Altitude as environmental filtering influencing phylogenetic diversity and species richness of plants in tropical mountains

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
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Original Article

Altitude as environmental filtering influencing phylogenetic diversity and species richness of plants in tropical mountains

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Abstract: Elucidating how multiple factors affect biodiversity and plant community assembly is a central issue in ecology, especially in vulnerable ecosystems such as tropical mountains. These studies are more relevant in global warming scenarios that induce the upward displacement of plant species towards reduced habitats and hostile environments in tropical mountains. This study aimed to analyze how altitude affects taxonomic and phylogenetic diversity in plant communities of tropical mountains. Thus, we tested if (i) increased altitude works as an environmental filtering promoting decreased species richness, decreased phylogenetic diversity, and increased phylogenetic clustering in these tropical mountains; and if (ii) plant communities of high altitude in tropical mountains are also result of recent diversification with plant species recently split shortening phylogenetic distances between closest related species. We tested effects of altitude on species richness and phylogenetic metrics using linear mixed-effects models. Mount Haleakala presented 114 species, Mount Kilimanjaro presented 231 species and Mount Purace presented 280 species. We found an environmental filtering effect with increasing altitude causing phylogenetic clustering, decreased phylogenetic diversity and decreased species richness. The decreasing phylogenetic distances between closest relatives are congruent with neo-endemics, suggesting recent plant diversification in high altitudes of tropical mountains, possibly driven by geographic isolation and environmental heterogeneity. Consequences of global warming should be monitored in tropical mountains focusing on distribution shifts.

Keywords: Tropical mountains; Global warming; Environmental filtering; Phylogenetic ecology; Assembly rules; Conservation; Mountaintop vegetation

1 Introduction

Understanding how multiple factors determine

the spatial variation of biodiversity is a central issue in ecology and biogeography (Anderson et al. 2011; Machac et al. 2011), which becomes more relevant under the global warming scenario (IPCC 2021a, b). Thus, the basic understanding of the causes and consequences of global warming in plant community assembly also becomes more relevant (Cavender-Bares et al. 2009) especially as rapid climate change challenges species in which evolutionary responses may not be rapid enough to cope with the change, being replaced by other species of warmer climates (Bradshaw and Holzapfel 2006). Mountain ecosystems have been recognized as highly threatened by climate change, and as remarkable distinct systems to evaluate ecological patterns, and their mechanisms (Körner et al. 2017). Thus, there is evidence of upward displacement of many plant and animal species in mountains caused by global warming (Feeley et al. 2011; Telwala et al. 2013; Zu et al. 2021) which alters the community composition, and ecosystem functioning (Fadrique et al. 2018; Gastauer et al. 2020). Consequently, habitat displacement and environmental filtering caused by shift of altitudinal zonal bands can induce many species extinctions (Galván-Cisneros et al. 2021; Zu et al. 2021). However, most previous studies on the altitudinal gradient in mountain ecosystems have been focused on taxonomic species diversity or distribution of few species responding to altitude. Most of these studies point out that there is a tendency to decrease the number of species as altitude increases, and, sometimes, showing a richness peak at intermediate altitudes (Villalba et al. 2005; Chawla et al. 2008; Toledo et al. 2012; Zhao et al. 2017a; Maharjan et al. 2022). Although a pattern emerges from these findings, they do not depict the environmental filtering of altitude as an evolutionary and ecological process that assembles communities.

One of the main causes of the altitudinal gradient in the mountain ecosystems being a driver of community assembly and plant adaptation is because altitude affects temperature (Seastedt & Oldfather 2021). Typically, tropical mountains have more uniform and stable temperature regimes than mountains in temperate regions (Fadrique et al. 2018) because summer and winter for them hardly change temperatures throughout the year, as they are close to the equator. Consequently, temperature stability in the tropics causes sharp temperature barriers in between zonal bands, creating an evolutionary

scenario for tropical species with narrower niches and more limited distribution (Janzen 1967) similar to continental islands (Qian et al. 2021). These stable bands can lead to the so-called 'Wallace Effect' prompting speciation because, differently from geographically isolated populations, isolation mechanisms between species may arise through natural selection between bands where incipient species overlap (Sawyer & Hartl 1981). In tropical mountains, vegetation above the forest line consists of dense shrub vegetation and herbaceous grasslands and is considered biogeographically as continental islands (Sklenář et al. 2014). These cold-climate plant communities are inserted within warm tropics with plant lineages originating from temperate regions contributing to the composition with plant lineages from tropical regions (Sklenář et al. 2014) possibly because of recent diversification in tropical lineages (Campos et al. 2021a, 2021b). Therefore, alpine vegetation bands compared to lower tropical vegetation bands have less species richness with most endemic species (Myers et al. 2000; Hofstede 2003; Carbutt & Edwards 2015) that may maximize phylogenetic effects in their communities. Thus, studying phylogenies of alpine plant communities in tropical mountains and their neo-endemic species can be a way to study altitude as an evolutionary/ ecological factor. Moreover, temperature change in mountains can promote a detectable vertical migration in altitude of plant distributions, since 500 m upwards counteract an increase of 3°C (Peñuelas et al. 2002) enabling studies of vegetation displacement caused by climate change.

