MAMMALS AND DUNG BEETLES ALONG ELEVATIONAL AND LAND USE GRADIENTS ON MOUNT KILIMANJARO: DIVERSITY, TRAITS AND ECOSYSTEM SERVICES

Dissertation
zur Erlangung des naturwissenschaftlichen Doktorgrades
der Julius-Maximilians-Universität Würzburg

vorgelegt von
Friederike Gebert
geboren in Schwäbisch Gmünd

Würzburg 2019

This document is licensed under the Creative Commons Attribution-ShareAlike 4.0 International License (CC BY-SA 4.0):
http://creativecommons.org/licenses/by-sa/4.0 This CC license does not apply to third party material (attributed to another source) in this publication.

Submitted/Eingereicht am: 12.09.2019

Members of the Doctoral Committee/Mitglieder der Promotionskommission:

Chair/Vorsitzender: Prof. Dr. Markus Sauer

Referee/Gutachter: Prof. Dr. Ingolf Steffan-Dewenter

Referee/Gutachter: Prof. Dr. Owen Lewis

Defence/Promotionskolloquium: 06.11.2019

Receipt of Certificates/Doktorurkunde ausgehändigt am:

"In other studies you go as far as others have gone before you, and there is nothing more to know; but in a scientific pursuit there is continual food for discovery and wonder"

Mary Wollstonecraft Shelley

© Friederike Gebert, *Diastellopalpus monapoides*

TABLE OF CONTENTS

AFFIDAVIT

I hereby declare that my thesis entitled: **“Mammals and dung beetles along elevational and land use gradients on Mt. Kilimanjaro: diversity, traits and ecosystem services”** is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis. Furthermore I verify that the thesis has not been submitted as part of another examination process neither in identical nor in similar form. Besides I declare that if I do not hold the copyright for figures and paragraphs, I obtained it from the rights holder and that paragraphs and figures have been marked according to law or for figures taken from the internet the hyperlink has been added accordingly.

EHRENWÖRTLICHE ERKLÄRUNG

Hiermit erkläre ich an Eides statt, die Dissertation: „**Säugetiere und Dungkäfer entlang von Höhen- und Landnutzungsgradienten am Kilimandscharo: Diversität, funktionelle Merkmale und Ökosystemdienstleistungen**“, eigenständig, d. h. insbesondere selbstständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen, als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben. Ich erkläre außerdem, dass die Dissertation weder in gleicher noch in ähnlicher Form bereits in einem anderen Prüfungsverfahren vorgelegen hat. Weiterhin erkläre ich, dass bei allen Abbildungen und Texten, bei denen die Verwertungsrechte (Copyright) nicht bei mir liegen, diese von den Rechtsinhabern eingeholt wurden und die Textstellen bzw. Abbildungen entsprechend den rechtlichen Vorgaben gekennzeichnet sind sowie bei Abbildungen, die dem Internet entnommen wurden, der entsprechende Hypertextlink angegeben wurde.

Würzburg, den 12.09.2019

SUMMARY

Despite belonging to the best described patterns in ecology, the mechanisms driving biodiversity along broad-scale climatic gradients, like the latitudinal gradient in diversity, remain poorly understood. Because of their high biodiversity, restricted spatial ranges, the continuous change in abiotic factors with altitude and their worldwide occurrence, mountains constitute ideal study systems to elucidate the predictors of global biodiversity patterns. However, mountain ecosystems are increasingly threatened by human land use and climate change. Since the consequences of such alterations on mountainous biodiversity and related ecosystem services are hardly known, research along elevational gradients is also of utmost importance from a conservation point of view. In addition to classical biodiversity research focusing on taxonomy, the significance of studying functional traits and their prominence in biodiversity ecosystem functioning (BEF) relationships is increasingly acknowledged. In this dissertation, I explore the patterns and drivers of mammal and dung beetle diversity along elevational and land use gradients on Mt. Kilimanjaro, Tanzania. Furthermore, I investigate the predictors of dung decomposition by dung beetles under different extinction scenarios.

Mammals are not only charismatic, they also fulfil important roles in ecosystems. They provide important ecosystem services such as seed dispersal and nutrient cycling by turning over high amounts of biomass. In chapter II, I show that mammal diversity and community biomass both exhibited a unimodal distribution with elevation on Mt.Kilimanjaro and were mainly impacted by primary productivity, a measure of the total food abundance, and the protection status of study plots. Due to their large size and endothermy, mammals, in contrast to most arthopods, are theoretically predicted to be limited by food availability. My results are in concordance with this prediction. The significantly higher diversity and biomass in the Kilimanjaro National Park and in other conservation areas

underscore the important role of habitat protection is vital for the conservation of large mammal biodiversity on tropical mountains.

Dung beetles are dependent on mammals since they rely upon mammalian dung as a food and nesting resource. Dung beetles are also important ecosystem service providers: they play an important role in nutrient cycling, bioturbation, secondary seed dispersal and parasite suppression. In chapter III, I show that dung beetle diversity declined with elevation while dung beetle abundance followed a hump-shaped pattern along the elevational gradient. In contrast to mammals, dung beetle diversity was primarily predicted by temperature. Despite my attempt to accurately quantifiy mammalian dung resources by calculating mammalian defecation rates, I did not find an influence of dung resource availability on dung beetle richness. Instead, higher temperature translated into higher dung beetle diversity.

Apart from being important ecosystem service providers, dung beetles are also model organisms for BEF studies since they rely on a resource which can be quantified easily. In chapter IV, I explore dung decomposition by dung beetles along the elevational gradient by means of an exclosure experiment in the presence of the whole dung beetle community, in the absence of large dung beetles and without any dung beetles. I show that dung decomposition was the highest when the dung could be decomposed by the whole dung beetle community, while dung decomposition was significantly reduced in the sole presence of small dung beetles and the lowest in the absence of dung beetles. Furthermore, I demonstrate that the drivers of dung decomposition were depend on the intactness of the dung beetle community. While body size was the most important driver in the presence of the whole dung beetle community, species richness gained in importance when large dung beetles were excluded. In the most perturbed state of the system with no dung beetles present, temperature was the sole driver of dung decomposition. In conclusion, abiotic drivers become more important predictors of ecosystem services the more the study system is disturbed.

In this dissertation, I exemplify that the drivers of diversity along broad-scale climatic gradients on Mt. Kilimanjaro depend on the thermoregulatory strategy of organisms. While mammal diversity was mainly impacted by food/energy resources, dung beetle diversity was mainly limited by temperature. I also demonstrate the importance of protected areas for the preservation of large mammal biodiversity. Furthermore, I show that large dung beetles were disproportionately important for dung decomposition as dung decomposition significantly decreased when large dung beetles were excluded. As regards land use, I did not detect an overall effect on dung beetle and mammal diversity nor on dung beetle-mediated dung decomposition. However, for the most specialised mammal trophic guilds and dung beetle functional groups, negative land use effects were already visible. Even though the current moderate levels of land use on Mt. Kilimanjaro can sustain high levels of biodiversity, the pressure of the human population on Mt. Kilimanjaro is increasing and further land use intensification poses a great threat to biodiversity. In synergy wih land use, climate change is jeopardizing current patterns and levels of biodiversity with the potential to displace communities, which may have unpredictable consequences for ecosystem service provisioning in the future.

ZUSAMMENFASSUNG (GERMAN)

Gradienten der Biodiversität, wie der Breitengradient der Artenvielfalt, gehören zu den bestbeschriebenen Mustern in der Ökologie. Dennoch bleiben die Mechanismen, die diese Gradienten steuern, unzureichend untersucht. Bergmassive eignen sich aufgrund ihrer hohen Artenvielfalt, ihrer räumlichen Begrenzung, der gleichmäßigen Veränderung abiotischer Faktoren mit der Höhe und ihres weltweiten Auftretens optimal zur Erforschung der Triebkräfte globaler Biodiversitätsmuster. Jedoch werden Gebirgs-Ökosysteme vermehrt durch menschliche Landnutzung und den Klimawandel bedroht. Da der Wissenstand über die Auswirkungen solcher Veränderungen auf die Biodiversität von Bergmassiven und zugehörigen Ökosystemdienstleistungen gering ist, nimmt die Erforschung von Höhengradienten auch aus der Perspektive des Artenschutzes eine besondere Bedeutung ein. In Ergänzung zur traditionellen, auf Taxonomie beruhenden Biodiversitätsforschung, wird die Wichtigkeit der Untersuchung funktioneller Merkmale und deren Bedeutung für Beziehungen zwischen Biodiversität und Ökosystemfunktionen (BEF) zunehmend anerkannt. In meiner Doktorarbeit untersuche ich entlang von Höhen- und Landnutzungsgradienten am Kilmandscharo (Tansania) die Muster und Triebkräfte der Artenvielfalt von Säugetieren und Dungkäfern als auch die Faktoren, die den Dungabbau durch Dungkäfer unter verschiedenen Aussterbe-Szenarien bestimmen.

Säugetiere sind nicht nur charismatisch, sie nehmen auch wichtige Rollen in Ökosystemen ein. So erfüllen Säugetiere wichtige Ökosystemdienstleistungen wie die Verbreitung von Samen und sind maßgeblich am Nährstoffkreislauf durch den Umsatz großer Mengen von Biomasse beteiligt. Im zweiten Kapitel dieser Arbeit stelle ich dar, dass die Diversität und Biomasse der Säugetiergemeinschaft am Kilimandscharo eine unimodale Verteilung mit der Höhe aufweist. Dieses Muster wurde vor allem durch die Nettoprimärproduktion, ein Maß für die Nahrungsverfügbarkeit der Säugetiere, und den Schutzstatus der

Untersuchungsgebiete bestimmt. Aufgrund ihrer Größe und Endothermie kann man schlussfolgern, dass für Säugetiere, im Unterschied zu den meisten Arthropoden, Nahrungsverfügbarkeit die Triebkraft der Diversität darstellt. Meine Resultate bestätigen diese Vorhersage. Die signifikant höhere Diversität und Biomasse der Säugetiere im Kilmandscharo Nationalpark und in anderen geschützten Gebieten unterstreicht die Wichtigkeit des Habitatschutzes für den Erhalt der Artenvielfalt großer Säugetiere in tropischen Bergmassiven.

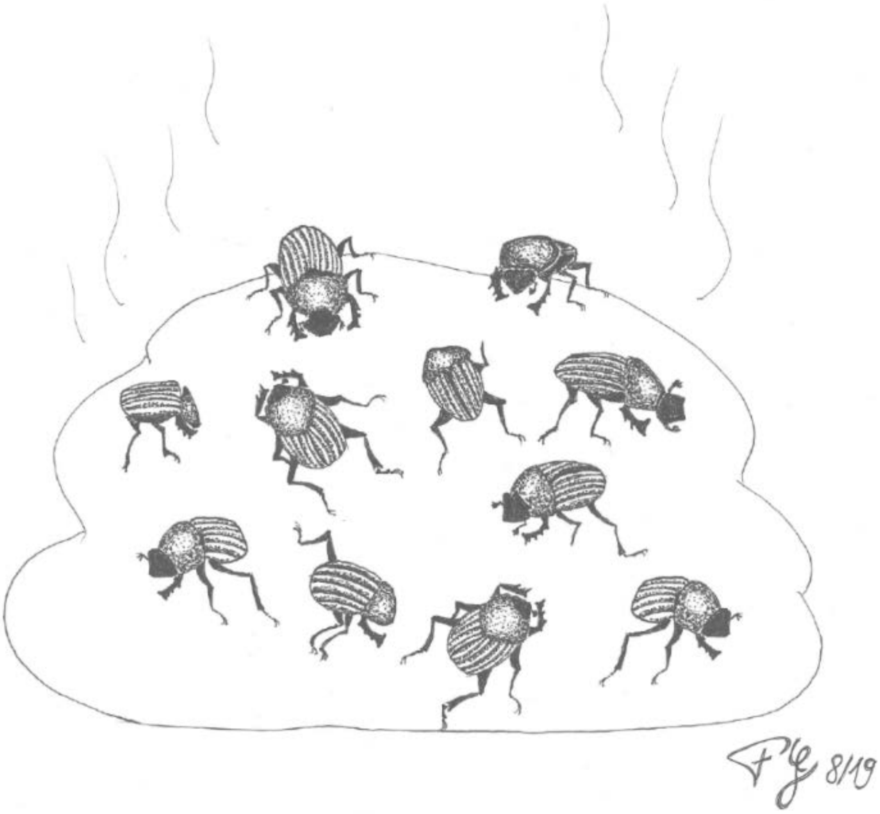
Dungkäfer stehen in enger Beziehung zu Säugetieren, da sie Säugetierdung als Nahrungs- und Nistmaterial benötigen. Dungkäfer übernehmen ebenfalls wichtige Ökosystemdienstleistungen: Sie spielen eine bedeutende Rolle im Nährstoffkreislauf und tragen entscheidend zur Bioturbation, der sekundären Verbreitung von Samen und der Unterdrückung von Schädlingen bei. Im dritten Kapitel weise ich nach, dass die Artenvielfalt der Dungkäfer mit der Höhe abnimmt, während die Abundanz der Käfer eine eingipfelige Verteilung zeigt. Im Unterschied zu den Säugetieren wurde die Diversität der Dungkäfer vor allem durch die Temperatur gesteuert. Obwohl ich versuchte, die vorhandenen Dungressourcen der Säugetiere möglichst genau durch die Berechung des Kotabsatzes zu quantifizieren, stellte ich keinen Einfluss von Ressourcenverfügbarkeit auf die Dungkäfer-Diversität fest. Stattdessen führte eine höhere Temperatur zu erhöhter Dungkäfer-Diversität.

Abgesehen von ihrer Rolle als wichtige Ökosystemdienstleister stellen Dungkäfer auch Modellorganismen für BEF-Studien dar, da sie eine leicht zu quantifizierende Ressource benötigen. Im vierten Kapitel untersuche ich den Dungabbau von Dungkäfern entlang des Höhengradienten mithilfe eines Ausschlussexperiments: in der Gegenwart der gesamten Dungkäfergemeinschaft, unter dem Ausschluss großer Dungkäfer und in der Abwesenheit aller Dungkäfer. Der Dungabbau war am größten, wenn der Abbau durch die gesamte Dungkäfergemeinschaft erfolgen konnte. Waren nur kleine Dungkäfer anwesend, waren die Dungabbauraten deutlich geringer als in der Gegenwart großer Dungkäfer, während sie im Falle des Ausschlusses aller Dungkäfer minimal wurden. Außerdem konnte ich nachweisen, dass die Triebkräfte des Dungabbaus von dem Zustand der Dungkäfergemeinschaft abhingen. Während die mittlere Körpergröße von Dungkäfern der wichtigste Faktor darstellte, wenn die Lebensgemeinschaft vollständig war, erlangte die Artenvielfalt an Bedeutung, wenn große Dungkäfer abwesend waren. Im gestörtesten Zustand des Systems, wo der Dungabbau ohne Dungkäfer erfolgte, war Temperatur der einzige Faktor, der den Dungabbau bestimmte. Abiotische Faktoren nehmen an Wichtigkeit als Triebkräfte von Ökosystemdienstleistungen zu, je mehr das System gestört ist.

Zusammenfassend wird in dieser Dissertation gezeigt, dass die Triebkräfte der Artenvielfalt entlang weitreichender klimatischer Gradienten am Kilimandscharo von der thermoregulatorischen Strategie der Organismen abhängen. Während die Diversität von Säugetieren vor allem durch die Nahrungsverfügbarkeit beeinflusst wurde, wurde die Dungkäfer-Diversität vor allem durch die Temperatur gesteuert. Außerdem sind geschützte Flächen für den Erhalt der Artenvielfalt großer Säugetiere unerlässlich. Weiterhin veranschauliche ich die herausragende Bedeutung großer Dungkäfer für den Dungabbau, da letzterer deutlich abnahm, wenn große Dungkäfer ausgeschlossen wurden. Betreffend der Landnutzung war insgesamt kein Einfluss auf die Dungkäfer- oder Säugetier-Diversität oder den Dungabbau durch Dungkäfer feststellbar. Anders sah es auf Ebene der am meisten spezialisierten trophischen Gilden der Säugetiere und funktionellen Gruppen der Dungkäfer aus: Hier waren bereits negative Auswirkungen sichtbar. Obwohl unter dem derzeitigen gemäßigten Ausmaß der Landnutzung am Kilimandscharo eine hohe Artenvielfalt aufrechterhalten werden kann, steigt der Druck durch das Bevölkerungswachstum, und eine zunehmende Intensivierung der Landwirtschaft stellt eine große Bedrohung für die Biodiversität dar. Im Zusammenspiel mit der Landnutzung gefährdet der Klimawandel das Niveau und die Verteilung der Biodiversität, mit dem Potential, Gemeinschaften von Organismen zu verdrängen, was unvorhersagbare Auswirkungen auf die Bereitstellung von Ökosystemdienstleistungen in der Zukunft haben könnte.

CHAPTER I

GENERAL INTRODUCTION



I.1 Patterns of global biodiversity

> “Among the scenes which are deeply impressed on my mind, none exceed in sublimity the primeval forests undefaced by the hand of man; […] no one can stand in these solitudes unmoved, and not feel that there is more in man than the mere breath of his body.”
>
> (Darwin 1862)

The fascination of biologists for the disparate distribution of biodiversity around the globe can be traced back to Charles Darwin, Alfred Russel Wallace and Alexander von Humboldt (Humboldt 1854, Darwin 1862, Wallace 1878). Probably the most pervasive pattern is the latitudinal diversity gradient with elevated species richness in the tropics and decreasing richness towards the poles (Hillebrand 2004). Despite being well-known, there is considerable controversy about the mechanisms driving the latitudinal diversity gradient and a unifying theory remains elusive until today (Willig & Presley 2013). In total, there are around 30 hypotheses trying to explain the latitudinal diversity gradient, many being controversial, specific or correlated to other hypotheses (Willig et al. 2003, Pontarp et al. 2018). Eventually, the latitudinal gradient in species richness is generated by historical, geographical, biotic, abiotic and stochastic processes (Willig et al. 2003).

Amongst the most topical hypotheses are the geographic area hypothesis, the productivity hypothesis, the ambient energy hypothesis, the Rapoport-Rescue hypothesis, the evolutionary speed hypothesis and the geometric constraints hypothesis (Willig & Presley 2013). The geographic area hypothesis is related to the species-area-theory and states that the highest species richness is found in the tropics since tropical regions are composed of more area than temperate regions due to the spherical nature of the globe (Rosenzweig 1995). Similarly, the productivity hypothesis or species – energy hypothesis is derived from the species-area-theory, suggesting that the tropics harbour the most productive ecosystems on earth as a consequence of receiving the highest amount of solar radiation, resulting in a positive relationship between productivity and species richness (Willig et al.

2003). The ambient energy hypothesis posits that physiological living conditions in the tropics are more amiable and less costly than at high latitudes where conditions are progressively more seasonal, harsh and variable (Rohde 1992). The Rapoport-rescue hypothesis asserts that species at high latitudes are characterized by large range sizes as a result of their broad climatic tolerances as an adaptation to the more variable climatic conditions. In contrast, tropical species show narrower distributional ranges and tolerances. The "rescue" part of the hypothesis implies that tropical species are prone to continuous dispersal into unfavourable habitat, thus raising species richness (Stevens 1989). The evolutionary speed hypothesis is based on the idea that increased temperatures in the tropics entail shorter generation times, a higher selection pressure and augmented mutation rates, resulting in higher rates of speciation (Rohde 1992). In contrast to the aforementioned hypotheses, the geometric constraints hypothesis is the only hypothesis which can be interpreted quantitatively and is not based on environmental gradients. This hypothesis suggests that the latitudinal gradient is the consequence of a mid-domain peak in species richness at the equator when species ranges are randomly distributed in a constrained domain, i.e. the earth, featuring hard boundaries, i.e. the poles (Colwell and Hurtt 1994).

Consensus has been reached that a pattern as complex as the latitudinal diversity gradient is most likely not caused by a single mechanism but that instead, many interrelated factors contribute to this gradient in biodiversity (Gaston 2000). However, not all taxa conform to the latitudinal diversity gradient. Noteworthy exceptions are parasitoid ichneumonid wasps, sawflies, braconids, ecto- and endoparasites, aphids, several groups of freshwater invertebrates, marine amphipods, procellariiforms as well as most aquatic plants (Gaston 2000, Willig et al. 2003).

I.2 Mountains: model systems for biodiversity research

> "The look of the mountains contributes no less than their form, their size, and the grouping of plants, nor less than the different species of animals […] in determining the character of a landscape and the general impression made upon man by the different zones of the earth."
>
> (Humboldt 1854)

From the lowlands to the highlands, mountains are characterised by fast successions of climates as well as of plant and animal communities. These impressive alterations have inspired the creation of numerous approved theories in ecology, such as island biogeography and the niche concept (Grytnes & McCain 2013). Indeed, the exploration of montane species richness patterns across the globe might be seminal in elucidating the driving forces of broad-scale patterns of biodiversity in general (Körner 2000b). In concordance with the latitudinal gradient in biodiversity, there is considerable debate about the mechanisms causing elevational gradients (Peters et al. 2016). Due to their limited spatial extents, the many separate ranges worldwide and the uniformity of change in abiotic factors along elevation, mountains offer ample opportunities for hypothesis-testing (Körner et al. 2017). Similar to the hypotheses explaining the latitudinal gradient, the most common hypotheses suggested for elevational gradients can be grouped into climatic, spatial, historical and biotic hypotheses (Grytnes & McCain 2013). Climatic hypotheses relate temperature, precipitation and productivity to elevational species richness patterns. Spatial hypotheses include area and the mid-domain effect, the former hypothesis states that the highest species richness should be found in the elevations encompassing the largest areas while the latter hypothesis can be equalled with the geometric constraint hypothesis for latitudinal gradients, suggesting that the highest species richness should be found at intermediate elevations. Biotic hypothesis comprise source-sink dynamics, habitat heterogeneity and variation in rates of biotic interactions (Grytnes & McCain 2013). The source-sink hypothesis supposes that ecotones act as species' sources, while the encompassing habitats act as species' sinks, also resulting in hump-shaped patterns of species richness because intermediate elevations gain sink populations from both low and high elevations, while the latter elevations only obtain species unidirectionally. Since the importance and kind of habitat heterogeneity is taxon-specific, general statements about the change of heterogeneity with elevation are challenging (Grytnes & McCain 2013). For example, forest bird species diversity in the Peruvian Andes has been shown to be related, amongst other factors, to canopy height and number of forest strata, which decreased with increasing elevation (Terborgh 1977).

I.3 Latitude versus elevation

Despite the many similarities between elevational and latitudinal gradients, there are also important differences. In contrast to the latitudinal diversity gradient with its almost universal decrease in species richness with increasing latitude, elevational gradients in diversity do not conform to such a consistent pattern. Instead, the shape of richness gradients along elevation varies depending on the study taxon (McCain & Grytnes 2010). Four main patterns of elevational gradients have been identified, the most common being a mid-elevational peak in species richness, followed by a decrease of species richness with increasing elevation (Rahbek 2005). The least common patterns include gradients with their highest diversity at a low plateau and gradients with their highest diversity at a midpeak following a low plateau (McCain & Grytnes, 2010). Non-volant small mammals show a virtually ubiquitous mid-elevational peak in species richness, whereas bats equally exhibit both mid-elevational peaks in diversity and decreasing diversity patterns with increasing elevation. Birds and reptiles feature all four richness patterns while salamanders and frogs indicate mid-elevational peaks and all four patterns, respectively (McCain & Grytnes 2010). No meta-analysis is yet available for elevational patterns displayed by insects and single studies show various patterns for diverse insect groups (McCoy 1990). Furthermore, due to their differing spatial scales – while entire latitudinal gradients extend over 10000 km, an entire elevational gradient hardly surmounts some kilometres – the importance of historical and ecological factors shaping latitudinal and elevational gradients probably varies (Rahbek 2005). Along elevational gradients, biotic factors are likely to be more important drivers of species richness patterns than along the large-scale latitudinal gradient, maybe accounting for the absence of a consistent elevational species richness pattern (Rahbek 2005). Moreover, as regards their evolutionary origin, contrasting hypotheses have been suggested for latitudinal and elevational gradients, respectively (Qian & Ricklefs 2016). While latitudinal gradients appear to have been shaped by the 'tropical niche conservatism hypothesis', elevational gradients in the tropics rather conform to the 'out of the tropics hypothesis' (Jablonski et al. 2006, Qian & Ricklefs 2016). The former hypothesis states that with increasing latitude, the clade age of species groups decreases and phylogenetic relatedness increases as tropical lineages retracted from high latitude habitats in the time of global cooling following the Eocene and were only sporadically capable to expand into high latitudes hereafter. Therefore, high latitudes are mostly inhabited by young, closely related clades. In contrast, the latter hypothesis assumes that along tropical elevational gradients, the clade age of species groups increases and phylogenetic relatedness decreases as species occurring at high elevations are derived from old clades that originated at low elevations. Young clades are mainly absent from high elevations as they more probably stem from low elevations due to the large area at low elevations and due to slow diversification rates at high elevations (Qian & Ricklefs 2016).

I.4 Climate change and land use: current threats to mountain biodiversity

In the light of global change, the conservation of tropical mountain ecosystems is of special importance as mountains harbour a disproportionate amount of biodiversity (Brooks et al. 2006). Even though mountains encompass only approximately 12 % of the terrestrial surface area, they are home to around 25 % of terrestrial biodiversity and comprise 50 % of the earth's biodiversity hotspots

(Spehn et al. 2010). Furthermore, mountains are indispensable for humans as about half of the population is dependent on clean water provided by mountain catchments (Messerli & Ives 1997). Despite the fact that mountain ecosystems are increasingly transformed by anthropogenic disturbances such as land use changes, the consequences of such perturbations on mountainous biodiversity are hardly known (Payne et al. 2017). Furthermore, mountain ecosystems are also affected by climate change, which may lead to biotic attrition in the lowlands and mountaintop extinctions (Colwell et al. 2008). Climate change may exacerbate the effect of land use on mountainous biodiversity (Peters et al. 2019). Therefore, it is pivotal to study the effects of land use and climate on tropical mountains, on their biodiversity and related ecosystem services.

I.5 Biodiversity – ecosystem functioning relationships (BEF)

As biodiversity today is threatened by a multitude of anthropogenic disturbances such as land use changes, overexploitation, invasive species, pollution and anthropogenic climate change (Barlow et al. 2018) and the consequences of impaired biodiversity on ecosystem service provision are not known (Gagic et al. 2015), it is pivotal to study biodiversity-ecosystem function relationships (BEF). While ecosystem functions comprise all ecosystem processes and their interactions in general, ecosystem services is a term used to describe ecosystem functions which are closely linked to human well-being (Quijas & Balvanera 2013). Ecosystem services can be divided into supporting (e.g. primary production, nutrient cycling, decomposition), provisioning (e.g. food, water), regulating (e.g. soil fertility, disease regulation) and cultural (non-material, e.g. recreational and aesthetical benefits) services (Millenium Ecosystem Assessment 2005). Nowadays, it is more and more realized that in addition to measuring traditional taxonomic metrics such as species richness and abundance, the incorporation of functional traits in BEF studies is important as functional traits have been shown to be superior in the prediction of ecosystem services and in making informed conservation decisions (Cadotte et al.

2011). Functional traits are quantifiable features of an organism that are related to its fitness and can be divided into effect functional traits and response functional traits. While effect traits support the functions an organism performs in an ecosystem, response traits control the reaction of organisms to environmental alterations (Naeem & Wright 2003). As regards BEF studies, response traits are probably most substantial in evaluating an organism's performance ensuing environmental disruptions (Naeem & Wright 2003). One of the most important functional traits is body size, being connected to many life-history traits and determining energetic demands and metabolic rates (Brown et al. 2004). Body size can act as both an effect and a response trait since large species are predicted to be disproportionately functionally important and more extinction prone than smaller species (Larsen et al. 2005).

I.6 Study system

In this dissertation, I was interested in exploring the diversity of endothermic and ectothermic organisms as well as a related ecosystem service. In chapters II and III of this study, I explore the patterns and drivers of mammal and dung beetle diversity along broad-scale climatic gradients on Mt. Kilimanjaro, respectively, while I investigate the predictors of dung decomposition by dung beetles in chapter IV. I chose mammals as endothermic study organisms because of their high diversity and their immense functional importance in ecosystems. Mammals provide ecosystem services such as pollination, seed dispersal and regulation of insect populations (Jones & Safi, 2011). Furthermore, by turning over high amounts of biomass, mammals are central for nutrient cycling and energy flow (Veldhuis et al. 2018). Many mammals are keystone species whose functions cannot be supplied by other species (Power et al. 1996), such as the maintenance of habitat heterogeneity by large herbivores (Lacher et al. 2019). Moreover, mammals are often used as flagship and umbrella species for conservation (Andelman and Fagan 2000). In chapter II, data on the distribution of mammals on Mt. Kilimanjaro was obtained from camera traps (Figure I.1) and from systematic transect walks to report mammalian tracks and faeces.

As an ectothermic group, I chose dung beetles since they are closely related to mammals and since they are important ecosystem service providers (Hanksi and Cambefort 1991). Dung beetles constitute a model taxon for biodiversity – ecosystem functioning relationships, primarily because they fulfil the basic requirement of BEF studies, which is the dependence on a clearly defined resource. Dung beetles rely on mammalian dung as a food and nesting resource for both larvae and adults. Mammalian dung is a versatile resource for BEF studies, since it occurs in ephemeral resource patches which can be replicated, manipulated and sampled easily (Slade et al. 2007).

Figure I.1: Camera trap for monitoring mammals. Photo © Gebert

Furthermore, dung beetles comprise an ideal focal taxon as they can be sampled efficiently according to standardized protocols, they are a taxonomically amenable group, have a wide geographic distribution, display graded responses to environmental disturbances, show correlations with other taxa such as mammals and are of huge ecological and economic importance (Hanksi & Cambefort 1991, Spector 2006). Dung beetles provide ecosystem services such as nutrient cycling, bioturbation, parasite suppression and secondary seed dispersal (Nichols et al. 2008) and their economic value has been estimated to be worth 380 M/year in the US cattle industry alone (Losey & Vaughan 2006). In chapter III, I sampled dung beetles with pitfall traps and used both human and cow dung as baits (Figure I.2). In chapter IV, I focus on dung decomposition by dung beetles since this central service is linked to virtually all other ecosystem services provided by dung beetles. Here, my aim is to explore the factors impacting dung decomposition along an extensive elevational gradient between the poles of species abundance and diversity, functional traits and climate variables.

Figure I.2: Pitfall traps for collecting dung beetles. The upper picture shows a pitfall trap baited with human dung, the lower picture a trap baited with cow dung. Photos © Gebert

1.7 Context of study

This dissertation was conducted within the framework of the KiLi Project (Kilimanjaro ecosystems under global change: Linking biodiversity, biotic interactions and biogeochemical ecosystem processes), a research unit funded by the DFG (FOR1246). The research objectives of this multidisciplinary unit were centred on investigating the impacts of climate change and anthropogenic perturbations on biodiversity and ecosystem processes along elevational and land use gradients on Mt. Kilimanjaro, Tanzania, the highest free-standing mountain in the world.

Mt. Kilimanjaro encompasses a northwest-southeast diameter of 90 km and covers elevations from the savanna habitats at its base at 700 m a.s.l. to the summit at 5895 m a.s.l.. The climate at Mt. Kilimanjaro is a typical equatorial day-time climate, which is due to its location 300 km south of the equator. There are two rainy seasons: the long rains between March and May and the short rains in November. The temperature on the mountain declines linearly with altitude at approximately 6.1° C for each 1000 m of elevation. Mean annual temperature (MAT) spans around 25 °C in the savanna to -8 °C at the top of the mountain. Mean annual precipitation (MAP) has a hump-shaped distribution on Mt. Kilimanjaro, peaking at 2700 mm and an approximate altitude of 2200m a.s.l. (Appelhans et al. 2016). The KiLi project has established 66 study plots on the southern slopes of Mt. Kilimanjaro along an elevational gradient from 870 to 4550 m a.s.l.. The study plots comprise all 6 natural and 7 anthropogenic habitats that can be found on the mountain (Figure I.3). Each study plot covers an area of 0.25 ha (50 x 50 m) and each habitat type is represented by 5 to 6 study plots. The natural habitats include 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.). The anthropogenic habitats comprise maize fields (866 – 1009 m a.s.l.), grasslands (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.) and burned *Podocarpus* (2770 – 3060 m a.s.l.) and *Erica* forests (3500 – 3880 m a.s.l.).

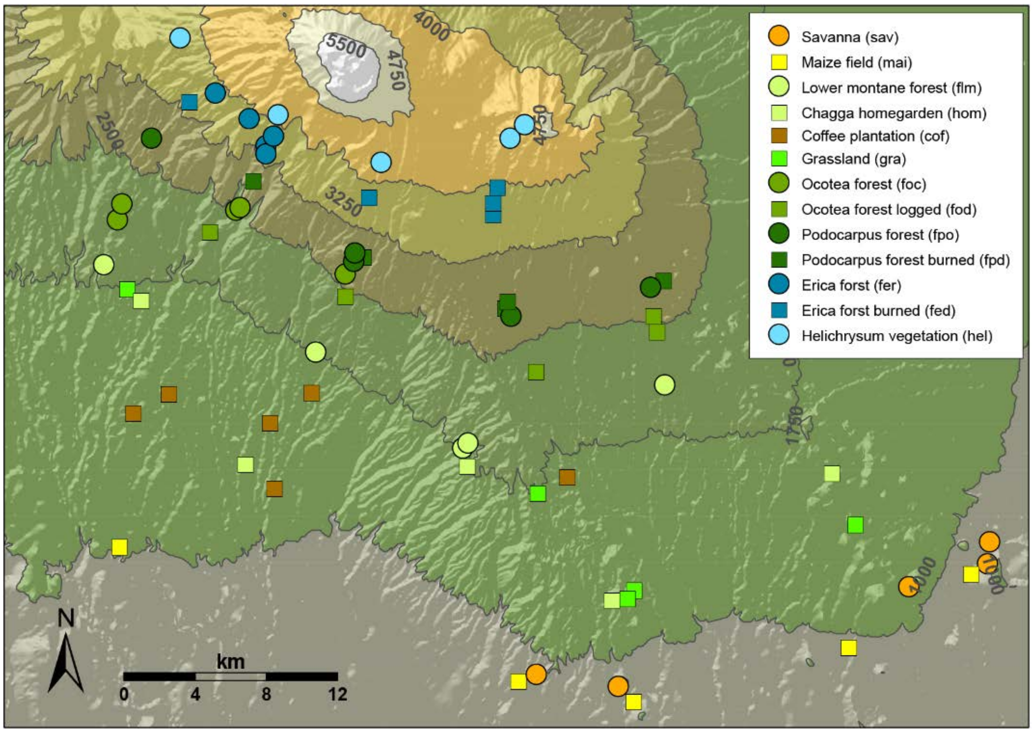
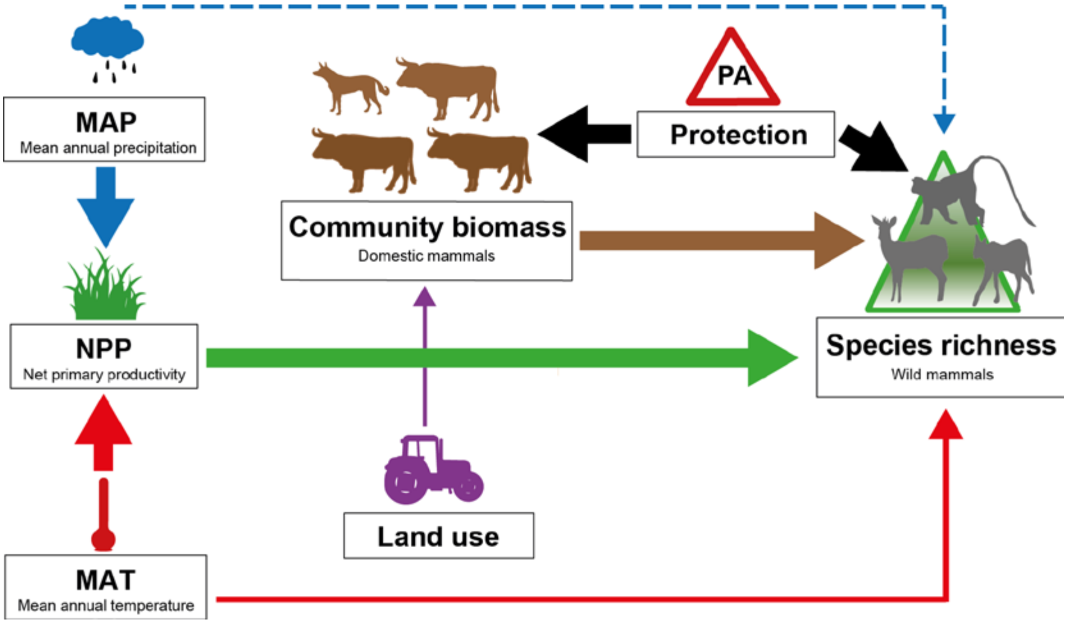


Figure I.3: The 66 study plots selected by the KiLi Project on Mt. Kilimanjaro. Graphic © Jie Zhang

CHAPTER II

PRIMARY PRODUCTIVITY AND HABITAT PROTECTION PREDICT ELEVATIONAL SPECIES RICHNESS AND COMMUNITY BIOMASS OF LARGE MAMMALS ON MT. KILIMANJARO



Despite their diversity and their large functional and cultural importance, the patterns and predictors of large mammal diversity along elevational gradients on tropical mountains remain poorly understood. Today, large mammals are threatened by human disturbances such as habitat destruction and hunting and may increasingly depend on the conservation of protected areas. Here, we use field data on the diversity of large mammals along a 3.6 km elevational gradient on Mt. Kilimanjaro to evaluate the importance of climate, net primary productivity and human impact for the distribution, species richness and community biomass of wild mammals. Mammal species richness was explored with camera traps on 66 study plots along an elevational gradient from 870 to 4550 m a.s.l.. We applied path analysis and variance partitioning analysis to unravel the direct and indirect effects of temperature, precipitation, primary productivity, land use, land area, the protection of habitats and the occurrence of domestic mammals on the diversity of wild mammals. Both species richness and community biomass of wild mammals showed a unimodal distribution with elevation, peaking in the montane zone of Mt. Kilimanjaro. However, the peak shifted significantly to lower elevations when only protected habitats were considered. Wild mammal diversity increased with net primary productivity, protection of habitats and temperature. Our study underscores the importance of energy resources for the establishment of diversity gradients in large mammals. While temperature has been revealed as a direct predictor of diversity in most ectothermic taxa, in endothermic organisms temperature has stronger indirect effects, via a modulation of net primary productivity. Moreover, our study reveals how patterns of diversity on tropical mountains are influenced by human impact, pointing to the pivotal role of protected areas for the long-term conservation of mountain biodiversity.

