variables with significant correlation with ordination axes are displayed. The darker the circle, the higher the elevation of the site. Abbreviations: CN, carbon to nitrogen ratio; MAP, mean annual precipitation; MAT, mean annual temperature; N, soil nitrogen content; OM, soil organic matter content; P, soil phosphorus content; pH, soil pH [Colour figure can be viewed at wileyonlinelibrary.com]

five regions, highlighting their complementarity in explaining fungal community composition.

When beta diversity was partitioned into replacement and nestedness components, we observed that replacement accounted for most of the observed beta diversity, with nestedness being negligible in all regions (Figure 2). Quadratic regressions indicated significant positive relationships between pairwise differences in replacement and elevation difference in all regions, with high replacement values being prevalent at <1000 m of elevation difference and increasing moderately thereafter. Conversely, nestedness were generally low even within the same elevation zone and decreased with increasing difference in elevation in all regions except Brazil, probably due to the relatively small number of samples from this latter region (Figure 2).

3.2 | Elevational patterns of fungal functional groups

All functional groups exhibited significant ($p < .05$) differences in community composition along the sampled elevation gradients, consistent with our general Hypothesis 2. The GNMDS ordinations of the four largest functional groups in terms of OTU richness are shown in Figure 3, with richness of taxonomic orders displayed as vectors. We did not find support for greater elevational community turnover in plant-associated than in nonplant-associated functional groups, in contrast to our expectations in Hypothesis 2a.

Elevational differences in richness also were observed in all functional groups in at least one region (Figure 4). Total fungal richness was generally similar along the gradients, except in Panama, where we observed a significant midelevation peak. The richness of plant pathogens and wood decomposers was generally correlated negatively with elevation in the sampled regions (Figure 4; Figure S7). ECM fungi and nonmycorrhizal root-associated fungi tended to be most diverse in mid- to high elevations, while richness of animal pathogens, mycoparasites and generalist saprotrophs did not differ significantly along elevation gradients except in Panama. Greater elevational differences observed in plant-associated fungi compared to nonplant-associated guilds were consistent with richness patterns of their hosts as phrased in Hypothesis 2a, despite the lack of such differences in community turnover rates among functional groups, as mentioned above.

Richness, proportional richness and proportional abundance of plant pathogens and wood decomposers tended to decrease with

TABLE 1 Proportion of variation (%) in fungal community composition explained by environmental variables calculated independently with permutational multivariate analysis of variance, based on the rarefied and Hellinger-transformed fungal community matrix

	All fungi	Animal path.	AM fungi	ECM fungi	Mycoparasites	Plant path.	Root fungi	Saprotrophs	Wood decomp.
Argentina									
Elevation	**19.91**	**24.72**	**17.13**	**15.01**	**12.37**	**17.26**	**9.76**	**15.84**	**15.31**
MAT	**15.97***	**22.85**	**12.49**	**11.95**	**11.80***	**15.77**	**8.48***	**14.04**	**13.82***
MAP	**13.18**	**24.39***	**14.51***	**12.90***	**14.86***	**17.47***	**7.83**	**15.21***	**12.95***
pH	**18.56***	**16.48**	10.63	**12.03**	**8.57**	**11.97**	**6.91**	**11.40**	**12.10**
OM	**13.29**	**10.04**	9.35	6.44	5.69	6.93	3.51	**7.49**	6.21
N	**12.72**	**11.15**	10.64	7.07	6.59	**7.78**	3.56	**8.01**	**6.71**
C/N	4.52	5.12	5.81	5.10	5.74	5.34	3.88	5.31	4.88
P	**9.41**	**10.67**	5.22	5.80	6.59	**7.37**	3.64	**7.26**	5.44
Brazil									
Elevation	**24.98**	**24.86**	–	**14.35**	**35.01**	**32.15**	18.02	**24.31**	**18.13**
MAT	**23.94***	**22.93**	–	**15.23**	**35.34***	**30.02***	15.28	**22.06***	**17.41***
MAP	**21.68**	**19.69**	–	**15.87***	**32.24**	**26.99**	14.92	**19.29**	**15.83***
pH	**22.42***	**25.04**	–	11.17	**28.63**	**22.98**	**30.37**	**26.09***	**15.07**
OM	**22.15**	**23.44**	–	11.87	**32.49***	**28.27***	**25.52**	**22.92***	**17.66***
N	**19.95**	**19.32**	–	12.17	**33.98**	**24.55***	12.31	**19.04**	**15.71**
C/N	15.06	12.51	–	10.34	17.57	15.69	**31.22***	**17.35**	11.75
P	13.56	10.14	–	12.08	**28.36**	12.47	10.29	14.28	11.38
Panama									
Elevation	**20.32**	**32.53**	**19.17**	**13.96**	**21.58**	**23.38**	**13.63**	**21.44**	**17.20**
MAT	**20.31***	**33.17***	**19.45***	**14.09***	**22.72***	**23.50***	**13.69***	**21.47***	**17.07***
MAP	**11.11**	11.84	11.05	7.34	13.44	**11.21**	8.92	**10.99**	**10.34**
pH	**12.03**	**14.40**	10.25	9.42	13.33	**11.66**	**10.57**	**12.63**	9.11
OM	**17.65**	**23.94**	**20.13**	**13.54**	**18.50**	**20.36**	**13.42***	**18.48**	**15.87**
N	8.32	5.30	11.66	8.60	5.58	7.61	8.87	8.79	8.17
C/N	8.04	10.78	11.41	7.80	8.04	7.96	7.01	8.54	8.31
P	**16.17**	**27.56**	**16.01**	**12.01**	**21.99**	**17.84**	**12.11***	**16.11**	**13.81**
Malaysian Borneo									
Elevation	**19.38**	**31.55**	**17.19**	**15.03**	**24.32**	**23.37**	**13.72**	**20.54**	**14.77**
MAT	**19.11***	**32.12***	**17.78***	**15.40***	**23.08***	**23.20***	**12.94***	**20.09***	**14.32***
MAP	6.91	6.43	12.81	6.67	6.06	6.55	7.66	7.23	5.89
pH	**14.32***	**14.02**	13.18	**10.06**	**15.14**	**15.66**	**13.86***	**15.36**	**13.28**
OM	8.18	5.99	11.58	**8.59***	**13.16**	7.61	**9.15***	8.51	6.79
N	7.34	6.36	12.66	7.69	7.54	7.25	**9.07**	7.69	5.71
C/N	**10.64**	9.77	11.85	8.19	**15.75**	**10.53**	**12.68**	**11.01**	**9.97**
Papua New Guinea									
Elevation	**10.04**	**7.53**	–	**7.38**	**8.92**	**11.76**	**8.29**	**10.25**	**6.96**
MAT	**9.91***	**7.31**	–	**7.33***	**9.16***	**11.55***	**8.22***	**10.11***	**6.96***
MAP	**8.82**	5.95	–	**7.91***	**7.03**	**9.61**	**7.46**	**9.14***	**6.59**
pH	**7.18***	**8.17**	–	**5.91**	**9.15***	**7.24***	**6.13***	**7.18***	**4.88***
OM	4.69	5.71	–	4.06	4.67	**6.58**	4.82	4.39	3.82
N	4.78	5.47	–	3.75	3.59	**6.88***	4.08	4.59	4.04
C/N	**6.96***	**9.31***	–	**6.48***	**10.52***	**6.72**	**6.39***	**6.79***	4.34

Notes: Significant results are in bold. Climatic and edaphic variables that remained significant in the final composite model (without elevation) for each fungal group are shown with an asterisk (*).

