Patterns and drivers of herbivore diversity and invertebrate herbivory along elevational and land use gradients at Mt. Kilimanjaro, Tanzania

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Contents

Affidavit

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich, Henry Kenneth Njovu, die vorliegende Dissertation mit dem Titel "Patterns and drivers of herbivore diversity and invertebrate herbivory along elevational and land use gradients at Mt. Kilimanjaro, Tanzania" selbstständig und ohne Hilfe eines kommerziellen Promotionsberaters angefertigt habe und dabei keine anderen, als die von mir angegebenen Quellen und Hilfsmittel verwendet habe. Ich erkläre außerdem, dass die vorliegende Dissertation weder in gleicher, noch in ähnlicher Form bereits in einem Prüfungsverfahren vorgelegen hat. Des Weiteren habe ich außer den mit dem Zulassungsantrag urkundlich vorgelegten Graden keine weiteren akademischen Grade erworben oder zu erwerben versucht.

Declaration

I, Henry Kenneth Njovu certify that the thesis entitled "Patterns and drivers of herbivore diversity and invertebrate herbivory along elevational and land use gradients at Mt. Kilimanjaro, Tanzania" results from my own work. I also certify that I did not receive any help or support from any commercial consulting firm and that all sources and materials applied are listed and specified in the thesis. Further to that, I certify that this thesis has not been submitted as part of another examination process in similar or dissimilar form.

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Summary

This thesis elucidates patterns and drivers of invertebrate herbivory, herbivore diversity, and community-level biomass along elevational and land use gradients at Mt. Kilimanjaro, Tanzania.

Chapter I provides background information on the response and predictor variables, study system, and the study design. First, I give an overview of the elevational patterns of species diversity/richness and herbivory published in the literature. The overview illuminates existing debates on elevational patterns of species diversity/richness and herbivory. In connection to these patterns, I also introduce several hypotheses and mechanisms put forward to explain macroecological patterns of species richness. Furthermore, I explain the main variables used to test hypotheses. Finally, I describe the study system and the study design used.

Chapter II explores the patterns of invertebrate herbivory and their underlying drivers along extensive elevational and land use gradients on the southern slopes of Mt. Kilimanjaro. I recorded standing leaf herbivory from leaf chewers, leaf miners and gall-inducing insects on 55 study sites located in natural and anthropogenic habitats distributed from 866 to 3060 meters above sea level (m asl) on Mt. Kilimanjaro. Standing leaf herbivory was related to climatic variables [mean annual temperature - (MAT) and mean annual precipitation - (MAP)], net primary productivity (NPP) and plant functional traits (leaf traits) [specific leaf area (SLA), carbon to nitrogen ratio (CN), and nitrogen to phosphorous ratio (NP)]. Results revealed an unimodal pattern of total leaf herbivory along the elevation gradient in natural habitats. Findings also revealed differences in the levels and patterns of herbivory among feeding guilds and between anthropogenic and natural habitats. Changes in NP and CN ratios which were closely linked to NPP were the strongest predictors of leaf herbivory. Our study uncovers the role of leaf nutrient stoichiometry and its linkages to climate in explaining the variation in leaf herbivory along climatic gradients.

Chapter III presents patterns and unravels direct and indirect effects of resource (food) abundance (NPP), resource (food) diversity [Functional Dispersion (FDis)], resource quality (SLA, NP, and CN rations), and climate variables (MAT and MAP) on species diversity of phytophagous beetles. Data were collected from 65 study sites located in natural and anthropogenic habitats distributed from 866 to 4550 m asl on the southern slopes of Mt. Kilimanjaro. Sweep net and beating methods were used to collect a total of 3,186 phytophagous beetles representing 21 families and 304 morphospecies. Two groups, weevils (Curculionidae) and leaf beetles (Chrysomelidae) were the largest and most diverse families represented with 898 and 1566 individuals, respectively. Results revealed complex (bimodal) and dissimilar patterns of Chao1-estimated species richness (hereafter referred to as species diversity) along elevation and land use gradients. Results from path analysis showed that temperature and climate-mediated changes in NPP had a significant positive direct and indirect effect on species diversity of phytophagous beetles, respectively. The results also revealed that the effect of NPP (via beetles abundance and diversity of food resources) on species diversity is stronger than that of temperature. Since we found that factors affecting species diversity were intimately linked to climate, I concluded that predicted climatic changes over the coming decades will likely alter the species diversity patterns which we observe today.

Chapter IV presents patterns and unravels the direct and indirect effects of climate, NPP and anthropogenic disturbances on species richness and community-level biomass of wild large mammals which represent endothermic organisms and the most important group of vertebrate herbivores. Data were collected from 66 study sites located in natural and anthropogenic habitats distributed from 870 to 4550 m asl on the southern slopes of Mt. Kilimanjaro. Mammals were collected using camera traps and used path analysis to disentangle the direct and indirect effects of climatic variables, NPP, land use, land area, levels of habitat protection and occurrence of domesticated mammals on the patterns of richness and community-level biomass of wild mammals, respectively. Results showed unimodal patterns for species richness and community-level biomass of wild mammals along elevation gradients and that the patterns differed depending on the type of feeding guild. Findings from path analysis showed that net primary productivity and levels of habitat protection had a strong direct effect on species richness and community-level biomass of wild mammals whereas temperature had an insignificant direct effect. Findings show the importance of climate-mediated food resources in determining patterns of species richness of large mammals. While temperature is among key predictors of species richness in several ectotherms, its direct influence in determining species richness of wild mammals was insignificant. Findings show the sensitivity of wild mammals to anthropogenic influences and underscore the importance of protected areas in conserving biodiversity.

In conclusion, despite a multitude of data sets on species diversity and ecosystem functions along broad climatic gradients, there is little mechanistic understanding of the underlying causes. Findings obtained in the three studies illustrate their contribution to the scientific debates on the mechanisms underlying patterns of herbivory and diversity along elevation gradients. Results present strong evidence that plant functional traits play a key role in determining invertebrate herbivory and species diversity along elevation gradients and that, their strong interdependence with climate and anthropogenic activities will shape these patterns in future. Additionally, findings from path analysis demonstrated that herbivore diversity, community-level biomass, and herbivory are strongly influenced by climate (either directly or indirectly). Therefore, the predicted climatic changes are expected to dictate ecological patterns, biotic interactions, and energy and nutrient fluxes in terrestrial ecosystems in the coming decades with stronger impacts probably occurring in natural ecosystems. Furthermore, findings demonstrated the significance of land use effects in shaping ecological patterns. As anthropogenic pressure is advancing towards more pristine higher elevations, I advocate conservation measures which are responsive to and incorporate human dimensions to curb the situation. Although our findings emanate from observational studies which have to take several confounding factors into account, we have managed to demonstrate global change responses in real ecosystems and fully established organisms with a wide range of interactions which are unlikely to be captured in artificial experiments. Nonetheless, I recommend additional experimental studies addressing the effect of top-down control by natural enemies on herbivore diversity and invertebrate herbivory in order to deepen our understanding of the mechanisms driving macroecological patterns along elevation gradients.

Zusammenfassung

In dieser Dissertation werden Muster und Determinanten von Herbivorendiversität, von Herbivorieraten durch Invertebraten sowie die Diversität und Gesamtbiomasse von Säugetieren entlang von Höhen- und Landnutzungsgradienten am Kilimandscharo (Tansania) untersucht.

Kapitel I liefert Hintergrundinformationen zu den betrachteten Variablen, dem Untersuchungssystem und dem generellen Studiendesign: Zuerst fasse ich den aktuellen Kenntnisstand über die Muster des Artenreichtums und der Herbivorie entlang von Höhengradienten zusammen und erläutere in diesem Zusammenhang verschiedene Hypothesen, die zur Erklärung von Gradienten des Artenreichtum herangezogen werden. Ich erkläutere verschiedene Variablen, die zum Testen dieser Hypothesen erhoben wurden und stelle dar, wie diese den Artenreichtum, die Herbivorieraten und die Biomasse beeinflussen könnten. Anschließend beschreibe ich das Untersuchungssystem, sowie das generelle Design der Studie.

In Kapitel II werden die Muster und Determinanten der Invertebratenherbivorie entlang von Höhen- und Landnutzungsgradienten an den südlichen Hängen des Kilimandscharos präsentiert. Auf insgesamt 55 Untersuchungsflächen, die sowohl natürliche als auch anthropogen genutzte Habitate am Kilimandscharo in Höhenlagen zwischen 866 und 3060 Meter über Normalnull (m ü. NN) umfassten, wurden die Herbivorieraten ektophager, minierender und gallbildener Insekten an Blättern erfasst. Die Blattherbivorie war sowohl mit klimatischen Variablen [Jahresmitteltemperatur und mittlere Jahresniederschlagsmenge], der Nettoprimärproduktivität (NPP) und mit funktionellen Blattmerkmalen von Pflanzen [spezifische Blattfläche (SLA), Kohlenstoff (C) / Stickstoff (N)-Verhältnis, sowie N / Phosphor (P)-Verhältnis] assoziiert. Die Gesamtherbivorie zeigte eine unimodale Verteilung über den Höhengradienten, wurde aber sowohl von der Herbivorengilde, als auch vom Habitattyp (natürlich *versus* anthropogen) beeinflusst. Das C/N-Verhältnis von Blättern war die stärkste

Determinante der Blattherbivorie und wurde selbst stark durch die NPP bestimmt. Herbivorieraten sanken mit steigendem C/N-Verhältnis. Das C/N Verhältnis nahm mit steigender NPP zu.- Letztere konnte fast vollständig durch Änderungen der mittleren Jahrestemperatur (MAT) und des Jahresniederschlags (MAP) entlang des Höhengradienten erklärt werden. Damit zeigt unsere Studie, dass sich durch klimatische Faktoren und Energie, welche ihrerseits die Blattchemie beeinflussen und so Variationen in der Blattherbivorie entlang großer Klimagradienten ergeben.

In Kapitel III werden die Muster im Artenreichtum phytophager Käfer entlang der Höhen- und Landnutzungsgradienten untersucht und die direkten und indirekten Effekte von klimatischen Faktoren (MAT, MAP), NPP und funktionellen Pflanzenmerkmalen (funktionelle Dispersion, SLA, C/N - und N/P - Verhältnisse) auf diese Muster analysiert. Die entsprechenden Daten wurden auf 65 Untersuchungsflächen, die sowohl natürliche als auch anthropogene Habitate entlang eines Höhengradienten am Kilimandscharo von 866 bis 4550 m ü. NN abdeckten, erhoben. Mittels Kescher wurden insgesamt 3186 phytophage Käfer aus 21 Familien gesammelt und in 304 Morphospezies eingeteilt. Der Artenreichtum phytophager Käfer zeigte eine komplexe, zweigipflige Verteilung entlang der Höhen- und Landnutzungsgradienten. Eine Pfadanalyse ergab, dass sowohl die MAT, als auch NPP positiven direkte bzw. indirekte Effekt auf die Artendiversität phytophager Käfer hatte. Die NPP war positiv mit der funktionellen Dispersion von Blattmerkmalen, ein Maß für die Diversität der Nahrungsressourcen, korreliert. Letztere hatte einen positiven Effekt auf die Diversität der Käfer. Die starken direkten und indirekten Effekte von Klima auf die Diversität und Abundanz von phytophagen Käfern, lassen vermuten dass der Klimawandel in den nächsten Dekaden großen Änderungen der Struktur von phytophagen Käfergemeinschaften bewirken wird.

In Kapitel IV untersuchen wir den Effekt von Klima, NPP und anthropogener Störung auf den Artenreichtum und die Gesamtbiomasse von Großwild. Dazu wurden auf 66

Untersuchungsflächen, welche natürliche und anthropogene Habitate in Höhenstufen zwischen 870 und 4550m ü. NN umfassten, Daten zum Artenreichtum un der Abundanz von Großwild mittels Kamerafallen erfasst. Mittels einer Pfadanalyse wurden die direkten und indirekten Effekte von klimatischen Variablen, NPP, Landnutzung, Größe und Schutzstatus der Flächen, sowie der Präsenz von domestizierten Säugetieren auf den Artenreichtum und die Biomasse von Großwild untersucht. Artenreichtum und Gesamtbiomasse dieser endothermen Organismen zeigten eine unimodale Verteilung über den Höhengradienten. Verschiedene Nahrungsgilden zeigten unterschiedliche Muster. Es konnte gezeigt werden, dass NPP und der Schutzstatus der Fläche, aber nicht die Temperatur einen direkten, positiven Einfluss auf den Artenreichtum und die Gesamtbiomasse des Großwildes hatte. Die vom Klima abhängige Nahrungsressourcenverfügbarkeit ist also eine wichtige Determinante im Artenreichtum von Großwild. Die Temperatur hingegen, die den Artenreichtum verschiedener ektothermer Organismen entscheidend prägt, hatte keinen direkten Einfluss auf den Artenreichtum des Großwildes Dafür reagiert das Großwild besonders sensibel auf anthropogene Einflüsse, was wiederum die Wichtigkeit von Schutzgebieten unterstreicht.

Obwohl die Muster im Artenreichtum und in Ökosystemfunktionen entlang großer klimatischer Gradienten bereits gut dokumentiert sind, ist das Wissen über die zu Grunde liegenden Prozesse nach wie vor unzureichend. Mit meinen drei Studien über die Muster und Determinanten der Herbivorendiversität, der Herbivorieraten und der Großwildbiomasse trage ich somit zur Verbesserung des mechanistischen Verständnisses solcher makroökologischer Muster bei. Wie die Pfadanalysen zeigten, wurden sowohl der Artenreichtum die Biomasse als auch ökologische Prozesse direkt oder indirekt vom Klima beeinflusst. Es ist somit zu erwarten, dass der vorhergesagte Klimawandel ökologische Muster, biotische Interaktionen, Energie- und Nährstoffkreisläufe in terrestrischen Ökosystemen wesentlich umstrukturieren wird, wobei natürliche Systeme wahrscheinlich besonders sensibel auf den Klimawandel reagieren werden. Meine Ergebnisse demonstrieren auch den Einfluss von Landnutzung auf Artenreichtum und ökologische Prozesse. Da der anthropogene Druck auf die natürlichen Ökosysteme des Kilimandscharos immer weiter zunimmt, sollten objektive Biodiversitätsmaße implementiert werden mit denen man Veränderungen in den Ökosystemen und in Ökosystemldienstleistungen schnell detektieren kann. Meine Ergebnisse basieren auf Beobachtungsdaten, die von bestimmten Nebenfaktoren im Feld beeinflusst werden können. Dennoch ist es mir gelungen mit korrelativen Methoden, Organismen in ihrem biotischen und abiotischen Interaktionsumfeld zu untersuchen – ein Szenario, welches in einem rein experimentellen Aufbau in dieser Form wahrscheinlich nicht geschaffen werden kann. Über weiterführende Experimente könnte jedoch zum Beispiel der Einfluss von Prädatoren auf die Herbivorendiversität und Herbivorieraten quantifiziert werden, welches unser Verständnis über die Determinanten makroökologischer Muster noch vertiefen würde.

