RESEARCH ARTICLE

The role of diversity, body size and climate in dung removal: A correlative and experimental approach

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Abstract

1. The mechanisms by which climatic changes influence ecosystem functions, that is, by a direct climatic control of ecosystem processes or by modifying richness and trait compositions of species communities, remain unresolved.

2. This study is a contribution to this discourse by elucidating the linkages between climate, land use, biodiversity, body size and ecosystem functions.

3. We disentangled direct climatic from biodiversity-mediated effects by using dung removal by dung beetles as a model system and by combining correlative field data and exclosure experiments along an extensive elevational gradient on Mt. Kilimanjaro, Tanzania.

4. Dung removal declined with increasing elevation, being associated with a strong reduction in the richness and body size traits of dung beetle communities. Climate influenced dung removal rates by modifying biodiversity rather than by direct effects. The biodiversity–ecosystem effect was driven by a change in the mean body size of dung beetles. Dung removal rates were strongly reduced when large dung beetles were experimentally excluded.

5. This study underscores that climate influences ecosystem functions mainly by modifying biodiversity and underpins the important role of body size for dung removal.

KEYWORDS

altitudinal gradients, biodiversity–ecosystem functioning relationship, body size, diversity gradients, ecosystem services, land use, Scarabaeidae, temperature

1 | INTRODUCTION

Global biodiversity is threatened by climatic and land use changes (Chapin III et al., 2000) with subsequent modifications of ecosystem functions and services (Hatfield et al., 2018). Experimental studies suggest strong linkages between biodiversity and ecosystem functions because of complementarity or sampling effects

and due to the detrimental effects of biodiversity loss on central ecosystem functions such as decomposition and primary production (Hooper et al., 2012). In contrast, the metabolic theory of ecology revealed strong linkages between rates of ecosystem processes and temperature, pointing to a predominant role of climate on rates of ecosystem functions across broad climatic gradients (Brown et al., 2004). Climatic changes may directly influence

ecosystem functioning due to effects of temperature and water availability on ectothermic metabolism and activity rates (Brown et al., 2004; Peters et al., 2019). Furthermore, climatic changes are often additionally associated with changes in species richness and the functional composition of species communities (Peters et al., 2016). Consequently, effects of climate on ecosystem functions can be mediated by alteration in the richness and trait composition of communities (Hevia et al., 2017). Despite an increasing number of studies testing biodiversity ecosystem functioning (BEF) relationships, the degree to which ecosystem functions are controlled by climate or by species diversity is still little resolved, as studies of ecosystem functions are largely constituted of small-scale manipulative experiments conducted in study regions with narrow climatic gradients (van der Plas, 2019). On the other hand, correlative studies of ecosystem function along broad scale climatic gradients in real-world ecosystems often fail to reveal clear evidence for direct effects of climate or of biodiversity because these are intimately correlated in natural ecosystems (Albrecht et al., 2021; Peters et al., 2019).

In recent years, the concept of BEF has been expanded by not only considering species richness but also the functional diversity of organisms (de Bello et al., 2010). When compared to analyses based on pure taxonomic diversity (considering only species richness and abundance), inclusion of functional traits of species has been shown to better predict ecosystem functions. Functional traits are features of an organism that influence its fitness and regulate its reaction to environmental impacts and ecosystem processes (Cadotte et al., 2011). A key functional trait of species is body size, which is associated with many life-history traits such as abundance, range size, trophic position and foraging, and positively correlated with metabolic rates and energy turnover of individuals (Brown et al., 2004). Communities dominated by larger organisms are predicted to show higher rates of ecosystem functions than communities dominated by smaller organisms (Manning & Cutler, 2020). However, larger-bodied species are more sensible to environmental perturbations than smaller-bodied species (Brose et al., 2017), making them more susceptible to human impact and adverse climatic conditions.

Here, we disentangled the linkages between climate, land use, biodiversity, body size and ecosystem functions by a combination of correlative field data and exclosure experiments. We used a model system of dung beetles performing the key ecosystem service dung removal along climatic and land use gradients on Mt. Kilimanjaro, Tanzania. Mountains are characterized by brisk changes in abiotic conditions and species distributions, offering unique study systems to elucidate the relationships between ecosystem functions, biodiversity and the environment (Nunes et al., 2018). Dung removal and dung burial by dung beetles is a central ecosystem service, affecting other ecosystem services such as nutrient cycling, bioturbation, plant growth enhancement, parasite suppression and secondary seed dispersal (Nichols et al., 2008). Furthermore, dung removal is an ecosystem service that has a huge economic dimension, being valued at £367M per year for the UK cattle industry alone (Beynon et al., 2015). Dung beetles have been reported to be the most important group responsible for dung removal, relying on dung as a food and nesting resource (Hanksi & Cambefort, 1991; Slade et al., 2007). Dung constitutes a model system to study BEF relationships since dung occurs in ephemeral resource patches that can be quantitatively measured and readily sampled, manipulated and replicated (Finn, 2001). Studies exploring the removal of dung along elevation are rare and either focus on the temperature dependency of general nutrient discharge from dung without considering dung beetles (Luo et al., 2010; Xu et al., 2010) or focus on intact dung beetle communities (Nunes et al., 2018). Recent studies suggest strong relations between body size of dung beetles and dung removal (Braga et al., 2013; Shahabuddin et al., 2010; Slade et al., 2007), between dung beetle richness, body size and land use (Nichols et al., 2013) and between dung beetle richness and climate (Gotcha et al., 2022). However, we are not aware of any study simultaneously exploring the interrelations between climate, land use, richness and body size of dung beetles on dung removal.

