



PHYLOGENETIC DIVERSITY OF PLANT COMMUNITIES IN RELATION TO ELEVATION AND HUMAN IMPACT AT MOUNT KILIMANJARO, TANZANIA

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ABSTRACT

Phylogenetic diversity (PD) of vascular plants in 30 natural communities along an elevation gradient (700 to 4600 m) at Mount Kilimanjaro compared with 30 human-influenced habitats was studied. Linear models were tested for phylogenetic diversity on elevational gradient while two-ways ANOVA was applied to compare phylogenetic diversity between human-influenced and natural habitats. PD was higher at intermediate elevation while its variation showed a unimodal increase with elevation up to 3500 m and slightly decreased in the alpine belt indicating uneven distribution of taxa at lower and highest elevations. At the angiosperm scale PD showed the same pattern while its variation decreased indicating the significance of Pteridophytes and Gymnosperms to PD at this elevation. In the savanna and montane elevational belts, natural and human-impacted communities were equally affected by climate conditions and human activities thus similar PD pattern. In the lower montane zone, phylogenetic diversity was lower in human-influenced habitats than in natural forest. This study showed that elevation modified the patterns of phylogenetic diversity of plant communities while human-influence had negative impact. Conservation efforts should consider those communities with higher PD below the National Park.

Key words: Climate and land use, change on elevational, gradient.

INTRODUCTION

Phylogenetic diversity can be used to explain the aspects of species similarity and difference (species relatedness) within communities which is one of the important aspects that may guide in making meaningful decisions towards biodiversity conservation prioritization and predicting ecosystem functioning beyond sheer species richness (Flynn *et al.* 2011, Raciol *et al.* 2014).

Climate and land-use changes could be among the most important driving factors for the changes in phylogenetic patterns within communities (Willis *et al.* 2008). It was found that, under benign environmental conditions, communities showed higher phylogeny diversity while being lower under straining conditions (Verdú 2007, Knapp *et al.* 2008, Dinnage 2009, Helmus *et al.* 2010). Thus, phylogenetic diversity patterns may play an important role in interpreting community responses to climatic or land use changes and in predicting community responses to future global change (Willis *et al.* 2008; Hoiss *et al.* 2012). Moreover, communities with higher phylogeny may be expected to contain distinct lineages which promote increased functional groups and thus increased ecosystem functioning (Faith and Baker, 2006; Winter *et al.* 2013, Raciol *et al.* 2014) and therefore be of high value both for conservation (Ohsawa and Ide 2008) and sustainable use (Forest *et al.* 2007).

Among the indices used for measuring different aspects of phylogenetic diversity, average taxonomic distinctness (Δ^+ or AvTD) and its variation (Λ^+ or VarTD) have shown the potential to be applied to a wider range of data in the form of species lists



(Clarke and Warwick 2001, Crozier *et al.* 2005). AvTD and its variation (VarTD) is one of the biodiversity measures which can be used to estimate the average degree to which species are related to each other based on Linnean classification system and how evenly the individual species are distributed within the community (Ellingsen *et al.* 2005, Anderson *et al.* 2013).

Mountains provide opportunity for studying the effects of climate change on biodiversity as they represent natural gradients of temperature and precipitation at small spatial scales (Lomolin, 2001, Rahbek 2005, Guo *et al.* 2013). Moreover, as humans impact mountain ecosystems at different elevations in different ways, mountains also constitute an arena for studying the impact of direct human intervention on plant communities (Fischer *et al.* 2008). Depending on habitat type, this impact can be due to conversion of natural habitats to agricultural land, to agro-forestry systems, to plantations, to grassland or due to burning or selective logging.

We studied phylogenetic diversity of plant communities at Mount Kilimanjaro, Africa's highest mountain (5895 m) on its exceptional elevational gradient. Kilimanjaro harbors a

wide range of different natural habitat types including savanna woodlands, cloud forest and alpine vegetation (Hemp 2006a). However, its vegetation has been strongly influenced by human impacts and there is a considerable variation in land-use types and intensities across the mountain (Hemp, 2006a). Hemp (2006c) studied species richness and diversity patterns, Rutten *et al.*, (2015b) vegetation structure, Ensslin *et al.* (2015) biomass and Rafael *et al.* (2020) phylogenetic diversity of usage guilds along elevation gradient and land use at Mount Kilimanjaro respectively, while phylogenetic diversity remains as a gap on understanding the patterns of plant diversity in communities along the elevation and land use gradients of this mountain We asked how phylogenetic diversity of natural habitats changes with elevation and with human impacts. To study human impacts, we compared the diversity in natural and human influenced habitats at four elevations: i) colline zone (ii) lower montane forest zone (iii) middle montane zone and (iv) upper montane zone. In the sub alpine and alpine elevational zones only, natural habitats were studied. The studied vegetation, land-use and disturbance types are shown in Table 1.

