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Community-weighted means and functional dispersion of plant functional traits along environmental gradients on Mount Kilimanjaro

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Community-weighted mean; Disturbance; Elevation; Environmental filtering; Environmental gradient; Functional dispersion; Null model; Precipitation; Soil nutrients; Temperature

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Abstract

Questions: How do community-weighted means of traits (CWM) and functional dispersion (FDis), a measure of trait variability, change in response to gradients of temperature, precipitation, soil nutrients and disturbance? Is the decrease in trait similarity between plots continuous or discontinuous? Is species turnover between plots linked to trait turnover?

Location: Mount Kilimanjaro, Tanzania, Africa.

Methods: Sixty plots were established in 12 major vegetation types on Mount Kilimanjaro, covering large gradients of temperature, precipitation, soil nutrients and anthropogenic disturbance representing the dominant ecosystems in East Africa. Environmental data, plant abundances and plant traits were recorded for each plot. Trait CWM and FDis were related to environmental factors with partial least squares regressions. Trait similarity between pairs of plots was assessed with a null model approach.

Results: Both CWM and FDis of most traits responded strongly to environmental factors, particularly to precipitation and disturbance. FDis of traits associated with growth and reproduction mostly increased with temperature and precipitation, and decreased with disturbance. Pair-wise plot comparisons revealed an inverse relationship of trait similarity with differences in temperature, precipitation and anthropogenic disturbance. However, changes in similarity were often discontinuous rather than continuous. Several vegetation types differed strongly in species composition but not in traits.

Conclusions: Trait dispersion indicating functional niches increased with productivity and temperature. Conversely, low-productivity conditions were characterized by trait convergence. Discontinuous changes in trait similarity between plots suggested tipping points at which trait expressions change strongly to adjust to environmental conditions. Large sections of the temperature gradient were characterized by species turnover with only minor changes in traits, indicating that the functional composition may be resilient to gradual environmental changes until a tipping point is reached.

Introduction

The response of plant functional traits to environmental change has been widely acknowledged to inform community assembly based on differential resource use, growth, regeneration and reproduction among species (McGill et al. 2006a). However, despite great advances, our understanding still remains fragmented, due to the

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wide diversity of habitats on Earth, the difficulty in finding traits suitable to indicate biological functions, and different methods used to analyse the response of traits to environmental variation.

At the community level, means and diversity of trait expression of co-existing species are frequently used to quantify trait responses (Leps et al. 2006). It is still an open question whether and how trait diversity co-varies with trait means on large environmental gradients. According to the productivity hypothesis, the number of available niches should increase towards the benign part of a gradient, suggesting that local functional diversity (FD) should also increase (e.g. Laliberté et al. 2013; Rabosky & Hurlbert 2015). Conversely, FD should decline towards environmental extremes due to stronger abiotic filtering. On the other hand, productive environments may allow competitive hierarchies to unfold (Grime 2001), resulting in stronger biotic filtering and decreasing FD among the species remaining in the community (Bernard-Verdier et al. 2012), whereas positive interactions might facilitate the co-existence of multiple life strategies at the stressful end of gradients (Bertness & Callaway 1994).

Both abiotic and biotic filtering restrict trait expressions to a subset of those available in the regional species pool. This process is often called convergence (Grime 2006). Conversely, if several life strategies co-exist in a given environment due to stabilizing niche differences (HilleRisLambers et al. 2012), spatial micro-heterogeneity (Raevel et al. 2012) or positive interactions (Boulangeat et al. 2012) the trait composition of a community can be divergent (Weiher & Keddy 1995; Weiher et al. 2011). Both convergence and divergence are generally assessed using null models based on random samples of a metacommunity species pool (Grime 2006; Mason et al. 2007; de Bello 2012). Apart from abiotic and biotic filtering, ecological drift, i.e. random walks of species' abundances in time, may generate different communities on distant sites with similar environmental conditions (Hubbell 2001). Variations in species occurrences should then be trait-independent, i.e. traits do not determine changes in species' abundances (Vellend et al. 2014). This process can potentially explain local community assembly if (1) environmental conditions are similar, (2) species identities vary across sites, and (3) trait expressions do not differ systematically from the null model distribution.

Changes from trait similarity to dissimilarity due to trait convergence should reflect changes in abiotic conditions, which could be either continuous or discontinuous (de Bello et al. 2009; Bermudez & Retuerto 2013). Land vegetation sometimes displays discontinuous patterns along continuous environmental gradients (Glavac et al. 1992; Collins et al. 1993; Danz et al. 2013). It is an open question whether these structural and compositional discontinuities are reflected by comparable discontinuities in traits. For instance, transitions between forest and savanna could be explained by complex feedback mechanisms (Hoffmann et al. 2012). If this were the case, sudden changes between similarity and dissimilarity rather than continuous changes with increasing environmental distance between vegetation types could be expected.