In this study we, first, reveal how dung removal increases simultaneously with temperature, species richness, abundance and changes in the body size of dung beetles along the extensive elevation gradient of Mt. Kilimanjaro. Second, we made use of path analyses to disentangle the linkages between climate, diversity and dung removal in real-world ecosystems and how these are impacted by current land use. We show that dung removal is largely driven by effects of climate on the composition of body size traits in communities rather than by direct climatic effects on dung removal. Third, exclosure experiments give further experimental evidence against direct climatic effects on dung removal and reveal a key role of dung beetle richness and correlated body size traits for dung removal in a tropical mountain ecosystem.

2 | MATERIALS AND METHODS

2.1 | Study plots

The study was carried out on 66 study plots of c. 50 × 50 m established by the KiLi project (DFG research unit FOR 1246) on the southern slopes of Mt. Kilimanjaro, Tanzania (2°54′–3°25′S, 37°0′–37°43′E; Figure 1). Mt. Kilimanjaro has a northwest–southeast diameter of 90 km and rises from the savanna plains at 700 m elevation to a snow-clad summit at 5895 m a.s.l. According to its location 300 km south from the equator, the climate on Mt. Kilimanjaro can be described as an equatorial day-time climate, characterized by two apparent rainy seasons: the long rains between March and May and the short rains around November. Mean annual temperature (MAT) decreases linearly with elevation at approximately 6.1°C per 1000 m of elevation from about 25°C at the base to −8°C at the summit. Mean annual precipitation (MAP) is unimodally distributed, reaching its maximum at ~2700 mm at around 2200 m a.s.l. in the forest belt (Appelhans et al., 2016). The study plots were located along an elevational gradient of
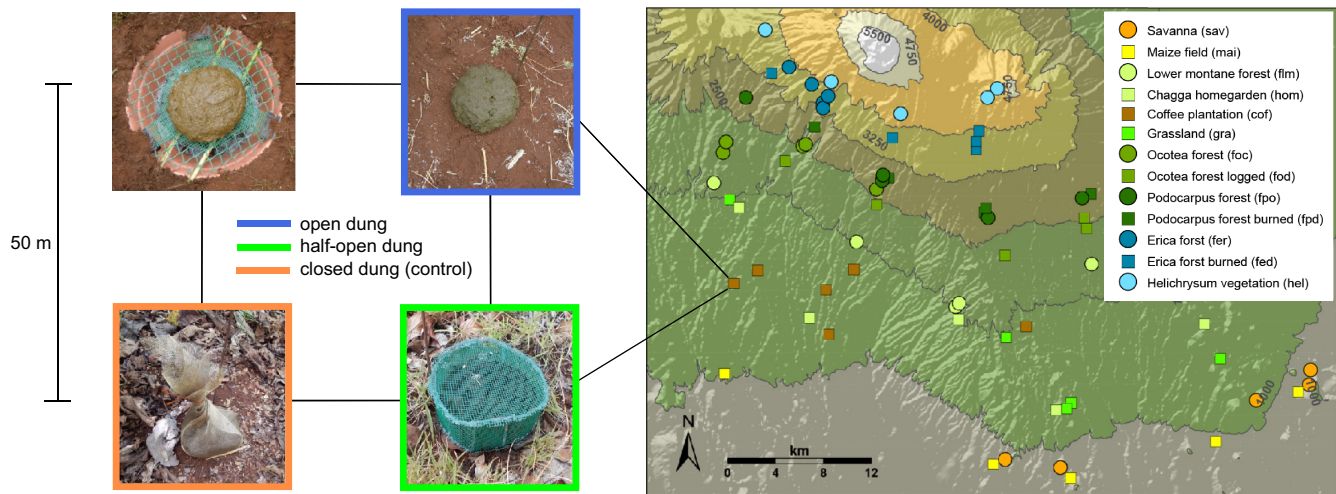
FIGURE 1 Map of Mt. Kilimanjaro showing the 66 study plots (right panel) and, enlarged, the experimental studies conducted on each study plot. The enlarged section shows clockwise from top left: Pitfall trap for collecting dung beetles, un-manipulated cow dung pat accessible to whole dung beetle community, half-open dung (treatment 'H' of exclosure experiment) excluding large dung beetles, closed dung (treatment 'C' of exclosure experiment) barring all dung beetles.

3.7 km from 870 to 4550 m a.s.l., and equally assigned to the 13 main natural and anthropogenic ecosystem types in the region (five to six study plots per ecosystem type, Figure 1; Table S1). Natural ecosystem types consisted of savanna (871–1153 m a.s.l.), lower montane forest (1560–2020 m a.s.l.), *Ocotea* forest (2120–2750 m a.s.l.), *Podocarpus* forest (2800–2970 m a.s.l.), *Erica* forest (3500–3900 m a.s.l.) and alpine *Helichrysum* scrub vegetation (3880–4550 m a.s.l.). Anthropogenic habitats comprised maize fields (866–1009 m a.s.l.), grasslands (regularly cut by hand for cattle feeding, 1303–1748 m a.s.l.), commercial coffee plantations (1124–1648 m a.s.l.) and Chagga agroforestry (1169–1788 m a.s.l.), selectively logged *Ocotea* forest (2220–2560 m a.s.l.), burned *Podocarpus* (2770–3060 m a.s.l.) and burned *Erica* forests (3500–3880 m a.s.l.). Anthropogenic habitats were further subdivided into agricultural habitats (maize fields, grasslands, coffee plantations, agroforestry) and disturbed habitats (logged *Ocotea* forest, burned *Podocarpus* and *Erica* forests), resulting in three land use levels (natural, agricultural, disturbed, Table S1). We used these land use types to explore the impact of land use on dung removal. The five to six study plots per ecosystem type were arranged along a within-habitat elevational gradient to account for fine scale changes in biodiversity with changing elevation. Distances among study plots amounted to at least 300 m, with 97% of all study plot pairs being more than 2 km apart. In order to lessen effects of transition zones, where feasible, study plots were situated in core zones of larger areas of the respective habitat type.