Table1: The studied natural vegetation with their type of disturbance/land use along elevational zones at the southern slopes of Mount Kilimanjaro

Elevational belt	Elevation range (m)	Vegetation zone	Natural vegetation	Disturbance or land use
6	4000 – 4600	Alpine	<i>Helichrysum</i> vegetation	No land use
5	3200 – 4000	Sub-alpine	<i>Erica</i> forest	Burned habitat was not studied
4	2800 – 3200	Upper montane	<i>Podocarpus</i> forest	Burned
3	2100 – 2800	Middle montane	<i>Ocotea</i> forest	Logged
2	1100 – 2100	Lower montane	Lower montane forest	Home gardens, Coffee plantations and grasslands
1	700 – 1100	Colline	Savanna woodlands	Maize fields

MATERIALS AND METHODS

Study area

This research was conducted on the southern slopes of Mount Kilimanjaro where climate gradients and various habitat types are most pronounced. Kilimanjaro the world's highest solitary mountain, is located in northern

Tanzania (between 2° 45' and 3° 25' South and 37° 00' and 37° 43' East). It has a very rich flora with about 2500-3000 vascular plant species (Hemp 2006a), representing almost one third of the approximately 12,000 known vascular plant species of Tanzania. Mean annual temperature ranges from about 23°C at 700 m in the savanna to minus 7°C at



5895 m at Uhuru-peak (Hemp 2006c). Precipitation also strongly changes with elevation, with dry foothills and afro-alpine heathlands, and a mid-elevational

precipitation peak at mid elevation at around 2200 m.

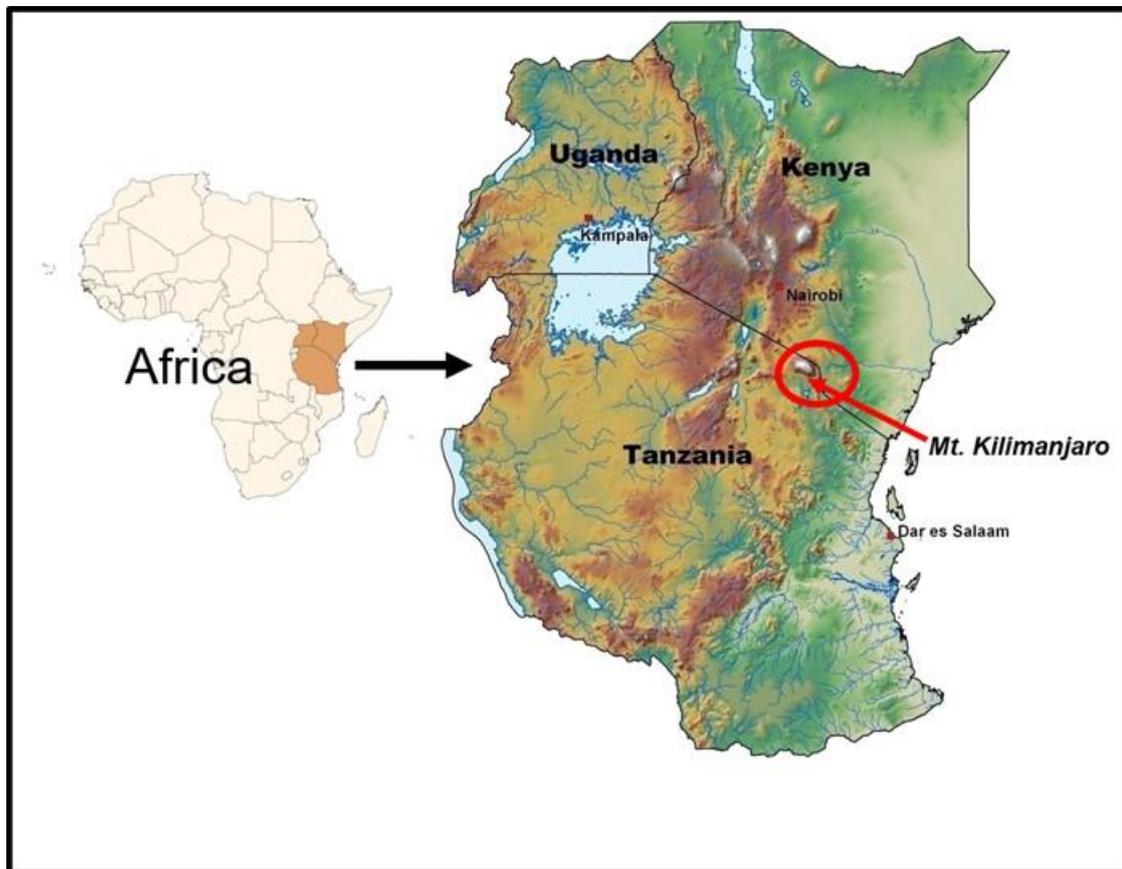


Figure 1: Map showing Location of Mount Kilimanjaro, in Tanzania, East Africa in African Continent