Evolutionary and ecological processes interact assembling plant communities and, thus, phylogenetic diversity can help to evidence processes from the evolutionary proximity between species of these communities (Webb et al. 2002; Cavender-Bares et al. 2009) generating hypotheses from the niche theory and neutral theory (Hubbell 2001; Webb et al. 2002; Soberón 2007). Phylogenetic diversity is a component of biodiversity measured in millions of years of each phylogenetic branch of a phylogenetic tree and expresses the set of evolutionary relationships between species and may reflect the diversity of traits (e.g., phenotypic and genetic) that they possess (Faith 1992). The neutrality-based hypothesis postulates that species are equivalent and that community assembly is driven by dispersal limitation and neutral drift within

biogeographical spaces (Hubbell 2001). The niche-based hypothesis suggests that competitive exclusion and environmental filtering are important processes in community assembly at a local scale (Kraft et al. 2015). This hypothesis postulates that abiotic filtering increases under environmental stress (e.g., temperature stress) and resource-limited scenarios (e.g., shallow soils), whereas competition increases as environmental stress decreases (Swenson & Enquist 2009; Violle et al. 2011; Götzenberger et al. 2012). The niche-based hypothesis postulates that species are more likely to be ecologically similar through relationship and niche conservatism (Losos 2008). Thus, less related species coexisting in a community tend to differ in their functional traits allowing resource partitioning (Leibold & McPeek 2006).

When niches are conserved within evolutionary lineages, a filtering promoted by the environment can select closely related, and ecologically similar species (Baraloto et al. 2012; Gastauer & Meira-Neto 2013). Under this assumption, environmental filtering would cause phylogenetic clustering, and species richness decreasing (Table 1), while competition would cause phylogenetic overdispersion and species richness decreasing (Webb et al. 2002). Alternatively, neutral theories suggest stochastic assembly of the community through a neutral process such as dispersal limitation, speciation, or local extinction (Hubbell 2001) that should result in a community that neither differs from the null expectation of random phylogenetic structure nor differs in species richness (Webb et al. 2002; Kembel & Hubbell 2006, Table 1). However, communities shaped by various deterministic processes operating simultaneously in species selection, such as environmental filtering and biotic interactions, can result in the same pattern of random phylogenetic structure (Webb 2000; Cavender-Bares et al. 2009) but species richness decreases. As taxonomic diversity variation along altitudinal gradients results from ecological and evolutionary processes as well (Lomolino 2001; Culmsee & Leuschner 2013), altitude can be a predictor for testing plant diversity patterns and community assembly under the environmental filtering hypothesis if species richness decreasing is

observed along with phylogenetic clustering (Qian et al. 2014; Manish & Pandit 2018; Galván-Cisneros et al. 2021). Environmental filtering has been reported causing phylogenetic clustering downwards in dry environments in mountains, assembling communities dominated by lineages adapted to hot and dry climates (Cornwell and Ackerly 2009; González-Caro et al. 2014; Galván-Cisneros et al. 2021). Upwards, the environmental filtering promotes phylogenetic clustering because it selects lineages adapted to cold environments and shortens phylogenetic distances (Li et al. 2014; Qian et al. 2014; Zhu et al. 2019). Additionally to phylogenetic clustering, the environmental filtering downwards or upwards also causes decreased species richness as less tolerant species are filtered out from communities (Laliberté et al. 2014; Galván-Cisneros et al. 2021).

This study aimed to analyze how altitude alone affects taxonomic and phylogenetic diversity in plant communities of three tropical mountain ecosystems on two continents and on an oceanic island. We tested if (i) increased altitude works as an environmental filtering triggering decreased species richness, decreased phylogenetic diversity, and increased phylogenetic clustering in these tropical mountains; and if (ii) plant communities of high altitude in tropical mountains can be a result of recent diversification with plant species recently split shortening phylogenetic distances between closest related species

2   Materials and Methods

2.1 Data collection

We used three mountains in this study because, to the best of our knowledge, they were the only studies with the appropriate published results to fulfill the meta-analysis that we performed. Checklists with altitude records from three tropical mountains were used as samples in Mount Puracé, Colombia (Rangel & Lozano 1986); Mount Kilimanjaro, Tanzania (Hemp 2006); and Mount Haleakalā, Hawaii, USA (Kitayama & Mueller-Dombois 1992)

Table 1 Phylogenetic structure and species richness of communities under different evolutionary backgrounds of ecological traits and ecological processes

Ecological processes	Conserved traits	Convergent traits	Species richness
Niche theory: Environmental filtering	Cluster dispersion	Overdispersion	Decreased
Niche theory: Limiting similarity	Overdispersion	Clustered or random dispersion	Decreased
Neutral theory: Neutral assembly	Random dispersion	Random dispersion	Unchanged

(Fig. 1). The survey of Mount Puracé (Rangel & Lozano 1986) aimed to describe the vegetation along the altitudinal gradient and consisted of a series of samples with species checklists of the vegetation in 11 different altitudes, from sub-Andean forests at 1020m ASL up to upper Paramo band at 4050m ASL. Only trees, shrubs, lianas and herbaceous species were considered; epiphytes and parasites were excluded. The Mount Kilimanjaro survey aimed to describe the vegetation, find endemic species and elucidate the

