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Climate rather than dung resources predict dung beetle abundance and diversity along elevational and land use gradients on Mt. Kilimanjaro

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Abstract

Aim: While elevational gradients in species richness constitute some of the best depicted patterns in ecology, there is a large uncertainty concerning the role of food resource availability for the establishment of diversity gradients in insects. Here, we analysed the importance of climate, area, land use and food resources for determining diversity gradients of dung beetles along extensive elevation and land use gradients on Mt. Kilimanjaro, Tanzania.

Location: Mt. Kilimanjaro, Tanzania.

Taxon: Scarabaeidae (Coleoptera).

Methods: Dung beetles were recorded with baited pitfall traps at 66 study plots along a 3.6 km elevational gradient. In order to quantify food resources for the dung beetle community in form of mammal defecation rates, we assessed mammalian diversity and biomass with camera traps. Using a multi-model inference framework and path analysis, we tested the direct and indirect links between climate, area, land use and mammal defecation rates on the species richness and abundance of dung beetles.

Results: We found that the species richness of dung beetles declined exponentially with increasing elevation. Human land use diminished the species richness of functional groups exhibiting complex behaviour but did not have a significant influence on total species richness. Path analysis suggested that climate, in particular temperature and to a lesser degree precipitation, were the most important predictors of dung beetle species richness while mammal defecation rate was not supported as a predictor variable.

Main conclusions: Along broad climatic gradients, dung beetle diversity is mainly limited by climatic factors rather than by food resources. Our study points to a predominant role of temperature-driven processes for the maintenance and origination of species diversity of ectothermic organisms, which will consequently be subject to ongoing climatic changes.

KEYWORDS
altitudinal gradients, diversity gradients, energy-richness hypothesis, food resources, insect abundance, land use, Scarabaeidae, species-area hypothesis, temperature-mediated resource exploitation hypothesis, temperature-richness hypothesis

1 | INTRODUCTION

In contrast with a nearly universal latitudinal decrease of species richness, patterns of diversity along elevation gradients on mountains are more variable, including patterns of monotonous decline, unimodal distributions or even increases of diversity with elevation. Despite two centuries of intensive mountain research, the drivers of montane species diversity gradients are still debated (Beck et al., 2017; Peters et al., 2016), with limited empirical field data explicitly testing the competing hypotheses.

On mountains, the land area which is available to populations changes strongly with elevation. The 'area hypothesis' posits that elevations with larger areas maintain more species at larger populations and have a higher probability of allopatric speciation than elevations with lower total land area (Rosenzweig, 1995).

The availability of energy resources is often considered the main factor limiting species richness (Beck et al., 2017; Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014). The 'more-individuals hypothesis' (Hutchinson, 1959) predicts a positive relationship between species richness and food resources as productive ecosystems with ample resources can sustain more and larger populations than ecosystems where resource availability is more limited. While the more-individuals hypothesis has gained some support in past macroecological research (Storch, Bohdalková, & Okie, 2018), tests of the hypothesis are often limited by the use of primary productivity (and its proxies) for estimating the food resource availability of consumer communities. However, most of the taxa typically studied in macroecology use specific kinds of food resources whose availability may not be linearly correlated with primary productivity (Storch et al., 2018).

In ectothermic organisms, temperature has been suggested as a major determinant of diversity gradients operating under two principal pathways: in the 'temperature-richness hypothesis', the maintenance and diversification of species richness is determined by positive effects of temperature on ecological and evolutionary rates (Belmaker & Jetz, 2015). In contrast, the 'temperature-mediated resource exploitation hypothesis' states that temperature regulates foraging rates and thereby the access of ectothermic consumers to food resources (Classen et al., 2015). Under this hypothesis, temperature is expected to have a positive effect on species richness, which is connected to a positive effect on the number of individuals of consumer assemblages (Storch et al., 2018). Lastly, the 'water availability hypothesis' proposes that species richness is dependent on the disposability of water, either by direct reliance on water supply or indirectly by impacts of precipitation on energy supply, for example on net primary productivity (Hawkins et al., 2003; Kreft & Jetz, 2007). On mountains, the amount of precipitation varies with elevation, often leading to systematic changes in the level of aridity (McCain & Grytnes, 2010).

Dung beetles provide an ideal taxon to study the importance of area, climate and energy resources for the establishment and maintenance of diversity gradients. A prerequisite for testing the influence of energy resources on diversity is a clearly defined resource which can be easily measured in the field. Since dung beetles rely upon ephemeral patches of mammalian dung characterized by distinct spatial bounds as a food and nesting resource for their offspring, they fulfil this criterion (Barlow et al., 2010; Finn, 2001). Moreover, dung beetles are useful as bioindicators and of huge ecological and economic importance as they provide ecosystem functions and services such as nutrient cycling, bioturbation, plant growth enhancement, parasite suppression and secondary seed dispersal (Nichols et al., 2008). According to their burial and breeding behaviour, dung beetles can be classified into the functional guilds termed dwellers, tunnellers, rollers and kleptoparasites. Dwellers (endocoprids) form their nests directly in the dung pad. Tunneller (paracoprid) species are characterized by digging tunnels and burying brood balls directly under a dung pad whereas rollers (telecoprids) move dung balls for a certain distance away from the original dung pad before burying them in the ground. Kleptoparasite dung beetles do not supply a nest but instead parasitize the brood balls of other rollers and tunnellers (Hanksi & Cambefort, 1991).