2.2 | Climate

On all 66 study plots of the KiLi project, temperature sensors were set up approximately 2 m above the ground (Appelhans et al., 2016). For a period of 2 years, temperature was measured every 5 min and

for each study plot, MAT (mean annual temperature) was computed as the average of all measurements. Data on MAP (mean annual precipitation) were collected with approximately 70 rain gauges distributed across the different ecosystem types and elevations on Mt. Kilimanjaro. These measurements were taken as a base to regionally interpolate MAP employing a co-kriging approach and to obtain MAP values for each study plot. More specific aspects on methodology and original data are featured in Appelhans et al. (2016) and Peters et al. (2016, 2019).

2.3 | Measuring dung removal and the exclosure experiment

For measuring the natural rate of dung removal, we placed one open, un-manipulated cow dung pat on each study plot (Lähteenmäki et al., 2015, Figure 1), which was accessible by dung beetles of all body sizes (treatment 'O' for open dung). Apart from dung beetles, the natural dung community is also composed of other decomposers, such as other beetles, flies and micro-organisms, among which dung beetles are considered the most important group for dung removal (Beynon et al., 2012; Hanksi & Cambefort, 1991). The exclosure experiment included two treatments: First, the exclusion of large dung beetles and, second, the exclusion of the whole dung beetle community. For the former treatment, one cow dung pat per study plot was surrounded by mesh wire with a mesh size of 0.5 cm (Figure 4c). This treatment represented a scenario where the more threatened large dung beetles are extinct but smaller beetles, as well as other small decomposers, are still present (treatment 'H' for half-open dung). We employed a mesh size of 0.5 cm since the average dung beetle species occurring in the Kilimanjaro region was found to have a pronotum width of around 0.5 cm (F.G., personal observation). Dung beetles smaller than 0.5 cm diameter, which

were able to move through the 0.5 cm mesh wire, were considered as 'small'. For excluding the whole dung beetle community, we encased dung pats with wire gauze with a mesh size of 0.1 cm (treatment 'C' for closed dung, Figure 4d). This treatment represented a touchstone for ecosystem functioning in the absence of dung beetles (Lähteenmäki et al., 2015). Although treatment C did not allow dung removal by dung beetles, other decomposers, such as flies, other small beetles and micro-organisms still had access to the dung, the former by placing eggs through the gauze (Kudavidanage & Qie, 2012). All dung pats consisted of 700 g of cow dung and were arranged into uniform pats (c. 15 cm in diameter and 6 cm high). Cow dung was the only kind of dung that could be obtained in large quantities at Mt. Kilimanjaro. Cow dung represents a suitable uniform resource for standardized exclosure experiments (Slade et al., 2007). Even though only small amounts of cow dung are expected to occur naturally at higher elevations, dung of other large grazers has been detected during the study time even in the afroalpine zone (Gebert et al., 2020). Cow dung was collected locally and frozen for at least 24 h prior to being exposed in the field, guaranteeing that any dung beetles dwelling in the dung were killed. On each study plot, one un-manipulated, one half-open and one closed dung pat were placed in three corners of a 50×50 m square, so that the distance between treatments amounted to at least 50 m, which is the minimum distance required to ensure independence of traps for dung beetles (Larsen & Forsyth, 2005). All dung pats and the pitfall trap were shielded with canvas from sun and rain. After 15 days of exposure, dung remains were dried until a constant dry weight at 60°C in a drying oven. For dung that was already dry in the field, such as dung collected in savanna habitats, constant dry weight was achieved on the second day while for wetter samples, this process could take up to 4 days. The exclosure experiment on all study plots was conducted twice between June 2015 and February 2016 and the mean dry weight values of the two sampling rounds were used for analyses. To obtain a control dry weight, we dried 10 fresh 700 g cow dung piles and calculated the mean dry weight, which amounted to 116 g.

2.4 | Trapping dung beetles

In the fourth corner of the 50×50 m square we placed a pitfall trap to collect the dung beetle community. Dung beetles were collected once on each study plot during the second round of the exclosure experiment from October 2015 to February 2016. Each pitfall trap (upper diameter 33 cm, lower diameter 24 cm, height 15 cm) was filled with 1.5 L of water to which we added detergent to lessen water surface tension, which resulted in a water height of c. 3 cm. The bait consisted of 700 g of fresh cow dung and was placed on a mesh positioned over the trap, resembling a natural dung pat with a diameter of approximately 15 cm. Even though most studies in the literature employ human dung for collecting dung beetles, even when conducting exclosure experiments with cow dung (e.g. Slade et al., 2007), we used cow dung to document the dung beetle community that was

removing the cow dung of the exclosure experiments. We found that on Mt. Kilimanjaro, the dung beetle communities attracted to human and cow dung differed only slightly (Gebert et al., 2020), which is why cow dung can be considered a suitable resource to record the dung beetle community on Mt. Kilimanjaro. We emptied traps after the first 72 h of the simultaneous exclosure experiment. We are aware that commonly, studies conducting exclosure experiments sample the dung beetle community after the functions have been assessed (e.g. Slade et al., 2007). However, we made sure that the spatial distance between the three exclosure treatments and the pitfall trap amounted to at least 50 m, which is the distance reported in the literature that is needed for assuming independence between treatments (Larsen & Forsyth, 2005). Collected specimens were stored in whirl packs filled with 70% ethanol. We sorted dung beetles to the species level; where this was not possible, specimens were identified to the genus level and assigned with a morphospecies number.