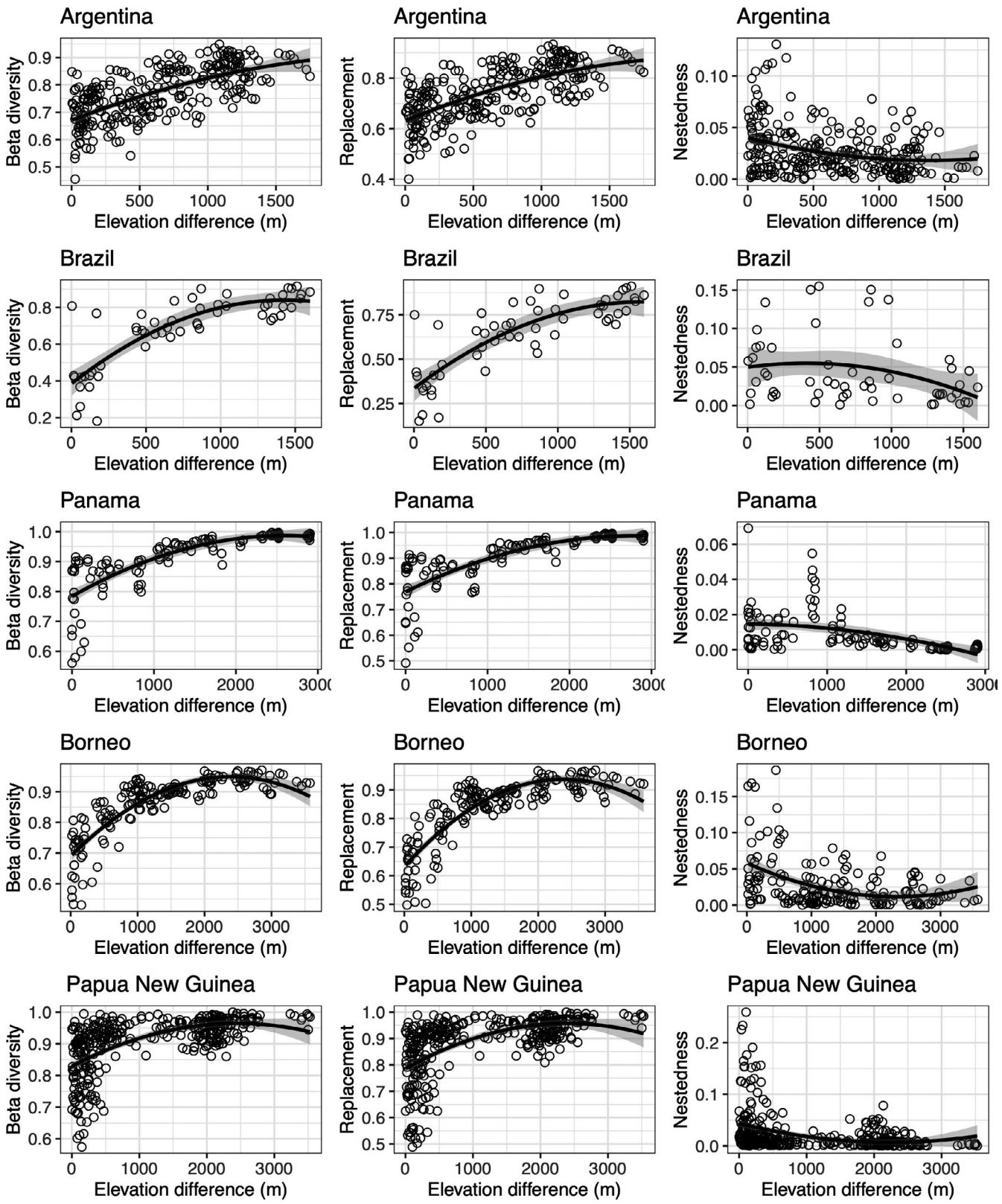

FIGURE 2 Correlation of total beta diversity and its replacement and nestedness components of fungal communities with pairwise differences in elevation among the sites, with 95% confidence intervals indicated by grey shading. All relationships, except that of nestedness in Brazil, are significant

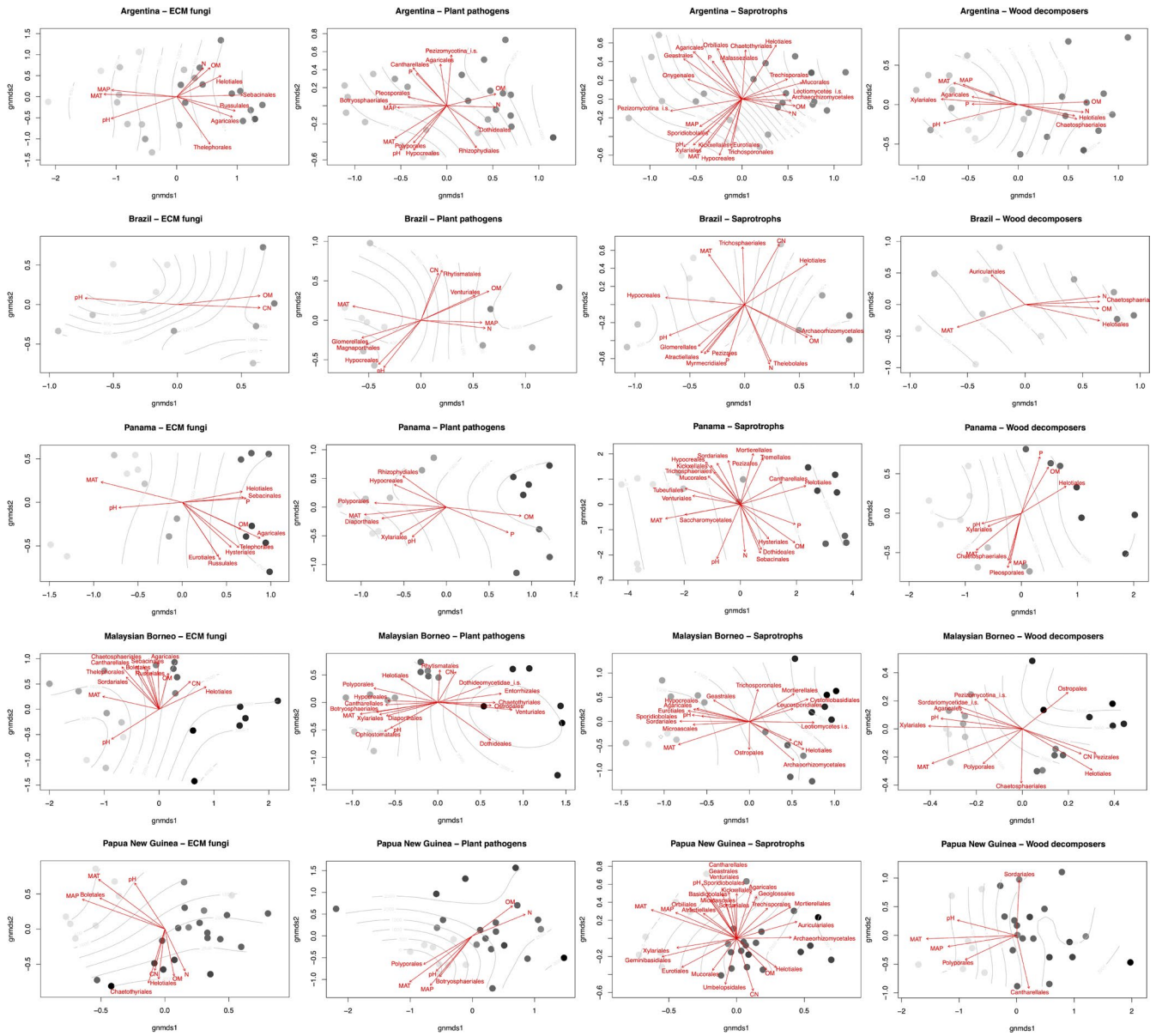

FIGURE 3 Global non-metric multidimensional scaling (GNMDS) ordination plots of fungal functional groups in the sampled regions based on Hellinger-transformed data, with elevation displayed as isolines. Vectors of environmental variables and taxonomic orders with significant correlation with ordination axes are displayed. The darker the circle, the higher the elevation of the site. Abbreviations: CN, carbon to nitrogen ratio; MAP, mean annual precipitation; MAT, mean annual temperature; N, soil nitrogen content; OM, soil organic matter content; pH, soil pH; P, soil phosphorus content [Colour figure can be viewed at wileyonlinelibrary.com]

elevation, largely consistent with Hypothesis 2b. In contrast, ECM fungi, mycoparasites and nonmycorrhizal root-associated fungi showed mixed patterns. For example, in Argentina and Panama, the highest richness of ECM fungi was observed at high elevations, but they showed a midelevation peak in Borneo and a similar, albeit nonsignificant, pattern in Brazil and Papua New Guinea (Figure 4; Figures S7 and S8).