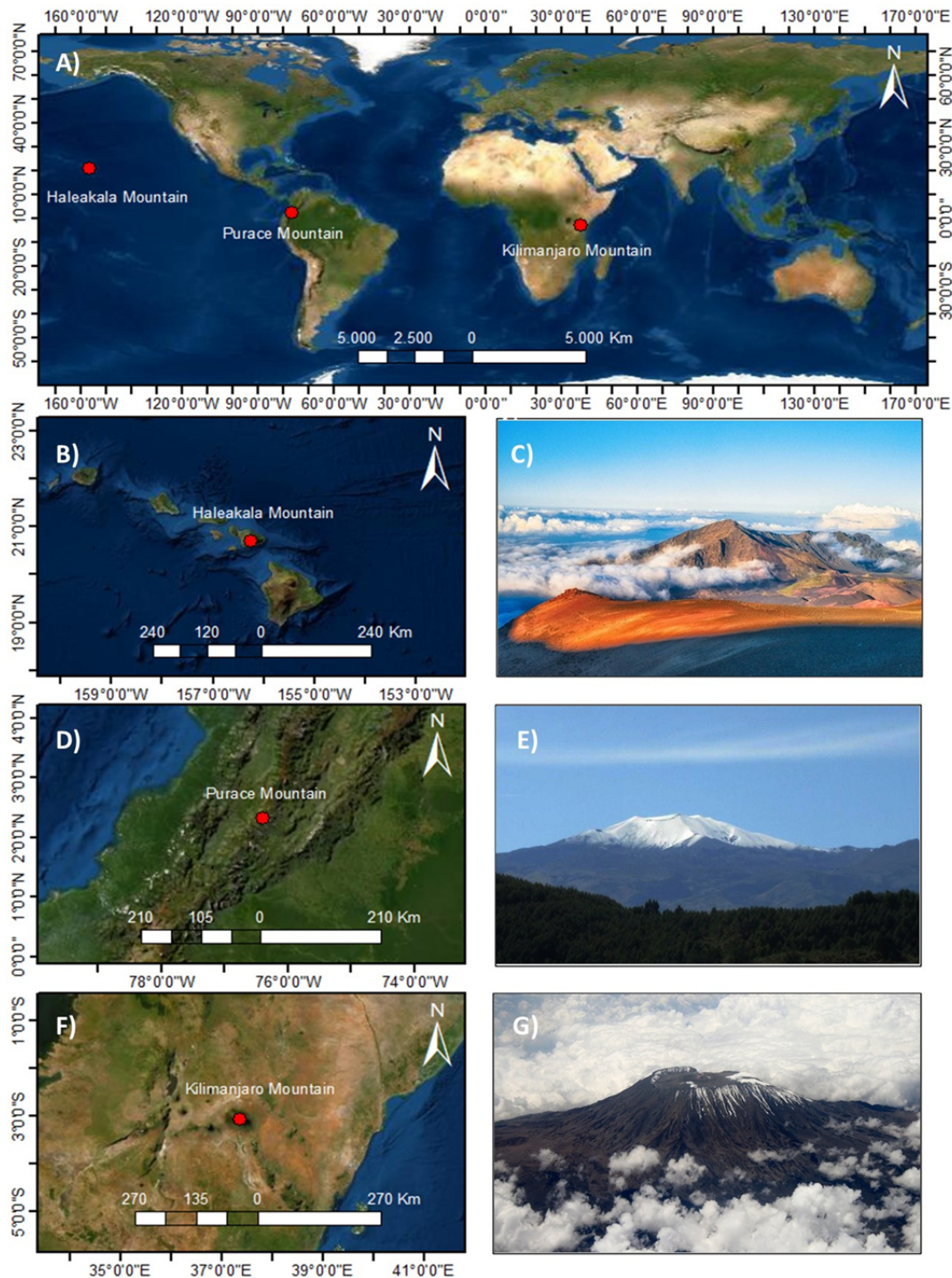**Fig. 1** Location of the study area. Global map (A), Hawaiian Islands indicating the Haleakalā volcano (B), Haleakalā volcano (Photographed by: Fernando Margolles, shutterstock) (C), Andean region of Colombia indicating the Puracé volcano (D), Puracé volcano (Photographed by: Diesalcedo, CC BY-SA 3.0) (E), Tanzania indicating the Mount Kilimanjaro (F) and Mount Kilimanjaro (Photographed by: Muhammad Mahdi Karim, GFDL 1.2) (G).

absence of bamboos band (Hemp 2006); that survey consisted of 21 species checklists of vegetation in different altitudes, from Lowland Forests at 889m ASL up to subalpine heathlands with *Erica* shrubs at 3893m ASL. The survey of Mount Haleakalā (Kitayama & Mueller-Dombois 1992) aimed to describe the vegetation and to study the similarity patterns between altitudinal zonal bands, from lowland forests at 350m ASL up to alpine deserts at 3055m ASL, presenting checklists for each of the eight altitudinal zonal bands (Table 2). As far as we know, these are the only studies in tropical mountains with detailed checklists of many different zonal bands and vegetation types in a range of altitude suitable to test our hypotheses. Altitude was used directly as an environmental factor, although it is a proxy for many associated environmental variables, such as temperature, umidity and soil depth.

2.2 Taxonomic and phylogenetic diversities and structure

In order to test the hypotheses of Table 1 concerning clustering, overdispersion or eveness of phylogenetic diversity and structure, we build phylogenetic trees and calculate the indices as described below.

A phylogeny of the studied species was generated from the largest dated mega-tree for vascular plants (Open Tree of Life) using the '*V.PhyloMaker*' package (Jin and Qian 2019). This mega-phylogeny was derived from two recently published, dated mega-trees, which were based on molecular markers and included 74,533 species representing all the families of extant vascular plants (Jin and Qian 2019). We used the p*hylo.maker* function that makes phylogenetic hypotheses under scenario 3, whereby the tips of a new genus or species not included in the mega-tree are bound at the half-point of the family or genus branch, representing the branch between the family and genus root node and the basal node (for further details, see Jin and Qian 2019). Scenario 3 adds species as polytomies within their parental clades and assigns branch lengths using BLADJ (Jin and Qian 2019).

For each vegetation strip or zone a taxonomic list

was extracted. From each phylogenetic tree, we calculated the lineage diversity as the total phylogenetic branch length [phylogenetic distance (PD)] for each vegetation zonal band (Faith 1992). We standardized PD for genus-level richness [i.e. standardized effect size of PD (ses.PD)]. The standardized PD measures how PD deviates from a null expectation generated by randomly shuffling the tips of the phylogeny and recalculating the PD in communities (Kembel 2015). We calculated mean pairwise phylogenetic distance (MPD) as a measure of the average phylogenetic distance between all combinations of pairs of individuals (including conspecifics); we calculated mean nearest taxon distance (MNTD) to be the mean phylogenetic distance from each taxon to its closest relative in the community (Webb 2000; Webb et al. 2002). We also evaluated the standardized effect size of MPD (ses.MPD) and the standardized effect size of MNTD (ses.MNTD). These derived metrics are equivalent to the inverse of the net relatedness index (NRI) and nearest taxon index (NTI), respectively, described by Webb (2000). Positive standardized effect size (ses) values indicate phylogenetic overdispersion (species more distantly related to each other than expected by chance), whereas negative values indicate clustering (species more closely related to each other than expected by chance). For the standardized effect size calculations, our tree was compared with 10,000 null model randomizations using the algorithm '*phylogeny pool*'. We calculated these metrics using the '*picante*' package (Kembel 2015). All phylogenetic analyzes were performed in R 4.0.4 (R Development Core Team 2021).