The necessary research permits (COSTECH 2015-178-NA-96-44 and TANAPA TNP/HQ/C.10/13) to conduct fieldwork were granted by the Tanzanian Commission for Science and Technology (COSTECH) and the Kilimanjaro National Park authority. This study did not require ethical approval.

2.5 | Functional traits of dung beetles

We used pronotum width as a proxy for the body size of dung beetles (Berson & Simmons, 2018; Tocco et al., 2019), which we measured using a measuring ocular in a Nikon SMZ 745 stereomicroscope. On each study plot, we took measurements of 10 individuals per species; if there were fewer than 10 individuals, all individuals were measured. We calculated the mean body size on each study plot as the average body size across all species (i.e. revealing a community mean body size).

To acquire the dry biomass of dung beetles (Chamberlain et al., 2015), the same individuals which were taken for size measurements were weighted with a microbalance with an accuracy of ±0.0001 g. Since beetles were already mounted, an average weight for the insect pin (0.1124 g) was calculated and subtracted from the weight of each pinned beetle (Radtke & Williamson, 2005). We always used the same type of pin from the same company. We calculated the total biomass of the dung beetle community per study plot by summing up the dry masses of all individuals. Where more than 10 individuals were collected per species, we multiplied the mean biomass of the 10 measured individuals with the total number of individuals to add their contribution to the community biomass.

2.6 | Statistical analysis

For all statistical analyses, we calculated dung removal as

$$\text{Dung removal} = \frac{\text{dry weight}[\text{control}] - \text{dry weight}[\text{treatment}]}{\text{dry weight}[\text{control}]}. \quad (1)$$

with the control dry weight amounting to 116 g. According to (1), dung removal is a value between 1 and 0, 1 signifying that all dung was decomposed and 0 the complete absence of dung removal. We analysed the pattern of dung removal and the distribution of dung beetle species richness, abundance, community biomass and body size with elevation by means of generalized additive models (GAMs). In GAMs, nonparametric smoothers are used to describe potential nonlinear or linear relationships between explanatory and response variables instead of assigning specific functional formula. We applied the 'gam' function from the R package MGCV to compute GAMs (Wood, 2006) setting the data family to 'poisson' for all count data. For dung beetle body size measures, we employed the Gaussian data family. When we detected overdispersion in the data, we used the family 'quasipoisson'. The dung removal data were modelled setting the data family to Gaussian (Figure S1). Furthermore, we tested whether land use affected dung removal by including land use type (factorial: natural vs. anthropogenic) as an interacting factor in the model. When the interaction effect was shown to be not significant, we maintained land use as an explanatory variable in the models. However, if the model dung removal ~ elevation + land use was also shown to be not significant (which was always the case), we simplified the model to dung removal ~ elevation.

For contrasting dung beetle community parameters for small dung beetles with the whole community, we also used GAMs. To avoid over parameterization, we set the basis dimension of the smoothing term (k) to five for all GAMs.

Using path analysis, we explored the direct and indirect effects of temperature, precipitation and the effects of abundance, species richness, body size and biomass of the dung beetle community on dung removal. In addition to temperature and precipitation, we included land use as a potential predictor of dung beetle abundance, species richness and body size in the path model (Figure 3a).

Potential path combinations were preselected by establishing a set of competitive explanatory models for each response variable (dung removal as well as dung beetle species richness, abundance, biomass and body size) using multi-model inference based on the Akaike information criterion (AIC). As our sample size was low compared to the number of estimated parameters, the AIC_c with a second-order bias correction for ranking individual models was applied. We employed the 'dredge' function of the R package MuMIn to obtain the AIC_c for the full model including all explanatory variables and for all nested models inferred from the null model. All models with a $\Delta AIC_c < 2$ were considered for constructing potential path models.

Since we used GLMs and the 'glm.nb' function in case of overdispersion, it was not possible to use traditional statistical applications for path analysis with normally distributed data as a prerequisite. Instead, we employed piecewise structural equation modelling (SEM) which is founded on the d-sep test (Shipley, 2009). We calculated the AIC_c for each path model with the 'sem.fit' function of the R package PIECEWISESEM (Lefcheck, 2016; Shipley, 2000, 2009, 2013). The path model with the lowest AIC_c represented the best path model (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.

For analysing whether there was a difference in dung removal between the whole dung beetle community and the two treatments of the exclosure experiment, we looked at low elevation (<2000 m) and high elevation study plots (>2000 m) separately. We wanted to explore dung removal in the presence and absence of the dung beetle community to find out whether dung beetles are the main group responsible for dung removal at Mt. Kilimanjaro and whether dung removal occurs in the absence of dung beetles. These two elevational ranges were selected because we documented most dung beetles below 2000 m (dung beetle community present) and only few dung beetles above 2000 m (dung beetle community nearly absent). For each elevation level, we calculated LMEs with the 'lme' function of the R package NLME with treatment (un-manipulated dung, treatment H and treatment C of the exclosure experiment) as a fixed factor and study plot as a random factor. The Tukey post hoc test was computed with the 'glht' function of R package MULTCOMP to check whether there are differences between treatments within and between elevational levels.