3.3 | Elevational patterns of taxonomic groups

In the Neotropics, all taxonomic orders of ECM and root-associated fungi that correlated significantly with the ordination axes showed positive relationships with elevation (e.g., ECM or root-associated Agaricales, Eurotiales, Helotiales, Hysteriales, Russulales, Sebacinales and Thelephorales). In Borneo, vectors of richness for most taxonomic orders of ECM and root-associated fungi were directed towards the midelevation sites, except for Sordariales and Thelephorales with highest richness at low and Helotiales at high elevations (Figure 3).

Vectors representing the richness of most taxonomic groups of plant pathogenic fungi (e.g., in plant pathogenic Botryosphaeriales, Cantharellales, Diaporthales, Hypocreales, Ophiostomatales, Polyporales, Rhizophydiales and Xylariales) correlated negatively with elevation, whereas putatively pathogenic Helotiales were richer in midelevation (Borneo) or high-elevation sites (Panama).

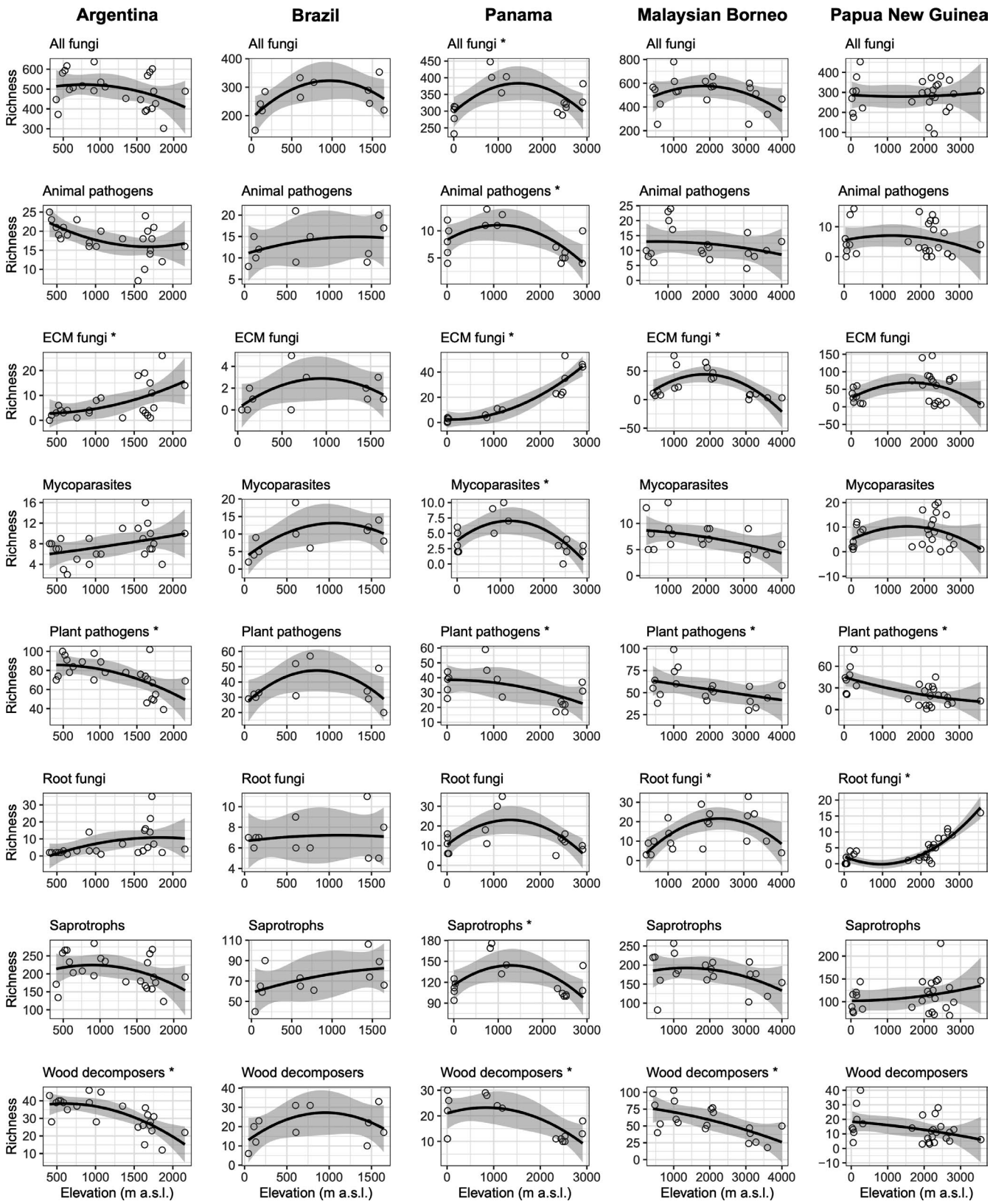

FIGURE 4 Quadratic regressions of elevation and richness of functional groups in the five sampled tropical montane regions, with 95% confidence intervals indicated by grey shading. Significant relationships are marked with an asterisk (*)

Orders of saprotrophic fungi that were richer in forests at lower elevations included Agaricales, Eurotiales, Geastrales, Hypocreales, Kickxellales, Saccharomycetales, Sporidiobolales and Sordariales, each with significant Pearson's correlation values in at least two regions. In contrast, vectors for saprotrophic Archaeorhizomycetales, Chaetothyriales, Helotiales and Sebacinales indicated higher

richness in montane forests. Among wood decomposers, Helotiales consistently showed highest richness in forests at higher elevations, and wood decomposer Agaricales and Xylariales at lower elevations (Figure 3).

3.4 | Pantropical relationships between fungal richness and environmental variables

In the combined GLMM analyses including all sampled regions, total fungal richness was weakly explained by the environmental variables considered here ($R^2 = .025$), with only pH showing a significant, but weak, positive effect on richness (Table 2). However, richness values of specific functional groups (ECM fungi, plant pathogens and wood decomposers) had much stronger relationships to environmental variables. ECM fungal richness showed significant negative correlations with pH and with the interaction of MAT and N content. Plant pathogen richness was most strongly explained by pH, with additional positive effects of MAT. Richness of saprotrophs showed a strong positive correlation with the interaction of pH and OM. Wood decomposer richness showed a strong unimodal response with MAT, with additional positive responses to pH and OM, and a negative response to N.

4 | DISCUSSION

Fungal biodiversity in tropical forests remains little known, and opportunities to compare data from similar guilds across diverse tropical forests at local and global scales are rare. The data presented here show that composition of the total fungal community in soil, as well as that of all functional groups, is strongly structured according to elevation in both the Neo- and Palaeotropics. In contrast to vascular plants, where forests at low to midelevations typically harbour more tree species than montane forests (Aiba & Kitayama, 1999; Brown et al., 2001; McCain & Grytnes, 2010), we did not find substantial differences in soil fungal richness along the elevation gradients in most sampled regions. The lack of a strong elevational pattern in fungal richness is similar to the lack of latitudinal differences in fungal richness on a global scale (Větrovský et al., 2019, but see Tedersoo et al., 2014). Panama was the only exception, where the midelevation peak in fungal richness is concordant with vascular plant richness in Central American mountains (Cardelús et al., 2006; Prada et al., 2017).

Overall, in all functional groups and in all regions, community composition appears to be driven by elevation and the resulting environmental filtering according to contrasting climatic and edaphic conditions, and associated differences in plant communities. Our data suggest that generally an elevation difference of 700–800 m of results in a high turnover of soil fungal communities, indicating that most fungi prefer a certain elevation zone along these gradients. This may be explained by the fact that organisms at a given elevation in the tropics are subjected to a lower variation in temperature than organisms in temperate mountains and thus are more likely to have a relatively narrow elevation range (Janzen, 1967).

