

Connecting plant evolutionary history and human well-being at Mt. Kilimanjaro, Tanzania

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Evolution is the source of all living organisms and hence the foundation for the ecosystem services that are directly supported by biodiversity. However, explicit connections between evolutionary history and human well-being are barely explored. Here, we focus on ethnobotanical data from Mt. Kilimanjaro (Tanzania) to identify significant associations between plant evolutionary lineages and six previously recognized usage guilds in the mountain (i.e. fodder, building material, fuelwood, food, ornamental/shading and traditional medicine), and further characterize the degree of phylogenetic overlap between the guilds using beta diversity metrics. In addition, we also explore how phylogenetic diversity of usage guilds varied along elevation and between natural and anthropized habitats. Our results suggest that the inhabitants of Mt. Kilimanjaro rely on multiple and deep lineages that specifically provide a certain type of service, supporting the notion that an increased number of lineages captures more current biodiversity benefits. However, we also found a few lineages that provided multiple benefits, indicating that particular efforts should be pursued in preserving individual multi-functional lineages of the phylogeny. Elevation was the most important factor explaining phylogenetic diversity of useful plants, whereas the effect of anthropogenic disturbance was comparatively weak. However, after controlling for the effect of elevation, a moderate negative effect of human disturbance was revealed, particularly for medicinal plants. Phylogenetic diversity of most guilds showed hump-shaped curves with elevation, revealing a major reservoir of useful plant lineages in the highly threatened montane forests of Mt. Kilimanjaro.

ADDITIONAL KEYWORDS: ecosystem – ethnobotany – evolution – phylogenetic diversity – phylogenetic domains – services.

INTRODUCTION

Evolution has enabled the extraordinarily diverse range of plant living variation that provides many essential goods for humans, including pharmaceutical products, fodder, fuelwood, timber, food and species with aesthetic features among others (MEA, 2005). This human-centric value of plant evolutionary legacy has brought to light the foundation that evolutionary history may inform sites or taxa that are particularly valuable for conservation (Forest *et al.*, 2007; Faith, 2016).

Theoretical arguments establishing causal relationships between high lineage diversity and human well-being rely on the assumption that the greater the number of lineages represented by a set of taxa, the greater the variety of biological features that are encapsulated, and therefore the greater the probability of retaining unknown benefits and evolutionary potential for future ones (i.e. the so-called ‘option values’; Faith *et al.*, 2010). However, despite theoretical foundations being deeply grounded in the literature since the 1990s (Vane-Wright, Humphries & Williams, 1991; Faith, 1992; Crozier, 1997), empirical evidence connecting plant evolutionary history and human-centric benefits is still scarce and fragmentary

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(Tucker *et al.*, 2019). To fill in this gap, we advocate the use of traditional ethnobotanical knowledge (Díaz *et al.*, 2018) in combination with modern phylogenetic methods (Garnatje, Peñuelas & Vallès, 2017).

It has been argued that species that are used to meet a certain human need (hereafter ‘usage guild’) may be over-represented in the so-called ‘hot nodes’ of the phylogeny (i.e. phylogenetic nodes including significantly more useful species than expected for a given usage guild), which would facilitate the direction of bioprospecting exercises (Garnatje *et al.*, 2017). To the extent that such hot nodes were guild-specific, preserving a multi-functional natural plant ‘storehouse’ would require the maintenance of multiple evolutionary lineages (Fig. 1). Alternatively, usage guilds might be clumped in a few multi-functional hot nodes (i.e. great phylogenetic overlap between guilds), in which case the latter should be major priority targets in conservation planning. Finally, if usage guilds were randomly distributed with respect to phylogeny, clade identity would not be informative on extant benefits, thus representing the worst-case scenario for phylogenetic bioprospecting (Rønsted *et al.*, 2012).

Here, we focused on ethnobotanical data from Mt. Kilimanjaro (Tanzania) to identify significant associations between plant evolutionary lineages and six previously recognized usage guilds in the mountain (i.e.

fodder, building material, fuelwood, food, ornamental/shading and traditional medicine: Hemp, 1999; Mollel, Fischer & Hemp, 2017) and further characterized the degree of phylogenetic overlap between the guilds using beta diversity metrics. In addition, we explored how phylogenetic diversity of usage guilds varied along the elevational gradient of Mt. Kilimanjaro and between natural and anthropized habitats (Table 1). This region represents an ideal setting for our study because the well-being of a substantial fraction of the local population depends on the direct collection of natural resources (Hemp, 1999; Mollel *et al.*, 2017). Further, Mt. Kilimanjaro encompasses the two main axes of variability of global change, i.e. a great climatic gradient (the highest elevational gradient in Africa) and dramatic changes in land-use intensity (Sala *et al.*, 2000), and thus it may serve as a natural laboratory to explore biodiversity change scenarios.

MATERIAL AND METHODS

STUDY AREA

Mt Kilimanjaro is a dormant stratovolcano located in northern Tanzania (between 2°45′ and 3°25′ South and 37°00′ and 37°43′ East) and forms part of the Afromontane biodiversity hotspot