Furthermore, we explored whether land use had an effect on dung removal for un-manipulated dung and the two treatments of the exclosure experiment by comparing residual plots. We calculated the residuals of the GAMs for these three response variables with elevation (treatment ~ elevation) separately for the three land use types (natural, agricultural, disturbed). Statistics were conducted in R version 4.0.2.

3 | RESULTS

3.1 | Dung removal and dung beetle communities

In total, we collected 1277 dung beetles, belonging to 87 species (Table S3). Of these, 88% were classified as small and 12% as large. Both the species richness and abundance of the dung beetle community decreased with increasing elevation [species richness: explained deviance (ED) = 69.2%, $p < 0.001$; Figure 2b, abundance: ED = 56.1%, $p = 0.07$]. The mean body size of the community exhibited a hump-shaped distribution with a peak at 1500 m (ED = 69.9%, $p < 0.001$, Figure 2d). The community biomass also showed a hump-shaped pattern, increasing to approximately 1800 m and decreasing to a value of 0 at c. 3000 m a.s.l. (ED = 60.5%, $p < 0.05$, Figure 2e). While there was no difference between natural and anthropogenic habitats for species richness, abundance and biomass, neither for small dung beetles nor for the whole dung beetle community, biomass showed differences between land use types (Figure S2). Dung removal was moderately high in the lowlands and peaked at 1500 m elevation (Table S2). After reaching its peak, dung removal decreased to 3000 m where it levelled off at a value of zero [explained deviance (ED) = 43%, $p < 0.001$; Figure 2a]. Dung removal rates, climate variables and biodiversity variables were correlated along the elevational gradient (Figures S3 and S4).
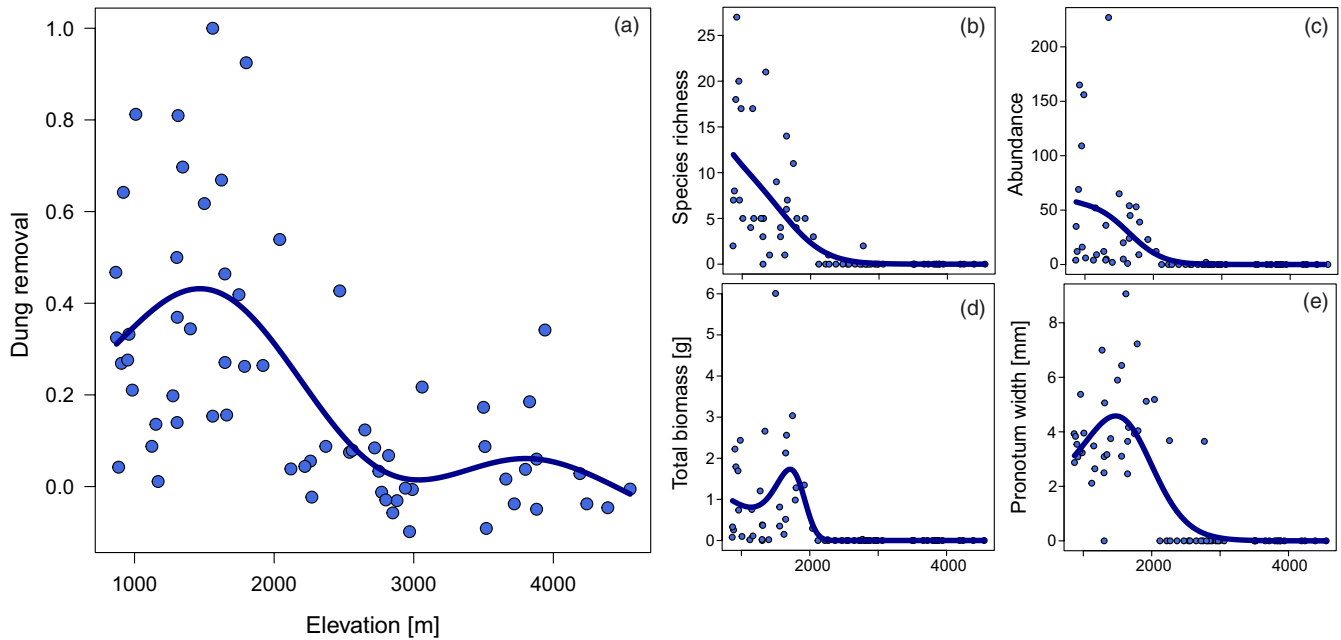
FIGURE 2 Pattern of dung removal with elevation (a) and elevational distribution of the dung beetle community parameters species richness (b), abundance (c), total biomass (d) and body size, measured as pronotum width (e). Dots represent original measurements on study plots. All trend lines were calculated with generalized additive models [basis dimension (k) = 5].
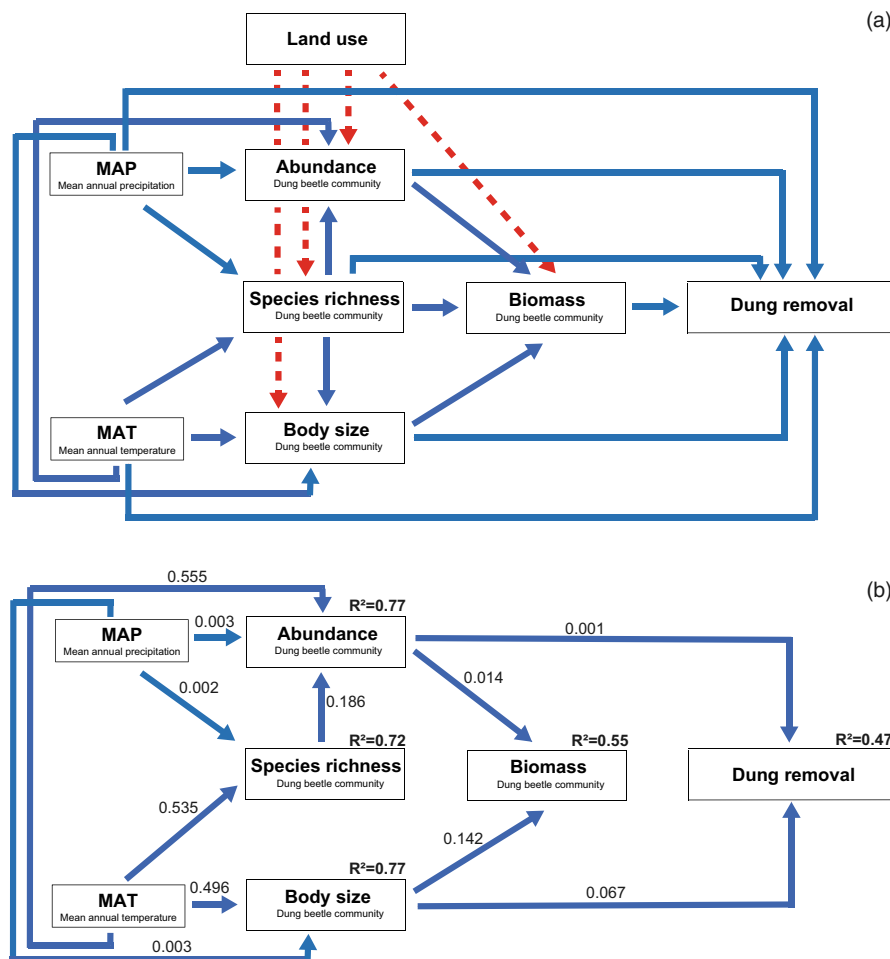