4.1 | Environmental drivers of community composition

Variation in fungal community composition and richness as a function of elevation is mediated by abiotic and biotic factors driven either directly or indirectly by differences in temperature, which strongly influences relative humidity, soil moisture and soil chemical processes. Consequently, forests found at different elevations have distinct mesoclimatic and edaphic conditions. Moreover, high-elevation habitats generally cover smaller areas than lower elevation ones and habitat area often is correlated positively with species

TABLE 2 Parameters of general linear mixed models on the richness of the functional groups (as response variables) in the combined analysis of all five sampled tropical montane regions

	All fungi	ECM fungi	Plant pathogens	Saprotrophs	Wood decomposers
R^2	.025	.106	.260	.099	.145
Environmental variables					
MAT	–	0.01; 0.57^{ns}	2.84; 3.58*	–	0.45; 14.51***
MAT^2	–	–	–	–	−0.19; 4.34*
pH	23.01; 4.35*	−0.31; 5.46*	10.75; 35.05***	0.82; 8.87**	0.42; 7.25**
OM	–	–	–	1.27; 4.55*	0.47; 4.95*
N	–	−0.15; 1.87^{ns}	–	−0.53; 3.75^{m}	−0.35; 3.41^{m}
MAT:N	–	−0.29; 11.64***	–	–	–
pH:OM	–	–	–	0.48; 7.18**	–

Notes: For each fungal group, only variables included in the final model are displayed. R^2: pseudocoefficient of determination of the fixed factors (marginal effect). Environmental variables: MAT, mean annual temperature; MAT^2, second order of MAT; N, soil nitrogen content; OM, soil organic matter content; pH, soil pH. The first parameter of the variables is the model estimate, the second one is the χ^2 value. The significance of the variables is indicated as: ***$p < .001$; **$p < .01$; *$p < .05$; m $p < .1$.

richness in many taxonomic groups (Gotelli, 1998). However, for fungi, the decreasing habitat area with increasing elevation does not seem to offer a satisfying explanation for the observed richness patterns: there were no statistical differences in total fungal richness between lowland and upper montane forests in any region, even though lowland forests cover much larger areas (Figures S1–S5). Although some functional groups decreased in richness with increasing elevation, other groups showed the opposite trend. Thus, it appears that climatic and edaphic factors, as well as the composition of biological communities, are far more influential drivers of fungal richness in mountains than habitat area alone.

Our results indicate that MAT and pH are the most influential drivers of fungal community composition across elevational gradients in neotropical and palaeotropical regions, while the roles of other variables seem to be more region-dependent (Figures 1 and 2, Table 1). In the pantropical GLMM analyses, MAT and pH also emerged as the main drivers of richness in most functional groups, followed by N and OM (Table 2). These findings differ somewhat from global drivers of fungal diversity and community composition: the influence of MAP in the sampled tropical montane forest tends to be specific to functional groups and to regions. Despite being the most influential climatic predictors of fungal richness and community composition on a global scale (Tedersoo et al., 2014), MAP did not contribute significantly to any final models explaining richness of various fungal groups in the pantropical analyses. On the other hand, MAP was the strongest contributor to the explained variation in community composition of most of the functional groups in Argentina and had moderately strong contribution in Brazil and Papua New Guinea, while it remained marginal or insignificant in Borneo and Panama. Except for Argentina, these trends do not seem to be explained by interregional differences in precipitation seasonality based on data from WorldClim (data not shown). Instead, MAP seems to be more important in regions where it was lower and/or had greater altitudinal variation (Figure S6).

Soil pH plays an important role in shaping below-ground fungal communities at both regional and global scales (e.g., Coughlan et al., 2000; Geml, 2019; Geml et al., 2014; Glassman et al., 2017; Lauber et al., 2008; Porter et al., 1987; Rousk et al., 2010; Tedersoo et al., 2014). Because many fungal species have a relatively wide pH optimum (e.g., Nevarez et al., 2009; Wheeler et al., 1991), it is likely that the observed correlation of pH with community composition is mainly indirect, such as by altering nutrient availability and competitive interactions between soil fungi and bacteria (Rousk et al., 2010) and other soil biota. In all regions, we observed some decrease in pH and increase in OM with elevation, and it is difficult to disentangle their effects from that of MAT. However, along with MAT, pH remained significant in explaining compositional differences of total fungal communities in four of the five sampled regions, and OM contributed significantly to the combined model for some functional groups in three regions (Table 1). The effect of pH on richness appears to be similarly strong: it was the only environmental variable that was correlated significantly with total fungal richness at a pantropical scale, and with significant contribution to the final model in all four major functional groups (Table 2). The relatively weak correlation of pH with total fungal richness seems to be explained by its negative correlation with ECM fungi, which counterbalanced the positive relationship with plant pathogens, saprotrophs and wood decomposers. With respect to saprotrophs, the positive effect of the significant interaction between pH and OM on richness suggests that saprotrophs may benefit more from the available organic carbon under less acidic conditions. This may partly be explained by lower levels of competition with ECM fungi for nutrient acquisition, i.e., "the Gadgil effect" (Fernandez & Kennedy, 2016; Gadgil & Gadgil, 1971), given the observed negative relationship between pH and ECM fungal richness. While the negative effect of available N on ECM fungal richness is well known (Lilleskov et al., 2002), in our analyses it was only evident at lower elevations, as shown by the strongly significant negative effect of the interaction between MAT and N on ECM richness. Overall, our observations suggest that despite the correlation with elevation, pH, N and OM play important roles in shaping fungal communities in tropical mountains in ways that are not explained by MAT.

4.2 | Elevational dynamics of fungal functional groups

The results presented here show that fungi with different life strategies are favoured by different environmental conditions. Even in functional groups with no significant differences in richness over the elevational gradients studied here, we observed strong differences in composition as a function of elevation. Similar elevational differences in richness and composition also have been observed in various functional groups of plants and animals (Cardelús et al., 2006; Guo et al., 2013; McCain, 2009; McCain & Grytnes, 2010).

With respect to ECM fungi in tropical mountains, the patterns reported here differ from those observed in temperate mountains, where ECM fungal richness tends to decrease monotonically with increasing elevation (Bahram et al., 2012; Nouhra et al., 2012; but see Bowman & Arnold, 2018). Based on the data presented here and on previous studies on tree community richness and composition of the sampled forests (e.gAiba & Kitayama, 1999; Malizia et al., 2012), ECM fungal richness appears to mirror host richness and density along the elevation gradients studied here in both the Neo- and Palaeotropics (as has been reported on a global scale; Tedersoo et al., 2014). This coupling of ECM fungi and host trees also results in important differences in the elevational patterns of ECM fungi between the Neo- and Palaeotropics. In the neotropical mountain ranges from Mexico to Argentina, high-elevation forests tend to harbour the highest density of trees that form ectomycorrhizal associations (e.g., *Alnus acuminata* as the principal ECM host in the Yungas in Argentina, and *Alnus acuminata* and several *Quercus* spp. in the mountains of southern Costa Rica and northern Panama) (Kappelle, 2016; Malizia et al., 2012; Nouhra et al., 2018; Wicaksono et al., 2017). These findings agree with sporocarp-based studies in other areas of the wet Neotropics that reported the highest richness

of ECM fungi in montane forests (Gómez-Hernández et al., 2012; Mueller et al., 2006). The Atlantic Forests in Brazil are different because they lack these ECM tree genera of northern origin, and native ECM trees and shrubs are relatively rare and little known (Sulzbacher et al., 2013, 2019; Vanegas-León et al., 2019). These differences in diversity and abundance of ECM hosts probably drive the differences in proportional richness and abundance of ECM fungi, which can reach 10% and 30% in Panama, 5% and 10% in Argentina, compared to 1% and 2% in Brazil, respectively. In Borneo, the richness and density of ECM trees are high in low- and midelevational forests, particularly Dipterocarpaceae and Fagaceae, respectively. ECM tree richness declines with further increases in elevation, which is reflected here and is discussed in detail by Geml et al. (2017). At high elevations, ECM host *Leptospermum recurvum* (Myrtaceae) tends to be dominant in ultramafic soils, occurring in lower abundance on granite (Aiba & Kitayama, 1999). In Papua New Guinea, ECM trees are relatively diverse and abundant throughout the elevation gradient, representing Dipterocarpaceae, Fagaceae, Nothofagaceae, Myrtaceae and Gnetaceae among others (Hope, 1976).

The richness of plant pathogenic and wood decomposer fungi often correlates positively with temperature (Gómez-Hernández et al., 2012; Tedersoo et al., 2014). In our study, the richness (both proportional and absolute) of wood decomposers, and to some extent plant pathogenic fungi, was predictably higher at lower elevations and correlated positively with MAT. However, saprotrophs did not show a consistent elevational pattern and lacked any significant relationship with MAT in the pantropical analysis. In all regions, the lowest proportional richness of saprotrophs always coincided with the highest proportional richness of ECM fungi, possibly partly because of "the Gadgil effect" mentioned above. We note that some of the fungi identified under the functional guilds of plant pathogens and saprotrophs may prove to be endophytes, raising an interesting direction for future study and highlighting an ongoing challenge with estimating functional modes based on barcode sequences alone. Our work suggests that given the ecological and phylogenetic overlap of endophytic, saprotrophic and pathogenic taxa in terms of ITS sequences, endophytes will broadly follow the patterns described here. A recent study by Oita et al. (2021) confirms these expectations, highlighting the importance of climate (MAT and MAP) and seasonality in shaping endophyte communities across an elevation gradient in Panama.