Today, many tropical mountain ecosystems are increasingly threatened by human habitat disturbance and land use (Körner, 2000). However, how land use affects montane biodiversity is still unresolved (Newbold et al., 2015). Due to their coprophagous life style, dung beetles are strongly linked to mammals, which are vulnerable to habitat loss and hunting (Andresen & Laurance, 2007). Conservation studies have shown that a depletion of the local mammalian fauna has resulted in co-declining dung beetle assemblages (Culot, Bovy, Zagury Vaz-de-Mello, Guevara, & Galetti, 2013).

Here, we explored the patterns and potential drivers of dung beetle diversity on Mt Kilimanjaro, Tanzania, comprising an elevational gradient of 3.6 km and covering major habitat types and climates from tropical to afro-alpine zones. We investigated the elevational distribution of the whole dung beetle community and separately for the different functional groups in all main natural and anthropogenic habitats found in the study area. To have a measure of dung resource availability for dung beetles, we calculated the defecation rate of the mammal community. The defecation rate is

equal to the mass-specific metabolic activity of animals (Peters et al., 1996), which scales to biomass$^{3/4}$ (Brown, Gillooly, Allen, Savage, & West, 2004).

By applying path analysis, we disentangled the direct and indirect effect of temperature, mammal defecation rates, precipitation, area and anthropogenic land use on dung beetle abundance and diversity and tested the following hypotheses:

1. As lower elevations consist of larger areas and offer more resources, higher habitat heterogeneity and more refugia for speciation than higher elevations (Lomolino, 2001), we expect dung beetle diversity to decrease with declining area, i.e. increasing elevation.
2. Food resources, as measured by mammal defecation rates, are principally limiting dung beetle species richness. We expect a positive effect of mammal defecation rates on dung beetle species richness.
3. Temperature is a driver of dung beetle species richness and abundance, either via a direct effect of temperature on dung beetle species richness (temperature-richness hypothesis) or via indirect abundance-mediated effects (temperature-mediated resource exploitation hypothesis; Buckley, Hurlbert, & Jetz, 2012).
4. Dung beetle richness is restricted by water availability, either directly or via a positive effect on mammal communities (Hawkins et al., 2003).
5. Human impact on mountains negatively influences dung beetle abundance and species richness. Such effects can be direct or indirect mediated by the mammal community structure. For example, landscape conversion to open habitats and hunting result in a depleted mammal fauna, entailing smaller and less diverse dung beetle assemblages (Feer & Boissier, 2015).

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted on Mount Kilimanjaro (2°54′–3°25′S, 37°0′–37°43′E), northern Tanzania. Mt. Kilimanjaro is located 300 km south from the equator and rises from 700 m to 5,895 m a.s.l. The mountain is characterized by an equatorial day-time climate with two rainy seasons, i.e. the long rains around March to May and the short rains around November. Temperature linearly declines with elevation at approximately 6.1°C per 1,000 m of elevation and reaches from about 25°C at the base to −8°C at the summit. The distribution of mean annual precipitation (MAP) is unimodal, with a peak of ~2,700 mm at around 2,200 m a.s.l. (Appelhans et al., 2016). For this project, 66 permanent study plots (50 m × 50 m) of the DFG research unit FOR1246 were selected on the southern slopes of Mt. Kilimanjaro (Peters et al., 2019). The study plots were evenly allocated among the 13 major natural and anthropogenic ecosystem types in the region (five to six study plots per ecosystem type) and covered an elevation gradient from 870 to 4,550 m a.s.l. (Appendix S1). Natural habitats comprised savanna (871–1,153 m a.s.l.), lower montane forest (1,560–2,020 m a.s.l.), *Ocotea* forest (2,120–2,750 m a.s.l.), *Podocarpus* forest (2,800–2,970 m a.s.l.), *Erica* forest (3,500–3,900 m a.s.l.) and alpine *Helichrysum* scrub vegetation (3,880–4,550 m a.s.l.). Anthropogenic habitats were represented by maize fields (866–1,009 m a.s.l.), grasslands (regularly cut by hand for cattle feeding, 1,303–1,748 m a.s.l.), commercial coffee plantations (1,124–1,648 m a.s.l.) and Chagga agroforestry systems (1,169–1,788 m a.s.l.), selectively logged *Ocotea* forest (2,220–2,560 m a.s.l.), burned *Podocarpus* (2,770–3,060 m a.s.l.) and burned *Erica* forests (3,500–3,880 m a.s.l.). In order to observe fine-scale changes in biodiversity with elevation, the five to six study plots per habitat type were distributed in a manner to form a within-habitat elevational gradient. All study plots were separated by more than 300 m with 97% of all distances between study plot pairs being larger than 2 km. As far as practicable, study plots were located in core zones of larger areas of the corresponding habitat type to diminish effects of transition zones. Anthropogenic habitats were subdivided into agricultural habitats (maize fields, grasslands, coffee plantations, agroforestry) and disturbed habitats (logged *Ocotea* forest, burned *Podocarpus* and *Erica* forests), so that there were three land use levels (natural, agricultural, disturbed). Furthermore, anthropogenic habitats were subdivided into 'low land use intensity' or 'high land use intensity' habitats according to their level of disturbance (Appendix S1). All study plots above 1,800 m a.s.l., which were located inside Mt. Kilimanjaro National Park, as well as two lowland savanna plots located in wildlife conservation areas, were categorized as 'protected'. All other study plots were considered as 'unprotected'.

2.2 | Climate and NPP

Temperature sensors were installed about 2 m above the soil surface on all 66 study plots of the KiLi project (Appelhans et al., 2016). Temperature was measured in intervals of 5 min for a duration of about 2 years and the mean annual temperature (MAT) was calculated for each study plot as the average of all measurements (Appelhans et al., 2016). Data on MAP was obtained with approximately 70 rain gauges allocated to the different ecosystem types and elevations on Mt Kilimanjaro (Appelhans et al., 2016). More details can be found in the supplement (Appendix S2).