Chapter I: General Introduction

Objectives and hypotheses of the studies

This thesis presents three important studies which in general elucidate patterns and drivers of invertebrate herbivory, herbivore diversity and community-level biomass along elevational and land use gradients at Mt. Kilimanjaro, Tanzania. The first study investigates patterns and drivers of community-level standing invertebrate (leaf) herbivory (Chapter II). This study hinges on four hypotheses which suggest that invertebrate (leaf) herbivory i) decline monotonically with elevation due to temperature; ii) peaks at mid-elevations due to high net primary productivity; iii) is highly influenced by leaf traits which vary with changing environmental conditions along the elevational gradient, and iv) declines with increased intensity of human land use. The second study investigates patterns and drivers of species diversity of phytophagous beetles (Chapter III). The study tests three hypotheses which suggest that diversity of phytophagous beetles i) peaks at mid-elevations due to high climate-mediated net primary productivity (i.e. resources abundance); ii) declines monotonically with elevation due to temperature-mediated foraging activity and speciation and iii) peaks at mid-elevation due to ambient environmental conditions which resources diversity and species coexistence. The third study investigates patterns and drivers of species richness and community-level biomass of large wild mammals (Chapter IV). The study tests four hypotheses which suggest that species richness and biomass of wild mammals i) correlate positively with net primary productivity which peaks at mid-elevations, ii) are positively correlated with climate-mediated net primary productivity (indirectly) and metabolic rate (directly), iii) decline with elevation due to decreased size of the available land area, and iv) increase with the level of habitat protection.

Mountain ecosystems

Mountains occupy approximately 12% of the earth's land surface (Körner 2007), they harbor extremely high biodiversity and provide ecosystem services to billion inhabitants in the world (Quintero and Jetz 2018, Woodwell 2004, Payne et al. 2017). Mountains also serve as hotspots of biological diversity and centers of endemism (Barthlott and al. 1996, Merckx et al. 2015). In tropical regions, it is not surprising to find mountains with several climatic and ecological zones of the globe compressed over a short horizontal distance (Körner 2000). Despite their importance, mountains have been subject to land use and climatic changes (Nogués-Bravo et al. 2008, Payne et al. 2017). However, the magnitude of the impact is not uniformly distributed along elevation gradients because lowlands often receive more impacts than the mid-elevations (Nogués-Bravo et al. 2008).

Elevational patterns of species diversity

Mountains provide useful elevation gradients which serve as a model template for testing hypotheses related to broad-scale patterns of species richness (Lomolino 2001, Rahbek and Graves 2001, McCain and Grytnes 2010). In the past, it was claimed that species richness declines monotonically from low to high elevations reflecting the latitudinal decline in species richness from the equator to the poles (Allen et al. 2002, Körner 2007). However, it has now been realized that several patterns of species richness exist (Rahbek 1995, McCain and Grytnes 2010, Rahbek 2005). Their understanding (Rowe 2009, Körner 2007) is an increasing challenge as an understanding of diversity patterns along broad climate gradients may shed light on the consequences of ongoing global climatic changes (Vitousek et al. 1997). Some of the factors accounting for the contemporary lack of consensus on the general pattern of elevational species diversity include variation in spatial scale attributed by sampling regimes and geographical area covered (Rahbek 2005, Nogués-Bravo et al. 2008), taxonomic group and geographic region being studied (Peters et al. 2016, McCain and Grytnes 2010), topography complexity (Werner and Homeier 2015, Thormann et al. 2018), presence of local or regional characteristics which are not related to altitude such as anthropogenic disturbances and drought (Körner 2007). So far, several dissimilar elevational patterns of species richness have been reported (Novillo and Ojeda 2014, Peters et al. 2016, Thormann et al. 2018), nevertheless, a monotonic decline and the unimodal "hump-shaped" patterns are well documented (Rahbek 2005, Yu et al. 2013). Several hypotheses and mechanisms have been proposed to explain patterns and drivers of species richness in mountain ecosystems, respectively (Peters et al. 2016). Most often, the proposed hypotheses and mechanisms are linked to climatic factors such as temperature and precipitation (Brown et al. 2004, Peters et al. 2016), spatial factors (Rahbek 1997, Colwell et al. 2004, McCain and Grytnes 2010), ecological processes such as primary productivity and herbivory (Rowe 2009), and evolutionary and historical processes (Li et al. 2009, McCain and Grytnes 2010, Yu et al. 2013).

Elevational patterns of herbivory

In contrast to elevational gradients of species richness, elevational gradients of insect herbivory have been rarely documented in the ecological and evolutionary literature (Galmán et al. 2018). To date, no consensus has been reached on the general patterns of herbivory along elevation gradients. At first, it was claimed that herbivore pressure and herbivory decline monotonically from low to high elevations (Andrew et al. 2012). But accumulating evidence suggests that there is no uniform elevational pattern of herbivory (Galmán et al. 2018). Some of the potential sources of variations in elevational patterns of herbivory include differences in local characteristics of the mountain, plant growth form (Galmán et al. 2018) and feeding guilds under investigation (Garibaldi et al. 2011) as well as differences in the way herbivory is measured (Anstett et al. 2016). The level of herbivory is influenced by both bottom-up and top-down controls (Castagneyrol et al. 2017, Vidal and Murphy 2018). Bottom-up controls include resources availability such as water and soil nutrients (Coley et al. 1985), plant defense such as phenolic compounds, primary productivity and plant nutritional traits such as leaf phosphorous and nitrogen concentration (Abdala-Roberts et al. 2016) whereas top-down controls encompasses the effect of predators and parasitoids on herbivores (Vidal and Murphy 2018). There are also several environmental (biotic and abiotic) factors (Bale et al. 2002, Abdala-Roberts et al. 2016) and land use practices which modulate the relative importance of the bottom and top-down controls on herbivores abundance and ultimately herbivory.

Environmental (abiotic) factors changing with elevation

Elevation gradients facilitate the acquisition of useful information which provides explanations for many ecological questions as it links biotic and abiotic factors in mountain ecosystems (McCain and Grytnes 2010). Abiotic factors such as air temperature, precipitation in the form of rain or snow, wind speed and atmospheric pressure are considered to be critical determinants of species distribution, diversity and ecosystem processes in mountain ecosystems (Hodkinson 2005, Merrill et al. 2008, McCain and Grytnes 2010). Along elevation gradients, some abiotic factors in particular atmospheric pressure and partial pressure of atmospheric gases and temperature change predictably with elevation while others such as precipitation do not change predictably with elevation (Körner 2007). It is reported that temperature and an atmospheric pressure of atmospheric gases decline by ~ 5.5 ºC and ~11% per kilometer gain in altitude, respectively (Körner 2007, Barry 1981). On the other hand, precipitation shows no clear pattern (Körner 2003, 2007). Abiotic factors act synergistically to produce unique environmental conditions within which mountain organisms reproduce and survive (Hodkinson 2005). The unique environment created by various abiotic factors can potentially limit not only species distribution and colonization but also influence species diversity, species interactions and ecological processes (Hodkinson 2005). As the world is experiencing climatic changes (Vitousek et al. 1997, Bale et al. 2002), abiotic factors are expected to become the strongest predictors of species range shifts (Chen et al. 2011), species distribution (Parmesan 1996, Merrill et al. 2008), species diversity and ecosystem processes in the future (Sala et al. 2000). However, the extent to which and the mechanisms through which species and ecosystem processes will be affected by the anticipated climatic changes remains poorly understood. Mountains provide a feasible natural experiment to test the influence of climate on ecosystem function (space for time approach) (Körner 2007) and thereby help to predict the consequences of climatic changes.

Land use changes along elevation gradients

Human land use and associated activities have often been reported to alter the earth and affect various ecosystems (Vitousek et al. 1997, Sala et al. 2000, Foster et al. 2003). Anthropogenic activities can independently or synergistically pose either a direct effect through land transformation, alteration of biogeochemistry and biotic composition, shaping species interactions, changing ecosystem structure and functions or indirect by changing climate (Vitousek et al. 1997, Foster et al. 2003, Jamieson et al. 2012). Mountain ecosystems are also not immune to anthropogenic influences (Nogués-Bravo et al. 2008, Payne et al. 2017). Reports show that foothills and lowland areas of several mountains (including Mt. Kilimanjaro) have been encroached by human settlements and their natural habitats have been transformed to agricultural fields and grazing land (Hemp 2006b, Kuppler et al. 2015). Empirical evidence also suggests that anthropogenic influences have now advanced to higher elevations shaping biota above the timberline zone through grazing and anthropogenic fire (Nogués-Bravo et al. 2008). Since mountains are hotspots of biodiversity (Quintero and Jetz 2018), the increasing land use intensification which is driven by the growing human population and associated demands are likely to affect species diversity, biomass and ecological processes (Hemp 2006c).

Plant functional traits

Plant functional trait refers to any morphological, anatomical, biochemical, physiological, structural, phenological or behavioral properties measured at an individual level which affects plant fitness indirectly through its effects on growth, reproduction, and survival (Violle et al. 2007). Plant functional traits provide useful information which can be used to characterize community responses to land use (Garnier et al. 2007) and environmental (biotic and abiotic) changes (Valladares et al. 2007, Kattge et al. 2011) and quantify the effect of community shifts on ecosystem processes (Kleyer et al. 2008, Nock et al. 2016). Furthermore, plant functional traits provide linkages between traits (Kleyer et al. 2008) and between species diversity and ecosystem functional diversity (Kattge et al. 2011, Becerra 2015). Accumulating evidence suggests that plant functional traits can be used to provide explanations on several ecological phenomena including functional diversity, plant-animal interactions, growth and reproductive investments (Wright et al. 2004, McGill et al. 2006, Costa et al. 2017).

Description of the study area

The study was conducted on the southern slopes of Mount Kilimanjaro which is the highest mountain [i.e. 5895 meters above sea level (m asl)] in Africa located on the northern part of Tanzania close to the Kenyan border (2°45' to 3°35'S and 37°00' to 37° 43'E). The study was conducted within the framework of the Research Unit FOR1246 titled *"Kilimanjaro ecosystems under global change: Linking biodiversity, biotic interactions, and biogeochemical ecosystem processes".* The project is commonly referred to as the "KiLi - Project" (https://www.kilimanjaro.biozentrum.uni-wuerzburg.de) and was funded by the Deutsche Forschungsgemeinschaft (DFG). The project aimed at developing an understanding on the interactive effects of climate and land use change on biodiversity, biotic interactions, and biogeochemical processes along elevation gradients of Mount Kilimanjaro. The project consisted of seven subprojects (SPs) and two central projects. My study fell under SP7 which had the main focus of analyzing the effects of climate and land use change on the diversity of invertebrates and associated ecosystem processes. One of the major strengths of the KiLi - Project is that all subprojects performed their studies on the same study sites, a situation which permitted amalgamation of many datasets; which is critical for developing a broad understanding of the consequences of climate and land use changes along elevation gradients of Mt. Kilimanjaro. Due to this setting, we were able to incorporate data on climatic variables from SP 1-3 and plant functional traits from SP 4 and 5.

The mean annual temperature (MAT) of the area declines quasi-linearly with elevation (lapse rate of 0.56°C per 100 m); at the foothills, it is ca. 25°C and the temperature declines to - 8°C at the peak of the mountain (Appelhans et al. 2016). Conversely, mean annual precipitation (MAP) in terms of rainfall is bimodal with periods of long and heavy rains between March and May and short rains around November (Hemp 2008). Annual precipitation peaks with ~2700 mm at mid-elevations in the montane forest belt (Appelhans et al. 2016), while in the lowlands it ranges from ca. 500-900 mm and ca. 200 mm in the alpine zone (Hemp 2006a).

Description of the study design

The general set up of the study design consisted of two distinct habitat categories namely natural and anthropogenic habitats. In the natural habitat category, we had six distinct habitat types while in the anthropogenic habitat category we had eight habitat types (Fig. I. 1). All habitats were distributed from 866 m asl to 4550 m asl but some were located inside and others outside the boundary (i.e. above ca. 1830 m asl) of the protected areas, namely Kilimanjaro national park and Lake Chala protected area. In the natural habitats, we included colline (lowland) Savannah (871-1153 m asl), lower montane rainforest (1560-2040 m asl), *Ocotea* forest (2120-2750 m asl), *Podocarpus* forest (2752-3060 m asl), *Erica* forest (3500-3880 m asl) and Alpine *Helichrysum* (3849-4548 m asl) as habitat categories.

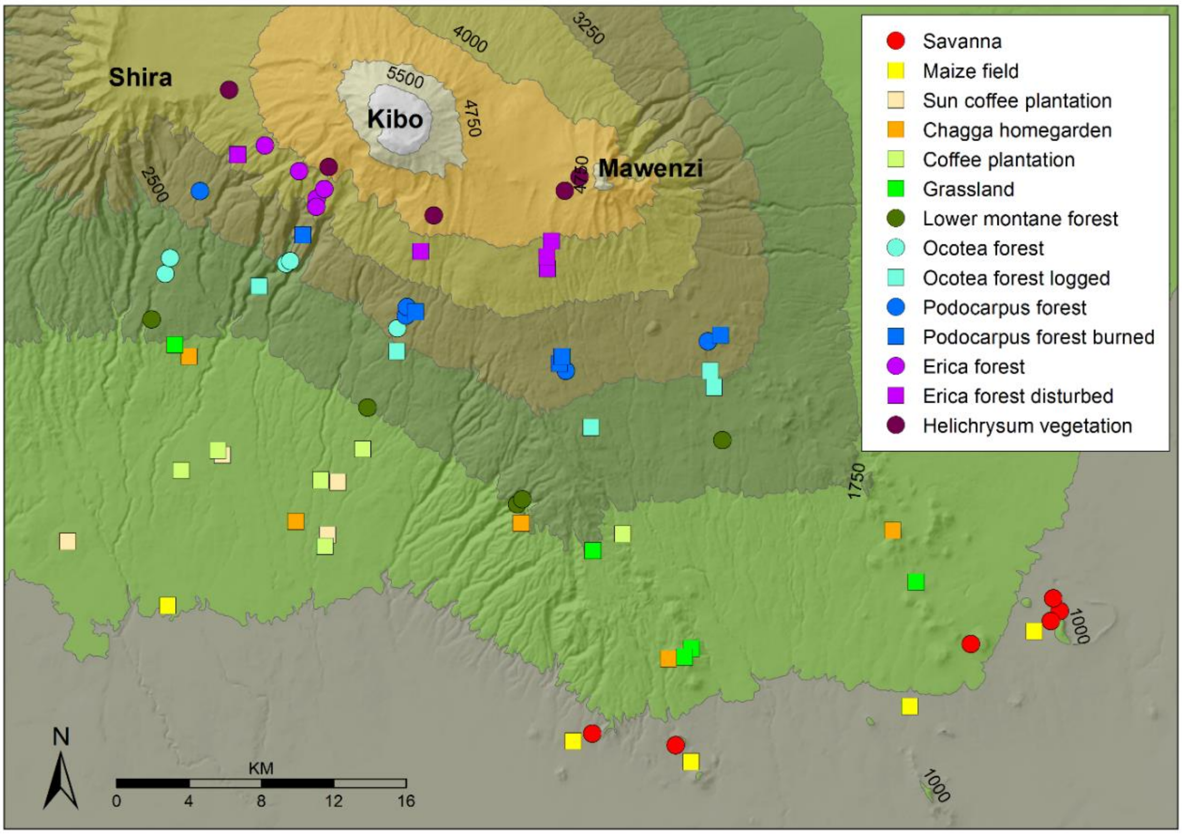


FIG. I. 1. Location of the 65 study sites distributed on the southern slopes of Mt. Kilimanjaro. Filled circles and squares indicate natural and anthropogenic habitat types respectively.