Regardless of differences in richness, the strong compositional changes as a function of elevation observed in all functional groups studied here is consistent with habitat specificity and elevational turnover of species within functional guilds. We observed several consistent patterns regarding the distribution of taxonomic groups across functional guilds, suggesting a certain level of phylogenetic conservatism with respect to environmental niches (Figure 3). For example, the consistently higher richness of Sordariomycetes, particularly Hypocreales, Sordariales and Xylariales, at lower elevations is apparent in various functional groups and agrees with higher host and substrate diversity for these fungi, which include plant pathogens as well as saprotrophs. Unlike in boreal and many temperate forests, Sordariomycetes (including common orders such as Chaetosphaeriales, Diaporthales, Glomerellales, Hypocreales, Sordariales and Xylariales) is the dominant class of plant endophytic fungi in tropical lowland forests (e.g., Arnold & Lutzoni, 2007; see also Oita et al., 2021), in agreement with their prevalence in soil at low elevations. In a similar manner, the higher richness of Leotiomycetes, particularly Helotiales, at high elevations is apparent in several functional groups, such as root-associated fungi, plant pathogens, saprotrophs and wood decomposers. Helotiales appears to be the most diverse order of ascomycetes in arctic tundra ecosystems (Semenova et al., 2015), and the above trend confirms that many Helotiales taxa thrive in relatively colder climates. The fact that habitat preference can be observed at the level of taxonomic ranks, often irrespective of functional guild, suggests shared physiological constraints and environmental optimum for certain phylogenetic lineages of fungi.

4.3 | Conclusions

This is the first study comparing the community composition of fungi along elevation gradients in the Neotropics and Palaeotropics. Climate, particularly temperature, and soil pH appear to be the driving factors shaping the distribution of fungi along elevational gradients in a variety of ways, such as by affecting microbial processes (e.g., decomposition), vegetation, nutrient availability and other edaphic factors, and by altering species interaction dynamics. Montane forests are among the most vulnerable terrestrial ecosystems to climate change and warming will undoubtedly affect fungal communities in these ecosystems. Given the contrasting habitat preferences of several taxonomic groups and the possible functional differences among them within the broad functional guilds, future communities at a given site may differ considerably from current ones not only in composition, but also in functionality. The habitat specificity exhibited by many fungi offers possibilities for monitoring and habitat characterization, and we advocate incorporating fungi in biodiversity assessments and conservation efforts. With the accumulating spatial data points for fungal taxa from metabarcoding studies, it will be possible, in the near future, to determine the climatic niches and model the suitable habitats for many fungi.

ACKNOWLEDGEMENTS

Financial support for the fieldwork was provided by E. Nouhra (SECYT Universidad Nacional de Córdoba 26/11; 162/12; 124/13), Naturalis and Sabah Parks as part of the Kinabalu-Crocker Range expedition, CNPq/Capes/FAPs/BC-Fundo Newton/PELD no. 15/2016 and FAPESC/2018TR0928 as part of the Brazilian expedition, and the National Science Foundation (NSF) GoLife grant (DEB 1541548) to F.L. A.E.A. acknowledges NSF DEB-1541496. Molecular work was financed by a Naturalis Research Initiative grant to J.G. and the above NSF GoLife grant to F.L. The authors thank staff members of all national parks, national reserves, provincial parks and provincial reserves sampled (listed in Table S1), the Panamanian Ministry

of Environment in Panama, and Sabah Biodiversity Center and Sabah Parks in Malaysia for issuing access and export permits. The authors are grateful to the Fundación ProYungas in Agentina, the Panamanian Institute for Scientific Research and High Technology Services (INDICASAT-AIP) and Dr O. López in Panama and Sabah Parks and Universiti Malaysia Sabah (UMS) in Malaysia for providing logistical support during fieldwork, and to Marcel Eurlings and Elza Duijm (Naturalis) for conducting the Ion Torrent sequencing. J.G. acknowledges support from the Lendület programme (no. 96049) of the Hungarian Academy of Sciences and the Eötvös Loránd Research Network. E.R.D.-S. is supported by CNPq (311158/2018-8).

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

J. Geml, E. R. Nouhra, F. Lutzoni and A. E. Arnold designed the research. J. Geml, E. R. Nouhra, F. Lutzoni, A. E. Arnold, A. Ibáñez, L. N. Morgado, R. Drechsler-Santos, A. Góes-Neto and L. Tedersoo performed the fieldwork. J. Geml and T. A. Semenova-Nelsen performed the laboratory work. L. Tedersoo contributed Papua New Guinea data. J. Geml completed the bioinformatics and the statistical analyses, to which O. Grau and L. N. Morgado contributed R scripts, except for the GLMM analyses, which were done by P. Ódor. B. Hegyi prepared the maps for Figures S1–S3. J. Geml wrote the first draft of the paper and all authors contributed to the revision of the manuscript.

DATA AVAILABILITY STATEMENT

The DNA sequence data that support the findings of this study are openly available in DDBJ/EMBL/GenBank at https://www.ncbi.nlm.nih.gov/genbank/, under Targeted Locus Study reference nos. KDPX01000000, KEXW01000000, KDPY01000000 and KDPZ01000000 (Geml, 2020, 2021). The OTU sequences for the Papua New Guinea samples can be downloaded from Tedersoo et al. (2014).

ORCID

József Geml https://orcid.org/0000-0001-8745-0423
Grau Oriol https://orcid.org/0000-0002-3816-9499
Leho Tedersoo https://orcid.org/0000-0002-1635-1249

REFERENCES

Aiba, S., & Kitayama, K. (1999). Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology*, *140*, 139–157.

Antonelli, A. (2015). Biodiversity: Multiple origins of mountain life. *Nature*, *524*, 300–301. https://doi.org/10.1038/nature14645

Arnold, A. E., & Lutzoni, F. (2007). Diversity and host range of foliar fungal endophytes: Are tropical leaves biodiversity hotspots? *Ecology*, *88*, 541–549. https://doi.org/10.1890/05-1459

Bagchi, R., Gallery, R. E., Gripenberg, S., Gurr, S. J., Narayan, L., Addis, C. E., Freckleton, R. P., & Lewis, O. T. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, *506*, 85–88. https://doi.org/10.1038/nature12911

Bahram, M., Põlme, S., Kõljalg, U., Zarre, S., & Tedersoo, L. (2012). Regional and local patterns of ectomycorrhizal fungal diversity and community structure along an altitudinal gradient in the Hyrcanian forests of northern Iran. *New Phytologist*, *193*, 465–473. https://doi.org/10.1111/j.1469-8137.2011.03927.x

Bakker, M. R., Brunner, I., Ashwood, F., Bjarnadottir, B., Bolger, T., Børja, I., Carnol, M., Cudlin, P., Dalsgaard, L., Erktan, A., Godbold, D., Kraigher, H., Meier, I. C., Merino-Martín, L., Motiejūnaitė, J., Mrak, T., Oddsdóttir, E. S., Ostonen, I., Pennanen, T. L., … Soudzilovskaia, N. A. (2019). Belowground biodiversity relates positively to ecosystem services of European forests. *Frontiers in Forests and Global Change*, *2*, 6. https://doi.org/10.3389/ffgc.2019.00006

Barry, R. G. (2008). *Mountain weather and climate*. Cambridge University Press.

Bartoń, K. (2019). *MuMIn: Multi-Model Inference*. R package version 1.43.15. Retrieved from https://CRAN.R-project.org/package=MuMIn

Baselga, A., & Orme, C. D. L. (2012). *betapart*: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*, 808–812.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Beaman, J. H., & Anderson, C. (2004). *The plants of Mount Kinabalu. 5. Dicotyledon families Magnoliaceae to Winteraceae*. Royal Botanic Gardens.

