

Plant traits mediate the effects of climate on phytophagous beetle diversity on Mt. Kilimanjaro

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Abstract. Patterns of insect diversity along elevational gradients are well described in ecology. However, it remains little tested how variation in the quantity, quality, and diversity of food resources influence these patterns. Here we analyzed the direct and indirect effects of climate, food quantity (estimated by net primary productivity), quality (variation in the specific leaf area index, leaf nitrogen to phosphorus and leaf carbon to nitrogen ratio), and food diversity (diversity of leaf traits) on the species richness of phytophagous beetles along the broad elevation and land use gradients of Mt. Kilimanjaro, Tanzania. We sampled beetles at 65 study sites located in both natural and anthropogenic habitats, ranging from 866 to 4,550 m asl. We used path analysis to unravel the direct and indirect effects of predictor variables on species richness. In total, 3,154 phytophagous beetles representing 19 families and 304 morphospecies were collected. We found that the species richness of phytophagous beetles was bimodally distributed along the elevation gradient with peaks at the lowest (~866 m asl) and upper mid-elevations (~3,200 m asl) and sharply declined at higher elevations. Path analysis revealed temperature- and climate-driven changes in primary productivity and leaf trait diversity to be the best predictors of changes in the species richness of phytophagous beetles. Species richness increased with increases in mean annual temperature, primary productivity, and with increases in the diversity of leaf traits of local ecosystems. Our study demonstrates that, apart from temperature, the quantity and diversity of food resources play a major role in shaping diversity gradients of phytophagous insects. Drivers of global change, leading to a change of leaf traits and causing reductions in plant diversity and productivity, may consequently reduce the diversity of herbivore assemblages.

Key words: altitudinal gradient; Chrysomelidae; Curculionidae; diversity gradients; elevation gradient; functional diversity; herbivorous beetles; herbivory; more-individuals hypothesis; phytophagous beetles; plant functional traits.

INTRODUCTION

Sharp changes in temperature, rainfall, and vegetation coupled with often restricted elevational ranges of species, make large tropical mountains the centers of biodiversity (Rahbek et al. 2019). Elevational diversity patterns have been a focus of ecology since the nineteenth century, but the major hypotheses to explain the changes in diversity along elevation gradients remain debated (McCain and Grytnes 2010, Peters et al. 2016). Unlike the nearly universal decline of species richness along latitudinal gradients (Hillebrand 2004), elevation

gradients show several contrasting diversity patterns, including monotonic declines and unimodal (“hump-shaped”) responses (Nogués-Bravo et al. 2008, Colwell et al. 2016). Climate and food resource availability are considered key factors driving the establishment and maintenance of diversity gradients (Ferber et al. 2014, Belmaker and Jetz 2015), but their relative importance and interdependencies remain poorly resolved. Past studies analyzing the influence of food resources were nearly exclusively restricted to measurements of total food availability (Ferber et al. 2014, Classen et al. 2015, Gebert et al. 2020) and did not integrate the complexity of food resources in natural ecosystems (Richards et al. 2015).

Food resources may vary in quantity, quality, and diversity with elevation and may influence consumer diversity in different ways (Behmer and Joern 2008).

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First, environments holding larger total amounts of food are assumed to be more species rich. This is because more food resources can sustain more individuals and larger populations, decreasing the risk of local extinction (“more-individuals hypothesis”) (Hurlbert and Stegen 2014, Storch et al. 2018). Therefore, on average, more species may persist in environments with high food availability. Second, food resources vary in terms of quality for consumers. Assuming the same amount of food quantity, food of higher quality (e.g. having a higher proportion of limiting nutrients) may sustain more individuals, larger populations, and therefore more species (Joern et al. 2012). Third, in cases of nutritional specialization among consumer species, environments providing more diverse types of food are expected to sustain more species (Novotny 2006, Behmer and Joern 2008, Richards et al. 2015, Volf et al. 2018).

Temperature and water have repeatedly been shown to be strongly correlated with species richness (Hawkins et al. 2003). Temperature is assumed to influence the diversity of ectotherms by its positive effect on metabolism, accelerating rates of ecological interactions and diversification (“temperature-diversity hypothesis”) (Allen et al. 2007, Brown 2014). Additionally, temperature is thought to limit species diversity by determining how much of the theoretically available resources can effectively be used by ectothermic taxa (the “temperature-mediated resource exploitation hypothesis”) (Classen et al. 2015). In this case, temperature is thought to influence species abundances positively, with consequent positive effects on the number of coexisting species (Hurlbert and Stegen 2014, Storch et al. 2018). Moreover, temperature and water availability are the predominant drivers of net primary productivity, which constitutes the energetic basis for consumers (Hawkins et al. 2003).

Over the last centuries, human land use has changed the natural sequence of ecosystems on mountains with consequences for biodiversity, ecosystem properties, and processes (Peters et al. 2019). Local land use practices, like plowing and the application of insecticides, detrimentally affect insect abundance and diversity on agricultural fields (Geiger et al. 2010). Conversely, the application of chemical fertilizer alters soil nutrient contents which in turn influence the leaf palatability for insects (Matson 1997, Poorter et al. 2004, Njovu et al. 2019). At large spatial scales, the loss of natural habitats and the simplification of landscapes may reduce natural enemies and accelerate the immigration and population growth of insects at lower trophic levels (Tscharrntke et al. 2005).