Due to human disturbances, in particular, agricultural activities, logging, and uncontrolled fire, many areas with natural habitats were converted into ‘anthropogenic habitat’ (Hemp 2006a). In the anthropogenic habitat category, we included maize fields (866-1009 m asl), coffee plantation (1124-1648 m asl), Sun coffee plantations (1124-1648 m asl), grasslands (1303-1748 m asl), and Chagga home gardens (1169-1788 m asl). The area above the park boundary (i.e. ca. 1830) experiences anthropogenic pressure as a result of selective logging of *Ocotea* forest (2220-2560 m asl) and human-induced fires in *Podocarpus* forest (2770-3060 m asl) and *Erica* forest (3500 – 3880 m asl). In each of the 14 (6 natural and 8 anthropogenic) habitat types, we had between 4 to 6 replicates making a total of 65 replicates hereafter referred to as study sites. Each study site had a size of 50 x 50 m from which various types of data were regularly collected.

Chapter II: Leaf traits mediate changes in invertebrate herbivory along broad environmental gradients on Mt. Kilimanjaro, Tanzania.

Summary

1. Temperature, primary productivity, plant functional traits, and herbivore abundances are considered key predictors of leaf herbivory but their direct and indirect contributions to community-level herbivory are not well understood along broad climatic gradients.

2. Here we determined elevational herbivory patterns and used a path analytical approach to disentangle the direct and indirect effects of climate, land use and plant functional traits on community-level invertebrate herbivory along the extensive elevational and land use gradients at Mt. Kilimanjaro, Tanzania.

3. We recorded standing leaf herbivory of leaf chewers, leaf miners, and leaf gallers on 55 study sites distributed in natural and anthropogenic habitats along a 3060 m elevation gradient. We then determined total and guild-specific community-level herbivory patterns and related the total community-level herbivory to climate (temperature and precipitation), net primary productivity, plant functional traits (specific leaf area, CN and NP ratios) and herbivore abundances.

4. Leaf herbivory ranged from 5 % to 11 % along the elevation gradient. Total leaf herbivory showed a unimodal pattern in natural habitats but a strongly contrasting bimodal pattern in anthropogenic habitats. We also detected some variation in the patterns of leaf herbivory along environmental gradients across feeding guilds with leaf chewers showing disproportionally large herbivory. Path analyses indicated that

the variation in leaf herbivory was mainly driven by changes in leaf CN and NP ratios which were closely linked to changes in NPP.

5. Our study elucidates the strong role of leaf nutrient stoichiometry and its linkages to climate and energy for explaining the variation in leaf herbivory along broad climatic gradients. Furthermore, the study suggests that climatic changes and nutrient inputs in the course of land use change may alter leaf herbivory and consequently energy and nutrient fluxes in terrestrial habitats.

Introduction

Herbivory is an important antagonistic interaction between plants and animals which has received a considerable attention in the ecological and evolutionary literature (Cebrian and Lartigue 2004, Turcotte Martin M. et al. 2014, Rossetti et al. 2017). Herbivory serves as a conduit through which chemical energy from autotrophs is made available to the entire food web (Agrawal 2004), modulates nutrient cycling and primary productivity (Zavala et al. 2013, Metcalfe et al. 2014), plant evolution (Boege 2005) and plant fitness (Lehndal and Ågren 2015). Invertebrate herbivores are often specialized and cause a relatively low but prolonged damage to plants (due to their small body and bite sizes relative to the plant size) compared to vertebrate herbivores (Kotanen and Rosenthal 2000). In agriculture, invertebrate herbivory reduces economic yields (Zavala et al. 2013), which in Africa alone, causes annual economic damages of more than US$ 4 billion (Oerke et al. 1994). The effects of and response to invertebrate herbivores and herbivory strongly vary along environmental gradients (Poorter et al. 2004, Metcalfe et al. 2014). While the understanding of patterns of invertebrate herbivory is of large importance for both basic and applied ecology (Bigger and Marvier 1998), the major factors causing variation in the levels of herbivory among plants across broad environmental gradients remain poorly understood. Knowledge of the broad-scale drivers of herbivory is, however, of high value to quantify the environmental level of herbivory and to predict changes in the functionality of ecosystems in a changing world.

The amount of plant biomass consumed by herbivores is a function of their abundance (Garibaldi et al. 2011) and feeding rate which is partly associated with feeding pattern and diet breadth (Schmitz 2008, Moreira et al. 2017). Abundance and feeding rate are constrained by a complex interplay of climate and plant functional traits which are associated with plant defense and food quality (Pellissier et al. 2016, Galmán et al. 2018). Climatic factors (e.g. precipitation) and availability of resources such as soil nitrogen, phosphorous and water influence net primary productivity and the ability of plants to defend against herbivory (Coley et al. 1985). For instance, herbivory is expected to be higher in resource-rich and productive habitats than in resource-poor and less productive habitats (Coley et al. 1985). Temperature may also influence herbivory and herbivore abundance by influencing invertebrates' metabolic activities and per capita consumption rates (Vucic-Pestic et al. 2011, Ehnes et al. 2011). Plant functional traits (leaf traits) such as specific leaf area, life lifespan (Zhang et al. 2017), concentrations of leaf carbon, nitrogen and phosphorous as well as the ratios of these elements determine leaf palatability, influence foraging decisions by herbivores and thus regulate susceptibility of plants to herbivory (Schädler et al. 2003, Behmer 2009, Paul et al. 2012, Leingärtner et al. 2014b). Furthermore, climate- and land use-driven changes in the relative importance of top-down control by natural enemies to bottom-up control might affect invertebrate herbivore communities and thus herbivory (Martin et al. 2013, Péré et al. 2013, Tylianakis and Morris 2017).

Human land use and associated anthropogenic activities like agriculture or forestry, changes in animal populations, and modification of natural disturbance regimes, in particular, fire have repeatedly been reported to affect various ecosystem processes (Foster et al. 2003). These anthropogenic activities have either independently or synergistically affected ecosystem structure, composition, functions, soil properties, carbon and nitrogen cycles, and species interactions (Foster et al. 2003, Tylianakis et al. 2008). Herbivory is influenced in various ways by anthropogenic activities. For instance, agricultural practices may influence herbivory directly by manipulating invertebrate abundance (both invertebrate herbivores and their natural enemies) through the application of insecticides or indirectly by altering soil properties through the application of fertilizers (Garibaldi et al. 2011, Gossner et al. 2014, Gagic et al. 2017). The application of chemical fertilizer alters soil nutrient content (soil nitrogen and phosphorous) which in turn influence leaf palatability and ultimately the amount of herbivory (Poorter et al. 2004). Conversely, it has been reported that fire can potentially trigger loss of nitrogen from the soil through volatilization (Foster et al. 2003). Linked to the aforementioned factors, there are several contrasting patterns of herbivory along elevation (and even latitude) gradient (Anstett et al. 2016). A monotonic decline in herbivory with increasing elevation is perhaps the pattern with most empirical support (Galmán et al. 2018). Evidence suggests that the monotonic pattern is often observed when herbivory is related to temperature and stable climates along an elevation gradient (Rasmann et al. 2014c, Galmán et al. 2018). However, alternative patterns occur particularly when factors such as herbivore feeding guilds (Anstett et al. 2014, Galmán et al. 2018), species and functional composition (Anstett et al. 2016), biogeographic zones (Kozlov et al. 2015), scale effects (truncated vs. full-scale elevation gradients) (Nogués-Bravo et al. 2008), shifts in vegetation types and position of more limiting conditions in relation to elevation (e.g. drought or arid conditions in lowlands) are taken into account (Rasmann et al. 2014a, Moreira et al. 2017).

Here we used a path analytical approach to disentangle the direct and indirect effects of climate, land use and plant functional traits on community-level invertebrate herbivory along the extensive elevational and land use gradients at Mt. Kilimanjaro, Tanzania. Mountains provide ideal conditions to study and test ecological hypotheses regarding broad scale gradients of ecosystem functions and biotic interactions (Sundqvist et al. 2013, Hoiss et al. 2015, Roslin et al. 2017). This is particularly true for large tropical mountains that allow standardized field studies along extensive climatic gradients at feasible spatial scales. Specifically, we tested the following non-exclusive hypotheses:

i. Leaf herbivory is related to temperature and shows a monotonic decline with increasing elevation.

ii. Leaf herbivory is related to net primary productivity and thus peaks at mid elevations.

iii. The elevational pattern of leaf herbivory is mainly influenced by leaf traits which vary with changing environmental conditions along the elevational gradient.

iv. Herbivore abundance and herbivory depend on the types and intensity of human land use. We expect herbivory to be lower in extensively managed, mixed anthropogenic habitats than in intensively managed agricultural habitats.

Methods

Study region

The study was conducted on the southern slopes of Mt. Kilimanjaro, Tanzania. Mount Kilimanjaro is a dormant stratovolcano which is located in the northeastern part of Tanzania contiguous to the Kenyan border (2°45' to 3°35'S and 37°00' to 37° 43'E, Fig. II. 1). 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 5895 m above sea level (asl). The mean annual temperature decreases quasi-linearly with elevation (lapse rate of 0.56°C per 100 m) starting with 25°C at the foothills and decreasing to - 8°C at the top of the mountain (Appelhans et al. 2016).

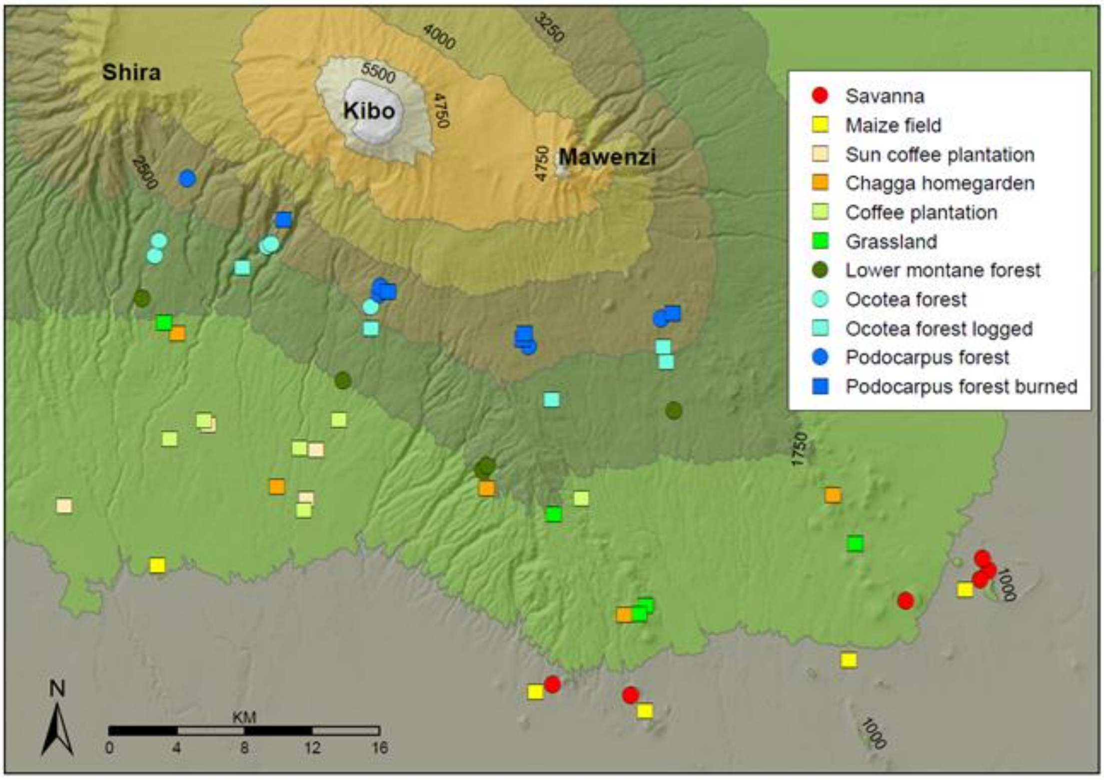


FIG. II. 1. Distribution of study sites on the southern slopes of the Mt. Kilimanjaro. Filled circles and squares indicate natural and anthropogenic habitat types respectively.

The annual pattern of rainfall is bimodal with periods of long-heavy rains between March and May and short rains around November (Hemp 2008). Annual precipitation shows a unimodal pattern along the elevation gradient with the peak of precipitation (~2700 mm) in the montane forest belt (Appelhans et al. 2016). The mountain encompasses several distinct vegetation zones (Fig. II. 1): colline (lowland) savannah (871-1153 m asl), lower montane rainforest (1560-2040 m asl), *Ocotea* forest (2120-2750 m asl), *Podocarpus* forest (2752-3060 m asl), *Erica* forest (3500-3880 m asl) and Alpine *Helichrysum* (3849-4548 m asl) habitats. Following human-induced disturbances, particularly agricultural activities, logging, and fire, many areas with natural habitats on the mountain were converted into 'anthropogenic habitat' (Hemp 2006c). The anthropogenic habitat includes maize fields (866-1009 m asl), coffee plantations (1124-1648 m asl), grasslands (1303-1748 m asl), Chagga home gardens (agroforestry systems; 1169-1788 m asl). Areas above 1830 m asl are protected by the Kilimanjaro National Park but face anthropogenic pressure by selective logging of *Ocotea* forest (2220-2560 m asl) and human-induced fires in *Podocarpus* forest (2770-3060 m asl).

Study sites and environmental data

We used the study sites of the DFG-funded research group FOR1246 (KiLi) distributed in all major natural and anthropogenic habitats on the southern slopes of Mt. Kilimanjaro (Classen et al. 2015). We had to exclude study sites from habitats situated above 3100 m asl because the leaf sizes of the plants found in these habitats were too small to provide reliable estimates of leaf herbivory by invertebrates with the visual estimation methods we used. We, therefore, restricted our analyses to 55 study sites from the eleven major habitat types found between 866 m asl and 3060 m asl (Fig. II.1). Twenty-one study sites were located in natural habitats and 34 study sites in anthropogenic habitats. The study sites differed in the level of land use which we estimated by calculating a composite index of human land use, hereafter called 'LUI'. The LUI is based on four major components of land use: agricultural treatments (including irrigation, application of fertilizers and pesticides, pesticides were only used in coffee plantations), land use at a landscape level (which was measured as a percentage of an area of agricultural habitats within 1.5 km from the study site center), alteration of vegetation structure (vegetation structure on the study sites relative to the potential natural vegetation), and biomass removal (through grazing, harvesting, cultivation and anthropogenic fires). For details, see (Classen et al. 2015).

At each study site, mean annual temperature (MAT) was measured for the duration of two years using temperature sensors erected approximately 2 m above the ground on each study site (Appelhans et al. 2016). Mean annual precipitation (MAP) was calculated using a co-kriging approach with rainfall data collected from a network of 70 rain gauges placed on the mountain for over 15 years. For details of climate measures see (Appelhans et al. 2016, Peters et al. 2016). The normalized difference vegetation index (NDVI) was used as a surrogate for net primary productivity (NPP) (Peters et al. 2016). Estimates of NDVI were calculated from a MODIS Aqua product MYD13Q1 with a horizontal resolution of 250 m by 250 m by averaging corrected NDVI measured of 10 consecutive years (2003 -2012) and extracting pixel values corresponding to the geographical positions of the study sites. For details see Detsch et al. (2016) and Peters et al. (2016).