Beaman, J. H., & Beaman, R. S. (1990). Diversity and distribution patterns in the flora of Mount Kinabalu. In P. Baas, P. Kalkman, & R. Geesink (Eds.), *The plant diversity of Malesia* (pp. 147–160). Kulwar Academic Publishers.

Blake, J. G., & Rougés, M. (1997). Variation in capture rates of understory birds in El Rey National Park, Northwestern Argentina. *Ornitología Neotropical*, *8*, 185–193.

Bowman, E. A., & Arnold, A. E. (2018). Distributions of ectomycorrhizal and foliar endophytic fungal communities associated with *Pinus ponderosa* along a spatially constrained elevation gradient. *American Journal of Botany*, *105*, 687–699.

Brown, A. D., Grau, H. R., Malizia, L. R., & Grau, A. (2001). Argentina. In M. Kappelle, & A. D. Brown (Eds.), *Bosques nublados del neotrópico* (pp. 623–659). INBio.

Brown, A. D., Pacheco, S., Lomáscolo, T., & Malizia, L. R. (2005). Ecoregión Yungas: situación ambiental en los bosques andinos yungueños. In A. D. Brown, U. Martinez Ortiz, M. Acerbi, & J. Corcuera (Eds.), *Situación ambiental Argentina* (pp. 53–72). Fundación Vida Silvestre Argentina.

Bueno, C. G., Gerz, M., Moora, M., Leon, D., Gomez-Garcia, D., de Leon, D. G., Font, X., Al-Quraishy, S., Hozzein, W. N., & Zobel, M. (2021). Distribution of plant mycorrhizal traits along an elevational gradient does not fully mirror the latitudinal gradient. *Mycorrhiza*, *31*, 149–159. https://doi.org/10.1007/s00572-020-01012-3

Cabrera, A. (1976). Regiones fitogeográficas de la República Argentina. *Enciclopedia De Agricultura, Jardinería Y Fruticultura*, *2*, 1–85.

Cardelús, C. L., Colwell, R. K., & Watkins, J. E. (2006). Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology*, *94*, 144–156. https://doi.org/10.1111/j.1365-2745.2005.01052.x

Castaño, C., Parladé, J., Pera, J., De Aragón, J. M., Alday, J. G., & Bonet, J. A. (2016). Soil drying procedure affects the DNA quantification of *Lactarius vinosus* but does not change the fungal community composition. *Mycorrhiza*, *26*, 799–808. https://doi.org/10.1007/s00572-016-0714-3

Coince, A., Cordier, T., Lengellé, J., Defossez, E., Vacher, C., Robin, C., Buée, M., & Marçais, B. (2014). Leaf and root-associated fungal assemblages do not follow similar elevational diversity patterns. *PLoS One*, *9*, e100668. https://doi.org/10.1371/journal.pone.0100668

Condit, R., Pérez, R., & Daguerre, N. (2011). *Trees of Panama and Costa Rica*. Princeton University Press.

Cordier, T., Robin, C., Capdeville, X., Fabreguettes, O., Desprez-Loustau, M. L., & Vacher, C. (2012). The composition of phyllosphere fungal assemblages of European beech (*Fagus sylvatica*) varies significantly along an elevation gradient. *New Phytologist*, *196*, 510–519.

Coughlan, A. P., Dalpé, Y., Lapoint, L., & Piché, Y. (2000). Soil pH-induced changes in root colonization, diversity, and reproduction of symbiotic arbuscular mycorrhizal fungi from healthy and declining maple forests. *Canadian Journal of Forest Research*, *30*, 1543–1554. https://doi.org/10.1139/x00-090

Davey, M. L., Heegaard, E., Halvorsen, R., Kauserud, H., & Ohlson, M. (2013). Amplicon-pyrosequencing-based detection of compositional shifts in bryophyte-associated fungal communities along an elevation gradient. *Molecular Ecology*, *22*, 368–383. https://doi.org/10.1111/mec.12122

Delavaux, C. S., Bever, J. D., Karppinen, E. M., & Bainard, L. D. (2020). Soil sample cold pack storage and DNA shipment up to 1 month does not impact metabarcoding results. *Ecololgy and Evolution*, *10*, 4652–4664.

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics*, *26*, 2460–2461. https://doi.org/10.1093/bioinformatics/btq461

Faraway, J. J. (2005). *Linear models with R*. Chapmann and Hall.

Faraway, J. J. (2006). *Extending the linear model with R*. Chapman and Hall.

Fernandez, C. W., & Kennedy, P. G. (2016). Revisiting the 'Gadgil effect': Do interguild fungal interactions control carbon cycling in forest soils? *New Phytologist*, *209*, 1382–1394. https://doi.org/10.1111/nph.13648

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression*, 3rd ed. Sage.

Gadgil, R. I., & Gadgil, P. D. (1971). Mycorrhiza and litter decomposition. *Nature*, *233*, 133. https://doi.org/10.1038/233133a0

Gai, J. P., Tian, H., Yang, F. Y., Christie, P., Li, X. L., & Klironomos, J. N. (2012). Arbuscular mycorrhizal fungal diversity along a Tibetan elevation gradient. *Pedobiologia*, *55*, 145–151. https://doi.org/10.1016/j.pedobi.2011.12.004

Geml, J. (2017). Altitudinal gradients in mycorrhizal symbioses – the current state of knowledge on how richness and community structure change with elevation. In L. Tedersoo (Ed.), *Ecological studies: Biogeography of mycorrhizal symbioses* (pp. 107–123). Springer.

Geml, J. (2019). Soil fungal communities reflect aspect-driven environmental structuring and vegetation types in a Pannonian forest landscape. *Fungal Ecology*, *39*, 63–79. https://doi.org/10.1016/j.funeco.2018.12.005

Geml, J. (2020). Soil metagenome; DDBJ/EMBL/GenBank; KDPX01000000, KDPY01000000, and KDPZ01000000.

Geml, J. (2021). Soil metagenome; DDBJ/EMBL/GenBank; KEXW01000000.

Geml, J., Morgado, L. N., Semenova-Nelsen, T. A., & Schilthuizen, M. (2017). Changes in richness and community composition of ectomycorrhizal fungi among altitudinal vegetation types on Mount Kinabalu in Borneo. *New Phytologist*, *215*, 454–468. https://doi.org/10.1111/nph.14566

Geml, J., Pastor, N., Fernandez, L., Pacheco, S., Semenova, T. A., Becerra, A. G., Wicaksono, C. Y., & Nouhra, E. R. (2014). Large-scale fungal diversity assessment in the Andean Yungas forests reveals strong community turnover among forest types along an altitudinal gradient. *Molecular Ecology*, *23*, 2452–2472. https://doi.org/10.1111/mec.12765

Ghalambor, C. K., Huey, R. B., Martin, P. R., & Wang, G. (2006). Are mountain passes higher in the tropics? Janzen's Hypothesis Revisited. *Integrative and Comparative Biology*, *46*, 5–17. https://doi.org/10.1093/icb/icj003

Glassman, S. I., Wang, I. J., & Bruns, T. D. (2017). Environmental filtering by pH and soil nutrients drives community assembly in fungi at fine spatial scales. *Molecular Ecology*, *26*, 6969–6973.

Gómez-Hernández, M., Williams-Linera, G., Guevara, R., & Lodge, D. J. (2012). Patterns of macromycete community assemblage along an altitudinal gradient: Options for fungal gradient and metacommunity analyses. *Biodiversity and Conservation*, *21*, 2247–2268.

Gotelli, N. J. (1998). *A primer of ecology*, 2nd ed. Sinauer Associates Inc.

Grau, O., Grytnes, J. A., & Birks, H. U. B. (2007). A comparison of elevational species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *Journal of Biogeography*, *34*, 1907–1915.

Grytnes, J. A., Beaman, J. H., Romdal, T. S., & Rahbek, C. (2008). The mid-domain effect matters: simulation analyses of range-size distribution data from Mount Kinabalu, Borneo. *Journal of Biogeography*, *35*, 2138–2147. https://doi.org/10.1111/j.1365-2699.2008.01952.x

Guo, Q., Kelt, D. A., Sun, Z., Liu, H., Hu, L., Ren, H., & Wen, J. (2013). Global variation in elevational diversity. *Scientific Reports*, *3*, 300.