II.1 Introduction

Elevational gradients in species richness are well depicted in ecology, yet there is no consensus about their major predictors (Rahbek 1995, Peters et al. 2016, Beck et al. 2017). A range of deterministic hypotheses have been suggested highlighting the influence of energy availability, climatic factors and history on biodiversity gradients (Pianka 1966, McCain 2007, Brown 2014). However, it is often unclear how such environmental factors operate, affecting species richness patterns either directly or indirectly, which hampers predictions on the influence of environmental changes on biodiversity (Classen et al. 2015).

Amongst the most supported predictors of species richness are temperature and the availability of energy resources (Mittelbach et al. 2007, Hurlbert & Stegen 2014). The 'temperature-richness hypothesis' predicts that temperature restricts species' occurrence by imposing physiological constraints and by influencing ecological and evolutionary processes (Belmaker & Jetz 2015). The 'energy-richness hypothesis', in contrast, states that in ecosystems that are highly productive, resources are predicted to be so abundant that more and larger populations are able to prevail than in less productive ecosystems (Hurlbert & Stegen 2014). Other hypotheses used for explaining gradients in species richness are the 'water availability hypothesis' and the 'area hypothesis'. The 'water availability hypothesis' assumes that access to water is limiting species richness, either via a direct dependence of species on water sources, or via energy-related effects such as the positive effect of precipitation on net primary productivity (Hawkins et al. 2003). The 'area hypothesis' rests on the idea that larger areas can sustain larger and more viable populations and offer more opportunities for allopatric speciation than smaller areas (Rosenzweig 1995, Romdal & Grytnes 2007).

Despite their fascinating diversity, and their large functional and cultural importance, little is known about the patterns and predictors of large mammal diversity along elevation gradients. Research on the distribution of mammal diversity on mountains has until now focused on small mammals (mostly on

Insectivora, Rodentia with body weights of 2 g – 5 kg), which nearly exclusively show unimodal distributions of elevational diversity (e.g. Brown 2001, McCain 2005, but see Di Bitetti et al. 2013, Ferreira de Pinho et al. 2017). In contrast, research on large mammals along altitudinal gradients has been scarce. Large mammals are of high ecological importance and are often used as flagship-species for conservation (Williams et al. 2000). They play a crucial role in controlling ecosystem processes such as nutrient cycling and energy flow by turning over high amounts of biomass (Veldhuis et al. 2018). Meta-analyses suggest that large mammals are particularly threatened by the loss of natural habitats and hunting (Hegerl et al. 2017). Of the known 5488 mammal species, 25 % have been categorized as threatened or extinct by the 2008 IUCN Red List (IUCN 2018). Four hundred fourteen of the 4086 non-volant placental mammal species listed in the panTHERIA data base can be categorized as large (body weight > 10 kg; Jones et al. 2009, Bogoni et al. 2016), of these, 184 (44 %) are categorized as at least "vulnerable" (IUCN 2018).

Here, we investigated the species richness of large mammal communities and its potential predictors along an elevational gradient spanning 3600 m and encompassing all major natural and anthropogenic habitats of the southern slopes of Mt. Kilimanjaro, Tanzania (Peters et al. 2019). Tropical mountains are ideal model systems to understand the factors driving biodiversity. They exhibit extreme climatic gradients at small spatial scales, which permit standardized, unbiased biodiversity assessments in differing environments. However, tropical mountains are under pressure by increasing human impact (Nogués-Bravo et al. 2008). Due to the high sensitivity of large mammal species to human impact, the occurrence of large mammals on mountains may strongly depend on the intensity of land use and the existence of large protected areas in mountain ecosystems. Large mammals are particularly vulnerable to extinction because of their body size (Davidson et al. 2009).

Most studies on elevational biodiversity focus on patterns of species richness although the utilization of mere taxonomic data may limit the predictive strength of assemblage studies (Fountain-Jones et al. 2015). The assessment of functionally relevant traits such as body mass may contribute to a more mechanistic understanding of the predictors of diversity and of the changes in mammal-mediated ecosystem functions (Storch 2012). Biomass is probably the single, most important characteristic of individuals and communities, which defines metabolic rates, energetic demands, and the susceptibility of animals to human impact (Brown et al. 2004).

Here, we unravelled the direct and indirect effects of climate, energy availability, area, and human impact on the species richness and biomass of wild mammals. We analysed the following predictions:

1. The biodiversity and community biomass of wild mammals is positively correlated to net primary productivity (NPP). At Mt. Kilimanjaro, NPP has a unimodal distribution with a peak at 2500 m (Peters et al. 2016). Due to their size and endothermic metabolism, large mammals have very high energetic demands, which limit population sizes and constrain the number of species which can coexist in local communities (Buckley et al. 2012).
2. Mammal species richness and community biomass is constrained by climate. Temperature and precipitation may influence species richness indirectly, through their influence on net primary productivity, or directly by influencing metabolic costs for endothermy (Buckley et al. 2012), filtering species from unsuitable climates (i.e. from extremely dry or cold elevations), or by a positive influence of temperature on speciation rates (Mittelbach et al. 2007). If mammal diversity followed the temperature gradient, we would expect a decline of mammal diversity with increasing elevation. If mammal diversity was correlated with the precipitation gradient on Mt. Kilimanjaro, we would expect a unimodal distribution as
3.

precipitation reaches its peak at approximately 2200 m (Appelhans et al. 2016).

4. Mammal species richness decreases with the decline in land area with increasing elevation. Smaller areas of land harbour fewer resources, less solar energy, less refugia and a lower habitat diversity than larger areas which may limit the number of individuals and species which can coexist (Lomolino 2001).
5. Mammal communities are influenced by human impact on mountains. We expect species richness and community biomass of wild mammals to be higher in protected than in unprotected areas. Additionally, we expect that the species richness of mammals decreases with increasing land use intensity and with the occurrence of domestic mammals (Di Bitetti et al. 2013).

II.2 Materials and methods

II.2.1 Study area

The study was carried out on Mount Kilimanjaro (2°54'-3°25'S, 37°0'-37°43'E) in northern Tanzania. Mt. Kilimanjaro is situated 300 km south from the equator and encompasses an elevational range from 700 m to 5895 m a.s.l.. The mountain is exposed to an equatorial day-time climate with two apparent rainy seasons: a long rainy season from around March to May and a short rainy season around November. Temperature decreases linearly with elevation at approximately 6.1 °C per 1000 m of elevation from about 25 °C at 870 m a.s.l. to -8 °C at the summit. Mean annual precipitation is unimodally distributed with a peak of ~2700 mm at around 2200 m a.s.l. (Appelhans et al. 2016).

Research was conducted on 66 study plots established in the framework of the KiLi project (research project of the German Research Foundation, DFG research unit FOR 1246) on the southern slopes of Mt. Kilimanjaro (Peters et al. 2016). The study plots ranged from near the base of Mt. Kilimanjaro at 870 m to 4550 m a.s.l.

and were equally distributed among the 13 major natural and anthropogenic habitat types in the region (5-6 study plots per habitat type). Each study plot covered an area of 0.25 ha. Natural habitats included 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 consisted of 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.) and burned *Podocarpus* (2770 – 3060 m a.s.l.) and *Erica* forests (3500 – 3880 m a.s.l.). 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). The five study plots per habitat type were distributed amongst differing elevations to reflect a within-habitat type elevational transect to detect fine scale changes in biodiversity with changing elevation. Spatial distances among study plots were larger than 300 m in all cases. If possible, study plots were established in core zones of larger areas of the respective habitat type, so that effects of transition zones were minimized. All study plots above 1800 m a.s.l., which were situated inside Mt. Kilimanjaro National Park, and additionally two lowland savanna sites, located in wildlife conservation areas, were classified as ‘protected’. All other study plots were classified as ‘unprotected’ (Supplementary Information Appendix II.S1).

II.2.2 Climate and Net Primary Productivity (NPP)

Study plots were equipped with temperature sensors installed approximately 2 m above the ground (Appelhans et al., 2016). The sensors measured temperatures in 5-min intervals over two years and mean annual temperature (MAT) was calculated as the average across all measurements per study plot (Appelhans et al. 2016). Mean annual precipitation (MAP) was collected with a network of about 70 rain gauges distributed over all habitat types and elevations on Mt. Kilimanjaro (Appelhans et al. 2016). We used the normalized difference vegetation index (NDVI) as a surrogate for net primary productivity (Detsch et al. 2016b, Peters et al. 2016). NDVI estimations were exclusively based on MODIS Aqua product MYD13Q1 with a horizontal resolution of 250 m x 250 m (Appelhans et al. 2016). More methodological details and original data are presented in Detsch et al. (2016), Appelhans et al. (2016) and Peters et al. (2016).

II.2.3 Monitoring of mammals

Mammal monitoring was carried out from May to September 2016 with a combination of camera trapping and standardized transect-based indirect observations on mammalian dung (Trolle et al. 2008). Five camera traps (Bushnell Trophy Cam HD Essential, model 119736) were installed (within a distance of 50 m) on each of the 66 study plots. Cameras were placed along trails or at animal latrine sites to increase the chance of mammal detection. The camera traps were left in the field for a duration of 14 days at each plot, amounting to 70 trap nights per plot and 4620 trap nights in total. Camera traps were activated through a motion sensor. After activation, the cameras were programmed to take videos of a length of 20 seconds, with a minimum interval of 10 seconds between sequences. At night, cameras operated with infrared light. For each plot, two videos of the same mammal were only considered to be independent shots if there was a time lapse of > 1 h between them. This so-called hourly event count is widely used to minimize the possibility of counting dwelling individuals numerous times (Hegerl et al. 2017). In addition to camera traps, systematic transect walks were conducted to document mammalian faeces. Each study plot was divided into 25 parallel transects, 2 m apart and with a length of 50 m. The observer walked all transects and recorded faeces located within a strip of 1 m each to the left and right from each transect. Transect walks were performed twice on each plot, once at the time of installing camera traps and once at the end of the experiment. We planned surveys in a way that study plots from each habitat type were equally distributed over the study period and that always four to five study plots from different elevations / habitat types were simultaneously surveyed. Faeces were identified using Stuart & Stuart (2000) while data on the corresponding mammal species' body weight and trophic guild was taken from Kingdon et al. (2013) and Kingdon (2015). In case of sexual dimorphism, we calculated the average body weight across sexes. On each study plot, species richness was obtained by counting the number of all species recorded by the five camera traps and by the systematic monitoring of faeces. Community biomass was computed by summing up the body weight of the individuals of all species across hourly event counts. For calculating community biomass, we only considered camera trap samples. Please note that the way we measured community biomass provides an estimate, which can only be evaluated relative to the estimates at other sites but not as an absolute measure of the community biomass. In addition to wild mammals, we also documented domestic mammals by means of camera trapping and transect walks.

II.2.4 Statistical analysis

To check the completeness of sampling of mammal communities we estimated asymptotic species richness from abundance data using a non-parametric species richness estimator (Chao 1; Colwell & Coddington 1994, Gotelli & Colwell 2011), calculated sampling coverage, and correlated observed species richness to the Chao 1-estimated diversity using Pearson correlations. Moreover, using data on the observed elevational ranges of species we calculated the total number of occurring mammal species for elevational bands of 250 m and compared elevational richness patterns to those detected from the study plot-based data.

The distribution of species richness and the community biomass of wild mammals (hereafter termed mammal community biomass) and trophic subgroups (herbivores, omnivores, carnivores) along the elevational gradient was examined with generalized additive models (GAMs). GAMs were conducted jointly for all mammals and separately for the three trophic guilds herbivores, omnivores and carnivores. Rather than designating a specific functional formula to the relationship between the response and explanatory variables, in GAMs, non-parametric smoothers are employed to characterize potential nonlinear or linear relationships between explanatory and response variables. GAMs were computed applying the 'gam' function from the R package 'mgcv' (Wood 2006). In case of species richness, we set the data family of GAMs to 'Poisson' and selected a log-link function. We checked for signs of overdispersion in the data but did not detect strong deviations from a Poisson distribution. For community biomass as the response variable we employed the Gaussian family. Due to the extreme variation in the data, biomass data was log-transformed (log (x +1)) prior to analyses. For both species richness and community biomass, the basis dimension of the smoothing term (k) was set to five to prevent over-parameterization of GAMs.

For each response variable we, first, constructed a model including elevation (continuous) and land use type (factorial: natural versus anthropogenic [combined variable of agricultural and disturbed habitat]) as interacting explanatory variables (using the 'by' command of the GAM function) which computes individual trend lines for each land use type. Using a backward selection approach we successively removed the interaction term, land use type or elevation as explanatory variables from models in case their significance level was $p > 0.1$. As we detected a significant effect of protected natural areas on all response variables in path analyses (see below), we additionally ran and visualized GAMs based on a data set including study plots situated in protected natural areas only.

Applying path analysis, we disentangled the direct and indirect effects of climate, net primary productivity (NPP), land area, land use, protection status, and the presence of domestic animals on the species richness and community biomass of wild mammals. As climate variables, both MAT and MAP were considered while for land use, we employed the factor levels natural, agricultural and disturbed. In contrast to the GAMs where we displayed elevational trends for anthropogenic and natural habitats, for path analysis, we employed three levels of land use to get a more differentiated result of land use effects.

Due to the overall low number of mammal species we conducted path analyses only for total mammal species richness and community biomass but not for single trophic guilds. We hypothesized that NPP along the elevational gradient is positively influenced by changes in mean annual temperature and mean annual precipitation (Peters et al. 2016). We also expected a negative impact of land use on NPP. Finally, we assumed that the community biomass of domestic mammals is positively influenced by land use (i.e. more animals on disturbed and agricultural plots than on natural plots), negatively by the protection status of study plots (i.e. less domestic animals in protected habitats) and positively by NPP. For the community biomass of wild mammals as the final response variable, the same model structure with the same response and explanatory variables as for species richness were used. Both the community biomass of domestic mammals and the community biomass of wild mammals was log-transformed (log (x+1)) prior to analyses.

As a first step before the actual path analysis, we pre-selected potential path combinations by defining for each response variable a set of competitive explanatory models using multi-model inference based on the Akaike information criterion (AIC). Due to a rather low sample size in comparison to the number of estimated parameters we used the AIC_c with a second-order bias correction for inferring the support of individual models. The ‘dredge’ function of the R package ‘MuMIn’ was applied to assess the AIC_c for the full model with all explanatory variables and for all nested models including the null model. All models within the range of $\Delta AIC_c < 3$ were considered for path analyses. Based on the set of best models we calculated for each explanatory variable the variable importance which is defined as the sum of the Akaike weights of all best-fit models which include the respective explanatory variable. The pre-selection of a set of competitive explanatory variables was conducted in order to limit the set of potential path models to a feasible number of most likely models and to increase the sample/parameter ratio of the path models.

We then used all pre-selected models to perform formal path analysis. Since species richness data of wild and domestic mammals followed a Poisson distribution, it was not possible to use statistical applications for path analysis which presume normally distributed data. Instead, we performed piecewise structural equation modelling (SEM) on the basis of the d-sep test for all best supported models ($\Delta AIC_c < 3$) with the ‘sem.fit’ function of the R package ‘piecewiseSEM’ (Shipley 2013, Lefcheck 2016). ‘PiceweiseSEM’ tests all combinations of explanatory variables for each response variable against all combinations of explanatory variables of the other response variables. For each path model, the AIC_c was calculated and the path model with the lowest AIC_c was selected as the best model (Shipley 2013). While we concentrated inference on the best selected path model, we documented all paths of competing path models ($\Delta AIC_c < 3$) in path diagrams. To assess whether path coefficients were significant and positive or negative, the ‘sem.coefs’ function was employed. This function offers the option to obtain standardized path coefficients. R^2- values were allocated to response variables with the ‘rsquared’ function. Since p-values obtained by path analysis for single factors are conditional on the presence of other factors in the model, we also tested the unique effect of all predictors on both species richness and community biomass of large mammals (Supplementary Information Appendix II.S2).

To complement path analysis, we performed variance partitioning analysis using the ‘varPart’ function of the R package ‘modEvA’ (Barbosa et al. 2016). The ‘varPart’ function only allows for the comparison of the unique and shared proportions of variance explained by three factor groups. We conducted variance partitioning with the factors that were significant in path analysis and combined variables into the three factor groups: NPP, 'human impact’ – including land use, protection status and domestic mammals – and ‘climate’, consisting of MAT and

MAP. To further elucidate the relationship between NPP and the two climate variables, we also conducted variance partitioning separately for MAT and MAP. We performed variance partitioning for both species richness and community biomass of wild mammals on GLMs with Poisson or Gaussian error family, respectively, using the pseudo-R^2-values obtained from the GLMs.

II.3 Results

II.3.1 Elevational patterns of species richness and community biomass

We recorded a total of 38 non-volant mammal species with 1601 video records and 178 dung samples (Figure II.1, Supplementary Information Appendix S3). Thirty-three species were wild mammals while the remaining five species were domestic mammals. Nineteen species were recorded with camera traps only, four were only present in dung samples and 15 species were documented using both camera traps and dung samples. Twenty-four of the 33 wild mammal species (73 %) were listed in the IUCN category of "least concern", three species (9 %: Eastern Tree Hyrax *Dendrohyrax validus*, Lesser Kudu *Tragelaphus imberbis*, Plains Zebra *Equus quagga burchelli* were listed as "near threatened", one species (Leopard *Panthera pardus*) was listed as "vulnerable", and one species (Abott's Duiker *Cephalophus spadix*) was listed as "endangered" (Figure 1, IUCN, 2016). The most common species was the Common Duiker *Sylvicapra grimmia hindei*, which was recorded at 31 of 66 study plots (Figure II.1, II.2), followed by the Zanzibar Syke's Monkey *Cercopithecus nicticans albogularis*, Figure II.1, II.2) and the Abbott's Duiker, which occurred on 19 and 13 plots, respectively (Figure II.1, II.2).

Figure II.1 Screenhsots of wild mammals on Mt. Kilimanjaro identified with cameras and mammalian dung. From upper left to lower right corner: Common Duiker *Sylvicapra grimmia hindei*, Zanzibar Syke's Monkey *Cercopithecus nicticans albogularis*, Abott's Duiker *Cephalophus spadix*, Leopard *Panthera pardus* (only faeces were recorded), Plains Zebra *Equus quagga burchelli* (only faeces was recorded), Lesser Kudu *Tragelaphus imberbis*.

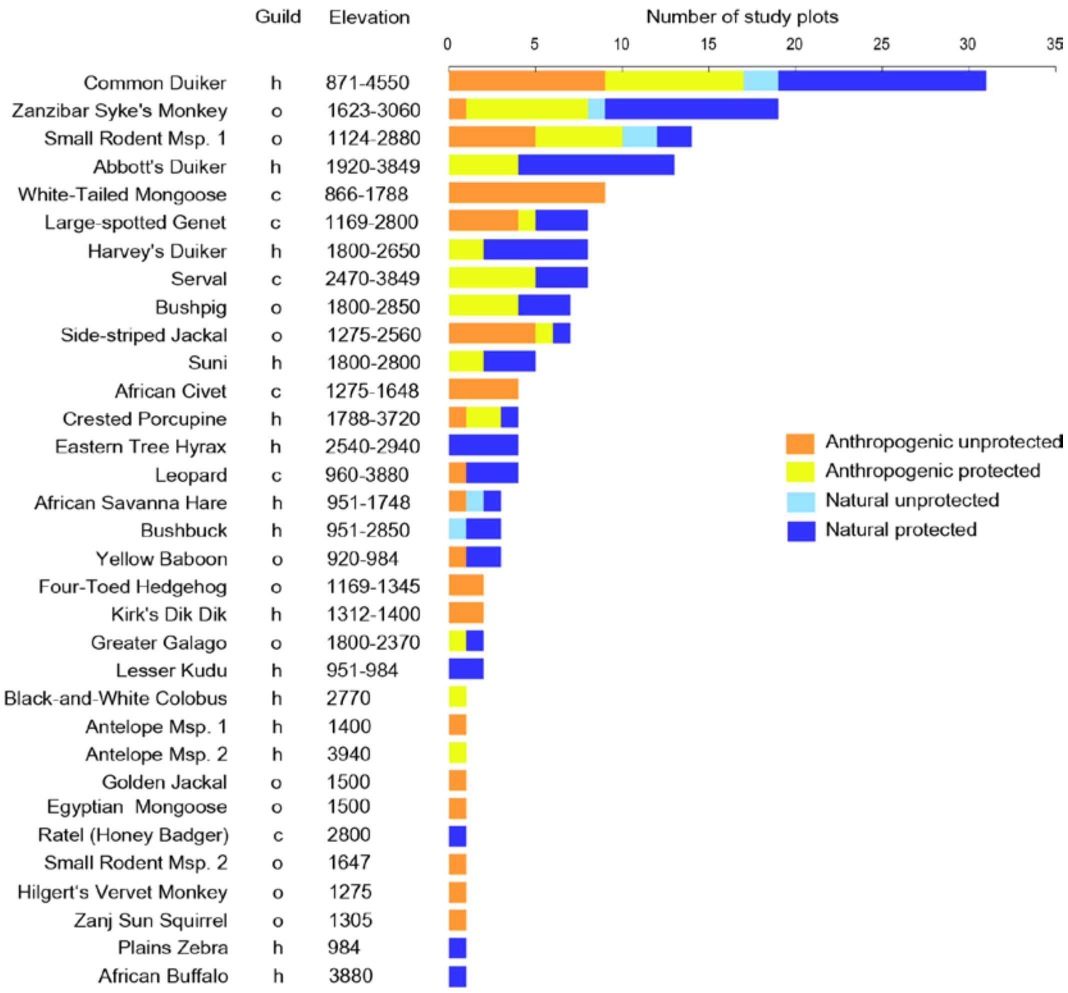


Figure II.2 Occurrence of wild mammals on the study plots on Mt Kilimanjaro recorded with camera traps and transect walks. Not shown are the 5 recorded domestic mammal species (Domestic Cat, Domestic Dog, Cattle, Sheep, Domestic Goat). The abbreviatons in the column "guild" refer to the trophic guilds h = herbivore, o = omnivore and c = carnivore. The elevational range of each species is given in m a.s.l.. Study plots are subdivided into natural and anthropogenic sites that are either classified as protected or not protected.

Species richness of wild mammals along the elevational gradient was unimodally distributed, with a peak in montane forests at mid elevations and no significant differences between natural and anthropogenic habitats (Figure II.3a, orange and blue dotted line, explained deviance (ED) = 20.1 %, $p_{\text{Elevation}} < 0.05$). However, if only study plots in protected natural areas were considered, the peak of the elevational diversity distribution shifted from elevations of ca. 2500 m to ca. 1500 m a.s.l., forming a low-elevation plateau pattern (Figure II.3a, dashed blue line, ED = 27.2 %, $p_{\text{Interaction}} < 0.05$). The observed species richness was highly correlated with Chao 1 estimated asymptotic species richness ($r = 0.93$, $p < 0.001$, Supplementary Information Appendix II.S4). Pooled species richness calculated for elevational bands of 250 m along the gradient also showed a unimodal pattern very similar to the one found for observed species richness on study plots (Figure II.4). A unimodal pattern similar to that of the species richness of all mammals was found for omnivores (Figure II.3c, ED = 48.8 %, $p_{\text{Elevation}} = 0.07$). In herbivores, species richness monotonically decreased with elevation in natural habitats but increased in anthropogenic habitats (Figure II.3b, ED = 19.2 %, $p_{\text{Interaction}} < 0.05$). For carnivores, no significant species richness trend with elevation could be detected (Figure II.3d, $p_{\text{Elevation}} = 0.44$).

The community biomass of wild mammals exhibited a unimodal distribution along the elevational gradient with no difference between natural and anthropogenic habitats (Figure II.3e, ED = 17.6 %, $p_{\text{Elevation}} < 0.05$). In herbivores, the pattern of community biomass along the elevation gradient mirrored the pattern of species richness with a higher biomass in natural habitats at low and mid elevations than in anthropogenic habitats (Figure II.3f, ED = 21.5 %, $p_{\text{Interaction}} < 0.05$). For omnivores, community biomass declined with elevation in natural habitats while there was a hump-shaped pattern in anthropogenic habitats (Figure II.3g, ED = 30.4 %, $p_{\text{Interaction}} = 0.055$). Protected natural areas showed a higher community biomass at low and mid elevations than unprotected areas (all mammals: Figure II.3e: ED = 18.8 %, $p_{\text{Interaction}} < 0.05$; herbivores: b: ED = 28 %, $p_{\text{Interaction}} < 0.001$; omnivores: c: ED = 41.3 %, $p_{\text{Interaction}} < 0.05$). The pattern was similar when all protected habitats (i.e. both natural and anthropogenic habitats) were considered (Supplementary Information Appendix II.S5). This result was largely driven by the mammal species with large body weight like the Lesser Kudu, which were regularly present in protected natural areas but absent from unprotected areas (Supplementary Information Appendix II.S6). For carnivores, at low elevations, community biomass was higher in anthropogenic habitats than in natural habitats (Figure II.3h, ED = 8.97 %, $p_{\text{Interaction}} = 0.09$).

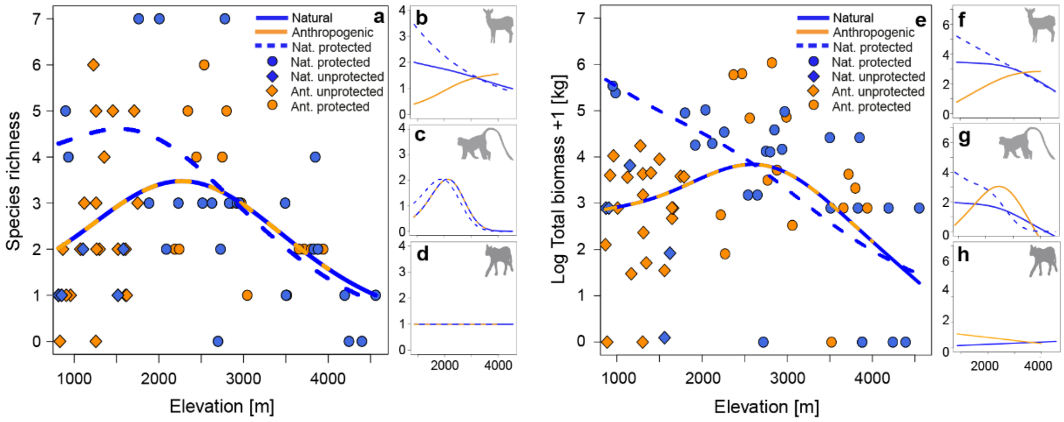


Figure II.3 Patterns of species richness and community biomass of wild mammals along the elevational gradient on Mt. Kilimanjaro. Shown are trends for all mammals (a, e) and patterns for individual trophic guilds: herbivores (b, f), omnivores (c, g) and carnivores (d, h). Trend lines for natural habitats are displayed in blue whilst trend lines for anthropogenic habitats are shown in orange. Dashed blue lines depict trends for natural habitats that were situated in protected areas. Trend lines were computed applying generalized additive models [Poisson family, basis dimension (k) = 5]. In (a) and (e), dots and diamonds depict original measurements on study plots. Natural habitats are subdivided into protected habitats (blue dots) and non-protected habitats (blue diamonds). Accordingly, anthropogenic habitats are subdivided into unprotected habitats (orange diamonds) and protected habitats (orange dots). In (a), (c), (d) and (e), the dashed blue and orange lines represent same trend lines for natural (blue) and anthropogenic (orange) habitats.

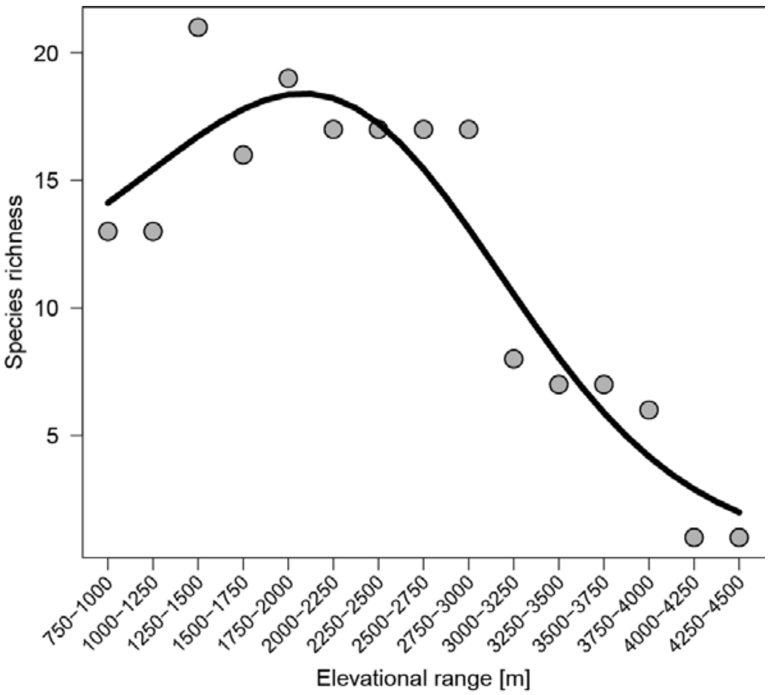


Figure II.4: Total number of species richness found in elevational bands of 250 m of elevation. The trend line was computed applying a generalized additive model [Poisson family, basis dimension (k) = 5].

II.3.2 Predictors of species richness and community biomass

For both species richness and community biomass of wild mammals, NPP and the protection status were the most important explanatory variables in path analysis (Figure II.5b, c) and their effect was consistently supported in all best models (Supplementary Information Appendix II.S7) and simple bivariate regression analysis (Supplementary Information Appendix II.S2). Species richness of wild mammals increased with net primary productivity (NPP) and was higher in protected natural habitats than in unprotected habitats (Figure II.5b). The best supported path models also implied positive direct effects of mean annual temperature (MAT) and the community biomass of domestic mammals on wild mammal species richness and community biomass (here only MAT was in the path model) but their effects were not consistently supported in competing models and bivariate regression analysis (Supplementary Information Appendix II.S2, II.S7).

The species richness of wild mammals was positively correlated to the community biomass of wild mammals ($r = 0.56$, $p < 0.001$).

Variance partitioning analysis mainly corroborated the results obtained with path analyses. The variable with the highest proportion of explained variance was human impact for both species richness and community biomass of wild mammals (16 % and 19 %, respectively; Figure II.6a, d). The shared variance between NPP and climate was the second strongest fraction (14 % and 11 %, respectively; Figure II.6a, d). The unique proportion of explained variance by climate and NPP was lower (climate: 3 % and 9 %, respectively; NPP: 8 % and 2 %, respectively; Figure II.6a, d). The rather low unique proportion of explained variance by NPP in variance partitioning analysis is related to the strong additive effect of MAT and MAP on NPP: When only MAT was considered instead of the combined climate variable, the proportion of variance explained uniquely by NPP increased for both species richness and community biomass of wild mammals (16 % and 7 %, respectively, Figure II.6b, e). When only regarding MAP as a climate variable, the sole contribution of NPP increased accordingly (21 % and 17 % for species richness and community biomass of wild mammals, respectively; Figure II.6c, f). As regards species richness of wild mammals, NPP rose to the factor with the highest proportional variance for both MAT and MAP (Figure II.6b, c). Concerning community biomass of wild mammals, MAT explained more variance than NPP (9 % and 7 %, respectively; Figure II.6e) and in the case of MAP, NPP constituted again the strongest fraction (Figure II.6f).

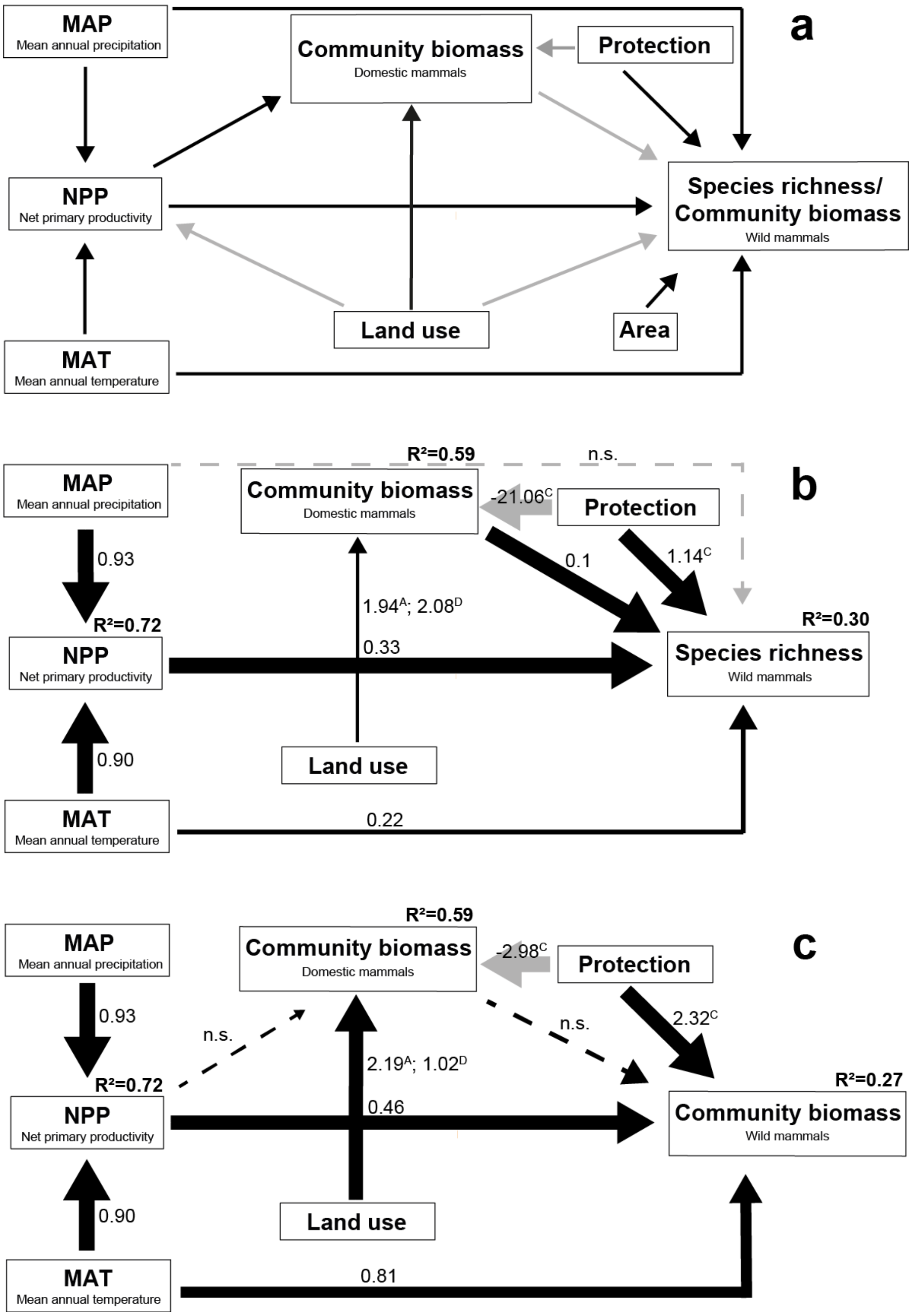


Figure II.5 Predictors of species richness and community biomass of wild mammals on Mt. Kilimanjaro. Black and grey lines represent positive and negative effects, respectively. Numbers above paths represent standardized path coefficients. The best path model with the lowest AIC_c is displayed with solid lines. The relative amount of explained variance (R^2, deduced from the best supported path model) is shown for all response variables. Dashed lines depict potential paths included in competing paths models (all path models with $\Delta AIC_c < 3$) but eliminated from the final path model. Non-significant paths are designated with 'n.s'. Arrow width indicates variable importance (specified as the sum of the Akaike weights of all best-fit models which include the respective explanatory variable) for each explanatory variable. (a) Expected path model showing anticipated effects of explanatory variables on species richness and community biomass of wild mammals. (b) Predictors of wild mammal species richness (best path model: $AIC_c = 41.54$). (c) Predictors of community biomass of wild mammals (best path model: $AIC_c = 42.85$). Please note that land use (three levels: natural, agricultural, disturbed, the latter two can be summarized as anthropogenic) and protection status (protected, unprotected) are factorial variables such that path coefficients are not standardized. ^{C} Explanatory variable is a factor, ^{A} Agricultural plots, ^{D} Disturbed plots.

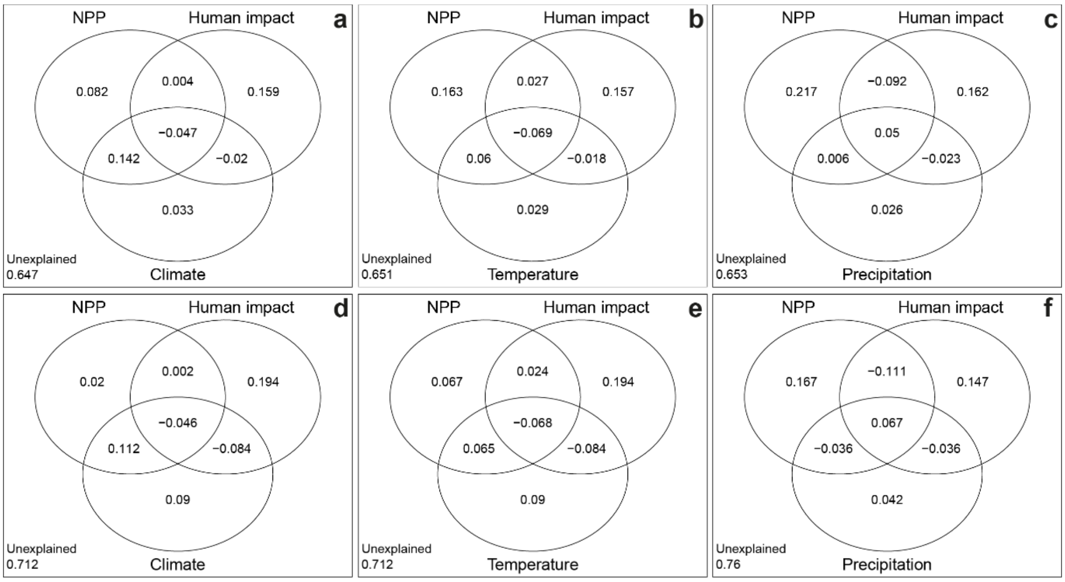


Figure II.6: Variance partitioning analysis for species richness (a, b, c) and community biomass (d, e, f) of wild mammals. (a) and (d) show the unique and shared proportions of explained variance for all explanatory variables that were significant in the path analysis ('human impact' includes land use, protection status and domestic mammals while 'climate' consists of MAT and MAP). (b) and (e) show the proportions of explained variance for the sole variable 'temperature' instead of the 'climate' variable for species richness (b) and community biomass of wild mammals (e), respectively. Accordingly, (c) and (f) show the proportions of explained variance for the variable 'precipitation' instead of the 'climate' variable. The proportions of explained variances and the unexplained variance add up to one. Negative interactions signify independence of factors.