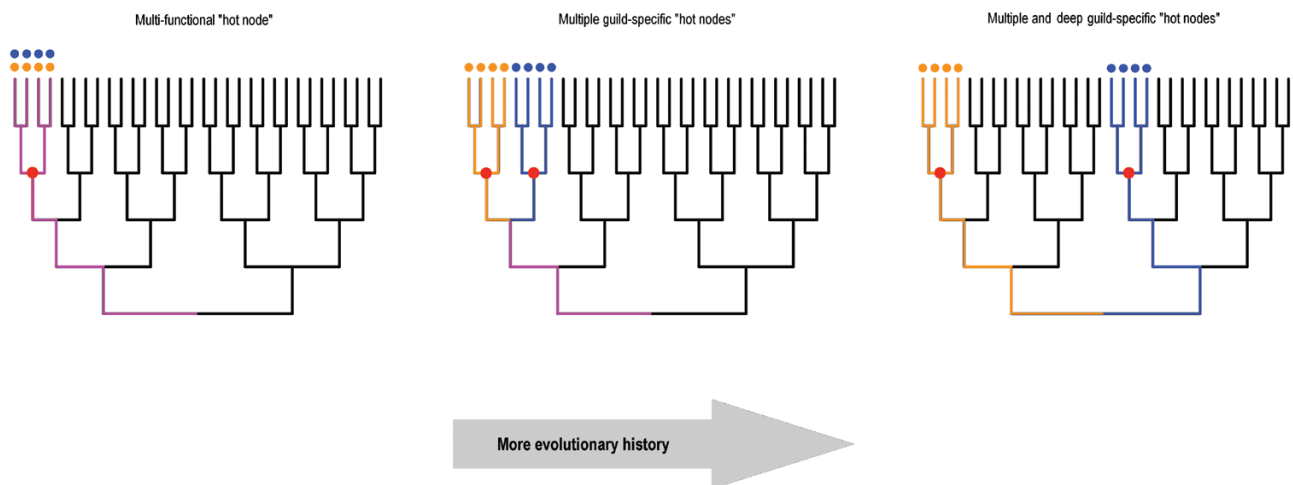


Figure 1. Hypothetical example showing the phylogenetic distribution of two usage guilds (circle symbols of the same colour on the phylogenetic tips, representing species) under three different scenarios. The most inclusive ‘hot nodes’ (phylogenetic nodes that include significantly more useful species than expected) are represented for each guild by red circles. The blue and orange branches of the phylogenetic tree are unique to each guild, whereas pink branches are shared. The nodes where the blue and orange colours meet represent the most recent common ancestors of the hot nodes in each scenario. In the first scenario (left phylogenetic tree), the only hot node includes both guilds (i.e. multi-functional hot node) and thus the phylogenetic overlap between the guilds is maximum. In the second scenario (central phylogenetic tree), each guild is included in a different hot node, but the most recent common ancestor of the hot nodes is relatively recent (intermediate phylogenetic overlap). In the third scenario (right phylogenetic tree), each guild is also included in a different hot node, but the most recent common ancestor of the hot nodes splits deep in the temporal scale (minimum phylogenetic overlap). Scenarios are sorted in increasing order of amount of evolutionary history that is encapsulated by the two guilds together (from left to right).

Table 1. Main natural and anthropized related habitats of Mt. Kilimanjaro (southern slope)

Elevational belt	Elevation range (m)	Natural ecosystems	Anthropized ecosystems
6	4000–4500	<i>Helichrysum</i> scrubland	-
5	3000–4000	<i>Erica</i> forest	<i>Erica</i> burned bushland
4	2700–3000	<i>Podocarpus</i> forest	<i>Podocarpus</i> burned forest
3	2100–2700	<i>Ocotea</i> forest	<i>Ocotea</i> logged forest
2	1100–1800	Lower montane forest	Grasslands Chaggas Coffee plantations
1	800–1100	Savanna woodlands	Maize fields

(Myers *et al.*, 2000). Here, we focused on the southern face of the mountain, where a higher number of habitat types can be recognized compared to the more homogeneous northern face (Hemp, 2006a; Table 1). The lowest vegetation belt is located between 800 and 1100 m, and the natural vegetation includes savanna fragments that are being increasingly transformed into maize fields (Hemp, 2006a). In the densely populated area between 1100 and 1800 m, the remnant natural vegetation is represented by patches of the lower montane forest, which has been progressively transformed into different land-uses. In this elevational range, the most abundant habitat is the traditional agroforestry system (the ‘Chagga’ homegardens), where farmers grow different smallholder crops under large forest trees (Hemp, 2006b). Coffee plantations also cover extensive areas of the lower montane belt, whereas the steepest parts of the landscape, which are not suitable for agriculture, are dominated by montane grasslands that are frequently cut to obtain forage for the livestock. At mid-elevations (2100–2700 m), the landscape is dominated by middle montane forests of *Ocotea usambarensis* Engl., which are undergoing serious transformation due to illegal logging. The upper montane zone (2700–3000 m) is home to cloud forests of *Podocarpus latifolius* (Thunb.) R.Br. ex Mirb., which are experiencing considerable shrinkage due to increasing aridity and human-induced fires (Hemp, 2005). As such, the resultant vegetation is a mix of slowly regenerating *Podocarpus latifolius* individuals under the canopy of shrubs and tree-like individuals of *Erica excelsa* Tausch. The natural vegetation of the subalpine zone (3000–4000 m) is represented by *Erica excelsa* forest remnants (single-stemmed trees that can reach up to 30 m) that are largely degenerated to small-shrubby vegetation due to recurrent fires (Hemp & Beck, 2001). Finally, the alpine vegetation (4000–4500 m) is shaped by cushion plants of *Helichrysum* Mill. and tussock grasses. Mean annual temperature ranges from 23 °C in the savanna lowlands to –7 °C at 5895 m at Uhuru-peak, and precipitation follows

a hump-shaped curve with a maximum peak at 2200 m (c. 2700 mm) with minimum values between 500–700 mm in savanna and alpine zones (Hemp, 2006a).

VEGETATION SURVEYS AND USEFUL PLANTS

We established five plots (50 × 20 m) in each of the habitats described above (65 plots in total), and recorded all native, naturalized and cultivated species of vascular plants (herbs, shrubs, trees, lianas and epiphytes) occurring in the plots. The surveys were conducted between 2010 and 2012, and plants were identified to the species level following nomenclatural criteria in *The Plant List v.1.1* (2013). Species were assigned to different categories of plant use (usage guilds) according to the information gathered by Molle *et al.* (2017), including publications on useful plants of East Africa and personal interviews with local people on Mt. Kilimanjaro. The usage categories include fodder, building material, fuelwood, food, ornamental/shading and traditional medicine.

PHYLOGENETIC TREE

We used a species-level time-calibrated molecular (DNA) phylogeny including all the species recorded in the study. The phylogenetic tree was inferred with maximum-likelihood methods based on a mixed supertree-supermatrix approach (Roquet, Thuiller & Lavergne, 2013). The maximum-likelihood tree was calibrated using the software TreePL (Smith & O’Meara, 2012) with 57 maximum and minimum divergence age estimations (95% highest posterior density intervals) of major lineages published in Magallón, Hilu & Quandt (2013), Magallón *et al.* (2015) and Rothfels *et al.* (2015). Full details on the phylogenetic procedure are described in Appendix 1.