Hope, G. S. (1976). The vegetational history of Mt. Wilhelm, Papua New Guinea. *Journal of Ecology*, *64*, 627–663. https://doi.org/10.2307/2258776

Ihrmark, K., Bödeker, I. T. M., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandström-Durling, M., Clemmensen, K. E., & Lindahl, B. D. (2012). New primers to amplify the fungal ITS2 region – evaluation by 454-sequencing of artificial and natural communities. *FEMS Microbiology Ecology*, *82*, 666–677. https://doi.org/10.1111/j.1574-6941.2012.01437.x

Janzen, D. H. (1967). Why mountain passes are higher in the Tropics? *American Naturalist*, *101*, 233–249. https://doi.org/10.1086/282487

Javis, S. G., Woodward, S., & Taylor, A. F. S. (2015). Strong altitudinal partitioning in the distributions of ectomycorrhizal fungi along a short (300 m) elevation gradient. *New Phytologist*, *206*, 1145–1155.

Kappelle, M. (2016). The Montane Cloud Forests of the Cordillera de Talamanca. In M. Kappelle (Ed.), *Costa Rican ecosystems* (pp. 451–491). The University of Chicago Press.

Kitayama, K. (1992). An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio*, *102*, 149–171. https://doi.org/10.1007/BF00044731

Kõljalg, U., Nilsson, R. H., Abarenkov, K., Tedersoo, L., Taylor, A. F. S., Bahram, M., Bates, S. T., Bruns, T. D., Bengtsson-Palme, J., Callaghan, T. M., Douglas, B., Drenkhan, T., Eberhardt, U., Dueñas, M., Grebenc, T., Griffith, G. W., Hartmann, M., Kirk, P. M., Kohout, P., … Larsson, K.-H. (2013). Towards a unified paradigm for sequence-based identification of fungi. *Molecular Ecology*, *22*, 5271–5277. https://doi.org/10.1111/mec.12481

Lauber, C. L., Strickland, M. S., Bradford, M. A., & Fierer, N. (2008). The influence of soil properties on the structure of bacterial and fungal communities across land-use types. *Soil Biology and Biochemistry*, *40*, 2407–2415. https://doi.org/10.1016/j.soilbio.2008.05.021

Lavilla, E. O., & Manzano, A. S. (1995). La batracofauna de las selvas de montaña del noroeste argentine. In A. D. Brown, & H. R. Grau (Eds.), *Investigación, conservación y desarollo en las selvas subtropicales de montaña* (pp. 157–162). Laboratorio de Investigaciones Ecológicas de las Yungas, UNT.

Liew, T. S., Schilthuizen, M., & Lakim, M. B. (2010). The determinants of land snail diversity along a tropical elevational gradient: Insularity, geometry and niches. *Journal of Biogeography*, *37*, 1071–1078. https://doi.org/10.1111/j.1365-2699.2009.02243.x

Lilleskov, E. A., Fahey, T. J., Horton, T. R., & Lovett, G. M. (2002). Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska. *Ecology*, *83*, 104–115.

Lomolino, M. V. (2001). Elevation gradients of species-density: Historical and prospective views. *Global Ecology and Biogeography*, *10*, 3–13. https://doi.org/10.1046/j.1466-822x.2001.00229.x

Malizia, L., Pacheco, S., Blundo, C., & Brown, A. D. (2012). Caracterización altitudinal, uso y conservación de las Yungas subtropicales de Argentina. *Ecosistemas*, *21*, 53–73.

McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, *19*, 346–360. https://doi.org/10.1111/j.1466-8238.2008.00443.x

McCain, C. M., & Grytnes, J.-A. (2010). Elevational gradients in species richness. *eLS*. https://doi.org/10.1002/9780470015902.a0022548

McMurdie, P. J., & Holmes, S. (2014). Waste not, want Not: Why rarefying microbiome data is inadmissible. *PLoS Computational Biology*, *10*, e1003531.

Meier, C. L., Rapp, J., Bowers, R. M., Silman, M., & Fierer, N. (2010). Fungal growth on a common wood substrate across a tropical elevation gradient: Temperature sensitivity, community composition, and potential for above-ground decomposition. *Soil Biology and Biochemistry*, *42*, 1083–1090. https://doi.org/10.1016/j.soilbio.2010.03.005

Merckx, V. S. F. T., Hendriks, K. P., Beentjes, K. K., Mennes, C. B., Becking, L. E., Peijnenburg, K. T. C. A., Afendy, A., Arumugam, N., de Boer, H., Biun, A., Buang, M. M., Chen, P.-P., Chung, A. Y. C., Dow, R., Feijen, F. A. A., Feijen, H., Soest, C.-V., Geml, J., Geurts, R., … Schilthuizen, M. (2015). Evolution of endemism on a young tropical mountain. *Nature*, *524*, 347–350. https://doi.org/10.1038/nature14949

Miyamoto, Y., Nakano, T., Hattori, M., & Nara, K. (2014). The mid-domain effect in ectomycorrhizal fungi: Range overlap along an elevation gradient on Mount Fuji, Japan. *ISME Journal*, *8*, 1739–1746. https://doi.org/10.1038/ismej.2014.34

Mueller, G. M., Halling, R. E., Carranza, J., Mata, M., & Schmit, J. P. (2006). Saprotrophic and ectomycorrhizal macrofungi of Costa Rican oak forests. *Ecological Studies*, *185*, 55–68.

Nevarez, L., Vasseur, V., Le Madec, A., Le Bras, M. A., Coroller, L., Leguérinel, I., & Barbier, G. (2009). Physiological traits of *Penicillium glabrum* strain LCP 08.5568, a filamentous fungus isolated from bottled aromatised mineral water. *International Journal of Food Microbiology*, *130*, 166–171. https://doi.org/10.1016/j.ijfoodmicro.2009.01.013

Neves, D. M., Dexter, K. G., Pennington, R. T., Valente, A. S. M., Bueno, M. L., Eisenlohr, P. V., Fontes, M. A. L., Miranda, P. L. S., Moreira, S. N., Rezende, V. L., Saiter, F. Z., & Oliveira-Filho, A. T. (2017). Dissecting a biodiversity hotspot: The importance of environmentally marginal habitats in the Atlantic Forest Domain of South America. *Diversity and Distributions*, *23*, 898–909. https://doi.org/10.1111/ddi.12581

Nor, S. M. D. (2001). Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. *Global Ecology and Biogeography*, *10*, 41–62. https://doi.org/10.1046/j.1466-822x.2001.00231.x

Nouhra, E., Soteras, F., Pastor, N., & Geml, J. (2018). Richness, community composition and functional groups of Agaricomycetes along a vegetation and elevational gradient in the Andean Yungas of Argentina. *Biodiversity and Conservation*, *8*, 1849–1871.

Nouhra, E., Urcelay, C., Longo, S., & Fontenla, S. (2012). Differential hypogeous sporocarp production from *Nothofagus dombeyi* and *N. pumilio* forests in southern Argentina. *Mycologia*, *104*, 45–52.

Oita, S., Ibáñez, A., Lutzoni, F., Miadlikowska, J., Geml, J., Lewis, L. A., Hom, E. F. Y., Carbone, I., U'Ren, J. M., & Arnold, A. E. (2021). Climate and seasonality drive the richness and composition of tropical fungal endophytes at a landscape scale. *Communications Biology*, *4*, 313. https://doi.org/10.1038/s42003-021-01826-7

Ojeda, R. A., & Mares, M. A. (1989). *A biogeographic analysis of the mammals of Salta Province, Argentina: Patterns of species assemblage in the Neotropics*. Texas Tech University Press.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2015). *Vegan: Community ecology package*. Version 2.3-2. Retrieved from http://cran.r-project.org. http://vegan.rforge.r-project.org/

Parris, B. S., Beaman, R. S., & Beaman, J. H. (1992). *The plants of Mount Kinabalu. 1. Ferns and fern allies*. Royal Botanic Gardens.