In this study, we determined the pattern of species diversity of phytophagous beetles along elevation gradients on Mt. Kilimanjaro and assessed the importance of climate, land use, and food resource quantity, quality, and diversity as predictors of diversity. As the highest free-standing mountain in the world, Mt. Kilimanjaro creates an extreme gradient in environmental conditions

at small spatial scales, which allows for a standardized assessment of biodiversity in a diverse set of environments (Peters et al. 2019). Phytophagous beetles are a major group of tropical herbivores and include some of the most species-rich families in the whole tree of life (Novotny 2006, Basset et al. 2012). Their often considerable specialization on host plants and large contribution to global biodiversity explain their key importance for estimating the total species richness on earth (Scheffers et al. 2012). Despite their high diversity, changes in phytophagous beetle diversity along elevation gradients have scarcely been investigated. Existing studies revealed humped-shaped distributions of species richness with elevation and point to the potential effects of climate and vegetation characteristics (e.g., net primary productivity, leaf traits, leaf trait diversity) as drivers of elevational diversity (Sánchez-Reyes et al. 2014, Thormann et al. 2018). The linkages between climate, vegetation characteristics, and phytophagous beetle diversity remain, however, untested.

Using a correlative approach, we first describe the patterns of species richness and abundance of phytophagous beetles along the extensive elevation gradient on Mt. Kilimanjaro and determine whether the patterns are influenced by human land use. Second, we test the effects of mean annual temperature and precipitation, land use intensity, and food resource variables (quantity, quality, and diversity) on species richness. We expect that the species richness of phytophagous beetles is determined by climate variables but that the influence of climate is mediated by changes in vegetation characteristics, i.e., the food resource quantity, quality, and diversity. We identify the major predictors of the species richness of phytophagous beetles and the linkages between climate and vegetation variables using a combination of multimodel inference and path analysis.

METHODS

Study area

We conducted the study on the southern slopes of Mt. Kilimanjaro, which is situated in the northeastern part of Tanzania at 2°45' to 3°35' S and 37°00' to 37°43' E (Appendix S1: Fig. S1). The mountain is a dormant stratovolcano with an elevation gradient ranging from the savanna plains of the foothills at ~700 m asl to the Kibo peak at 5,895 m asl. Mean annual temperature (MAT) declines quasilinearly with elevation at an overall lapse rate of 0.56°C per 100 m spanning from 25°C at the foothills to -8°C at the peak (Appelhans et al. 2016). The area experiences a bimodal rainfall pattern with the main rainy season occurring between March and June and more variable short rains occurring around November. Mean annual precipitation shows a hump-shaped pattern along the elevation gradient with the maximum precipitation of ~2,700 mm at 2,300 m asl (Appelhans et al. 2016). The mountain encompasses

distinct natural habitats along the elevational gradient: the lowland is characterized by colline savanna (800–1,200 m asl), followed by lower montane rainforest (1,500–2,100 m asl), *Ocotea* forest (2,100–2,800 m asl), *Podocarpus* forest (2,700–3,100 m asl), *Erica* forest (3,500–3,900 m asl) and alpine *Helichrysum* vegetation (3,800–4,600 m asl). Following anthropogenic disturbances, in particular, subsistence and commercial farming activities, illegal logging and fire, large parts of the natural habitats on the mountain were converted into “anthropogenic habitat” (Peters et al. 2019) including maize fields (800–1,100 m asl), coffee plantations (1,100–1,700 m asl), sun coffee plantations (1,100–1,400 m asl), grasslands (1,300–1,800 m asl), agroforestry systems (Chagga home gardens; 1,100–1,800 m asl), logged *Ocotea* forest (2,200–2,600 m asl) and burned *Podocarpus* forest (2,700–3,100 m asl) (Peters et al. 2019).

Study design

This study is a part of the KiLi research project (Peters et al. 2019) from which we used a total of 65 study sites to sample phytophagous beetles, plant traits, and environmental data (Appendix S1: Fig. S1). Each study site was 50 × 50 m in size with a minimum distance of 300 m between any two sites. Ninety-seven percent of all study sites had pairwise distances of more than 2 km. Study sites were located between 866 and 4,550 m asl in the six natural and seven major anthropogenic habitats on the south-southeastern slopes of Mt. Kilimanjaro. Each habitat type was represented by five replicate study sites which formed a small-scale within-habitat elevation gradient. We used a composite land use index to describe the land use intensity (hereafter termed “LUI”) at each study site based on the level of chemical inputs, removal of plant biomass, the difference of the vegetation structure to natural habitats, and the proportion of agricultural land in a 1.5 km buffer zone surrounding each study site. Details on the calculation of the LUI can be found in Peters et al. (2019).

Temperature was recorded every 5 minutes for the duration of 2 years using temperature sensors positioned approximately 2 m above the ground on each study site (Appelhans et al. 2016). MAT was calculated by averaging all individual temperature measurements per study site. Data on precipitation (rainfall) was estimated for each study site from a total of 70 rain gauges distributed on Mt. Kilimanjaro for over 15 years. From these data, mean annual precipitation (MAP) was mapped across the area using a co-kriging approach. For a detailed description of how climatic variables were measured, please see Appelhans et al. (2016).