To increase our understanding of trait response functions, we were interested in three questions: (1) how do CWM of traits and FD change in response to environmental gradients; (2) is the decrease in trait similarity between plots continuous or discontinuous; and (3) can we detect species turnover without corresponding changes in traits? To answer these questions, we linked CWM and FD of a wide range of traits to gradients in temperature, precipitation, soil nutrients and disturbance on Mount Kilimanjaro, East Africa. This analysis yielded linear relationships along these gradients. We also assessed patterns of trait similarity with pair-wise comparisons of plots within and across vegetation types using null models to assess deviations of plot trait expression from the common species pool. Finally, we compared taxonomic and trait β-diversities across vegetation types. Communities with similar species and trait compositions should simply belong to the same vegetation type, but similarity in traits combined with dissimilarities in species composition may indicate trait-independent changes in species composition.

Methods

Study site and data collection

Data collection took place on Mount Kilimanjaro, northern Tanzania. We investigated 12 major vegetation types on the southern slopes of the mountain and established five plots in each of them (Table 1). The average distance between plots of the same vegetation type was 14 km. The highest sites were situated in alpine *Helichrysum* shrubland (HEL; see Hemp 2006a). Descending, plots were located in *Erica* cloud forest (FER), joined by upper montane *Podocarpus* (FPO) and *Ocotea* forest (FOC) at lower elevations. Besides these undisturbed sites, plots were also established in fire-disturbed *Podocarpus* (FPD) and selectively logged *Ocotea* forests (FOD), covering substantial parts of the mountain. The lowest forest belt is formed by lower montane forest (FLM), characterized by high heterogeneity due to its disturbance history. In populated areas, forest has been replaced by home gardens (HOM), the traditional agroforestry systems of the local Chagga people. Grasslands (GRA) and coffee plantations (COF) were the most disturbed habitats at these elevations. In the lowlands, savanna fragments (SAV) were selected, together with maize fields (MAI). Cultivated plants were excluded from all analyses because their growth does not exclusively

Table 1. Dominant vegetation types on Mount Kilimanjaro and abiotic environmental conditions.

Vegetation Type	Elevation (m a.s.l.)	Annual Precipitation (mm·yr^{-1})	Mean Temperature (°C)	Disturbance	Soil Nutrients
Helichrysum shrub (HEL)	3880–4550	1208–1411	2.9–5.3	0.00–0.02	−1.65 to −1.36
Erica forest (FER)	3500–3890	1393–1716	4.5–8.1	0.01–0.04	−1.54 to −1.30
Disturbed *Podocarpus* forest (FPD)	2770–3060	1936–2116	9.0–10.8	0.15–0.26	−1.35 to −0.83
Podocarpus forest (FPO)	2720–2970	1946–2136	9.0–10.3	0.00–0.00	−1.31 to −1.17
Ocotea forest (FOC)	2120–2750	2117–2552	9.9–12.1	0.00–0.02	−1.33 to −0.92
Disturbed *Ocotea* forest (FOD)	2220–2560	2202–2413	11.0–13.0	0.07–0.10	−1.33 to −1.05
Lower montane forest (FLM)	1620–2040	2089–2305	14.4–16.5	0.10–0.21	−1.04 to −0.18
Grasslands (GRA)	1300–1750	1248–2022	16.5–20.8	0.49–0.57	−0.57 to 1.49
Home gardens (HOM)	1150–1840	1152–2244	16.2–20.8	0.41–0.63	−0.42 to 2.63
Coffee plantations (COF)	1120–1660	1115–1736	17.4–22.6	0.59–1.00	−0.16 to 3.24
Savanna (SAV)	871–1130	657–957	22.3–24.6	0.16–0.42	−0.57 to 6.15
Maize fields (MAI)	860–1020	588–785	22.6–24.8	0.54–0.91	−0.40 to 5.25

Value ranges are given for each vegetation type. Disturbance was calculated considering biomass removal, input of chemicals and landscape composition (Appendix S1). Soil nutrients is the value of the first axis of a PCA including plant available Ca^{2+}, K^{+}, Na^{+}, N and P (Appendix S2). Larger values indicate higher nutrient availability.

depend on their response traits. On all 60 plots, continuous temperature and humidity measurements were made from 2010 to 2014 and combined with long-term precipitation measurements (Mwangomo et al. 2014). Productivity of the vegetation increases with precipitation on Mount Kilimanjaro (Ensslin et al. 2015). Disturbance was measured as a compound variable including the combined effects of fertilization, biomass removal and differences in the surrounding habitat matrix (Appendix S1).

Soil and plant samples were taken between 2010 and 2012. Vegetation surveys were performed at all plots using the Braun-Blanquet scale to assess abundance (Braun-Blanquet & Schoenichen 1964). Abundance classes were converted to percentage cover. As plant diversity was too high to make complete sampling feasible, the most abundant species making up 80% of total plant biomass at a plot were selected for trait measurements. Plant functional trait measurement followed the LEDA protocols (Kleyer et al. 2008; www.leda-traitbase.org). Fifteen individuals per species were sampled from different plots, if possible, to account for intraspecific variability. Traits were selected to mirror aspects of plant life strategies (Table 2). Traits related to the worldwide leaf economics spectrum (Wright et al. 2004) describing fast vs slow growth and nutrient

Table 2. Plant functional traits. Sampling and measurements followed the LEDA protocols (Kleyer et al. 2008). Means are given for all traits except leaf pubescence and spinescence, where medians are given, and categorical traits. Specific leaf area, canopy height, relative seed number and leaf area values were log-transformed prior to analyses.