To study plant communities at Mount Kilimanjaro, we took vegetation records of 60 plots (20 x 50 m) covering six natural habitats and six human-influenced habitats across the southern slope of Kilimanjaro. These plots covered an elevational gradient from colline to alpine (700-4600 m) and the major land-use gradient from heavily used to natural habitats. Each habitat type was represented by 5 plots (Fig.2, Table 1)

A distinct assemblage of natural and anthropogenically affected habitat types are shaping the mountain's southern slopes. Savanna woodlands in the colline part of the mountain dominate the natural landscape between 700 to 1100 m which have largely been transformed to crop fields for local food

production, and only smaller patches of natural savanna woodland remain intermingling with the crop fields. In the densely populated sub-montane and lower montane zone (1100-2100 m) several major land-use types are found. The first is the traditional Chagga agroforestry (home gardens) which is a multi-layered system with a forest-like structure consisting of a tree layer, which provides firewood, fodder and shadow, banana trees are grown and under the bananas coffee shrubs, and under these vegetables. The second land-use type in the lower montane zone is grassland where the Chagga people frequently cut grass as fodder for livestock.

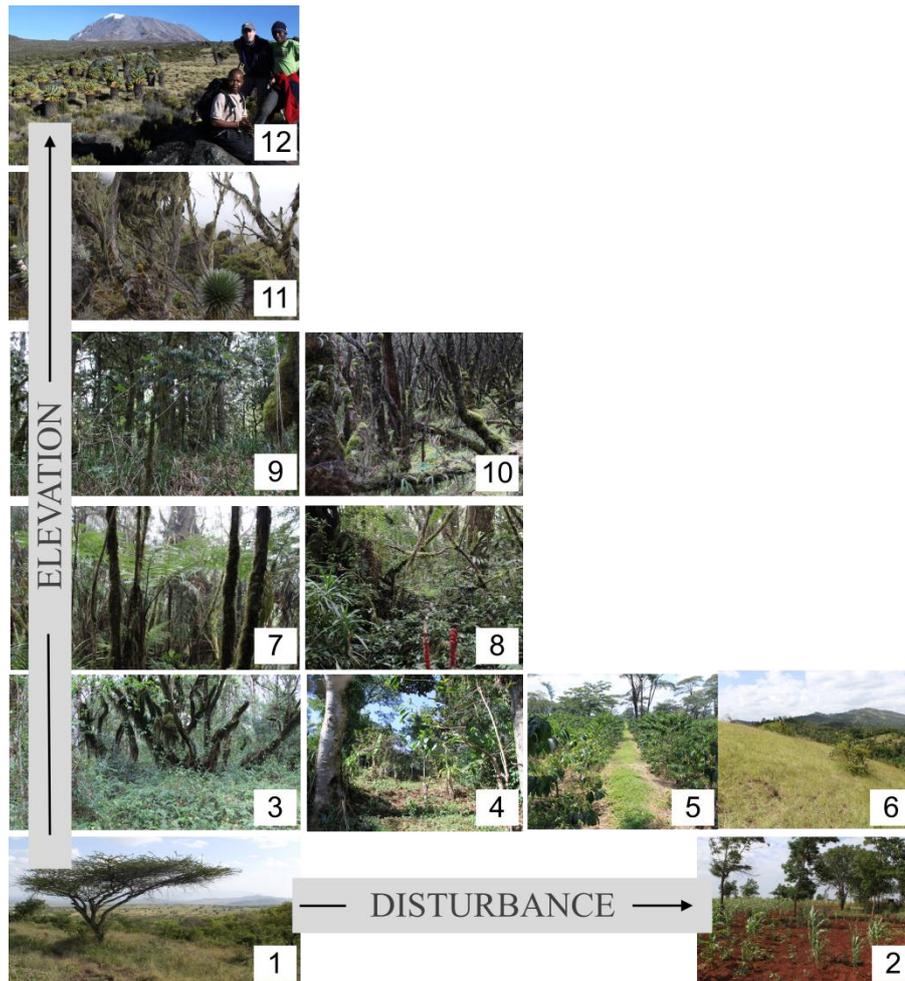


Figure 2: Mount Kilimanjaro and its main habitat types and disturbances at different elevations. Savanna¹ zone (700 and 1100 m) is used for crop production (e.g., maize²). In the lower montane³ zone (1100 and 2100 m) there are homegardens⁴ (traditional agroforestry systems), commercial coffee farms⁵ and grass lands⁶. In the montane *Ocotea*⁷ zone (2100 to 2800 m), commercial logging⁸ occurred until 1984. In the upper montane *Podocarpus*⁹ zone (2800 to 3200 m), and previously burned¹⁰ *Podocarpus* areas. In the subalpine, *Erica trimera*¹¹ zone (3200 to 4000 m), Africa's highest forests can be found. Higher up is *Helichrysum*¹² zone (4000 to 4600 m). Each habitat type consisted of five sites which were distributed over an east-west gradient along the southern slope and elevation gradient within each vegetation zone.