Standing leaf herbivory

We assessed standing leaf herbivory in four sampling occasions from April 2014 to May 2016. Data were collected twice during the rainy season and twice during the dry season to capture the full seasonal amplitude of herbivory levels. At each study site, we randomly selected 15 trees or shrubs of a relatively small size of up to 5 m. The selected woody plants were permanently marked with tags bearing an individual code and each plant was identified to species level. During each sampling round, we randomly picked 30 mature leaves from every selected woody plant. We randomly took one leaf at a time from the upper, middle and lower part of the selected plants or branches in a spiral fashion repeatedly until 30 leaves were obtained. Leaves were temporarily stored in plastic zip bags until measurements of herbivory were taken. This method of sampling leaves by picking or removing some leaves from a plant for leaf herbivory estimation is referred to as a discrete sampling method which yields a type of herbivory known as standing herbivory or point herbivory (Lowman 1984, Anstett et al. 2016). Although the method underestimates herbivory as it does not capture completely defoliated leaves and herbivory over time (i.e. cumulative herbivory) (Anstett et al. 2016), it is a relatively fast, simple, accurate and frequently used method in large-scale studies (Anstett et al. 2016). Individual-level leaf herbivory was quantified visually by estimating the percentage leaf area damaged or consumed by invertebrates for each of the 15 selected plants per site across the 55 study sites.

We then calculated a percentage community-level leaf herbivory by averaging individual-level leaf herbivory of the 15 plants in each study site per phase. Because we had four sampling phases, we eliminated non-independence of our data among years by averaged community-level leaf herbivory resulting in one herbivory score for each of the 55 study sites. We grouped leaf damages into three categories based on the feeding guilds of herbivores i.e. invertebrate leaf chewers, leaf miners or gall-inducing insects (leaf gallers). We determined the level of accuracy of this method by comparing the visual herbivory estimates for 108 leaves (36 small, 36 medium, and 36 large leaves) to those obtained by quantifying the damaged leaf area using a computer-aided image analysis (using the program ImageJ) as suggested by (Robertson and Duke 1987) (Supplementary Fig. II. 1).

Plant functional traits

The Plant functional traits (hereafter referred to as leaf traits) we considered in our study were specific leaf area (SLA, a measure of leaf surface area per leaf dry mass which includes rachis and petiole), leaf carbon to nitrogen (CN) ratio and the leaf nitrogen to phosphorus (NP) ratio. We chose these traits because they were found to be closely associated with susceptibility of plants to herbivore attack (Poorter et al. 2004, Dussourd 2017). Within a study of plant functional traits along elevation gradients of Mt. Kilimanjaro, a total of 758 woody plant individuals, including the most abundant woody plant species from all study sites, have been studied for plant functional traits (Schellenberger Costa et al. 2017). The studied species collectively made up over 80 % of the maximum photosynthetic biomass on each study site.

Leaf traits were determined following protocols established by LEDA (www.leda-traitbase.org) and as described by (Schellenberger Costa et al. 2017). From this trait data set, we derived leaf traits of 640 (84 %) plant individuals screened for herbivory, representing 51 plant species. Leaf traits data for an additional 13 plant species representing a further 9 % of all individuals were obtained from the TRY plant trait database (Kattge et al. 2011). A comparison of leaf traits data for species that were sampled on study sites and for which data was additionally available in the TRY database revealed a high overlap, justifying the use of the additional trait data from the TRY database in our analyses. We did not manage to get leaf traits data for 25 plant species of low general abundance which represented 7 % of individual plants included in this study. However, these plants were randomly distributed along the elevational gradient. For each study site, we calculated the mean species CN ratio, the mean NP ratio, and the mean SLA by averaging the leaf traits of the fifteen plant individuals for which we measured the percentage of leaf area damaged or missing and for which leaf trait data was available. A comparison of the average leaf traits of the fifteen selected plants well reflected community-level trait patterns calculated from all major plant species found on the study sites (Supplementary Fig. II. 2).

Abundance of invertebrate herbivores

We used a sweep net sampling technique to sample invertebrates from two parallel, permanently marked, 50 m long transects per study site. On each transect, we made 100 sweeps using a 30 cm diameter sweep net to get a subsample. All invertebrates ≥ 1 mm collected from two subsamples per site were put together to get one sampling unit per study site per season (Ferger et al. 2014). Invertebrate sampling was conducted once in the dry and once in the wet season. Invertebrate samples were pooled per site and identified at the order or family level. For each study, we summed up the number of individuals belonging to taxa characterized by a predominately herbivorous diet Coleoptera (Beetles), Hemiptera (Cicada and Sternorryncha), Orthoptera (Grasshoppers and Crickets), Phasmatodea (Stick insects), Lepidoptera (Larva), Thysanoptera (Thrips), and Gastropods).

Statistical analyses

Data were analyzed using the R statistic platform version 3.3.1 (R Core Team 2016). We used generalized additive models (GAMs) from the *mgcv* R package to visualize and determine relationships between invertebrate herbivory (total herbivory, herbivory by leaf chewers, leaf miners and leaf gallers and elevation. We used Gaussian data family and set the basis dimension of the smoothing function to k = 5 to estimate patterns of invertebrate herbivory along the elevation gradient. We constructed three different model types for each response variable:

i. herbivory ~ elevation
ii. herbivory ~ elevation + land use (additive effect)
iii. herbivory ~ elevation * land use (interactive effect)

In the GAMs the main habitat type was included as a factorial variable (natural versus anthropogenic habitats) as we aimed here at testing for and visualizing general differences in herbivory between natural and anthropogenic habitats along the elevation gradient. For each response variable, we selected the best-supported model type based on the Akaike-information criterion (AIC). The AIC is based on the information theory and evaluates models on the basis of model fit and model complexity (Burnham and Anderson 2004). As our sample size was relatively low in comparison with the number of estimated parameters we used the AIC with a second-order bias correction (AIC_C) instead of the standard AIC.

Path analysis was used to examine causal relationships (Shipley 2016) and untangle the direct and indirect effects of explanatory variables (Classen et al. 2015, Herbst et al. 2017). The term "direct effect" in a statistical context refers to the magnitude (strength) of change in a response variable caused by a unit change in a predictor variable independently of an intervening variable(s) in causal relationships, while, indirect effect refers to the magnitude of change in a response variable caused by a unit change in a predictor variable completely through an intervening variable(s) (Olobatuyi 2006). Based on an ecological understanding of invertebrate herbivory, we postulated and constructed a conceptual path diagram that climatic factors (MAT and MAP) and land use influence invertebrate herbivory directly or indirectly via changes in NPP, herbivore abundance and leaf traits (SLA, CN and NP ratios) (see conceptual path diagram Fig. II. 4a). In order to limit a large number of potential path models which can be used to construct the final path model from the set of exogenous and endogenous variables, we first determined for each response variable the best-supported paths using multi-model inference based on AIC_C. For the construction of competitive path models, we just included models which showed AIC_C values of < 2 in comparison to the best-supported model. The multi-model inference was done using the function 'dredge' in R package *MuMIn.* We compared all path models which could be constructed from the set of best supported linear models and identified the best path model based on the AIC. For path analysis, the R package *lavaan* was used.

Results

We estimated leaf herbivory from ≈99,000 leaves collected from 825 woody plants along environmental gradients of Mt. Kilimanjaro. Mean leaf herbivory ranged from 5 % to 11 % in the natural habitats and from 5 % to 9 % in anthropogenic habitats. We found contrasting patterns of herbivory between natural and anthropogenic habitats and across feeding guilds of invertebrates (GAM; n = 55, explained deviance (ED) = 46.4 %, $F_{interaction\ term}$ = 5.1, $P_{interaction\ term}$ < 0.0001; Fig. II. 2a). In natural habitats, total leaf herbivory exhibited a unimodal pattern with elevation: leaf herbivory peaked in lower montane forests (at ca. 1700 m asl) and was significantly lower in lowland savannah and higher montane forests (Fig. II. 2a). In anthropogenic habitats, we found a bimodal pattern which strongly opposed the pattern detected along the natural habitats. In anthropogenic and disturbed habitats, herbivory was highest in the lowlands of Mt. Kilimanjaro (ca. 871 m asl) and in the mid-montane forests (at ca. 2400 m asl).

Leaf chewers were responsible for the majority of total leaf herbivory (mean 6.7 %) and therefore their patterns closely followed patterns of total leaf herbivory (GAM; n = 55, ED = 43.9%, $F_{interaction\ term}$ = 4.7, $P_{interaction\ term}$ < 0.001; Fig. II. 2b). Leaf herbivory by leaf gallers declined monotonically with elevation in natural habitat but not in anthropogenic habitat, where values were consistently low (GAM; n=55, ED = 18.3 %, $F_{interaction\ term}$ = 4.6, $P_{interaction\ term}$ < 0.01; Fig. II. 2c). Leaf miners depicted a unimodal pattern of herbivory which did not significantly differ between natural and anthropogenic habitats (GAM; n = 55, ED = 14.9 %, $F_{elevation}$ = 2.3, $P_{elevation}$ < 0.07; Fig. II. 2d).

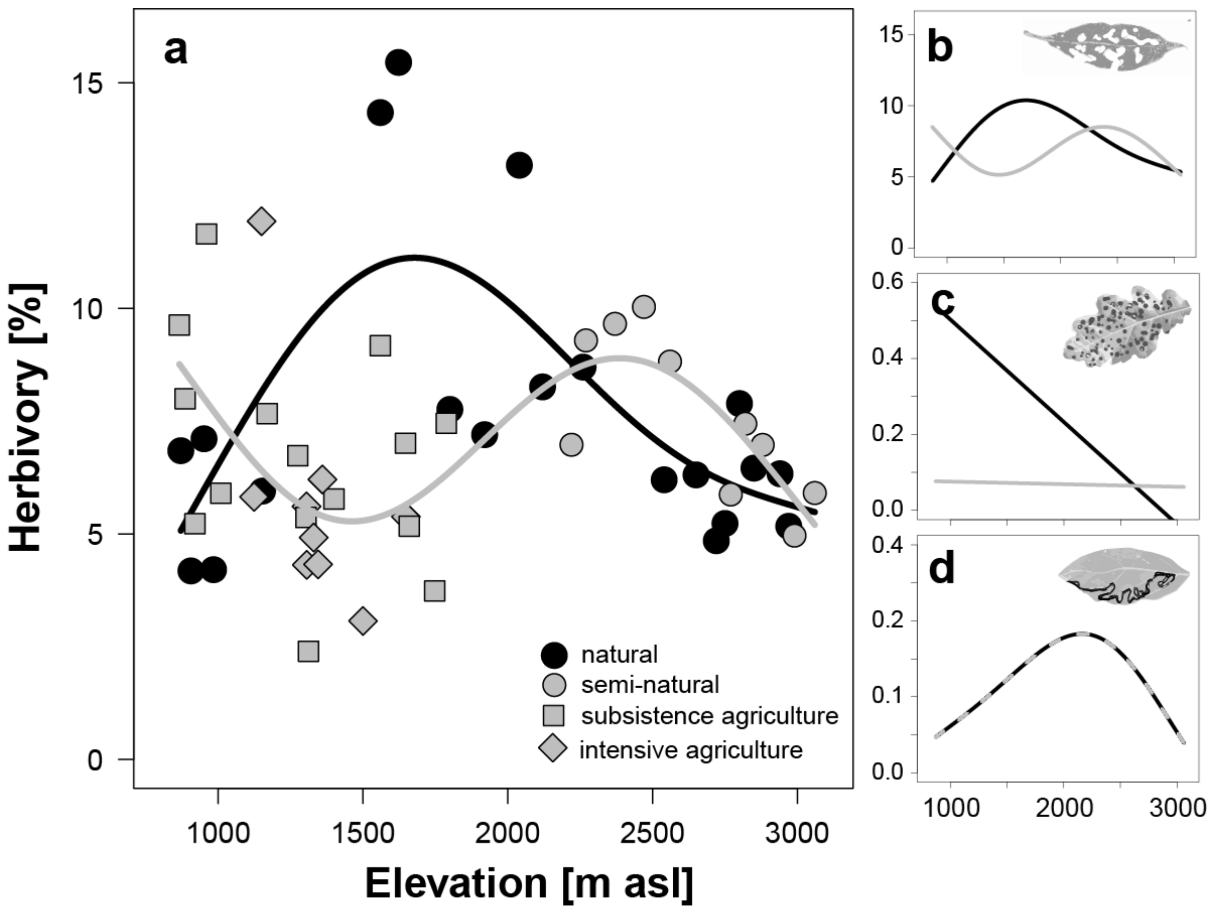


FIG. II. 2. Patterns of invertebrate herbivory in natural and anthropogenic habitats along the elevational gradient at Mt. Kilimanjaro. Black and gray lines show the patterns of invertebrate herbivory in natural and anthropogenic habitats, respectively: (a) total herbivory, (b) leaf herbivory caused by leaf chewers, (c) leaf gallers, and (d) leaf miners. Trend lines were calculated using generalized additive models (GAMs) with a basis dimension of $k = 5$. In case of significant interactions between elevation and land use individual trend lines are shown for natural (black) and anthropogenic (white) habitats, separately (in Fig. II. 2a-c). In case of no significant land use effect (interaction nor additive), one interrupted black-gray trend line was drawn (Fig. II. 2d).

We also detected considerable variation in the distribution of potentially influential response variables (CN, NP, MAP, MAT and NPP) along the elevation gradient. In natural habitat the CN ratio was high at lower elevations and low at mid-elevation, whereas the distribution of MAP, NP ratio and NPP peaked at mid elevations. Only MAT declined consistently with increasing elevation (GAMs; CN ratio: n = 60, ED = 66.8 %, $F_{interaction\ term}$ = 7.3, $P_{interaction\ term}$ < 0.001; NP ratio: n = 60, ED = 72.7 %, $F_{interaction\ term}$ = 4.4, $P_{interaction\ term}$ < 0.001; MAP: n = 61, ED = 97 %, $\mathrm{F}_{interaction\ term}$ = 3.6, $\mathrm{P}_{interaction\ term}$ < 0.001; MAT: n = 67, ED = 99.1 %, $F_{interaction\ term}$ = 3.1, $P_{interaction\ term}$ < 0.01; NPP: n = 60, ED = 91.6 %, $F_{elevation}$ = 132.4, $P_{elevation}$ < 0.001; Fig. II. 3a-e). With exception of NPP, the distribution of other variables differed between natural and anthropogenic habitats along elevation gradient.