II.4 Discussion

In this study, we showed that wild mammal species richness and community biomass displayed a unimodal distribution with elevation on Mt. Kilimanjaro, a pattern which remarkably reflects the nearly universal unimodal diversity gradient observed in small mammals along elevation gradients (McCain 2005). Mammal species richness increased with NPP and was positively influenced by protected areas. The number of species per study plot was low in relation to the total number of species, probably a result of high rates of turnover. On Mt. Kilimanjaro, the elevational gradient changes from open habitats (savanna) at the base of the mountain to forested habitats at mid- elevations to open alpine *Helichrysum* shrub vegetation at high elevations. As most species are either open habitat or forest specialists, this will lead to a high turnover along the elevation gradient, which has also been observed in other vertebrate taxa like birds (Ferger et al. 2017). The high turnover is mirrored in the small elevational ranges of most mammals on Mt. Kilimanjaro. Accordingly, only the Common Duiker occurs over the whole elevational gradient. Our data suggests that the unimodal distribution of wild mammals is largely influenced by human impact at low elevations. In protected natural habitats mammal diversity was high even in the lowlands and the pattern of elevational diversity consequently more strongly resembled a lower plateau pattern (McCain & Grytnes 2010).

To the best of our knowledge, this is the first study which combines data on the elevational diversity of large mammals with detailed tests of multiple macroecological hypothesis for explaining diversity gradients.

II.4.1 Net primary productivity as a predictor for endothermic species richness

Species richness and community biomass of wild mammals were predicted by net primary productivity (NPP), the protection status of study plots, and climate. The unique contribution of NPP was small while the combined effect of NPP and climate amounted to approximately 15 % of the explained variation. However, when considering MAT and MAP separately instead of the combined climate variable, the proportion of variance explained uniquely by NPP increased for both species richness and community biomass of wild mammals, underscoring the dependence of NPP on MAT and MAP and highlighting the importance of NPP as a factor which is driving mammal diversity. In accordance with the energy-richness hypothesis (Currie et al. 2004), both wild mammal species richness and community biomass peaked at around 2500 m a.s.l. in the lower forest belt, an elevation which approximately coincidences with the highest amount of NPP along the elevational gradient on Mt. Kilimanjaro (Peters et al. 2016). This finding suggests that productive ecosystems with high amounts of resources can sustain communities with higher species richness and larger biomass than less productive ecosystems. In contrast to ectothermic organisms, for which tight correlations between temperature and species richness are often detected (Classen et al. 2015, Peters et al. 2016), endotherms appear to be more strongly depending on resource availability (Buckley et al. 2012). In accordance with these findings, Ferger et al. (2014) showed that for birds, another group of endothermic organisms, species richness on Mt Kilimanjaro was best explained by the availability of food resources. The energy-richness hypothesis (Currie et al. 2004, Storch 2012) is also supported by the strong correlation between species richness and biomass / abundance of wild mammals on Mt. Kilimanjaro. The effect of NPP supports the view that food resources are a key factor limiting the number of coexisting large mammal species along tropical elevation gradients.

II.4.2 The importance of climate and domestic mammals

In addition to the effect of NPP, we found a positive effect of temperature on wild mammal species richness and community biomass, both direct and indirect via primary productivity, which probably accounts for the large combined effect of NPP and climate. Temperature is a critical factor for endotherms, setting limits of species' distributional ranges (Fernández & Vrba 2005). At low temperatures, there are increased metabolic costs for endotherms which may result in reduced population densities (Buckley et al. 2012).

In addition, we expected the presence of domestic mammals to have a negative effect on wild mammals, either directly via competition for the same resources and space, or indirectly via the transmission of diseases (Pryke et al. 2016). However, we found a positive effect of the community biomass of domestic mammals on the species richness of wild mammals. This effect was unexpected and may be due to the relatively high species richness of omnivorous wild mammals in the cultivated zone, where most domestic mammals are found.

Overall, the variance explained by our models for species richness and community biomass of wild mammals was rather low. One reasons for this could be that other predictors of mammal richness were not considered in the study. For example, there could be spatial variation in hunting pressure on Mt. Kilimanjaro, which we could not measure appropriately in the field. Moreover, despite a high sampling completeness in the study period, seasonal migrations of mammals may occur which may have increased or decreased species richness and community biomass on some plots in the study period and thus increased variation in the data. Future studies conducted over longer periods, ideally over the whole year, could account for seasonal differences of animal activity.

II.4.3 Implications for conservation

In protected habitats, both species richness and community biomass of wild mammals were higher than in unprotected areas (Jones et al. 2019). In unprotected habitats, large mammals are particularly vulnerable to losses through hunting, either through bush meat hunting or retaliatory killing for crop losses (Schipper et al. 2008). As a result, the species richness, abundance and body size of wild mammals is often lower in unprotected than in protected habitats (Kinnaird & O'Brien 2012). Compared to the protection status of study plots, the impact of land use on the species richness and the biomass of large mammals was low. One reason for the small influence of land use on wild mammal diversity might be that at low elevations, the landscape on the mountain is still characterized by a diverse farmland mosaic consisting of small fields of different cropping systems used for subsistence farming and of semi-natural habitat and forest remnants in between (Mmbaga et al. 2017), which may sustain a rather high diversity of mammals. For most large mammals with large home ranges, the landscape mosaic may be more important than the features of single study plots, potentially obscuring the observed richness pattern. Nevertheless, increasing agricultural intensification at the local and landscape scale with the augmented use of pesticides and heavy machinery poses a growing threat to the maintenance of biodiversity on the mountain (Newmark & IUCN Tropical Forest Programme 1991). Interestingly, the effect of land use and the protection status of study plots differed between trophic guilds. Herbivores were the only guild which was negatively affected by land use, evident mainly on mid and low elevation sites. In contrast to herbivores, the richness and biomass of omnivores was barely influenced by human land use activities, a pattern which was also found by Kinnaird & O'Brien (2012). Carnivores were the guild with the fewest detected species in this study, which might have been a reason why we observed no significant trend in species richness or biomass with elevation and human impact. Commonly, carnivores are expected to show both lower species diversity and smaller body sizes in anthropogenically modified landscapes

(Kinnaird & O'Brien 2012). A reason for this discrepancy with the expected patterns could be that the monitoring applied in our study was not intense enough to adequately measure the distribution of carnivores, which typically occur at very low densities. We suspect that increases in monitoring intensity would lead to better estimates of carnivore species richness on study plots, reduced variation and clearer trends along gradients of elevation and human impact.

We recorded 29 (70 %) of the 41 large mammal species reported to occur on the southern slopes of Mt. Kilimanjaro in 1995 (Grimshaw et al. 1995). Ten of the 12 species we did not detect were restricted to lower elevations (Supplementary Information Appendix S8), and may have become rare due to an increase in land use. As four of the undetected species were arboreal, we consider the patterns which we found to be representative for ground-dwelling mammals. Other species which we did not detect were either extremely rare or not recorded since 1995. The documented high presence of the Abbott's Duiker in the forests of Mt. Kilimanjaro National Park is worth a special note, since hitherto the distribution of this endangered antelope on Mt. Kilimanjaro was hardly known. Our results suggest that Mt. Kilimanjaro could be, apart from the Udzungwa Mountains (Bowkett et al. 2014), a second population stronghold of this species.

II.5 Conclusions

Our study shows that there is not a single factor influencing mammal diversity and community biomass along an extensive elevational gradient. Rather, net primary productivity, habitat protection and climate variables determine elevational diversity of large mammals on tropical mountains. We could show that whilst most of the variance in species richness and community biomass of wild mammals remained unexplained, human impact contributed the highest proportion of explained variance, with its effect on richness and community biomass of wild mammals being independent of that of climate and NPP. The latter two factors combined constituted the second strongest fraction of explained variance. In conclusion, these results show that both anthropogenic impacts and climatic / productivity processes are driving mammal species richness and community biomass.

Our data confirmed that more mammal species, particularly those of large body size, are able to persist in protected than in unprotected areas (Ferreira de Pinho et al. 2017). Due to their high significance as keystone and umbrella species (Caro 2010), the loss of large mammals from unprotected areas is probably connected to changes in the structure of species communities and a decline of ecosystem functions (Dirzo et al. 2014). Therefore, the maintenance and expansion of protected areas will be of vital importance for the conservation of the diverse mammal fauna of Mt. Kilimanjaro and other mountains.

Data accessibility

The data that support the findings of this study are documented and archived in the PANGAEA database at: https://doi.pangaea.de/10.1594/PANGAEA.903710 (Gebert et al. 2019b).

II.6 Supplementary Information

Appendix II.S1 Ecosystem types on Mt. Kilimanjaro

Supplementary Table II.S1 Ecosystem types studied on Mt. Kilimanjaro. The 66 study plots were located in six natural and seven anthropogenic habitats (further subdivided into agricultural and disturbed habitats) along an elevational gradient of 3679 m. While there was no human impact in natural habitats, there was low to high land use intensity in anthropogenic habitats.

habitat	# plots	type	elevation[1]	intensity	protection
savanna	5	natural	871-1153	none	protected (2)
maize fields	5	anthropogenic (agri.)	866-1009	high	unprotected
lower montane forest	5	natural	1560-2020	none	unprotected
Chagga agroforestry	5	anthropogenic (agri.)	1169-1788	high	unprotected
coffee plantations	6	anthropogenic (agri.)	1124-1648	high	unprotected
grasslands	5	anthropogenic (agri.)	1303-1748	high	unprotected
Ocotea forest	5	natural	2120-2750	none	protected
logged *Ocotea* forest	5	anthropogenic (dist.)	2220-2560	low	protected
Podocarpus forest	5	natural	2800-2970	none	protected
burned *Podocarpus* f.	5	anthropogenic (dist.)	2270-3060	low	protected
Erica forest	5	natural	3500-3900	none	protected
burned *Erica* forest	5	anthropogenic (dist.)	3500-3880	low	protected
Helichrysum	5	natural	3880-4550	none	protected

Note:[1] Elevation is shown in m a.s.l.

Appendix II.S2 Single predictors

Supplementary Table II.S2 Effect of single predictors on species richness/community biomass of wild mammals. For species richness of mammals, glms with poisson family, for community biomass, glms with Gaussian family were computed.

predictor	Pseudo-R^2	p
MAP	0.06/0.04	**0.03***/0.12
MAT	0.001/0.002	0.74/0.74
Domestic	0.001/0.01	0.77/0.44
Protection	0.03/0.05	0.12/**0.058***
Land use	0.006/0.015	>0.05/>0.05
NPP	0.18/0.09	<**0.001*/0.02***
Area	0.0003/0.002	0.87/0.75

Note. Bold numbers depict significant results

Appendix II.S3 Mammals on Mt. Kilimanjaro

Supplementary Table II.S3 Recorded mammal species on Mt. Kilimanjaro. Animal body weight is shown in kg, elevation in m a.s.l.

Order	Family	Common Name	Species	Trophic Guild	Weight	Records	Plots	Elevation
Hyracoidea	Procaviidae	Eastern Tree Hyrax	*Dendrohyrax validus*	herbivore	2.75	15	4	2540-2940
Primates	Galagonidae	Small-eared greater Gallago #	*Otolemur garnetti panganiensis*	omnivore	0.8	3	2	1800-2370
	Cercopithecidae	Yellow Baboon #	*Papio cynocephalus*	omnivore	18.63	10	3	920-984
		Hilgert's Vervet Monkey #	*Chlorocebus pygerythrus hilgerti*	omnivore	5.18	33	1	1275
		Zanzibar Sykes's Monkey #	*Cercopithecus nicticans albogularis*	omnivore	5.73	46; 7	19	1623-3060
		Black-and-White Colobus #	*Colobus guereza caudatus*	herbivore	9.23	1	1	2770
Rodentia	Sciuridae	Zanj Sun Squirrel	*Heliosciurus undulatus*	omnivore	0.32	3	1	1305
		Sciuridae sp. 1	Rodentia sp. 1*	omnivore	0.1	1	1	1124-2880
		Sciuridae sp. 2	Rodentia sp. 2*	omnivore	0.1	95; 3	14	1647
	Leporidae	African savanna Hare	*Lepus victoriae*	herbivore	2.31	6; 7	3	951-1748
	Histricidae	Crested Porcupine	*Hystrix cristata*	herbivore	19.5	7	4	1788-3720
Eulipotyphla	Erinaceidae	Four-toed Hedgehog	*Atelerix albiventris*	omnivore	0.93	10	2	1169-1345
Carnivora	Felidae	Serval #	*Leptailurus serval*	carnivore	9.75	6; 7	8	2470-3849
		Leopard #	*Panthera pardus*	carnivore	55	3; 3	4	960-3880
		Domestic Cat #	*Felis catus*	carnivore	4,05	35	7	866-1788
	Herpestidae	Egyptian Mongoose #	*Herpestes ichneumon*	omnivore	3.15	2	1	1500
		White-tailed Mongoose	*Ichneumia albicauda ibeana*	carnivore	3.6	37	9	866-1788
	Viverridae	African Civet #	*Civettictis civetta*	carnivore	13.5	11	4	1275-1648
		Large-spotted Genet	*Genetta maculata*	carnivore	2.35	15	8	1169-2800

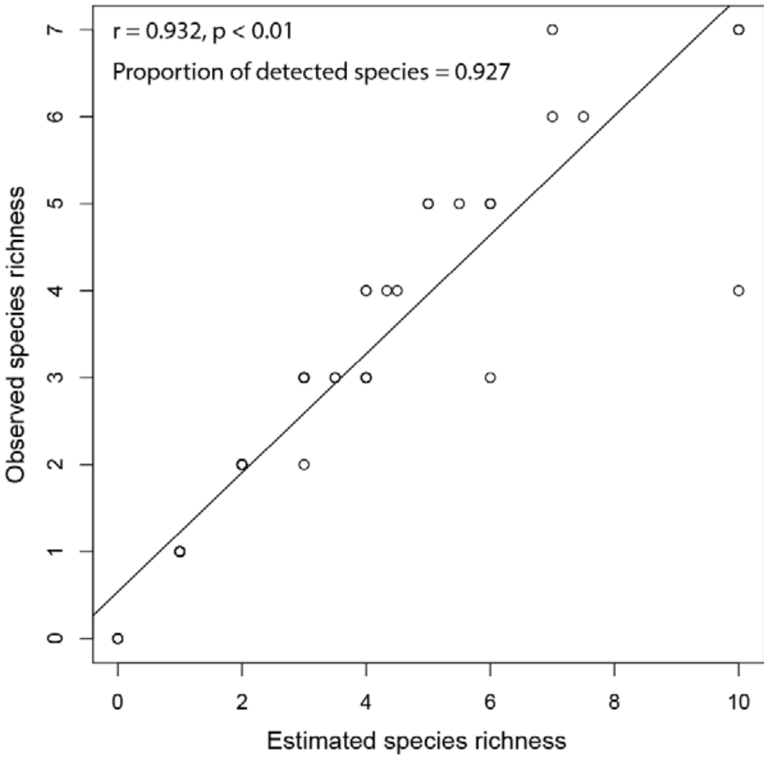
	Canidae	Side-striped Jackal #	*Canis adustus*	omnivore	9.65	29	7	1275-2560
		Golden Jackal #	*Canis aureus*	omnivore	10.5	4	1	1500
		Domestic Dog #	*Canis lupus familiaris*	carnivore	15	206;4	17	866-1788
	Mustelidae	Ratel (Honey Badger) #	*Mellivora capensis*	carnivore	9.85	1	1	2800
Perissodactyla	Equidae	Plains Zebra #	*Equus quagga boehmi*	herbivore	241.8	0; 1	1	984
Artiodactyla	Suidae	Bushpig	*Potamochoerus larvatus daemonis*	omnivore	97.5	16; 6	7	1800-2850
	Bovidae	Harvey's Duiker	*Cephalophus harveyi*	herbivore	14.5	54; 7	8	1800-2650
		Abbott's Duiker	*Cephalophus spadix*	herbivore	55	73; 15	13	1920-3849
		Common Duiker #	*Sylvicapra grimmia hindei*	herbivore	17.1	102; 37	31	871-4550
		Suni	*Nesotragus moschatus*	herbivore	5	202; 11	5	1800-2800
		Kirk's Dik-Dik #	*Madoqua kirkii*	herbivore	5.5	2; 3	2	1312-1400
		Bovidae sp. 1	Bovidae sp. 1*	herbivore	17.1	0; 1	1	1400
		Bovidae sp. 2	Bovidae sp. 2*	herbivore	17.1	0; 3	1	3940
		Bushbuck #	*Tragelaphus scriptus*	herbivore	42	4	3	951-2850
		Lesser Kudu #	*Tragelaphus imberbis*	herbivore	81.5	14	2	951-984
		African Buffalo #	*Syncerus caffer*	herbivore	637.5	0; 1	1	3880
		Cattle #	*Bos spp.*	herbivore	385	127; 49	10	920-2800
		Sheep #	*Ovis aries*	herbivore	45	32; 3	6	920-3510
		Domestic Goat #	*Capra aegagrus hircus*	herbivore	20	396;10	5	920-1788

Note. The first number listed under records depicts the number of animals on videos shot of each species with an interval of 1 hour between consecutive videos; the second number represents the number of dung pats for species where dung was present. Plots imply the number of study plots on which each species was recorded. Elevation shows the elevational range of the study plots on which species were present.

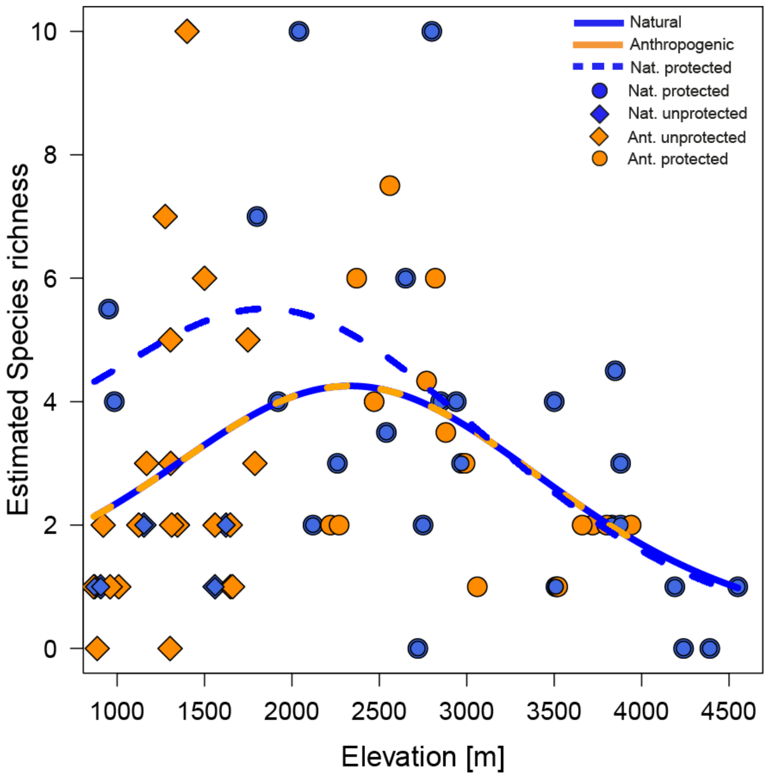
# Denotes species with sexual dimorphism. In the case of the African Civet, the Common Duiker, and Kirk's Dik Dik, the female is larger than the male. In all other cases, males are heavier than females. Species were characterized as dimorphic if the size difference between sexes was larger than 10% (Lindorfs et al. 2007).

*Amongst the wild mammals sampled with camera traps, two small rodents could only be identified to morphospecies level while there were dung samples of apparently two small antelopes which could not be further identified and were therefore designated as morphospecies.

Appendix II.S4 Species richness estimations

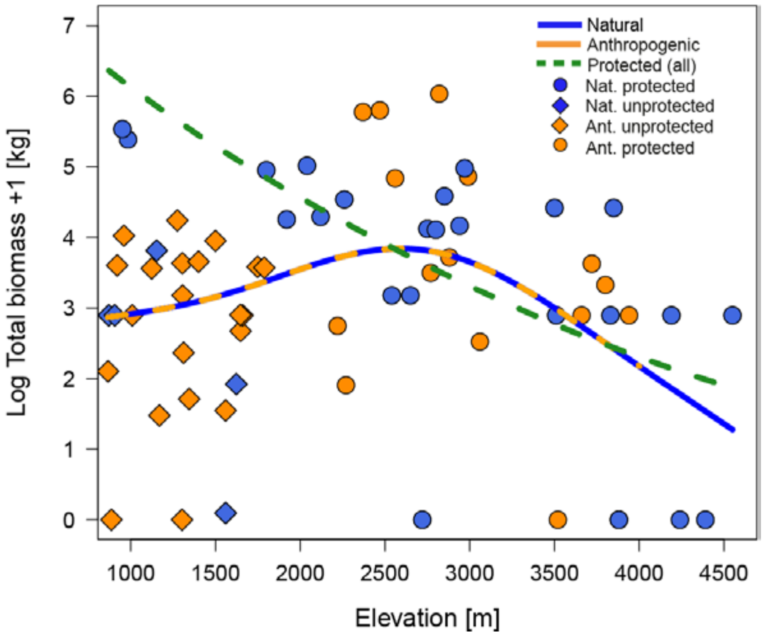


Supplementary Figure II.S4.1 Correlation between estimated and observed species richness. Species richness was estimated with the Chao 1 estimator.



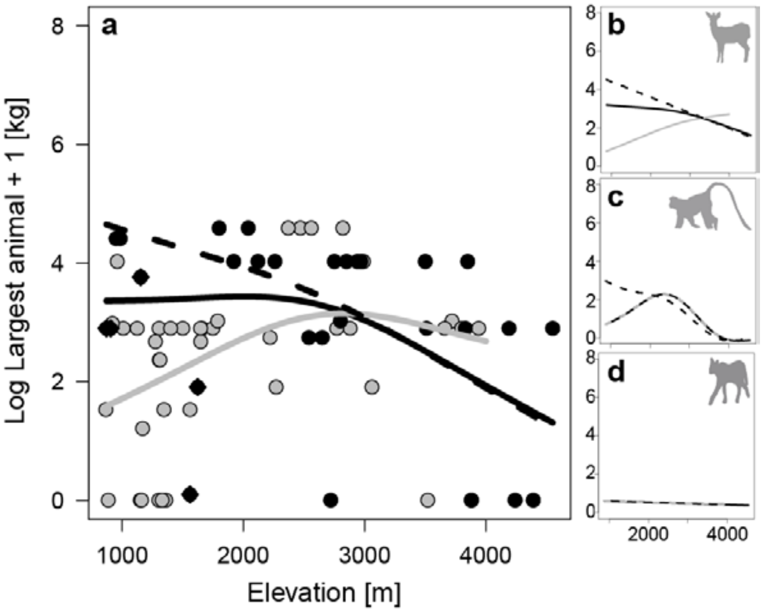
Supplementary Figure II.S4.2 Pattern of estimated species richness with elevation. Dots (blue: natural protected habitats, orange: anthropogenic protected habitats) and diamonds (blue: natural habitat, unprotected, orange: anthropogenic habitat, unprotected) depict original measurements on study sites. Trend lines were computed applying generalized additive models [Gaussian family, basis dimension (k) = 5]. The dashed blue lines depicts the trend for natural habitats that were situated in protected areas. The dashed blue and orange line represents the trend line for natural (blue) and anthropogenic (orange) habitats.

Appendix II.S5 Protected habitats



Supplementary Figure II.S5 Pattern of community biomass with elevation for natural and anthropogenic habitats (yellow and blue dashed line) as well as for protected habitats (green dashed line). Trend lines were computed applying generalized additive models [Gaussian family, basis dimension (k) = 5].

Appendix II.S6 Elevational distribution of the maximum biomass of the largest mammals on Mt. Kilimanjaro.



Supplementary Figure II.S6 Distribution of the maximum biomass of the largest animal species per study plot on Mt Kilimanjaro. (**a**) Dots (black: natural habitat, protected; grey: anthropogenic habitat) and diamonds (natural habitat, unprotected) depict original measurements on study sites. Trend lines were computed applying generalized additive models [Gaussian family, basis dimension (k) = 5]. Black solid lines represent trends for natural habitats, grey lines trends for anthropogenic habitats. Dashed black lines depict trends for natural habitats that were additionally situated in protected areas. For all mammals, animals were larger in natural compared to anthropogenic habitats ($p_{\mathrm{Interaction}} < 0.05$, ED = 23.8%). When only protected areas were considered, the size of animals increased at low elevation sites ($p_{\mathrm{Interaction}} < 0.05$, ED = 25.3%). **(b)** Likewise, herbivores were larger in natural than in anthropogenic habitats ($p_{\mathrm{Interaction}} < 0.05$, ED = 24.7%). Again, animals were larger at low elevations when only protected habitats were taken into consideration ($p_{\mathrm{Interaction}} < 0.001$, ED = 27%). **(c)** The largest omnivores showed the same unimodal distribution for both natural and anthropogenic habitats ($p_{\mathrm{Elevation}} < 0.001$, ED = 28.5%). In protected areas, the size of omnivores increased at low elevation sites. ($p_{\mathrm{Interaction}} < 0.05$, ED = 40.3%). **(d)** Regarding carnivores, there was no relationship between the distribution of the largest mammals and elevation ($p_{\mathrm{Interaction}} = 0.54$, ED = 0.6 %).

Appendix II.S7 Model support

Supplementary Table II.S7.1 Model support for all response variables in path diagram with species richness of wild mammals as the final response variable (Figure 6b)

(a): Model support for all models with $\Delta AIC_C < 3$ for species richness of wild mammals

Model (glm with Poisson distribution)	AIC_C	$\mathbf{\Delta_i}$	w_i	R^2
Area + protection + NPP + domestic	232.72	0.00	0.38	0.37
Area + protection + MAT + NPP + domestic	234.59	1.87	0.15	0.38
Protection + MAT + NPP + domestic	234.94	2.22	0.13	0.35
Protection + MAP + NPP + domestic	235.04	2.32	0.12	0.35
Area + protection + MAP + MAT + NPP + domestic	235.14	2.42	0.11	0.38
Protection + NPP + domestic	235.25	2.53	0.11	0.32

Note. NPP = net primary productivity, MAT = mean annual temperature, MAP = mean annual precipitation, domestic = community biomass of domestic mammals. $\Delta_i = \Delta AIC_c$, w_i = weight.

(b) Model support for all models with $\Delta AIC_C < 3$ for community biomass of domestic mammals

Model (glm with Gaussian distribution)	AIC_C	$\mathbf{\Delta_i}$	w_i	R^2
Protection + land use	275.09	0.00	0.77	0.59
Protection + land use + NPP	277.52	2.42	0.23	0.59

(c) Model support for all models with $\Delta AIC_C < 3$ for NPP

Model (glm with Gaussian distribution)	AIC_C	$\mathbf{\Delta_i}$	w_i	R^2
MAT + MAP	-99.46	0.00	0.80	0.72
MAT + MAP + land use	-96.68	2.78	0.2	0.73

Supplementary Table II.S7.2: Model support for all response variables in path diagram with community biomass of wild mammals as the final response variable (Figure 6c)

(a): Model support for all models with $\Delta AIC_C < 3$ for community biomass of wild mammals

Model (glm with Gaussian distribution)	AIC_C	$\mathbf{\Delta_i}$	w_i	R^2
Protection + MAT + NPP	239.33	0.00	0.21	0.27
Area + protection + NPP	239.64	0.31	0.18	0.27
Protection + MAT +NPP + domestic	240.30	0.97	0.13	0.29
Area + protection + NPP + domestic	240.51	1.18	0.12	0.29
Protection + MAP + MAT	241.21	1.88	0.08	0.25
Area + protection + MAT + NPP	241.33	2.00	0.08	0.28
Protection + MAP + MAT + NPP	241.75	2.42	0.06	0.27
Area + protection + MAP + NPP	242.07	2.74	0.05	0.27
Protection + MAP + MAT + domestic	242.12	2.79	0.05	0.27
Area + protection + MAT + NDVI + domestic	242.27	2.94	0.05	0.29

Note. NPP = net primary productivity, MAT = mean annual temperature, MAP = mean annual precipitation, domestic = community biomass of domestic mammals. $\Delta_i = \Delta AIC_c$, w_i = weight.

(b) Model support for all models with $\Delta AIC_C < 3$ for community biomass of domestic mammals

Model (glm with Gaussian distribution)	AIC_C	$\mathbf{\Delta_i}$	w_i	R^2
Protection + land use	275.09	0.00	0.77	0.59
Protection + land use + NPP	277.52	2.42	0.23	0.59

(c) Model support for all models with $\Delta AIC_C < 3$ for NPP

Model (glm with Gaussian distribution)	AIC_C	$\mathbf{\Delta_i}$	w_i	R^2
MAT + MAP	-99.46	0.00	0.80	0.72
MAT + MAP + land use	-96.68	2.78	0.2	0.73

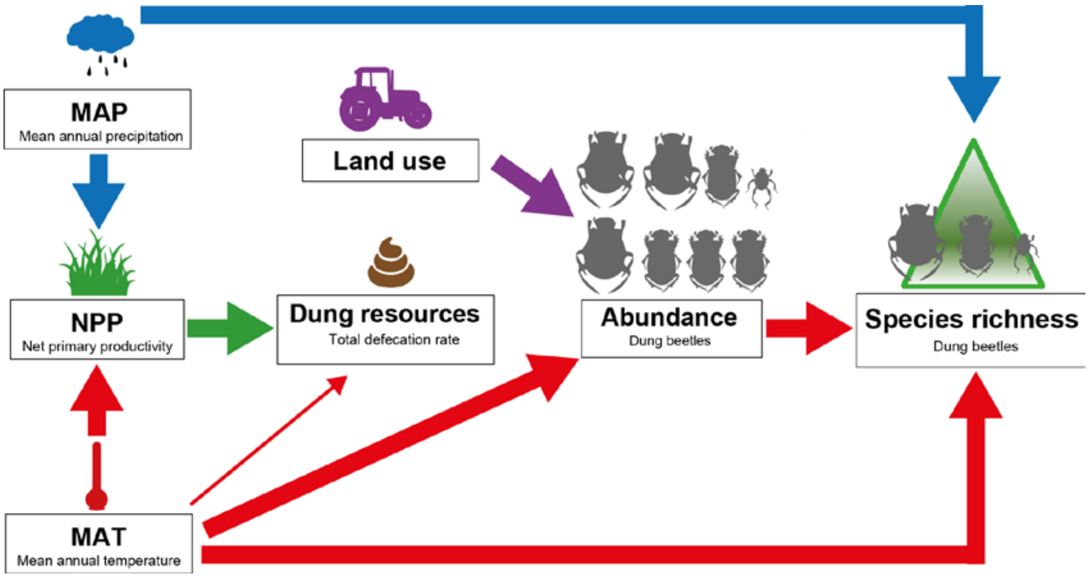
Appendix II.S8 Mammal species that were not detected

Supplementary Table II.S8: Not recorded mammal species reported to occur on the southern slopes of Mt. Kilimanjaro. After Grimshaw et al. (1995).

Species	Elevation/ habitat
Zanzibar Gallago	1500-1600 m
Hunting Dog	Bushland, low elevations
Zorilla	Cultivated zone
African Palm Civet	Cultivated zone
Slender Mongoose	Forest, cultivated zone
Marsh Mongoose	1200 m
Aardwolf	980 – 1350 m, cultivated zone, dry bush zone
African Wild Cat	Bushland, cultivated zone
Lion	Up to 4000 m
African Elephant	Up to 2900 m
Huet's Buhs Squirrel	Cultivated zone
Kilimanjaro Mountain Squirrel	1900 m up to heath zone

CHAPTER III

CLIMATE RATHER THAN DUNG RESOURCES PREDICT DUNG BEETLE ABUNDANCE AND DIVERSITY ALONG ELEVATIONAL AND LAND USE GRADIENTS ON MT. KILIMANJARO



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. 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. 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. 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.

III.1 Introduction

In contrast to 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 (Peters et al. 2016, Beck et al. 2017), 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 (Ferger et al. 2014, Beck et al. 2017). 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 et al. 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 to 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 2010b).

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 (Finn 2001, Barlow et al. 2010). 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 2000a). 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 et al. 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 et al. 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 et al., 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).

III.2 Materials and Methods

III.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 5895 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 1000 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 ~2700 mm at around 2200 m a.s.l. (Appelhans et al., 2016). For this project, sixty-six permanent study plots (50 m x 50 m) of the DFG research unit FOR1246 were selected on the southern slopes of Mt. Kilimanjaro (Peters et al. 2019b). 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 4550 m a.s.l. (Supporting Information Appendix III.S1). Natural habitats comprised 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 were represented by 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 systems (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.). 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 (Supporting Information Appendix III.S1). All study plots above 1800 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'.

III.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 five minutes for a duration of about two 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 (Supporting Information Appendix III.S2).

III.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 (Supporting Information Appendix III.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.

III.2.4 Assessment of mammal communities

We collected data on mammal communities from May to September 2016 using camera trapping and 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 the supplementary materials (Supporting Information Appendix III.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 (Peters et al. 1996, Brown et al. 2004). 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.

III.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 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 versus anthropogenic habitat), depicting specific trend lines for the two land use categories. GAMs calculate Chi-square 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 ($p > 0.05$), 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 $p > 0.05$. 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 et al. 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 the supplement (Supplementary Information Appendix III.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. Further, 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' (Shipley 2000, 2009, 2013, Lefcheck 2016). 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 two 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 two months in 2015 and 2016.

III.3 Results

We collected a total of 10432 dung beetles across the 66 study plots (Supporting Information Appendix III.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 (Supporting Information Appendix III.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; Supporting Information Appendix III.S7). The total biomass of mammal communities varied over 2000-fold (mean ± standard deviation: 49.6 ± 121.8), depicting strong variation in the availability of resources for dung beetles across study plots (Supporting Information Appendix III.S7).

III.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 III.1a, ED = 89.7 %, $p_{\text{Elevation}} < 0.001$). For tunnellers and kleptoparasites, abundance decreased with elevation in both natural and anthropogenic habitats (tunnellers: Figure III.1b, ED = 87.9 %, $p_{\text{Elevation}} < 0.001$; kleptoparasites: Figure III.1e, ED = 84.3 %, $p_{\text{Elevation}} < 0.001$). The elevational reduction in abundance was more pronounced for kleptoparasites (Figure III.1e). In rollers, abundance was higher in natural compared to anthropogenic habitats at low elevations. (Figure III.1b, ED = 79.5 %, $p_{\text{Interaction}} < 0.05$). Dweller abundance was unimodally distributed for both natural and anthropogenic habitats with a higher abundance in anthropogenic habitats and peaked at around 1500m (Figure III.1d, ED = 77.7 %, $p_{\text{Interaction}} < 0.05$).

Species richness of dung beetles declined exponentially with elevation with no significant difference between natural and anthropogenic habitats (Figure III.2a, explained deviance (ED) = 90 %, $p_{\text{Elevation}} < 0.001$). 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 III.2b, ED = 91 %, $p_{\text{Elevation}} < 0.001$). 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 III.2e, ED = 79.6 %, $p_{\text{Elevation}} < 0.05$) Rollers exhibited a decline in species richness with elevation with higher species richness in natural than anthropogenic habitats at low elevations (Figure III.2c, ED = 80%, $p_{\text{Elevation + Land use}} < 0.05$). In contrast to the other feeding guilds, species richness of dwellers showed a unimodal distribution with elevation with a peak at around 1500 m. Dweller richness did not differ between natural and anthropogenic habitats (Figure III.2d, ED = 72.2 %, $p_{\text{Elevation}} < 0.001$). Dung beetle abundance and dung beetle species richness were highly correlated ($r = 0.80$, $p < 0.001$).

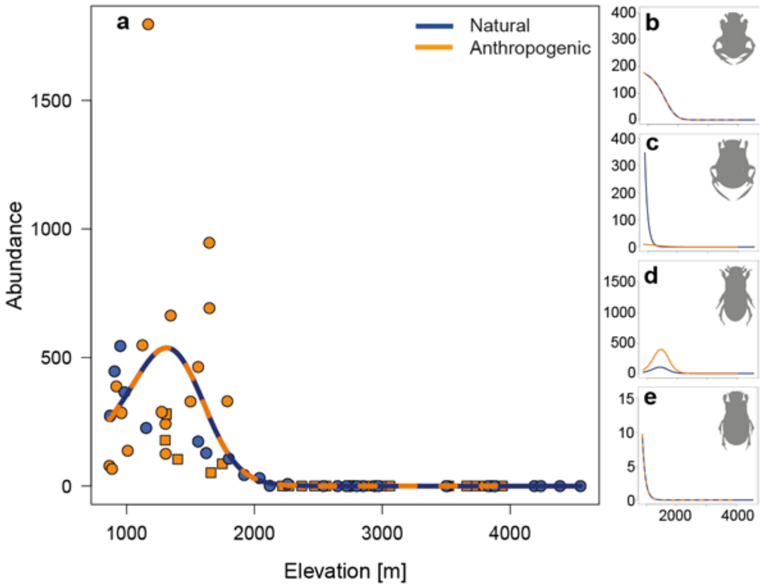


Figure III.1 Patterns of dung beetle abundance along the elvational gradient on Mt. Kilimanjaro (**a**) and patterns for separate feeding guilds: tunnellers (**b**), rollers (**c**), dwellers (**d**) and kleptoparasites (**e**). In (**a**), dots and squares delineate original measurements of abundance 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.

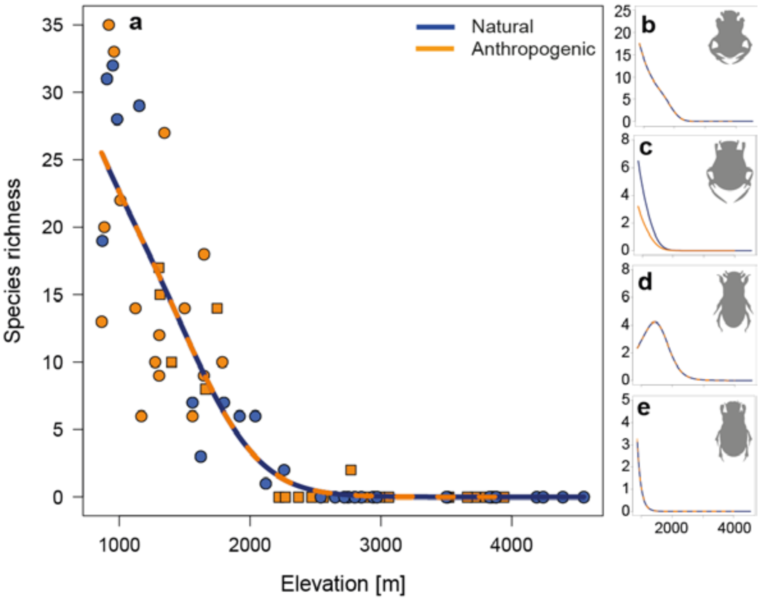


Figure III.2 Elevational distribution of dung beetle species richness on Mt. Kilimanjaro (**a**) and patterns for individual feeding guilds: tunnellers (**b**), rollers (**c**), dwellers (**d**) and kleptoparasites (**e**). In (**a**), dots and squares illustrate original measurements of species richness 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.