Food resources

For each study site, we determined food quantity, quality, and diversity. As phytophagous beetles feed on

plant leaves, we used net primary productivity (NPP) of ecosystems as a proxy for food resource quantity. NPP was estimated by determining the normalized difference vegetation index (NDVI) as a proxy (Peters et al. 2016). The NDVI was derived from the MODIS Aqua product MYD13Q1 with a horizontal resolution of 250 × 250 m by averaging corrected NDVI measures of 10 consecutive years (2003–2012) and extracting pixel values corresponding to the geographical positions of the study sites. The effect of food quality was determined by measuring the community-level averages of three leaf traits which are indicators of food quality for herbivores (C:N ratio, N:P ratio, specific leaf area) (Joern et al. 2012). We used the LEDA protocol to measure plant functional traits from the most abundant plant species making up 80% of total plant biomass found on each study site (Schellenberger Costa et al. 2017). To account for intraspecific variability, we sampled 15 individuals per species from different sites when possible. Details on these traits and descriptions of trait measurements can be found in Schellenberger Costa et al. (2017). Specific leaf area (SLA) (mm²/mg) is the ratio of leaf area to dry mass. Low SLA values are typically associated with long leaf lifespan, high investment in physical defenses (Callis-Duehl et al. 2017) and low nutritional value (Schuldt et al. 2012). The N:P ratio indicates the mass of nitrogen relative to those of phosphorus in plant leaves, whereas the C:N ratio indicates the mass of leaf carbon in relationship to nitrogen (Mattson 1980). These traits play a crucial role in regulating the nutritional value of food resources for herbivores, which in turn influences the susceptibility of plants to herbivore attacks (Schuldt et al. 2012, Leingärtner et al. 2014a). The food diversity available to phytophagous beetles was estimated by calculating the functional diversity of plant leaves at the community level using the three leaf traits (FD) (Schellenberger Costa et al. 2017) and the functional dispersion (FDis) (a measure of the functional dispersion of traits) as a functional diversity measure (Laliberté and Legendre 2010). FDis is considered to be highly flexible, as it accommodates traits of any number or type (qualitative, quantitative, or semiquantitative) and those taken from any distance or dissimilarity measure (Laliberté and Legendre 2010). If species of phytophagous beetles are specialized on plants with certain functional traits, we would expect strong correlations between the functional diversity of plant leaves (FD) and the species richness of phytophagous beetles.

Richness and abundance of phytophagous beetles

We sampled phytophagous beetles on 65 study sites in two sampling sessions between March 2011 and October 2012 and in three sampling sessions from April 2014 to May 2016. Beetles were collected in both dry and rainy seasons and all sampling activities were restricted to between 09:00 h and 16:00 h, when most insects are believed to be active. Within each sampling session, each

study site was visited once under a similar “seasonal climate” (dry season or rainy season). To collect a wide spectrum of phytophagous beetles in different vegetation types, a sweep-net method was used in tandem with a beating method (Thormann et al. 2018). We used a 30 cm diameter sweep net to sample mainly active and flying insects from two parallel, permanently marked, 50 m transects per study site. In each sampling session, 200 sweep-net samples were taken per study site (i.e., 100 sweep-net samples per 50 m transect).

In the last three sampling sessions, we also used a beating method to dislodge and sample insects resting or feeding on woody plants. At each study site, we sampled insects from 15 randomly selected woody plants (trees or shrubs) of a relatively small size of up to 5 m. Each of the small-sized trees or shrubs was heavily hit five times (in case of relatively large trees or shrubs, three branches were selected and each was hit five times) with a club to dislodge insects onto a 72 cm diameter hand-held sample collection sheet. The collected insects were sorted immediately from the vegetation debris and killed using ethyl acetate. All collected insects were then counted and stored in vials with 70% ethanol for further processing. For each study site, we pooled all insects collected by the two sampling methods over the five sampling sessions.

Out of the collected insect specimens, we focused on adult beetles (Coleoptera) for further taxonomic identification. All beetles were mounted and identified to the family level. All beetles from mainly phytophagous beetle families—including Curculionidae, Chrysomelidae, Buprestidae, Cerambycidae, and Elateridae—were further identified to species or morphospecies level by T.W. (Thormann et al. 2016, 2018). We calculated the abundance and observed species richness for each study site as the cumulative number of specimens and species, respectively, detected across all five sampling sessions.

Statistical analyses

We used the R statistical platform v. 3.3.1 to perform statistical analyses. To overcome the problem of incomplete sampling of beetle species, we estimated asymptotic species richness (from this point forward referred to as estimated species richness) for each study site using the Chao1 index, implemented in the R package *iNext* (Hsieh et al. 2016). The Chao1 index has been shown to perform well in other studies on phytophagous beetles (Sánchez-Reyes et al. 2014, Thormann et al. 2018) and Chao1-estimated species richness was strongly correlated with other diversity measures (Fisher α : $P < 0.001$, ACE: $P < 0.001$). Generalized additive models (GAMs) calculated with the *mgcv* package (Wood 2006) were used to examine the distribution of diversity and abundance of all phytophagous beetles, and additionally of the two most abundant families, weevils and leaf beetles, along the elevational gradient. In the GAMs the two major categories of habitat (natural and anthropogenic habitats) were included as factors as we wanted to

visualize potential differences in trends of estimated species richness between the two habitat categories. As our data showed signals of overdispersion, we used the quasi-Poisson data family for modeling count data. We set the basis dimension of the smoothing functions to $k = 5$ to prevent overparameterization of the GAM models.