2.3 Statistical analysis

We used linear mixed-effects models (LMMs, with random and fixed effects) to test the main effects of altitude on different phylogenetic metric (PD, MPD, ses.MNTD) and species richness (response variables). Predictors with fixed effects (continuous explanatory variables) were grouped into two categories of diversity dimensions, such as taxonomic (i.e. species richness), and phylogenetic metrics (PD, MPD, ses.MNTD). The three mountains were considered as

Table 2 Mountains' location and altitude range of the data used in the analyses.

References	Mountain	Location	Altitude (m)
Rangel & Lozano 1986	Puracé	Huila, Colombia	1020-4050
Hemp 2006	Kilimanjaro	Kilimanjaro Region, Tanzania	998-3893
Kitayama & Mueller-Dombois 1992	Haleakalā	Maui Island, Hawai, EUA	350-3055

a random effect (1│Mountain) in all models (i.e. Campos et al. 2021a, b). The most suitable distribution and function was tested (i.e., normality was confirmed by the Q-Q graph and Shapiro–Wilk test); after that the distributions of residuals were checked. Thus, the Gaussian error distribution could be confirmed (Crawley 2009; Zuur et al. 2009).

The main effect of altitude as explanatory variable on each response variable using the following Eq. 1:

$$lmer(formula=ntaxa \sim Altitude+(1|mountain)) \quad (1)$$

where ntaxa= species richness that can be changed by phylogenetic metrics as response variable. Each response variable was used in different univariate models based on the LMM (equation1). All models were calculated using the package "lme4" (Bates et al. 2014) in the platform R (R Development Core Team 2021). We also used the estimates of the predictors' coefficients to interpret parameter estimates on a comparable scale using the "jtools" package (Long 2021). For example, Adjusted R2 is a corrected goodness-of-fit (model accuracy) measure for classical linear models. To produce the graphs for this study, we used the "ggplot2" package (Wickham 2016). All analyses were run in R 4.0.1 (R Development Core Team 2021).

3 Results

3.1 Species richness

A total of 626 angiosperms species were compiled across all the vegetation surveys of the three mountains. A total of 114 angiosperms species were compiled in samples of the Mount Haleakalā, which belonged to 81 genera, 40 families and 22 orders; the most species-rich families in the Mount Haleakalā species pool were Poaceae (N = 14), Cyperaceae (N = 10), and Rubiaceae (N = 9) (Fig. 2, Appendix 1). A total of 280 angiosperms species were compiled in samples of the Mount Puracé, which belonged to 181 genera, 78 families and 39 orders; the most species-rich families in the Mount Puracé species pool were Asteraceae (N = 28), Rubiaceae (N = 18) and Poaceae
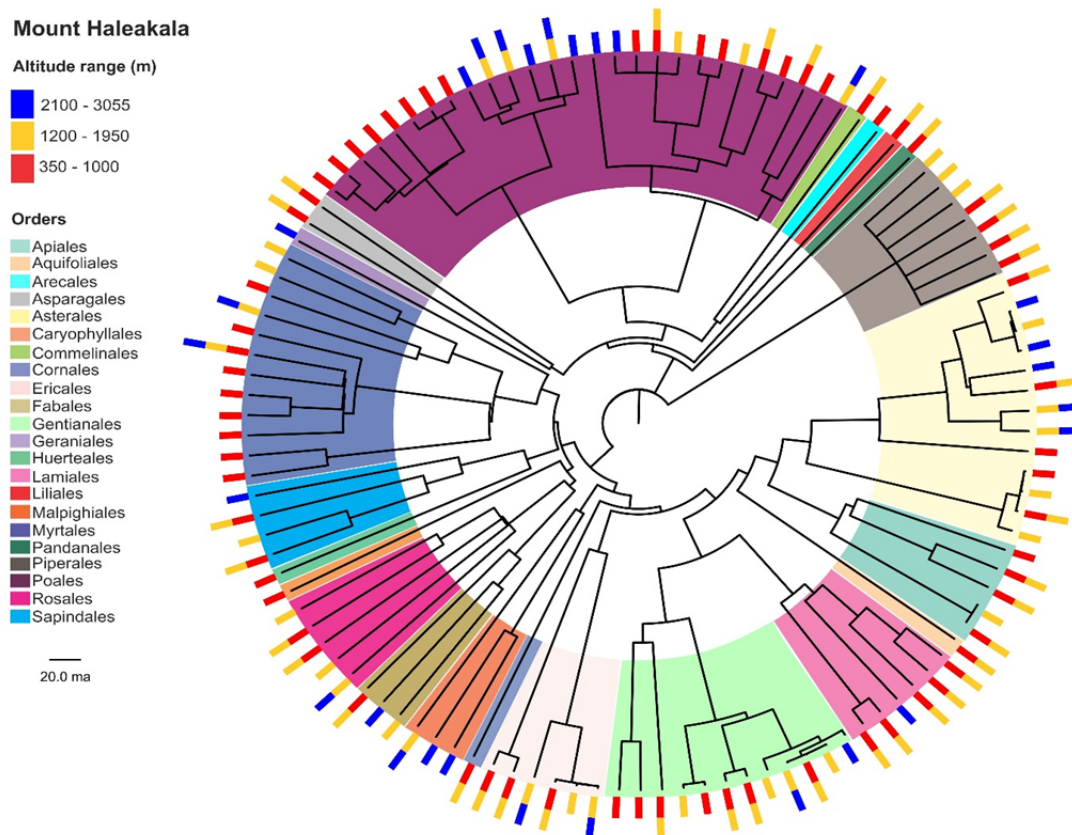

Fig. 2 Phylogenetic tree of plant communities of Mount Haleakala. Orders and altitudinal ranges are indicated by colors, and lineages ages are indicated by branch lengths according to the legend. Phylogenetic divergence scale is indicated in millions of years (ma).