The degree of nestedness was low as the NODF-values were closer to zero than to 100 (Fig.III.3 a, 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 (Supplementary Information Appendix III.S5, NODF entire community = 9.24, turnover = 0.91, nestedness = 0.07).

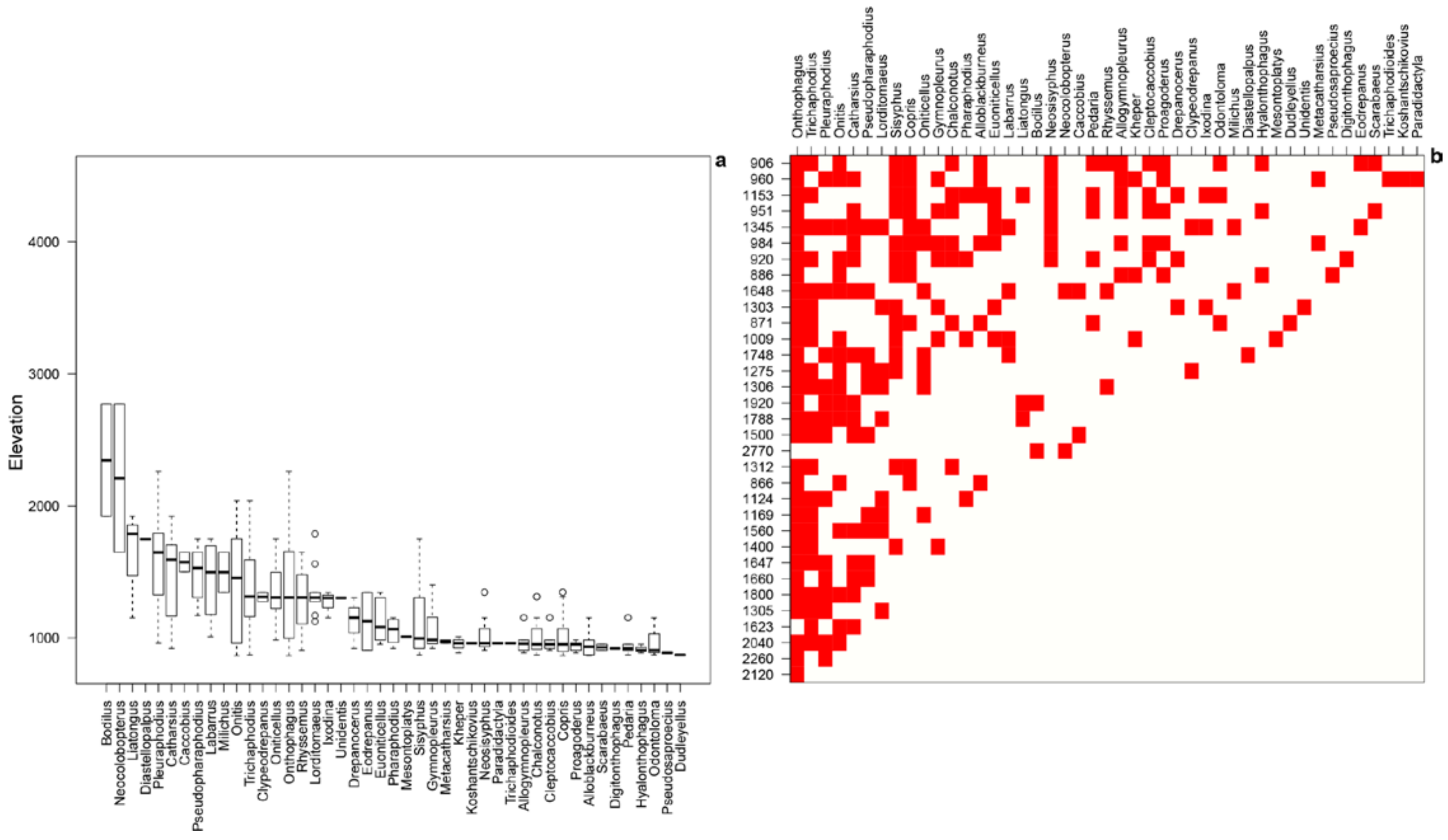


Figure III.3 Elevational range of dung beetle genera (a) and composition of dung beetle communities at the genus level for all elevations (study plots) where dung beetles were present (b). In (b), coloured squares signify that a genus was present at a given elevation while blank squares represent absence of a genus.

III.3.2 Drivers of species richness and abundance

Path analysis showed that the main predictor for dung beetle species richness and abundance was mean annual temperature (MAT; Figure III.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 to mean annual precipitation (MAP). Scatterplots showing the relations between all response and predictor variables can be found in the supplement (Supplementary Information Appendix III.S8.1). The relationship between dung beetle species richness and MAP was negative (Supplementary Information Appendix III.S8.2).

Besides a strong effect of MAT, dung beetle abundance was correlated to 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 III.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 ($r = 0.77$, $p < 0.01$; Supplementary Information Appendix III.S9), as was abundance ($r = 0.81$, $p < 0.01$; Supplementary Information Appendix III.S10). Species composition hardly changed between the two sampling events (Supplementary Information Appendix III.S11, III.S12) and path analysis produced the same patterns for both cow and human dung as for the pooled data set (Supplementary Information Appendix III.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 (Supplementary Information Appendix III.S14).

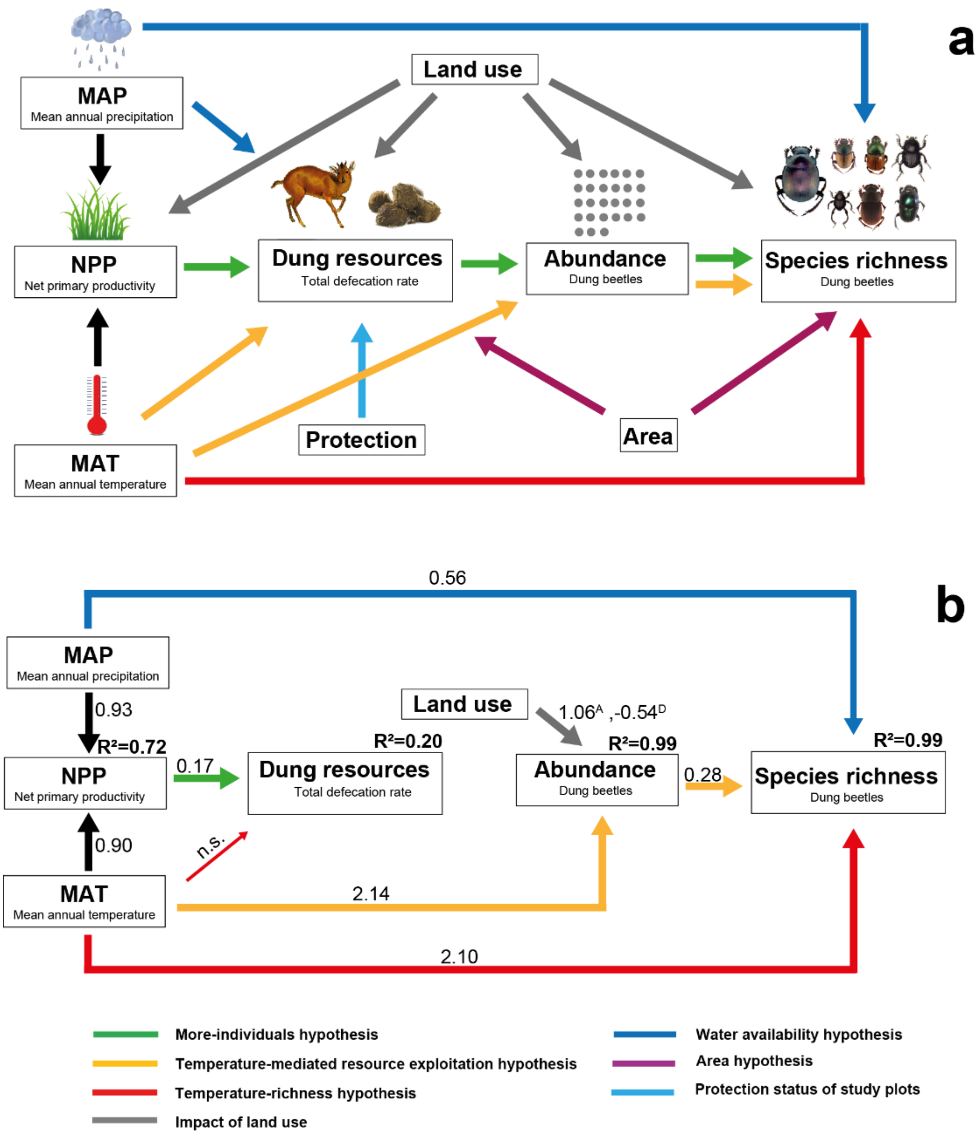


FIGURE III.4 Path models illustrating the direct and indirect effects of predictor variables on the species richness of dung beetles on Mt. Kilimanjaro. (**a**) Starting path model showing all hypothesized effects of predictor variables on the species richness and abundance of dung beetles. (**b**) Path 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 ($p < 0.05$). 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, $p < 0.05$. ^{D} Disturbed plots, n.s.

^{A,D} As land use is a factorial variable, the path coefficients are not standardized.

III.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.

III.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 2260 m (*Onthophagus incantatus*) while the highest Aphodiinae dung beetles were found at 2770 m (*Bodilus vittifer*, *Neocolobopterus stefenellii*), patterns which reflect elevational distributions of dung beetles on other African mountains (Davis et al. 1999, Muhirwa et al. 2018). Interestingly, in the new world, the highest record for a Scarabaeinae dung beetle was found in the Colombian Andes at 4550 m in a mountain system reaching 5330 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 et al. 2018), reaching their highest richness in temperate latitudes (Martín-Piera et al. 1992, Chamberlain et al. 2015). Turnover was mainly responsible for the changes in species composition with elevation while nestedness only played an inferior role.

III.4.2 Drivers of dung beetle diversity

We found that species richness of dung beetles was mainly influenced by mean annual temperature (MAT) and to a lesser degree by mean annual precipitation (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 et al. 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 (Muhirwa et al. 2018, Frank 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 et al. 2005, Herzog et al. 2013).The temperature-richness hypothesis assumes that temperature is positively correlated to 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 (Frazier et al. 2006, Classen et al. 2015), 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, 2005). 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).

III.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 1345 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 et al. 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 et al. 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.

III.4.4 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 to 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.

Data availability statem

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 et al. 2019a).

III.5 Supplementary Information

Appendix III.S1: Ecosystem types on Mt. Kilimanjaro

Table III.S1: Ecosystem types studied on Mt. Kilimanjaro. The 66 study plots were located in six natural and seven anthropogenic habitats along an elevational gradient of 3679 m. While there was no human impact in natural habitats, there was low to high land use intensity in anthropogenic habitats.

habitat	# plots	land use type	elevation[1]	land use intensity
savanna	5	Natural	871-1153	none
maize fields	5	Anthropogenic	866-1009	high
lower montane forest	5	Natural	1560-2020	none
Chagga agroforestry	5	anthropogenic	1169-1788	high
coffee plantations	6	anthropogenic	1124-1648	high
grasslands	5	anthropogenic	1303-1748	high
Ocotea forest	5	natural	2120-2750	none
logged *Ocotea* forest	5	anthropogenic	2220-2560	low
Podocarpus forest	5	natural	2800-2970	none
burned *Podocarpus* f.	5	anthropogenic	2270-3060	low
Erica forest	5	natural	3500-3900	none
burned *Erica* forest	5	anthropogenic	3500-3880	low
Helichrysum vegetaton	5	natural	3880-4550	none

Note. [1] Elevation is shown in m a.s.l.

Appendix III.S2: Climate and NPP

MAP was regionally interpolated applying a co-kriging approach and MAP values were extracted for each study plot (Appelhans et al. 2016). As a proxy for net primary productivity (NPP), we utilized the normalized difference vegetation index (NDVI; Detsch et al. 2016a,b, Peters et al. 2016). NDVI estimates were derived from MODIS Aqua product MYD13Q1, which provides data of a horizontal resolution of 250 m x 250 m (Detsch et al. 2016a,b, Peters et al. 2016). For more details on methodology and original data, refer to Appelhans et al. (2016) and Peters et al. (2016).

Appendix III.S3: Trapping of dung beetles

In the first sampling round, we buried two pitfall traps in opposite corners of the study plots. The upper rim of the cup was placed in the ground so that it was even with the soil surface, assuring that beetles were hindered from perceiving the trap as an obstacle. We filled each trap with water to approximately its half and added a small amount of unscented detergent to lessen water surface tension. As bait, ca. 20 g of human dung was wrapped in mosquito net and fastened to a stick over the cup, simulating a natural dung pad (Halffter & Favila 1993). For the second round, one large pitfall trap (plastic bowls with an upper diameter of 33 cm and a depth of 15 cm) was used per study plot. We filled traps with 1.5 L of water and detergent, resulting in a water height of 3 cm. As bait, 700 g of fresh cow dung were placed on a mesh over the trap. Dung was frozen for at least 24 hours prior to the experiment, ensuring that any dung beetles already in the dung were killed. In both sampling rounds, traps were covered by a canvas shielding the bait from sun and rain. All pitfall traps were operated for 72 h. After this time, all captured specimens were sieved and stored in whirl packs filled with 70% ethanol. Later, dung beetles were pinned, sorted to morphospecies and identified at species level (86.7 % of all collected species).

Appendix III.S4: Assessment of mammal communities

We placed five camera traps (Bushnell Trophy Cam HD Essential, model 119736) on or in the direct vicinity (within a distance of 50 m) of all 66 study plots. For improving the likelihood of mammal detection, we installed cameras near trails or animal latrine sites. Cameras were attached to trees or posts at a height between 70 cm and 140 cm depending on local topography. We ran cameras for a period of 14 days, amounting to 70 trap nights per plot. Cameras were activated with a motion sensor and set up to shoot videos with a duration of 20 seconds and a minimum gap of ten seconds between consecutive videos. At night, cameras operated with infrared light. We used the hourly event count approach to avoid listing the same individuals several times (Hegerl et al. 2017). Accordingly, we solely regarded two shots of the same mammal as independent if there was an interval of one hour in between. All mammals were identified to the species level using Kingdon et al. (2013) and Kingdon (2015).

For carrying out systematic transect-based searches for mammalian dung, we split every study plot into 25 transects with a length of 50 m and a distance of two meters between adjacent transects. We documented mammalian faeces situated up to one metre left and right from every transect. On all study plots, transect walks were conducted twice, once whilst setting up camera traps and once at the day of terminating the experiment. We measured and photographed faeces and froze samples for subsequent identification after Stuart & Stuart (2000).

Appendix III.S5: Dung beetle community compositoin

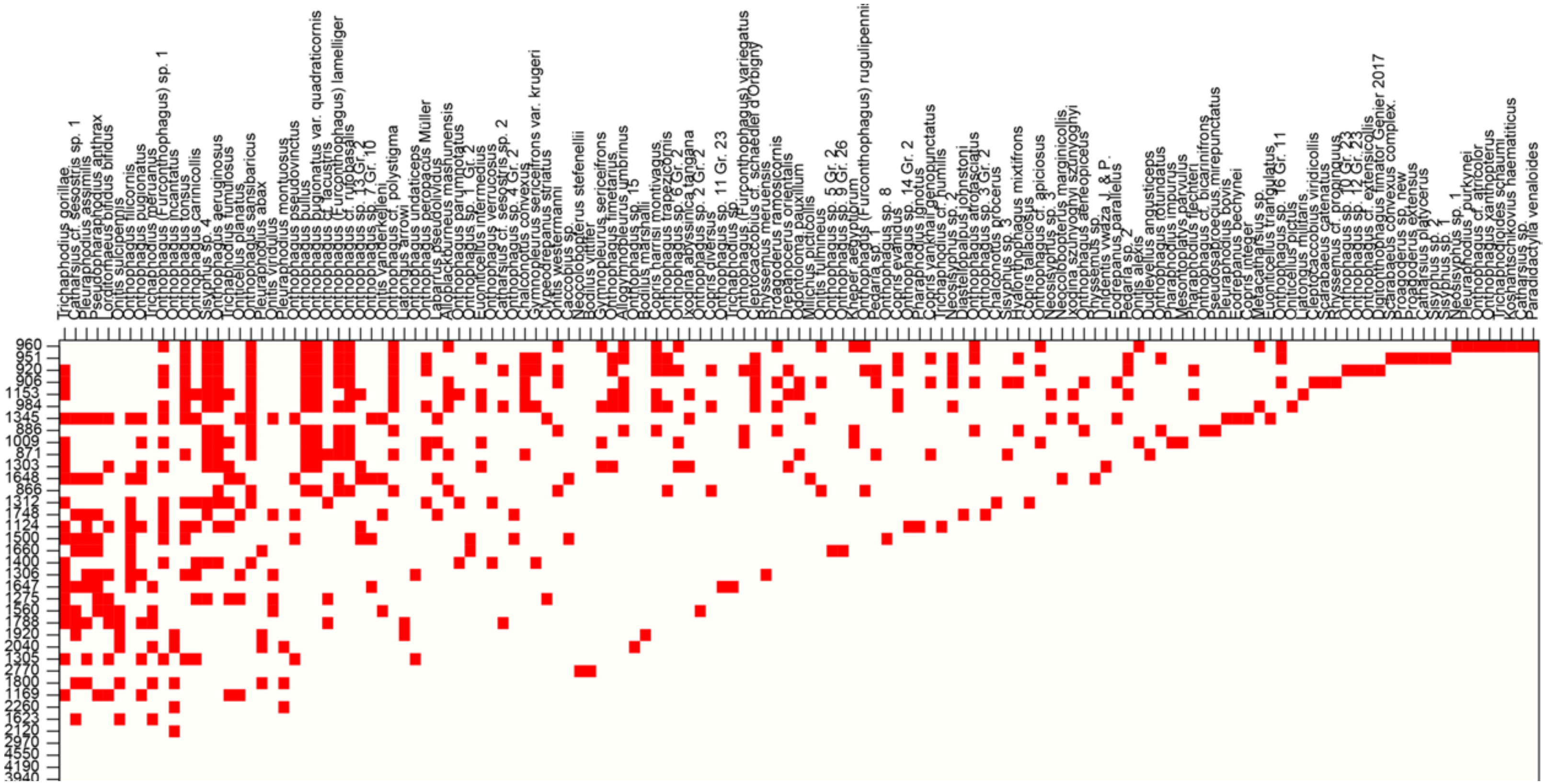


Figure III.S5: Dung beetle species composition. Coloured squares signify that a species was present at a given elevation while blank squares represent absence of a species. The degree of nestedness was low (NODF species = 10.51, NODF study sites = 3.53, NODF entire community = 9.24). The components of multiple-site dissimilarities showed a high amount of turnover (turnover [Simpson dissimilarity] = 0.91, nestedness= 0.07).

Appendix III.S6: Dung beetles of Mt. Kilimanjaro

Table III.S6: Recorded dung beetle species on Mt. Kilimanjaro. Elevation is shown in m a.s.l.

Subfamily	Tribe	Species	Total[1]	Plots[2]	Elevation[3]	Guild[4]
Scarabaeinae	Dichotomiini	*Pedaria sp. 1*	6	3	871-920	k
		Pedaria sp. 2	11	3	920-1153	k
	Coprini	*Catharsius cf. sesostris sp. 1*	215	12	1345-1920	t
		Catharsius cf. sesostris sp. 2	4	3	920-1788	t
		Catharsius platycerus	1	1	951	t
		Catharsius sp.	1	1	960	t
		Copris diversus	6	3	866-984	t
		Copris evanidus	7	4	920-1153	t
		Copris fallaciosus	1	1	1312	t
		Copris harrisi montivagus	10	6	886-1153	t
		Copris integer	1	1	1345	t
		Copris vankhaii genopunctatus	4	3	871-951	t
		Metacatharsius sp.	26	2	960-984	t
	Canthonini	*Chalconotus convexus*	126	6	871-1153	r
		Chalconotus procerus	3	1	1312	r
		Odontoloma pauxillum	15	3	871-1153	u
	Gymnopleurini	*Allogymnopleurus umbrinus*	15	6	886-1153	r
		Gymnopleurus sericeifrons	24	4	960-1303	r
		Gymnopleurus sericeifrons var. krugeri	42	4	920-1400	r
	Scarabaeini	*Kheper aegyptiorum*	4	3	886-1009	r
		Scarabaeus catenatus	8	1	906	r
		Scarabaeus convexus complex.	1	1	951	r
	Sisyphini	*Neosisyphus sp. 1*	1	1	960	r
		Neosisyphus sp. 2	12	4	906-984	r
		Neosisyphus sp. 3	7	2	1153-1345	r
		Sisyphus sp. 1	7	1	951	r
		Sisyphus sp. 2	1	1	951	r
		Sisyphus sp. 3	4	2	871-906	r
		Sisyphus sp. 4	486	14	871-1748	r
	Onitini	*Onitis alexis*	2	2	960-1009	t
		Onitis fulmineus	6	3	866-960	t
		Onitis sulcipennis	34	6	1560-2040	t
		Onitis vanderkelleni	9	4	1345-1748	t
		Onitis viridulus	15	6	1275-1748	t
		Onitis westermanni	34	5	866-960	t
	Onthophagini	*Caccobius sp.*	2	2	1500-1648	t
		Cleptocaccobius cf. schaedlei	16	5	906-1153	k.
		Cleptocaccobius viridicollis	1	1	906	k.

Diastellopalpus johnstoni	2	1	1748	t
Digitonthophagus fimator	3	1	920	t
Hyalonthophagus mixtifrons	7	2	886-906	k
Milichus picticollis	3	2	1345-1648	t
Onthophagus (Furconthophagus) lamelliger	465	10	866-1648	t
Onthophagus (Furconthophagus) rugulipennis	8	3	866-960	t
Onthophagus (Furconthophagus) sp. 1	175	13	906-1748	t
Onthophagus (Furconthophagus) variegatus	11	3	886-1009	t
Onthophagus aeneopiceus	23	2	886-906	t
Onthophagus aeruginosus	123	14	866-1400	t
Onthophagus atrofasciatus	34	4	886-960	t
Onthophagus carinicollis	33	8	1124-1400	t
Onthophagus cf. apiciosus	6	3	920-1009	t
Onthophagus cf. atricolor	2	1	960	t
Onthophagus cf. bicarifrons	1	1	886	t
Onthophagus cf. extensicollis	1	1	920	k.
Onthophagus cf. lacustris	7	4	871-1788	t
Onthophagus cf. polystigma	199	9	866-1153	t
Onthophagus cf. rufobasalis	94	8	866-1153	t
Onthophagus filicornis	195	10	1124-1748	t
Onthophagus fimetarius	20	5	920-1303	t
Onthophagus incantatus	80	6	1560-2260	t
Onthophagus parumnotatus	15	3	1153-1400	t
Onthophagus peropacus	58	6	871-1312	t
Onthophagus pseudovinctus	359	5	1305-1748	t
Onthophagus pugionatus	120	9	1009-1788	t
Onthophagus pugionatus var. quadraticornis	105	11	866-1303	t
Onthophagus pullus	55	9	866-1303	t
Onthophagus rotundatus	2	2	886-951	t
Onthophagus sansibaricus	358	13	866-1400	t
Onthophagus sp. 1 Gr. 2	4	2	1500-1660	t
Onthophagus sp. 2 Gr. 2	3	1	1560	t
Onthophagus sp. 3 Gr. 2	1	1	1748	t
Onthophagus sp. 4 Gr. 2	4	2	1500-1748	t
Onthophagus sp. 5 Gr. 2	1	1	1660	t
Onthophagus sp. 6 Gr. 2	15	4	920-1303	t
Onthophagus sp. 7 Gr. 10	44	4	1345-1648	t
Onthophagus sp. 8	1	1	1500	t
Onthophagus sp. 9 Gr. 26	1	1	1660	t
Onthophagus sp. 10 Gr. 23	1	1	920	t

		Onthophagus sp. 11 Gr. 23	1	1	1647	t
		Onthophagus sp. 12 Gr. 23	3	1	920	t
		Onthophagus sp. 13 Gr. 2	10	5	1124-1648	t
		Onthophagus sp. 14 Gr. 2	1	1	1124	t
		Onthophagus sp. 15	1	1	2040	t
		Onthophagus sp. 16 Gr. 11	5	3	906-960	k.
		Onthophagus tonsus	297	13	871-1500	t
		Onthophagus trapezicornis	9	4	866-984	t
		Onthophagus undaticeps	7	2	1305-1306	t
		Onthophagus verrucosus	135	2	1312-1400	t
		Onthophagus xanthopterus	2	1	960	t
		Proagoderus extensus	1	1	951	t
		Proagoderus ramosicornis	12	4	886-984	t
		Proagoderus sp. new	1	1	951	t
		Pseudosaproecius mirepunctatus	1	1	886	u
		Unidentis vwaza J. & P.	1	1	1303	u
	Oniticellini	*Clypeodrepanus striatus*	3	2	1275-1345	t
		Drepanocerus orientalis	8	3	920-1303	t
		Eodrepanus bechynei	1	1	1345	t
		Eodrepanus parallelus	2	2	906-1345	t
		Euoniticellus intermedius	7	5	951-1303	t
		Euoniticellus triangulatus	1	1	1345	t
		Ixodina abyssinica tangana	3	3	1153-1345	t
		Ixodina szunyoghyi szunyoghyi	7	2	1153-1345	t
		Liatongus arrowi	6	2	1788-1920	t
		Liatongus militaris	1	1	1153	t
		Oniticellus pictus	2	1	984	d
		Oniticellus planatus	19	6	1169-1748	d
Aphodiinae		*Alloblackburneus mashunensis*	77	6	866-1153	d
		Bodilus marshalli	5	1	1920	d
		Bodilus vittifer	1	1	2770	d
		Dudleyellus angusticeps	2	1	871	d
		Koshantschikovius haematiticus	1	1	960	d
		Labarrus pseudolividus	20	4	1009-1748	d
		Lorditomaeus bifidus bifidus	237	9	1124-1788	d
		Mesontoplatys parvulus	2	1	1009	d
		Neocolobopterus marginicollis	1	1	1648	d
		Neocolobopterus stefenellii	1	1	2770	d
		Paradidactylia venaloides	2	1	960	d
		Pharaphodius fiechteri	2	2	920-1153	d
		Pharaphodius ignotus	1	1	1124	d
		Pharaphodius impurus	1	1	1009	d

Pleuraphodius abax	28	4	1660-2040	d
Pleuraphodius assimilis	687	11	1124-1800	d
Pleuraphodius bovis	1	1	1345	d
Pleuraphodius montuosus	7	3	1800-2260	d
Pleuraphodius purkynei	1	1	960	d
Pseudopharaphodius anthrax	31	10	1169-1748	d
Rhyssemus cf. propinquus	1	1	906	d
Rhyssemus meruensis	1	1	1306	d
Rhyssemus sp.	1	1	1648	d
Trichaphodioides schaumi	2	1	960	d
Trichaphodius cf. humilis	1	1	1124	d
Trichaphodius fumulosus	349	8	1009-1648	d
Trichaphodius gorillae	4068	19	871-1788	d
Trichaphodius meruanus	546	6	1560-2040	d
Trichaphodius sp.	1	1	1647	d

Note. [1]Total number of individuals collected. [2]Number of study plots on which species were collected. [3]Elevational range of study plots on which species were collected. [4]k = kleptoparasite, t = tunneller, d = dweller, r = roller, u = unknown

Appendix III.S7: Mammals of Mt. Kilimanjaro

Table III.S7: Recorded mammal species on Mt Kilimanjaro. Weight and metamass (metabolic mass) are shown in kg, elevation in m a.s.l.

Order	Family	Common Name	Species	Weight	Metmass^{1}	Records^{2}	Plots^{3}	Elevation^{4}
Hyracoidea	Procaviidae	Eastern Tree Hyrax	*Dendrohyrax validus*	2.75	2.14	15	4	2540-2940
Primates	Galagonidae	Small-Eared Greater Gallago	*Otolemur garnetti panganiensis*	0.8	0.85	3	2	1800-2370
	Cercopithecidae	Yellow Baboon	*Papio cynocephalus*	18.63	8.97	10	3	920-984
		Hilgert's Vervet Monkey	*Chlorocebus pygerythrus hilgerti*	5.18	3.43	33	1	1275
		Zanzibar Sykes's Monkey	*Cercopithecus n. albogularis*	5.73	3.70	46; 7	19	1623-3060
		Black-and-White Colobus	*Colobus guereza caudatus*	9.23	5.30	1	1	2770
Rodentia	Sciuridae	Zanj Sun Squirrel	*Heliosciurus undulatus*	0.32	0.43	3	1	1305
		Sciuridae sp. 1	Rodentia sp. 1*	0.1	0.18	1	1	1647
		Sciuridae sp. 2	Rodentia sp. 2*	0.1	0.18	95; 3	14	1124-2880
	Leporidae	African Savanna Hare	*Lepus victoriae*	2.31	1.87	6; 7	3	951-1748
	Histricidae	Crested Porcupine	*Hystrix cristata*	19.5	9.28	7	4	1788-3720
Eulipotyphla	Erinaceidae	Four-Toed Hedgehog	*Atelerix albiventris*	0.93	0.95	10	2	1169-1345
Carnivora	Felidae	Serval	*Leptailurus serval*	9.75	5.52	6; 7	8	2470-3849
		Leopard	*Panthera pardus*	55	20.20	3; 3	4	960-3880
		Domestic Cat	*Felis catus*	4,05	2.85	35	7	866-1788
	Herpestidae	Egyptian Mongoose	*Herpestes ichneumon*	3.15	2.36	2	1	1500
		White-tailed Mongoose	*Ichneumia albicauda ibeana*	3.6	2.61	37	9	866-1788
	Viverridae	African Civet	*Civettictis civetta*	13.5	7.04	11	4	1275-1648
		Large-spotted Genet	*Genetta maculata*	2.35	1.90	15	8	1169-2800
	Canidae	Side-striped Jackal	*Canis adustus*	9.65	5.48	29	7	1275-2560
		Golden Jackal	*Canis aureus*	10.5	5.83	4	1	1500

		Domestic Dog	*Canis lupus familiaris*	15	7.62	206,4	17	866-1788
	Mustelidae	Ratel (Honey Badger)	*Mellivora capensis*	9.85	5.56	1	1	2800
Perissodactyla	Equidae	Plains Zebra	*Equus quagga boehmi*	241.8	61.32	0; 1	1	984
Artiodactyla	Suidae	Bushpig	*Potamochoerus larvatus daemonis*	97.5	31.03	16; 6	7	1800-2850
	Bovidae	Harvey's Duiker	*Cephalophus harveyi*	14.5	7.43	54; 7	8	1800-2650
		Abbott's Duiker	*Cephalophus spadix*	55	20.20	73; 15	13	1920-3849
		Common Duiker	*Sylvicapra grimmia hindei*	17.1	8.41	102; 37	31	871-4550
		Suni	*Nesotragus moschatus*	5	3.34	202; 11	5	1800-2800
		Kirk's Dik-Dik	*Madoqua kirkii*	5.5	3.59	2; 3	2	1312-1400
		Bovidae sp. 1	Bovidae sp. 1*	17.1	8.41	0; 1	1	1400
		Bovidae sp. 2	Bovidae sp. 2*	17.1	8.41	0; 3	1	3940
		Bushbuck	*Tragelaphus scriptus*	42	16.50	4	3	951-2850
		Lesser Kudu	*Tragelaphus imberbis*	81.5	27.12	14	2	951-984
		African Buffalo	*Syncerus caffer*	637.5	126.87	0; 1	1	2120-3880
		Cattle	*Bos spp.*	385	86.92	127; 49	10	920-2800
		Sheep	*Ovis aries*	45	17.37	32; 3	6	920-3510
		Domestic Goat	*Capra aegagrus hircus*	20	9.46	396;10	5	920-1788

Note.[1]Metabolic mass was calculated by the weight of the respective mammal to the power of ¾. [2]The first number listed under records depicts the number of animals on videos shot of each species with an interval of 1 hour between consecutive videos; the second number represents the number of dung pats for species where dung was present. [3] Implies the number of study plots on which each species was recorded.[4] Shows the elevational range of the study plots on which species were present. [*]Amongst the wild mammals sampled with camera traps, two small rodents could only be identified to morphospecies level while there were dung samples of apparently two small antelopes which could not be further identified and were therefore designated as morphospecies.

Appendix III.S8: Correlations between response and predictor variables

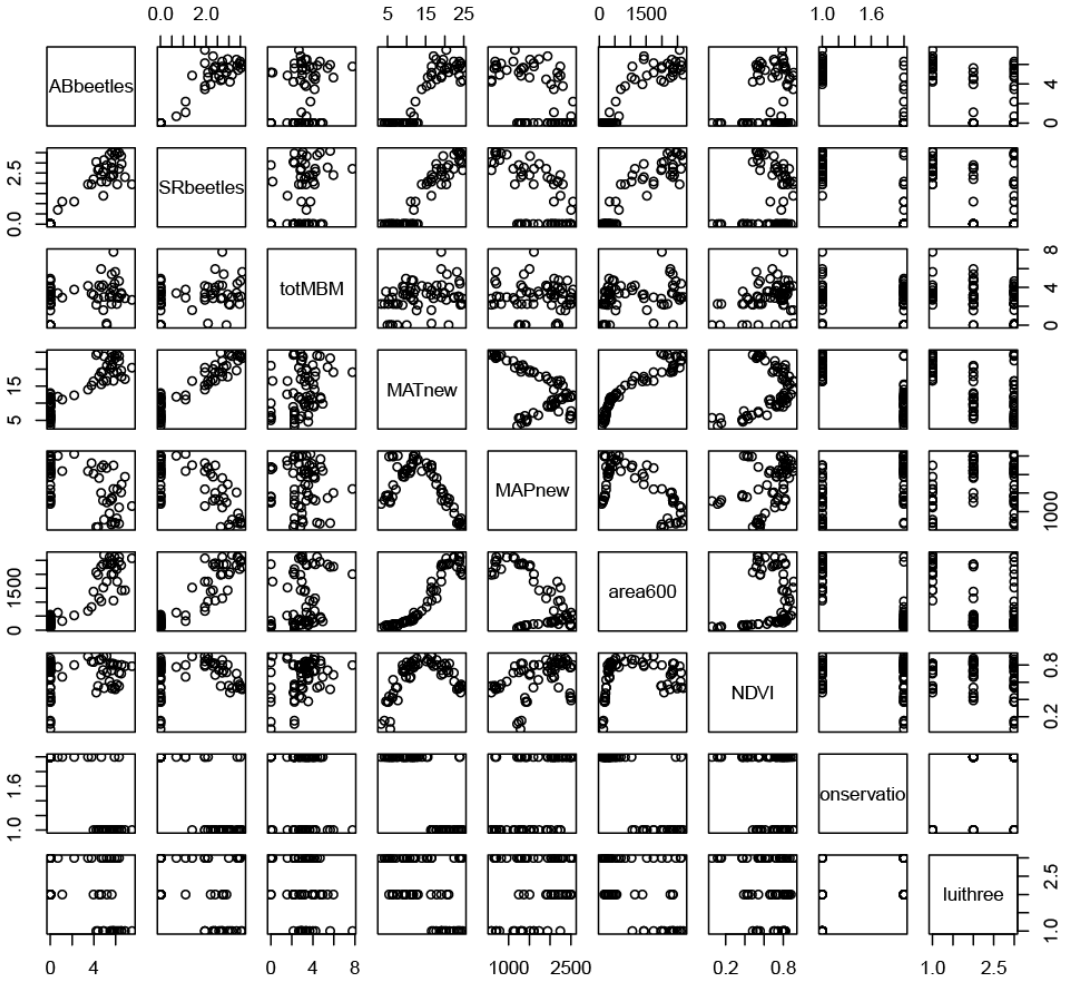


Figure III.S8.1: Pairwise scatterplots of all response variables (ABbeetles, SRbeetles, totMBM) and predictor vairables (MATnew, MAPnew, area600, NDVI, conservation, luithree).

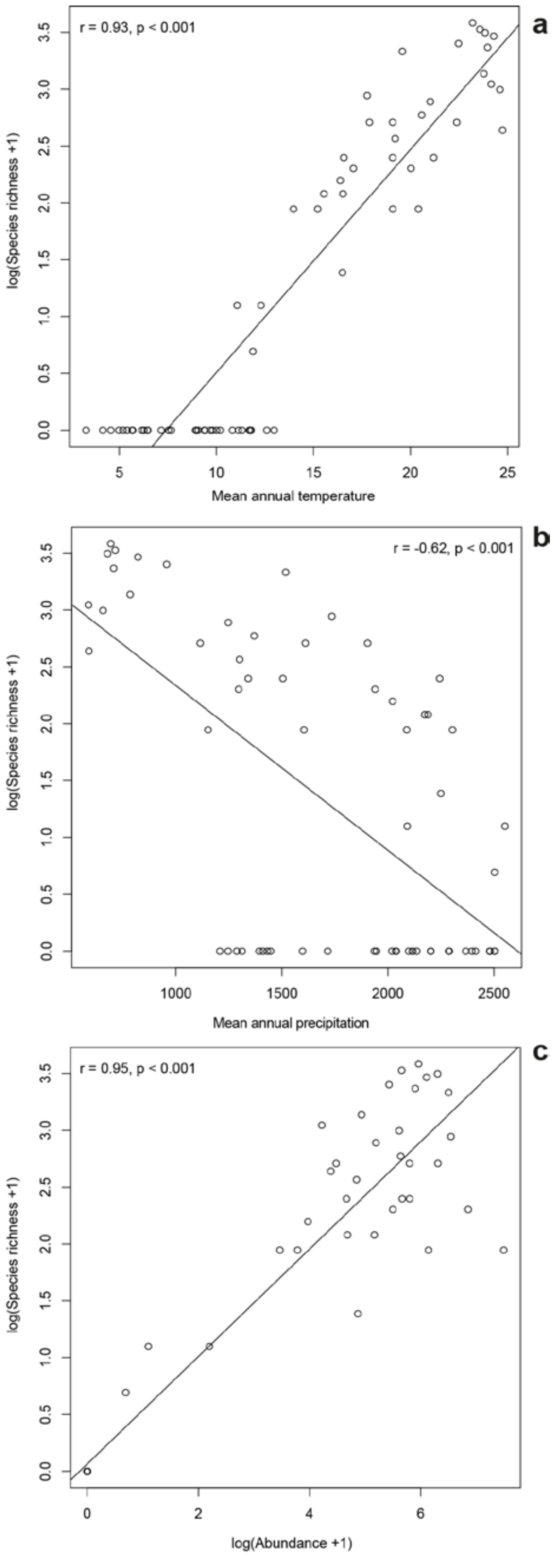


Figure III.S8.2: Relationships between dung beetle species richness and mean annual temperature (a), mean annual precipitation (b) and dung beetle abundance (c).