FIGURE 3 Path model illustrating the direct and indirect effects of predictor variables on dung removal on Mt. Kilimanjaro. (a) Starting path model showing all hypothesized effects of predictor variables on dung removal. (b) Path model best supported by the data. Blue solid lines depict positive relationships while red dashed lines illustrate negative effects. The relative amount of explained variance (R^2) is given for all response variables. Numbers above paths represent standardized path coefficients. Model support for all response variables and alternative best path models can be found in the supplement (Table S4; Figure S7).
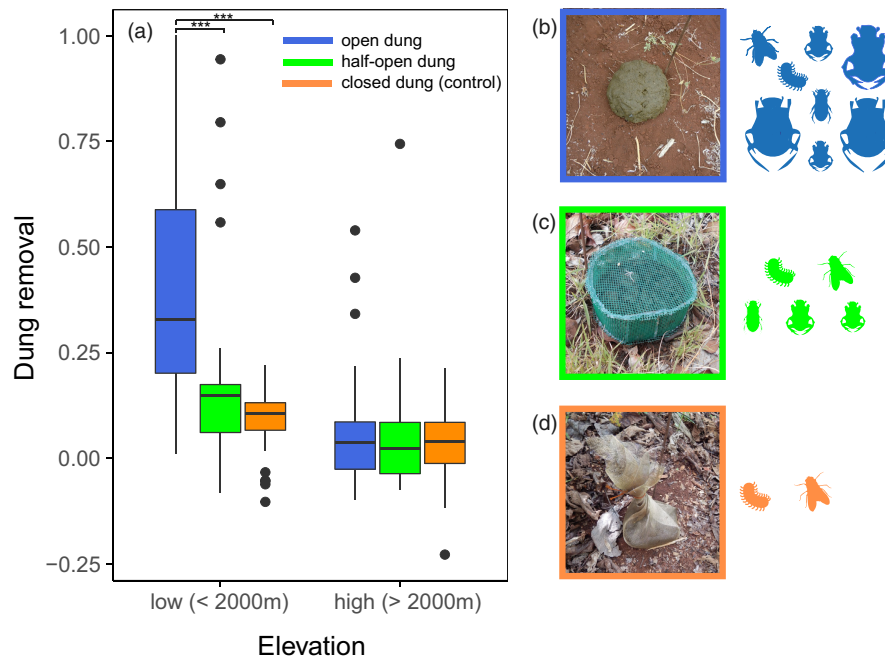
FIGURE 4 (a) Dung removal for intact dung beetle communities (shown in blue) and for the two treatments of the exclosure experiment (treatment H shown in green, treatment C in orange), separated into two elevation levels: Low (<2000 m) and high (>2000 m). The boxplots show the median and the Q1–Q3 range (25%–75% of data) inside the box. The whiskers represent minimum and maximum values without outliers. Outliers are displayed with dots (outliers defined as Q1–1.5 × IQR, Q3 + 1.5 × IQR). Significant differences are only shown for low elevation treatments and are depicted with '***'. (b–d) Experimental setup and illustration of the effects of exclosures on dung beetle communities. (b) Open, un-manipulated cow dung pats were used for assessing dung removal by naturally occurring decomposer communities, consisting of large and small dung beetles as well as other decomposers, here represented by a fly and a micro-organism. (c) Treatment H, excluding large dung beetles. The reduced decomposer community consisted of small dung beetles and other small decomposers. (d) Treatment C, barring all dung beetles. Here, only small decomposers, such as flies and micro-organisms, could still access the dung.