2.3 | Trapping of dung beetles

Dung beetles were collected with baited pitfall traps in two sampling rounds, from April to June 2015 and from October 2015 to February 2016. Even though most dung beetle species are regarded as trophic generalists, we used two different baits (human dung, cow dung) in the first and second round, respectively in order to increase the sampling completeness of local species assemblages. Refer to the supplement for more details (Appendix S3). Species were allocated to the trophic guilds dwellers, tunnellers, rollers and kleptoparasites based on their mode of food allotment for reproduction (Halffter & Edmonds, 1982). The data of both sampling rounds per study plot were pooled for all further calculations. Species richness per study

plot was calculated as the total number of species recorded during both human and cow dung sampling rounds. Accordingly, for each study plot, dung beetle abundance was calculated as the sum of the number of individuals found in the human and cow dung baited traps.

2.4 | Assessment of mammal communities

We collected data on mammal communities from May to September 2016 using standardized transect-based searches for mammalian dung. Since the amount of mammalian dung occurring in different habitats along the elevational gradient cannot be quantified through transect walks alone, we additionally used camera trapping. Methodological details are described in Appendix S4. The biomass of the mammal community was calculated per study plot by multiplying the biomass of each mammal species with its estimated abundance and summing up these values across all species observed per study plot. Mammal defecation rates were then calculated by raising these values per study plot to the power of ¾ (Brown et al., 2004; Peters et al., 1996). We consulted Kingdon et al. (2013) and Kingdon (2015) for data on average species' body masses. To calculate abundances, we used the maximum number of simultaneously observed individuals during camera trapping for each species on each study plot to avoid overestimation.

2.5 | Statistical analysis

We examined the distribution of species richness and abundance of dung beetles along the elevational gradient with generalized additive models (GAMs). In GAMs, non-parametric smoothers are used to define the relationship between a response and a predictor variable, allowing flexible estimations of both linear and non-linear relationships. We computed GAMs of the total abundance and species richness for the whole dung beetle assemblage, and for each of the functional guilds of dung beetles, i.e. dwellers, tunnellers, rollers and kleptoparasites, respectively. The R package 'mgcv' was used to calculate the GAMs (Wood, 2006). As species richness and abundance is count data, we used the Poisson data family with a log-link function in GAM models. As we detected signals of overdispersion in the data, we used the negative binomial data family rather than the Poisson family for modelling. To avoid over-parametrization of GAMs, we set the basis dimension of the smoothing term (k) to $k = 5$ (Peters et al., 2016).

In GAMs, we created a 'starting model' comprising elevation and land use type as interacting explanatory variables, the latter being factorial (natural vs. anthropogenic habitat), depicting specific trend lines for the two land use categories. GAMs calculate chi-squared tests to test for significance. We used the 'summary' function on our models to calculate the significance level of predictor variables. In case of non-significance of the interaction term ($p > .05$), we deleted it and utilized a simple additive effect model ($y \sim$ elevation + land use). In this instance, the trend lines in natural and anthropogenic habitats would be the same, though the intercepts might be different. We consecutively discarded elevation, land use or both explanatory variables from the model if their significance level was higher than $p > .05$. When the interaction term was significant, we designated the p-value as $p_{\text{Interaction}}$. In cases where the simple additive model was significant, we labelled the p-value as $p_{\text{Elevation + Land use}}$. If elevation was the only significant predictor variable, the p-value was named $p_{\text{Elevation}}$.

To analyse the role which nestedness and turnover play for the change in species composition with elevation, we applied the nestedness metric depending on overlap and decreasing fill ('NODF'; Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008). The outcome of this metric is a value between zero and 100 with NODF = 100 implying a completely nested community. NODF computes nestedness both between columns (species) and between rows (the study plots), as well as for the entire community matrix. We calculated NODF with the 'nestednodf'-function of the 'vegan' package (Oksanen et al., 2019). In addition, we used the function 'nestedbetasor' which detects multiple-site dissimilarities and brakes these down into components of turnover and nestedness (Baselga, 2012). We computed a graph for community composition with the 'nestedtemp' function. For simplification, we calculated NODF on the level of dung beetle genera. NODF for species can be found in Appendix S5.

Using path analysis, we unravelled the direct and indirect effects of temperature, precipitation, mammalian dung resources (calculated as mammal defecation rates: body mass$^{3/4}$), land area and land use on the species richness and abundance of dung beetles. Furthermore, we assumed that the mammal communities are dependent on climate, NPP, land area, land use intensity and in addition on the protection status of study plots (either situated in protected or unprotected areas). Moreover, we presumed that NPP along the elevational gradient is driven by changes in MAT and MAP (Peters et al., 2016).

For each response variable (dung beetle species richness, dung beetle abundance, mammal defecation rate, NPP), we pre-selected possible path combinations by constructing a compilation of competitive explanatory models applying multi-model inference based on the Akaike information criterion. Since the sample size was low compared to the number of estimated parameters, we employed the AIC_c with a second-order bias correction for ranking individual models. We used the 'dredge' function of the R package 'MuMIn' to infer the AIC_c for the full model comprising all explanatory variables and for all nested models including the null model. All models with a $\Delta AIC_c < 2$ were selected for path analyses. In cases where we detected overdispersion—for the models with species richness and mammalian defecation rate as response variables—we employed the negative binomial family implemented in the 'glm.nb' function instead of the glm function.