Appendix III.S9: Relationship between communities sampled with human dung and communities sampled with cow dung: species richness

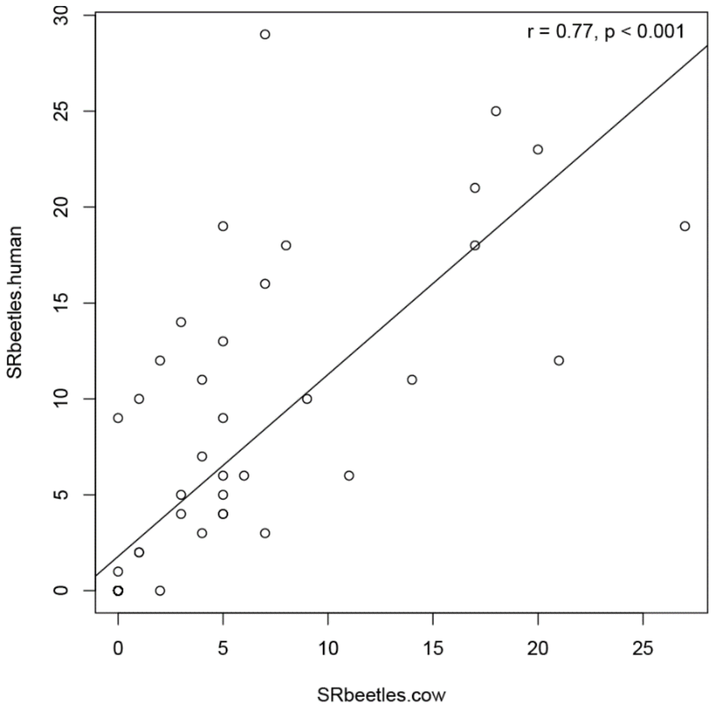


Figure III.S9: Relationship between species richness of communities sampled with human dung (SRbeetles.human) and species richness of communities sampled with cow dung (SRbeetles.cow)

Appendix III.S10: Relationship between communities sampled with human dung and communities sampled with cow dung: abundance

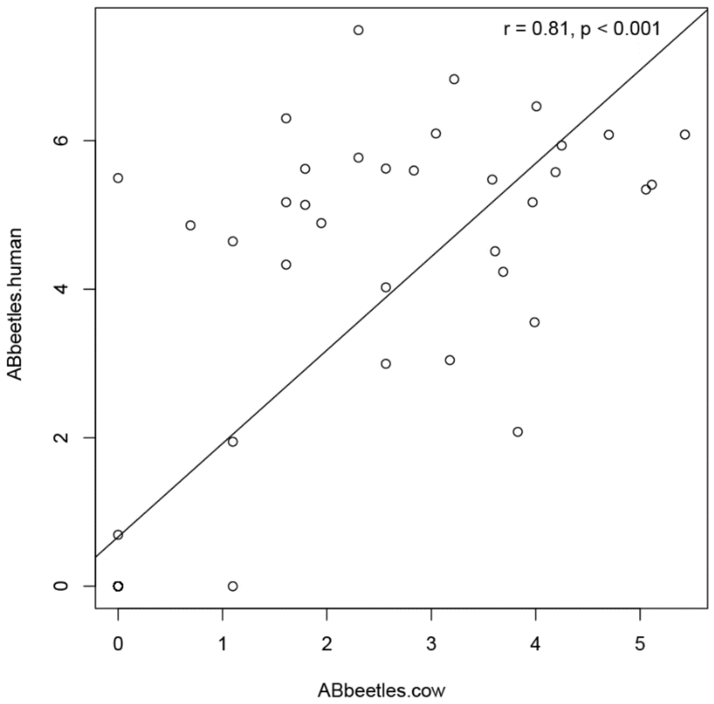


Figure III.S10: Relationship between abundance of communities sampled with human dung (ABbeetles.human) and abundance of communities sampled with cow dung (ABbeetles.cow)

Appendix III.S11: Comparison of species composition between cow and human dung

The species composition of the two sampling events was compared with the 'multivariate_change' function of the R package 'codyn'. This function produces a metric called 'composition_change' which ranges between 0 (identical communities) and 1 (completely different communities). The result of the comparison between the community sampled with human dung and the community sampled with cow dung was a compositional change of 0.29 – this result leans towards the zero end of the range – therefore, the communities hardly differ.

Appendix III.S12: Community composition for human and cow dung

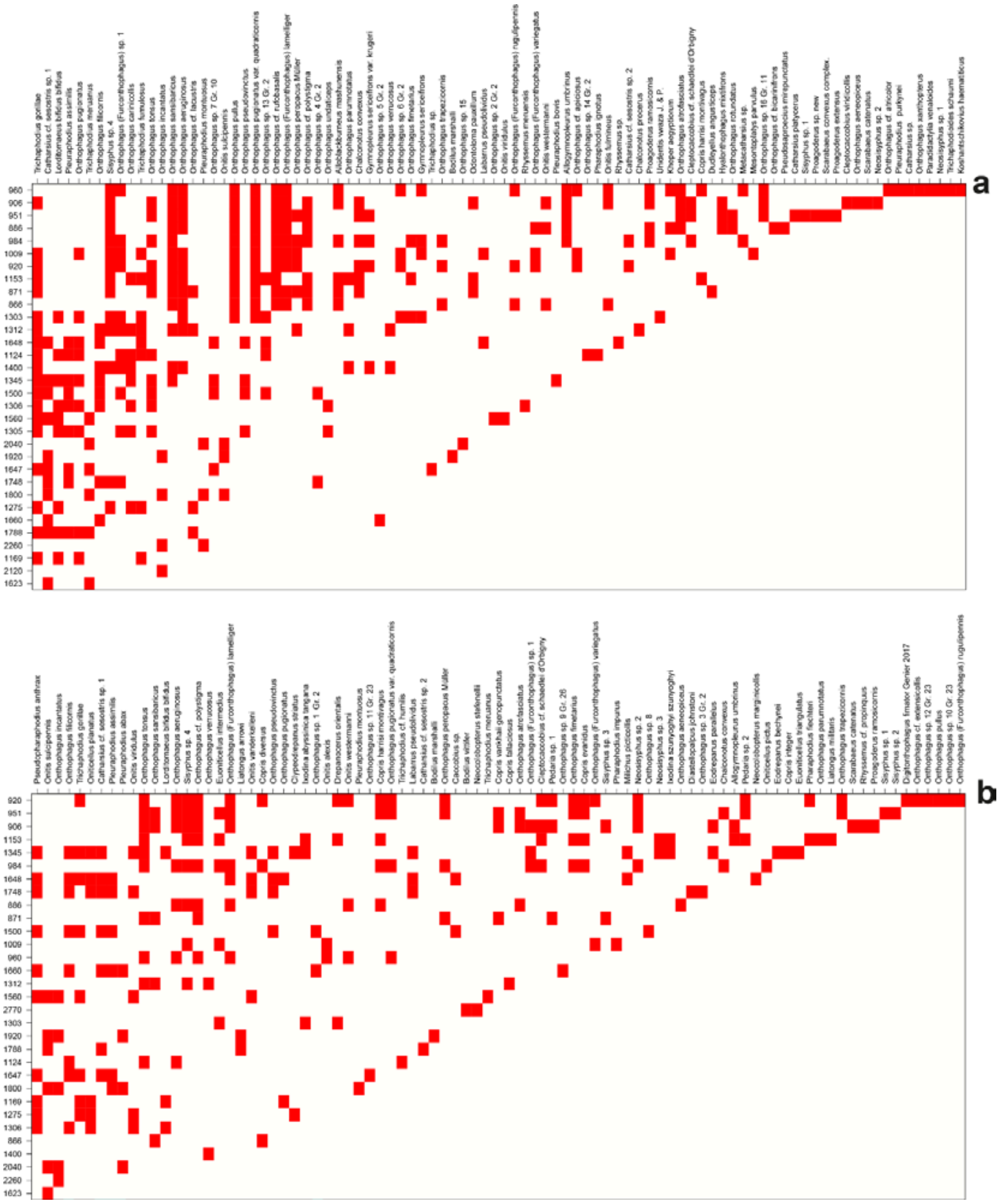


Figure III.S12: Community composition of community sampled with human dung **(a)** and cow dung **(b)**. Coloured squares signify that a species was present at a given elevation while blank squares represent absence of a species.

Appendix III.S13: Path analysis for communities sampled with cow and human dung

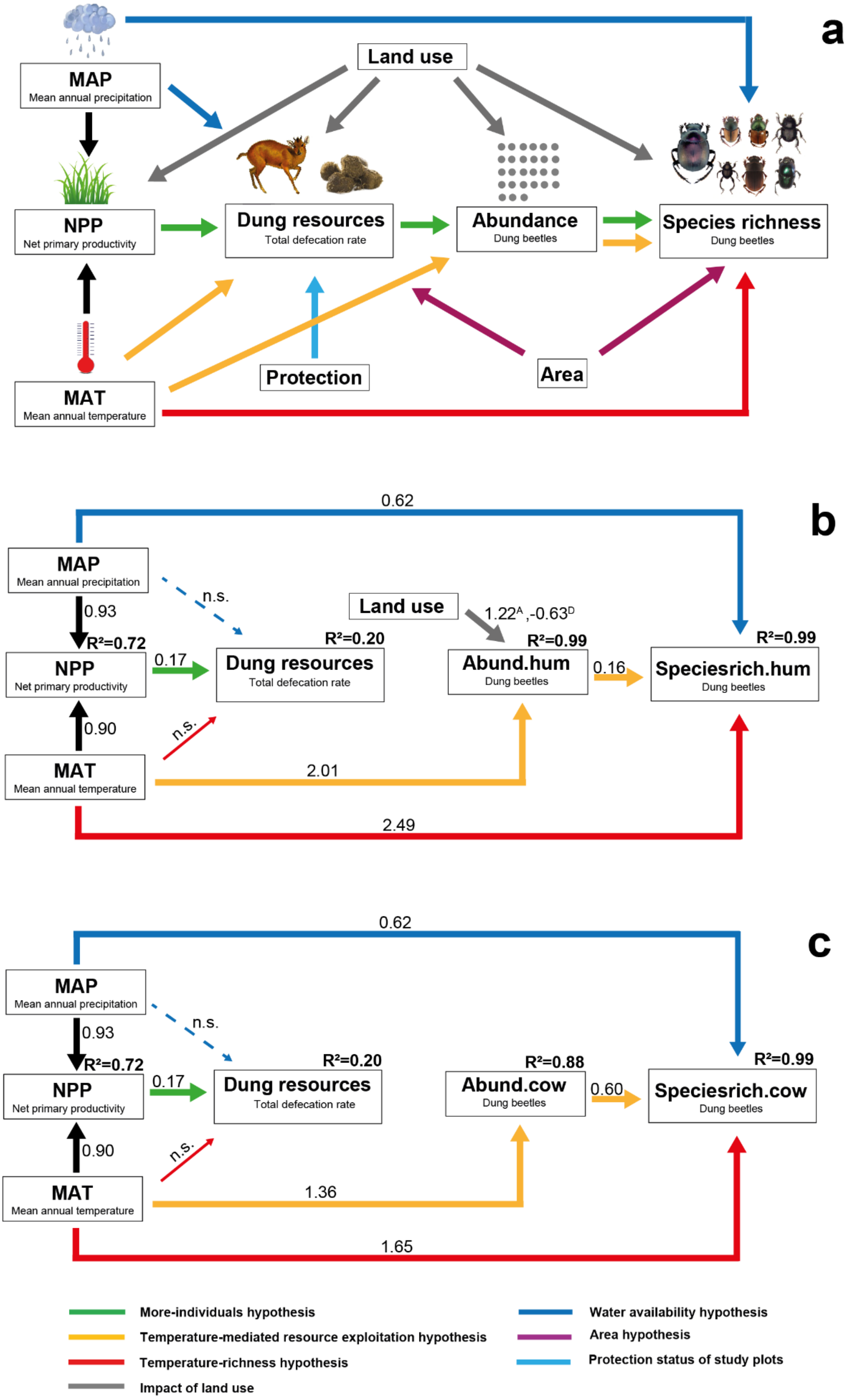


Figure III.S13: Path models illustrating the direct and indirect effects of predictor variables on the species richness of dung beetles on Mt. Kilimanjaro. **(a)** Starting path model showing all hypothesized effects of predictor variables on the species richness and abundance of dung beetles. **(b)** Path model best supported by the data ($AIC_c = 67.93$) for the dung beetle community sampled with human dung. **(c)** Path model best supported by the data ($AIC_c = 51.63$) for the dung beetle community sampled with cow dung. Different coloured arrows depict different expected linkages between environmental variables and dung beetle communities. 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. **(b)** ^{A,D} As land use is a factorial variable, the path coefficients are not standardized. Additional paths from the best supporting path models ($AIC_c = 69.83$ for human dung, $AIC_c = 53.30$ for cow dung) are shown with dashed lines.

Appendix III. S14: Path analysis for overlapping period of mammal and dung beetle sampling

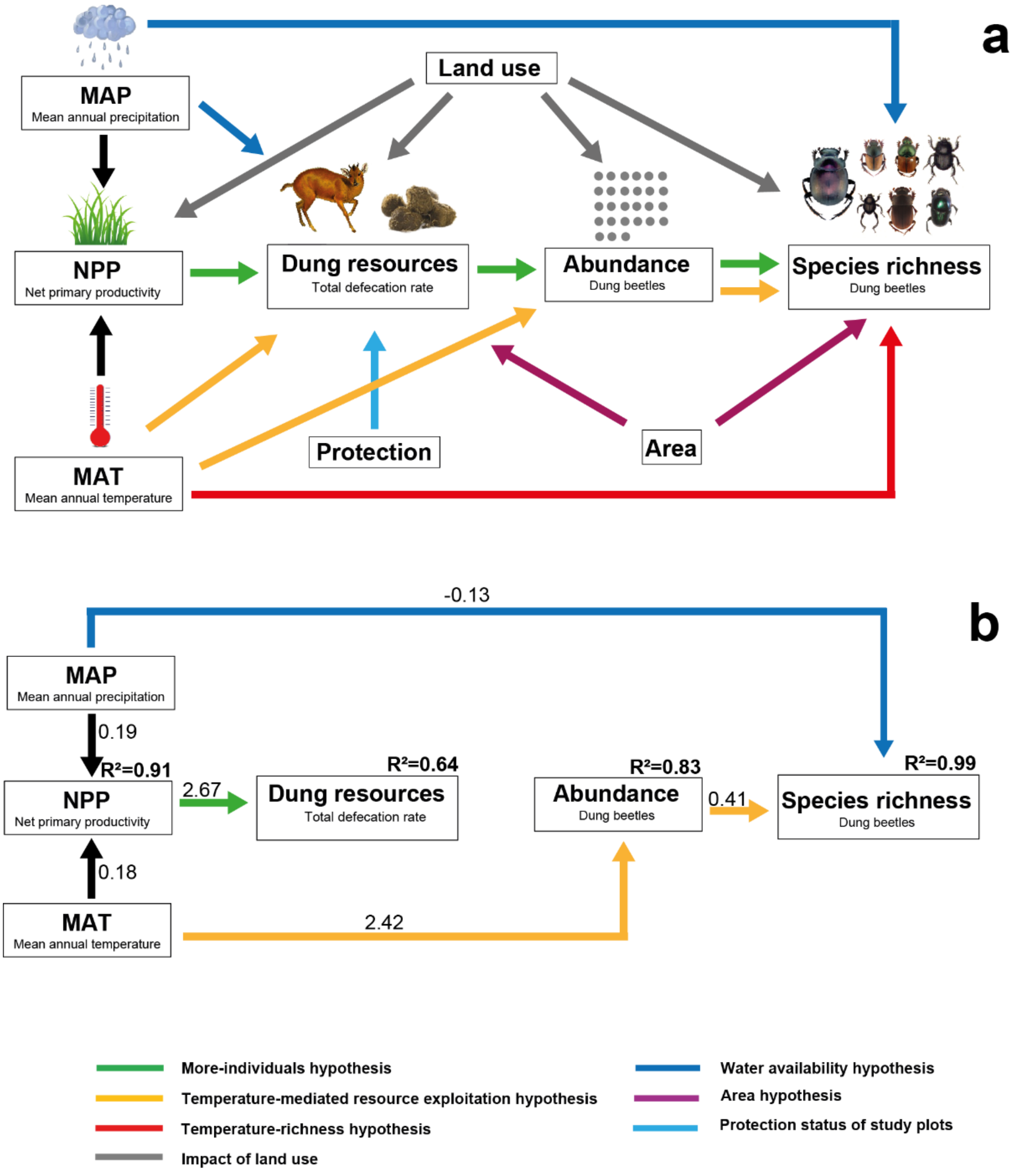
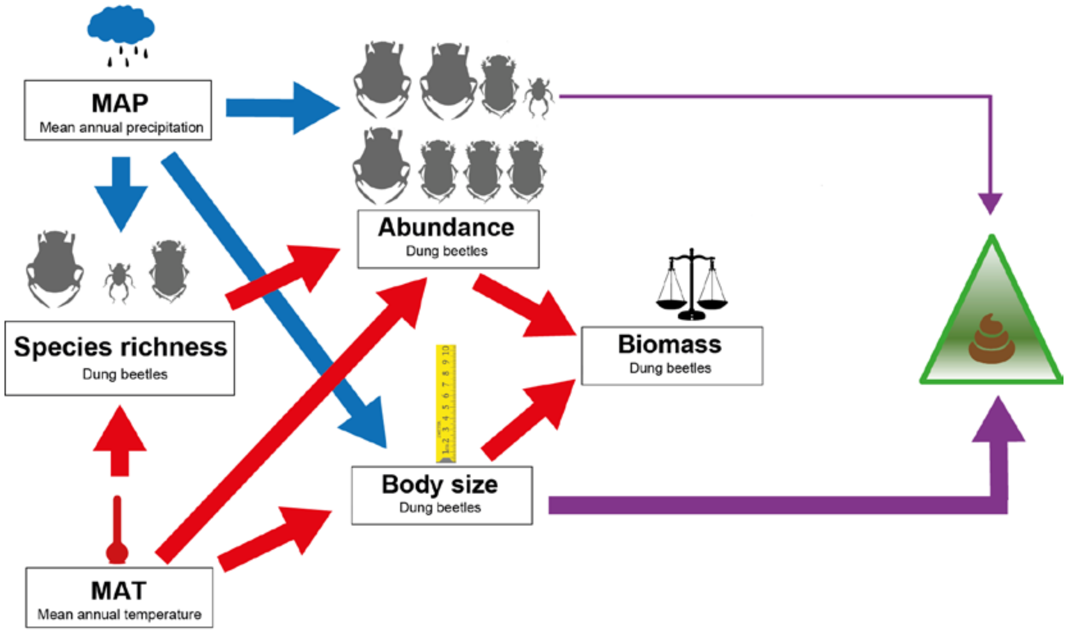


Figure III.S14: Path models illustrating the direct and indirect effects of predictor variables on the species richness of dung beetles on Mt. Kilimanjaro for the period of overlapping mammal and dung beetle sampling (May, June 2015, 2016). **(a)** Starting path model showing all hypothesized effects of predictor variables on the species richness and abundance of dung beetles. **(b)** Path model best supported by the data (AIC_c = -367.15) Different coloured arrows depict different expected linkages between environmental variables and dung beetle communities. The relative amount of explained variance (R^2) is given for all response variables. Numbers above paths represent standardized path coefficient

CHAPTER IV

CHANGES IN BODY SIZE AND SPECIES RICHNESS OF DUNG BEETLES DETERMINE RATES OF DUNG DECOMPOSITION ON MT. KILIMANJARO



Tropical biodiversity is increasingly threatened by anthropogenic climate and land use changes, with little understood consequences for ecosystem functions. Using a combination of experiments and field data along extensive elevation and land use gradients on Mt. Kilimanjaro, we investigate the direct and indirect effects of changes in climate and the structure of dung beetle assemblages on rates of dung decomposition. Dung beetles were collected with baited pitfall traps on 66 study plots along a 3.6 km elevation gradient in natural and anthropogenic habitats. Simultaneously, we conducted exclosure experiments to explore the impact of different extinction scenarios on dung decomposition, consisting of three treatments: the first comprised cow dung pads accessible to the whole dung beetle community, the second excluded large dung beetles, while the third did not allow decomposition by any dung beetles. We applied path analysis to unravel the effects of climate, dung beetle richness, abundance and body size on decomposition. Dung decomposition rates declined with increasing elevation and were highest for open pads, intermediate for treatments excluding large dung beetles and lowest for treatments barring all dung beetles. Path analysis revealed that climate- and species richness-mediated changes in dung beetle abundance and body size were the major drivers of dung decomposition by whole dung beetle communities, while species richness became important when large dung beetles were excluded from the dung. Temperature was the main determinant of dung decomposition when the whole dung beetle community was absent. This study shows that the functional composition of species assemblages, mediated by climate, strongly influences ecosystem functions. Our results emphasize the importance of large dung beetles for maintaining high rates of dung decomposition. The loss of large dung beetles from ecosystems will probably lead to a strong decline in decomposition rates. Therefore, the conservation of intact dung beetle communities in mountain ecosystems is pivotal to ensure ecosystem service provision in the future.

IV.1 Introduction

Global biodiversity is threatened by anthropogenic disturbances such as climate change and land use (Chapin et al. 2000) with subsequent expected declines in ecosystem functions and services (Hatfield et al. 2018). Experimental studies suggest strong linkages between biodiversity and ecosystem functions because of negative relationships between biodiversity loss and 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). 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 conducted in small-scale manipulative experiments and in study regions with narrow climatic gradients (van der Plas 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 pure taxonomic diversity considering only species richness and abundance, inclusion of functional traits of species has been shown to better predict ecosystem functions (Gagic et al. 2015). Functional traits are defined as the features of an organism influencing its fitness and regulating its reaction to environmental impacts and ecosystem processes (Reiss et al. 2009, Cadotte et al. 2011). One of the most important functional traits is body mass. Not only is body mass associated with many life-history traits, but it also regulates metabolic rates and energetic requirements (Brown et al. 2004). Moreover, species losses happen non-randomly with larger-bodied species often being more extinction-prone than smaller-bodied species (Brose et al. 2017). In order to better predict the consequences of biodiversity loss on ecosystem functions, it is important to identify potential linkages between body size and ecosystem functions (Woodward et al. 2005).

In this study, we explored the drivers of ecosystem functions along the extensive climate and land use gradient on Mt. Kilimanjaro, Tanzania. Since mountain ecosystems are particularly vulnerable to human-induced land use and climate change (Messerli & Ives 1997), it is pivotal to study BEF relationships also along elevational gradients. 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). We focused on dung decomposition by dung beetles, a central ecosystem function linked to nutrient cycling, bioturbation, plant growth enhancement, parasite suppression and secondary seed dispersal (Nichols et al. 2008).

Studies exploring the decomposition of dung along elevation are rare and either focus on the temperature-dependency of general nutrient discharge from dung without considering dung beetles (Xu et al. 2010) or focus on intact dung beetle communities (Nunes et al. 2018). To our best knowledge, our study is the first to conduct an exclosure experiment along a broad-scale elevational gradient to investigate the importance of biodiversity, functional traits and climate as drivers of dung decomposition. In addition to exploring decomposition by the whole dung beetle community, we both simulated a future scenario where large dung beetles have become extinct and imitated the extinction of the whole dung beetle community, resulting in an exclosure experiment with three treatments: Treatment O (open dung) consisted of cow dung pats accessible for the whole dung beetle community, treatment H (half-open dung) excluded large dung beetles from dung pats and treatment C (closed dung) did not allow decomposition by any dung beetles. In the closed treatment, decomposition by microorganisms might play a dominant role. Applying path analysis, we unravelled the direct and indirect effects of climate and biodiversity on dung decomposition along elevational and land use gradients. As regards biodiversity, we did not only analyze dung beetle community parameters such as species richness and abundance, but also included dung beetle body size and community biomass to account for the possible influence of functional traits on decomposition processes. We expected climate to either affect decomposition rates directly, or indirectly via a positive effect on species richness, abundance and functional traits of dung beetles.

IV.2 Methods

IV.2.1 Study plots

The study was carried out on 66 study plots of ca. 50 x 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). Mt. Kilimanjaro has a northwest-southeast diameter of 90 km and rises from the savannah plains at 700 m elevation to a snow-clad summit at 5,895 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 to 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 (700 m a.s.l.) to -8 °C at the summit (5895 m a.s.l.). 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 3.6 km from 870 to 4550 m a.s.l., and equally assigned to the 13 main natural and anthropogenic ecosystem types in the region (5-6 study plots per ecosystem type, Supplementary Information Appendix IV.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 sudivided 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). 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.

IV.2.2 Climate and NPP

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 two years, temperature was measured every five minutes and for each study plot, MAT was computed as the average of all measurements (Appelhans et al. 2016). Data on MAP was collected with approximately 70 rain gauges distributed across the different ecosystem types and elevations on Mt. Kilimanjaro (Appelhans et al. 2016). 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 (Appelhans et al. 2016). More information can be found in the supplement (Supplementary Information Appendix IV.S2).

IV.2.3 Measuring dung decomposition: exclosure experiment

For measuring dung decomposition rates, 700 g of fresh cow dung were placed on study plots and remains were recollected after 15 days. Cow dung was collected locally and frozen for at least 24 hours prior to the experiment, guaranteeing that any dung beetles dwelling in the dung were killed. To test the contribution of large dung beetles and the whole dung beetle community to decomposition, respectively, we applied three different treatments to the dung pads: To assess dung decomposition by the whole decomposer community, an open (non-caged) cow dung pad was used (O). Since open dung pads could be accessed by all organisms present, this treatment depicted the natural rate of dung decomposition (Lähteenmäki et al. 2015). To exclude large dung beetles, the cow dung pad was surrounded by a mesh wire with a mesh size of 0.5 cm (H for half-open dung). This treatment represented a scenario where more threatened large dung beetles have become extinct but smaller beetles are still present. We employed a mesh size of 0.5 cm since the average dung beetle 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 consequently termed ‘small’. Dung beetles with a pronotum width larger than 0.5 cm were designated as ‘large’. In a third treatment the whole dung beetle community was excluded by surrounding dung pads with a wire gauze with a mesh size of 0.1 cm (C for closed dung). Although treatment C did not allow decomposition by dung beetles, other decomposers like flies, fungi and microorganisms still had access to the dung; the former by placing eggs through the gauze into the dung (Kudavidanage et al. 2012). This treatment represented a touchstone for ecosystem functioning in the absence of dung beetles (Lähteenmäki et al. 2015). All dung pads were arranged into uniform pads (ca. 15 cm in diameter and 6 cm high) and shielded with canvas from rain and sun. On each 50 x 50 m study plot, one open, one half-open and one closed dung pad were placed in three corners so that the distance between treatments amounted to 50 m, the minimum distance required to ensure independence of traps for dung beetles (Larsen and Forsyth 2005). The arrangement of the three treatments as well as a pitfall trap was randomized with regard to the slope and vegetation characteristics on study plots. After 15 days, dung remains were carried to the laboratory and dried in a drying oven at 60°C for at least two days prior to calculating dry weights. To obtain a reference dry weight, we dried ten 700 g piles consisting of fresh cow dung and calculated the mean dry weight. For all statistical analyses, we used the remaining dry weight of dung as a measure of dung decomposition rate. We conducted the exclosure experiment from June 2015 to February 2016.

IV.2.4 Trapping dung beetles

In addition to the three dung decomposition treatments, we placed a baited pitfall trap in the fourth corner of each study plot to simultaneously collect data on dung beetle diversity. We collected dung beetles from October 2015 to February 2016. One pitfall trap (upper diameter 33 cm, lower diameter 24 cm, height 15 cm) was employed per study plot. We filled each trap with 1.5 L of water with detergent to lessen water surface tension, obtaining a water height of 3 cm. As baits, we also applied fresh cow dung here (frozen for at least 24 hours prior to the experiment). The 700 g of fresh cow dung were placed on a mesh positioned over the trap, resembling a natural dung pad with a diameter of approximately 15 cm. To shelter traps from sun and rain, they were covered with canvas. Traps were emptied after a duration of 72 hours. Collected specimens were sieved and stored in whirl packs filled with 70% ethanol. Dung beetles were sorted to species level. Where identification to species level was not possible, specimen were assigned a morphospecies number.

IV.2.5 Functional traits of dung beetles

We used pronotum width as a proxy for dung beetle body size (Berson & Simmons 2018). We measured pronotum width with a measuring ocular. On each study plot, we took measurements of ten individuals per species. If the number of collected individuals of a species on a study plot was smaller than ten, all individuals were measured. For each species on each study plot, we calculated the mean body size. The mean body size of dung beetles for each study plot was computed as the average body size across all species (i.e. revealing a species-weighted 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 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 then calculated the total biomass of the dung beetle community of each study plot by summing up the dry masses of all individuals. In cases where more than ten individuals were collected per species, we multiplied the mean biomass of the ten measured individuals with the total number of individuals in order to add their proper contribution to the community biomass.

IV.2.6 Statistical analysis

We analyzed dung decomposition rates (i.e. the dry mass of remaining dung) along the elevation gradient with generalized additive models (GAMs). In GAMs, non-parametric smoothers are used to depict potential nonlinear or linear relationships between explanatory and response variables rather than assigning a specific functional formula to the relationship between response and predictor variables. We utilized the R package ‘mgcv‘ with its ‘gam‘ function to compute GAMs (Wood 2006) and fitted a Gaussian data family. To prevent over-parametrization of GAMs, we restricted the dimension of the smoothing term to $k \leq 5$. We calculated separate models for each of the dung exclosure treatments (i.e. for the O, H, and C treatment). We also explored whether land use had an effect on dung decomposition for the three treatments by comparing residual plots.

Using path analysis, we explored the direct and indirect effects of temperature, precipitation, as well as the effects of abundance, species richness, body size and biomass of the dung beetle community on dung decomposition. Path analysis was conducted separately for the three different treatments of the exclosure experiment to explore whether there are different drivers of dung decomposition for dung beetle communities composed of different size classes and to explore dung decomposition in the absence of dung beetles. For treatment O and C, biomass, abundance, body size and species richness data of the whole dung beetle community was considered while for treatment H, only data on small dung beetles (pronotum width < 5 mm) was included in path analysis.

Potential path combinations were pre-selected by establishing a set of competitive explanatory models for each response variable (dung beetle species richness, abundance, body size, biomass and remaining dry weight) 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.

As species richness and abundance of dung beetles had a negative binomial error distribution, 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' (Shipley 2000, 2009, 2013, Lefcheck 2016). 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. In addition, we visualized the relationships between dung decomposition and its main predictors obtained by the path analysis for the three treatments To analyze the distribution of the dung beetle community metrics species richness, abundance, total biomass and body size with elevation, we employed GAMs. We calculated separate GAM models for the elevational distribution of mean, maximum and minimum body size of dung beetles. For body size of dung beetles, we explored elevational patterns only considering study plots where dung beetles were present. Statistics were conducted in R version 3.5.1 (R Core Team 2018).

IV.3 Results

IV.3.1 Patterns of dung decomposition along elevation

Averaged over the whole elevational gradient, in open treatments 21.4 % of available dry mass of dung was lost, in half-open treatments 11.6 %, and in closed treatments 5.5 %. Dung decomposition decreased with increasing elevation for all three treatments, i.e. the remaining dry weight increased with rising elevation (Fig. IV.1d, treatment O (open dung, Fig. IV.1a): ED = 30.2 %, $p_{Elevation} < 0.001$; treatment H (half-open dung, Fig. IV.1b): ED = 14.6 %, $p_{Elevation} < 0.05$, treatment C (closed dung, Fig. IV.1c): ED = 16.3 %, $p_{Elevation} < 0.001$).

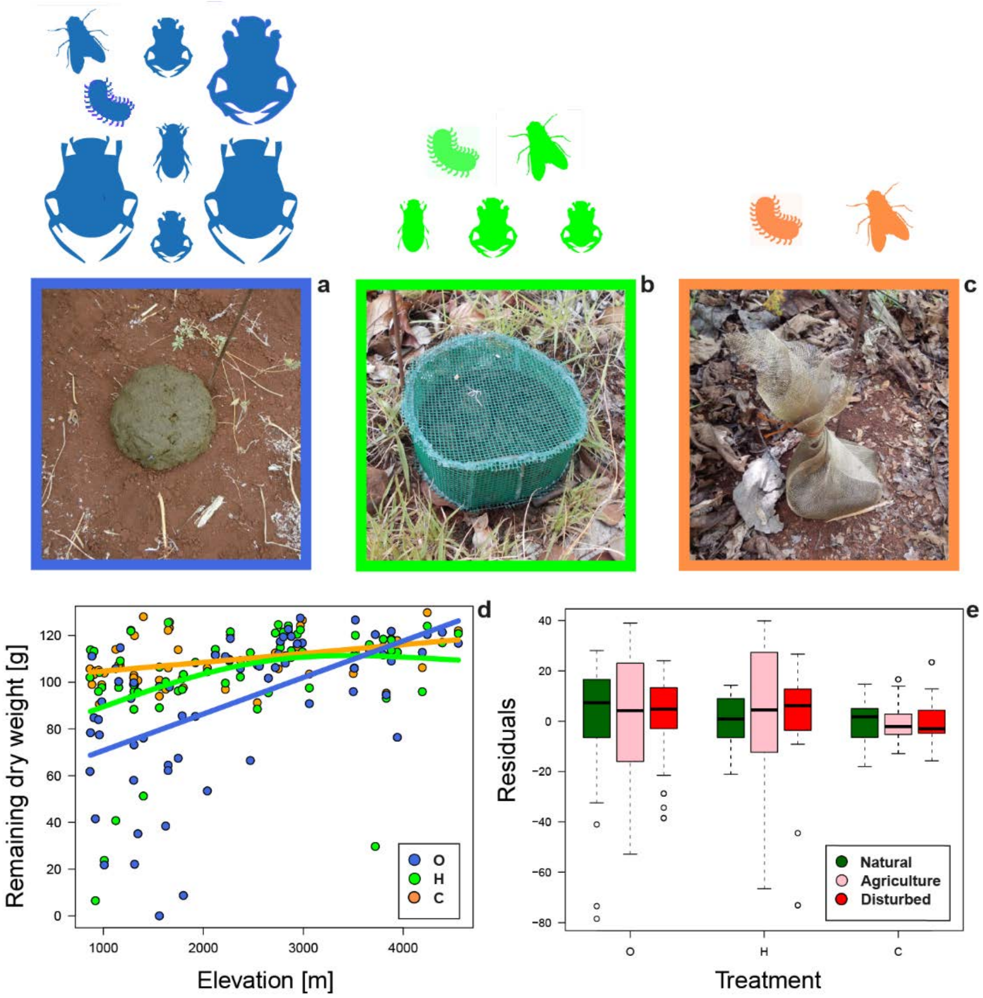


Figure IV.1 The three different treatments of the dung exclosure experiment and the pattern of dung decomposition with elevation. **(a)** In treatment O (open dung) dung was accessible to the whole dung beetle community as well as to flies and microorganisms. **(b)** Treatment H (half open dung) only allowed decomposition by small dung beetles, flies and microorganisms. **(c)** In treatment C, the whole dung beetle community was excluded, yet decomposition by small decomposers like fly larvae and microorganisms was still possible. **(d)** Dung decomposition along elevation measured as remaining dry weight for the three different treatments of the exclosure experiment (O, H and C). Dots represent original measurements on study plots. Blue represents trend lines for treatment O (open dung), green depicts treatment H (half-open dung) and orange treatment C (closed dung). Trend lines were calculated with generalized additive models (Gaussian family). The black dotted line depicts the reference dry weight. **(e)** Residual variation in dung decomposition rates (after controlling for the effect of elevation) for the three treatments (O, H and C), separated into natural, agricultural and disturbed habitats.

The difference between treatments was highest at low elevations and decreased with increasing elevation (Fig. IV.1d). At low elevations, open dung pads (O) accessible to the whole dung beetle community constituted the lightest pads while closed pads (C) excluding all dung beetles were the heaviest. Treatments where only small dung beetles could enter (H, half-open dung) were of intermediate weights. Dung decomposition did not differ between natural, agricultural and disturbed habitats (Fig. IV.1e).

IV.3.2 Patterns of dung beetle community metrics

We collected a total of 1277 dung beetles belonging to 87 species (Supplementary Information Appendix IV.S3). Species richness, abundance and total biomass of dung beetle communities declined with increasing elevation (species richness: Fig. IV.2a, ED = 51.9 %, $p_{\text{Elevation}} < 0.001$; abundance: Fig. IV.2b, ED = 27.8 %, $p_{\text{Elevation}} < 0.001$; total biomass Fig. IV.2c, ED = 19.9 %, $p_{\text{Elevation}} < 0.001$) and was higher in natural compared to anthropogenic habitats at low elevations (Supplementary Information Appendix IV.S4). When all study plots were considered, dung beetle maximum, mean and minimum body size decreased with increasing elevation (Supplementary Information Appendix IV.S5). Considering only study plots where dung beetles were present, maximum, mean and minimum body size did not change with elevation (Fig. IV.2d, maximum body size: ED = 8.1 %, p = 0.396; mean body size: ED = 11.9 %, p = 0.234; minimum body size: ED = 1.83 %, p = 0.468). Mean body size was not significantly affected by land use (Supplementary Information Appendix IV.S4). However, when considering the functional groups tunnellers, rollers, dwellers and kleptoparasites separately, for rollers and dwellers, mean body size was higher in natural compared to anthropogenic habitat while there was no difference between habitat types for tunnellers and kleptoparasites (Supplementary Information Appendix IV.S4). Overall, tunnellers comprised the functional group with most species and the most abundant, largest and heaviest individuals. Both species richness and abundance of tunnellers was higher in natural compared to anthropogenic habitats at low elevations (Supplementary Information Appendix IV.S4).