EVOLUTIONARY LINEAGES AND USAGE GUILDS

We seek the existence of hot nodes in the phylogeny for each usage guild, this is, monophyletic clades with

a significantly high number of useful species (Saslis-Lagoudakis *et al.*, 2011). For each guild, the number of useful species descending from each node i of the phylogeny was counted and compared to a null distribution of values generated by shuffling trait values (i.e. 1 and 0 for useful and non-useful plants for the given guild, respectively) across the tips of the phylogeny 999 times (i.e. standardized effect size (SES) scores):

$$SES.i = \frac{SR_i - \bar{x}_{null}}{\sigma_{null}}$$

where SR_i is the observed number of useful species of a certain guild descending from node i , and \bar{x}_{null} and σ_{null} are the mean and standard deviation of the null distribution (Kembel, 2009). For a nominal alpha of 5%, the richness of useful plants in clade i will be higher than expected for the given null model if the corresponding SES score is > 1.96 . We only evaluated those clades that included ten species or more, since previous studies have documented unacceptable rates of statistical errors for smaller lineages (Parra, McGuire & Graham, 2010).

It is important to note that (1) statistical significance for hot nodes is based on relative richness of useful plants rather than absolute values (i.e. a node including the same number of useful species for two different guilds may not necessarily show the same statistical output for the two guilds), and (2) hot nodes can be nested in the phylogenetic hierarchy. Thus, we defined ‘dense’ phylogenetic domains as the most inclusive hot nodes (MIHNs) that showed a relatively high fraction of useful species ($> 70\%$ of the species descending from the MIHN), ‘soft’ domains as the MIHNs that showed intermediate levels of useful species (50–70% of the species descending from the MIHN) and ‘weak’ domains as the MIHNs that showed a lower fraction of useful species ($< 50\%$ of the species descending from the MIHN). The term ‘phylogenetic domain’ was recently coined by Graham, Storch & Machac (2018) to refer to clades within which a certain attribute of interest (here a high richness of species that provide a specific type of benefit to humans) stays relatively unchanged. Of course, our thresholds are arbitrary and should be modified according to the aim of the study. For example, if the purpose is prioritizing lineages for a resource-consuming bioprospecting project, using higher thresholds would minimize the probability of type I errors (i.e. prioritizing the wrong lineages). Alternatively, the user may also set a smaller nominal alpha to determine the statistical significance of the hot nodes (e.g. nominal alpha of 1% instead of 5%). The computer code to conduct the hot node analysis is provided in Appendix 2 as an R function.

To assess the degree of phylogenetic overlap between the guilds, we explored phylogenetic beta diversity (PBD) between them using the PhyloSor index (Bryant *et al.*, 2008) as a distance metric. The PhyloSor index represents the fraction of evolutionary units (typically branch lengths) that is shared between two samples (here usage guilds), and it ranges between 0 (no branch lengths are shared, minimum overlap) and 1 (all branch lengths are shared, maximum overlap). Thus, PBD is defined as $1 - \text{PhyloSor index}$. PBD can be decomposed into two additive components, namely ‘true’ phylogenetic turnover (hereafter ‘turnover’) and nestedness, which represent different aspects of beta diversity (Leprieur *et al.*, 2012). Briefly, the nestedness component represents the fraction of PBD that is simply due to differences in phylogenetic diversity (PD, the minimum spanning path connecting a set of taxa; Faith, 1992) between the samples (Leprieur *et al.*, 2012). In contrast, the turnover component implies the replacement of an exact amount of evolutionary history (i.e. phylogenetic branches) between the samples, the branches that are replaced being exclusive to each sample. As such, the turnover component represents the fraction of PBD that is independent from differences in PD between the samples. Because PBD and taxonomic beta diversity (TBD) are intrinsically correlated (Bryant *et al.*, 2008; Leprieur *et al.*, 2012), we evaluated whether the observed turnover and nestedness components of PBD were lower or higher than expected for the given species composition in the guild \times species matrix by computing SES scores for each component of PBD and pairwise comparison as:

$$SES.PBD = \frac{PBD_{obs} - \bar{x}_{null}}{\sigma_{null}}$$

where PBD_{obs} is the observed component of PBD (i.e. turnover or nestedness) between the two guilds being compared, and \bar{x}_{null} and σ_{null} are the mean and standard deviation of a null distribution of values generated by shuffling species names across the tips of the phylogeny 999 times (Kembel, 2009). For a nominal alpha of 5%, the observed component of PBD will be significantly lower or higher than expected for the given null model when SES.PBD is lower or higher than -1.96 and $+1.96$, respectively.

According to this null model, lower than expected values in the turnover component would indicate that the replacement of lineages tends to occur towards the tips of the phylogeny (i.e. high phylogenetic overlap between the guilds), whereas higher than expected values would indicate that the replacement involves deeper nodes of the phylogeny (i.e. low phylogenetic

overlap) (Molina-Venegas *et al.*, 2015). To further complement PBD patterns, we also computed TBD using the Sorensen index as a distance metric. The Sorensen index represents the fraction of species that is shared between two samples, and it ranges between 0 (no species are shared) and 1 (all species are shared). Thus, TBD is defined as $1 - \text{Sorensen index}$. Alike PBD, TBD can be decomposed into 'true' turnover and nestedness, the former representing the actual replacement of species as it is corrected for differences in species richness between the samples (Baselga, 2010).