Perrigo, A., Hoorn, C., & Antonelli, A. (2020). Why mountains matter for biodiversity. *Journal of Biogeography*, *47*, 315–325. https://doi.org/10.1111/jbi.13731

Põlme, S., Abarenkov, K., Henrik Nilsson, R., Lindahl, B. D., Clemmensen, K. E., Kauserud, H., Nguyen, N., Kjøller, R., Bates, S. T., Baldrian, P., Frøslev, T. G., Adojaan, K., Vizzini, A., Suija, A., Pfister, D., Baral, H.-O., Järv, H., Madrid, H., Nordén, J., … Tedersoo, L. (2020). FungalTraits: A user-friendly traits database of fungi and fungus-like stramenopiles. *Fungal Diversity*, *105*, 1–16. https://doi.org/10.1007/s13225-020-00466-2

Porter, W. M., Robson, A. D., & Abbott, L. K. (1987). Field survey of the distribution of Vesicular-arbuscular mycorrhizal fungi in relation to soil pH. *Journal of Applied Ecology*, *24*, 659–662. https://doi.org/10.2307/2403900

Prada, C. M., Morris, A., Andersen, K. M., Turner, B. L., Caballero, P., & Dalling, J. W. (2017). Soils and rainfall drive landscape-scale changes in the diversity and functional composition of tree communities in premontane tropical forest. *Journal of Vegetation Science*, *28*, 859–870. https://doi.org/10.1111/jvs.12540

Prado, D. E. (2000). Seasonally dry forests of tropical South America: From forgotten ecosystems to a new phytogeographic unit. *Edinburgh Journal of Botany*, *57*, 437–461. https://doi.org/10.1017/S096042860000041X

R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, *8*, 224–239. https://doi.org/10.1111/j.1461-0248.2004.00701.x

Ribeiro, M. C., Martensen, A. C., Metzger, J. P., Tabarelli, M., Scarano, F., & Fortin, M. J. (2011). The Brazilian Atlantic forest: A shrinking biodiversity hotspot. In F. Zachos, & J. Habel (Eds.), *Biodiversity hotspots* (pp. 405–434). Springer.

Rincón, A., Santamaría-Pérez, B., Rabasa, S. G., Coince, A., Marçais, B., & Buée, M. (2015). Compartmentalized and contrasted response of ectomycorrhizal and soil fungal communities of Scots pine forests along elevation gradients in France and Spain. *Environmental Microbiology*, *17*, 3009–3024. https://doi.org/10.1111/1462-2920.12894

Rojas-Jimenez, K., Hernandez, M., Blanco, J., Vargas, L. D., Acosta-Vargas, L. G., & Tamayo, G. (2016). Richness of cultivable endophytic fungi along an altitudinal gradient in wet forests of Costa Rica. *Fungal Ecology*, *20*, 124–131. https://doi.org/10.1016/j.funeco.2015.12.006

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press.

Rousk, J., Bååth, E., Brookes, P. C., Lauber, C. L., Lozupone, C., Caporaso, J. G., Knight, R., & Fierer, N. (2010). Soil bacterial and fungal communities across a pH gradient in an arable soil. *The ISME Journal*, *4*, 1340–1351. https://doi.org/10.1038/ismej.2010.58

Schön, M. E., Nieselt, K., & Garnica, S. (2018). Belowground fungal community diversity and composition associated with Norway spruce along an altitudinal gradient. *PLoS One*, *13*, e0208493. https://doi.org/10.1371/journal.pone.0208493

Semenova, T. A., Morgado, L. N., Welker, J. M., Walker, M. D., Smets, E., & Geml, J. (2015). Long-term experimental warming alters community composition of ascomycetes in Alaskan moist and dry arctic tundra. *Molecular Ecology*, *24*, 424–437. https://doi.org/10.1111/mec.13045

Shearer, C. A., Zelski, S. E., Raja, H. A., Schmit, J. P., Miller, A. N., & Janovec, J. P. (2015). Distributional patterns of freshwater ascomycetes communities along an Andes to Amazon elevational gradient in Peru. *Biodiversity and Conservation*, *24*, 1877–1897. https://doi.org/10.1007/s10531-015-0911-y

Siddique, A. B., & Unterseher, M. (2016). A cost-effective and efficient strategy for Illumina sequencing of fungal communities: A case

study of beech endophytes identified elevation as main explanatory factor for diversity and community composition. *Fungal Ecology*, *20*, 175–185. https://doi.org/10.1016/j.funeco.2015.12.009

Spehn, E. M., Rudmann-Maurer, K., & Körner, C. (2012). Mountain biodiversity. *Plant Ecology and Diversity*, *4*, 301–302. https://doi.org/10.1080/17550874.2012.698660

Stevens, G. C. (1992). The elevational gradient in elevational range: An extension of Rapoport's latitudinal rule to altitude. *American Naturalist*, *140*, 893–911.

Sulzbacher, M. A., Grebenc, T., Jacques, R. J. S., & Antoniolli, Z. I. (2013). Ectomycorrhizal fungi from southern Brazil – A literature-based review, their origin and potential hosts. *Mycosphere*, *4*, 61–95. https://doi.org/10.5943/mycosphere/4/1/5

Sulzbacher, M. A., Grebenc, T., Nouhra, E. R., Giachini, A. J., Martín, M. P., & Baseia, I. G. (2019). *Hysterangium atlanticum* sp. nov., forms ectomycorrhizae with *Coccoloba* species (Polygonaceae) from the Atlantic rainforest of Northeastern Brazil. *Symbiosis*, *78*, 275–286. https://doi.org/10.1007/s13199-019-00617-3

Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N. S., Wijesundera, R., Ruiz, L. V., Vasco-Palacios, A. M., Thu, P. Q., Suija, A., Smith, M. E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., … Abarenkov, K. (2014). Global diversity and geography of soil fungi. *Science*, *346*, 1256688. https://doi.org/10.1126/science.1256688

Truong, C., Gabbarini, L. A., Corrales, A., Mujic, A. B., Escobar, J. M., Moretto, A., & Smith, M. E. (2019). Ectomycorrhizal fungi and soil enzymes exhibit contrasting patterns along elevation gradients in southern Patagonia. *New Phytologist*, *222*, 1936–1950. https://doi.org/10.1111/nph.15714

Vanegas-León, M. L., Sulzbacher, M. A., Rinaldi, A. C., Roy, M., Selosse, M.-A., & Neves, M. A. (2019). Are Trechisporales ectomycorrhizal or non-mycorrhizal root endophytes? *Mycological Progress*, *18*, 1231–1240. https://doi.org/10.1007/s11557-019-01519-w

Veloso, H. P. (1992). *Manual técnico da vegetação brasileira*. IBGE.

Větrovský, T., Kohout, P., Kopecký, M., Machac, A., Man, M., Bahnmann, B. D., Brabcová, V., Choi, J., Meszárošová, L., Human, Z. R., Lepinay, C., Lladó, S., López-Mondéjar, R., Martinović, T., Mašínová, T., Morais, D., Navrátilová, D., Odriozola, I., Štursová, M., … Baldrian, P. (2019). A meta-analysis of global fungal distribution reveals climate-driven patterns. *Nature Communications*, *10*, 1–9. https://doi.org/10.1038/s41467-019-13164-8

Wheeler, K. A., Hurdman, B. F., & Pitt, J. I. (1991). Influence of pH on the growth of some toxigenic species of *Aspergillus*, *Penicillium* and *Fusarium*. *International Journal of Food Microbiology*, *12*, 141–150. https://doi.org/10.1016/0168-1605(91)90063-U

White, T. J., Bruns, T., Lee, S., & Taylor, J. W. (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In M. A. Innis, D. H. Gelfand, J. J. Sninsky, & T. J. White (Eds.), *PCR protocols: A guide to methods and applications* (pp. 315–322). Academic Press Inc.

Wicaksono, C. Y., Aguirre Gutierrez, J., Nouhra, E. R., Pastor, N., Raes, N., Pacheco, S., & Geml, J. (2017). Contracting montane cloud forests: A case study of the Andean alder (*Alnus acuminata*) and associated fungi in the Yungas. *Biotropica*, *49*, 141–152.

Wood, J. J., Beaman, R. S., & Beaman, J. H. (1993). *The plants of Mount Kinabalu. 2. Orchids*. Royal Botanic Gardens.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. (2009). *Mixed effects models and extension in ecology with R*. Springer.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Geml, J., Arnold, A. E., Semenova-Nelsen, T. A., Nouhra, E. R., Drechsler-Santos, E. R., Góes-Neto, A., Morgado, L. N., Ódor, P., Hegyi, B., Oriol, G., Ibáñez, A., Tedersoo, L., & Lutzoni, F. (2022). Community dynamics of soil-borne fungal communities along elevation gradients in neotropical and palaeotropical forests. *Molecular Ecology*, 31, 2044–2060. https://doi.org/10.1111/mec.16368