Since species richness data of dung beetles followed a negative binomial distribution, we could not employ traditional statistical applications for path analysis based on normally distributed data. Alternatively, we carried out piecewise structural equation modelling (*SEM*) which is founded on the d-sep test for all best supported models using the 'sem.fit' function of the R package 'piecewiseSEM' (Lefcheck, 2016; Shipley, 2013). We computed the AIC_c for each path model and chose the best model as the one with the lowest AIC_c (Shipley, 2013). To scale path coefficients, we used the 'sem.coefs' function while the 'rsquared' function was employed to assign R^2-values to the response variables.

We collected mammal data and dung beetle data in different periods of the year. While dung beetles were sampled both in 2015 and 2016, mammal data was only collected during 2016. However, mammal sampling in 2016 overlapped for 2 months with the dung beetle sampling in 2015 (Mai and June). To ensure that we did not miss any relationship between mammals and dung beetles, we conducted an additional path analysis exclusively with the data collected during these 2 months in 2015 and 2016.

3 | RESULTS

We collected a total of 10,432 dung beetles across the 66 study plots (Appendix S6). Forty-two percent and 58% of all individuals belonged to the subfamilies Scarabaeinae and Aphodiinae, respectively. We recorded 135 species of which 79% were Scarabaeinae dung beetles and 21% belonged to the subfamily Aphodiinae (Appendix S6). Thirty-one species were dwellers, 79 tunnellers, 15 rollers and 7 were kleptoparasite species (for three species the trophic guild was unknown). We detected a total of 38 non-volant mammal species with a biomass range of 0.1 kg (small rodents) to 637.5 kg (African Buffalo; Appendix S7). The total biomass of mammal communities varied over 2,000-fold (mean ± SD: 49.6 ± 121.8), depicting strong variation in the availability of resources for dung beetles across study plots (Appendix S7).

3.1 | Elevational patterns of abundance and species richness

Dung beetle abundance showed a hump-shape pattern with a peak in the premontane part of the elevational gradient and no differences between natural and anthropogenic habitats (Figure 1a, ED = 89.7%, $p_{Elevation} < .001$). For tunnellers and kleptoparasites, abundance decreased with elevation in both natural and anthropogenic habitats (tunnellers: Figure 1b, ED = 87.9%, $p_{Elevation} < .001$; kleptoparasites: Figure 1e, ED = 84.3%, $p_{Elevation} < .001$). The elevational reduction in abundance was more pronounced for kleptoparasites (Figure 1e). In rollers, abundance was higher in natural compared to anthropogenic habitats at low elevations. (Figure 1b, ED = 79.5%, $p_{Interaction} < .05$). Dweller abundance was unimodally distributed for both natural and anthropogenic habitats with a higher abundance in anthropogenic habitats and peaked at around 1,500 m (Figure 1d, ED = 77.7%, $p_{Interaction} < .05$).

Species richness of dung beetles declined exponentially with elevation with no significant difference between natural and anthropogenic habitats (Figure 2a, explained deviance (ED) = 90%, $p_{Elevation} < .001$). As tunneller species richness made up the largest proportion of the total species, this functional group displayed a similar distribution along the elevation gradient with no significant difference between land use categories (Figure 2b, ED = 91%, $p_{Elevation} < .001$). Kleptoparasites also showed a decrease in species richness with elevation for both natural and anthropogenic habitats. As with abundance, the decrease in species richness was more pronounced for kleptoparasites than for tunnellers (Figure 2e, ED = 79.6%, $p_{Elevation} < .05$). Rollers exhibited a decline in species richness with elevation with higher species richness in natural than anthropogenic habitats at low elevations (Figure 2c, ED = 80%, $p_{Elevation + Land use} < .05$). In contrast with the other feeding guilds, species richness of dwellers showed a unimodal distribution with elevation with a peak at around 1,500 m. Dweller richness did not differ between natural and anthropogenic habitats (Figure 2d, ED = 72.2%, $p_{Elevation} < .001$). Dung beetle abundance and dung beetle species richness were highly correlated ($r = .80$, $p < .001$).

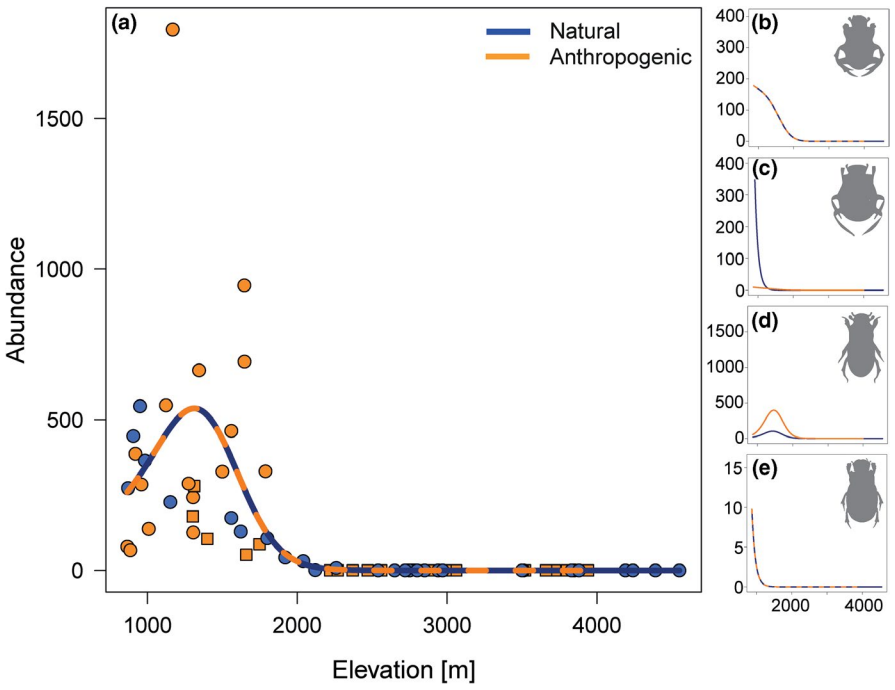

FIGURE 1 Patterns of dung beetle abundance along the elvational gradient on Mt. Kilimanjaro (a) and patterns for separate feeding guilds: tunnellers (b), rollers (c), dwellers (d) and kleptoparasites (e). In (a), dots and squares delineate original measurements of abundance on study plots. Natural habitats are indicated in blue whilst anthropogenic habitats are depicted in orange. Anthropogenic habitats are further subdivided into agricultural habitats (dots) and disturbed forest sites (squares). Trend lines were calculated using generalized additive models [Colour figure can be viewed at wileyonlinelibrary.com]