PHYLOGENETIC DIVERSITY OF USAGE GUILDS ALONG ELEVATION AND LAND-USE

We evaluated whether the amount of evolutionary history (i.e. PD) encapsulated by each usage guild varies along the elevational gradient of the mountain and between natural and anthropized habitats. To do so, we pooled all the useful species recorded in the plots into one single sample per habitat type (five plots per habitat, $N = 13$ habitats in total, Table 1), and computed SES.PD scores for each habitat and guild using the complete list of species in the same guild as the reference pool (i.e. a different 'pool phylogeny' for each guild). Then, we fitted different linear and quadratic models using the SES.PD scores as the response variable and elevation (mean elevation of the plots) and land-use type (natural or anthropized) as explanatory variables. We included a quadratic term for elevation in the models because previous studies have reported hump-shaped responses of diversity along the elevational gradient of the mountain (e.g. Ensslin *et al.*, 2015; Mollel *et al.*, 2017). The most complex models included elevation, land-use type and the interaction between them, and the simplest model included only the intercept (Supporting Information, Appendix 3). The performance of each set of models was evaluated using AICc, and the model that showed the highest explanatory power (adjusted R^2) and statistical significance ($P < 0.05$) within delta AICc < 2 was selected as the most likely (Burnham & Anderson, 2002). Complementarily, we also conducted the analyses using richness of useful species (SR) as the response variable.

Finally, we tested for differences in PD due to changes in land-use after controlling for the effect of elevation. To do so, we computed SES.PD scores for each habitat and guild using all the species in the same guild that occurred within the elevational belt of the focal habitat as the reference pool (Table 1). Differences in SES.PD between natural and anthropized habitats were tested using paired t -tests, because the latter are degraded states of the former.

It is important to note that distance-based indices of phylogenetic structure such as PD and Phylosor can strongly vary with the phylogenetic scale of the analysis (Münkemüller *et al.*, 2014; Graham *et al.*, 2018). Thus, to assess the effect of non-angiosperm lineages in PD and PBD patterns, we conducted the analyses at two different phylogenetic scales; the vascular plants (all the species recorded in the plots) and the angiosperms (i.e. after removing gymnosperms and ferns). All the analyses were conducted in R v.3.4.3 (R Core Team, 2017) using the packages picante (Kembel *et al.*, 2010), phytools (Revell, 2012), betapart (Baselga *et al.*, 2018), MuMIn (Bartoń, 2018) and our own code (Supporting Information, Appendix 2).

RESULTS

EVOLUTIONARY LINEAGES AND USAGE GUILDS

Of the 980 species recorded in the study, 538 (55%) were assigned to at least one of the usage guilds. Of this pool, traditional medicine (70%) and fodder (59%) were the most species-rich guilds, followed by fuelwood (21%), building material (19%), food (16%) and ornamental/shading (7%) (Supporting Information, Fig. S1 in Appendix S3). Most fodder, edible and medicinal plants were herbs, whereas plants used as building material, fuelwood and ornamental/shading were predominantly trees and shrubs. Edible and medicinal trees and shrubs were also relatively abundant (Supporting Information, Fig. S1 in Appendix S3).

The fodder guild showed five dense phylogenetic domains (i.e. MIHNs with $> 70\%$ of useful species), two in the eupolypod ferns (Aspleniaceae and Dryopteridaceae), two in the monocots (Poaceae and Commelinaceae) and one in the subfamily Faboideae within the Fabaceae (*Indigofera* L.) (Fig. 2). Further, the commelinids (Poales + Arecales + Commelinales + Zingiberales), Faboideae and the fern clade as a whole constituted three soft domains (MIHNs with 50–70% of useful species). We also detected two minor soft domains in Asteraceae and Lamiaceae, respectively. The building material and fuelwood guilds showed a great similarity in species composition. As such, both guilds shared the *Acacia* Mill. + *Albizia* Durazz. (Fabaceae) and the Anacardiaceae (Sapindales) clades as dense domains and the magnoliids as a soft domain (the entire Sapindales constituted a dense domain in the case of the fuelwood guild). Also, Myrtales represented a dense and soft domain in the building material and fuelwood guilds, respectively. The ornamental/shading and food guilds only showed weak domains (MIHN with $< 50\%$ of useful species), but some of these domains were exclusive, such as Asparagales for ornamental/shading plants and Caryophyllales for