The third land-use type along this zone is commercial coffee plantations with scattered trees shadowing the coffee shrubs. Natural forests in this zone are restricted to steep valleys and gorges and dominate above 1700 m (Hemp 2006a, Hemp 2006b, Hemp 2009).

The middle montane (2100 – 2800 m) is the zone of highest precipitation and the main habitat of *Ocotea usambarensis* trees. In this zone commercial logging took place until 1984 when the National park was established however, illegal logging continued in recent

years, especially in areas within the National Park that are close to local settlements (Hemp 2006c). With increasing elevation, between 2800-3200 m, *O. usambarensis* is replaced by *Podocarpus latifolius*, a gymnosperm tree which dominates the upper montane zone. A substantial area of *Podocarpus* forest had been destroyed by fire during the last decades and replaced by *Erica excelsa* in the tree layer (Hemp 2005, 2009). In the sub-alpine zone (3200-4000 m), most of the former *Erica* forest was destroyed by regular fires which occurred every year over the last three



decades (Hemp 2005) and replaced by ericaceous shrub-land. In the alpine zone up to 4600 m, dominant vegetation contains cushion plants of the genus *Helichrysum* and tussock grasses (Fig. 2; Table 1).

Vegetation records

We established 60 (20 x 50 m) study plots between 2011 and 2012, five replicates in each of the six most prominent natural and six human-influenced habitats described above (Fig 2; Table 1). The selection of study plots was based on representativeness of the respective habitat type, accessibility and security. Plot positions were recorded with GPS coordinates and permanently marked with subterranean iron nails. The distances between the plots ranged from 0.3 to 54 km. To estimate the diversity and composition of plant communities, we recorded all vascular plant species and their abundances in all study plots during the dry and rainy seasons using the Braun-Blanquet (1964) method. Specimens of species that could not be identified in the field were collected and brought to the herbarium at the research station in Kidia (Old Moshi) and National Herbarium of Tanzania (NHT) in Arusha for identification, verification and preservation. Here we compared the collected plants with already identified specimens and used taxonomic keys from various volumes of the Flora of Tropical East Africa (FTEA 1952 - 20016). Replicate specimens were deposited at the East African herbarium Nairobi (Kenya), Kew (England), Berlin (Germany), Copenhagen (Denmark), Stockholm (Sweden), Paris (France) and Vienna (Austria). Nomenclatural criteria and taxonomic hierarchy followed The Plant List (2019) and the Catalogue of life annual checklist (2019).

Statistical analysis

The taxonomic hierarchy matrix was formed based on five levels of classification: classes (6), orders (48), families (135), genera (539) and species (962). The taxonomic hierarchy and species abundance matrices were used to calculate the two phylogenetic diversity

indices using 'Vegan' package 2.4-0' (Oksanen *et al.* 2013) in 'R' Version 3.3.1 (R Core Team 2017). The indices were average taxonomic distinctness (AvTD or Δ^+) and its variation (varTD or Λ^+).

AvTD measures taxonomic coverage for each study plot calculated as taxonomic distances through a classification tree between all pairs of species. Higher values of AvTD suggest that a community consists of more distantly related species thus, higher phylogenetic breadth. varTD measures even distribution of taxa within the community (Clarke and Warwick 1998 & 2001, Crozier, *et al.* 2005, Chen *et al.* 2019), whereas higher values of VarTD suggest even distribution of taxa in a community (Clarke and Warwick, 2001; Tolimieri and Anderson 2010)

Linear regressions were tested for the effect of elevation on phylogenetic diversity while treating AvTD and VarTD as response variables. The best fitting linear model over elevation was sought using R^2 as the measure of fit and allowing for a quadratic term. Linear and quadratic models were compared using a likelihood test ratio. Two-ways ANOVA was applied to test whether diversity was affected by human activities by comparing human-influenced with natural habitats in the colline zone (savanna woodlands against maize fields); lower montane zone (one natural against the three human-influenced), the middle montane (natural against logged *Ocotea*) and the upper montane zone (undisturbed against burnt *Podocarpus* forest) separately. For the sub-alpine (*Erica*) and alpine (*Helichrysum*) zones only natural habitats were studied (Table 1). To test for differences between the four habitats types in the lower montane zone, we performed post-hoc (Tukey's HSD method) tests. All analyses were performed using R Version 3.3.1 (R Core Team 2017).



RESULTS

Relationship of phylogenetic diversity and elevation for natural habitats

Species richness declined linearly with elevation increase ($F_{1,28} = 102$, $P < 0.001$; $R^2 = 0.77$; Fig.3). In contrast, AvTD showed a strong quadratic relationship ($F_{2,27} = 70$; $P < 0.001$; $R^2 = 0.90$) with elevation showing a unimodal pattern peaking at intermediate elevation at about 2300 m (Fig.4A & B) where the highest phylogenetic diversity was detected. When all pteridophytes and gymnosperms species were excluded in the analysis, AvTD showed the same pattern where $F_{2,27} = 43.1$; $R^2 = 0.76$; $P < 0.001$ (Fig 4B).