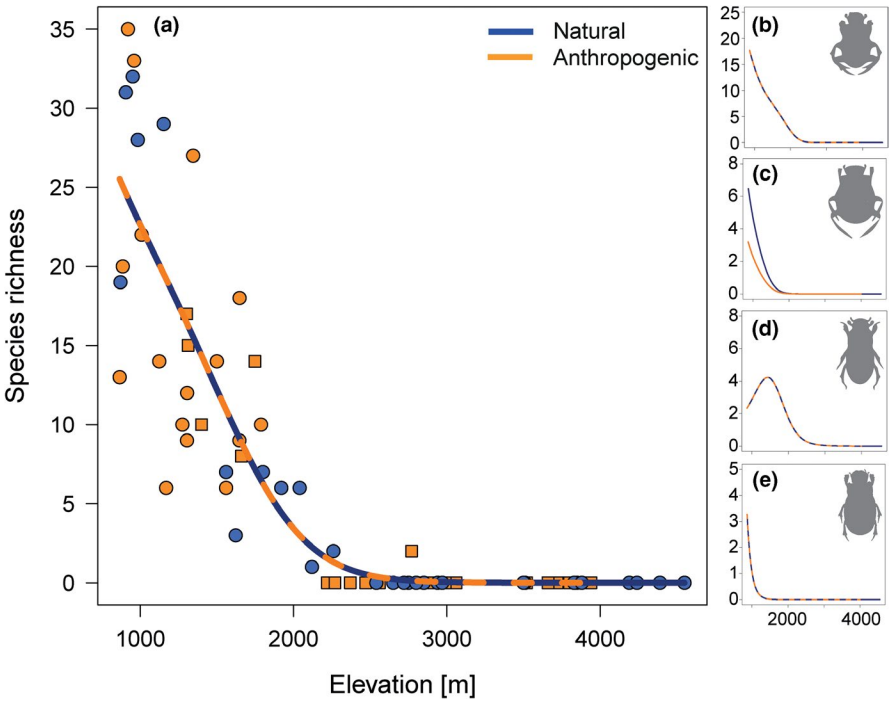

FIGURE 2 Elevational distribution of dung beetle species richness on Mt. Kilimanjaro (a) and patterns for individual feeding guilds: tunnellers (b), rollers (c), dwellers (d) and kleptoparasites (e). In (a), dots and squares illustrate original measurements of species richness on study plots. Values in natural habitats are displayed in blue whilst anthropogenic habitats are shown in orange. Anthropogenic habitats are further sectioned into agricultural habitats (dots) and disturbed forest sites (squares). Trend lines were calculated using generalized additive models [Colour figure can be viewed at wileyonlinelibrary.com]