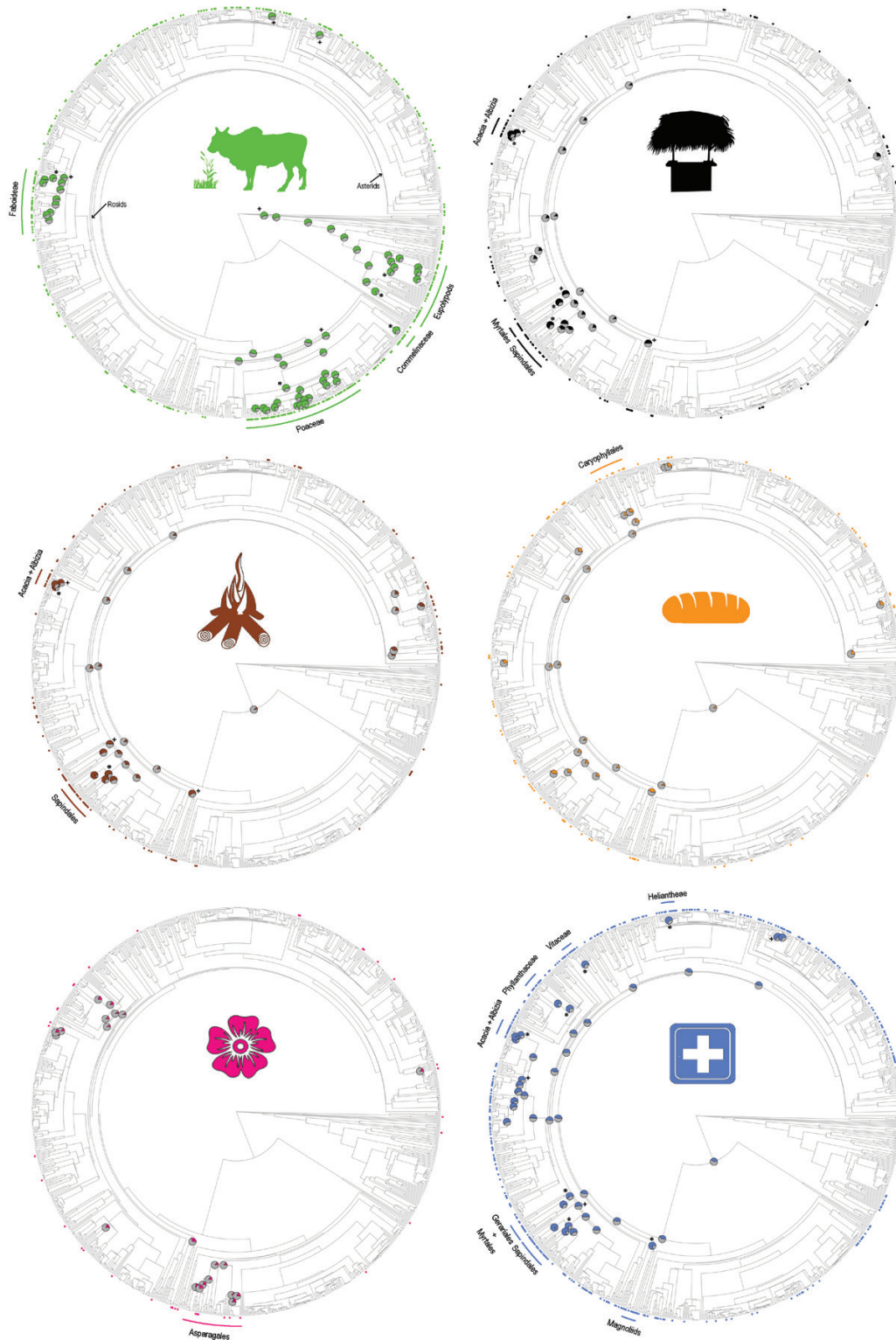


Figure 2. Phylogenetic domains of useful plants for the vascular flora of Mt. Kilimanjaro. The circle symbols on the phylogenetic tips represent the phenotypic state 'useful' for the different usage guilds (binary trait). The phylogenetic nodes that included a significantly high number of useful species (i.e. SES scores > 1.96) are marked with pie charts (hot nodes). The pie charts represent the fraction of useful species descended from each hot node. The pie charts marked with asterisk

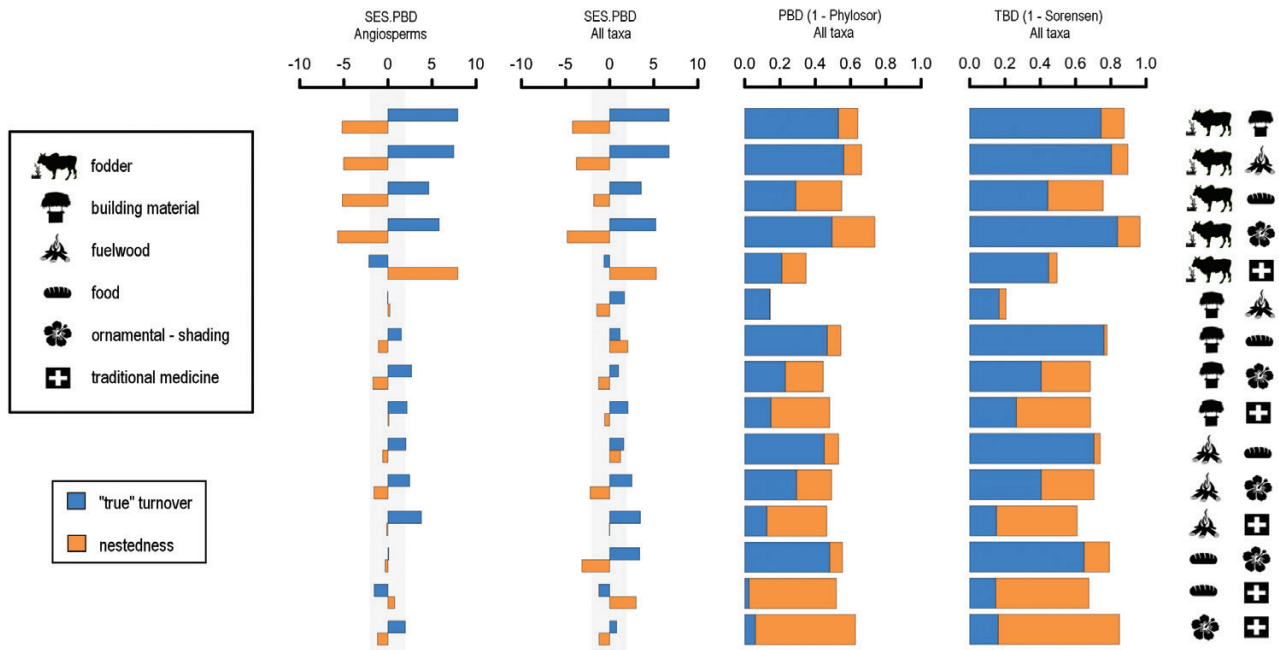


Figure 3. Taxonomic (TBD) and phylogenetic (PBD) beta diversity between the usage guilds analysed in the study, and standardized effect size values (SES scores) for the 'true' turnover (blue) and nestedness (orange) additive components of PBD. The bars protruding from the shaded area represent significant comparisons for a nominal alpha of 5% (SES scores $> |1.96|$).

edible species. The traditional medicine guild showed multiple and scattered dense domains, either shared with other guilds (Sapindales, Myrtales, magnoliids and *Acacia* + *Albizia*) or exclusive as medicinal (Phyllanthaceae, Vitaceae and Heliantheae).