(N = 18) (Fig. 3, Appendix 2). A total of 232 angiosperms species were compiled in the samples of the Mount Kilimanjaro, which belonged to 176 genera, 72 families and 33 orders; the most species-rich families in the Mount Kilimanjaro species pool were Asteraceae (N = 22), Rubiaceae (N = 21) and Poaceae (N = 14) (Fig. 4, Appendix 3).

3.2 Phylogenetic diversity and structure

We found a phylogenetic clustering associated with the altitude based on the tested model. Thus, species richness, ses.PD, ses.MPD and ses.MNTD are explained by the altitude, which consistently suggested a significative and negative effect in all tested models (Fig. 5, Table 3). The first model show that altitude significantly and negatively affected the

species richness (LMM, Estimate = -0.01, t = -4.83, p = 0.001) (Fig. 5A, Table 3). The ses.PD was negatively (i.e., phylogenetic clustering) influenced by the altitude (LMM, Estimate = -0.01, t = -3.73, p = 0.001) (Fig. 5B). Moreover, we observed that variation of ses.MPD was significantly and negatively affected by Altitude (LMM, Estimate = -0.01, t = -3.84, p < 0.001) (Fig. 5C, Table 3). Finally, the altitude had a weak negative effect on ses.MNTD (LMM, Estimate = -0.001, t = -2.86, p = 0.01) (Fig 5D, Table 3).

4 Discussion

We used only three mountains to produce results, the only three studies with adequate data to use. Although there is no statistical limitation in terms of
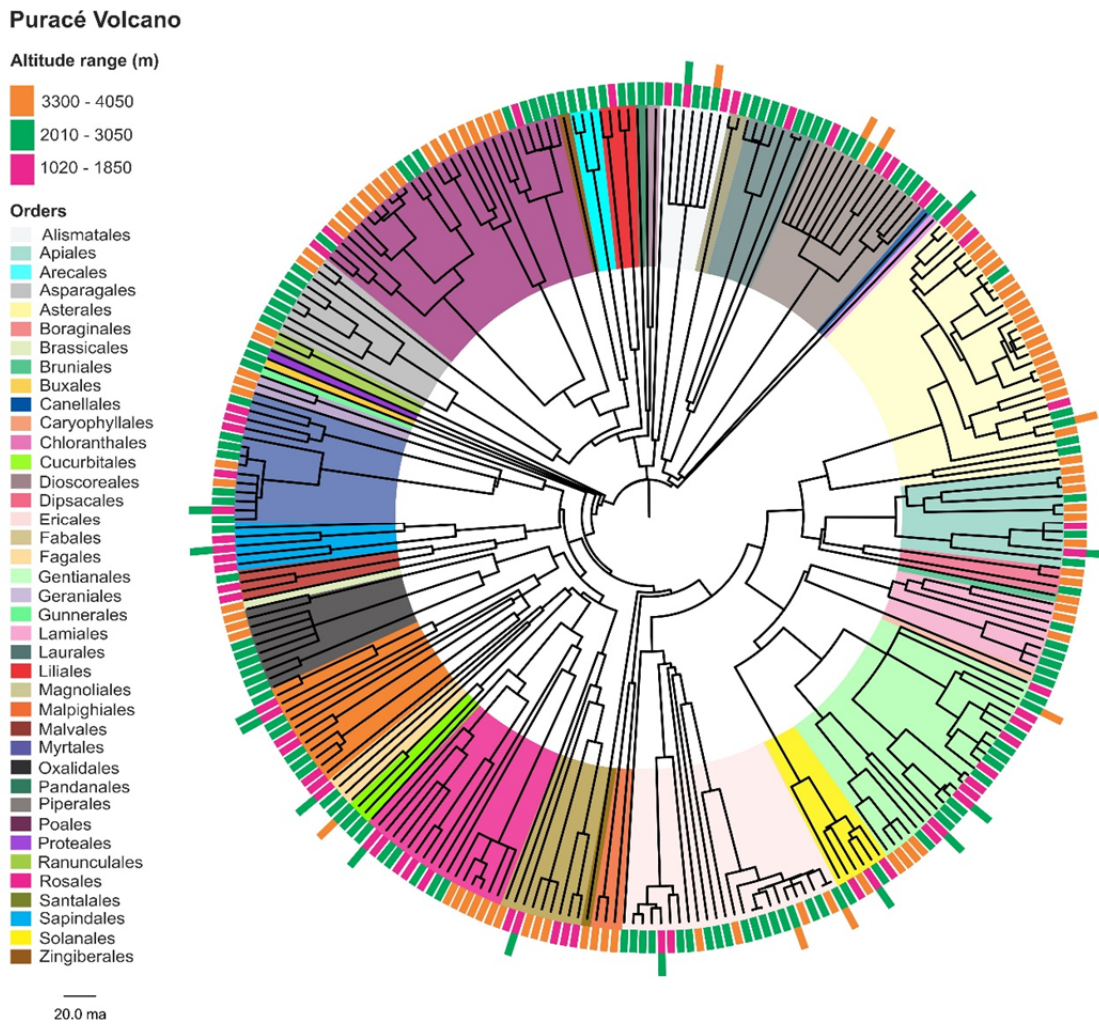