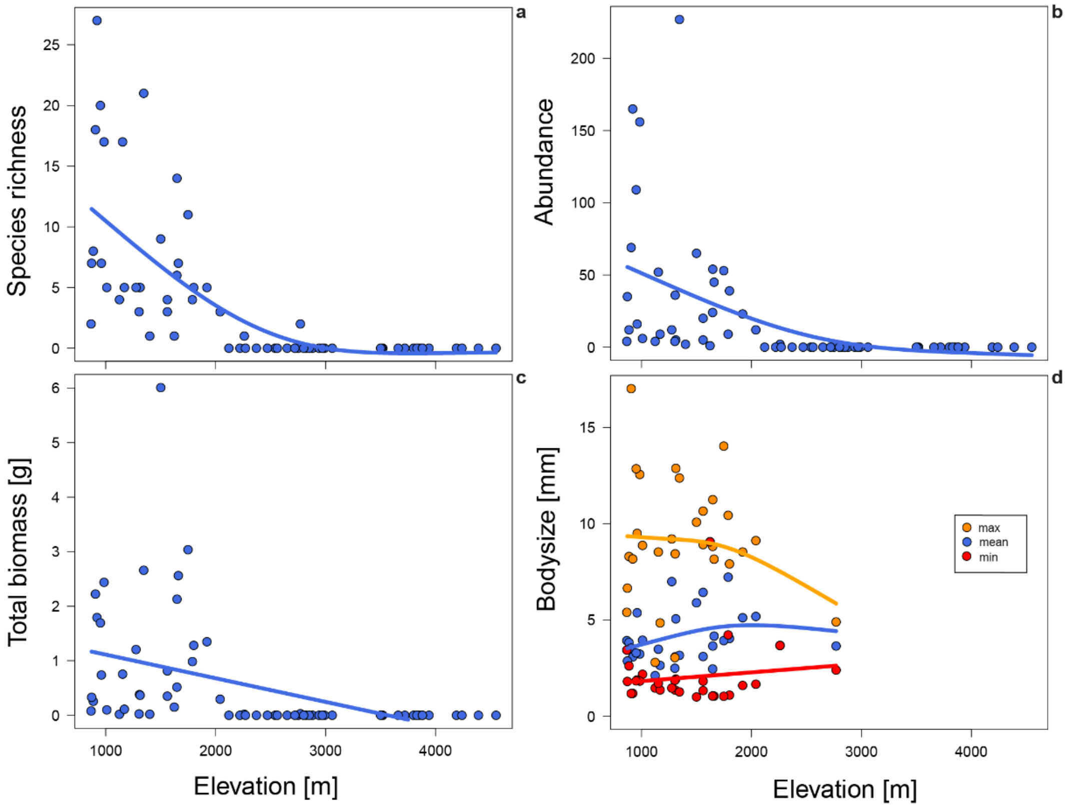


Figure IV.2 Elevational distribution of dung beetle community parameters. Patterns of species richness **(a)**, abundance **(b)**, total biomass **(c)** and body size **(d)** of dung beetles on

Mt. Kilimanjaro are shown. Dots represent original measurements on study plots. Trend lines were calculated with generalized additive models (Poisson family for **a, b**; Gaussian family for **c, d**). **(d)** Different colours were used for mean (blue), maximum (orange) and minimum (red) body size.

IV.3.3 Drivers of dung decomposition along elevation

Path analysis illustrated that the factors influencing dung decomposition differed between the three treatments of the dung exclosure experiment. For fully open dung pads (treatment O) the remaining dry weight was mainly influenced by the mean body size of dung beetle communities and, secondly, by the abundance of dung beetles (Fig. IV.3b). The latter trend was not significant in the path analysis ($p = 0.13$). However, we found a correlation between the remaining dry weight and dung beetle abundance ($r = -0.37$, $p < 0.05$). Dung beetle abundance was strongly correlated to dung beetle species richness ($r = 89$, $p < 0.001$). Decomposition rates were higher where dung beetle communities were composed of many individuals with large body sizes (Supplementary Information Appendix IV.S5: mean body size: $p < 0.001$; abundance: $p < 0.05$). When only considering study plots where dung beetles were present for treatment O, there was a non-significant relationship between decomposition rates and dung beetle abundance. (Supplementary Information Appendix IV.S6). The trend of increasing dung beetle size with rising decomposition became also non-significant in this case (Supplementary Information Appendix IV.S5a, red dotted line, $p = 0.12$) and does not appear in the path diagram (Supplementary Information Appendix IV.S6). When large dung beetles were excluded (treatment H), decomposition was solely driven by species richness (Fig. IV.3c), implying that a higher species richness resulted in augmented decomposition (Fig. IV.3c, Supplementary Information Appendix IV.S5: $p < 0.001$) When no dung beetles had access to the dung pad (treatment C), dung decomposition was best predicted by mean annual temperature (MAT), resulting in higher decomposition rates at higher temperatures (Fig. IV.3d; Supplementary Information Appendix IV.S5, $p < 0.05$).

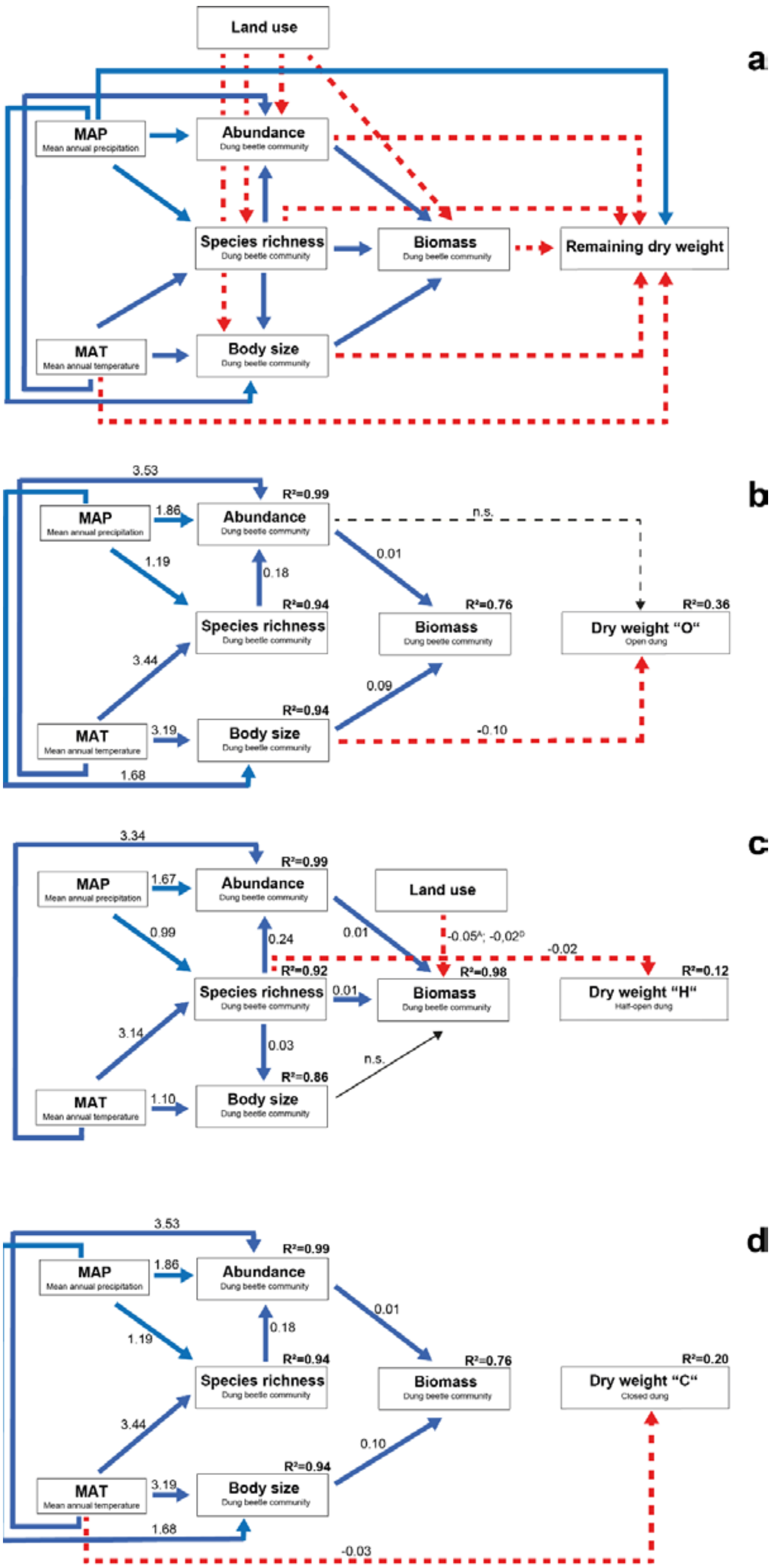


Figure IV.3 Path model illustrating the direct and indirect effects of predictor variables on dung decomposition on Mt. Kilimanjaro for the three different treatments of the exclosure experiment (Treatment O, treatment H and treatment C). Remaining dry weight was employed as a measure for dung decomposition. **(a)** Starting path model showing all hypothesized effects of predictor variables on dung decomposition. **(b)** Path model best supported by the data for treatment O (open dung, $AIC_c = 94.7$), **(c)** for treatment H (half open dung, $AIC_c = 91.32$) and **(d)** for treatment C (closed dung, $AIC_c = 89.18$). Different coloured arrows depict different expected linkages between predictor variables and dung decomposition. Blue solid lines depict positive relationships while red dashed lines illustrate negative effects. Non-significant relationships are featured with thin lines. **(b, c)** Black arrows depict relationships that appeared in alternative path models that could not be statistically distinguished from the best model ($\Delta AIC_c < 2$). The relative amount of explained variance (R^2) is given for all response variables. Numbers above paths represent standardized path coefficients. Please note that land use (three levels: natural, agricultural, disturbed, the latter two can be summarized as anthropogenic) is a factorial variable such that path coefficients are not standardized. ^{A} Agricultural plots, ^{D} Disturbed plots. Model support for all response variables for the three treatments can be found in the supplement (Supplementary Information Appendix IV.S7).

IV.4 Discussion

In this study, we found that dung decomposition rates decreased with increasing elevation. At low elevations, decomposition differed between treatments with different dung beetle communities. Dung decomposition was the highest where the whole dung beetle community was present, intermediate where large dung beetles were excluded and the lowest in the absence of dung beetles. To our knowledge, this is the first elevational study comparing decomposition by naturally occurring dung beetle communities to experimentally manipulated assemblages. Our study contributes to the current debate about the importance of abundance and species richness in mediating ecosystem services (Dainese et al. 2019) and also discusses the importance of incorporating functional traits into BEF studies (Gagic et al. 2015). We show that the drivers of ecosystem services change with augmented disturbance of the study system. In undisturbed communities, functional traits were the main drivers for ecosystem services. Temperature influenced decomposition rates indirectly, i.e. by its effect on dung beetle communities. Species richness raised to the main predictor in the absence of the main ecosystem service providers, i.e. large dung beetles. A direct temperature effect was supported under complete beetle exclosure when decomposition was restricted to fly larvae and microbial decomposers.

Dung beetle-mediated decomposition was highest at low elevations where dung beetle diversity reached its peak, a result consistent with the hypothesis that more diverse communities are superior in ecosystem service provisioning to less diverse communities (Hooper et al., 2005). Accordingly, the experimental exclusion of dung beetles strongly reduced decomposition rates, emphasizing the importance of intact dung beetle communities for dung decomposition (Slade et al. 2007). In general, dung decomposition decreased with increasing elevation, mirroring the decline of dung beetle richness with rising elevation (Davis et al. 2005). Where no dung beetles were present, as was the case in the highest elevations, no considerable dung decomposition was observed.

In the presence of the entire dung beetle community, both dung beetle body size and to a lesser extend dung beetle abundance were the drivers of dung decomposition, pointing to the pivotal role of large dung beetles for decomposition (Slade et al. 2011b, Nervo et al. 2014). The exclusion of large dung beetles had huge functional consequences as larger dung beetles are more efficient in decomposition than smaller dung beetles (Braga et al. 2013). Larger dung beetles have also been shown to be more extinction prone than smaller beetles (Braga et al. 2013). Because of their huge importance in decomposition, the extinction of large dung beetles may have negative repercussions on other dung beetle-mediated ecosystem services such as nutrient cycling and secondary seed dispersal (Slade et al. 2007), as well as on ecosystem functioning in general (Piccini et al. 2018).

When large dung beetles were experimentally excluded, dung decomposition rates were lower and species richness became the main determinant of dung decomposition, highlighting that communities consisting of only small dung beetles could not compensate for the absence of large dung beetles (Slade et al. 2007). Furthermore, MAT rose to the sole driver for dung decomposition when all dung beetles were excluded. In studies investigating dung decomposition without considering dung beetles, MAT was also reported as one major driver of dung decomposition (Xu et al. 2010). In general, the amount of variance explained for dung decomposition in the dung beetle exclosure treatments was very low, indicating a lower predictability of dung decomposition rates under impoverished dung beetle communities. In our study, the effect of microorganisms, flies and other small organisms on dung decomposition was very low in comparison to the effect of dung beetles. However, a limitation of our approach might have been the comparatively short sampling period of 15 days which could either under- or overestimate long-term differences between treatments. Older dung is mainly decomposed by mostly small-bodied endocoprid species (Hanksi & Cambefort 1991) and microorganisms which show a strong seasonality in activity (Becker et al. 2015). This could lead to decreased disparities between treatments over time and to a higher relevance of microorganisms over long time periods for decomposition.

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 et al. 2000, Loreau 2001). In our study, we found that land use led to a change in the characteristics of dung beetle communities but did not significantly influence dung decomposition rates. While the species richness and abundance of dung beetles was reduced, the mean body size of dung beetles remained consistent along the land use gradient. A loss of species and individuals was largely due to the decrease of the behaviorally most specialized groups of dung beetles, rollers and kleptoparasites. In contrast, tunnellers, who dominated in terms of abundance and species richness, were relatively insensitive towards land use and were probably key for the maintenance of dung decomposition in anthropogenic habitats (Slade et al. 2007). Current land use at Mt. Kilimanjaro is still moderate. Nevertheless, 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 decomposition. Huge conservation efforts will be necessary to guarantee the continuity of diversity in the Mt. Kilimanjaro biodiversity hotspot (Mmbaga et al. 2017). Overall, it is paramount to conserve the whole dung beetle community including all functional guilds to ensure the long-term stability of ecosystem service provisioning in the future (Manning et al. 2016, Piccini et al. 2018).

Our study shows that diversity is more important than a direct climate effect in driving decomposition processes when dung beetle communities are intact. However, when dung beetle communities are impoverished or absent, climate may increase in relevance. To conclude, our results indicate that the drivers of ecosystem functions along broad climatic gradients strongly depend on the state of the community in question and may become more biased towards climatic factors the more the community is perturbed.

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 crucial to gain better insight into ecosystem functioning (Nunes et al. 2018). 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 the importance of drivers changes with increased disturbance of the system. In this study, functional traits were the main determinants of ecosystem services in unperturbed communities while species richness was the main predictor when large dung beetles were excluded. Incorporating functional traits into our analysis made it possible to explore the extinction order of dung beetles and the detrimental effects the exclusion of large dung beetles had on ecosystem service provisioning. Therefore, our study emphasizes that it is pivotal to incorporate functional traits into future conservation research to better predict the effect of species extinctions on ecosystem functions and services.

IV.5 Supplementary Information

Appendix IV.S1. Ecosystem types on Mt. Kilimanjaro

Supplementary Table IV.S1: Ecosystem types studied on Mt. Kilimanjaro. The 66 study plots were located in six natural and seven anthropogenic habitats (further subdivided into agricultural and disturbed study plots) along an elevational gradient of 3679 m. While there was no human impact in natural habitats, there was low to high land use intensity in anthropogenic habitats.

habitat	# plots	land use type	elevation[1]	land use intensity
savanna	5	natural	871-1153	none
maize fields	5	anthropogenic (agricultural)	866-1009	high
lower montane forest	5	natural	1560-2020	none
Chagga agroforestry	5	anthropogenic (agricultural)	1169-1788	high
coffee plantations	6	anthropogenic (agricultural)	1124-1648	high
grasslands	5	anthropogenic (agricultural)	1303-1748	high
Ocotea forest	5	natural	2120-2750	none
logged *Ocotea* forest	5	anthropogenic (disturbed)	2220-2560	low
Podocarpus forest	5	natural	2800-2970	none
burned *Podocarpus* forest	5	anthropogenic (disturbed)c	2270-3060	low
Erica forest	5	natural	3500-3900	none
burned *Erica* forest	5	anthropogenic (disturbed)	3500-3880	low
Helichrysum vegetation	5	natural	3880-4550	none

[1] Elevation is shown in m a.s.l.

Appendix IV.S2: Climate and NPP

We used the normalized difference vegetation index (NDVI; Detsch et al. 2016a,b, Peters et al. 2016) as a surrogate for net primary productivity (NPP). NDVI estimates were inferred from MODIS Aqua product MYD13Q1 supplying data of a horizontal resolution of 250 m x 250 m (Kerr and Ostrovsky 2003, Appelhans et al. 2015, 2016). More specific aspects on methodology and original data are featured in Appelhans et al. (2016), Detsch et al. (2016a, b) and Peters et al. (2016).

Appendix IV.S3: Dung beetles of Mt. Kilimanjaro

Supplementary Table IV.S3: Recorded dung beetle species on Mt. Kilimanjaro. Elevation is shown in m a.s.l.

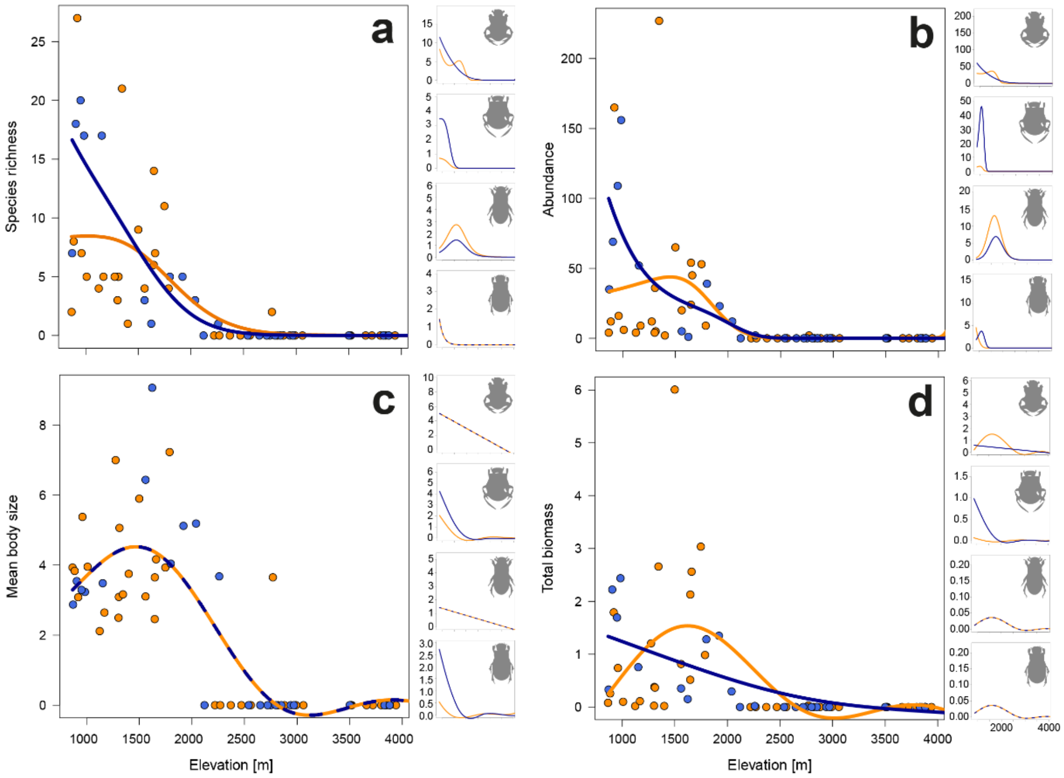
Subfamily	Tribe	Species	Total	Plots[1]	Elevation[2]	Guild[3]
Scarabaeinae	Dichotomiini	*Pedaria sp. 1*	6	3	871-920	k
		Pedaria sp. 2	11	3	920-1153	k
	Coprini	*Catharsius cf. sesostris sp. 1*	60	12	1345-1920	t
		Catharsius cf. sesostris sp. 2	1	3	920-1788	t
		Copris diversus	6	3	866-984	t
		Copris evanidus	7	4	920-1153	t
		Copris fallaciosus	1	1	1312	t
		Copris harrisi montivagus	8	6	886-1153	t
		Copris integer	1	1	1345	t
		Copris vankhaii genopunctatus	4	3	871-951	t
	Canthonini	*Chalconotus convexus*	3	6	871-1153	r
	Gymnopleurini	*Allogymnopleurus umbrinus*	6	6	886-1153	r
		Scarabaeus catenatus	3	1	906	r
		Neosisyphus sp. 2	9	4	906-984	r
		Neosisyphus sp. 3	7	2	1153-1345	r
		Sisyphus sp. 1	1	1	951	r
		Sisyphus sp. 2	1	1	951	r
		Sisyphus sp. 3	4	2	871-906	r
		Sisyphus sp. 4	122	14	871-1748	r
	Onitini	*Onitis alexis*	2	2	960-1009	t
		Onitis sulcipennis	28	6	1560-2040	t
		Onitis vanderkelleni	9	4	1345-1748	t
		Onitis viridulus	14	6	1275-1748	t
		Onitis westermanni	8	5	866-960	t
	Onthophagini	*Caccobius sp.*	2	2	1500-1648	t
		Cleptocaccobius cf. schaedlei	11	5	906-1153	k
		Diastellopalpus johnstoni	2	1	1748	t
		Digitonthophagus fimator	3	1	920	t
		Milichus picticollis	3	2	1345-1648	t
		Onthophagus (Furconthophagus) lamelliger	58	10	866-1648	t
		Onthophagus (Furconthophagus) rugulipennis	1	3	866-960	t
		Onthophagus (Furconthophagus) sp. 1	13	13	906-1748	t

		Onthophagus (Furconthophagus) variegatus	6	3	886-1009	t
		Onthophagus aeneopiceus	1	2	886-906	t
		Onthophagus aeruginosus	15	14	866-1400	t
		Onthophagus atrofasciatus	10	4	886-960	t
		Onthophagus cf. extensicollis	1	1	920	k
		Onthophagus cf. polystigma	105	9	866-1153	t
		Onthophagus filicornis	98	10	1124-1748	t
		Onthophagus fimetarius	15	5	920-1303	t
		Onthophagus incantatus	23	6	1560-2260	t
		Onthophagus parumnotatus	3	3	1153-1400	t
		Onthophagus peropacus	10	6	871-1312	t
		Onthophagus pseudovinctus	183	5	1305-1748	t
		Onthophagus pugionatus	3	9	1009-1788	t
		Onthophagus pugionatus var. quadraticornis	6	11	866-1303	t
		Onthophagus pullus	1	9	866-1303	t
		Onthophagus sansibaricus	10	13	866-1400	t
		Onthophagus sp. 1 Gr. 2	4	2	1500-1660	t
		Onthophagus sp. 3 Gr. 2	1	1	1748	t
		Onthophagus sp. 8	1	1	1500	t
		Onthophagus sp. 9 Gr. 26	1	1	1660	t
		Onthophagus sp. 10 Gr. 23	1	1	920	t
		Onthophagus sp. 11 Gr. 23	1	1	1647	t
		Onthophagus sp. 12 Gr. 23	3	1	920	t
		Onthophagus tonsus	133	13	871-1500	t
		Onthophagus trapezicornis	3	4	866-984	t
		Onthophagus verrucosus	3	2	1312-1400	t
		Proagoderus ramosicornis	3	4	886-984	t
	Oniticellini	*Clypeodrepanus striatus*	3	2	1275-1345	t
		Drepanocerus orientalis	8	3	920-1303	t
		Eodrepanus bechynei	1	1	1345	t
		Eodrepanus parallelus	2	2	906-1345	t
		Euoniticellus intermedius	7	5	951-1303	t
		Euoniticellus triangulatus	1	1	1345	t
		Ixodina abyssinica tangana	3	3	1153-1345	t
		Ixodina szunyoghyi szunyoghyi	7	2	1153-1345	t
		Liatongus arrowi	6	2	1788-1920	t
		Liatongus militaris	1	1	1153	t
		Oniticellus pictus	2	1	984	d
		Oniticellus planatus	19	6	1169-1748	d
Aphodiinae		*Bodilus marshalli*	4	1	1920	d
		Bodilus vittifer	1	1	2770	d
		Labarrus pseudolividus	17	4	1009-1748	d

Lorditomaeus bifidus bifidus	13	9	1124-1788	d
Neocolobopterus marginicollis	1	1	1648	d
Neocolobopterus stefenellii	1	1	2770	d
Pharaphodius fiechteri	2	2	920-1153	d
Pharaphodius impurus	1	1	1009	d
Pleuraphodius abax	28	4	1660-2040	d
Pleuraphodius assimilis	18	11	1124-1800	d
Pleuraphodius montuosus	2	3	1800-2260	d
Pseudopharaphodius anthrax	31	10	1169-1748	d
Rhyssemus cf. propinquus	1	1	906	d
Trichaphodius cf. humilis	1	1	1124	d
Trichaphodius gorillae	36	19	871-1788	d
Trichaphodius meruanus	1	6	1560-2040	d

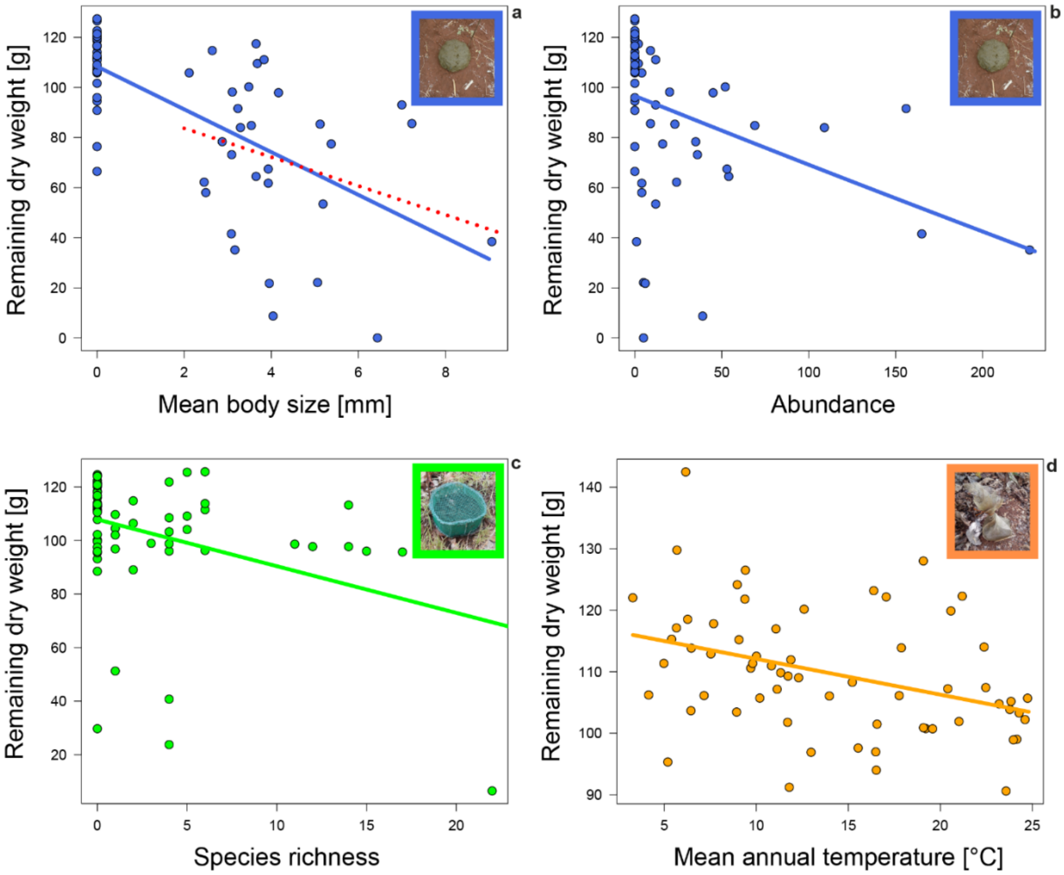
Note. [1]Indicates the number of study plots on which species were caught. [2]Implies the elevational range of study plots on which species were present. [3]k = kleptoparasite, t = tunneller, d = dweller, r = roller, u = unknown

Appendix IV.S4: Dung beetle community metrics



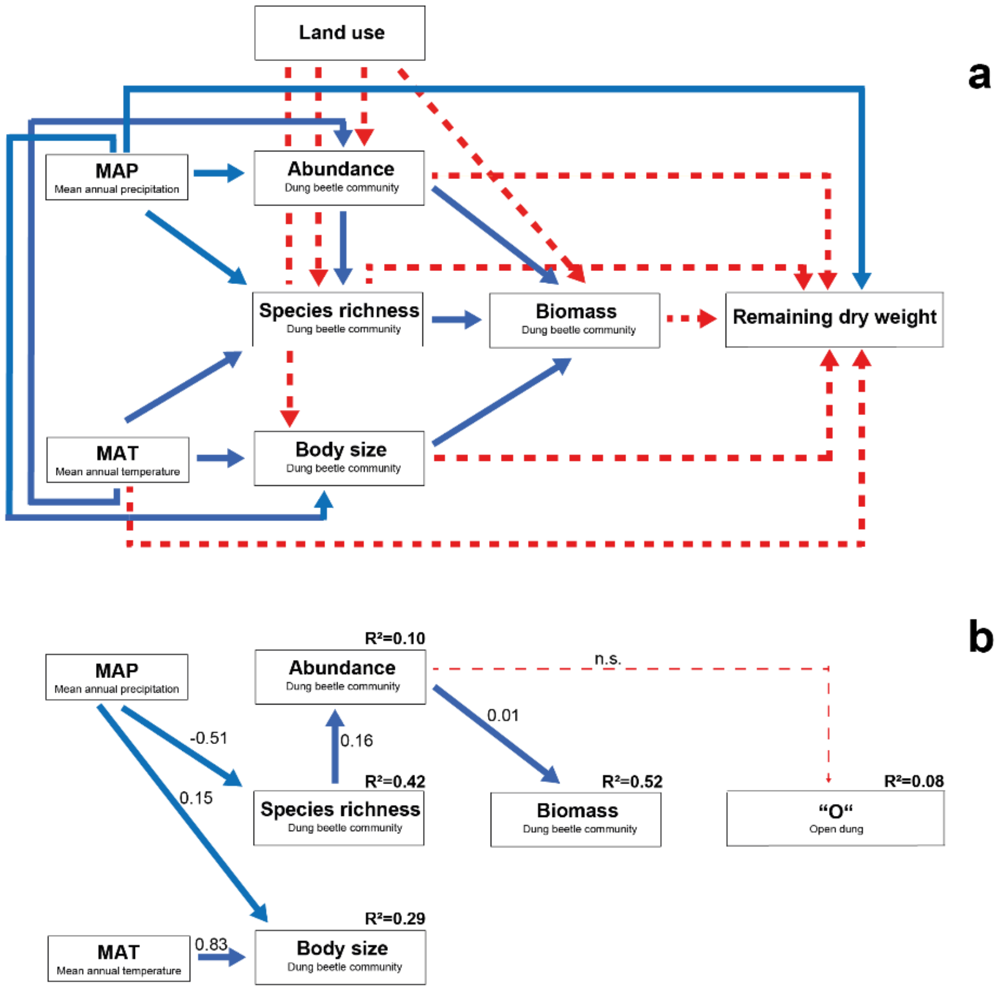
Supplementary Figure IV.S4: Dung beetle community metrics along elevation for natural and anthropogenic habitats. Shown are species richness (a), abundance (b), mean body size (c) and total biomass (d). On the right-hand side, the four small graphs represent trends for the trophic guilds tunnellers, rollers, dwellers and kleptoparasites (from top to bottom) for each community metric, respectively. Dots depict original measurements on study plots. Natural habitats are shown in blue while anthropogenic habitats are shown in orange. Trend lines were computed with generalized additive models (GAMs) with a basis dimension of k = 5 with a Poisson (a, b) or Gaussian family (b, d).

Appendix IV.S5: Relationship between dung decomposition and main predictors



Supplementary Figure IV.S5: Illustration of relationships between decomposition and the main predictors for the three different treatments: Treatment O (blue; **a, b**), treatment H (green, **c**) and treatment C (orange, **d**). Remaining dry weight is used as a measure for dung decomposition. For treatment O (open dung), the main predictors were **(a)** mean body size and **(b)** abundance. For treatment H (half open dung), the main driver was mean annual temperature **(c)** and for treatment C (closed dung) mean annual temperature as well **(d)**. Dots represent original measurements on study plots. Trend lines were calculated with linear models.

Appendix IV.S6: Path model only for study plots where dung beetles were present



Supplementary Figure IV.S6: Path model for open dung pads when only the study plots where dung beetles were present were considered. Starting path model (a) and best supported path model (b) for open dung (“O”). Positive relationships are shown in blue, negative relationships are depicted with red dashed lines.

Appendix IV.S7: Model support

Supplementary Table IV.S7.1: Model support for all response variables in path diagram with remaining dung weight of open dung pads ("O") as the final response variable (Figure 3b).

(a): Model support for all models with $\Delta AIC_C < 2$ for remaining dry weight of "O"

Model (glm.nb)	AIC_C	Δ_i	w_i	R^2
MWbodysize	636.61	0.00	0.30	0.24
ABbeetles. + MWbodysize	636.94	0.33	0.25	0.27
ABbeetles. + MWbodysize + totalbiomass	637.54	0.93	0.19	0.29
MWbodysize + SRbeetles	638.29	1.68	0.13	0.25
ABbeetles. + MWbodysize + SRbeetles	638.36	1.75	0.13	0.28

Note. ABbeetles = abundance of dung beetle community, MWbodysize = mean body size of dung beetle community, SRbeetles = species richness of dung beetle community, $\Delta_i = \Delta AIC_c$, w_i = weight.

(b) Model support for all models with $\Delta AIC_c < 2$ for abundance of dung beetle communities

Model (glm.nb)	AIC_C	Δ_i	w_i	R^2
MAT + MAP + SRbeetles	290.7	0.00	0.847	0.77

Note. MAT = mean annual temperature, MAP = mean annual precipitation.

(c) Model support for all models with $\Delta AIC_c < 2$ for species richness of dung beetle communities

Model (glm.nb)	AIC_C	Δ_i	w_i	R^2
MAT + MAP	211.2	0.00	0.87	0.70

(d) Model support for all models with $\Delta AIC_c < 2$ for mean body size of dung beetle communities

Model (glm.nb)	AIC_C	Δ_i	w_i	R^2
MAT + MAP	160.4	0.00	0.76	0.75

(e) Model support for all models with $\Delta AIC_c < 2$ for total biomass of dung beetle communities

Model (glm with Gaussian distribution)	AIC_C	Δ_i	w_i	R^2
ABbeetles + MWbodysize + SRbeetles	82.27	0.00	0.44	0.71
ABbeetles. + MWbodysize + SRbeetles + landuse	83.02	0.76	0.30	0.73
ABbeetles. + MWbodysize	82.25	0.98	0.27	0.70

Supplementary Table IV.S7.2: Model support for all response variables in path diagram with remaining dung weight of half-open dung pads (“H”) as the final response variable (Figure 3c).

(a): Model support for all models with $\Delta AIC_C < 2$ for remaining dry weight of “H”

Model (glm.nb)	AIC_C	Δ_i	w_i	R^2
SRbeetles	619.87	0.00	0.31	0.08
MAT	620.64	0.77	0.21	0.07
MAT + SRbeetles	621.60	1.73	0.13	0.09
Totalbiomass	621.70	1.90	0.12	0.05
MWbodysize	621.82	1.95	0.12	0.05
MWbodysize + SRbeetles	621.87	2.00	0.11	0.09

(b) Model support for all models with $\Delta AIC_c < 2$ for abundance of dung beetle communities

Model (gm.nb)	AIC_C	Δ_i	w_i	R^2
MAT + MAP	273.8	0.00	0.88	0.76

(c) Model support for all models with $\Delta AIC_c < 2$ for species richness of dung beetle communities

Model (glm.nb)	AIC_C	Δ_i	w_i	R^2
MAT + MAP	194.2	0.00	0.81	0.67

(d) Model support for all models with $\Delta AIC_c < 2$ for mean body size of dung beetle communities

Model (glm with Gaussian distribution)	AIC_C	Δ_i	w_i	R^2
MAT	163.47	0.00	0.69	0.66
MAT +SRbeetles	165.05	1.58	0.31	0.67

(e) Model support for all models with $\Delta AIC_c < 2$ for total biomass of dung beetle communities

Model (glm with Gaussian distribution)	AIC_C	Δ_i	w_i	R^2
ABbeetles + Land-use + SRbeetles	-208.97	0.00	0.56	0.98
ABbeetles + Land-use + MWbodysize +SRbeetles	-208.47	0.50	0.44	0.98

Supplementary Table IV.S7.3: Model support for all response variables in path diagram with remaining dung weight of closed dung pads (“C”) as the final response variable (Figure 3d).