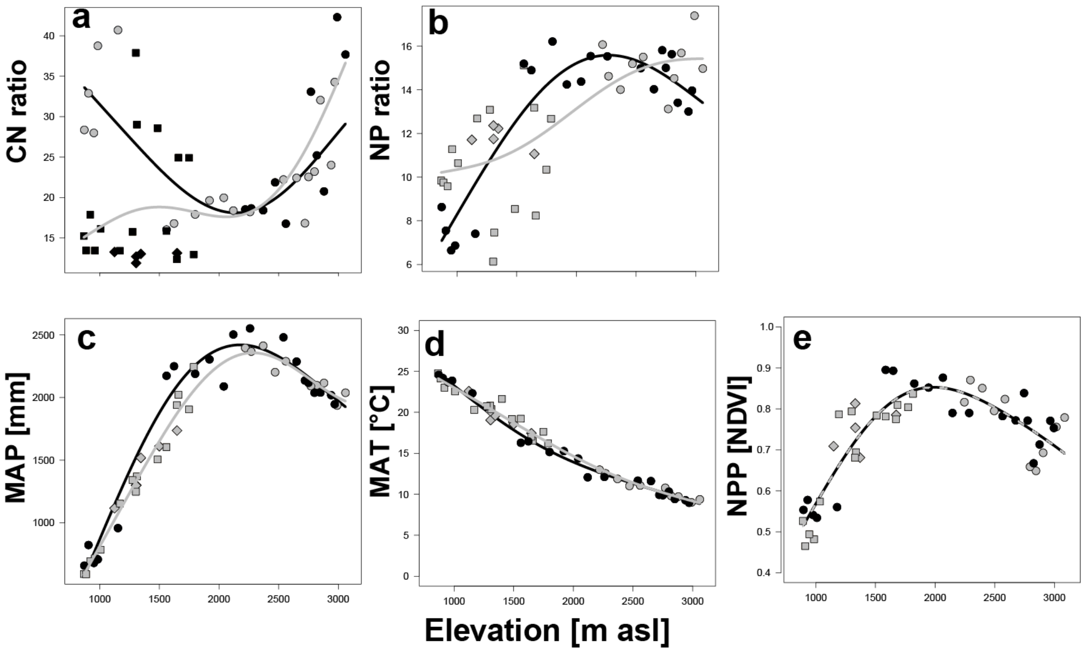


Fig. II. 3. Distribution of (a) CN ratio (b), NP ratio, (c) MAP, (d) MAT and (e) NPP along the elevational gradient. Symbols denote study sites in natural (filled dots) and anthropogenic (filled squares) habitats. Black trend lines describe distribution in natural habitats and gray trend lines describe distribution in anthropogenic habitats. Where no significant land use effect (interaction nor additive) was detected, one interrupted black-gray trend line was drawn (Fig. II. 3e).

Path analysis suggested that leaf herbivory was most strongly influenced by leaf traits (CN and NP ratios), which were linked to climate-mediated changes in NPP. High CN and NP ratios were associated with low levels of invertebrate herbivory (Supplementary Fig. II. 2). Net primary productivity did not directly influence leaf herbivory but was a strong predictor of leaf nitrogen concentration (AICc = 278.67, *P* (RMSEA) = 0.153, *P* (χ^2 - test) = 0.1040; Fig. II. 4b): study sites with higher NPP were characterized by higher NP and lower CN ratios.

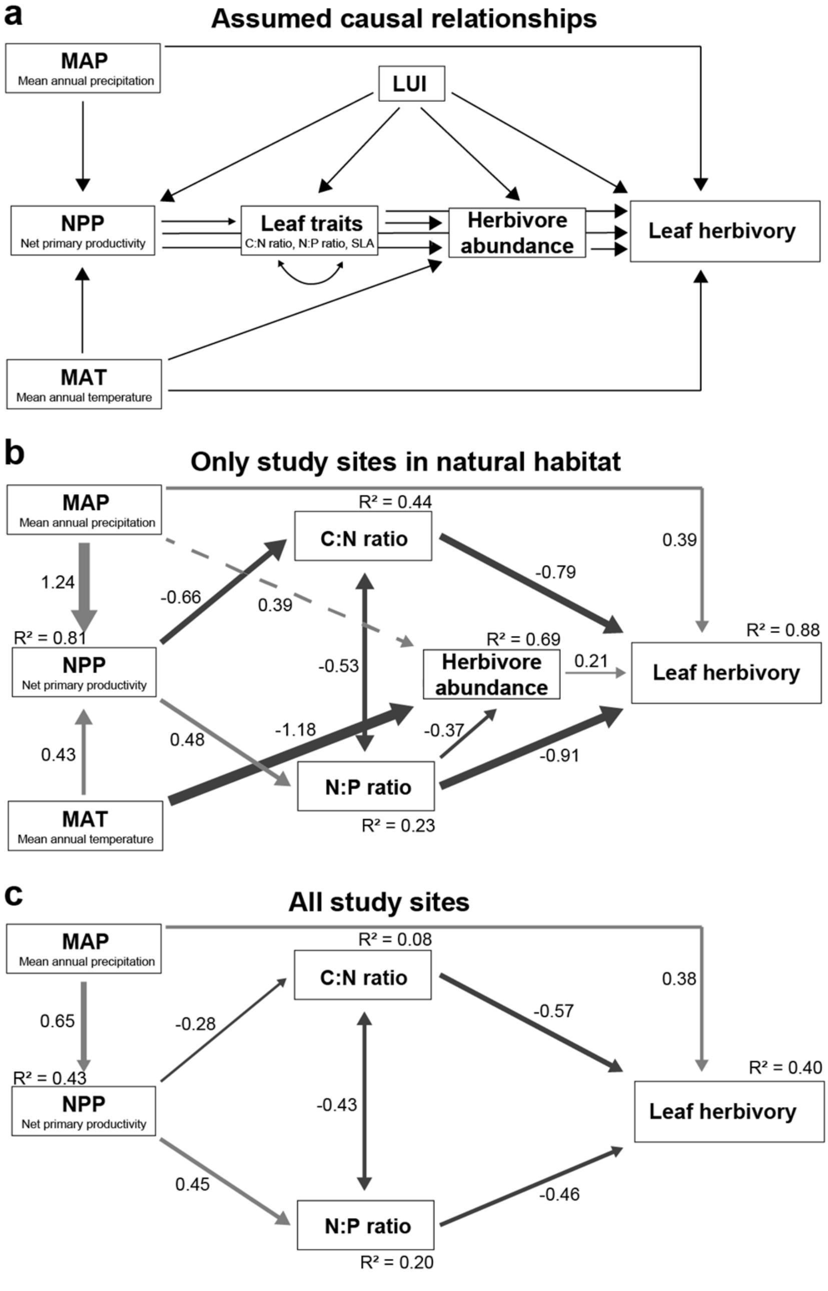


FIG. II. 4. Path diagrams showing direct and indirect effects of predictor variables on leaf herbivory. The numbers displayed near each arrow represent standardized path coefficients. Single-headed arrows connect response and explanatory variables while double-headed arrows indicate covariation between variables. Arrow width is proportional to the relative effect strength and the number on or below the box (R^2) show amount of variation explained by the predictor variable where the arrow comes from. The solid lines and dashed lines represent path described by the best supported path model (the most parsimonious model) and an additional variable appearing in the best competitive model, respectively (a) Input path model showing assumed causal relationships between predictor variables (MAT, MAP, NPP, LUI, SLA, CN and NP ratio, herbivore abundance) and a response variable (leaf herbivory). (b) Output path diagram from the best supported model (AICc= 278.67, *P* (RMSEA) = 0.153, *P* (χ^2 - test) = 0.1040) illustrating direct and indirect effects of predictor variables (MAT, MAP, NPP, CN ratio, NP ratio and herbivore abundance) on a response variable (leaf herbivory) in natural habitats, c) Output path diagram from the best supported model (AICc=650.805, *P*(RMSEA) = 0.322, *P* (χ^2 - test) = 0.268) showing direct and indirect effects detected of predictor variables (MAT, MAP, CN ratio and NP ratio) on a response variable (leaf herbivory) in all habitats (i.e. anthropogenic and natural habitats).

Climate variables (MAP and MAT) had moderate direct and indirect effects on leaf herbivory. First, leaf herbivory was positively correlated to MAP. Second, MAP and MAT were strong predictors of NPP. For natural habitats, we additionally found a positive effect of herbivore abundances on leaf herbivory, but the effect was rather small in comparison to the effects of leaf traits and MAP. Although the patterns of leaf herbivory for natural and disturbed habitats differed significantly, the differences in herbivory due to land use were best explained by indirect effects on NP and CN ratios and perhaps also unknown variation e.g. in pest management. With the exception of the effect of herbivore abundance, the final path models and the main pathways by which leaf herbivory was determined were highly similar between a dataset restricted to an elevation gradient of natural habitat and the one including data from the extensive land use gradient on Mt. Kilimanjaro (AICc = 650.805, *P* (RMSEA) = 0.322, *P* (χ^2 - test) = 0.268; Fig. II. 4c). The main difference between the final path models was found in the predictability of endogenous variables (R^2 values in Fig. II. 3), which were much higher for the natural habitat than for the complete data set.

Discussion

We found that leaf herbivory strongly varied along the elevational gradient of Mt. Kilimanjaro with striking differences between natural and anthropogenic habitats. Contrary to our hypothesis, herbivory was not directly related to temperature and did not monotonically decline with elevation. Instead, herbivory in natural habitats peaked at mid-elevations whereas anthropogenic habitats showed a nearly inverse pattern. The variation in leaf herbivory along the elevational gradient could be explained by the direct and indirect effects of climate and net primary productivity on leaf nutrient stoichiometry. Our study provides new insights into the mechanisms linking between climate and community-level leaf herbivory across broad climatic gradients.

Along the natural habitats gradient, total leaf herbivory showed a unimodal distribution with a peak in the lower montane forest and significantly low values in colline (lowland) savannah and higher elevations. The observed pattern is incongruent with the widespread view that herbivory declines monotonically with elevation (Andrew et al. 2012). One of the possible reasons could be that Mount Kilimanjaro (and other mountains in East Africa) experiences moist conditions at mid-elevations but an arid environment at lower elevations in addition to harsh conditions at higher elevations (i.e. low temperatures, low nutrients, high wind speed) (Rasmann et al. 2014a, Moreira et al. 2017). This situation causes net primary productivity to peak at mid elevations. Evidence suggests that plants in resource-rich and productive habitats are often associated with high plant growth rates and low investments less in plant defense both of which promote herbivory (Coley et al. 1985, Abdala-Roberts et al. 2016). Conversely, under limiting environmental conditions plant growth and plants' investments in defense against herbivory are elevated due to the high cost of replacement of the damaged tissues (Coley et al. 1985, Pellissier et al. 2016).

At lower elevations where a relatively fire-prone and drought stressed savannah habitat is found, plants produce tougher leaves and carbon-based defensive compounds such as terpenes or alkaloids, both of which negatively affect foliage nutritional quality, to avoid herbivory (Coley and Barone 1996, Rasmann et al. 2009). Likewise, at high elevation, the climatically harsh conditions might increase plant physical defense traits against climatic and mechanical stress which increase leaf toughness, lower leaf palatability and decrease ultimately herbivory (Körner 1989, Rasmann et al. 2014b)

Results from path analysis show that in natural habitat precipitation and temperature had moderate direct and indirect effects on herbivore abundance and leaf herbivory. Precipitation showed a direct positive effect on herbivory while both precipitation and temperature exhibited an indirect effect on herbivory via its influence on NPP and herbivore abundance. The rather low effect of herbivore abundance on leaf herbivory could have been attributed by the limitation of our study in capturing a wide range of invertebrate herbivores. Collecting a wide spectrum of invertebrate herbivores in different vegetation types is a very challenging task and a combination of different sampling methods could possibly lead to a higher linkage between herbivory, MAT and herbivore abundance. Importantly, herbivory rates are not only driven by the bottom-up process but may also be under top-down control (Marczak et al. 2011, Terborgh 2015, Castagneyrol et al. 2017). Regulation of herbivore abundance by natural enemies could be related to temperature with higher predation rates at lower elevations (Roslin et al. 2017). Based on the relationship between temperature and predation rates, the strong negative effect of MAT on herbivore abundance we observed in our study could be associated with a stronger positive effect of temperature on predators and predation rates than on herbivores abundance which could lead to a negative correlation between herbivore abundance and MAT. We are not aware of other studies that have systematically assessed the relative contribution of various environmental parameters on herbivory rates in tropical elevational gradients and thus provide novel insights into the determinants of plant herbivory.

In anthropogenic habitats, the bimodal pattern in leaf herbivory strongly opposed the unimodal pattern detected in the natural habitat. In this habitat, leaf herbivory was relatively high on woody plants found in the maize fields in the lowlands (ca. 866-1009 m asl), decreased in agricultural habitats in the submontane zone of the mountain and increased again in the disturbed *Ocotea* forest (ca. 2500 m asl). The high level of herbivory in the maize fields was probably due to elevated leaf N content relative to leaf C content (i.e. low CN ratio), and elevated leaf P content relative to leaf N content (i.e. low NP ratio) which is linked to fertilizer applications. There is ample evidence suggesting that addition of N or P-rich fertilizers to the soil can potentially increase levels of leaf nutrients (Marquis & Clark, 1989), lower plants commitment to defenses against herbivory (Coley et al. 1985), and ultimately promote herbivory (Gagic et al. 2017). Conversely, the lower level of herbivory in the anthropogenic habitat at ca. 1500 m asl could be due to a dominance of domesticated plant species showing high CN ratios (e.g. coffee, *Eucalyptus* trees) and the application of insecticides which negatively affect invertebrate abundance (Garibaldi et al. 2017).

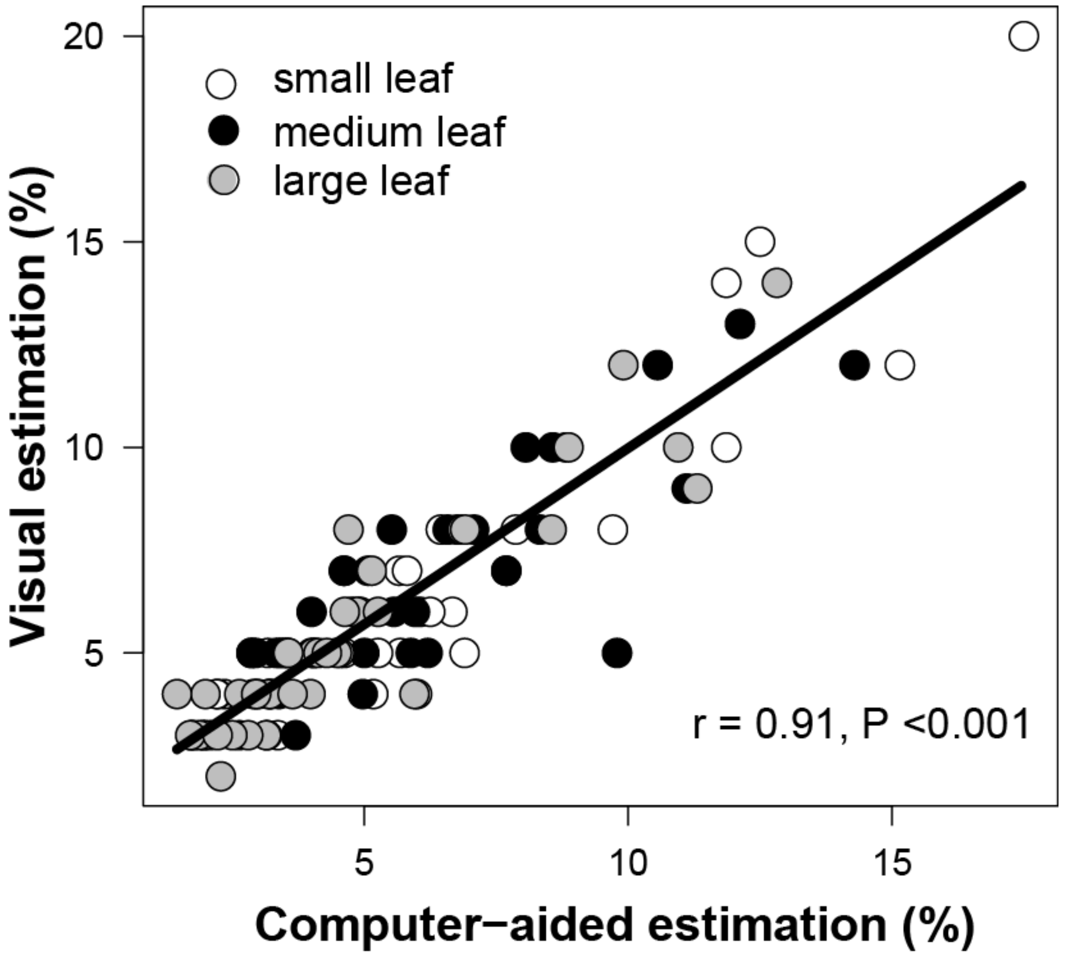
We also detected some variation in the patterns of leaf herbivory along environmental gradients across feeding guilds. Differences in the patterns of herbivory among different guilds of herbivores have also been reported in studies conducted in temperate and tropical regions (Novotny et al. 2010, Anstett et al. 2014). However, there are also studies which reported similar patterns of herbivory by different feeding guilds along an elevation gradient (Garibaldi et al. 2011). In our study, leaf chewers showed disproportionately high levels of leaf herbivory compared to other feeding guilds, a situation which strongly influenced the overall patterns of leaf herbivory in both habitats. The dominance of herbivory caused by leaf chewers over that caused by leaf miners and leaf gallers has also been reported in other studies (Schuldt et al.