Group	Trait	Unit	Mean (Range)	Description
GI	Specific leaf area (SLA)	cm^{2}·g^{-1}	18.9 (4.9 to 89.1)	Leaf area per g leaf dry weight
GI	Leaf dry matter content (LDMC)	mg·g^{-1}	0.31 (0.06 to 0.61)	Leaf dry matter per g fresh leaf tissue
GI	Stem-specific density (SSD)	g·cm^{-3}	0.41 (0.05 to 0.82)	Dry weight per unit volume
GI	Leaf N_{mass}	mg·g^{-1}	22 (6.2 to 47.9)	Leaf N content per g dry tissue
GI	Leaf C_{mass}	mg·g^{-1}	441.7 (362.1 to 551)	Leaf C content per g dry tissue
GI	Leaf P_{mass}	mg·g^{-1}	2 (0.5 to 7.5)	Leaf P content per g dry tissue
GI	Canopy height	m	1.03 (0.05 to 44.92)	Height of highest leaves
RI	Relative seed number	cm^{-1}	8.08 (0.04 to 99707)	Number of seeds per m canopy height
RI	Seed crop frequency	yr^{-1}	1.57 (0.2 to 12)	Number of seed production events per year
PAI	Spinescence	–	0 (0 to 4)	Size and density of spines (0 = no spines, . . ., 4 = medium density of large spines)
PAI	Dispersal syndrome	–	Categorical (5)	Type of transport of dispersal unit
PAI	Diaspore colour	–	Categorical (14)	Colour of fleshy or dry fruit, seed or spore
PAI	Flower colour	–	Categorical (9)	Colour of flower petals, if present
O	Leaf area	cm^{2}	10.28 (0.02 to 10097)	One-sided leaf area
O	Leaf pubescence	–	0 (0 to 2)	Density of leaf hairs (0 = no or few hairs, 1 = hairy, 2 = densely covered with hairs)
O	Leaf $\delta^{13}C$	–	−26.2 (−35 to −10.7)	Proxy of water-use efficiency (discrimination of C_3 vs C_4/CAM plants)

GI, Growth investment; RI, Reproductive investment; PAI, Plant–animal interactions; O, Others.

turnover were termed 'growth investment traits'. 'Reproductive investment traits' separate plants with fast generation cycles and high seed number from those with slow reproduction and reliance on few, often large, seeds. Seed number was weighted by canopy height to account for their inherent correlation (Moles & Westoby 2004). 'Plant–animal interaction traits' describe adaptations of plants both to avoid predation by herbivores and to enhance pollen and seed dispersal, which may involve animals.

Laboratory analyses for leaf C, N and P contents were done at Oldenburg University, Germany. Leaf C stable isotopes were analysed at the Karlsruhe Institute of Technology in Garmisch-Partenkirchen, Germany. We collected soil samples and measured plant-available Ca^{2+}, K^{+}, Na^{+}, N and P concentrations at the Department of Soil Science of the University of Goettingen, Germany. The first axis of a PCA was termed 'soil nutrients' and reflected overall soil nutrient availability for plants, high values indicating high nutrient availability (Appendix S2).

Statistical analyses

Community-weighted means (CWM) and functional dispersion of traits of co-occurring species (FDis; Laliberté & Legendre 2010) were dependent variables in the analysis of trait–environment relationships. FDis is unaffected by the number of species present in a community. It is a measure of functional divergence, following Mason et al. (2005). According to Butterfield & Suding (2013), single trait diversity indices can outperform those calculated from multiple traits. We therefore calculated CWM and abundance-weighted FDis for each plant functional trait on the 60 plots separately, as well as for all traits together ('multivariate FDis') using the dbFD function in the R package FD (Laliberté & Legendre 2010; R Foundation for Statistical Computing, Vienna, AT).

We analysed changes in CWM and FDis on environmental gradients with partial least squares (PLS) regression. PLS can deal with correlated predictors, which was the case in our study system (Appendix S3). As PLS is an ordination method, no *P*-values are given. Explained variance and the signs of coefficients indicate the strength and directionality of relationships. Calculations were carried out using the plsr function in the R package pls. Standard errors for coefficient estimates were calculated with leave-one-out cross-validation using the var.jack R function (pls package).

Trait similarity between plots was assessed comparing CWM (Garnier et al. 2007) and FDis values. In a null model approach, we performed a pair-wise comparison of the 60 plots, testing for similarity in terms of CWM and FDis as well as for the occurrence of convergence or divergence patterns (see Appendix S4 for details of our null model approach). We refrained from incorporating environmental distance into this analysis, because relationships of traits and environment were already revealed with the PLS approach and it would not have been trivial to weight the environmental factors.

As similarity is the inverse of β-diversity, we derived trait β-diversity from the similarity calculated previously. As we were interested in the relationship of taxonomic β-diversity and overall trait space, trait β-diversity was derived from all traits. Taxonomic β-diversity was assessed using the Hill number approach, whose use has been recommended because of its intuitive properties, among them its doubling property, i.e. communities sharing half as many species as others have exactly the double β-diversity (Jost 2007; Chao et al. 2014). Hill numbers rely on a parameter q that defines how much weight is given to species' abundances. We chose $q = 1$, which weights rare and abundant species proportionally (R package vegetarian).