Fig. 3 Phylogenetic tree of plant communities of Mount Puracé. Orders and altitudinal ranges are indicated by colors, and lineages ages are indicated by branch lengths according to the legend. Phylogenetic divergence scale is indicated in millions of years (ma).
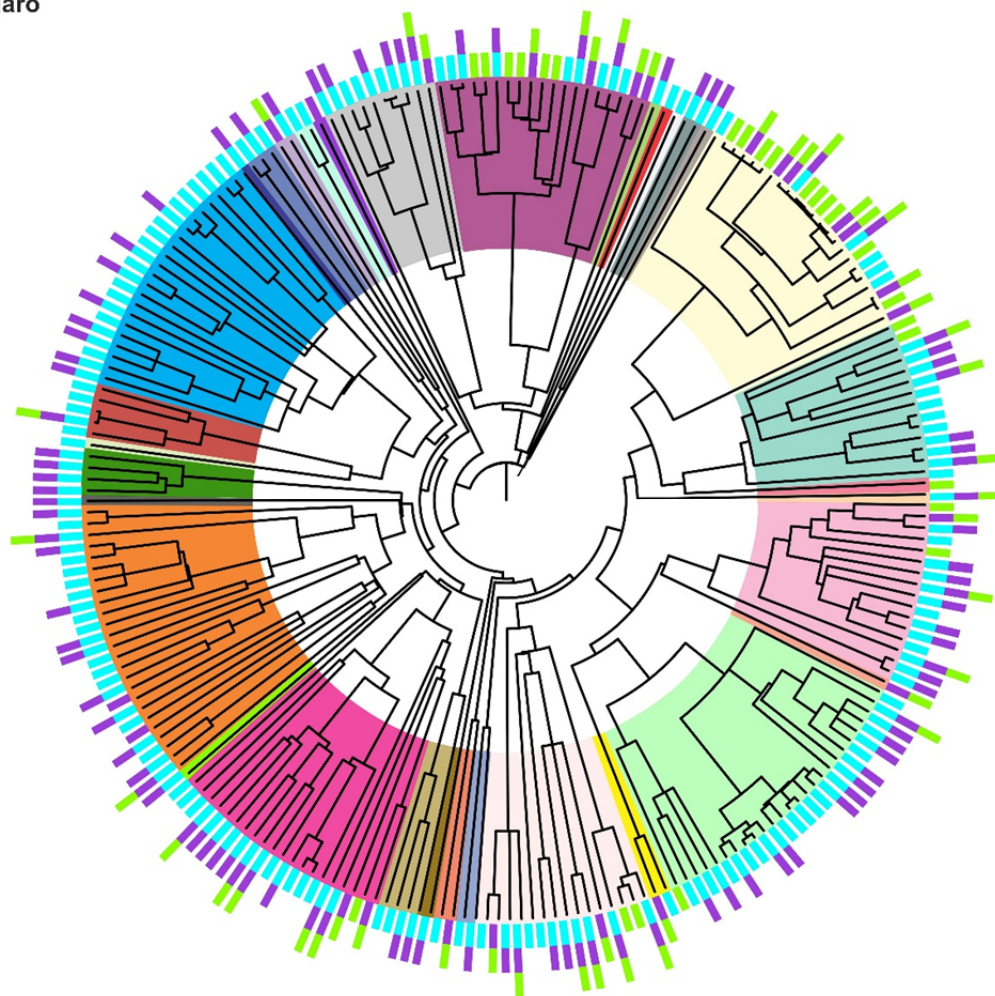
Fig. 4 Phylogenetic tree of plant communities of Mount Kilimanjaro. Orders and altitudinal ranges are indicated by colors, and lineages ages are indicated by branch lengths according to the legend. Phylogenetic divergence scale is indicated in millions of years (ma).

repetition, the few tropical mountains in this study require that the interpretation be made recognizing its limitations. The results show that as altitude increases in the studied tropical mountains, the plant communities show a general pattern of decreasing species richness, decreasing phylogenetic diversity, decreasing mean phylogenetic distance between species and decreasing phylogenetic distances between the closest related species. Therefore, the results suggest that the two working hypotheses were confirmed. The results show expected effects of environmental filtering in high altitudes of tropical mountains that are commonly referred as harsh (Bremer & Sander 2000; Neri et al. 2017; Gastauer et al. 2020). Therefore, the results are congruent with the environmental filtering promoted by increasing altitude with negative effects on species richness, phylogenetic diversity and phylogenetic distances

(Laliberté et al. 2014; Aldana et al. 2017). Congruent results of taxonomic diversity and phylogenetic structure were found in some temperate mountains (Qian et al. 2014, 2020; Zhao et al. 2017b; Xu et al. 2017; Manish & Pandit 2018), and to a lesser extent in tropical mountains (Cuesta et al. 2017; Worthy et al. 2019). Especially relevant in our results is that the environmental filtering at high altitudes generates plant communities with shortened phylogenetic distances between closest relatives. This is an expected pattern in communities with many species originated from recent diversification (see Beaman & Beaman 1990). Additionally, as high altitude regions tend to be more sensitive to the global warming forecasted for the 21st century than low altitude regions (Rangwala and Miller 2012), the results suggest a highly adapted mountaintop flora facing a strong influence of global warming. However, further

studies are needed to deepen our understanding of the status of the threatened tropical mountaintop flora.

Our results suggest that in tropical mountains the pronounced environmental filtering in high altitudes assembles communities with shortened phylogenetic distances between closest relatives (Machac et al. 2011). Although more studies are needed to reaffirm the causes of such shortened phylogenetic distances, our results are congruent with the hypothesized recent diversification in these continental islands of cold climate surrounded by warm tropical zones. These neighboring zones can generate areas of quick speciation and one of the possible causes is the 'Wallace Effect' that split incipient species occupying bordering zones that quickly isolate from each other due to strong selective pressure for reproductive isolation where their distributions overlap (Sawyer & Hartl 1981). A recurrent generation of species in higher altitudes coming from the same phylogenetic lineages of lower altitudes could explain the expressive number of species arisen recently (neo-endemics) (see Beaman & Beaman 1990) as well as could explain the closest phylogenetic distances among closest relatives found in communities of high altitudes. These findings are congruent with mountains as major centers of endemism at a global scale influenced by the high environmental heterogeneity and strong geographic isolation (Trigas et al. 2013; Noroozi et al. 2018).