As expected, taxonomic and PBD were highly correlated (Pearson's $R = 0.99$). PBD was relatively high for most pairwise comparisons between the guilds (Fig. 3). Further, phylogenetic dissimilarities between the guilds were mainly due to true turnover of lineages except for comparisons involving the traditional medicine guild, where the nestedness component predominated in most of the comparisons. The turnover component of PBD was higher than expected (SES $> +1.96$) in 8 out of 15 comparisons, indicating significantly deep phylogenetic turnover (i.e. low phylogenetic overlap). Quantitatively, such significant comparisons were particularly noticeable (i.e. PBD > 0.5 and predominantly due to turnover) between (1) fodder and any other guild (except traditional medicine) and (2) between ornamental/shading and both fuelwood and food guilds. In contrast, the turnover fraction of PBD between the traditional medicine and both the building material and fuelwood guilds was reduced (i.e. PBD was predominantly

due to nestedness) despite being significantly high (SES $> +1.96$), indicating that the fraction of PBD that was owing to turnover between these guilds, though reduced, involved deep nodes of the phylogeny. The comparisons between the traditional medicine and both the fodder and food guilds showed greater differences than expected in the nestedness component, but such differences were only quantitatively important in the latter comparison, where PBD was rather high (0.52) and almost exclusively due to nestedness. The number of comparisons that were significantly high in the turnover component of PBD was even higher at the angiosperm scale (10 out of 15 comparisons).

PHYLOGENETIC DIVERSITY OF USAGE GUILDS ALONG ELEVATION AND LAND-USE

Elevation was the most important factor explaining both PD and SR of useful plants across the habitats of the study, whereas the effect of anthropogenic disturbance was comparatively weak and non-significant (Fig. 4, Table S1 in Appendix 3). SR of fodder, food and traditional medicine guilds decreased linearly with elevation. In contrast, the

symbols represent the most inclusive hot nodes (MIHNs) that included $> 70\%$ of useful species (dense domains), and those marked with plus symbols represent the MIHNs that included 50–70% of useful species (soft domains). The phylogenetic placement of the rosids and asterids, two major eudicot clades, is indicated in the top-left phylogenetic tree.

building material, fuelwood and ornamental/shading guilds showed hump-shaped relationships with peaks at 2000 m (Fig. 4). PD followed hump-shaped relationships in all cases (peaks between 2500 and 3000 m) except for the food and ornamental/shading guilds, which showed non-significant relationships. However, the relationships between PD and elevation weakened for the fodder and fuelwood guilds when the analyses were scaled at the angiosperm clade (Fig. 4).

After controlling for the effect of elevation, we found that changes in land-use towards increased anthropization significantly reduced PD of the fodder ($t = 2.58, P < 0.05$) and traditional medicine guilds ($t = 2.76, P < 0.05$) (Fig. 5). Differences for the building material and fuelwood guilds were only marginally significant ($t = 2.21, P = 0.06$ for building material and $t = 2.40, P = 0.05$ for fuelwood), whereas the food and ornamental guilds showed non-significant differences.

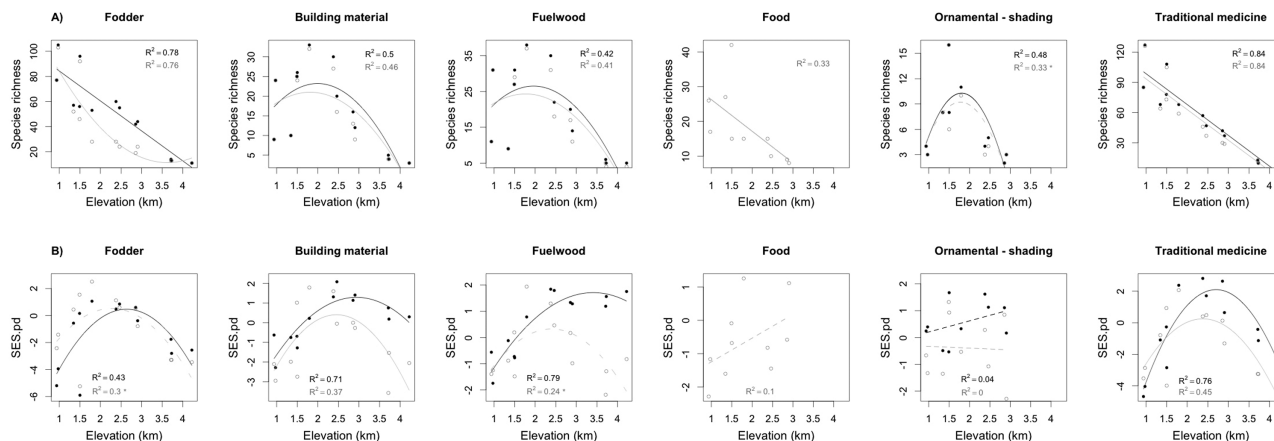


Figure 4. Scatterplots showing the relationship between A, species richness and B, phylogenetic diversity of useful plants and elevation. The solid and open dots represent the observed values for vascular plants and angiosperms, respectively (note that the food guild only included angiosperm plants). The regression lines correspond to the models that showed the highest explanatory power (adjusted R^2) and statistical significance ($P < 0.05$) within $\Delta AICc < 2$ (black and grey for vascular plants and angiosperms, respectively). The dotted lines represent non-significant relationships ($P > 0.05$), and the symbol ‘*’ indicates marginally significant relationships (i.e. $0.05 < P < 0.1$). Note that no edible or ornamental species were found above 3000 m.