We used path analysis to examine causal relationships (Shipley 2016) and unravel the direct and indirect effects of all predictor variables on the diversity of phytophagous beetles. Before the analysis, we $\ln(x + 1)$ -transformed estimated species richness and abundance of phytophagous beetles in order to conform to the assumption of normal distributions. As we did not have data on some explanatory variables for all 65 study sites, for analyzing causal relationships, we had to reduce the dataset to 59 study sites with complete data. Based on our assumed linkages between climate, food resource variables, and phytophagous beetle diversity we hypothesized and constructed a conceptual path diagram based on the following linkages:

1. $NPP = MAT + MAP + LUI$
2. $FD/C:N/N:P/SLA = LUI + NPP$
3. $Abundance = MAT + NPP + LUI + FD + N:P + C:N + SLA$
4. $Estimated\ species\ richness = MAT + LUI + NPP + FD + Abundance + N:P + C:N + SLA$

We then preselected possible path combinations, by analyzing the response variables of our path models (NPP, FD, C:N ratio, N:P ratio, SLA, abundance, and estimated species richness) with their respective predictor variables using multimodel inference of linear models. For each linear model, we employed the *dredge* function of the R package *MuMIn* to identify a set of competitive models based on the Akaike information criterion ($AIC < 2$). The AIC is conceptually based on information theory and evaluates statistical models on the basis of model fit and complexity (Burnham and Anderson 2004). We used the AIC_C (AIC with a second-order bias correction) instead of the standard AIC because our sample size was relatively small compared with the number of estimated parameters. We then constructed all possible path models based on all identified competitive models and, as a second selection criterion, included only variables which were supported with summed Akaike weights of $\sum AIC\ weights = 0.7$ (which in our models equaled the predictor variables showing a significance level of $P < 0.05$ in multimodel averaging). By this approach, we selected all predictors of estimated species richness that were well supported across the full model space. For path analysis, the *sem* function in the R package *lavaan* (Rosseel 2012) was used. The goodness of fit of the path models was calculated based on χ^2 -test statistics and was used to compare the support for all competitive path models. For path analysis, all variables were standardized such that the direct and indirect effect

strength of all variables can be directly assessed by comparing the path coefficients.

RESULTS

We collected 3,154 phytophagous beetles representing 19 families and grouped them into 304 morphospecies (Appendix S1: Table S1). Curculionidae (weevils) and Chrysomelidae (leaf beetles) were the largest families, with 895 and 1,566 individuals, respectively. The Chao1-estimated species richness of all phytophagous beetles showed a bimodal pattern (Fig. 2a, Appendix S1: Table S2). The pattern of the observed species richness with elevation was very similar (Appendix S1: Fig. S2). Estimated species richness was highest in the lowlands, then declined in the lower montane zone up to ~2,200 m

asl and rose to a second peak at ~3,200 m asl (GAM: $n = 65$, explained deviance (ED) = 35.1%, $F_{\text{elevation}} = 4.0$, $P_{\text{elevation}} < 0.001$). Above 3,200 m asl, estimated species richness steeply declined with elevation. We did not detect significant differences in the elevational distribution of estimated species richness of phytophagous beetles between natural and anthropogenic habitats ($P > 0.1$). Mean abundance of herbivorous beetles was unimodally distributed with a peak at ~3,100 m asl and with no significant differences between natural and anthropogenic habitats (Fig. 1d).

Leaf beetles showed an elevational diversity pattern similar to that of the total phytophagous beetle community (Fig. 2c, GAM: $n = 65$, explained deviance (ED) = 33.5%, $F_{\text{elevation}} = 5.6$, $P_{\text{elevation}} < 0.0001$). Weevils, in contrast, exhibited a unimodal pattern, with a