We used a path analytical modelling approach to disentangle causal relationships among climate, dung beetle diversity and dung removal. The best path model (AIC$_c$ = 100.137) revealed that dung removal of natural dung beetle communities (i.e. dung pats to which all dung beetles had access) was mainly predicted by the mean body size of dung beetle communities (standardized path coefficient = 0.067, $p < 0.001$) and, secondly, by the abundance of dung beetles (standardized path coefficient = 0.001, $p < 0.05$; Figure 3b; Table S4). Climate influenced dung removal indirectly; mainly by its effect on species richness (MAT: standardized path coefficient = 0.535, $p < 0.001$; MAP: standardized path coefficient = 0.002, $p < 0.001$), abundance (MAT: standardized path coefficient = 0.555, $p < 0.001$; MAP: standardized path coefficient = 0.003, $p < 0.001$) and body size (MAT: standardized path coefficient = 0.496, $p < 0.001$; MAP: standardized path coefficient = 0.003, $p < 0.001$) of dung beetle communities. Dung beetle abundance was strongly correlated with dung beetle species richness ($r = 0.89$, $p < 0.001$). Apart from the best path model, there was one competing path model that received similar support by the data ($\Delta AIC_c < 2$). Here, dung removal was solely predicted by dung beetle body size (Figure S5).

Regarding land use, dung removal did not differ between natural, agricultural and disturbed habitats for both intact dung beetle communities and the two treatments of the exclosure experiment (Figure S6). Land use was not supported as a predictor variable in path models (Figure 3).

3.2 | Experimental exclusion of dung beetles

Dung removal was significantly reduced if large dung beetles or all dung beetles were excluded from the dung pat (Figure 4). This effect was absent at elevations exceeding the maximum of dung beetle elevational ranges (c. 2000 m a.s.l.; Figure 2, Supporting Information S8). At higher elevations above 2000 m, also slightly negative values of dung removal were reported (Figures 2a and 4a; Figure S1). Since it was not always possible in the field to obtain an exact wet weight of 700 g of cow dung, in cases where hardly any or no dung removal occurred, the obtained dry weight could be slightly higher than the reference dry weight, resulting in negative dry weights according to formula (1). Soil attached to dung pats by termites was not the reason for these negative weights as termites only occurred below 2000 m and we made sure to remove any soil from the dung pats at point of collection. Across all samples, the whole dung beetle community removed 22% of the dung (treatment O), a further 11% could be attributed to medium- and small-sized dung beetles (treatment H), while smaller organisms contributed 5% of dung removal (treatment C). Under the complete

exclosure of dung beetles, dung removal slightly increased with temperature (slope $= 0.005 \pm 0.0016$, $R^2 = 0.14$, $p < 0.01$). Extending the access to the dung pat to small dung beetles doubled the slope estimate for the relationship between temperature and dung removal rate (slope $= 0.011 \pm 0.004$, $R^2 = 0.12$, $p < 0.01$); this additional temperature effect can be attributed to the higher number of small dung beetles at higher temperatures. Giving additionally large dung beetles access to the dung again more than doubled the effect of temperature on dung removal (slope $= 0.023 \pm 0.004$, $R^2 = 0.30$, $p < 0.01$), revealing that the effects of climate on dung removal are mediated by the positive effects of temperature on the average body size in dung beetle communities.

A path model including data from all exclosure treatments underscored that the effects of climate on dung removal are mediated by the positive effect of climate on average body size and biomass of dung beetle communities (Figure S7). Univariate correlations revealed a stronger correlation between dung removal rates with average body size ($r = 0.66$, $p < 0.001$, Figure S3) than with dung beetle species richness ($r = 0.41$, $p < 0.05$, Figure S6), biomass of the total dung beetle community ($r = 0.39$, $p < 0.05$, Figure S3) or dung beetle abundance ($r = 0.38$, $p < 0.05$. Figure S3).

4 | DISCUSSION

To the best of our knowledge, this is the first study combining the study of natural dung beetle communities with an exclosure experiment to disentangle the effects of climate and biodiversity in dung removal along a broad-scale climatic gradient. Our study is a vital contribution to the current debate on the role of climate and biodiversity-related factors as drivers of ecosystem services (Brown et al., 2004; Dainese et al., 2019; Gagic et al., 2015; Hooper et al., 2012; Nunes et al., 2018; van der Plas, 2019). Community body size and biomass were the main drivers of dung removal while temperature and precipitation influenced dung removal rates indirectly, that is, via their effect on dung beetle body size and abundance.

Dung removal followed a hump-shaped distribution with elevation with a peak in the lower part of the elevation gradient at *c.* 1500 m. Dung removal was strongly correlated with the mean body size of dung beetle communities, which showed a similar elevational distribution. Our study thus corroborates the results of small-scale experimental studies focusing on few dung beetle species only, which reported dung beetle biomass as a major factor impacting dung removal (O'Hea et al., 2010; Tixier et al., 2015).