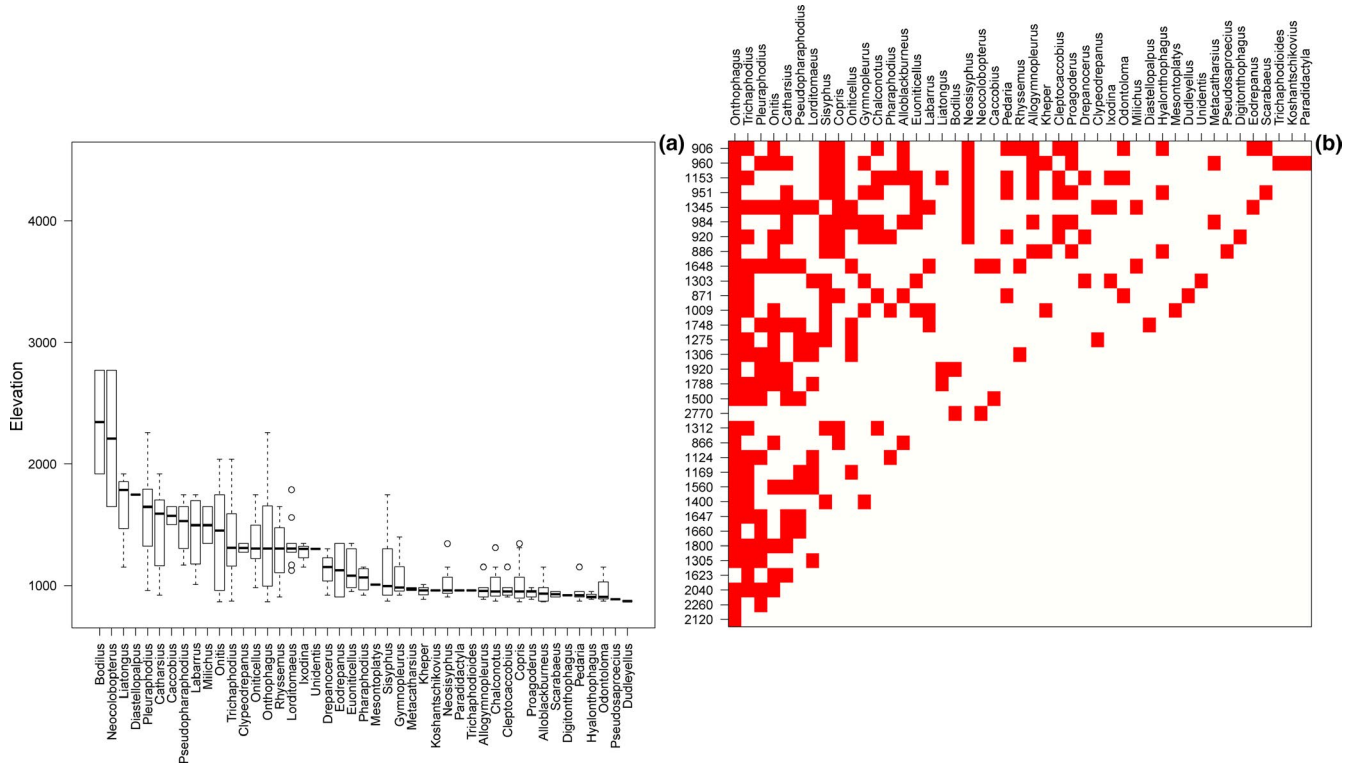

FIGURE 3 Elevational range of dung beetle genera (a) and composition of dung beetle communities at the genus level for all elevations (study plots) where dung beetles were present (b). In (b), coloured squares signify that a genus was present at a given elevation while blank squares represent absence of a genus [Colour figure can be viewed at wileyonlinelibrary.com]

The degree of nestedness was low as the NODF-values were closer to zero than to 100 (Figure 3a,b; NODF genera = 15.61, NODF study plots = 36.86, NODF entire community = 23.00). The components of multiple-site dissimilarities showed a high amount of turnover (turnover [Simpson dissimilarity] = 0.86, nestedness = 0.07). For species-level community composition, nestedness was even lower (Appendix S5, NODF entire community = 9.24, turnover = 0.91, nestedness = 0.07).

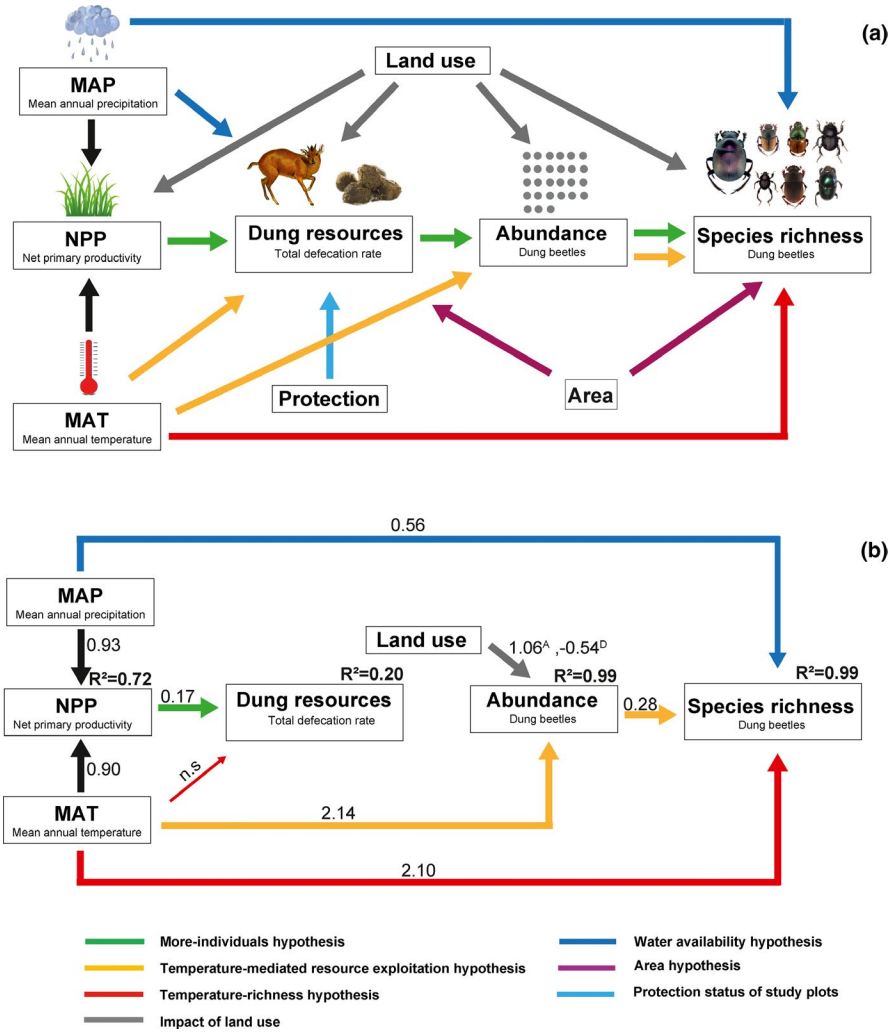

FIGURE 4 Path models illustrating the direct and indirect effects of predictor variables on the species richness of dung beetles on Mt. Kilimanjaro. (a) Starting path model showing all hypothesized effects of predictor variables on the species richness and abundance of dung beetles. (b) Path model best supported by the data (AIC_c = 67.18). Different coloured arrows depict different expected linkages between environmental variables and dung beetle communities. Details on the hypotheses behind the expected linkages are given in the introduction. All paths with numbers imply significant relationships ($p < .05$). Non-significant relationships are featured with thin lines. The relative amount of explained variance (R^2) is given for all response variables. Numbers above paths represent standardized path coefficients. [A]Agricultural plots, $p < .05$. [D]Disturbed plots, n.s. [A,D]As land use is a factorial variable, the path coefficients are not standardized. [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Drivers of species richness and abundance

Path analysis showed that the main predictor for dung beetle species richness and abundance was MAT (Figure 4b). Temperature had both direct effects on dung beetle species richness and indirect effects modulated by its positive influence on dung beetle abundance, supporting both the temperature-richness and the temperature-mediated resource exploitation hypothesis. In addition, dung beetle species richness was correlated with MAP. Scatterplots showing the relations between all response and predictor variables can be found in the supplement (Appendix S8.1). The relationship between dung beetle species richness and MAP was negative (Appendix S8.2).