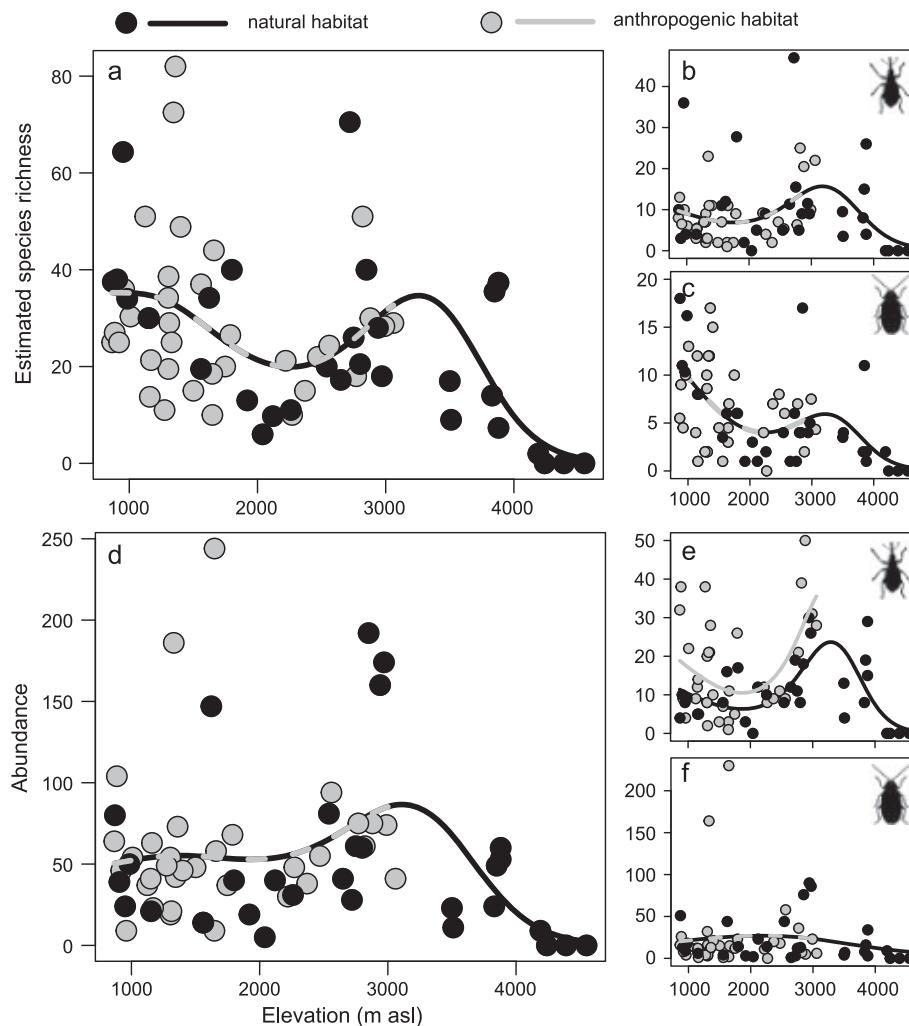


FIG. 1. Patterns of estimated species richness (Chao1 estimates of asymptotic species richness; a–c) and abundance (number of individuals; d–f) of phytophagous beetles in natural and anthropogenic habitats along the elevation gradient of Mt. Kilimanjaro. Subpanels show data and trend lines for all phytophagous beetles (a, d), and separately for the two most abundant subfamilies, i.e., weevils (b, e) and leaf beetles (c, f). Trend lines are predictions of generalized additive models (GAMs; basis dimension of $k = 5$). For no significant difference in trends between habitat types, a dashed black-and-gray line is displayed.

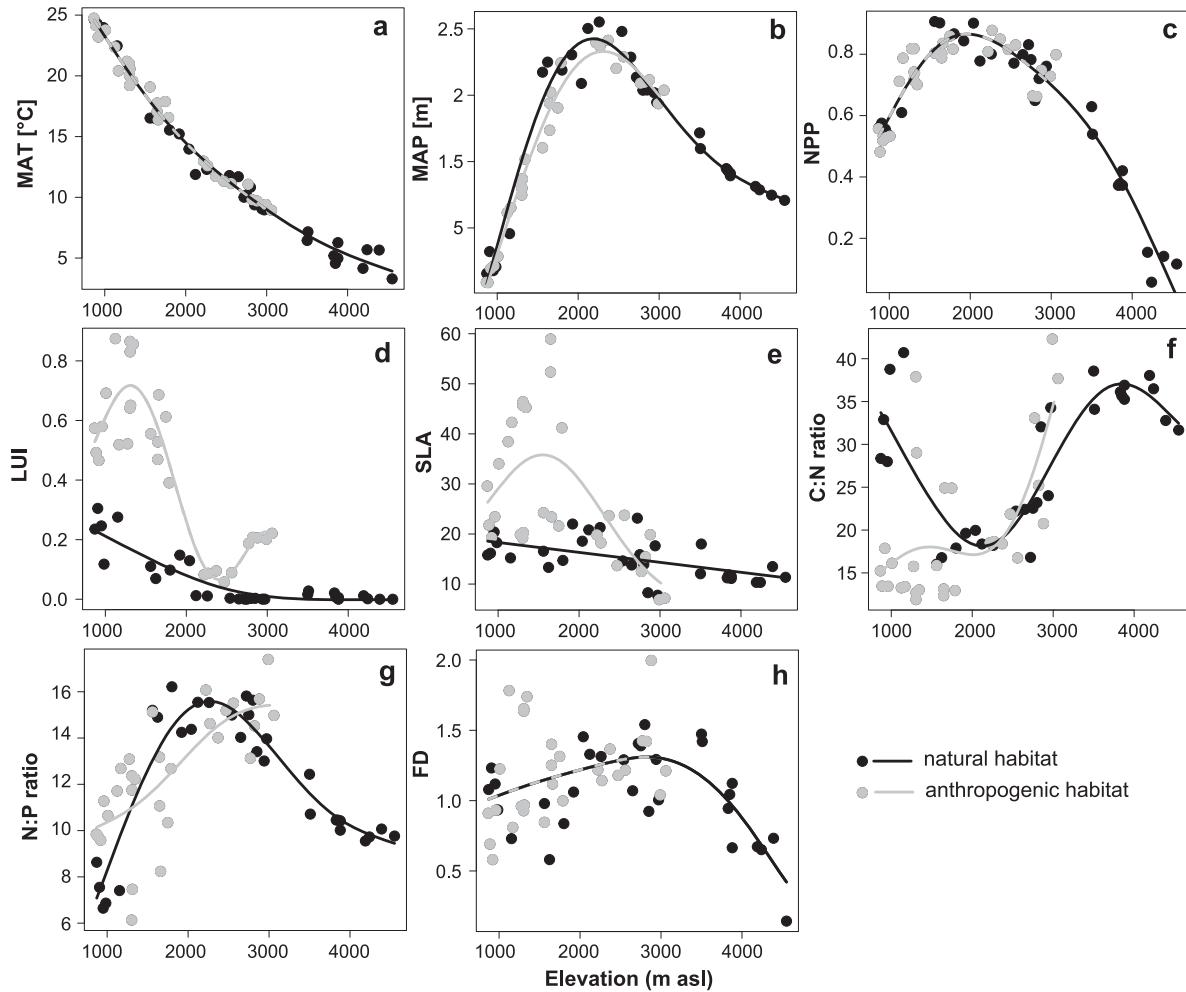


FIG. 2. Distribution of abiotic and biotic variables, which were used to explain variation in estimated species richness and abundance, along the elevation gradient: (a) mean annual temperature (MAT), (b) mean annual precipitation (MAP), (c) net primary productivity (NPP), (d) land use intensity (LUI), (e) specific leaf area (SLA), (f) leaf C:N ratio, (g) leaf N:P ratio, and (h) a measure of the functional diversity in leaf traits (FD). Detailed descriptions of the variables are given in the method section. Trend lines are predictions of generalized additive models (GAMs; basis dimension of $k = 5$). If no significant land use effect (i.e. no significant interactive or additive effect of LUI) was detected, a single dashed black-gray trend line is displayed (Fig. 2a, c, h).