VarTD showed a unimodal increase with elevation up to 3500 m and slightly decreased or leveled-off with increasing elevation in the alpine belt ($F_{2,27} = 25.63$; $P < 0.001$; $R^2 = 0.65$; Fig. 5A). When pteridophytes and gymnosperms species were excluded in the analysis, VarTD showed a trough-shaped pattern decreasing at the middle elevation ($F_{2,22} = 70$; $P < 0.001$; $R^2 = 0.83$; Fig. 5B)

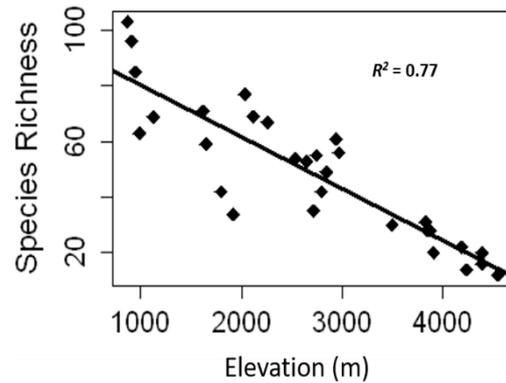


Figure 3: Relationship between species richness and elevation for 30 plots of natural vegetation at Mount Kilimanjaro.

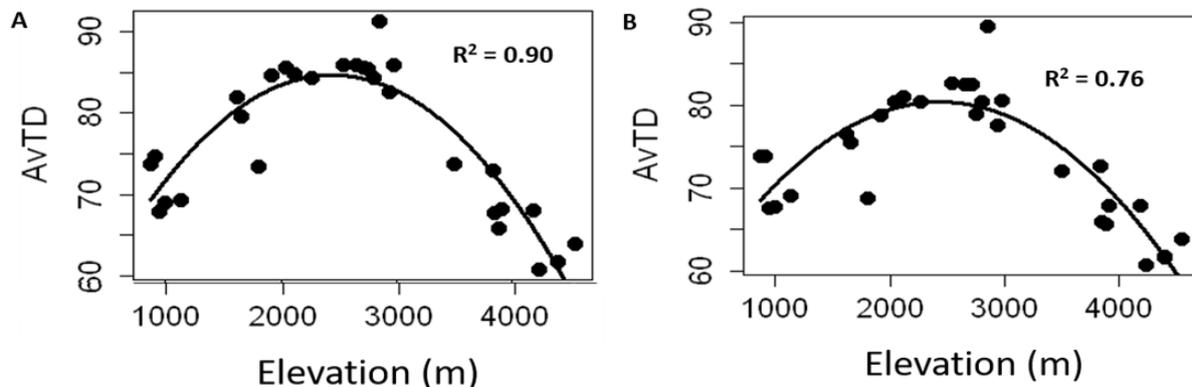


Figure 4: A – B: Elevational diversity of the means of AvTD for 30 plots of natural vegetation at Mount Kilimanjaro. Both unimodal relationships are highly significant.

4A - all species included ($F_{2,27} = 124$; $P < 0.001$);

4B - when only angiosperms species were analyzed ($F_{2,27} = 43.1$; $P < 0.001$)

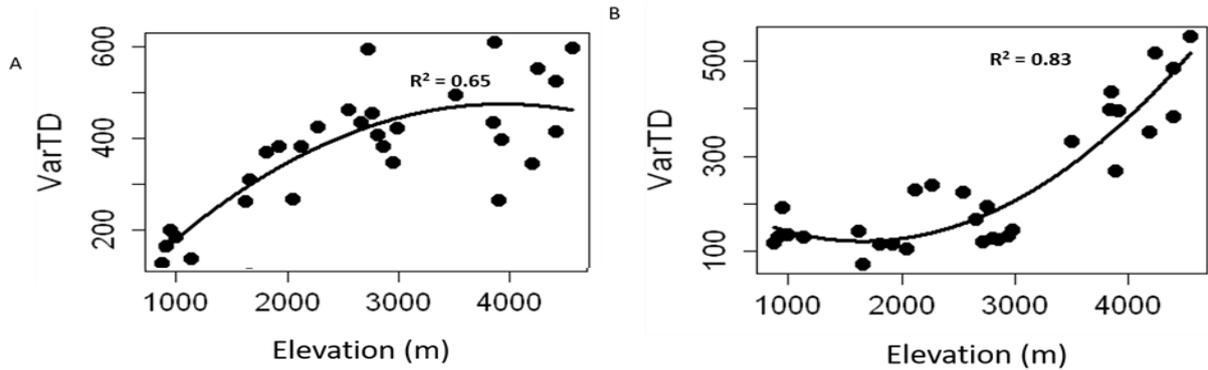


Figure 5A – B: Elevational diversity of the means of VarTD for 30 plots of natural vegetation at Mount Kilimanjaro. Both unimodal relationships are highly significant.