Results

Community-weighted means and functional dispersion along environmental gradients

Functional dispersion (FDis) was moderately and community-weighted means (CWM) very well explained by temperature, precipitation and disturbance, and to a lesser extent by soil nutrients (Fig. 1). Individual R^2 values ranged from 0.13 to 0.56 (Appendices S5 and S6). Multivariate FDis had an R^2 value of only 0.08. Considering CWM, 'growth investment' and 'other' traits were equally well explained ($0.42 \leq R^2 \leq 0.72$; Appendix S6). 'Reproductive investment' and 'plant–animal interaction' traits had slightly lower R^2 values on average ($0.45 \leq R^2 \leq 0.54$). Thus, CWM showed a stronger response to the environmental gradients than FDis.

Temperature, precipitation and disturbance had stronger effects on CWM and FDis than soil nutrients, as shown by the number of significant coefficients (Appendices S5 and S6). The effects of temperature and disturbance were mostly opposite, i.e. CWM or FDis values, increasing with temperature, decreasing with disturbance. The relationships of precipitation, temperature and soil nutrients with CWM and FDis were mostly similar.

Low temperatures favoured high leaf C_{mass}, leaf pubescence and relative seed number, whereas canopy height, leaf area, spinescence and leaf $\delta^{13}C$, a proxy for water-use efficiency, increased with temperature. FDis decreased or increased in the same direction as CWM for leaf pubescence and leaf $\delta^{13}C$, but in opposite directions for relative seed number and leaf area. The leaf area of the most dominant species thus increased with temperature, but low

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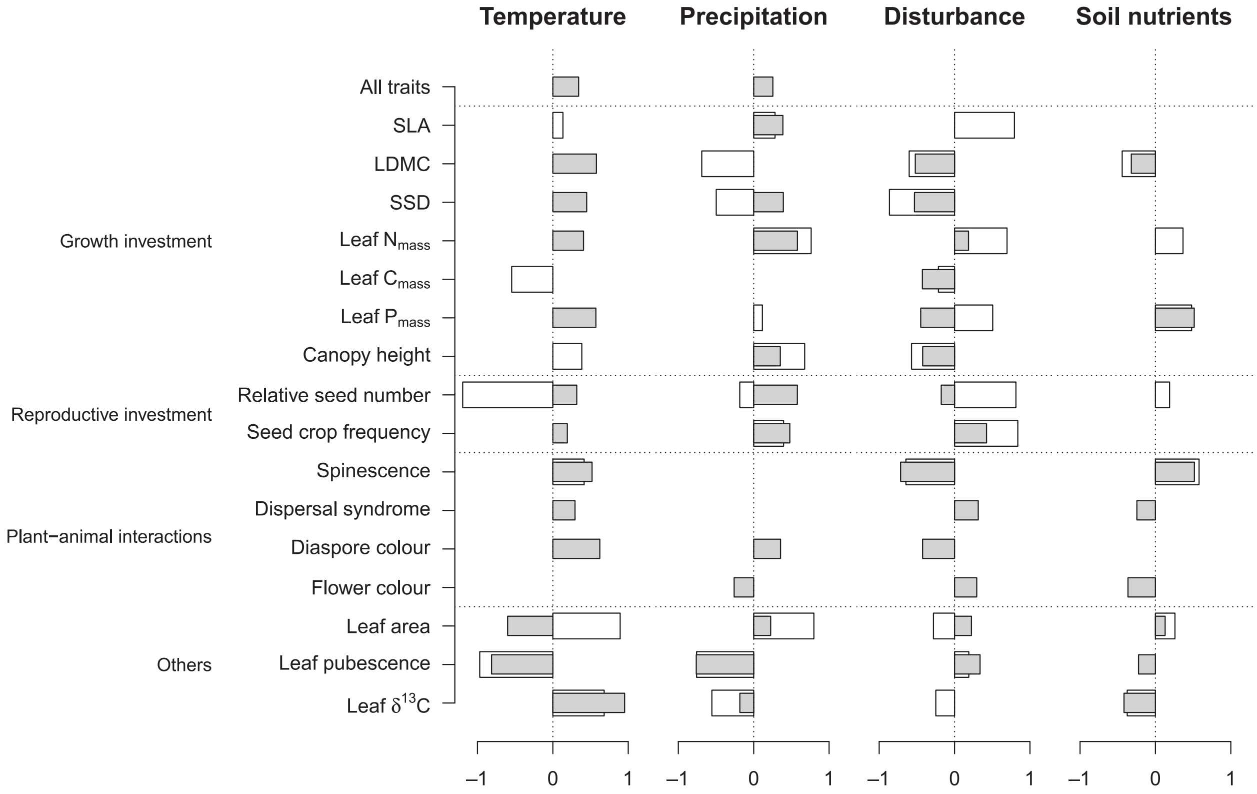

Fig. 1. Relationship of plant functional trait CWM and FDis to environmental factors. Bars represent coefficients of a multivariate PLS regression. Both environmental factors and plant functional traits were standardized. Coefficients are thus comparable between traits and environmental factors. Grey bars are FDis values, white bars are CWM. Only values of coefficients larger than their corresponding cross-validation SE (see Appendices S5 and S6) are shown. No CWM could be calculated for categorical traits and in a multivariate format ('All traits').

temperature favoured both large and small leaves within a plot. FDis of other growth traits and diaspore colour increased with temperature. Overall trait space measured with the multivariate FDis also increased with temperature.