2010, Souza et al. 2013), and it is associated with their enhanced ability to overcome the barrier posed by physical leaf structure (Schuldt et al. 2012).

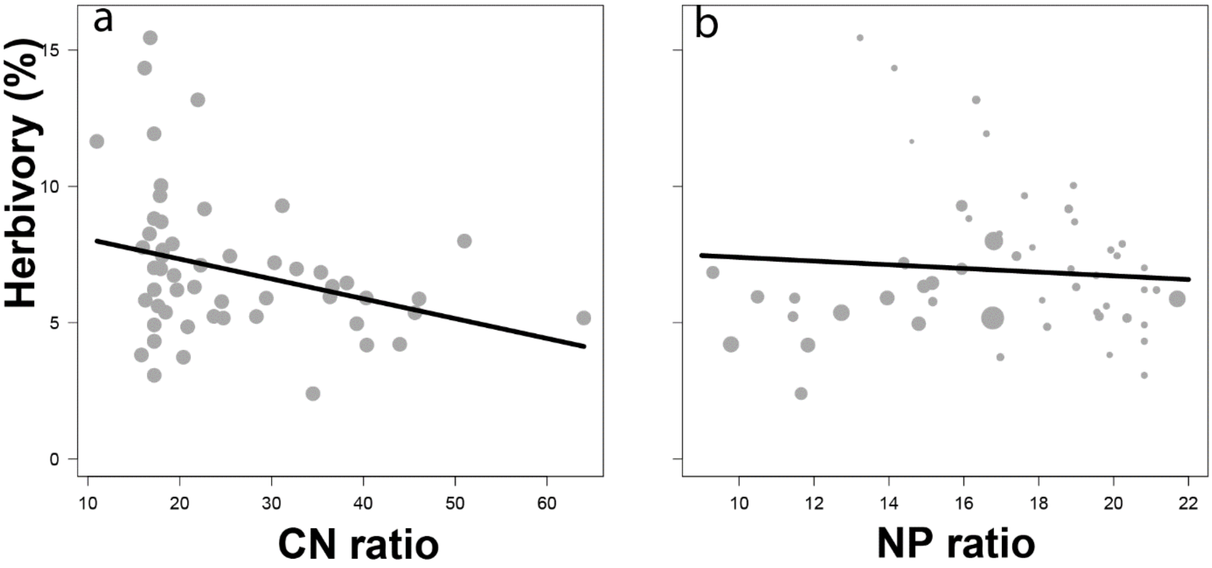
Besides a high similarity in the main pathways by which leaf herbivory was determined, we found a much higher predictability of endogenous variables when we restricted the analyses to natural habitats than for a complete data set, which also included anthropogenic habitats. The lower predictability of invertebrate herbivory in anthropogenic habitats may be due to variation in the composition of managed plants which may differ in defensive plant traits which we did not measure (Kost and Heil 2006) or due to a higher stochasticity in herbivory due to pest management.

Despite the fact that the magnitude of herbivory is influenced by bottom-up and top-down controls (Marczak et al. 2011, Pellissier et al. 2016), the latter influences herbivory through trophic cascade (Hoset et al. 2014, Roslin et al. 2017) and was beyond the scope of this study. Our study elucidates the strong role of leaf macronutrient stoichiometry and its linkages to climate and energy for explaining the extensive variation in leaf herbivory along broad climatic gradients. Our results suggest that the predicted changes in climate and nutrient inputs over the coming decades may significantly alter the levels of leaf herbivory, energy and nutrient fluxes in terrestrial habitats. Although we have managed to show the influence of leaf CN and NP ratios, climate and herbivore abundance on leaf herbivory by a correlative approach, experimental studies, also addressing changes in top-down control by natural enemies, should deepen our understanding of plant-herbivore interactions along elevational gradients.

Supplementary Information



Supplementary FIG. II. 1. Correlation between herbivory measured by visual estimation method and a computer-aided program (Image J).



Supplementary FIG. II. 2. Relationships between insect herbivory and leaf traits, i.e. for the (a) leaf CN ratio and (b) leaf NP ratio dots show mean levels of leaf herbivory per study site. In the right panel, dot size is proportional to the CN ratio of leaves (larger dots = higher CN ratios). Trend lines are derived from simple linear regression models of herbivory (response) against CN and NP ratios.

Chapter III: Temperature and resource diversity predict the diversity of phytophagous beetles along elevation and land use gradients on Mt. Kilimanjaro.

Summary

Patterns of diversity along elevational gradients are well depicted in ecology but it remains little tested on how variation in the quantity, quality, and diversity of food resources modulate these patterns. Here we use phytophagous beetles as a model taxon to unravel direct and indirect effects of climate, food resource abundance (estimated by net primary productivity), resource quality (specific leaf area index, leaf nitrogen to phosphorus and leaf carbon to nitrogen ratio), resource diversity (functional dispersion of leaf traits), on Chao1-estimated species richness (here referred to as species diversity) of phytophagous beetles along extensive elevation and land use gradients of Mt. Kilimanjaro. We sampled phytophagous beetles in 65 study sites positioned in natural and anthropogenic habitats which were distributed from 866 - 4550 m asl. We used path analysis to unravel the direct and indirect effects of predictor variables on species diversity. A total of 3,186 phytophagous beetles representing 21 families and 304 morphospecies were collected. We found that the elevational diversity of phytophagous beetles was bimodally distributed along the elevation gradient with peaks at lowest (~800 m asl) and high elevations (~3000 m asl). Results from path analysis revealed temperature, climate-mediated changes in resource abundance and resource diversity to be the best predictors of the changes in the diversity of phytophagous beetles. We did not find an effect of land use intensity on resource abundance, resource diversity, phytophagous beetle abundance, and species diversity or of leaf quality traits (leaf SLA, CN and NP ratios of plant communities) on abundance and species diversity of phytophagous beetles. The species diversity of phytophagous beetles was related to temperature and the diversity of food resources suggesting that future climate change and human-driven plant diversity loss will influence species diversity and distribution patterns of herbivorous insects.

Keywords: climate change, elevation gradient, functional dispersion, land-use change, plant functional traits, net primary productivity, phytophagous beetles, species richness, species diversity

Introduction

The idea to understand mechanisms underlying variation in species diversity along elevational gradients dates back to the 19th Century (Rahbek 2005, Yu et al. 2013, Peters et al. 2016). Since then elevational gradients have become an integral part of ecological, evolutionary and biogeographic studies (Rahbek 1995, Wang et al. 2011, Sundqvist et al. 2013). In such macroecological studies, mountains play a central role as they host relatively natural habitats composed of compressed life zones which are exposed to a great variation of climatic conditions within a short horizontal distance (Spehn and Körner 2005, Hodkinson 2005). Tropical mountains, in particular, harbor a significant amount of biodiversity with a unique evolutionary history (Spehn and Körner 2005, Merckx et al. 2015). These mountains are often used as both, observational and experimental study sites to identify ecological patterns and reveal mechanisms underlying these patterns (McCoy 1990, McCain 2007, Körner 2007, Beck et al. 2017), to disentangle direct and indirect effects of biotic and abiotic factors on biological diversity (Colwell et al. 2008, Sundqvist et al. 2013, Classen et al. 2015, Peters et al. 2016) and to test several biological hypotheses (Wang et al. 2011, Dulle et al. 2016, Thormann et al. 2018).

Studies on species diversity along elevational gradients regardless of the taxon have revealed several contrasting patterns (Rahbek 1995, Nogués-Bravo et al. 2008, Yu et al. 2013, Thormann et al. 2018). So far, a monotonic decline and unimodal "hump-shaped" patterns of species diversity along elevation gradients are most common (Nogués-Bravo et al. 2008, González-Megías et al. 2009, Yu et al. 2013, Beck et al. 2017). However, it has now been established that variation in the patterns of species diversity along elevation gradients may as well arise from spatiotemporal settings of a given study (McCoy 1990, Rahbek 1995, Nogués-Bravo et al. 2008). In connection to these patterns, there are several competing hypotheses which incorporate over 30 explanatory variables attempting to explain mechanisms underlying patterns of species diversity (González-Megías et al. 2009, Novillo and Ojeda 2014, Leingärtner et al. 2014b). Although commentaries suggest that patterns of species diversity are influenced by interactive effects of numerous factors (Baur et al. 2014, Novillo and Ojeda 2014), temperature, precipitation, and availability of foraging resources (in terms of quantity and quality) are considered key bottom-up factors driving the pattern of species diversity of insects along elevation gradients (Hodkinson 2005, McCain 2007, Beck et al. 2017). Conversely, studies have also shown that top-down control through predation plays an important role in shaping species diversity patterns of insect herbivores (Vidal and Murphy 2018).

For ectothermic animals like insects, temperature imposes severe physiological constraints particularly at higher altitudes (Brown et al. 2004); a situation which limits species colonization (McCoy 1990, Fiedler et al. 2008) and modulates efficiency with which foraging resources can be utilized (Suzuki 1998, Kaspari et al. 2000). Conversely, precipitation influences not only net primary productivity, quality and quantity of foraging resources but also plant functional traits which in turn could affect the abundance and species diversity of primary consumers such as insect herbivores (Hodkinson 2005, Cardinale et al. 2009, Beck et al. 2017). The influence of productivity on species diversity has been well-documented in ecology (Abrams 1995) and several contrasting mechanisms have been proposed to explain productivity-richness relationships (Rosenzweig and Abramsky 1993, Abrams 1995, Mittelbach et al. 2001). For instance, studies on diversity-productivity relationships have closely associated productivity with plant functional traits (Šímová and Storch 2017). Plant functional traits have been frequently used in ecological studies as they provide insights on several aspects of plant life strategies such as plant-animal interactions (incl. spinescence, dispersal syndrome, diaspore and flower colors), growth (incl. leaf nitrogen, leaf phosphorous, canopy height) and reproductive (incl. relative seed number, seed crop frequency) investments (Costa et al. 2017). In addition, functional traits have also been linked to competition and functional diversification. As various ecosystems are subjected to land-use and climatic changes (Vitousek et al. 1997), environmental variables, net primary productivity (forage resources) and plant functional traits are expected to respond to these changes (Vitousek et al. 1997, Hendrickx et al. 2007, Garnier et al. 2007, Garibaldi et al. 2017) and cause some consequences to various animal species.

Here we determined the underlying reasons for various patterns of species diversity of phytophagous beetles (Order: Coleoptera) along land use and elevation gradients and unraveled direct and indirect effects of environmental factors (temperature and precipitation), net primary productivity, plant functional traits and land use on species diversity. We used phytophagous beetles because they are taxonomically hyperdiverse and a major herbivorous insect taxon in the world (Rosenberg et al. 1986, Hunt et al. 2007, Fiedler et al. 2008, Stork et al. 2015). The use of hyperdiverse groups in ecological studies is worth the effort as it presents an opportunity to understand mechanisms underlying variation in the patterns of species diversity. We tested the following non-exclusive hypotheses stating that

(i) Species diversity peaks at mid-elevation due to high climate-mediated net primary productivity (*i.e. the resource availability hypothesis*);

(ii) Species diversity declines monotonically with elevation due to temperature-mediated foraging activity (*the temperature-mediated resource exploitation hypothesis*) and temperature-mediated speciation (*i.e the temperature–speciation hypothesis*).

(iii) Species diversity peaks at mid-elevation due to ambient environmental conditions which promote persistence of a wider range of plant functional strategies (*i.e. physiological tolerance hypothesis*) (Spasojevic et al. 2014).

Methods

Study Area

We conducted the study on the southern slopes of Mt. Kilimanjaro in the northeastern part of Tanzania at 2°45' to 3°35'S and 37°00' to 37° 43'E (Fig. III. 1). The mountain is a dormant stratovolcano and the highest free-standing mountain in the world. Its elevation gradient ranges from the savanna plains on the foothill at approximately 700 m above sea level (asl) to the Kibo peak at 5895 m asl Mean annual temperature (MAT) declines quasi-linearly with elevation at an overall lapse rate of 0.56°C per 100 m spanning from 25°C at the foothills to - 8°C at the peak (Appelhans et al. 2016).

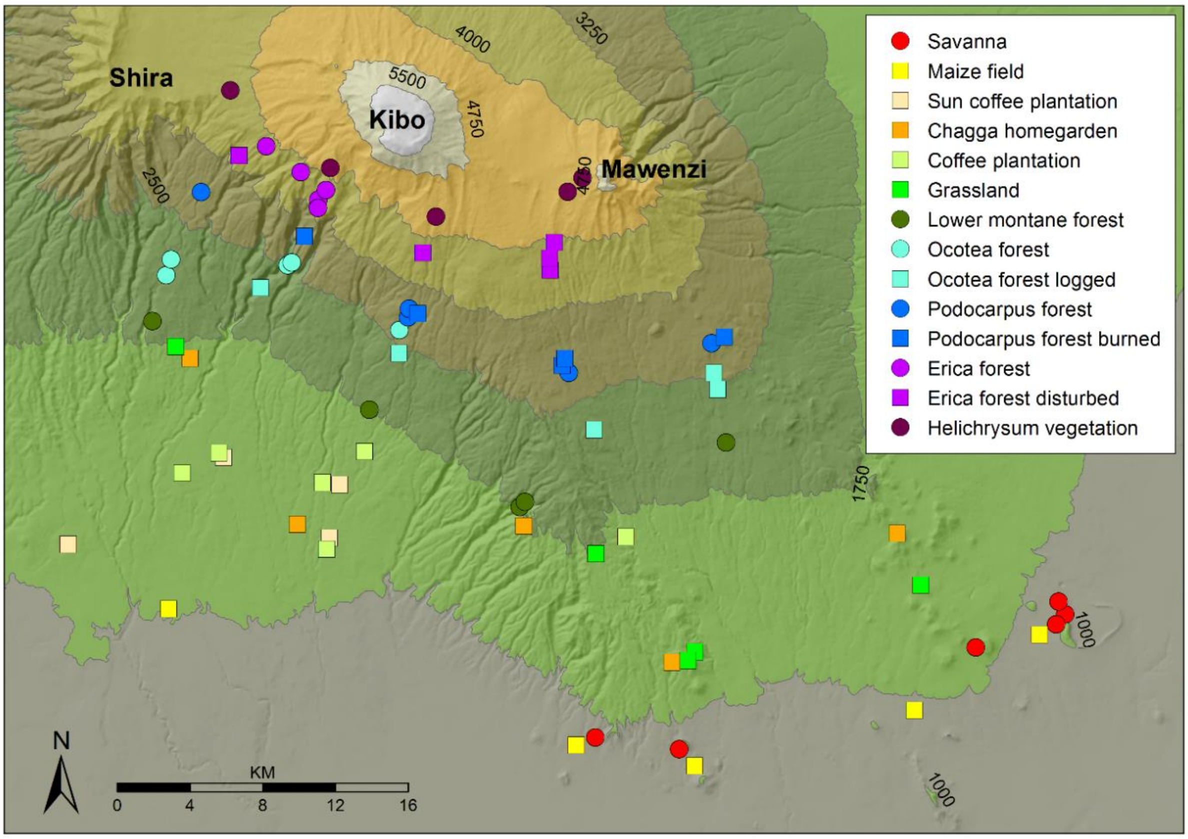


FIG. III. 1. Location of the 65 study sites distributed on the southern slopes of Mt. Kilimanjaro. Filled circles and squares indicate natural and anthropogenic habitat types respectively.