(a): Model support for all models with $\Delta AIC_C < 2$ for remaining dry weight of “C”

Model (glm.nb)	AIC_C	Δ_i	w_i	R^2
MAT	467.1	0.00	0.16	0.12

(b) Model support for all models with $\Delta AIC_c < 2$ for abundance of dung beetle communities

Model (glm.nb)	AIC_C	Δ_i	w_i	R^2
MAT + MAP + SRbeetles	290.7	0.00	0.85	0.77

(c) Model support for all models with $\Delta AIC_c < 2$ for species richness of dung beetle communities

Model (glm.nb)	AIC_C	Δ_i	w_i	R^2
MAT + MAP	211.2	0.00	0.87	0.70

(d) Model support for all models with $\Delta AIC_c < 2$ for mean body size of dung beetle communities

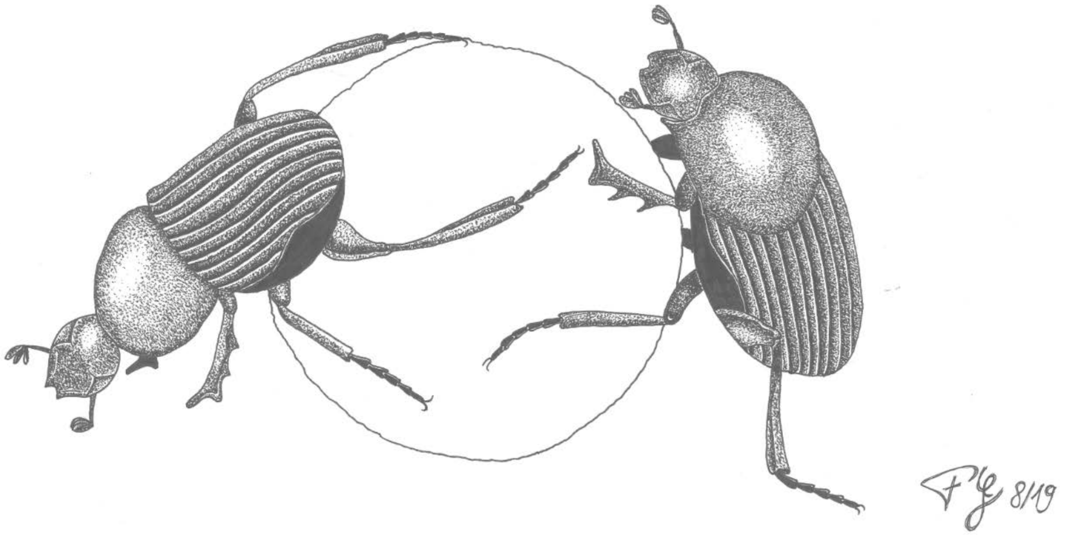
Model (glm.nb)	AIC_C	Δ_i	w_i	R^2
MAT + MAP	160.4	0.00	0.68	0.75

(e) Model support for all models with $\Delta AIC_c < 2$ for total biomass of dung beetle communities

Model (glm with Gaussian distribution)	AIC_C	$\mathbf{\Delta_i}$	w_i	R^2
ABbeetles + MWbodysize + SRbeetles	82.27	0.00	0.44	0.71
ABbeetles. + MWbodysize + SRbeetles + landuse	83.02	0.76	0.30	0.73
ABbeetles. + MWbodysize	83.25	0.98	0.27	0.70

CHAPTER V

GENERAL DISCUSSION



Global biodiversity patterns belong to the best-described ecological phenomena, yet the mechanisms driving biodiversity remain controversial until today (Peters et al. 2016). However, the status of global biodiversity is rapidly deteriorating (Díaz et al. 2019), rendering the investigation of its drivers paramount to be able to implement appropriate conservation actions (Chun and Lee 2018). Moreover, the linkages between biodiversity and ecosystem services are poorly resolved and the significance of the diversity measures species richness, abundance and functional traits in modulating ecosystem services has hardly been investigated (Gagic et al. 2015). Here, I explored the factors predicting mammal and dung beetle diversity and drivers of ecosystem services provided by dung beetles along elevational and land use gradients on Mt. Kilimanjaro. To the best of my knowledge, these are the first studies to integrate the exploration of elevational patterns with meticulous testing of different macroecological hypotheses along broad-scale climatic gradients for dung beetles and large mammals, respectively. Moreover, I exemplify the ramifications of different extinction scenarios on dung decomposition by dung beetles for the first time along an extensive elevational gradient.

V.1 Opposing drivers for endothermic and ectothermic diversity

By choosing one endothermic and one ectothermic taxon, it was possible to investigate the drivers of biodiversity for two organismal groups representing the two main strategies for thermoregulation (Shabtay 2005). Amongst the many hypotheses explaining diversity gradients, special emphasis has been placed on the importance of resource availability versus the importance of temperature when exploring endothermic and ectothermic diversity patterns (Buckley et al. 2012).

I found that for mammals, the paragon for endotherms, net primary productivity (NPP) was a major driver for species richness and community biomass. Mammal diversity showed a unimodal distribution along the elevational gradient, closely following the pattern of NPP at Mt. Kilimanjaro and therefore supporting the ‘more individuals hypothesis’ (Currie et al. 2004). According to this hypothesis, higher species diversity and biomass can be maintained in productive ecosystems as compared to ecosystems harbouring less quantities of resources. The strong impact of NPP illustrates the significance of food resources in maintaining mammal diversity at Mt. Kilimanjaro and probably other tropical mountains. The strong dependence on food resources has also been demonstrated for birds, another endothermic taxon (Ferger 2014). However, I did not only find an effect of NPP on mammal diversity, but also a direct and indirect impact of temperature. The direct influence of temperature was not as powerful as the NPP effect. Still, as NPP itself was strongly impacted by climate variables, the combined influence of NPP and climate was stronger than the sole effect of NPP. Consequently, temperature is also crucial for endotherms, posing metabolic constraints on species' distributions, for example in extreme climates (Buckley et al. 2012).

In contrast to endothermic mammals where I reported a predominant role of resource availability in driving diversity patterns, for ectothermic dung beetles, temperature constituted the main factor predicting elevational species richness and abundance. Temperature affected dung beetle diversity both directly and indirectly via a positive effect on dung beetle abundance. Corresponding to the 'temperature-richness hypothesis', temperature directly contributes to the perpetuation of species richness by modulating ecological and evolutionary processes (Belmaker & Jetz 2015). Instead, the 'temperature-mediated resource exploitation hypothesis' (Classen et al. 2015) assumes an indirect temperature effect on species richness, acting on the level of abundances. According to this second hypothesis, temperature restricts the foraging activity of ectotherms by influencing metabolic rates, resulting in a temperature-dependent exploitation of resources. Therefore, ectotherms will probably be more impacted by the temperature-mediated resource utilisation than by resource disposability in a habitat per se (Buckley et al. 2012). My results support both temperature hypotheses.

One shortcoming of many macroecological studies investigating the influence of resources on species distributions is the usage of primary productivity or related measures as an approximation for the resources consumed by the organisms in question. However, the food resource availability for the target taxon may not correspond well with primary productivity (Storch et al. 2018). For studies on dung beetles, the absence of an adequate assessment of resource availability is a common problem (Nichols et al. 2007). Despite my attempt to overcome this shortcoming by accurately measuring mammalian dung resources available for dung beetles by calculating mammalian defecation rates, I did not find an impact of resource availability on elevational patterns of dung beetle diversity. Even so, it is important to stress that my study was conducted along a broad-scale climatic gradient and that patterns might well be different at smaller spatial scales and in single climates. For example, strong linkages between dung beetles and mammals have been reported in non-elevational studies (e.g. Bogoni et al. 2016). Furthermore, temperature and resource availability have been identified as drivers of dung beetle diversity of equal importance in studies along small-scale elevational gradients (e.g. Muhirwa et al. 2018). Dung beetle diversity was not only positively impacted by temperature, but also negatively by mean annual precipitation (MAP). Both positive and negative effects of MAP on dung beetles have been reported. Positive effects include larger larval and adult dung beetles, resulting in higher reproductive success while negative effects accompanied by excessive rains entail reduced dung beetle survival, for example due to high mortality rates of dung beetle larvae and eggs (Edwards 1986, Vessby 2001). On Mt. Kilimanjaro, the highest amount of MAP is shed at mid-elevations, where the dung beetle fauna was nearly absent, probably accounting for the negative relationship.

V.2 The importance of protected areas for mammal conservation

Apart from NPP, another major determinant of mammal diversity was the protection status of study plots with higher mammal diversity and community biomass in protected than in unprotected habitats. On Mt. Kilimanjaro, I could only detect mammals with high body mass in protected habitats. Outside Mt.

Kilimanjaro National park, two savanna study plots, which were located in a wildlife conservation area, were of special importance for the distribution of large mammals. Here, I frequently detected large-bodied mammals like the Lesser Kudu and the Plains Zebra. Even though the remaining savanna habitats retain the majority of the natural vegetation cover, I did not find equally large mammals there. In unprotected habitats, especially large-bodied mammals are threatened by anthropogenic encroachments like hunting (Harrison 2011). In Africa, common reasons for hunting include bush meat hunting (Knapp et al. 2017) as well as killing mammals to requite damages to crops (Nyirenda et al. 2013) or livestock (Kissui 2008). Mammals provide key ecosystem services such as nutrient cycling, pollination and seed dispersal. Furthermore, they contribute to maintining habitat heterogeneity, regulating insect populations, and reducing disease transmission (Jones & Safi 2011, Lacher et al. 2019). Therefore, the absence of mammals from unprotected habitats most likely has far reaching consequences such as cascading effects on other trophic levels, altered species assemblages and decreased ecosystem service provisioning (Pringle et al. 2007). My study underscores the importance of protected areas for the preservation of mammal diversity on tropical mountains. From a scientific point of view, the maintenance and extension of protected areas is indispensable for the conservation of biodiversity in the future.

V.3 Ecosystem services: the larger the beetle, the better

Currently, the drivers of ecosystem services are subject to controversial discussion (Gagic et al. 2015). The role of climate on the one hand and biodiversity-related drivers including species richness, abundance and functional traits on the other hand in prediction ecosystem services remains unresolved (Brown et al. 2004, Hooper et al. 2012, van der Plas 2019, Dainese et al. 2019). My exclosure experiment contributes to this discourse by investigating the direct and indirect impacts of climate, dung beetle diversity and functional traits on dung decomposition under different disturbance scenarios. By contrasting dung decomposition in intact dung beetle communities with dung decomposition in depauperate communities consisting of small dung beetles and with decomposition in the absence of dung beetles, I exemplify how the drivers of dung decomposition changed with increasing disturbance of the dung beetle community. In unperturbed systems, dung decomposition was the highest and mainly impacted by dung beetle body size and to a lesser extent by dung beetle abundance, implying that larger dung beetles removed most of the dung. Following the extinction order of dung beetles with larger beetles being the most likely to go extinct first (Gardner et al. 2008), in the sole presence of small dung beetles, decomposition rates were reduced and species richness became the main driver of dung decomposition. Both dung beetle body size and species richness were impacted by temperature. In the absence of the whole dung beetle community, decomposition was the lowest and predicted by temperature. I show that the drivers of dung decomposition differed according to the level of perturbation, changing from biodiversity-related drivers under no and intermediate levels of disturbance to climate-related drivers under the worst-case scenario where no dung beetle community is remaining. My study illustrates the importance of including functional traits in studies investigating ecosystem services. Without the incorporation of the functional trait body size in my experiment, the consequences of the exclusion of the functionally most important large dung beetles on ecosystem service provisioning would have been missed. Since large dung beetles are both most functionally efficient and most extinction prone, body size is both an effect and a response functional trait (Piccini et al. 2018). Especially in the light of global change, not only considering the status quo in experiments, but also possible future extinction scenarios, is vital to better predict ecosystem service provisioning in the future.

V.4 Land use: no effect on overall richness, idiosyncratic patterns for guilds

When considering overall species diversity and dung decomposition, land use had no effect on mammals, nor on dung beetles, nor dung beetle-mediated ecosystem services. While mammal diversity showed a mid-elevation peak for both species richness and community biomass in both natural and anthropogenic habitats, closely following the distribution of net primary productivity on Mt. Kilimanjaro, dung beetle species richness declined with increasing elevation, resembling the pattern of decreasing temperature with elevation. In contrast, dung beetle abundance showed a hump-shaped pattern in both natural and anthropogenic habitats. However, when looking at different trophic guilds of mammals, i.e. herbivores, omnivores and carnivores, or at different functional groups of dung beetles, i.e. rollers, tunnellers, dwellers and kleptoparasites, the impact of land use was not homogenous.

For mammals, herbivores were the only guild negatively impacted by land use, showing higher species richness and community biomass in natural as compared to anthropogenic habitats. This result was mostly due to large herbivores being absent at low elevation habitats where land use was most intense. Herbivores have also been found to be more susceptible to land use changes than omnivores in other studies (Kinnaird & O'Brien 2012), probably because herbivorous mammals are more specialized in their foraging behaviour than omnivorous species (Price et al. 2012). However, the result that carnivores were not affected by anthropogenic alterations was surprising as they are commonly reported to be negatively impacted by land use changes (Kinnaird & O'Brien 2012). One reason for this lack of impact of land use might be that I only recorded few carnivorous species. As carnivores have larger home ranges and smaller population sizes than either omnivores or herbivores (Harestad & Bunnel 1979, Van Valkenburgh 1999), my sampling of each study plot for the duration of a fortnight was probably too short to report all carnivores present. Subsequent studies over longer monitoring periods should be more suited to collect data on carnivores and to compare carnivore diversity along land use and elevational gradients.

For dung beetles, it was the rollers, which were larger, more abundant and showed a higher species richness in natural as compared to anthropogenic habitats. Kleptoparasites were also larger in natural habitats. Arguably, these two groups are more behaviourally specialized and therefore more vulnerable to land use changes than the other functional groups of dung beetles (Halffter & Edmonds 1982). Rollers build shallower nests than tunnellers, which might render them especially susceptible to drier and hotter conditions in converted habitats (Nichols et al., 2013). Moreover, rollers are mainly comprised of large-bodied species, which may be more vulnerable than smaller species to land use changes as their surface to volume ratio is smaller than that of tinier beetles and therefore, larger species are less efficient in thermal emission (Clusella Trullas et al. 2007). Thus, larger species may be facing abiotic conditions beyond their physiological tolerance in non-shaded anthropogenic habitats. Since kleptoparasites predominantly parasitize large species (Simmons & Ridsdill-Smith 2011), they may be negatively influenced by the absence of large roller species in anthropogenic habitats. In contrast, smaller-bodied species may profit from anthropogenic land use changes. Especially dwellers, which are less affected by microclimatic changes due to their lifestyle in dung pats, insulating them from more extreme climatic conditions, can reach high abundances in anthropogenic habitats. Moreover, the absence of larger-bodied species can favour the diversity and abundance of smaller-bodied species as the former replace the latter in anthropogenic habitats as a form of density compensation (Larsen et al. 2008). Accordingly, I reported by far the highest dung beetle abundance at one high land-use intensity study plot on a commercial coffee plantation, which was mainly due to the prevalence of few small-bodied species.

One reason for the absence of a land use effect on overall mammal and dung beetle diversity and on dung decomposition may be that at present, the anthropogenic influence on Mt. Kilimanjaro is still moderate. At low elevations outside Mt. Kilimanjaro National Park, the landscape is composed of a patchwork of small-scale agricultural fields where different crops are grown, semi natural habitat and forest fragments (Mmbaga et al., 2017). This highly heterogeneous landscape matrix may be responsible for maintaining high biodiversity despite high levels of fragmentation by facilitating dispersal or by sustaining viable populations inside the matrix (Nichols et al., 2007). Therefore, even at landscape fragments with high land use intensity, such as maize fields, a high diversity can be found. Differences in both mammal and dung beetle diversity between study sites and habitats was mainly due to turnover, which may indicate that landscape heterogeneity facilitates high levels of diversity on the one hand (Ramírez-Ponce et al. 2019), but that in modified landscapes, species typical for natural habitats are replaced by open- habitat specialists on the other hand. Mostly, the latter species are small-bodied and despite occurring in high abundances, it is doubtful that they can replace larger-bodied species in terms of ecosystem service provisioning in the long term. (Nichols et al., 2007). Overall, I did not detect an effect of land use on dung decomposition. However, I showed that smaller-bodied dung beetles are less efficient in dung removal than larger-bodied dung beetles. Therefore, I would anticipate negative consequences for ecosystem service provisioning if land use at Mt. Kilimanjaro increases and if communities are more shifting to smaller-bodied species as a reaction to land use conversion to more open habitats. Indeed, the anthropogenic pressure on the mountain is rising (Kulkarni et al. 2016) and augmented agricultural intensification entailing enhanced application of pesticides and heavy machines are progressively jeopardizing the current high levels of sustained biodiversity. Furthermore, the fact that land use effects are already visible on the level of trophic guilds of mammals and functional groups of dung beetles, respectively, implies that negative changes to communities are already taking place. Perhaps it is just a matter of time until land use will affect mammals and dung beetles as a whole as well as ecosystem services provided by dung beetles.

V.5 Implications for climate change

Apart from land use changes such as habitat loss and fragmentation, climate change is one of the major threats to global biodiversity (Chapin et al. 2000). Due to their different thermoregulatory strategies, endothermic and ectothermic organisms are predicted to show differing reactions to climate change. While endothermic mammals are more buffered against rising temperatures because of their metabolism being largely independent from ambient temperatures, ectothermic dung beetles are expected to be more susceptible to climate change since their physiology and activity time is strongly dependent on ambient temperature (Deutsch et al. 2008, Buckley et al. 2012). However, endothermic organisms might also be negatively affected by climate change as the prevalence of extreme heat events increases. Nevertheless, while the vulnerability of ectothermic organisms to climate change is largely due to the danger of overheating, for endothermic organisms, water loss will be more of a restraint to activity and endurance in a changing world (Buckley et al. 2012).

For ectothermic dung beetles, I showed that temperature was the major driver of diversity. While this relationship was positive, higher temperatures could have detrimental effects, pushing species beyond their thermal limit (Deutsch et al. 2008). On tropical mountains like Mt. Kilimanjaro, species of the lowlands may expand their range upwards as a reaction to climate change, tracking their optimal temperature range (Chen et al. 2011). Therefore, species richness in middle altitudes may be increasing. However, while expanding upwards, species might restrict their lower range, causing biotic attrition in the lowlands as absent species are not being replaced by new species (Colwell et al. 2008). Interestingly, I only reported dung beetles at Mt. Kilimanjaro up to a height of 2700 m. Since Mt. Kilimanjaro is a relatively young mountain, dung beetle species may still be in the process of colonization and moving up the mountain.

As regards ecosystem services, I would expect a corresponding pattern with climate change, resulting in less ecosystem service provisioning at low altitudes and a possible positive effect on services at middle altitudes, profiting from higher diversity. However, it has been proposed that under higher temperatures, a higher biodiversity does not necessarily ensure increased ecosystem service provisioning, since higher biodiversity also translates into increased competition in ectothermic organisms, actually causing a levelled or even negative BEF relationship (Parain et al. 2019). Ecosystem service provisioning at low altitude sites may also be reduced because of the dependence of dung decomposition on large dung beetles, which are not only the functional group most vulnerable to land use changes, but also to climate change because of their body size (Braga et al. 2013). In general, ectothermic organisms are predicted to get smaller and more generalised with climate change (Isaac and Williams 2013, Ohlberger 2013) Since dung decomposition in the absence of the dung beetle community was solely driven by temperature, I expect dung decomposition in high altitude sites where no dung beetles are (yet) present to profit from augmented temperatures.

Across taxa and ecosystem services on Mt. Kilimanjaro, the effect of land use was dependent on climate and was greatest at low elevations, leading to decreased species richness and modified ecosystem services at the elevations coinciding with the highest diversity (Peters et al. 2019). This result has implications for global change as both land use and climate change are acting in synergy and are predicted to increase, with the potential to essentially rearrange ecological communities and their associated ecosystem services (Peters et al. 2019).

V.6 Conclusions

On Mt. Kilimanjaro, the drivers of diversity were dependent on the thermoregulatory strategy of organisms. While mammal species richness and community biomass was mainly predicted by energy availability and the protection status of study plots, dung beetle species richness and abundance was primarily impacted by climate variables. While across taxa at Mt. Kilimanjaro, temperature was found to be the main predictor for species richness along elevation, I could confirm that at the level of single taxa, e.g. mammals and dung beetles, the predictors were idiosyncratic (Peters et al. 2016). Furthermore, I showed that the drivers of dung decomposition, an important ecosystem service, change with increasing disturbance of the community of ecosystem service providers. While dung decomposition in undisturbed communities was mainly impacted by body size, in communities excluding large dung beetles, species richness was the main predictor of decomposition. In the absence of dung beetles, decomposition was mainly impacted by temperature. Currently, the impact of land use on Mt. Kilimanjaro is still moderate. However, changes in species diversity and functional traits due to land use change are already visible at the level of trophic guilds of mammals and functional groups of dung beetles, respectively, affecting the most behaviourally specialised groups. Further intensification of land use changes, such as agricultural intensification and landscape homogenization, which is very likely due to the increasing population at Mt. Kilimanjaro (Hemp 2006), may thus augment the negative impacts already visible today, leading to changes at the community level and negative repercussions on mammal and dung beetle mediated ecosystem services. Moreover, I stressed the importance of protected areas on Mt. Kilimanjaro by showing that large mammals mainly occur in protected habitats. In unprotected habitats, the reduction of large mammals is probably due to anthropogenic impacts such as hunting. To conclude, this study is part of the contemporary discourse on the drivers of biodiversity and ecosystem services, underscoring the importance of investigating different taxa and functional traits for elucidating the predictors of species richness and ecosystem services. Such an integrated approach is the prerequisite to be able to make informed conservation decisions in the light of contemporary and future global change and to ensure ecosystem integrity in the era of the Anthropocene.

REFERENCES

Almeida-Neto, M., P. Guimarães, P. R. Guimarães, R. D. Loyola, & W. Ulrich. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117:1227–1239.

Alvarado-Roberto, F., & J. Arias-Buriticá. 2015. Highest elevation recorded for a nesting dung beetle (Coleoptera: Scarabaeidae: Scarabaeinae) in the Americas. The Coleopterists Bulletin 69:789–792.

Andelman, S. J., & W. F. Fagan. 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences 97:5954–5959.

Andresen, E., & S. G. W. Laurance. 2007. Possible indirect effects of mammal hunting on dung beetle assemblages in Panama. Biotropica 39:141–146.

Appelhans, T., F. Detsch, & T. Nauss. 2015. remote: Empirical Orthogonal Teleconnections in R. Journal of Statistical Software 65:1-9.

Appelhans, T., E. Mwangomo, I. Otte, F. Detsch, T. Nauss, & A. Hemp. 2016. Eco-meteorological characteristics of the southern slopes of Kilimanjaro, Tanzania. International Journal of Climatology 36:3245–3258.

Arriaga-Jiménez, A., M. Rös, & G. Halffter. 2018. High variability of dung beetle diversity patterns at four mountains of the Trans-Mexican Volcanic Belt. PeerJ 6:e4468.

Barbosa, A. M., J. A. Brown, A. Jimenez-Valverde, & R. Real. 2016. modEvA: Model evaluation and analysis. R package version 1.3.2. https://CRAN.R-project.org/package=modEvA.

Barlow, J., F. França, T. A. Gardner, C. C. Hicks, G. D. Lennox, E. Berenguer, L. Castello, E. P. Economo, J. Ferreira, B. Guénard, C. Gontijo Leal, V. Isaac, A. C. Lees, C. L. Parr, S. K. Wilson, P. J. Young, & N. A. J. Graham. 2018. The future of hyperdiverse tropical ecosystems. Nature 559:517–526.

Barlow, J., J. Louzada, L. Parry, M. I. M. Hernández, J. Hawes, C. A. Peres, F. Z. Vaz-de-Mello, & T. A. Gardner. 2010. Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles: Dung beetles in Amazonian forest strips. Journal of Applied Ecology 47:779–788.

Baselga, A. 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness: Species replacement and nestedness. Global Ecology and Biogeography 21:1223–1232.

Beck, J., C. M. McCain, J. C. Axmacher, L. A. Ashton, F. Bärtschi, G. Brehm, S.-W. Choi, O. Cizek, R. K. Colwell, K. Fiedler, C. L. Francois, S. Highland, J. D. Holloway, J. Intachat, T. Kadlec, R. L. Kitching, S. C. Maunsell, T. Merckx, A. Nakamura, E. Odell, W. Sang, P. S. Toko, J. Zamecnik, Y. Zou, & V. Novotny. 2017. Elevational species richness gradients in a hyperdiverse insect taxon: a global meta-study on geometrid moths: Geometrid moth richness on elevational gradients. Global Ecology and Biogeography 26:412–424.

Becker, J., H. Pabst, J. Mnyonga, & Y. Kuzyakov. 2015. Annual litterfall dynamics and nutrient deposition depending on elevation and land use at Mt. Kilimanjaro. Biogeosciences 12:5635–5646.

Beiroz, W., E. M. Slade, J. Barlow, J. M. Silveira, J. Louzada, & E. Sayer. 2017. Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change. Insect Conservation and Diversity 10:94–106.

de Bello, F., S. Lavorel, S. Díaz, R. Harrington, J. H. C. Cornelissen, R. D. Bardgett, M. P. Berg, P. Cipriotti, C. K. Feld, D. Hering, P. Martins da Silva, S. G. Potts, L. Sandin, J. P. Sousa, J. Storkey, D. A. Wardle, & P. A. Harrison. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. Biodiversity and Conservation 19:2873–2893.

Belmaker, J., & W. Jetz. 2015. Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. Ecology Letters 18:563–571.

Berson, J. D., & L. W. Simmons. 2018. A costly chemical trait: phenotypic condition dependence of cuticular hydrocarbons in a dung beetle. Journal of Evolutionary Biology.

Bogoni, J. A., M. E. Graipel, P. V. de Castilho, F. M. Fantacini, V. V. Kuhnen, M. R. Luiz, T. B. Maccarini, C. B. Marcon, C. de Souza Pimentel Teixeira, M. A. Tortato, F. Z. Vaz-de-Mello, & M. I. M. Hernández. 2016. Contributions of the mammal community, habitat structure, and spatial distance to dung beetle community structure. Biodiversity and Conservation 25:1661–1675.

Bowkett, A., T. Jones, F. Rovero, M. Nielsen, T. Davenport, D. Hawkins, A. Plowman, & J. Stevens. 2014. Distribution and genetic diversity of the endangered Abbott's duiker Cephalophus spadix in the Udzungwa Mountains, Tanzania. Endangered Species Research 24:105–114.

Braga, R. F., V. Korasaki, E. Andresen, & J. Louzada. 2013. Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: A rapid assessment of ecological functions associated to biodiversity. PLoS ONE 8:e57786.

Brooks, T. M., R. A. Mittermeier, G. A. B. da Fonseca, J. Gerlach, M. Hoffmann, J. F. Lamoreux, C. G. Mittermeier, J. D. Pilgrim, & A. S. L. Rodrigues. 2006. Global biodiversity conservation priorities. Science 313:58–61.

Brose, U., J. L. Blanchard, A. Eklöf, N. Galiana, M. Hartvig, M. R. Hirt, G. Kalinkat, M. C. Nordström, E. J. O'Gorman, B. C. Rall, F. D. Schneider, E. Thébault, & U. Jacob. 2017. Predicting the consequences of species loss using size-structured biodiversity approaches. Biological Reviews 92:684–697.

Brown, J. H. 2001. Mammals on mountainsides: elevational patterns of diversity. Global Ecology and Biogeography 10:101–109.

Brown, J. H. 2014. Why are there so many species in the tropics? Journal of Biogeography 41:8–22.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, & G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Buckley, L. B., A. H. Hurlbert, & W. Jetz. 2012. Broad-scale ecological implications of ectothermy and endothermy in changing environments: Ectothermy and endothermy. Global Ecology and Biogeography 21:873–885.

Cadotte, M. W., K. Carscadden, & N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48:1079–1087.

Cambefort, Y. 1984. Etude écologique des coléoptères Scarabaeidae de Côte d'Ivoire.

Caro, T. 2010. Conservation by Proxy: Indicator, umbrella, keystone, flagship, and other surrogate species. Island Press, Washington.

Chamberlain, D., C. Tocco, A. Longoni, S. Mammola, C. Palestrini, & A. Rolando. 2015. Nesting strategies affect altitudinal distribution and habitat use in Alpine dung beetle communities. Ecological Entomology 40:372–380.

Chapin III, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, & S. Díaz. 2000. Consequences of changing biodiversity. Nature 405:234.

Chen, I.-C., J. K. Hill, R. Ohlemuller, D. B. Roy, & C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026.

Chown, S. L., & J. Klok. 2011. The Ecological Implications of Physiological Diversity in Dung Beetles. In: Ecology and evolution of dung beetles. John Wiley & Sons, Ltd, Chichester, UK.

Chun, J.-H., & C.-B. Lee. 2018. Partitioning the regional and local drivers of phylogenetic and functional diversity along temperate elevational gradients on an East Asian peninsula. Scientific Reports 8:2853.

Classen, A., M. K. Peters, W. J. Kindeketa, T. Appelhans, C. D. Eardley, M. W. Gikungu, A. Hemp, T. Nauss, & I. Steffan-Dewenter. 2015. Temperature versus resource constraints: which factors determine bee diversity on Mount Kilimanjaro, Tanzania? Global Ecology and Biogeography 24:642–652.

Clusella Trullas, S., J. H. van Wyk, & J. R. Spotila. 2007. Thermal melanism in ectotherms. Journal of Thermal Biology 32:235–245.

Colwell, R. K., G. Brehm, C. L. Cardelus, A. C. Gilman, & J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258–261.

Colwell, R. K., & J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 345:101–118.

Colwell, R. K., & G. C. Hurtt. 1994. Nonbiological Gradients in Species Richness and a Spurious Rapoport Effect. The American Naturalist 144:570–595.

Culot, L., E. Bovy, F. Zagury Vaz-de-Mello, R. Guevara, & M. Galetti. 2013. Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biological Conservation 163:79–89.

Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J.-F. Guegan, B. A. Hawkins, D. M. Kaufman, J. T. Kerr, T. Oberdorff, E. O'Brien, & J. R. G. Turner. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7:1121–1134.

Dainese, M., E. A. Martin, M. Aizen, M. Albrecht, I. Bartomeus, R. Bommarco, L. G. Carvalheiro, R. Chaplin-Kramer, V. Gagic, L. A. Garibaldi, J. Ghazoul, H. Grab, M. Jonsson, D. S. Karp, C. M. Kennedy, D. Kleijn, C. Kremen, D. A. Landis, D. K. Letourneau, L. Marini, K. Poveda, R. Rader, H. G. Smith, T. Tscharntke, G. K. S. Andersson, I. Badenhausser, S. Baensch, A. D. M. Bezerra, F. J. J. A. Bianchi, V. Boreux, V. Bretagnolle, B. Caballero-Lopez, P. Cavigliasso, A. Cetkovic, N. P. Chacoff, A. Classen, S. Cusser, F. D. da Silva e Silva, G. A. de Groot, J. H. Dudenhoffer, J. Ekroos, T. Fijen, P. Franck, B. M. Freitas, M. P. D. Garratt, C. Gratton, J. Hipolito, A. Holzschuh, L. Hunt, A. L. Iverson, S. Jha, T. Keasar, T. N. Kim, M. Kishinevsky, B. K. Klatt, A. Klein, K. M. Krewenka, S. Krishnan, A. E. Larsen, C. Lavigne, H. Leire, B. Maas, M. Nesper, R. E. Mallinger, E. Martinez, A. Martinez-Salinas, T. D. Meehan, M. G. E. Mitchell, G. A. R. Molina, L. Nilsson, M. O'Rourke, M. K. Peters, M. Plecas, Si. G. Potts, D. de L. Ramos, J. A. Rosenheim, M. Rundlof, A. Rusch, A. Saez, J. Scheper, M. Schleuning, J. Schmack, A. R. Sciligo, C. Seymour, D. A. Stanley, R. Stewart, J. C. Stout, L. Sutter, M. B. Takada, H. Taki, G. Tamburini, M. Tschumi, B. F. Viana, C. Westphal, B. K. Wilcox, S. D. Wratten, A. Yoshioka, C. Zaragoza, W. Zhang, Y. Zou, & I. Steffan-Dewenter. In press. A global synthesis reveals biodiversity-mediated benefits for crop production. Science Advances.

Darwin, Charles. 1862. The Voyage of the Beagle. Doublebay, Garden City, NJ.

Davidson, A. D., M. J. Hamilton, A. G. Boyer, J. H. Brown, & G. Ceballos. 2009. Multiple ecological pathways to extinction in mammals. Proceedings of the National Academy of Sciences 106:10702–10705.

Davis, A. L. V., & C. F. Dewhurst. 1993. Climatic and biogeographical associations of Kenyan and northern Tanzanian dung beetles (Coleoptera: Scarabaeidae). African Journal of Ecology 31:290–305.

Davis, A. L. V., C. H. Scholtz, & S. L. Chown. 1999. Species turnover, community boundaries and biogeographical composition of dung beetle assemblages across an altitudinal gradient in South Africa. Journal of Biogeography 26:1039–1055.

Davis, A. L. V., C. H. Scholtz, & C. Deschodt. 2005. A dung beetle survey of selected Gauteng nature reserves : implications for conservation of the provincial scarabaeine fauna. African Entomology 13:1–16.

Davis, A. L. V., C. H. Scholtz, & C. Deschodt. 2008. Multi-scale determinants of dung beetle assemblage structure across abiotic gradients of the Kalahari-Nama Karoo ecotone, South Africa. Journal of Biogeography 35:1465–1480.

Detsch, F., I. Otte, T. Appelhans, A. Hemp, & T. Nauss. 2016a. Seasonal and long-term vegetation dynamics from 1-km GIMMS-based NDVI time series at Mt. Kilimanjaro, Tanzania. Remote Sensing of Environment 178:70–83.

Detsch, F., I. Otte, T. Appelhans, & T. Nauss. 2016b. A Comparative Study of Cross-Product NDVI Dynamics in the Kilimanjaro Region—A Matter of Sensor, Degradation Calibration, and Significance. Remote Sensing 8:159.

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, & P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences 105:6668–6672.

Di Bitetti, M. S., S. A. Albanesi, M. J. Foguet, C. De Angelo, & A. D. Brown. 2013. The effect of anthropic pressures and elevation on the large and medium-sized terrestrial mammals of the subtropical mountain forests (Yungas) of NW Argentina. Mammalian Biology - Zeitschrift für Säugetierkunde 78:21–27.

Díaz, S., J. Settele, E. Brondízio, H. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. Brauman, S. Butchart, K. Chan, L. Garibaldi, K. Ichii, J. Liu, S. Subrmanian, G. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Chowdhury, Y. Shin, I. Visseren-Hamakers, K. Wilis, & C. Zayas. 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, & B. Collen. 2014. Defaunation in the Anthropocene. Science 345:401–406.

Edwards, P. B. 1986. Phenology and field biology of the dung beetle *Onitis caffer* Boheman (Coleoptera: Scarabaeidae) in southern Africa. Bulletin of Entomological Research 76:433–446.

Feer, F., & O. Boissier. 2015. Variations in dung beetle assemblages across a gradient of hunting in a tropical forest. Ecological Indicators 57:164–170.

Ferger, S. W., M. K. Peters, T. Appelhans, F. Detsch, A. Hemp, T. Nauss, I. Otte, K. Böhning-Gaese, & M. Schleuning. 2017. Synergistic effects of climate and land use on avian beta-diversity. Diversity and Distributions 23:1246–1255.

Ferger, S. W., M. Schleuning, A. Hemp, K. M. Howell, & K. Böhning-Gaese. 2014. Food resources and vegetation structure mediate climatic effects on species richness of birds: Climate and bird species richness. Global Ecology and Biogeography 23:541–549.

Fernández, M. H., & E. S. Vrba. 2005. Rapoport effect and biomic specialization in African mammals: revisiting the climatic variability hypothesis: Rapoport effect and biomic specialization. Journal of Biogeography 32:903–918.

Ferreira de Pinho, F., G. Braga Ferreira, & A. Pereira Paglia. 2017. Influence of vegetation physiognomy, elevation and fire frequency on medium and large mammals in two protected areas of the Espinhaço Range. Zoologia 34:1–11.

Finn, J. A. 2001. Ephemeral resource patches as model systems for diversity-function experiments. Oikos 92:363–366.

Fountain-Jones, N. M., S. C. Baker, & G. J. Jordan. 2015. Moving beyond the guild concept: developing a practical functional trait framework for terrestrial beetles. Ecological Entomology 40:1–13.

Frank, K., A. Brückner, A. Hilpert, M. Heethoff, & N. Blüthgen. 2017. Nutrient quality of vertebrate dung as a diet for dung beetles. Scientific Reports 7.

Frank, K., F.-T. Krell, E. M. Slade, E. H. Raine, L. Y. Chiew, T. Schmitt, C. S. Vairappan, P. Walter, & N. Blüthgen. 2018. Global dung webs: high trophic generalism of dung beetles along the latitudinal diversity gradient. Ecology Letters 21:1229–1236.

Frazier, M. R., R. B. Huey, & D. Berrigan. 2006. Thermodynamics constrains the evolution of insect population growth rates: “Warmer Is Better.” The American Naturalist 168:512–520.

Gagic, V., I. Bartomeus, T. Jonsson, A. Taylor, C. Winqvist, C. Fischer, E. M. Slade, I. Steffan-Dewenter, M. Emmerson, S. G. Potts, T. Tscharntke, W. Weisser, & R. Bommarco. 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proceedings of the Royal Society B: Biological Sciences 282:20142620–20142620.

Gardner, T. A., M. I. M. Hernández, J. Barlow, & C. A. Peres. 2008. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. Journal of Applied Ecology 45:883–893.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405:220–227.

Gaston, K. J., & S. L. Chown. 1999. Elevation and Climatic Tolerance: A Test Using Dung Beetles. Oikos 86:584.

Gebert, F., Steffan-Dewenter, & M. K. Peters. 2019a. Data from: Climate rather than dung resources predict dung beetle abundance and diversity along elevational and land use gradients on Mt. Kilimanjaro. PANGAEA. https://doi.org/10.1594/PANGAEA.905168.

Gebert, F., I. Steffan-Dewenter, & M. K. Peters. 2019b. Data from: Primary productivity and habitat protection predict elevational species richness and community biomass of large mammals on Mt. Kilimanjaro. PANGAEA. https://doi.pangaea.de/10.1594/PANGAEA.903710.

Gotelli, N. J., & R. K. Colwell. 2011. Estimating species richness. In: Biological diversity: frontiers in measurement and assessment 12.

Grimshaw, J. M., N. J. Cordeiro, & C. A. H. Foley. 1995. The mammals of Kilimanjaro. Journal of East African Natural History 84:105–139.

Grytnes, J.-A., & C. M. McCain. 2013. Elevational trends in biodiversity. In: Levin,S (Ed.) Encyclopedia of Biodiversity. Academic Press, Amsterdam, Oxford.

Halffter, G., & W. D. Edmonds. 1982. The nesting behaviour of dung beeltes (Scarabaeinae): an ecological and evolutionary approach. México: Instituto de Ecología.

Halffter, G. & M. E. Favila. 1993. The Scarabaeinae (Insecta : Coleoptera) an animal group for analyzing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. Biology International 27:15–21.

Hanksi, I., & Y. Cambefort. 1991. Dung beetle ecology. Princeton University Press, Princeton.

Harestad, A. S., & F. L. Bunnel. 1979. Home range and body weight-A reevaluation. Ecology 60:389–402.

Harrison, R. D. 2011. Emptying the forest: Hunting and the extirpation of wildlife from tropical nature reserves. BioScience 61:919–924.

Hatfield, J. H., M. L. K. Harrison, & C. Banks-Leite. 2018. Functional diversity metrics: How they are affected by landscape change and how they represent ecosystem functioning in the tropics. Current Landscape Ecology Reports 3:35–42.

Hawkins, B. A., R. Field, H. V. Cornell, D. J. Currie, J.-F. Guégan, D. M. Kaufman, J. T. Kerr, G. G. Mittelbach, T. Oberdorff, E. M. O'Brien, E. E. Porter, & J. R. G. Turner. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.

Hegerl, C., N. D. Burgess, M. R. Nielsen, E. Martin, M. Ciolli, & F. Rovero. 2017. Using camera trap data to assess the impact of bushmeat hunting on forest mammals in Tanzania. Oryx 51:87–97.

Hemp, A. 2006a. The banana forests of Kilimanjaro: biodiversity and conservation of the Chagga homegardens. Biodiversity and Conservation 15:1193–1217.

Hemp, A. 2006b. Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. Plant Ecology 184:27–42.