The experimental exclusion of both large dung beetles and the whole dung beetle community strongly reduced dung removal rates, emphasizing the importance of intact dung beetle communities and the disproportionate role of large dung beetles for dung removal (Nervo et al., 2014; Slade et al., 2007, 2011). Furthermore, dung removal was highest at low elevations where dung beetle richness was most pronounced, confirming the hypothesis that more diverse communities are superior in ecosystem service provisioning (Hooper et al., 2005). The general decrease in dung removal with increasing elevation mirrors the common decline

of dung beetle diversity with rising elevation (Davis et al., 2005; Gebert et al., 2020; Muhirwa et al., 2018; Nunes et al., 2016). Our results highlight that communities consisting of only small dung beetles could not compensate for the absence of large dung beetles (Braga et al., 2013; Shahabuddin et al., 2010; Slade et al., 2007), even though small dung beetles accounted for 67% of the total biomass across study plots.

A limitation of our study might be that we did not measure the contribution of other small decomposers to dung removal, which could still access the dung in the exclosure treatments. However, the effect of micro-organisms, flies and other small organisms on dung degradation proved to be low in comparison to the effect of dung beetles, corroborating dung beetles as the most important organismal group facilitating dung decomposition (Slade et al., 2007). Another possible limitation of our approach may be the comparatively short sampling period of 15 days, which may either under- or overestimate long-term differences between treatments. Since older dung is mainly decomposed by small-bodied endocoprid dung beetle species (Hanksi & Cambefort, 1991) and micro-organisms, which show a strong seasonality in activity (Becker et al., 2015), disparities between treatments could be decreasing and micro-organisms could gain in importance as dung decomposers over longer time periods.

Anthropogenic land use change is regarded as one of the major threats for global biodiversity and consequently for the provisioning of ecosystem functions and services (Chapin III et al., 2000; Loreau, 2001). As opposed to other studies (e.g. Frank et al., 2017), we found that land use did not significantly influence dung removal. This result is most likely due to the current moderate land use regimes at Mt. Kilimanjaro. However, especially ecosystems at lower elevations outside Mt. Kilimanjaro National Park are vulnerable to further human encroachment and agricultural intensification (Newmark & IUCN Tropical Forest Programme, 1991; Peters et al., 2019), which could lead to impoverished dung beetle communities and the loss of dung beetle-mediated ecosystem functions, such as dung removal. Larger dung beetles have been shown to be more extinction prone than smaller beetles (Braga et al., 2013; Larsen et al., 2005). Because of their huge importance in dung removal, the extinction of large dung beetles may have negative repercussions on other dung beetle-mediated ecosystem services such as nutrient cycling, secondary seed dispersal and parasite suppression (Klein, 1989; Slade et al., 2007), as well as on ecosystem functioning in general (Piccini et al., 2018). Especially large dung beetles are vulnerable to land use changes since they are more likely to overheat in open agricultural landscapes as compared to smaller beetles (Clusella Trullas et al., 2007). Because of these imminent threats, huge conservation efforts will be necessary to guarantee the continuity of diversity in the Mt. Kilimanjaro biodiversity hotspot (Mmbaga et al., 2017).

Presently, species together with their affiliated functions are disappearing at unparalleled pace (Woodward et al., 2005). Most studies exploring BEF relationships concentrate on mere taxonomic data without considering other aspects of biodiversity (Larsen et al., 2005). However, especially in the light of global change, the investigation of functional traits is paramount to gain better insight

into ecosystem functioning (Nunes et al., 2018). Only the incorporation of body size into our analysis made it possible to show the detrimental effects of excluding large dung beetles on ecosystem service provisioning.

In natural systems, it is difficult to disentangle the effects of climate and biodiversity on ecosystem functions as both are often correlated (Peters et al., 2019; van der Plas, 2019). Most studies to date that investigate the effects of climate and biodiversity on ecosystem functions focus on plants (e.g. Ratcliffe et al., 2017) and most are conducted as small-scale experiments, making inferences to natural system difficult (van der Plas, 2019). Here, in a natural setting along a broad environmental gradient, we illustrate that dung removal by dung beetles, a major ecosystem service, is mainly driven by a biodiversity-related functional trait, that is, body size, while climate-related factors are secondary as indirect predictors.

Currently, there is no consensus about the relative importance of species richness, abundance and functional traits as drivers of ecosystem services and the interplay between these three components of biodiversity has rarely been tested in the field (Gagic et al., 2015). Our study sheds light to this ongoing debate by illustrating that along broad-scale climatic gradients, functional traits such as body size are the main drivers of ecosystem services. In order to ensure the long-term stability of ecosystem service provisioning in the future (Manning et al., 2016; Piccini et al., 2018) it will be paramount to conserve intact, functionally diverse species communities.

AUTHOR CONTRIBUTIONS

Friederike Gebert, Marcell K. Peters and Ingolf Steffan-Dewenter developed the study; Friederike Gebert, Ingolf Steffan-Dewenter and Marcell K. Peters designed the study; Friederike Gebert collected the data; Friederike Gebert and Patrick Kronbach conducted taxonomic identification and measured traits, Friederike Gebert analysed the data with input from Marcell K. Peters; Friederike Gebert wrote the first version of the manuscript; all authors contributed to the final version of the manuscript and gave final approval for publication.

CONFLICT OF INTEREST

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.z08kprrgf (Gebert et al., 2022).

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SUPPORTING INFORMATION

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