The area experiences a bimodal rainfall pattern with the main rainy season occurring between March and June and the more variable short rains occurring around November (Peters et al. 2016). Mean annual precipitation shows a hump-shaped pattern along the elevation gradient with the maximum precipitation of ~2700 mm at 2300 m asl (Appelhans et al. 2016).

The mountain encompasses distinct natural habitats along the elevational gradient: the lowland is characterized by colline savanna (871 - 1153 m asl), followed by lower montane rainforest (1560-2040 m asl), *Ocotea* forest (2120 - 2750 m asl), *Podocarpus* forest (2752 - 3060 m asl), *Erica* forest (3500 - 3880 m asl) and alpine *Helichrysum* vegetation (3849 - 4548 m asl). Following anthropogenic disturbances, in particular, subsistence and commercial farming activities, illegal logging, and fire, large parts of the natural habitats on the mountain were converted into 'anthropogenic habitat' (Hemp 2006c) including maize fields (866 - 1009 m asl), coffee plantations (1124 - 1648 m asl), sun coffee plantations (1150 - 1360 m asl), grasslands (1303 -1748 m asl), Chagga home gardens (agroforestry systems; 1169 - 1788 m asl), logged *Ocotea* forest (2220 - 2560 m asl) and burned *Podocarpus* forest (2770 - 3060 m asl).

Study design

This study is part of a larger research project (Kili Research Unit FOR1246 (https://www.kilimanjaro.biozentrum.uni-wuerzburg.de) from which we used a total of 65 study sites to sample phytophagous beetles, plant traits, and environmental data. Each study site had a size of 50 x 50 m and was placed at least 300 m apart of each other with 97% of all study site pairs being larger than 2 km. The study sites were located between 866 and 4550 m asl in the six natural and eight major anthropogenic habitats on the south-southeastern slopes of the Kilimanjaro (mentioned above). Each habitat type was represented with not less than five study sites (with exception of Savannah and Coffee plantations which were 6 each, and Sun coffee plantations and Helichrysum which were 4 each) which formed a small-scale within-habitat elevation gradient (Fig. III. 1). We used a composite land use index established by the KiLi Research Unit to described the land use intensity at each study site based on the level of chemical inputs, removal of plant biomass, the difference of the vegetation structure to natural habitats, and the proportion of agricultural land in a 1.5 km buffer zone surrounding each study site (Classen et al. 2015).

The temperature was recorded every 5 minutes for the duration of two years using temperature sensors positioned approximately 2 m above the ground on each study site (Classen et al. 2015, Appelhans et al. 2016). Mean annual temperature (MAT) was calculated by averaging all individual temperature measurements per study site (Classen et al. 2015). Data on precipitation (rainfall) was estimated for each study site from a total of 70 rain gauges distributed on Mt. Kilimanjaro for over 15 years. From this data, mean annual precipitation (MAP) was mapped across the area using a co-kriging approach (Appelhans et al. 2016). For a detailed description of how climatic variables were measured, please see Appelhans et al. (2016) and Peters et al. (2016).

Richness and abundance of herbivorous beetles

We sampled phytophagous insects on all study sites in two sampling phases between March 2011 and October 2012 and in three sampling phases from April 2014 to May 2016. Insects were collected in both dry and wet seasons and all sampling activities were restricted to hours between 0900 and 1600 when most diurnal insects were believed to be active. In order to collect a wide spectrum of insect herbivores in different vegetation types, a sweep net method in tandem with a beating method was used to sample insects on each study site. We used a 30 cm diameter sweep net to sample mainly active and flying insects from two parallel, permanently marked, 50 m long transects per study site. A sampling unit constituted a total of 200-sweep sample specimens (i.e. 100-sweep sample specimens from each transect).

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

Out of the collected insect specimens, we dealt with adult beetles (Order: Coleoptera) for further taxonomic identification. All beetles were mounted and identified to the family level. All beetles from mainly phytophagous beetle families including Curculionidae, Chrysomelidae, Buprestidae, Cerambycidae, and Elateridae were then identified to species or morphospecies level by Thomas Wagner (Hasenkamp and Wagner 2000, Wagner 2007, Thormann et al. 2016, 2018).

Food resource abundance, food resource quality, and food resource diversity

For each study site, we estimated measures of the food resource abundance (approximated by the normalized difference vegetation index (NDVI), food resource quality (resource quality) (leaf traits assumed to influence the digestibility of leaves for herbivores) and food resource diversity (resource diversity) (approximated by the functional dispersion of leaf traits). The NDVI is a proxy for the net primary productivity [food resource abundance (resource abundance)] of ecosystems (Evans et al. 2005, Peters et al. 2016) and a measure for the overall food resource availability of phytophagous insects. The NDVI was estimated from a MODIS Aqua product MYD13Q1 with a horizontal resolution of 250 m by 250 m by averaging corrected NDVI measures of 10 consecutive years (2003-2012) and extracting pixel values corresponding to the geographical positions of the study sites. For details see Detsch et al. (2016) and Peters et al. (2016).

We also determined a specific leaf area (SLA) (mm^2 mg^{-1}) as the ratio of leaf area to dry mass. Low SLA scores are typically representative of leaves with a long lifespan, high investments in physical defenses (Callis-Duehl et al. 2017) and low nutritional value (Schuldt et al. 2012). The NP ratio indicates plant phosphorous availability per unit of nitrogen available to herbivores whereas the CN ratio indicates plant nitrogen availability per unit of carbon available to herbivores (Mattson 1980). These traits play a crucial role in regulating the nutritional value of food resources for herbivores which in turn influence susceptibility of plants to herbivore attacks (Schuldt et al. 2012, Leingärtner et al. 2014a). We used the LEDA protocol to measure plant functional traits from the most abundant plant species making up 80% of total plant biomass found on each study site. In order to account for intraspecific variability, we sampled 15 individuals per plant species from different sites where possible. Details on these traits and descriptions of trait measurements can be found in Costa et al. (2017) and Kleyer et al. (2008).

We also used Functional Dispersion (FDis) of leaf traits (SLA, NP and CN ratios) as a measure of resource diversity. FDis is a multidimensional functional diversity index which uses data of multiple functionally relevant traits (Laliberté Etienne and Legendre Pierre 2010). FDis is considered to be highly flexible as it accommodates traits of any number, type (qualitative, quantitative or semi-quantitative) and those taken from any distance or dissimilar measures (Laliberté Etienne and Legendre Pierre 2010). If species of phytophagous beetles are specialized to feed on plants with certain functional traits, we expect strong correlations between the functional diversity of plant leaves (FDis) and the diversity of phytophagous beetles.

Statistical analyses

We used the R statistical platform version 3.3.1 to perform statistical analyses (R Core Team 2016). In order to counteract the potential problem of incomplete sampling of beetles' species, we estimated asymptotic species richness for each study site using the Chao1 index, implemented in *estimate* function of the R-package *vegan*. The Chao1-estimated species richness is hereafter referred to as species diversity. Generalized additive models (GAMs) calculated with the *mgcv* package were used to examine the distribution of species diversity and abundance of all phytophagous beetles, and additionally of weevils and leaf beetles along the elevational gradient. In the GAMs the two major categories of habitat (natural and anthropogenic habitats) were included as factor levels since we wanted to visualize potential differences in species diversity trends between the two habitat categories. As our data showed a signal of overdispersion we used the quasipoisson data family for modeling count data in GAMs. We set the basis dimension of the smoothing function to k = 5 to prevent overparameterization of GAM models (Peters et al. 2016).

We used path analysis to examine causal relationships (Shipley 2016) and unravel the direct and indirect effects of all predictor variables on the species diversity of phytophagous beetles (Herbst et al. 2017). Before analysis, we log-transformed Chao1- estimated species richness (hereafter referred to as species diversity) and abundance of phytophagous beetles in order to conform to the assumptions of a normal distribution. Based on our assumed linkages between climate, plant resource variables and phytophagous beetle diversity we hypothesized and constructed a conceptual path diagram (Fig. III. 3a) based on the following linkages:-

1) NDVI~MAT + MAP + LUI
2) Herbivore abundance ~MAT + MAP + LUI + NDVI + FDis + NP + CN + NDVI + SLA
3) Species diversity~ MAT + LUI + NDVI + FDis + Abundance + NP + CN + NDVI + SLA
4) FDis ~ LUI + NDVI

We then pre-selected possible path combinations, by analyzing the four response variables of our path models (NDVI, FDis, herbivore abundance, and species diversity) with their respective predictor variables using linear models. For each path model, we employed the *‘dredge’* of the R package *MuMIn* to identify a set of competitive models based on the Akaike information criterion (AIC). The AIC is conceptually based on information theory and evaluates statistical models on the basis of model fit and complexity (Burnham and Anderson 2004). We used the AICc (AIC with a second-order bias correction) instead of the standard AIC because our samples were relatively low compared with the number of estimated parameters. For the construction of competitive path models, we just included models which showed AIC_C values of < 2 in comparison to the best-supported model. We compared all path model combinations which could be constructed from the set of the best supported linear models and identified the best path model based on the AIC.

Results

We collected 3,186 phytophagous beetles representing 21 families and grouped them into 304 morphospecies. Two groups, weevils (Curculionidae) and leaf beetles (Chrysomelidae) were the largest and most diverse families represented with 898 and 1566 individuals, respectively. Findings show that abundance of phytophagous beetles peaked in the *Podocarpus* forests located at ca. 3200 m asl (Fig. III. S1). The species diversity of all phytophagous beetles showed a tendentially declining but bimodal pattern. Species diversity was highest in the lowlands, then declined sharply in the lower montane zone up to ca. 2200 m asl Diversity then peaked again at ca. 3400 m asl, in the area of upper montane *Podocarpus* forests (GAM: n = 65, explained deviance (ED) = 35.1 %, $F_{elevation}$ = 4.0, $P_{elevation}$ < 0.001, Fig. III. 2a).

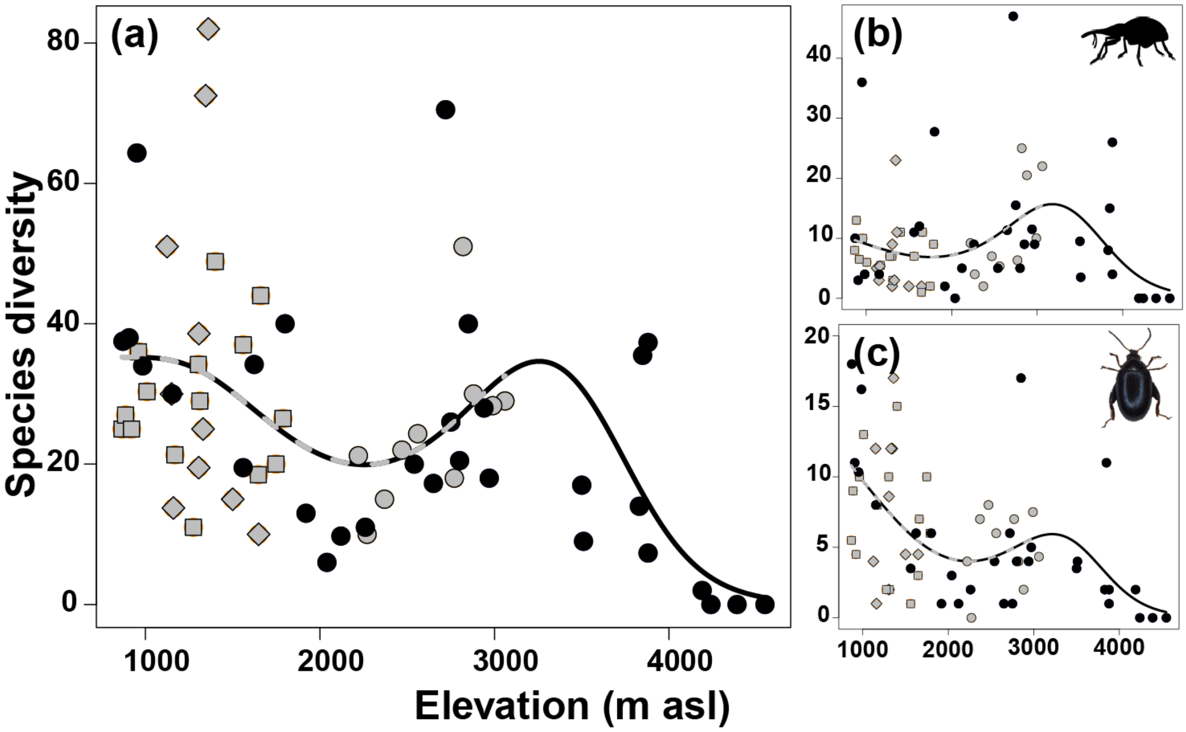


FIG. III. 2. Patterns of species diversity of phytophagous beetles in natural and anthropogenic habitats along the elevation gradients. Filled (black) and broken (gray) trend lines indicate patterns of elevational species diversity in natural and anthropogenic habitats, respectively. (a)

Represents patterns of species diversity as described by all phytophagous beetles; (b) represents patterns of species diversity for weevils; (c) represents patterns of species diversity for leaf beetles. We used generalized additive models (GAMs) with a basis dimension of k = 5 to calculate the trend lines.

We did not detect differences in the elevational distribution of phytophagous beetles between natural and anthropogenic habitats ($P > 0.1$). Weevils exhibited a unimodal pattern, with rather low diversity in the lowlands and the highest diversity at 3400 m asl (GAM: n = 65, explained deviance (ED) = 19 %, $F_{elevation} = 2.1$, $P_{elevation} < 0.05$, Fig. III. 2b). Leaf beetles, in contrast, showed an elevational diversity pattern similar to that of the total phytophagous beetle community (GAM: n = 65, explained deviance (ED) = 33.5 %, $F_{elevation} = 5.6$, $P_{elevation} < 0.0001$, Fig. III. 2c). Patterns for the observed (actual) species richness for the overall, weevils and leaf beetles datasets were also similar to that of species diversity (i.e. Chao1-estimated species richness) (Fig. III. S2 a-c).