5A - all species included ($F_{2,27} = 25.6$; $P = 0.007$);

5B - when only angiosperms species were analyzed ($F_{2,27} = 69.8$; $P < 0.001$).

Human impact on phylogenetic diversity at different elevations

In the savanna zone, there was no significant difference in AvTD and VarTD between natural savanna and maize fields even when pteridophytes and gymnosperm species were excluded in the analysis (Table 2).

In the lower montane zone AvTD decreased from natural forest over home gardens and

coffee plantations to grasslands ($F_{1,19} = 26.1$; $P < 0.001$); Tukey's HSD test in the lower montane elevation indicated that the two human-impacted habitat types had significantly lower AvTD than natural forest (Fig 6A & B; Table 2). VarTD also decreased from natural forest over home gardens and coffee plantations to grasslands ($F_{1,19} = 14.8$; $P < 0.001$; Fig 7A & B Table 2).

Table 2: ANOVA summaries. The means of two measures of Phylogenetic diversity (Average taxonomic distance AvTD and its Variation VarTD) between natural and human-influenced habitat types for four elevation zones at Mt. Kilimanjaro. Significant differences are shown in bold.

Zone	AvTD			VarTD		
	Df	F-value	P-value	Df	F-value	P-value
Colline	1;6	1.19	0.3	1;6	0.23	0.6
Lower Montane	1;19	26.1	0.001	1;19	14.8	0.001
Middle montane	1;18	2.82	0.13	1;8	3.2	0.1
Upper montane	1;8	0.9	0.34	1;8	1.77	0.2
Result when only angiosperms species were analysed						
Middle montane	1;8	6.8	0.3	1;8	6.8	0.03
Upper montane	1;8	7.9	0.005	1;8	7.6	0.02

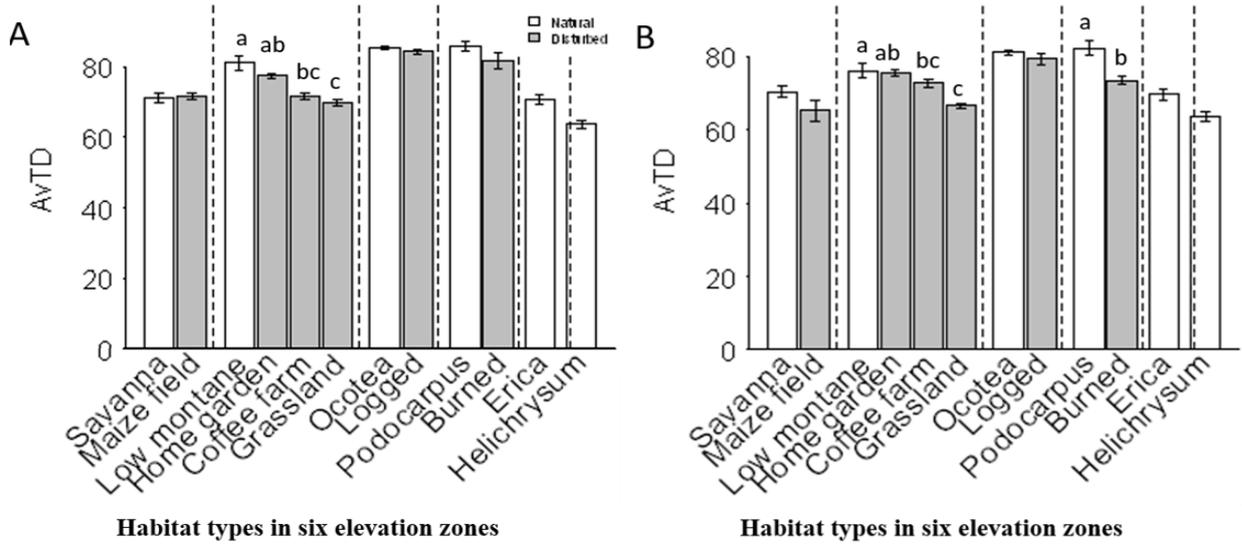


Figure 6: A – B: Means of AvTD comparing phylogenetic diversity for natural and human-influenced habitat types in six elevation zones at Mt. Kilimanjaro.

- - - separating vegetation zones are by dotted lines.
- white bars: Natural habitat types
- grey bars: human- influenced habitat types.
- Columns with letters: represent statistically significant differences (Tukey’s HSD test in the lower montane elevational belt)
- columns not sharing a letter are significantly different.

NOTE:

- 6A all species included in the analysis;
- 6B = angiosperms species only (Pteridophytes and gymnosperm species excluded).