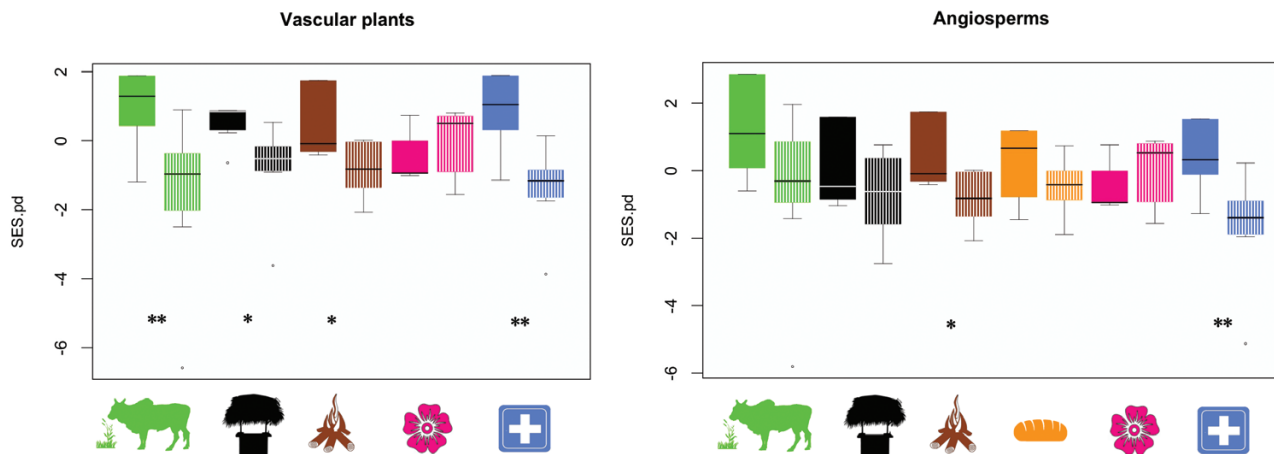


Figure 5. Boxplots showing differences in phylogenetic diversity (SES.PD) of useful plants between natural (solid) and anthropized (striped) habitats of Mt. Kilimanjaro after controlling for the effect of elevation. The analyses were conducted at two different phylogenetic scales, this is, including all vascular plants recorded in the study and only the angiosperms. The symbols ‘**’ and ‘*’ indicate significant differences for a nominal alpha of 5% (i.e. $P < 0.05$) and marginal significance ($P < 0.07$), respectively.

At the angiosperm scale, differences in PD remained significant for medicinal plants ($t = 2.55$, $P < 0.05$) but were drastically narrowed for fodder plants ($t = 1.58$, $P = 0.16$).

DISCUSSION

Ethnobotanical legacy is perhaps one of the most palpable proofs of the reality of the ecosystem services that are directly provided by plant biodiversity, and thus represents an excellent opportunity to explore connections between biodiversity and human well-being. However, while most previous ethnobotanical studies have focused on taxonomic diversity patterns (e.g. Mollel *et al.*, 2017), efforts to link evolutionary history with plant-related benefits remain scarce (Tucker *et al.*, 2019). Here, we have combined ethnobotanical data from Mt. Kilimanjaro with molecular phylogenetic information to fill in this gap. Specifically, we evaluated the extent to which plant-related services provided by the flora of this emblematic mountain are lineage-specific. Also, we have determined whether PD of usage guilds (the evolutionary basis of natural resources; Faith *et al.*, 2010) varies across the major habitats of Mt. Kilimanjaro, which may help to inform spatially explicit conservation efforts.

EVOLUTIONARY LINEAGES AND USAGE GUILDS

We found some specificity in the relationship between plant-related services and evolutionary lineages (Fig. 2), which suggests that preserving a multi-functional natural plant ‘storehouse’ at Mt. Kilimanjaro would require the maintenance of multiple evolutionary lineages. However, we also detected a few multi-functional lineages that deserve special attention in conservation planning. On the other hand, we found significantly deep phylogenetic true turnover (i.e. low phylogenetic overlap) between many of the guild pairwise comparisons (Fig. 3). All in all, our results suggest that the inhabitants of Mt. Kilimanjaro rely on multiple and relatively deep lineages that specifically provide a certain type of service (although a few clades provided multiple benefits), which may have important implications for human well-being in the future. As such, environmental stressors might jeopardize the delivery of plant-related services if closely related species are similarly vulnerable to ongoing pressures as a result of conserved evolution (Thuiller *et al.*, 2011; Molina-Venegas *et al.*, 2018).

Poaceae and Faboideae constituted two different phylogenetic domains of fodder plants in the angiosperm lineage (Gemedo-Dalle, Maass & Isselstein,

2005) (Fig. 2). Grasses (Poaceae) are well recognized for their capacity to modify environments via positive feedback from grazing fauna (Linder *et al.*, 2018), which may have driven the evolution of this lineage as a worldwide phylogenetic domain of fodder plants. On the other hand, many species of Faboideae (e.g. species of *Indigofera* and *Tephrosia* Pers.) are important sources of high-quality protein for livestock in Africa (Coughenour *et al.*, 1990; Mbomi *et al.*, 2011) and also worldwide (Duc *et al.*, 2015) due to the evolution of a sophisticated mechanism to fix atmospheric nitrogen (Doyle, 2011). The presence of fodder domains in the eupolypod ferns is more surprising, since ferns are generally believed to be of low nutritional value. However, a few fern lineages such as *Osmunda* L. and *Angiopteris* Hoffm. have been recognized as rich energy sources for Mesozoic herbivores (Hummel *et al.*, 2008). Therefore, future studies may also confirm the nutritional value of eupolypod ferns, which represent a great fraction of total plant biomass in the montane forests of Mt. Kilimanjaro (Hemp, 2001).

Dracaena Vand. ex L. (Asparagaceae) contributed much to defining Asparagales as an ornamental-specific domain in our study (50% of all the Asparagales ornamental species in the dataset were affiliated to *Dracaena*). *Dracaena* is a predominantly African lineage, and it includes a few species with great cultural significance not only in the study area but in northern Tanzania in general. For example, shrubs of *Dracaena fragans* (L.) Ker Gawl. are ubiquitous in the Tanzanian ‘Chagga’ social landscape, where they are used for delimiting family land properties as strong indicators of ancestral authority. *Dracaena* shrubs are also planted on graves, featuring in witchcraft detection and peace-making rituals. As such, it is said that presenting a single leaf of *Dracaena* in a dispute will suffice to invoke peace between the opponents (Hemp, Hemp & Winter, 2009; Sheridan, 2016). On the other hand, *Dracaena* includes monumental tree-like species [e.g. *Dracaena draco* (L.) L.] that have a direct economic impact on some African islands, where they act as tourist appeals (Symon, 1974). The emblematic ‘dragon tree’ (*Dracaena draco*) of Icod de los Vinos (Tenerife, Canary Islands) is perhaps the greatest exponent of its kind.