At high precipitation values, we found high SLA, leaf N_{mass}, canopy height and leaf area together with low LDMC, SSD, leaf $\delta^{13}C$ and leaf pubescence. FDis of almost all traits increased with precipitation. Exceptions were spinescence and flower colour, which showed the opposite pattern.

Disturbance favoured high values of traits indicating rapid growth and reproduction (SLA, leaf N_{mass}, leaf P_{mass}, relative seed number), whereas canopy height, leaf area, LDMC and SSD decreased. In contrast to the precipitation gradient, FDis of many traits decreased with increasing disturbance.

As expected, leaf N_{mass} and leaf P_{mass} increased with soil nutrients. For leaf P_{mass}, FDis also increased. LDMC and leaf $\delta^{13}C$ decreased, while spinescence increased both in CWM and FDis with increasing soil nutrients. Flower colour variability decreased at high soil nutrient concentrations, as shown in low FDis.

Trait similarity among pairs of plots

Similarity or dissimilarity among pairs of plots was often related to vegetation type, i.e. plots from one vegetation type showed the same degree of similarity to those from another in pair-wise comparisons (Fig. 2, upper triangles). Convergence (Fig. 2, blue fill, lower triangles) of the observed trait values from two communities relative to the null models did not increase gradually but in discontinuous steps (Fig. 2, blue fill of lower triangle). However, convergence was not linearly related to temperature. These discontinuities were congruent for growth investment traits, while other traits showed a more variable pattern. Vegetation types with tall trees, i.e. *Ocotea* (FOC, FOD) and lower montane forests (FLM), formed a group that was similar in most traits (white in Fig. 2), except for *Podocarpus* forests (FPO, FPD), which differed in leaf chemical traits and leaf area. Similarity in traits was also found for alpine scrub (HEL) and *Erica* forest (FER). Savanna (SAV) and home gardens (HOM) showed some ties to forests, but also to maize fields (MAI) and grasslands (GRA). Coffee plantations (COF) were distinct from other vegetation types for most traits. In contrast to convergence, divergence