Besides a strong effect of MAT, dung beetle abundance was correlated with anthropogenic land use. Dung resource availability, measured by mammal defecation rates, neither influenced dung beetle abundance nor dung beetle species richness. In contrast to dung beetle diversity, mammalian dung resources were mainly predicted by net primary productivity, whereas temperature only played a minor role here. We did not find any effect of area, neither on dung beetle diversity nor on mammalian dung resources (Figure 4b). Considering the communities collected during the two sampling events separately resulted in the same patterns for both the community sampled with human dung and the community sampled with cow dung: Species richness was well-correlated between the two sampling events ($r = .77$, $p < .01$; Appendix S9), as was abundance ($r = .81$, $p < .01$; Appendix S10). Species composition hardly changed between the two sampling events (Appendices S11 and S12) and path analysis produced the same patterns for both cow and human dung as for the pooled data set (Appendix S13).

Analogous to the path analysis of the complete data set, an analysis with data from the time period where dung beetles and mammals were sampled in parallel in consecutive years revealed no effect of mammal defecation rate on dung beetle species richness and abundance (Appendix S14).

4 | DISCUSSION

In this study, we found that dung beetle abundance showed a hump-shaped pattern while species richness declined exponentially with increasing elevation with no significant differences between natural and anthropogenic habitats. The variation in dung beetle abundance and species richness was best explained by changes in temperature but not by the amount and diversity of dung resources, supporting the view that the diversity of ectothermic

taxa is mostly limited by temperature and not by energy resources (Brown, 2014). Therefore, our results are in concordance with the 'temperature richness hypothesis' and the 'temperature-mediated resource exploitation hypothesis, while lending no support to the 'more individuals hypothesis'. To the best of our knowledge, this is the first study that directly compares the relative influence of climate and resource availability for dung beetle diversity across broad climatic gradients.

4.1 | Elevational patterns of diversity

The majority of elevational studies on dung beetle species richness report a decrease of species richness with increasing elevation (e.g. Chamberlain et al., 2015; Nunes et al., 2018). However, hump-shaped distributions of dung beetle diversity along elevation have also been observed (Herzog et al., 2013). For Scarabaeinae dung beetles, we recorded the highest species at 2,260 m (*Onthophagus incantatus*) while the highest Aphodiinae dung beetles were found at 2,770 m (*Bodilus vittifer*, *Neocolobopterus stefenellii*), patterns which reflect elevational distributions of dung beetles on other African mountains (Davis, Scholtz, & Chown, 1999; Muhirwa, Maniragaba, Maniragaba, & Kaplin, 2018). Interestingly, in the new world, the highest record for a Scarabaeinae dung beetle was found in the Colombian Andes at 4,550 m in a mountain system reaching 5,330 m, a height comparable to Mt. Kilimanjaro (Alvarado-Roberto & Arias-Buriticá, 2015). One reason for this striking difference could be that Mt. Kilimanjaro is a relatively young mountain with an age of 1.5–2 Ma years (Nonnotte et al., 2008). Likewise, the high mountains in the neighbourhood of Mt. Kilimanjaro are relatively young compared to the Andes. Dung beetles may still be colonizing Mt. Kilimanjaro or adapt to the environment at higher elevations. Alternatively, the area at higher elevation may have been too small in east Africa over evolutionary relevant time-scales to facilitate the diversification of a high elevation dung beetle fauna.

The pattern of abundance and species richness along elevation differed between functional guilds and subfamilies of dung beetles. Scarabaeinae dung beetles, composed of tunnellers, rollers and kleptoparasites, showed a decrease of species richness with elevation. In contrast, Aphodiinae dung beetles, consisting of dwellers, showed a hump-shaped distribution of both abundance and species richness with elevation. This pattern mirrors trends along latitudinal gradients: The warm-adapted Scarabaeinae dung beetles reach their highest species richness in tropical savannas (Hanksi & Cambefort, 1991) while cold-adapted Aphodiine dwellers replace Scarabaeinae dung beetles in cold climates (Arriaga-Jiménez, Rös, & Halffter, 2018), reaching their highest richness in temperate latitudes (Chamberlain et al., 2015; Martín Piera, Veiga, & Lobo, 1992). Turnover was mainly responsible for the changes in species composition with elevation while nestedness only played an inferior role.

4.2 | Drivers of dung beetle diversity

We found that species richness of dung beetles was mainly influenced by MAT and to a lesser degree by MAP. As opposed to endothermic organisms for which resource availability is often found to be a key limiting factor (Buckley et al., 2012), our study gives further evidence for the predominant role of temperature in determining the richness of ectothermic taxa (Brown, 2014; Peters et al., 2016).