rather low diversity in the lowlands and highest diversity at 3,400 m asl (Fig. 2b, GAM: $n = 65$, explained deviance (ED) = 19%, $F_{\text{elevation}} = 2.1$, $P_{\text{elevation}} < 0.05$). Patterns of observed species richness of leaf beetles and weevils reflected those of Chao1-estimated species richness (Appendix S1: Fig. S2). Except for the highest elevations, the abundance of leaf beetles was relatively homogeneous along the elevation gradient (Fig. 1f); however, at a few study sites leaf beetles reached extremely high abundances (4–5 times the average). Weevils showed a unimodal distribution of abundance with a peak at ~3,000–3,200 m asl, with significantly higher values in anthropogenic than in natural habitats (Fig. 1e).

Climate, land use and food resource variables showed distinct distributions along the elevation and land use

gradients (Fig. 2). Measures of food resource quantity, quality, and diversity were moderately to strongly connected to climate and land use intensity (Fig. 3, Appendix S1: Table S3). Results from the final path analysis ($\chi^2 = 11.1$, $P = 0.13$) showed that the estimated species richness of phytophagous beetles was influenced by MAT, food quantity (NPP) and food diversity (FD) (Fig. 3). Climatic variables (i.e., MAT and MAP) had both a direct and indirect effect on the estimated species richness of phytophagous beetles. MAT showed a strong direct positive effect on estimated species richness. In addition, both MAT and MAP showed a strong combined positive effect on the estimated species richness through their positive effects on NPP and, subsequently, on herbivore abundance. Additionally, we found a positive effect of FD on estimated species richness, i.e.