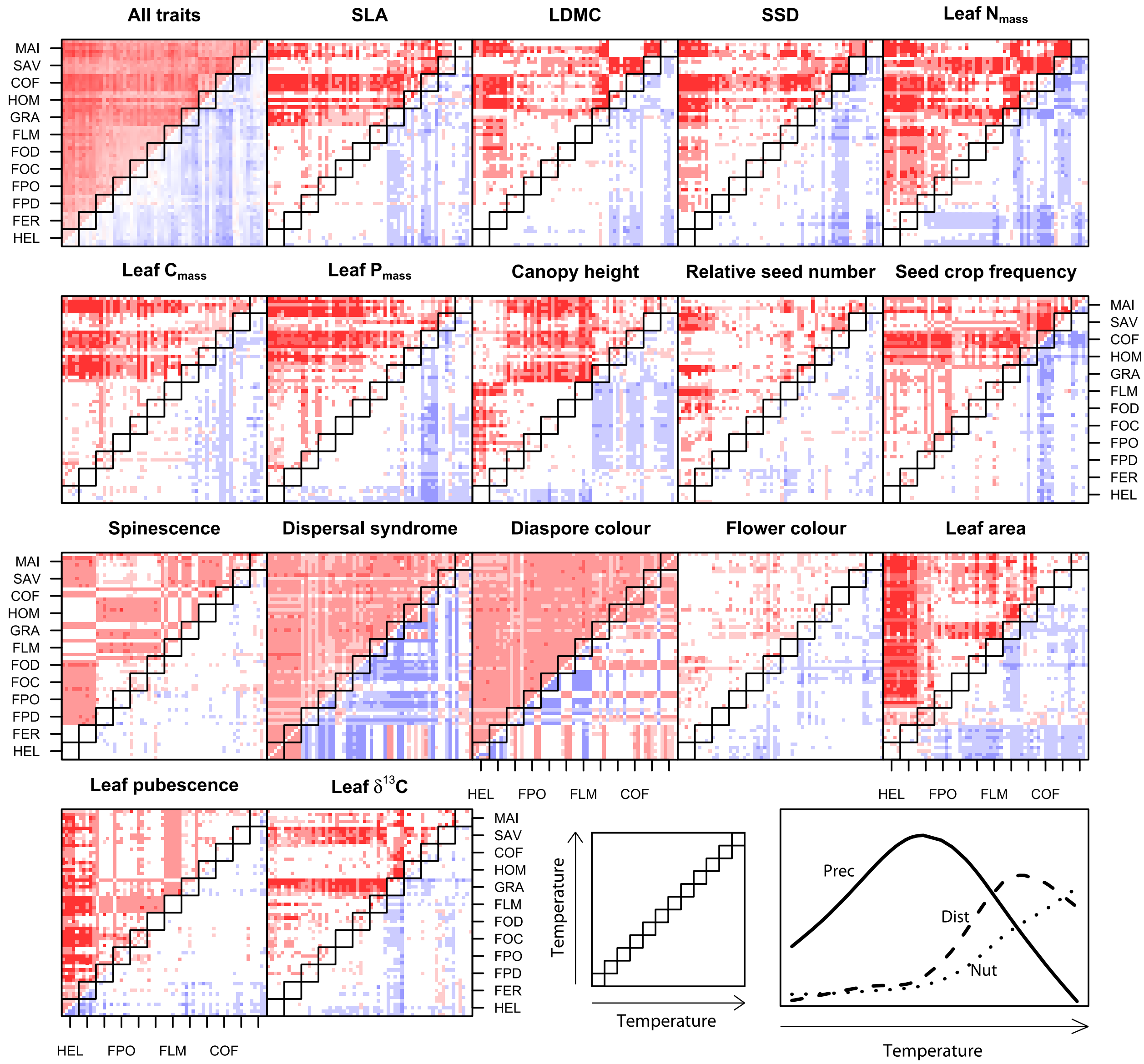

Fig. 2. Trait similarity, convergence and divergence within and between vegetation types. Vegetation types are arranged according to their elevational distribution (see Table 1), with elevation decreasing from left to right and bottom to top. Upper triangle: White areas represent complete trait similarity, i.e. both CWM and FDis of the respective plot pairs lie within null model CI, while red shading indicates that CWM, FDis, or both, are outside null model CI. Lower triangle: The colour scale shows trait convergence and divergence. FDis values below null model distribution CI are blue (convergence), while those above are red (divergence). Dark colours show both plot FDis values were below or above CI, while light colours represent pairs where one plot was within FDis CI. Note that upper and lower triangles are not mirror images: plots may differ in terms of CWM, but have similar FDis values. In this case, the lower triangle would be white while the upper triangle would be red. Black squares frame within-vegetation type comparisons. The lower right panel shows the approximate distribution of precipitation (Prec), disturbance (Dist) and soil nutrients (Nut) along the temperature gradient.

occurred rather infrequently and not in distinct patterns, except for diaspore colour and dispersal syndrome.

Relationship of trait and taxonomic β-diversity

Taxonomic β-diversity was lowest within vegetation types (Fig. 3, diagonal elements). Starting from the diagonal elements representing within-vegetation type β-diversities, both trait and taxonomic across-vegetation type β-diversities increased from left to right and top to bottom with increasing elevational distance. Increases were generally strong for taxonomic β-diversity (horizontal ellipse diameters). Trait β-diversity increased less strongly than taxonomic β-diversity (vertical ellipse diameters).

Difference in disturbance intensity added to elevational distance: comparisons of forest types with COF, MAI and GRA showed larger trait β-diversity than with HOM or SAV. Trait-independent species turnover, i.e. higher species β-diversity than trait β-diversity, occurred between FPD and FPO, whereas FOD and FOC differed neither in species nor in traits. FLM differed strongly from the other rain forests in terms of species, but not in traits. Among vegetation types of the lower elevations, COF shared species and traits with HOM, and GRA with SAV. Interestingly, SAV and FPD had especially low trait β-diversity. This was probably due to similar leaf size and similar growth forms in the understorey vegetation, although the elevational distance between these communities is about 2000 m.

Discussion

We assumed that plant functional traits respond to environmental gradients, both community means and dispersion. We found support for this assumption for a broad range of traits, with a stronger response of CWM than FDis. In line with these results, plots often showed convergence when compared with ecologically distant plots in their common null model. Sudden shifts from trait similarity to convergence appeared that were often, but not always, associated with strong changes in environmental conditions. Pairs of plots with similar trait values could still be dissimilar is species composition, indicating trait-independent turnover.

Community-weighted means and functional dispersion along environmental gradients

Community weighted means of SLA, leaf N_{mass} and leaf P_{mass} increased, and LDMC and SSD decreased with precipitation, disturbance or soil nutrients. The correlations between these traits support the plant economics spectrum, indicating higher acquisition and turnover of resources in plants with increasing soil resources or disturbances (Appendix S2; Wright et al. 2004; Freschet et al. 2010; Díaz et al. 2016). Similar relationships were also found by e.g. Fonseca et al. (2000), Lienin & Kleyer (2012) and Moles et al. (2014). FDis of these ‘growth investment’