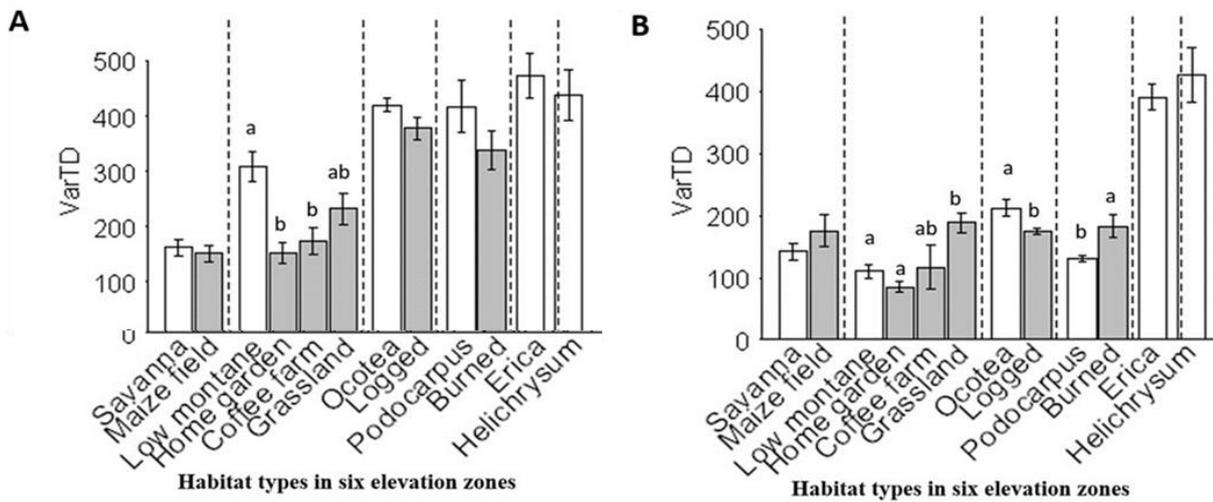


Figure 7 A – B: Means of VarTD comparing phylogenetic diversity for natural and human-influenced habitat types in six elevation zones at Mt. Kilimanjaro.

- - - separating vegetation zones are by dotted lines.
- white bars: Natural habitat types
- grey bars: human- influenced habitat types.
- Columns with letters: represent statistically significant differences (Tukey’s HSD test in the lower montane elevational belt)
- columns not sharing a letter are significantly different.

NOTE:

- 7A all species included in the analysis;
- 7B = angiosperms species only (Pteridophytes and gymnosperm species excluded).



AvTD of home gardens increased at $P = 0.02$ over grassland while both coffee plantations and grasslands decreased significantly than natural forests at $P < 0.001$); coffee and home gardens were not significantly different (Fig. 6A & B). In the montane zone, there was no significant difference in AvTD and VarTD between natural and selectively logged *Ocotea* forests, (Table 2; Fig. 6A & B; Fig 7A & B).

Similarly, in the upper montane zone, there was no significant difference in AvTD and VarTD between natural and burnt *Podocarpus* forest (Table 2; Fig. 6A & B; Fig 7A & B). In subalpine *Erica* and alpine *Helichrysum* zones, only undisturbed natural vegetation was studied (Table 1). When Pteridophytes and Gymnosperms species were excluded in the analysis the AvTD and VarTD remained the same for savanna and lower montane zones. Tukey's HSD test in the savanna and lower montane showed that the AvTD was not different from the results with all species included in the analysis, (Fig. 6B; Table 2). There was an increase of AvTD from undisturbed to burnt *Podocarpus* forest ($P = 0.005$; Table 2; Fig. 6B). In the montane zone, VarTD was significantly lower in selectively logged forests than in undisturbed *Ocotea* forests, ($P = 0.03$; Table 2; Fig. 7B) while, in the upper montane zone, VarTD decreased from undisturbed to burnt *Podocarpus* forests ($P = 0.02$; Table 2; Fig. 7B). In subalpine *Erica* and alpine *Helichrysum* zones, only undisturbed natural vegetation was studied.

DISCUSSION

Phylogenetic diversity of natural habitats at different elevations

Increased AvTD at intermediate elevations around 2300 m at Mount Kilimanjaro indicates higher phylogenetic diversity of plant communities at this belt (Fig.4 A - B). Interestingly, the elevational pattern of AvTD observed here did not match with that of species richness which declined linearly with elevation (Fig.3). Accordingly, the