Herzog, S. K., A. C. Hamel-Leigue, T. H. Larsen, D. J. Mann, R. W. Soria-Auza, B. D. Gill, W. D. Edmonds, & S. Spector. 2013. Elevational distribution and conservation biogeography of Phanaeine Dung Beetles (Coleoptera: Scarabaeinae) in Bolivia. PLoS ONE 8:e64963.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. The American Naturalist 163:192–211.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. K. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, & M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, & D. A. Wardle. 2005. effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75:3–35.

Humboldt, A. 1854. Volcans des Cordillères de Quito et du Mexique. Gide et J. Baudry, Paris.

Hurlbert, A. H., and J. C. Stegen. 2014. When should species richness be energy limited, and how would we know? Ecology Letters 17:401–413.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93.

Isaac, J. L., & S. E. Williams. 2013. Climate change and extinctions. 73–78. In: Levin, S. (Ed.) Encyclopedia of Biodiversity. Academic Press, Amsterdam, Oxford.

IUCN. 2018. The IUCN red list of threatened species. Version 2018-2. <http://www.iucnredlist.org>. Downloaded on 21 January 2019.

Jablonski, D., K. Roy, &J. W. Valentine. 2006. Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. Science 314:102–106.

Jay-Robert, P., J. M. Lobo, & J.-P. Lumaret. 1997. Altitudinal turnover and species richness variation in European montane dung beetle assemblages. Arctic and Alpine Research 29:196.

Jones, K. E., J. Bielby, M. Cardillo, S. A. Fritz, J. O'Dell, C. D. L. Orme, K. Safi, W. Sechrest, E. H. Boakes, C. Carbone, C. Connolly, M. J. Cutts, J. K. Foster, R. Grenyer, M. Habib, C. A. Plaster, S. A. Price, E. A. Rigby, J. Rist, A. Teacher, O. R. P. Bininda-Emonds, J. L. Gittleman, G. M. Mace, & A. Purvis. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090-184. Ecology 90:2648–2648.

Jones, K. E., & K. Safi. 2011. Ecology and evolution of mammalian biodiversity. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2451–2461.

Jones, T., J. E. Hawes, G. W. Norton, & D. M. Hawkins. 2019. Effect of protection status on mammal richness and abundance in Afromontane forests of the Udzungwa Mountains, Tanzania. Biological Conservation 229:78–84.

Kerr, J. T., & M. Ostrovsky. 2003. From space to species: ecological applications for remote sensing. Trends in Ecology & Evolution 18:299–305.

Kingdon, J. 2015. The kingdon field guide to African mammals. Princeton University Press, Princeton, NJ.

Kingdon, J., T. M. Butynski, T. Pokora, D. C. D. Happold, M. Happold, & M. Hoffmann. 2013. Mammals of Africa. Bloomsbury, London; New York.

Kinnaird, M. F., & T. G. O'Brien. 2012. Effects of private-land use, livestock management, and human tolerance on diversity, distribution, and abundance of large African mammals. Conservation Biology 26:1026–1039.

Kissui, B. M. 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. Animal Conservation 11:422–432.

Knapp, E., N. Peace, & L. Bechtel. 2017. Poachers and poverty: Assessing objective and subjective measures of poverty among illegal hunters outside Ruaha National Park, Tanzania. Conservation and Society 15:24.

Koike, S., M. Soga, H. Enari, C. Kozakai, & Y. Nemoto. 2013. Seasonal changes and altitudinal variation in deer fecal pellet decay. European Journal of Wildlife Research 59:765–768.

Körner, C. 2000a. The alpine life zone under global change. Gayana. Botánica 57:1-17.

Körner, C. 2000b. Why are there global gradients in species richness? Mountains might hold the answer. Trends in Ecology & Evolution 15:513–514.

Körner, C., W. Jetz, J. Paulsen, D. Payne, K. Rudmann-Maurer, & E. M. Spehn. 2017. A global inventory of mountains for bio-geographical applications. Alpine Botany 127:1–15.

Kreft, H., & W. Jetz. 2007. Global patterns and determinants of vascular plant diversity. Proceedings of the National Academy of Sciences 104:5925–5930.

Kulkarni, M. A., R. E. Desrochers, D. C. Kajeguka, R. D. Kaaya, A. Tomayer, E. J. Kweka, N. Protopopoff, & F. W. Mosha. 2016. 10 Years of environmental change on the slopes of Mount Kilimanjaro and its associated shift in malaria vector distributions. frontiers in public health 4.

Lacher, T. E., A. D. Davidson, T. H. Fleming, E. P. Gómez-Ruiz, G. F. McCracken, N. Owen-Smith, C. A. Peres, & S. B. Vander Wall. 2019. The functional roles of mammals in ecosystems. Journal of Mammalogy 100:942–964.

Lähteenmäki, S., E. M. Slade, B. Hardwick, G. Schiffler, J. Louzada, J. Barlow, & T. Roslin. 2015. MESOCLOSURES - increasing realism in mesocosm studies of ecosystem functioning. Methods in Ecology and Evolution 6:916–924.

Larsen, T. H., & A. Forsyth. 2005. Trap spacing and transect design for dung beetle biodiversity studies. Biotropica 37:322–325.

Larsen, T. H., A. Lopera, & A. Forsyth. 2008. Understanding trait-dependent community disassembly: Dung beetles, density functions, and forest fragmentation. Conservation Biology 22:1288–1298.

Larsen, T. H., N. M. Williams, & C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters 8:538–547.

Lefcheck, J. S. 2016. PiecewiseSEM : Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography 10:3–13.

Loreau, M. 2001. Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294:804–808.

Losey, J. E., & M. Vaughan. 2006. The economic value of ecological services provided by insects. BioScience 56:311.

Manning, P., E. M. Slade, S. A. Beynon, & O. T. Lewis. 2016. Functionally rich dung beetle assemblages are required to provide multiple ecosystem services. Agriculture, Ecosystems & Environment 218:87–94.

Martín-Piera, F., C. M. Veiga, & J. M. Lobo. 1992. Ecology and biogeography of dung-beetle communities (Coleoptera, Scarabaeoidea) in an Iberian Mountain Range. Journal of Biogeography 19:677.

McCain, C. M. 2005. Elevational gradients in the diversity of small mammals. Ecology 86:366–372.

McCain, C. M. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. Global Ecology and Biogeography 16:1–13.

McCain, C. M., & J.-A. Grytnes. 2010. Elevational gradients in species richness. In: Encyclopedia of Life Sciences. John Wiley & Sons, Ltd, Chichester, UK.

McCoy, E. D. 1990. The Distribution of insects along elevational gradients. Oikos 58:313.

Messerli, B., & J. D. Ives. 1997. Mountains of the world: a global priority. Parthenon Publishing, New York and Carnforth.

Millenium Ecosytem Assessment. 2005. Ecosystems and human well-being:
synthesis.

Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, H. A. Lessios, C. M. McCain, A. R. McCune, L. A. McDade, M. A. McPeek, T. J. Near, T. D. Price, R. E. Ricklefs, K. Roy, D. F. Sax, D. Schluter, J. M. Sobel, & M. Turelli. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. Ecology Letters 10:315–331.

Mmbaga, N. E., L. K. Munishi, & A. C. Treydte. 2017. How dynamics and drivers of land use/land cover change impact elephant conservation and agricultural livelihood development in Rombo, Tanzania. Journal of Land Use Science 12:168–181.

Moczek, A. P., & D. J. Emlen. 2000. Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative reproductive tactics favour alternative phenotypes? Animal Behaviour 59:459–466.

Muhirwa, F., Rwanda Abias Maniragaba, Abias Maniragaba, & B A Kaplin. 2018. Dung beetle distribution, abundance, and diversity along an elevation gradient in Nyungwe National Park, Rwanda: A preliminary survey.

Naeem, S., & J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. Ecology Letters 6:567–579.

Nervo, B., C. Tocco, E. Caprio, C. Palestrini, & A. Rolando. 2014. The effects of body mass on dung removal efficiency in dung beetles. PLoS ONE 9:e107699.

Newbold, T., L. N. Hudson, S. L. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, D. J. Bennett, A. Choimes, B. Collen, J. Day, A. De Palma, S. Díaz, S. Echeverria-Londoño, M. J. Edgar, A. Feldman, M. Garon, M. L. K. Harrison, T. Alhusseini, D. J. Ingram, Y. Itescu, J. Kattge, V. Kemp, L. Kirkpatrick, M. Kleyer, D. L. P. Correia, C. D. Martin, S. Meiri, M. Novosolov, Y. Pan, H. R. P. Phillips, D. W. Purves, A. Robinson, J. Simpson, S. L. Tuck, E. Weiher, H. J. White, R. M. Ewers, G. M. Mace, J. P. W. Scharlemann, & A. Purvis. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

Newmark, W. D., & IUCN Tropical Forest Programme. 1991. The conservation of Mount Kilimanjaro. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.

Nichols, E., T. A. Gardner, C. A. Peres, S. Spector, & The Scarabaeinae Research Network. 2009. Co-declining mammals and dung beetles: an impending ecological cascade. Oikos 118:481–487.

Nichols, E., T. Larsen, S. Spector, A. L. Davis, F. Escobar, M. Favila, & K. Vulinec. 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. Biological Conservation 137:1–19.

Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amezquita, & M. E. Favila. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation 141:1461–1474.

Nichols, E., M. Uriarte, D. E. Bunker, M. E. Favila, E. M. Slade, K. Vulinec, T. Larsen, F. Z. Vaz-de-Mello, J. Louzada, S. Naeem, & S. H. Spector. 2013. Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. Ecology 94:180–189.

Nogués-Bravo, D., M. B. Araújo, T. Romdal, & C. Rahbek. 2008. Scale effects and human impact on the elevational species richness gradients. Nature 453:216–219.

Nonnotte, P., H. Guillou, B. Le Gall, M. Benoit, J. Cotten, & S. Scaillet. 2008. New K–Ar age determinations of Kilimanjaro volcano in the North Tanzanian diverging rift, East Africa. Journal of Volcanology and Geothermal Research 173:99–112.

Nunes, C. A., R. F. Braga, J. E. C. Figueira, F. de S. Neves, & G. W. Fernandes. 2016. Dung beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity. PLoS ONE 11:e0157442.

Nunes, C. A., R. F. Braga, F. de Moura Resende, F. de Siqueira Neves, J. E. C. Figueira, & G. W. Fernandes. 2018. Linking biodiversity, the environment and ecosystem functioning: ecological functions of dung beetles along a tropical elevational gradient. Ecosystems 21: 1244-1254

Nyirenda, V. R., W. J. Myburgh, B. K. Reilly, & A. I. Phiri. 2013. Wildlife crop damage valuation and conservation: conflicting perception by local farmers in the Luangwa Valley, Eastern Zambia. International Journal of Biodiversity and Conservation 5: 741-750

Ohlberger, J. 2013. Climate warming & ectotherm body size - from individual physiology to community ecology. Functional Ecology 27:991–1001.

Oksanen, J., F. Guillaume Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, & H. Wagner. 2019. vegan: community Ecology Package.

Parain, E. C., R. P. Rohr, S. M. Gray, & L.-F. Bersier. 2019. Increased temperature disrupts the biodiversity–ecosystem functioning relationship. The American Naturalist 193:227–239.

Payne, D., E. M. Spehn, M. Snethlage, & M. Fischer. 2017. Opportunities for research on mountain biodiversity under global change. Current Opinion in Environmental Sustainability 29:40–47.

Peters, M. K., A. Hemp, T. Appelhans, J. N. Becker, C. Behler, A. Classen, F. Detsch, A. Ensslin, S. W. Ferger, S. B. Frederiksen, F. Gebert, F. Gerschlauer, A. Gütlein, M. Helbig-Bonitz, C. Hemp, W. J. Kindeketa, A. Kühnel, A. V. Mayr, E. Mwangomo, C. Ngereza, H. K. Njovu, I. Otte, H. Pabst, M. Renner, J. Röder, G. Rutten, D. Schellenberger Costa, N. Sierra-Cornejo, M. G. R. Vollstädt, H. I. Dulle, C. D. Eardley, K. M. Howell, A. Keller, R. S. Peters, A. Ssymank, V. Kakengi, J. Zhang, C. Bogner, K. Böhning-Gaese, R. Brandl, D. Hertel, B. Huwe, R. Kiese, M. Kleyer, Y. Kuzyakov, T. Nauss, M. Schleuning, M. Tschapka, M. Fischer, & I. Steffan-Dewenter. 2019. Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions. Nature 568:88–92.

Peters, M. K., A. Hemp, T. Appelhans, C. Behler, A. Classen, F. Detsch, A. Ensslin, S. W. Ferger, S. B. Frederiksen, F. Gebert, M. Haas, M. Helbig-Bonitz, C. Hemp, W. J. Kindeketa, E. Mwangomo, C. Ngereza, I. Otte, J. Röder, G. Rutten, D. Schellenberger Costa, J. Tardanico, G. Zancolli, J. Deckert, C. D. Eardley, R. S. Peters, M.-O. Rödel, M. Schleuning, A. Ssymank, V. Kakengi, J. Zhang, K. Böhning-Gaese, R. Brandl, E. K. V. Kalko, M. Kleyer, T. Nauss, M. Tschapka, M. Fischer, & I. Steffan-Dewenter. 2016. Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nature Communications 7:13736.

Peters, R. H., G. Cabana, B. Choulik, T. Cohen, S. Griesbach, & S. J. McCanny. 1996. General models for trophic fluxes in animals based on their body size. Ecoscience 3:365–377.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. The American Naturalist 100:33–46.

Piccini, I., B. Nervo, M. Forshage, L. Celi, C. Palestrini, A. Rolando, & T. Roslin. 2018. Dung beetles as drivers of ecosystem multifunctionality: Are response and effect traits interwoven? Science of the Total Environment 616–617:1440–1448.

van der Plas, F. 2019. Biodiversity and ecosystem functioning in naturally assembled communities. Biological Reviews.

Pontarp, M., L. Bunnefeld, J. S. Cabral, R. S. Etienne, S. A. Fritz, R. Gillespie, C. H. Graham, O. Hagen, F. Hartig, S. Huang, R. Jansson, O. Maliet, T. Münkemüller, L. Pellissier, T. F. Rangel, D. Storch, T. Wiegand, & A. H. Hurlbert. 2018. The Latitudinal Diversity Gradient: Novel Understanding through Mechanistic Eco-evolutionary Models. Trends in Ecology & Evolution 34:211–223.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, & R. T. Paine. 1996. Challenges in the Quest for Keystones. BioScience 46:609–620.

Price, S. A., S. S. B. Hopkins, V. L. Roth, & K. K. Smith. 2012. Tempo of trophic evolution and its impact on mammalian diversification. Proceedings of the National Academy of Sciences 109: 7008-7012

Pringle, R. M., T. P. Young, D. I. Rubenstein, & D. J. McCauley. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. Proceedings of the National Academy of Sciences 104:193–197.

Pryke, J. S., F. Roets, & M. J. Samways. 2016. Wild Herbivore Grazing Enhances Insect Diversity over Livestock Grazing in an African Grassland System. PLoS ONE 11:e0164198.

Qian, H., & R. E. Ricklefs. 2016. Out of the Tropical Lowlands: Latitude versus Elevation. Trends in Ecology & Evolution 31:738–741.

Quijas, S., & P. Balvanera. 2013. Biodiveresity and ecosystem services. In: Levin, S (Ed.) Encyclopedia of Biodiversity. Academic Press, Amsterdam, Oxford.

Radtke, M. G., & G. B. Williamson. 2005. Volume and linear measurements as predictors of dung beetle (Coleoptera: Scarabaeidae) biomass. Annals of the Entomological Society of America 98:548–551.

Rahbek, C. 1995. The elevational gradient of species richness: a uniform pattern? Ecography 18:200–205.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns. Ecology Letters 8:224–239.

Ramírez-Ponce, A., J. M. Calderón-Patrón, H. M. G. Vásquez, & C. E. Moreno. 2019. Biotic heterogeneity among scarab beetle communities in an anthropized landscape in the Central Valleys of Oaxaca, Mexico. Journal of Insect Conservation: 1-12

Reiss, J., J. R. Bridle, J. M. Montoya, &G. Woodward. 2009. Emerging horizons in biodiversity and ecosystem functioning research. Trends in Ecology & Evolution 24:505–514.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514.

Romdal, T. S., & J.-A. Grytnes. 2007. An indirect area effect on elevational species richness patterns. Ecography 30:440–448.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, New York.

Schipper, J., J. S. Chanson, F. Chiozza, N. A. Cox, M. Hoffmann, V. Katariya, J. Lamoreux, A. S. L. Rodrigues, S. N. Stuart, H. J. Temple, J. Baillie, L. Boitani, T. E. Lacher, R. A. Mittermeier, A. T. Smith, D. Absolon, J. M. Aguiar, G. Amori, N. Bakkour, R. Baldi, R. J. Berridge, J. Bielby, P. A. Black, J. J. Blanc, T. M. Brooks, J. A. Burton, T. M. Butynski, G. Catullo, R. Chapman, Z. Cokeliss, B. Collen, J. Conroy, J. G. Cooke, G. A. B. da Fonseca, A. E. Derocher, H. T. Dublin, J. W. Duckworth, L. Emmons, R. H. Emslie, M. Festa-Bianchet, M. Foster, S. Foster, D. L. Garshelis, C. Gates, M. Gimenez-Dixon, S. Gonzalez, J. F. Gonzalez-Maya, T. C. Good, G. Hammerson, P. S. Hammond, D. Happold, M. Happold, J. Hare, R. B. Harris, C. E. Hawkins, M. Haywood, L. R. Heaney, S. Hedges, K. M. Helgen, C. Hilton-Taylor, S. A. Hussain, N. Ishii, T. A. Jefferson, R. K. B. Jenkins, C. H. Johnston, M. Keith, J. Kingdon, D. H. Knox, K. M. Kovacs, P. Langhammer, K. Leus, R.

Lewison, G. Lichtenstein, L. F. Lowry, Z. Macavoy, G. M. Mace, D. P. Mallon, M. Masi, M. W. McKnight, R. A. Medellin, P. Medici, G. Mills, P. D. Moehlman, S. Molur, A. Mora, K. Nowell, J. F. Oates, W. Olech, W. R. L. Oliver, M. Oprea, B. D. Patterson, W. F. Perrin, B. A. Polidoro, C. Pollock, A. Powel, Y. Protas, P. Racey, J. Ragle, P. Ramani, G. Rathbun, R. R. Reeves, S. B. Reilly, J. E. Reynolds, C. Rondinini, R. G. Rosell-Ambal, M. Rulli, A. B. Rylands, S. Savini, C. J. Schank, W. Sechrest, C. Self-Sullivan, A. Shoemaker, C. Sillero-Zubiri, N. De Silva, D. E. Smith, C. Srinivasulu, P. J. Stephenson, N. van Strien, B. K. Talukdar, B. L. Taylor, R. Timmins, D. G. Tirira, M. F. Tognelli, K. Tsytsulina, L. M. Veiga, J.-C. Vie, E. A. Williamson, S. A. Wyatt, Y. Xie, & B. E. Young. 2008. The Status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322:225–230.

Shabtay, A. 2005. Ectothermy and endothermy: evolutionary perspectives of thermoprotection by HSPs. Journal of Experimental Biology 208:2773–2781.

Shahabuddin, P. Hidayat, S. Manuwoto, W. A. Noerdjito, T. Tscharntke, & C. H. Schulze. 2010. Diversity and body size of dung beetles attracted to different dung types along a tropical land-use gradient in Sulawesi, Indonesia. Journal of Tropical Ecology 26:53–65.

Shipley, B. 2000. A New inferential test for path models based on directed acyclic graphs. Structural Equation Modeling: A Multidisciplinary Journal 7:206–218.

Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.

Shipley, B. 2013. The AIC model selection method applied to path analytic models compared using a d-separation test. Ecology 94:560–564.

Simmons, L. W., & T. J. Ridsdill-Smith. 2011. Ecology and Evolution of Dung Beetles. John Wiley & Sons.

Slade, E. M., D. J. Mann, & O. T. Lewis. 2011. Biodiversity and ecosystem function of tropical forest dung beetles under contrasting logging regimes. Biological Conservation 144:166–174.

Slade, E. M., D. J. Mann, J. F. Villanueva, and O. T. Lewis. 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. Journal of Animal Ecology 76:1094–1104.

Spector, S. 2006. Scarabaeine Dung Beetles (coleoptera: Scarabaeidae: Scarabaeinae): An invertebrate focal taxon for biodiversity research and conservation. The Coleopterists Bulletin 60:71–83.

Spehn, E. M., Rudmann-Maurer, C. Körner, & Maselli. 2010. Mountain biodiversity and global change. GMBA-DIVERSITAS, Basel.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. The American Naturalist 133:240–256.

Storch, D. 2012. Biodiversity and its energetic and thermal controls. Pages 120–131 *in* R. M. Sibly, J. H. Brown, and A. Kodric-Brown, editors. Metabolic Ecology. John Wiley & Sons, Ltd, Chichester, UK.

Storch, D., E. Bohdalková, & J. Okie. 2018. The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity-diversity relationship. Ecology Letters 21:920–937.

Stuart, C., & T. Stuart. 2000. A field guide to the tracks and signs of Southern and East African wildlife. Struik, Cape Town.

Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. Ecology 58:1007–1019.

Trolle, M., A. J. Noss, J. L. P. Cordeiro, & L. F. B. Oliveira. 2008. Brazilian tapir density in the pantanal: a comparison of systematic camera-trapping and line-transect surveys. Biotropica 40:211–217.

Van Valkenburgh, B. 1999. Major patterns in the history of carnivorous mammals. Annual Review of Earth and Planetary Sciences 27:463–493.

Veldhuis, M. P., M. I. Gommers, H. Olff, & M. P. Berg. 2018. Spatial redistribution of nutrients by large herbivores and dung beetles in a savanna ecosystem. Journal of Ecology 106:422–433.

Vessby, K. 2001. Habitat and weather affect reproduction and size of the dung beetle Aphodius fossor. Ecological Entomology 26:430–435.

Wallace, A R. 1878. Tropical nature and other essays. Macmillan, London.

Williams, P. H., N. D. Burgess, & C. Rahbek. 2000. Flagship species, ecological complementarity and conserving the diversity of mammals and birds in sub-Saharan Africa. Animal Conservation 3:249–260.

Willig, M. R., D. M. Kaufman, & R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273–309.

Willig, Michael R, & Presley, Steven J. 2013. Latitudinal Gradients of Biodiversity. In: Levin, S. (Ed.) Encyclopedia of Biodiversity. Academic Press, Amsterdam, Oxford.

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton, FL.

Woodward, G., B. Ebenman, M. Emmerson, J. Montoya, J. Olesen, A. Valido, & P. Warren. 2005. Body size in ecological networks. Trends in Ecology & Evolution 20:402–409.

Xu, G., Z. Chao, S. Wang, Y. Hu, Z. Zhang, J. Duan, X. Chang, A. Su, C. Luo, Y. Li, & M. Du. 2010. Temperature sensitivity of nutrient release from dung along elevation gradient on the Qinghai–Tibetan plateau. Nutrient Cycling in Agroecosystems 87:49–57.

AUTHOR CONTRIBUTIONS

CHAPTER II

This chapter is published as

Gebert F*, Njovu HK, Treydte AC, Steffan-Dewenter I,Peters MK (2019) Primary productivity and habitat protection predict elevational species richness and community biomass of large mammals on Mt. Kilimanjaro. Journal of Animal Ecology. *Corresponding author (contributed ca. 80 % of this study)

Authors' contributions

F.G., M.K.P. and I.S.-D. conceived the idea for the study; F.G., A.C.T, I.S.-D. and M.K.P. designed the study; F.G. collected the data; F.G, H.K.N. and A.C.T. conducted taxonomic identification, F.G. and M.K.P. analysed the data; F.G. wrote the first version of the manuscript; all authors contributed to the final version of the manuscript.

Acknowledgements

We would like to thank the Tanzanian Comission for Science and Technology (COSTECH), the Tanzanian Wildlife Research Institute (TAWIRI) and the Kilimanjaro National Park authority for their support and the necessary research permit (COSTECH 2015-178-NA-96-44 and TANAPA TNP/HQ/C.10/13). We are thankful to Zacharia Mwanga, Daudi Lusiba, Bahati Charles and all other Tanzanian field assistants for their help in the field and two anonymous reviewers for providing helpful comments to improve the manuscript. We would like to thank Katrin Böhning-Gaese for the provision of camera traps.

Funding

This study was accomplished within the scope of the Research Unit FOR1246 (Kilimanjaro ecosystems under global change: linking biodiversity, biotic interactions and biogeochemical processes, https://www.kilimanjaro.biozentrum.uni-wuerzburg.de) and funded by grants of the Deutscher Akademischer Austauschdienst (DAAD) and by the Deutsche Forschungsgemeinschaft (DFG).

Friederike Gebert	Dr. Henry K. Njovu
PD Dr. Anny C. Treydte	Prof. Dr. Ingolf Steffan-Dewenter
PD DR. Marcell Peters	

CHAPTER III

This chapter is published as

Gebert, F*, Steffan-Dewenter, I, Moretto, P, Peters, MK. Climate rather than dung resources predict dung beetle abundance and diversity along elevational and land use gradients on Mt. Kilimanjaro. Journal of Biogeography *Corresponding author (contributed ca. 80-90 % of this study)

Authors' contributions

F.G., M.K.P. and I.S.-D. developed the study; F.G., I.S.-D. and M.K.P. designed the study; F.G. collected the data; F.G. and P.M. conducted taxonomic identification, F.G. analysed the data with input from M.K.P.; F.G. wrote the first version of the manuscript; all authors contributed to the final version of the manuscript.

Acknowledgements

We would like to thank the Tanzanian Comission for Science and Technology (COSTECH), the Tanzanian Wildlife Research Institute (TAWIRI) and the Kilimanjaro National Park authority for their continous support and granting the necessary research permits (COSTECH 2015-178-NA-96-44 and TANAPA TNP/HQ/C.10/13). We are thankful to Zacharia Mwanga, Daudi Lusiba, Bahati Charles and all other Tanzanian field assistants for their help in the field. We would like to thank Patrice Bordat for the identification of Aphodiinae dung beetles and Katrin Böhning-Gaese for the provision of camera traps.

Funding

This study was accomplished within the scope of the Research Unit FOR1246 (Kilimanjaro ecosystems under global change: linking biodiversity, biotic interactions and biogeochemical processes, https://www.kilimanjaro.biozentrum.uni-wuerzburg.de) and funded by grants of the Deutscher Akademischer Austauschdienst (DAAD) and by the Deutsche Forschungsgemeinschaft (DFG).

Friederike Gebert	Prof. Dr. Ingolf Steffan-Dewenter
Phillipe Moretto	PD Dr. Marcell Peters

CHAPTER IV

This chapter has been submitted to Ecology as

Gebert , F*, Steffan-Dewenter, I, Kronbach, P, Peters MK (under review). Changes in body size and species richness of dung beetles determine rates of dung decomposition on Mt. Kilimanjaro. *Corresponding author (contributed ca. 90 % of this study)

Author's contributions

F.G., M.K.P. and I.S.-D. developed the study; F.G., I.S.-D. and M.K.P. designed the study; F.G. collected the data; F.G. and P.K. conducted species measurements, F.G. analysed the data; F.G. wrote the first version of the manuscript; all authors contributed to the final version of the manuscript.

Acknowledgements

We would like to thank the Tanzanian Comission for Science and Technology (COSTECH), the Tanzanian Wildlife Research Institute (TAWIRI) and the Kilimanjaro National Park authority for their continous support and granting the necessary research permits (COSTECH 2015-178-NA-96-44 and TANAPA TNP/HQ/C.10/13). We are thankful to Zacharia Mwanga, Daudi Lusiba, Bahati Charles and all other Tanzanian field assistants for their help in the field. We would like to thank Philippe Moretto for the identification of Scarabaeinae dung beetles and Patrice Bordat for the identification of Aphodiinae dung beetles, respsectively.

Funding

This study was accomplished within the scope of the Research Unit FOR1246 (Kilimanjaro ecosystems under global change: linking biodiversity, biotic interactions and biogeochemical processes, https://www.kilimanjaro.biozentrum.uni-wuerzburg.de) and funded by grants of

the Deutscher Akademischer Austauschdienst (DAAD) and by the Deutsche Forschungsgemeinschaft (DFG).

Friederike Gebert	Prof. Dr. Ingolf Steffan-Dewenter
Patrick Kronbach	PD Dr. Marcell Peters

ACKNOWLDGEMENTS

I would like to thank Ingolf Steffan-Dewenter and Marcell Peters for granting me the opportunity to join the fantastic Zoo 3 team and to work on my subject of choice in Tanzania. Thank you both for the great supervision and the continuous advancement of my project. Thanks for also including camera traps and mammals in this project – this has really broadened my horizon! Thank you Ingolf for your enduring support and funding. Thank you Marcell for introducing me to R and for the valuable advice on all science matters! Thanks to you both also for the two wonderful excursions to Kenya. Thanks to Owen Lewis for reviewing my thesis and for coming all the way from the UK for my defence.

Next, I would like to thank the Zoo 3 team for the great working atmosphere and for making me feel at home. Thanks to Elena for sharing the office of laughter and joy with me. Thanks to Elena and Toni for the nice discussions about life, R and everything! Thanks to Elena, Laura, Ludmilla, Amy, Mariela and Fabian for being my lunchtime mates. Thanks to Patrick for doing his bachelor thesis with me and for mounting and measuring thousands of dung beetles. Thanks also to my HiWis Monika, Pia, Lara and Selma. Thanks to Birgit for her help with all administrative obstacles. Thanks to Norbert for his practical help in designing the covers of the traps.

In Tanzania, a huge thank you goes out to Zacharia, Daudi, Bahati, Esrom, Raymundi, Frederik and Johannes for being my field assistants. Without you, the practical part of this work would not have been possible. Thank you all for becoming friends, for carrying a total of 185 kg of cow dung up Mt. Kilimanjaro without complaint, for building tents, cooking ugali and spending many weeks with me on the mountain. Thanks to the drivers Wilberd, William, Nelson and August – no matter whether the car got stuck in the mud or whether the road was blocked by trees, in the end you always got me savely to the study plots. Thanks to Marion, Sophia and all other students, our station tiger Mimi as well as to Mamatuma and Veronika for the amazing time in Nkweseko. Thanks to COSTECH and TANAPA for granting research permits.

This PhD would have been a lot harder without my stay at the Natural History Museum London beforehand. Thanks to Max Barclay for the three wonderful months there. I am grateful to Sally-Anne Spence and Darren Mann for sharing their passion for dung beetles with me.

Thanks to Philippe Moretto for his help in identifying Scarabaeinae dung beetles and his hospitality during my stay in Toulon. I would also like to thank Patrice Bordat for the identification of Aphodiinae dung beetles. Thanks also to the Association Catharsius for the nice meetings and fruitful discussions in Paris and Olivier Montreuil for the identification of Sisyphini.

Thanks to the DAAD for funding. Thank you also to the SCIENTIA mentoring programme and my mentor Eleanor Slade for the many tips about the academic way of life.

Abigale and Dominik: Thank you for being my besties on whom I can always rely on.

Last but not least, I would like to thank my family for their continuous support and for always believing in me. Thanks especially to my partner Sebastian for making me laugh even from far away and the many hikes and adventures that gave me the necessary distraction to fully concentrate on this project.

PUBLICATION LIST

Publications as part of doctoral thesis

Gebert F, Njovu HK, Treydte AC, Steffan-Dewenter I, Peters MK (2019) Primary productivity and habitat protection predict elevational species richness and community biomass of large mammals on Mt. Kilimanjaro. Journal of Animal Ecology. https://doi.org/10.1111/1365-2656.13074

Gebert, F, Steffan-Dewenter, I, Moretto, P, Peters, MK (2019) Climate rather than dung resources predict dung beetle abundance and diversity along elevational and land use gradients on Mt. Kilimanjaro. Journal of Biogeography. https://doi.org/10.1111/jbi.13710

Gebert, F, Steffan-Dewenter, I, Kronbach, P, Peters MK (under review) Changes in body size and species richness of dung beetles determine rates of dung decomposition on Mt. Kilimanjaro. Ecology.

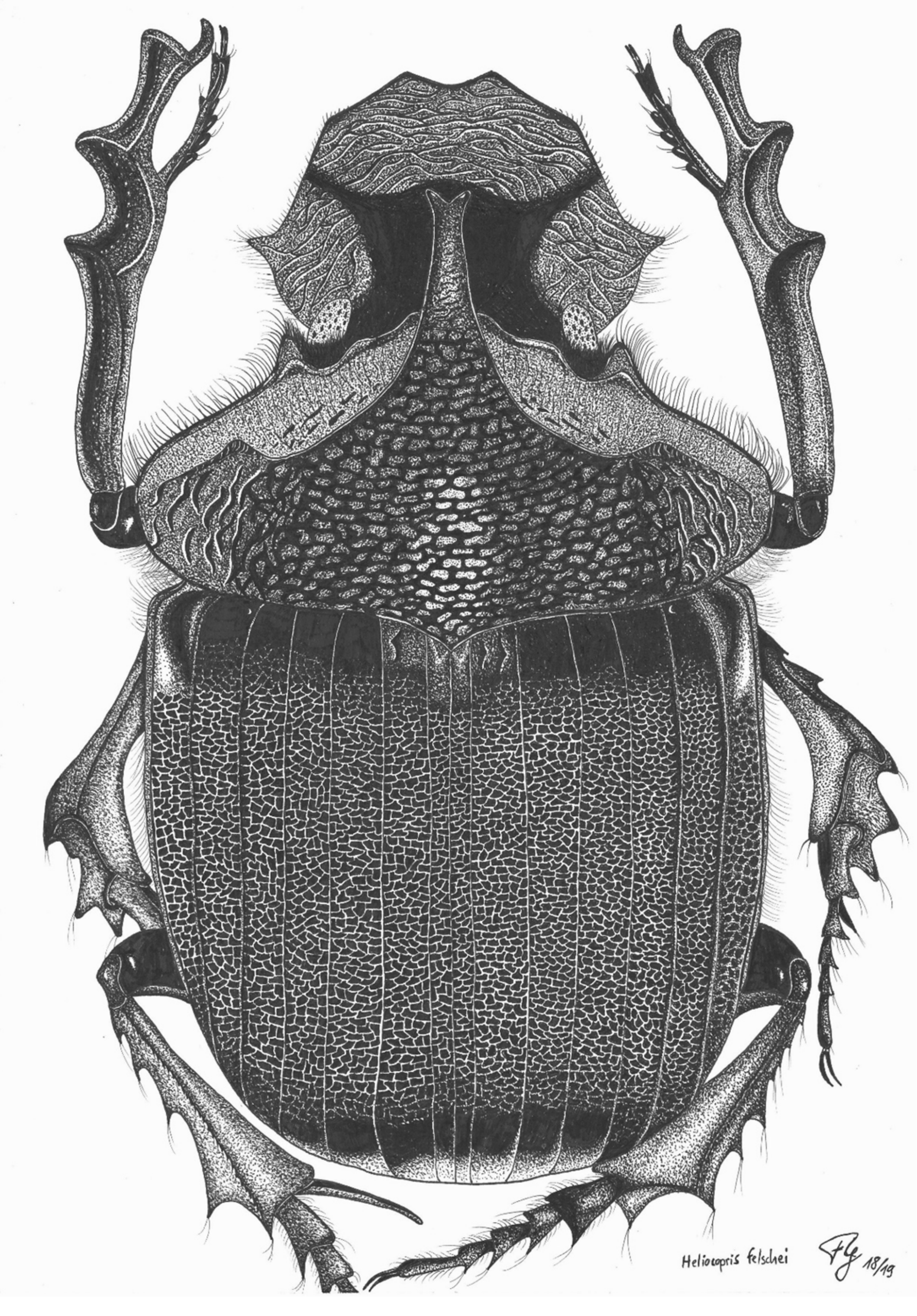
Additional publications

Peters MK, Hemp A, Appelhans T, Becker JN, Behler C, Classen A, Cornejo NS, Detsch F, Ensslin A, Ferger SW, Frederiksen SB, **Gebert F**, Gerschlauer F, Gütlein A, Haas M, Helbig-Bonitz M, Hemp C, Kindeketa WJ, Kühnel A, Mayr A, Mwangomo E, Ngereza C, Njovu HN, Otte I, Pabst H, Renner M, Röder J, Rutten G, Schellenberger Costa D, Vollstädt MGR, Eardley CD, Keller A, Peters RS, Ssymank A, Kakengi V, Zhang J, Bogner C, Böhning-Gaese K, Brandl R, Hertel D, Huwe B, Kiese R, Kleyer M, Kuzyakov Y, Nauss T, Schleuning M, Tschapka M, Fischer M, Steffan-Dewenter I (2019) Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. Nature 568:88-92.

Peters MK, Hemp A, Appelhans T, Behler C, Classen A, Detsch F, Ensslin A, Ferger SW, Frederiksen SB, **Gebert F**, Haas M, Helbig-Bonitz M, Hemp C, Kindeketa WJ, Mwangomo E, Ngereza C, Otte I, Roeder J, Rutten G, Schellenberger Costa D, Tardanico J, Zancolli J, Deckert J, Eardley CD, Peters RS, Rooedel M-O, Schleuning M, Ssymank A, Kakengi V, Zhang J, Boehning-Gaese K, Brandl R, Kalko EKV , Kleyer M, Nauss T, Tschapka M, Fischer M, Steffan-Dewenter I (2016) Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nature Communications 7: 13736. OPEN ACCESS.

Conference talks

03/2019	Climate-mediated changes in the functional composition of dung beetle communities determine rates of dung decomposition along extensive environmental gradients on Mt. Kilimanjaro, Tanzania Macroecology 2019, Würzburg, Germany
07/2018	Dung beetles (Coleoptera: Scarabaeidae) along elevational and land use gradients on Mt. Kilimanjaro: Which factors predict species richness and abundance? 55th Annual Meeting of the Association of Tropical Biology and Conservation (ATBC), Kuching, Malaysia
03/2018	Predictors of species richness and community biomass of large mammals along elevational and land use gradients on Mt. Kilimanjaro. European Conference of Tropical Ecology (GTÖ), Paris, France
02/2017	Can differences in dung beetle diversity and ecosystem services provided by dung beetles be explained by mammal diversity? AfroMont Congress, Moshi, Tanzania
02/2017	Mammals and dung beetles along an elevation and land use gradient at Mt Kilimanjaro. European Conference of Tropical Ecology (GTÖ), Brussels, Belgium. Maria Sibylla Merian Award in the category "Best Presentations Talk"
02/2016	Dung beetle assemblages and their contribution to decomposition along elevational and land use gradients on Mt. Kilimanjaro European Conference of Tropical Ecology (GTÖ), Göttingen, Germany



© Friederike Gebert, *Heliocopris felschei*