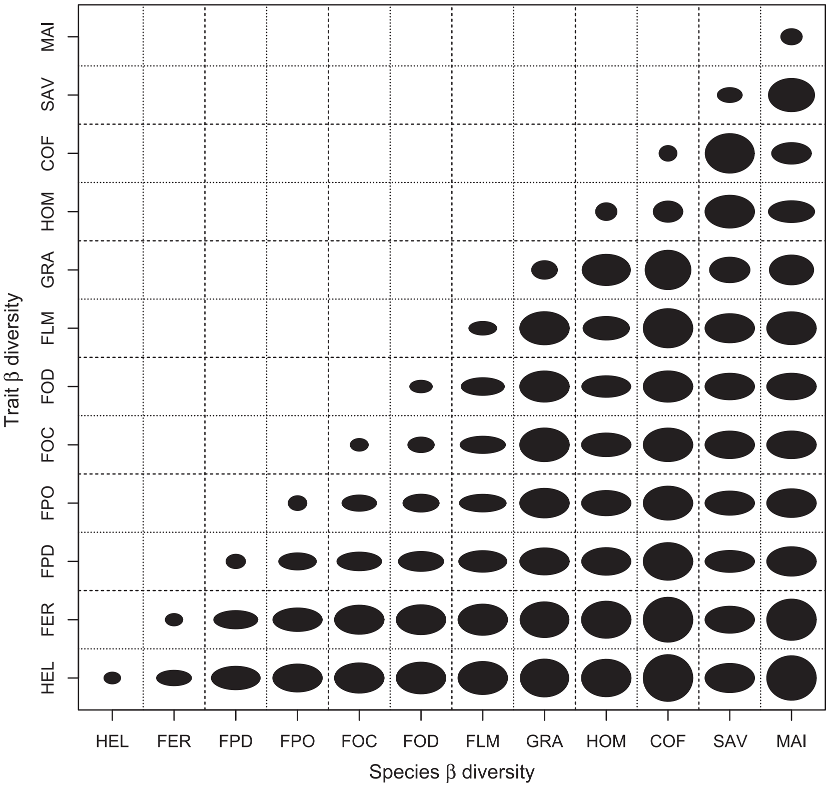

Fig. 3. Trait and taxonomic β-diversity. Vegetation types are arranged according to their elevational distribution (see Table 1), with elevation decreasing from left to right and bottom to top. Trait and taxonomic β-diversity represent averages across all pairs of plots classified to vegetation types. Horizontal ellipse diameters represent taxonomic β-diversity (Jost 2007). Vertical ellipse diameters show trait β-diversity, the inverse of trait similarity. Both variables were scaled to the interval [1,2].

traits also increased with precipitation, because the upper end of the precipitation gradient was occupied by rain forests comprising multiple co-occurring growth forms, such as trees, ferns, epiphytes and lianas, and thus high FDis. Conversely, low temperatures, low precipitation and high disturbance were associated with low FDis values, indicating a decrease in viable plant life strategies under environmentally extreme conditions (Weiher & Keddy 1995). A study from Cornwell & Ackerly (2009) along a precipitation gradient in California showed the same directionality in functional diversity. Our results suggest that niche space increases with available resources on Mount Kilimanjaro, which supports higher trait dispersion (Rabosky & Hurlbert 2015).

Evidence was weaker for soil nutrients than for the other environmental factors, although soil nutrients are known to be important drivers of species distributions in tropical ecosystems (Swaine 1996; John et al. 2007). Tropical mountain soils are typically N-limited (Tanner et al. 1998); this is not the case in the volcanic soils of Mount Kilimanjaro (Gerschlauer et al. 2016), suggesting less importance of nutrient limitation compared to other regions.

Savanna remnants were rich in C_4 grasses with high leaf $\delta^{13}C$, whereas fertilized maize fields were dominated by dicotyledonous weeds, which may be better adapted to disturbed environments through shorter generation time. This led to a decrease in the leaf $\delta^{13}C$ CWM with increasing nutrient levels. Seed crop frequency CWM and FDis increased with disturbance, as plants need to reproduce quickly to survive disturbance as seed (Jakobsson & Eriksson 2000; Schippers et al. 2001; Lehsten & Kleyer 2007).

In contrast to most other traits, FDis of leaf area and pubescence increased with decreasing temperature. It is often stated that leaves should be small under cold and dry conditions to decrease transpiration (Harrington et al. 2010; Peppe et al. 2011). However, the growth of large-leaved giant groundsel (*Lobelia* spp. L.) and *Dendrosenecio* spp. B. Nord. in many African high-elevation ecosystems (Hedberg 1969) shows that large, hairy leaves can be successful even where regular night frosts occur (Geller & Smith 1982; Smith & Young 1987). Leaf pubescence helps to avoid heat loss and tissue damage from intense UV light and is therefore linked to low temperatures and high elevations.

Dispersal syndrome, diaspore and flower colour showed idiosyncratic responses to the environmental gradients, probably due to co-evolution with pollinators, seed dispersers and herbivores (Schaefer et al. 2004), which are only indirectly linked to environmental gradients. To resist herbivory, many plant species feature spines in savanna habitats, where large herbivores have detrimental effects on vegetation (Hanley et al. 2007). Thus, the number of spiny taxa increased in the relatively nutrient-rich and hot savanna and in the disturbed maize fields.

Like most individual traits, the whole trait space (multivariate FDis) decreased with decreasing temperature and precipitation. Other studies have reported different results, such as bowl- or hump-shaped trait spaces (Spasojevic & Suding 2012; Lamanna et al. 2014). The PLS approach of our study is essentially limited to detecting linear relationships, which can be expected for large environmental distances as on Mount Kilimanjaro. Lamanna et al. (2014) corrected trait space for species richness, which affects tropical regions more than temperate or arctic ones due to higher species number in the former. The resulting measure can be seen as the average trait space occupied per species, while we quantified absolute dimensions.