highest biomass and most diverse vegetation structure were also reported at this elevation at Mount Kilimanjaro by Ensslin *et al.* (2015) and Rutten *et al.* (2015b) respectively. The hump-shaped pattern of AvTD along the elevational gradient at Mount Kilimanjaro may therefore reflect the structural diversity and to a much lesser degree the species richness of our research plots. All plots around the elevational peak of AvTD are highly structured, multi-layered montane forests which consist of several distinct layers harboring different niches, life forms and functional groups distributed along a huge gradient of 40 m of tree height (Hemp 2006c). These functionally very different plant groups belong to different, distantly related taxa, enhancing higher phylogenetic diversity at this zone of Mount Kilimanjaro. This might ultimately be due to more benign climate conditions at intermediate elevation, where precipitation peaks and where temperatures are neither stressfully (Hemp, 2006c). Furthermore, the peak of AvTD is congruent with the main distribution of pteridophytes which is also related to precipitation and humidity (Hemp 2002). Because pteridophytes belong to an ancient and systematically very different class than the other more modern vascular plants, their main occurrence in these forests adds also to higher phylogenetic breadth (high AvTD) within the range of 1800-3000 m. Furthermore, the decrease in the AvTD at lower and upper altitudes in our study area might be due to hot and dry climate conditions in the savanna and low temperatures in the alpine zone (Hemp 2006c) which could cause strong environmental filtering (Dinnage 2009).

Together with the relatively low species richness at higher elevations (2500-3500 m), increased VarTD represent even distribution of taxa in communities at this elevation with specialized species of similar adaptations that belong to similar clades (Fig. 5A); while indicating uneven distribution of taxa for the communities at lower and highest elevations. When only angiosperms were analyzed (gymnosperms and pteridophytes excluded)



VarTD showed a strong decrease in mid elevations (Fig. 5B) where pteridophytes play an important role in wet montane forests. This means that the pteridophytes (82 species) added only moderately to AvTD but significantly to VarTD. This reflects the huge species diversity of Pteridophytes and gymnosperms (only one species – *Podocarpus latifolius* – was present in our plots) which belongs on the other hand to one major clade only.

Effect of human activities on phylogenetic diversity at different elevations

In the colline zone AvTD and VarTD did not differ between the savanna woodlands and maize fields (Table 2; Fig. 6 A & B; 7A & B). Although land use can change plant species composition and dominance including higher numbers of ruderals in maize fields, they were not less phylogenetically diverse than natural savanna at Kilimanjaro. This may reflect that environmental filtering by the hot and dry savanna conditions is equally affecting both natural habitats and maize fields.

In the lower montane zone, the significant decrease of AvTD and VarTD observed in human-influenced habitats (Fig. 6 A & B; Fig. 7A & B), is an indication that human influence resulted in communities of more closely related species and uneven distribution compared to the nearby natural habitats. Earlier studies of the same study plots showed that home gardens and some coffee plantations had a similar vegetation structure and produced similar amounts of biomass, which was considerably lower than the one of natural forest, and that grasslands had clearly the least pronounced structure and lowest biomass (Rutten *et al.* 2015b, Ensslin *et al.* 2015). The species compositions of natural and of human impacted habitats do not differ in the *Ocotea* zone (Hemp 2006c) likewise, AvTD and VarTD of the natural and previously selectively logged forest were not significantly different from each other (Fig. 6A & Fig. 7A).

In a parallel study, using the same study plots, the natural and the previously selectively logged forests were also similar in biomass, but found to be still more open than the unlogged forests (Ensslin *et al.* 2015; Rutten *et al.* 2015a). This reflects that exploitation of the forest has resulted in forests free of mature *Ocotea* trees but still with the same species composition.

In the *Podocarpus* zone, there was no significant difference in phylogenetic diversity between previously burned and non-burned forests (Table 2; Fig. Fig. 6A & Fig. 7A). Fire can largely influence species composition by eliminating fire susceptible species in some layers and maintain a composition of rather fire-resistant species (Hemp 2005). The result of this study may reflect that species replacement by fire happened within orders and families rather than by distinct species. *Erica excelsa*, which is favored by fires and becomes dominant in fire regeneration stage, occurs always in undisturbed *Podocarpus* forests as well, although in low frequency and cover (Hemp and Beck 2001).

CONCLUSIONS

Mount Kilimanjaro provided the natural field arena for studying the effects of climate change on biodiversity as the elevation represented natural gradients of temperature and precipitation at small spatial scales while demonstrating how human activities impacted phylogenetic diversity in plant communities at different elevations in different ways.

The decrease in phylogenetic diversity in the lower and upper elevations might be a result of environmental filtering due to hot and dry climate conditions in the savanna and low temperatures in the alpine zone. We also found that phylogenetic diversity of natural habitats at Mount Kilimanjaro is driven more by vegetation structural diversity than by species richness. This might be due to more benign climate conditions at intermediate



elevation, where precipitation peaks and where temperatures are neither stressfully.

Human influence at Mount Kilimanjaro had moderate negative impact on phylogenetic diversity in the lower montane, middle and upper montane zones. In the colline zone environmental filtering due to hot and dry savanna conditions is equally affecting both natural and human influenced habitats (maize fields).

As areas with higher phylogenetic diversity are considered to be of high conservation value and important for ecosystem functioning and services, conservation at Mount Kilimanjaro should care for communities with higher phylogenetic diversity along with conserving remaining lower montane forests below the National Park.

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