Nevertheless, the 'more-individuals hypothesis', stating that abundance and species richness is dependent on the amount of available energy resources, was corroborated by several studies along gradients of increasing defaunation stressing the link between the occurrence of dung beetles and mammals generating dung (e.g. Bogoni et al., 2016; Frank, Brückner, Hilpert, Heethoff, & Blüthgen, 2017). Other studies discussing the relationship between dung beetle diversity, resource availability and climate conclude that both temperature and mammal diversity constitute drivers of dung beetle diversity (Frank et al., 2018; Muhirwa et al., 2018). However, these studies were conducted along small climatic scales compared to our large-scale 3.6 km elevational and 21°C temperature gradient on Mt. Kilimanjaro. Still, one reason for the lack in causality between dung beetles and mammals in our study could be the only partial overlap in sampling periods of dung beetles and mammals. However, we could show that even when only considering the two months in which dung beetle and mammal sampling overlapped in consecutive years, mammal defecation rate did not affect dung beetle diversity, which was instead impacted by climate even under this scenario.

The results of our path analyses are in agreement with two principle pathways by which temperature may influence species richness: In accordance with the 'temperature-richness hypothesis', we found a strong direct impact of temperature on dung beetle species richness. Temperature was also found to be a main driver of dung beetle diversity in other elevational studies across regional scales (Davis, Scholtz, & Deschodt, 2005; Herzog et al., 2013).The temperature-richness hypothesis assumes that temperature is positively correlated with ecological interactions and evolutionary rates (Brown, 2014). In addition to the direct effect of temperature on dung beetle species richness, we found an abundance-mediated indirect effect, supporting the temperature-mediated resource exploitation hypothesis (Classen et al., 2015). This hypothesis states that temperature, by influencing metabolic rates of ectothermic organisms, limits rates of resource use and the net productivity of consumers (Classen et al., 2015; Frazier, Huey, & Berrigan, 2006), predicting increases of species richness with increasing temperatures which are mediated by increasing consumer abundances.

MAP constituted the second strongest direct predictor for dung beetle species richness. The importance of water for dung beetles is supported by the observation that dung beetles reach their highest activity in the rainy season (Davis & Dewhurst, 1993). The dependence of dung beetle distributions on MAP has also been documented by several other studies (Davis et al., 1999,). Furthermore, moisture levels have been linked to the size of dung beetles and to reproductive success as dung beetles tended to be larger, time for egg laying to be longer and the number of surviving larvae higher under moist compared to dry conditions (Vessby, 2001). However, the relationship between MAP and dung beetle diversity was negative in our study. The

influence of MAP on dung beetles is dependent on the time of year and species (Cambefort, 1984). In this perspective, it is possible that too moist conditions on Mt Kilimanjaro during the rainy season may have negative consequences for dung beetle survival. Especially larval dung beetles as well as dung beetle eggs have been shown to be vulnerable to heavy rains causing increased mortality (Edwards, 1986).

4.3 | Land use effects

Overall, land use had no effect on dung beetle species richness. However, different functional groups of dung beetles showed different reactions to land use, probably due to differing sensitivities to biotic and abiotic changes in anthropogenic habitats as compared to natural habitats (Nichols et al., 2013). Rollers constituted the only functional group negatively influenced by land use, probably since they are behaviourally more specialized than other functional groups (Hanksi & Cambefort, 1991). As rollers build shallower nests than tunnellers, they may be especially vulnerable to augmented air and soil temperatures typical of anthropogenic habitats (Halffter & Edmonds, 1982). Furthermore, rollers are mainly comprised of large-bodied species which may be pushed to their physiological limit and therefore less abundant in anthropogenic habitats (Chown & Klok, 2011). In contrast, other groups dominated by smaller dung beetles, like dwellers, may profit from land use and compensate the decline of large rollers. The highest abundance of dung beetles was found on a study plot located on a commercial coffee plantation at 1,345 m a.s.l., mainly attributed to the predominance of few small tunneller and dweller species (e.g. *Onthophagus pseudovinctus*, *Trichaphodius gorillae*) which reached extreme abundances. Perturbed habitats have already been reported to host high dung beetle abundances caused by the dominance of few small-bodied species (Culot et al., 2013). If there is exploitative competition between dung beetles, the absence of large rollers from anthropogenic habitats could promote the diversity and abundance of smaller species as a form of density compensation (Nichols, Gardner, Peres, & Spector, 2009), which may explain the acute increase of few small species. However, due to their body size, large rollers are of huge functional significance unlikely to be substituted by smaller species (Slade, Mann, & Lewis, 2011). Since they process disproportional large amounts of dung compared to smaller-bodied species, the absence of large dung beetles in anthropogenic habitats may have negative consequences for associated ecosystem services such as fly control and suppression of diseases (Slade et al., 2011). Another reason for the exceptionally high abundance of dung beetles on the coffee study plot may be the close proximity of the plantations to settlements, providing a constant supply of animal and human excrements to few adapted species.

5 | CONCLUSION

While the diversity of endothermic organisms like birds and mammals is mainly limited by food resources (Buckley et al., 2012; Ferger et al., 2014), we show in this study that temperature-mediated processes have a higher relevance in constraining the diversity of ectothermic dung beetles.

The strong linkage between temperature, abundance and species richness points to a strong sensitivity of dung beetles towards climatic warming. Even though temperature was positively correlated with species richness within the studied temperature range, further increases of temperature may push lowland species beyond their physiological limits (Deutsch et al., 2008), urging them to progressively colonize higher altitudes, if possible. Furthermore, the vulnerability of ectothermic organisms to climate change might even worsen if anthropogenic disturbances are increasing simultaneously to augmented temperatures (Beiroz et al., 2017). A better understanding of the physiological and ecological response of insect communities towards more extreme temperatures and land use changes and studies on the evolutionary limits of adaptation will be mandatory for a better understanding of the ecological consequences of climatic changes in mountain ecosystems.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are documented and archived in the PANGAEA database at: https://doi.org/10.1594/PANGAEA.905168 (Gebert, Steffan-Dewenter, & Peters, 2019).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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