A shortcoming of our study could be that our trait collection was limited to a subset of all species. Vegetation surveys on Mount Kilimanjaro suggest that over 1200 species of vascular plant occur on the southern slopes (Hemp 2006b), about ten times as many as were sampled. Nevertheless, as we sampled the most abundant species (Garnier et al. 2007), the remaining species had very low frequencies, and their influence on both CWM and FDis should be rather low. A consequence of the restricted sampling was that epiphytes could not be included, although they exhibit trait expression not covered by other life forms (Benzing 1990; Petter et al. 2015). Considering their abundance on Mount Kilimanjaro, their inclusion in a larger sampling programme would probably influence results quantitatively, but not qualitatively.

Trait similarity among pairs of plots

We found strong discontinuities in trait similarity, and therefore in convergence and divergence patterns among pairs of plots. This is contrary to a monotonic decrease in similarity between low- and high-elevation sites found by Swenson et al. (2011) on an elevation gradient from 300 to 1000 m a.s.l. in Puerto Rico. Shifts from similarity to dissimilarity due to convergence at upper elevations for leaf N_{mass}, leaf P_{mass}, canopy height and leaf area were probably due to an array of adaptations to very cold and dry conditions above 3300 m a.s.l. (Beck et al. 2007; Harrison et al. 2010) that were not present in Puerto Rico. Other sudden shifts can be explained by changes in disturbance regime at lower elevations, for instance between rain forests (FLM), home gardens (HOM) and grasslands (GRA) or between savanna (SAV) and maize fields (MAI) (Pakeman et al. 2011; Ding et al. 2012; Guedo & Lamb 2013). These shifts indicate abrupt changes in abiotic filtering. However, sudden shifts between similar and dissimilar trait values also occurred on continuous environmental gradients, such as between *Podocarpus* (FPO) and other forests on gradients of

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temperature and precipitation (Table 1). Discontinuities in trait expressions on continuous latitudinal gradients were also found for seed size and plant height (Moles et al. 2007, 2009).

Relationship of trait and taxonomic β-diversity

Overall, there was strong evidence for environmental filtering on Mount Kilimanjaro, in line with findings from other tropical mountains (e.g. Swenson et al. 2011). However, we observed trait-independent species turnover for a considerable environmental distance (compare Figs 2 and 3). For instance, over an elevation gradient of about 1100 m with significant changes in precipitation and temperature, the functional composition of the rain forest types remained very similar (Fig. 3) and most traits did not deviate from null model expectations (Fig. 2), whereas species composition varied considerably.

Further up, the 0° isotherm around 3000 m a.s.l., where *Podocarpus* forests changed to *Erica* forests, marked a strong shift in trait filtering, resulting in high taxonomic and trait β-diversity across the plots belonging to these vegetation types. Above this elevation and up to the *Helichrysum* alpine zone, where regular frosts occur each night, trait-independent species turnover occurred again, as different species shared similar traits indicating adaptations to a cold and dry climate.

Trait-independent species turnover under similar environmental conditions may indicate neutral processes such as ecological drift, dispersal limitation or historical contingency (Chase & Leibold 2003; Vellend et al. 2014). However, most plots belonging to the same vegetation type showed low taxonomic β-diversity combined with low trait β-diversity (Fig. 3). Different vegetation types were also different in environmental conditions that break neutrality (McGill et al. 2006b). An alternative explanation for the apparent trait-independent species turnover may be filtering on traits that were not taken into account. Candidate traits known to respond to extreme climate are e.g. leaf surface albedo, xylem conductivity and frost sensitivity (Harrison et al. 2010). However, trait-independent species turnover might also be due to a buffered trait response to gradual environmental changes, i.e. species change but their traits form discrete clusters remaining stable or resilient in the face of gradual environmental changes. There is some evidence from modelling studies for trait clustering (Scheffer & van Nes 2006; Leimar et al. 2008), but empirical tests are largely lacking.

Conclusions

Functional diversity of most traits increased with productivity represented by temperature and precipitation, and decreased towards the extreme ends of environmental gradients. This indicates an increase in functional niches with higher temperature, precipitation and lower disturbance. Plant communities were characterized by trait-specific and abrupt shifts between similarity and dissimilarity due to convergence, rather than gradual changes. These patterns were similar for correlated traits associated with the leaf economics spectrum. However, relatively large sections of the elevation gradient were characterized by trait-independent species turnover. Changes between species turnover with and without changes in traits were discontinuous, indicating that the functional composition may be buffered against gradual environmental changes until a tipping point is reached, where strong trait filtering occurs and a new functional composition is established.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Disturbance index calculation.

Appendix S2. Principal components analysis (PCA) of soil nutrients.

Appendix S3. Pearson correlations between environmental factors and plant functional traits.

Appendix S4. Null model description.

Appendix S5. The response of functional dispersion (FDis) to the environmental gradients.

Appendix S6. The response of trait community-weighed means (CWMs) to environmental gradients Predictors and responses were standardized prior to the analysis.