The phylogenetic trees show that the environmental filtering promoted by the altitude allows that most of the species occur only in one or two zonal bands, suggesting an upwards decreasing species richness, as well as suggesting a specialized flora of each zonal band. The environmental filtering promoted by the increasing altitude in tropical mountains suggest that other factors associated with altitude, such as temperature, are drivers (Buytaert et al. 2006; Rada et al. 2019) which affect community composition and species richness patterns (Kerkhoff et al. 2014; Klanderud et al. 2015; Bagousse - Pinguet et al. 2017; Qian et al. 2021). Congruently with other findings, our results suggest that as altitude varies, temperature varies in tropical mountains, causing downward or upward environmental filtering (Galván-Cisneros et al. 2021). Environmental filtering downwards is an observed pattern for forests in dry
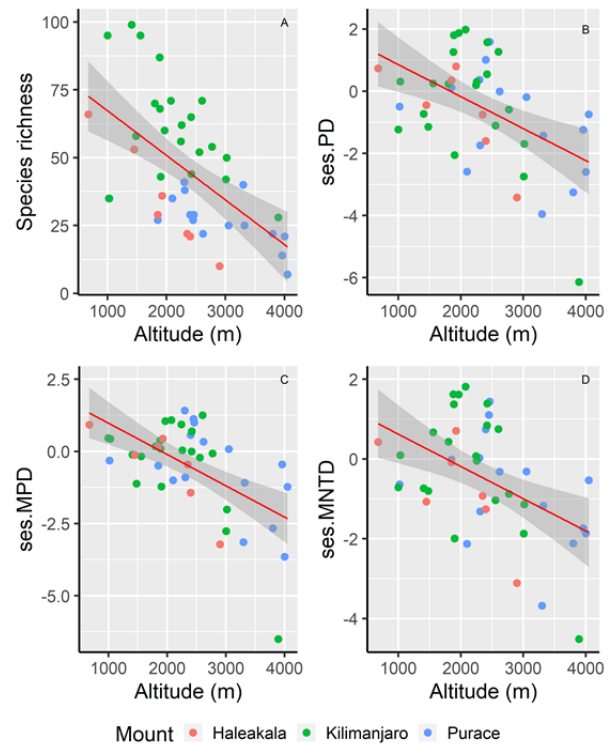

Fig. 5 Relationships between altitude and (A) species richness, (B) standardized effect size of phylogenetic distance - ses.PD, (C) standardized effect size of mean pairwise phylogenetic distance - ses.MPD, and (D) standardized effect size of mean nearest taxon - ses.MNTD. Solid lines represent fitted (predicted) model's values, and the shaded polygons are the 95% confidence interval associated with the modeled predictions.

Table 3 Linear mixed models (LMM) explain the relationships between phylogenetic metrics (PD, MPD, MNTD, ses.PD, ses.MPD, ses.MNTD) altitude. ses.PD: standard effective size of phylogenetic diversity; ses.MPD: standard effect size of mean pairwise distance); ses.MNTD: the standard effective size of mean nearest taxon. Models with significant effects (*) are indicated.

Random effects (variance)	Model	R^2	Estimate	t	p
0.50	Richness ~ Altitude	0.63	-0.01	-4.83	0.001*
0.54	PD ~ Altitude	0.68	-0.90	-5.76	0.001*
0.09	ses.PD ~ Altitude	0.24	-0.01	-3.73	0.01*
0.38	MPD ~ Altitude	0.58	-0.01	-5.14	0.001*
0.02	ses.MPD ~ Altitude	0.34	-0.01	-3.84	0.001*
0.30	MNTD ~ Altitude	0.29	-0.010	-0.20	0.84
0.05	ses.MNTD ~ Altitude	0.23	-0.001	-2.86	0.01*

and hot environments in zonal bands of low altitudes (Cornwell & Ackerly 2009; González-Caro et al. 2014), and was not suggested by our results in the three studied sites possibly because it is not the predominant environmental filtering or because the altitude range of this study was not suitable to detect the environmental filtering in the lowest zonal bands (see Galván-Cisneros et al. 2021). Our results suggest an environmental filtering that increases upwards from communities that have high species richness and high phylogenetic diversity below forest lines (Qian et al. 2014; Campos et al. 2021a) contrasting with alpine vegetation of higher altitudes, and above the forest line with lower species richness, lower phylogenetic diversity, and phylogenetically clustered (Li et al. 2014; Qian et al. 2014; Zhu et al. 2019). Therefore, the suggested environmental filtering in the studied tropical mountains associated with the increasing altitude could be caused by other environmental factors as decreasing temperatures that negatively affect species richness, phylogenetic diversity, and phylogenetic distances.

Downwards, below the treeline, phylogenetic overdispersion of plant communities is possibly caused by the increasing abundance of eudicots and magnoliids clades. Below the treeline, the Rubiaceae family (eudicot) showed the highest number of species. Below the treeline, Rubiaceae was followed in number of species by Piperaceae (magnoliid) on Mount Kilimanjaro and Mount Haleakala. The importance of the Rubiaceae family in mountain forest systems is widely known, having representation as trees, shrubs and herbs (Anderson 1995; Richter 2008; Cirimwami et al. 2019). However, Asteraceae was the dominant family in our analyses because it is the best represented family in alpine ecosystems of the world (Pegoraro et al. 2020; Lencinas et al. 2021; Brochmann et al. 2021). The species richness of Asteraceae is assigned to their ability to colonize harsh environments under severe stress conditions with a broad array of adaptations (Knox & Palmer 1995; Ornellas et al. 2019; Zhang et al. 2021). Monocots as Poaceae, Cyperaceae, and Juncaceae stood out in the alpine vegetation of the three mountains, where genus such as *Carex* and *Luzula* were common. These lineages are diversified and dominant above the treeline in phylogenetically clustered communities of alpine vegetation (Ndiribe et al. 2013; Venn et al. 2014; Schubert et al. 2020).