The fuelwood and building material guilds shared most of the species (Figs 2 and 3), especially in the *Acacia* + *Albizia*, Sapindales and magnoliid clades, which also represented medicinal domains (i.e. multi-functional lineages). The properties of *Acacia* trees have been well-known since the ancient times, and especially in Africa, where Egyptians extensively used them as a source of timber and gum Arabic for embalming and burial rituals (Baumann, 1960). Many members of Sapindales are economically important as raw material for construction, fuel

and furniture production (Porter & Sytsma, 2016), with the outstanding role of Meliaceae as a source of the precious mahogany wood (*Swietenia* Jacq. in South and Central America and *Khaya* A.Juss. and *Entandrophragma* C.DC. in Africa). The coveted wood of magnoliid species (here detected as a soft domain for the building material and fuelwood guilds) represents a threat to the montane forests of Mt. Kilimanjaro, which have long attracted the attention of illegal loggers (Lambrechts *et al.*, 2002). Several members of Sapindales are well-known for their edible fruits [e.g. *Sclerocarya birrea* (A.Rich.) Hochst.; Mariod & Abdelwahab, 2012], which was also reflected in our hot node analysis (Fig. 2). Caryophyllales was detected as an exclusive domain of edible species, with a major contribution of Polygonaceae [e.g. *Oxygonum sinuatum* (Hochst. & Steud ex Meisn.) Dammer, *Persicaria nepalensis* (Meisn.) Miyabe] and Amaranthaceae (e.g. *Amaranthus hybridus* L.). As such, the latter family provides highly nutritious crops worldwide such as beet (*Beta vulgaris* L.), spinach (*Spinacia oleracea* L.) and quinoa (*Chenopodium quinoa* Willd.). Finally, we found multiple and scattered medicinal domains. Previous studies have documented a strong phylogenetic signal in multiple subcategories of African medicinal plants (Yessoufou, Daru & Muasya, 2015), suggesting that the medicinal domains detected here might be disease-specific, although such an hypothesis remains to be tested.

Although we focused on the detection of lineages that showed a significantly high number of useful species (i.e. positive phylogenetic domains), detecting 'negative' domains may help to delineate evolutionarily relevant lineages (from a human-centred perspective) more accurately. For example, although both the building material and fuelwood guilds showed a deep (weak) domain coincident with the rosid clade, Faboideae represented a noticeable 'gap' (in terms of useful species as building material or fuelwood) nested in the former (Fig. 2).

PHYLOGENETIC DIVERSITY OF USAGE GUILDS ALONG ELEVATION AND LAND-USE

PD of most usage guilds showed hump-shaped curves along the elevational gradient that peaked between 2500 and 3000 m (Fig. 4), thus revealing a phylogenetic hotspot of useful lineages in the middle (*Ocotea*) and upper (*Podocarpus* Labill.) montane forests of Mt. Kilimanjaro (Table 1). Accumulating evidence suggests that vegetation belts are experiencing a general upward shift in mountainous ecosystems worldwide due to global warming and increasing levels of carbon dioxide and nitrogen (Shugart *et al.*, 2001; Leonelli *et al.*, 2011). However, Hemp (2005) reported an over-riding downslope migration of the alpine (*Helichrysum*

scrubland) and subalpine (*Erica* bushland) vegetation belts of Mt. Kilimanjaro due to climate-change induced fires. On the other hand, land-use change represents a pervasive threat to the remnants of the lower montane forest of Mt. Kilimanjaro, which are immersed in a densely populated matrix of cultivated areas (i.e. Chagga homegardens and coffee plantations) where demographic pressure is steadily increasing (Hemp *et al.*, 2017). Thus, our findings outline an alarming scenario for the preservation of many useful plant lineages of Mt. Kilimanjaro, as montane forests may experience substantial shrinking in coming decades, trapped between the 'hammer and the anvil' of climate and land-use change.

Although elevation was the main predictor of PD across the ecosystems of the study, our analyses revealed significant differences in PD between natural and human-disturbed habitats for some of the guilds (i.e. fodder and traditional medicine) after controlling for the effect of elevation (Fig. 5). This result adds to previous evidence that anthropogenic disturbance may reduce PD due to exclusion of disturbance-intolerant lineages (Dinnage, 2009; Ding *et al.*, 2012; D'agata *et al.*, 2014). However, differences in PD narrowed (particularly for fodder plants) when the analyses were scaled at the angiosperm clade. Human disturbance reduces vertical structure and shading of the understory among other effects (Rutten *et al.*, 2015), which may negatively affect the diversity of sciophilous and epiphytic fern species in anthropized habitats. Thus, differences in PD between natural and human-disturbed plots seem to emerge largely owing to exclusion of disturbance-intolerant fern lineages. However, we found that differences in PD remained significant for the traditional medicine guild regardless of the phylogenetic scale of the analysis, suggesting that the evolutionary legacy of the medicinal flora of Mt. Kilimanjaro is threatened by ongoing land-use change. The negative effects of land-use change on useful medicinal plants have already been perceived in other tropical regions (Rodríguez *et al.*, 2018), and conservation planning should pay particular attention to preserve the option values for the genetic medicinal resources on which the health of future generations may depend.

CONCLUSIONS

We have documented a relatively high specificity in the relationship between plant-related ecosystem services and evolutionary lineages of the flora of Mt. Kilimanjaro, suggesting that the inhabitants of this mountain rely on multiple and deep lineages that specifically provide a certain type of service. However, we also detected a few multi-functional lineages

that may deserve special attention in conservation planning. Our analyses revealed an important reservoir of useful lineages in the montane forests of Mt. Kilimanjaro. Given the current well-documented threats to these forests, our findings outline an alarming scenario for the preservation of the option values they treasure, which may be trapped between the ‘hammer and the anvil’ of climate and land-use change.

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AUTHOR CONTRIBUTION STATEMENT

MF and AH conceived the exploration of plant-related ecosystem services at Mt. Kilimanjaro and the sampling design, AH conducted the vegetation survey, AH and NPM elaborated the ethnobotanical dataset, RMV conceived the ideas, designed the structure of the manuscript, conducted all the analyses and led the writing. All the authors read and commented on the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

- Appendix 1.** Phylogenetic reconstruction methods.
Appendix 2. R function to run the hot node analysis.
Appendix 3. Supplementary results.