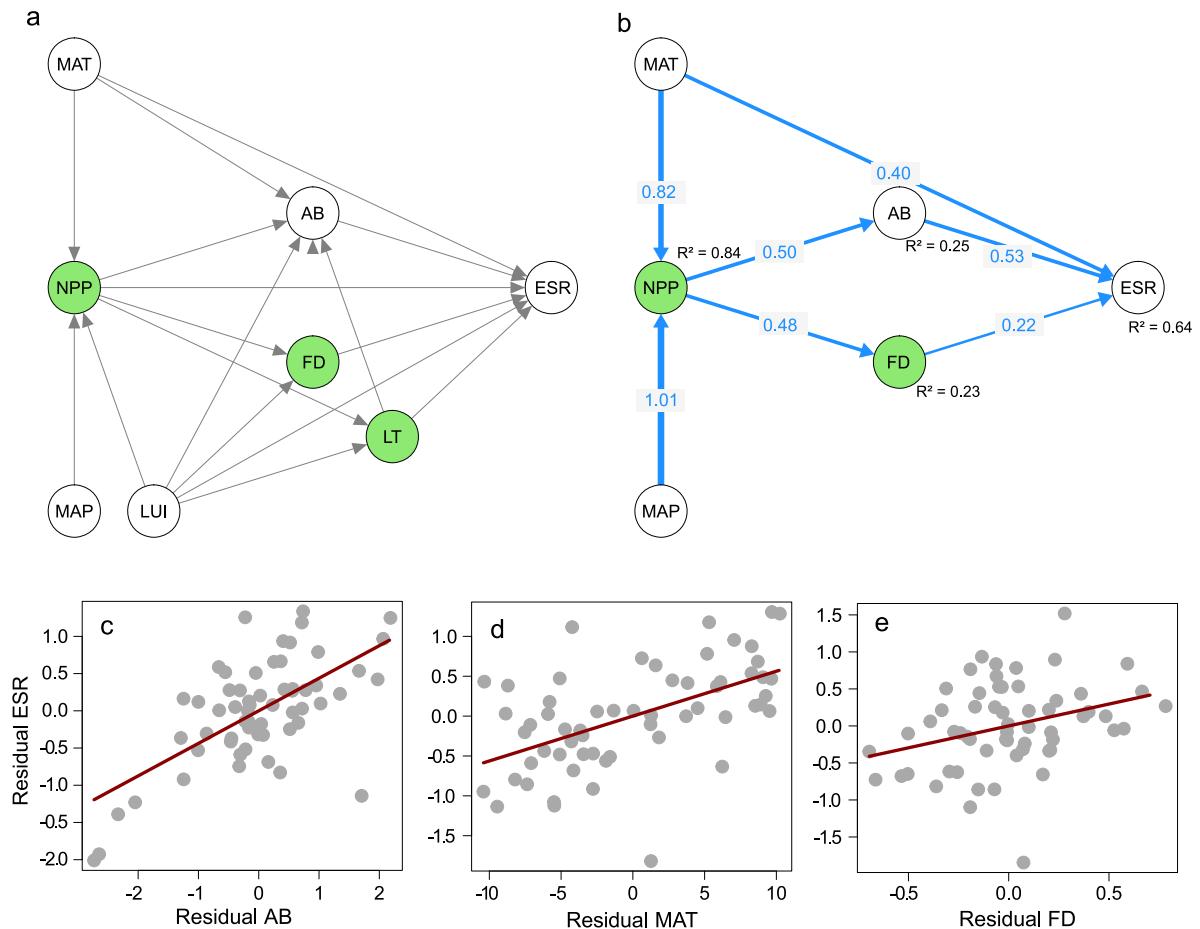


FIG. 3. Path diagrams displaying (a) the anticipated and (b) detected links between climate (MAT, mean annual temperature; MAP, mean annual precipitation), net primary productivity (NPP), functional diversity of leaf traits (FD), leaf traits (LT) and phytophagous beetle abundance (AB), and estimated species richness (ESR). The path model shows the most supported path model characterized by AIC_C-based model selection and χ^2 tests on the goodness of fit ($\chi^2 = 11.1$, $P = 0.13$). Numbers on arrows represent standardized path coefficients. All path coefficients were significant at a level of $P < 0.001$. Positive effects are indicated by blue arrows. Line width of arrows is proportional to the absolute size of standardized path coefficients. For each endogenous variable the explained variance is shown (R^2). Green color indicates endogenous plant-related variables. Panels (c–e) show partial regression plots displaying the effect of each of the three predictor variables on ESR (shown in b) after controlling for the other two predictor variables. Please note that abundance and ESR were ln-transformed in all models.

species richness was higher in environments characterized by a vegetation with a high leaf trait diversity. A second competitive path model (Appendix S1: Fig. S3) also showed a negative effect of SLA on estimated species richness, implying higher beetle diversity in environments characterized by thicker leaves. The SLA was positively influenced by LUI. However, this path model with the additional linkages between LUI, SLA, and estimated species richness was not supported in a goodness-of-fit test ($\chi^2 = 33.12$, $P = 0.001$). Neither path model supported the direct effects of LUI on phytophagous beetle abundance nor diversity.

DISCUSSION

Estimated species richness of phytophagous beetles showed two distinct peaks (at the lowest and upper mid-

elevations) and steeply decreased at elevations above 3,200 m asl. This bimodal pattern of elevational diversity could be explained by an interaction of direct, positive effects of temperature on species richness and by climate-driven changes in food resource quantity (NPP) and food resource diversity (functional diversity of leaf traits).

The bimodal elevational diversity pattern shown by phytophagous beetles was more complex than the majority of elevation diversity patterns detected for other taxonomic groups on Mt. Kilimanjaro (including other beetles groups) (Peters et al. 2016, Gebert et al. 2020) and other mountains (Rahbek 1995, McCain and Grytnes 2010, Colwell et al. 2016, Beck et al. 2017). However, it is similar to patterns found for geometrid moths, a second major group of phytophagous insects, on Mt. Kilimanjaro (Axmacher et al. 2004, Axmacher and Fiedler

2008). The first peak of the estimated species richness on Mt. Kilimanjaro was detected in the savanna zone at the lowest elevations and the second peak at higher mid-elevations, where *Podocarpus* forests are found. Estimated species richness was particularly low in the lower mid-elevation submontane and montane *Ocotea* forests. Studies on other phytophagous beetles (Sánchez-Reyes et al. 2014, Thormann et al. 2018) and other phytophagous insects (Colwell et al. 2016, Beck et al. 2017) on both tropical and extratropical mountains have often revealed unimodal or, less often, decreasing patterns of diversity with elevation (Leingärtner et al. 2014b, Peters et al. 2016). Our finding of a nonunimodal pattern of elevational diversity and the differences to the patterns found in other studies on phytophagous beetle diversity cast doubt on the relevance of geometric constraints in determining patterns of elevational diversity (Colwell et al. 2016). Instead, it suggests that environmental drivers, which differ among mountain regions, are determining the variation in species diversity of phytophagous beetles. We did not find a significant difference in the species richness of phytophagous beetles between natural and anthropogenic habitats, which was similarly observed also for bees on the same mountain (Classen et al. 2015). A major reason for the high richness in anthropogenic habitats could be that land use intensity is currently rather moderate on Mt. Kilimanjaro when compared with the intensified farming practices in many western countries. Subsistence farming is the dominant agricultural system and sustains a high proportion of seminatural habitats. The small size of fields and the diversity of different cropping systems shape a mosaic-like heterogeneous landscape from which many phytophagous beetle species may profit.

What are the factors driving the diversity of phytophagous beetles along elevation gradients, and how are they linked to each other? We found strong support for the positive effects of temperature, food resource quantity, and food resource diversity on the species richness of phytophagous beetles. Thus, climate variables had both direct effects on species richness and indirect effects, i.e., by modifying the quantity, quality, and diversity of food resources of the phytophagous beetle assemblage. Our final model, which was only based on three explanatory variables, could explain a large proportion of the total variation in estimated species richness ($R^2 = 68\%$; $R^2 = 81\%$, if only data from natural habitats are considered). Temperature had a strong exponential effect on the estimated species richness of phytophagous beetle species, increasing estimated species richness by ~ 0.6 species per $^{\circ}\text{C}$ at the lower limit of the temperature range of the elevation gradient and by ~ 2 species at the highest temperatures. Our finding of a positive effect of MAT is broadly in agreement with data found for other animal taxa, in particular for ectothermic taxa, whose diversity closely correlates with temperature along both elevational or latitudinal gradients (Dunn et al. 2009, McCain 2010, Brown 2014, Classen

et al. 2015, Peters et al. 2016, Gebert et al. 2020, Mayr et al. 2020). The low influence of MAT on beetle abundance and its strong direct effect on species richness suggests that temperature influences phytophagous beetle diversity mainly by accelerating evolutionary rates and fostering diversification (Allen et al. 2007, Brown 2014) rather than by increasing net energy uptake (Classen et al. 2015). In addition to the effect of temperature described above, temperature together with MAP was the main driver of NPP, which had strong positive effects on species richness of phytophagous beetles via increasing species abundances and the functional diversity of leaf traits. This additional indirect effect contributes nearly as much to explaining the species richness of phytophagous beetles (sum of the path effects of MAT via $\text{NPP} = 0.30$) as the direct effect (~ 0.40).