The results show some species of high altitude closely related to other of lower altitudes in the three studied mountains suggesting neo-endemisms, as *Carex* species in Mount Haleakala, *Senecio* species in Mount Kilimanjaro and *Lachemilla* species in Mount Puracé. Another example of possible neo-endemism in Andes is the genus *Lupinus*, Fabaceae, that has at least 81 endemic species in Andes (Hughes and Eastwood 2006), with three species occurring in Mount Puracé. It is also remarkable that Asterales, Poales and Ericales orders (all eudicots) have many adapted species to high altitude in the three studied mountains. These examples are among many other that can be observed in the presented phylogenetic trees. Although it is not certain that these examples are actual neo-endemics, the results of the phylogenetic trees with shortened phylogenetic distances between closest relatives are congruent with neo-endemisms. If this congruence is true, such evolutionary feature could be prompted because the temperature stability in tropical mountains harbors species with narrow niches and limited distribution driven by sharp temperature barriers in between band zones (Janzen 1967; Cuesta et al. 2020).

A possible explanation of the different species number among the studied mountains is given by the classical model of species number provided by the Island Biogeography Theory (MacArthur & Wilson 1967). For example, the Hawaian Mount Haleakala has the fewer surveyed plant species by far (114 species) compared to Mount Kilimanjaro (231 species) and Mount Purace (280 species), congruently to a tropical mountain that creates an island of cold climate in tropics inside an oceanic island. Species richness of Mount Kilimanjaro in Africa and Mount Puracé in South America might be boosted during glacial periods when alpine vegetation occupied lower altitudes in a much larger continental area with merging alpine islands that mixed floras and promoted rapid species diversification (Madriñán et al. 2013). Such species richness booster would not be possible in Mount Haleakala, an island in the middle of the largest ocean on Earth.

Global warming can be a major conservation threat to the specialized flora of the tropical mountains, especially on mountaintops (Hamid et al. 2020; Steinbauer et al. 2022; Kidane et al. 2022). Firstly, as the zonal bands move upwards they would face a decreasing distribution area, a threat *per se* because species-area relationships states the smaller the area, the smaller the species number (see

Rosenzweig 1995). Secondly, the zonal bands of vegetation besides smaller with their upwards displacement would be more disconnected, with lower immigration rates and with higher extinction rates (Sklenář et al. 2014), decreasing the species richness (MacArthur & Wilson 1963, 1967) in an opposite way to the glacial periods. During the glacial periods, the downward displacement of zonal bands possibly merged islands of mountain vegetation on much larger areas (Madriñán et al. 2013). Finally, if global warming is causing an upward movement of zonal bands, plants populations could be displaced to recently deglaciated areas with thin, poor and exposed soils, a situation that initiates centuries-long primary successions (FAO - Food and Agriculture Organization of the United Nations 2015; Llambí et al. 2021). For many purposes, including conservation and restoration, the boundaries of species distributions will be especially useful to check range shifts (Parmesan & Yohe 2003). For example, habitat suitability models predicted an altitude increase of trees species distributions in mountains and a concomitant decrease in cover of tussock grasses, caulescent rosettes and small-leaved sclerophyllous shrubs (Arzac et al. 2019). The Tropical Andean alpine species showed highest vulnerability to climate change because the spatially more restricted species near the equator (e.g., Páramo endemics) are at the same time the most vulnerable to warming (Cuesta et al. 2020). Altitudinal changes in zonal bands of tropical mountains could occur in a time scale that may overwhelm ecological and evolutionary processes, especially among mountaintop species (see Parmesan 2006) of the most specious families and orders. Thus, some threats could not to be overcome only by ecological and evolutionary processes and the scenario is that the tropical mountain vegetation could be highly impacted with loss of evolutionary history. More studies, efforts and actions are needed to deepen the knowledge of the current threatened status of tropical mountain flora, especially the mountaintop flora. Global warming and its consequences should be monitored in tropical mountains worldwide, focusing on range shifts and prioritizing mountain vegetation's highest zonal bands. If the worst scenario discussed above is true, dead-ends around tropics will threaten mountaintop floras very soon.

5 Conclusions

Our results of taxonomic and phylogenetic diversity analyses suggest that environmental filtering could be the predominant force that structures the distribution of plant communities along elevational gradients in three tropical mountains, two continental and one oceanic. As a general result, increasing altitude could cause negative effects on species richness, phylogenetic diversity, and phylogenetic distances promoting phylogenetic clustering.

The findings highlight the patterns of diversity and phylogenetic structure as essential in tropical mountains conservation especially because these ecosystems are increasingly more susceptible to climatic changes and anthropic pressures. Tropical mountains harbor a rich endemic flora, and the distribution of plant species would be changing triggered by global temperature changes. As a consequence, plant species located in the highest bands of vegetation might be threatened as they would not have higher altitudes to move to. Therefore, plant lineages occurring at high altitudes, many of them endemic and recently originated might be at greater risk of succumbing to climate change. For this reason, the selection of areas for protection should consider the prioritization of communities with high endemism, high taxonomic and high phylogenetic diversity to improve the chances of biodiversity conservation, especially the mountaintop vegetation of tropical mountains.

Electronic supplementary material: Supplementary material (Appendixes 1-3) is available in the online version of this article at https://doi.org/10.1007/s11629-022-7687-9.

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