Our findings, of a positive relationship between NPP and phytophagous beetle abundance, and of a positive relationship between phytophagous beetle abundance and estimated species richness are in agreement with the “more-individuals hypothesis” (Storch et al. 2018), which explains higher consumer species richness by the reduced extinction probability of larger populations in energy-rich environments (Hurlbert and Stegen 2014). An increase of 10% in the NDVI (our proxy for NPP/food resource quantity) was associated with an increase in estimated species richness of 1.1 species at the lower limit of the NDVI gradient and 2.6 species at the upper limit. A recent meta-analysis on geometrid moths recognized area-integrated net primary productivity as a major driver of the elevational diversity pattern of these phytophagous insects, while NPP alone received considerably lower support (Beck et al. 2017). This difference might be due to particularities of the studied taxa (geometrid moths vs. phytophagous beetles), differences in spatial scale (global analysis vs. one mountain), or differences in analytical approaches (we revealed an indirect effect of NPP via beetle abundance and functional diversity of plant communities while Beck et al. (2017) exclusively tested for direct effects of NPP).

In addition to food resource quantity, food resource diversity, measured as the community-wide functional dispersion of leaf traits, positively influenced phytophagous beetle richness. Plant communities characterized by higher variation in leaf C:N ratios, N:P ratios, and SLA had a higher diversity of phytophagous beetles (a 10% increase in FD at the lower limit of FD values was associated with an increase in estimated species richness of 1.6 species; at the higher limit of FD values the increase was 3.6 species), supporting the hypothesis that more diverse food resources permit more niches for the coexistence of animal species (Kissling et al. 2007). While the way we sampled beetles did not allow for the analysis of host specialization and niche partitioning (Novotny 2006), this result is in line with recent studies revealing a positive influence of divergence in plant anti-herbivore traits on herbivore diversity, specialization, and coexistence (Becerra 2015, Richards et al. 2015, Volf

et al. 2018). In this regard, the high functional diversity of leaf traits in the *Podocarpus* elevational zone at mid-elevations on Mt. Kilimanjaro correlated with an exceptionally high richness of phytophagous beetles, forming the second diversity peak of the bimodal diversity distribution along the elevation gradient. This zone is also characterized by a change from a predominately forested to an increasingly open vegetation at higher elevations, which may positively affect leaf trait diversity. An ecotone or edge effect could also explain a second diversity peak in geometrid moths at the same elevational level (Axmacher et al. 2004, Axmacher and Fiedler 2008), pointing to a potential consensus in the driver of phytophagous insect diversity across two different insect orders.

A second competitive path model (Appendix S1: Fig. S3) additionally included a negative effect of SLA on the estimated species richness of phytophagous beetles. Specific leaf area increased with land use intensity. The negative correlation between SLA and estimated species richness indicates that softer, thinner leaves were associated with a reduced diversity of phytophagous beetles. In close correspondence with this result, a study conducted along a gradient of increasing climatic harshness in Australia found a significant influence of SLA on leaf miner diversity (Bairstow et al. 2010). In the Neotropics, leaf beetle diversity on Andean mountains peaked in ridge crest habitats characterized by plants with hard, thick leaves (low SLA values) (Thormann et al. 2018). Hard, thick leaves, which are less digestible for herbivores (Njovu et al. 2019) may foster food specialization of phytophagous insects and local diversity (Volf et al. 2018).

One important aspect, which we could not cover in our analysis, was the influence of other phytochemical compounds (other than the tested C:N ratio and N:P ratios) on the species richness of phytophagous beetles. Recent studies could link elevated chemical diversity of plants with more specialized assemblages of herbivores and higher herbivore diversity (Richards et al. 2015). Plant communities with higher phytochemical diversity could, therefore, be associated with a higher number of species of phytophagous beetles, which could explain parts of the unexplained variation in estimated species richness observed in this study. However, phytochemical compounds, including those associated with plant defense against herbivores, may also systematically change with climate and NPP (Coley 1987). In this case, parts of the variation that is currently explained by NPP or climate could be mediated by a change in phytochemical compounds. Future studies, including extensive analyses of phytochemical traits could help to clarify the linkages between climate, NPP, and phytochemical diversity on the species richness of phytophagous insects (Richards et al. 2015, Volf et al. 2018).

The mean number of phytophagous beetles per study site (mean = 47.2 individuals) was rather low, which could have biased patterns of elevational diversity. The low number can be explained in two ways. First, the

studied climatic gradient was extensive and included extreme environments where we only sampled very few phytophagous beetles and sometimes not even a single individual. Second, we used a sampling design that balanced sampling intensity per study site and the total number of replicates (study sites). A large number of replicates allowed the parallel statistical analyses of multiple predictor variables and multiple linkages between endogenous and exogenous variables in path analysis. Nevertheless, the high similarity between elevational diversity patterns of observed species richness and those resulting from estimates of asymptotic species richness support the robustness of the results.

Our findings elucidate how climate variables directly and indirectly, by influencing vegetation characteristics, determine the species richness of phytophagous beetles. In the light of ongoing global change, detailed knowledge of the mechanisms driving species richness is critical for biodiversity conservation. Our study shows that increasing temperature, within the limits of the studied environmental gradient, has a positive effect on the species richness of phytophagous beetles but that the effect is also dependent on correlated changes in rainfall that both determine plant growth and leaf diversity. Climate and land use changes leading to a decrease in NPP and the functional diversity of plants will probably be associated with a loss of species in the group of phytophagous beetles.

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