Path analysis revealed that MAT, food resource abundance (NPP) and diversity of food resources (FDis) were the strongest predictors of species diversity of phytophagous beetle. Out of the two climatic variables (MAT and MAP), only MAT showed a strong direct positive effect on species diversity (standardized path coefficient = 0.39, P = 0.0001). In addition, both MAT and MAP showed a strong combined effect on species diversity through their positive effects on resource abundance (MAT: standardized path coefficient = 0.83, P = 0.0001; MAP: standardized path coefficient = 1.01, $P = 0.0001$). Conversely, the results also revealed a significant direct effect of resource diversity (standardized path coefficient = 0.22, P = 0.007) and herbivore abundance (standardized path coefficient = 0.54, P = 0.001) on species diversity of phytophagous beetles. However, the effects of resource diversity and herbivore abundance on species diversity were mediated by resource abundance (Fig. III. 3b). We did not find a direct effect of MAT on beetle abundance or an effect of LUI on NPP, leaf traits, phytophagous beetle abundance, and species diversity. Furthermore, we did not find a significant effect of leaf quality traits (leaf SLA, CN and NP ratios of plant communities) on the abundance and species diversity of phytophagous beetles.

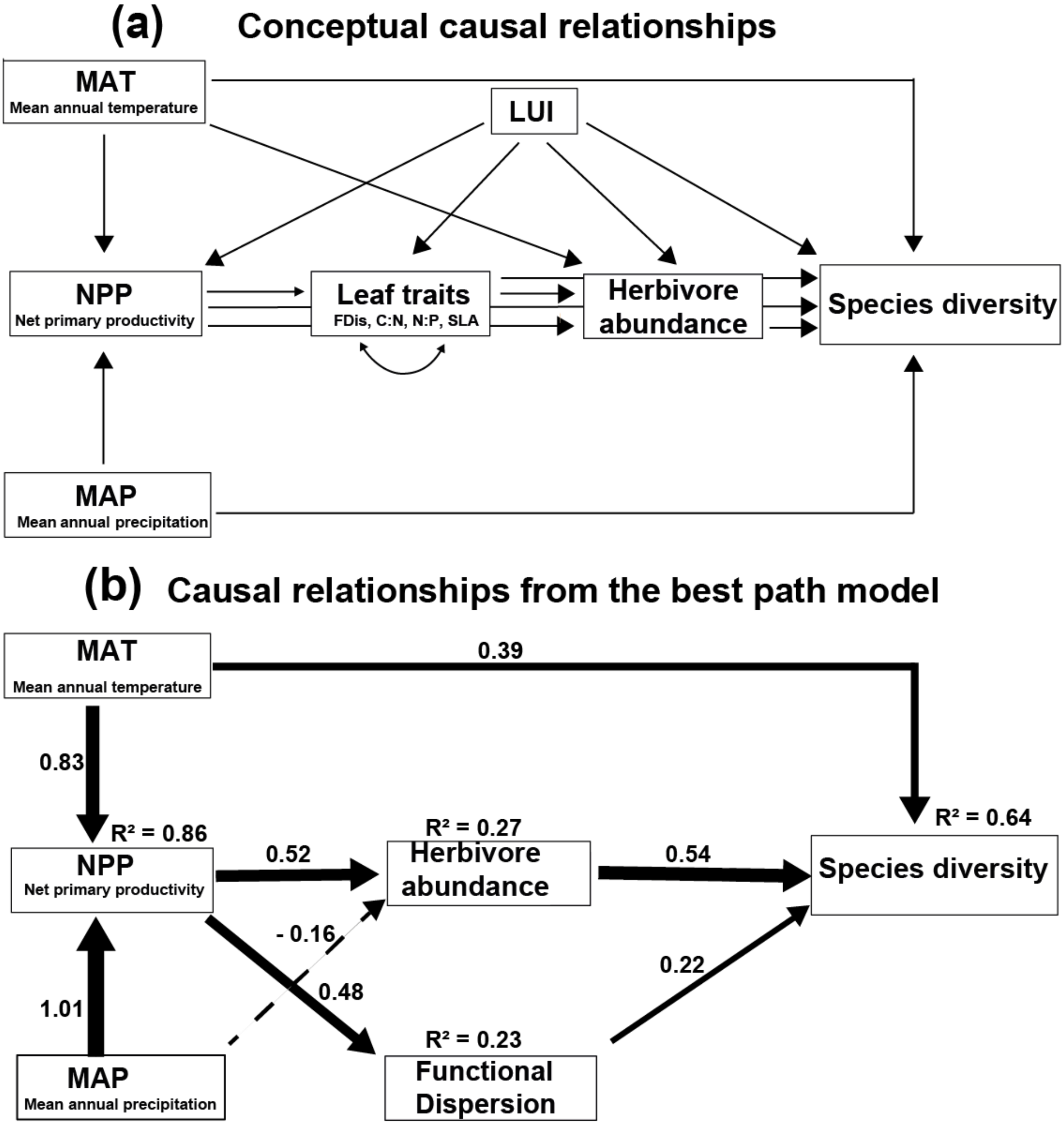


FIG. III. 3. Path diagram displaying predictors of herbivore abundance and species diversity on Mt. Kilimanjaro. The solid and dashed arrows represent paths described by the best-supported path model (the most parsimonious model) and an additional variable appearing in the best competitive model, respectively. Arrow width (and the path coefficient on it) is proportional to the relative strength of the effect of a particular predictor variable on the response variable (species diversity). The number on the box (R^2) shows the total explained the variation of species diversity by predictors. (**a**) Shows a conceptual path diagram indicating possible causal relationships between all predictor variables used in our path models (MAP, MAT, NPP, LUI, FDis, herbivore abundance, SLA, CN, and ratios) and species diversity. (**b**) Path diagram displaying directions of predictor variables on species diversity of phytophagous beetles. The diagram with solid arrows was constructed from the best path model which had the lowest AIC of 791.05 The relative amount of explained variation (R^2, deduced from the best-supported path model) is shown. The dashed arrow represents an additional variable (included in one of the competing path models) to the best-supported model (Competing models are the ones which had ΔAIC < 2 calculated against the best-supported path model). In our case, the additional variable (MAP) had a negative but insignificant effect on abundance.

In addition, findings showed that one competing path model (AIC = 791.68) showed results similar to the ones shown by the best model (AIC = 791.05), however, the competing path model had an additional predictor variable (MAP) which showed an insignificant effect on beetle abundance (Fig. III. 3b).

Discussion

Our results show that species diversity of the overall phytophagous beetles community exhibited a bimodal pattern and tendentially declined along the elevation gradient. In addition, this study found less significant support for hypotheses advocating monotonic decline pattern (i.e. *temperature-mediated resource exploitation hypothesis* and *the temperature–speciation hypothesis)* and more significant support for hypotheses advocating hump-shaped patterns along elevation gradients (*i.e. the resource availability hypothesis* and *physiological tolerance hypothesis)*. Conversely, findings revealed that food resource abundance (NPP) and diversity of food resources (FDis of plant communities) were the strongest predictors of species diversity of phytophagous beetle beside MAT.

Patterns of species diversity

Our results revealed complex patterns of species diversity for overall phytophagous beetles and the most dominant groups, leaf beetles (Chrysomelidae) and weevils (Curculionidae). Both, overall and leaf beetles had a similar elevational pattern of species diversity which contrasts that of weevils. Although our patterns slightly differed from the widely found pattern of monotonous diversity decline with elevation (Rahbek 1995, Trigas et al. 2013), high elevations were characterized by low species diversity of overall and individual phytophagous beetle taxa. We also found that temperature and climate-mediated resources abundance (NPP) at different elevations were the most important predictors of species diversity of the overall phytophagous beetles. Importantly, the effect of climate-mediated resource abundance on the diversity of the overall phytophagous beetle was indirect through the abundance of phytophagous beetles and resources diversity (FDis of plant communities), whereas temperature had a direct effect on species diversity.

The overall species diversity of phytophagous beetles showed bimodal peaks along the elevation gradient but we detected no modification of the diversity pattern by human land use. A similar pattern was also observed in leaf beetles suggesting that the overall pattern of species diversity for phytophagous beetles might have been shaped by the species diversity of leaf beetles which were the most abundant among families of phytophagous beetles. In these (the overall and leaf beetles) patterns, the first peak was detected at low elevations ca. 866m asl where Savannah and maize fields are found and the second peak at left-skewed mid-elevations where *Podocarpus* forests are found. Similar patterns to that of the overall and leaf beetles were also observed for predators (spiders) and some plant groups in studies conducted in the same region (Peters et al. 2016). The presence of high species diversity at low elevations and low species diversity at high elevations could be associated with high and low temperatures, respectively (Hodkinson 2005, Beck and Chey 2008, Classen et al. 2015). High temperature at low elevations creates environments that enable high colonization, speciation, reproduction and survival rates of ectothermic species whereas at high elevations, low temperature creates a harsh and inhospitable environment which poses a barrier for colonization, gene flow, and speciation particularly for ectothermic species (Baker and Williams 1988, Hodkinson 2005, Mittelbach et al. 2007).

Conversely, high species diversity at the left-skewed mid-elevations could be associated with high productivity of the forests which are found on mountains with dry and arid conditions at the lowlands (McCain 2007). Evidence suggests high species diversity in habitats with a larger resource base and vice versa in habitats with low resource base (Mittelbach et al. 2001, Allen et al. 2002, Beck et al. 2017). Resource-rich habitats enhance bottom-up determinants of species richness through trophic cascades, provide more diverse niche space in which more species can coexist, and support larger herbivore populations which lower extinction risk. Thus the detected bimodal pattern of beetle diversity along elevations was presumably shaped by superimposed patterns driven by temperature (resulting in a monotonic decline) and resource abundance (resulting in hump-shaped diversity patterns).

In the lowlands of Mt. Kilimanjaro, anthropogenic activities have cleared vegetation in favor of settlement and agriculture; also the presence of fire-prone and dry savannah ecosystem presumably has exerted a profound negative effect on resources abundance. Low resource abundance at higher elevation particularly above the timberline could also be associated with frequent anthropogenic fires and grazing pressure (Nogués-Bravo et al. 2008).

Interestingly, we observed a rarely described pattern with low species diversity in the lower montane forests found at ca. 2000 m asl. We suspect variation in microclimate associated with temperature and light availability within forest microhabitat could account for the situation. The forest canopy cover (opened vs. closed) is likely to have a profound effect on temperatures of the forest-floor (Frenne et al. 2013, Jiang et al. 2015, Scheffers et al. 2016, Scheffers and Williams 2018). Temperature experienced by organisms living within the closed-canopy forest is cooler than that of open surroundings (Frenne et al. 2013, Jiang et al. 2015). Available evidence suggests that microhabitats have a differential buffering effect along elevation and latitude gradients (Scheffers et al. 2014, Scheffers and Williams 2018). The effect of temperature on organisms living in the forest-floor is likely to be even higher in montane (than lowland) forests - due to the already low temperatures associated with altitude, in tropical (than temperate) regions and in ectothermic (than endothermic) organisms. Thus the observed pattern of low species diversity of phytophagous beetles in the denser and closed-canopy of the lower montane forests could be due to cooler canopy-mediated temperatures within the lower montane forests (as opposed to contiguous species-rich open-canopy *Podocarpus* forests in our study system).

Additionally, forest canopy cover can also prevent penetration of sunlight to understorey plants a situation which reduces availability of resources to understorey plants (Bartels and Chen 2010), negatively affects species diversity of plants (Šímová and Storch 2017) and ultimately that of primary consumers as described in plant diversity hypothesis (Novotny et al. 2006, Basset et al. 2012).

Factors influencing species diversity of phytophagous beetles

We found that temperature and climate-mediated resource abundance (NPP) were the strongest predictors of species diversity. Temperature had a significant direct positive effect on species diversity while climate-mediated resource abundance had a stronger but indirect effect on species diversity through beetles' abundance and resource diversity (FDis of plant communities). The positive effect of temperature on species diversity along elevation gradients has also been proposed in other studies (McCain 2007, Classen et al. 2015, Peters et al. 2016) and is consistent with our conceptual diagram. Temperature poses differential physiological effects on organisms by influencing metabolic rates along elevation gradients (Brown et al. 2004, Hodkinson 2005). At higher elevations, low temperatures limit species diversity because species colonization is severely constraints (McCoy 1990) and resource consumption rates are reduced (Kaspari et al. 2000, Brown et al. 2004). According to the diversification rate hypothesis, low temperature slows rates of speciation as it limits biotic interactions, slows molecular evolution and increases extinction rates (Mittelbach et al. 2007) and the reversed trend is expected at low elevations.

We found strong evidence suggesting that climate-mediated changes in resource abundance (NPP) had a positive effect on species diversity through herbivore abundance and resources diversity (FDis of plant communities) as hypothesized, but we did not detect a direct effect of climate-mediated changes in resource abundance on species diversity. Other studies have elucidated the influence of resource abundance on species diversity, however, only a few have managed to disentangle the direct and indirect effects of resource abundance on biodiversity. The missing direct effect of resource abundance on species diversity underscores the need to unravel direct and indirect effects when attempting to explain mechanisms affecting ecological relationships along environmental gradients. Despite existing controversies on the patterns and mechanisms by which productivity affects species diversity (Abrams 1995, Mittelbach et al. 2001, Šímová et al. 2013), empirical evidence suggests that productivity may affect species diversity by influencing the abundance of resources and enhancing the population sizes of rare species which are often prone to demographic and genetic stochastic events (Rosenzweig 1992), thereby promoting co-existence of species (Tilman 1982, Chesson 2000, Brown et al. 2016). In our study, evidence for species co-existence is shown by a strong direct positive effect of resource diversity (FDis of plant communities) on species diversity of phytophagous beetles. FDis measures the diversity of plant functional traits in ecosystems which reflects the degree of functional variability and complementarity of co-occurring species (Petchey and Gaston 2002, Schleuter et al. 2010). The observed relationships support the physiological tolerance hypothesis which posits higher diversity of phytophagous beetles in suitable environmental conditions (Spasojevic et al. 2014). Empirical evidence suggests that high resource diversity is usually observed in a community which experiences an intense competition for resources, a situation which leads to a greater functional diversification and coexistence of species (Grime 2006, Laliberté et al. 2013) rather than exclusion (Janzen 1970, Bagchi et al. 2014). FDis is often positively correlated with resource abundance and temperature suggesting that at mid-elevations where temperature and productivity are at optimum, species diversity of plants (Jiang et al. 2016, Costa et al. 2017) and consumers such as phytophagous beetles are expected to be highest (Crutsinger et al. 2006, Novotny et al. 2006, Haddad et al. 2011, Moreira et al. 2016).

Although our results revealed the effect of climate variables on species diversity of phytophagous beetles through a bottom-up control, there is also strong evidence which unearths the effect of biotic and abiotic factors on insect herbivores through top-down control (Martin et al. 2013, Roslin et al. 2017, Vidal and Murphy 2018). Studies have also shown that temperature can have an indirect effect on insect herbivore populations through a top-down control particularly at lower elevations where higher temperatures play a crucial role in fostering predator activity and hunting success (Roslin et al. 2017).

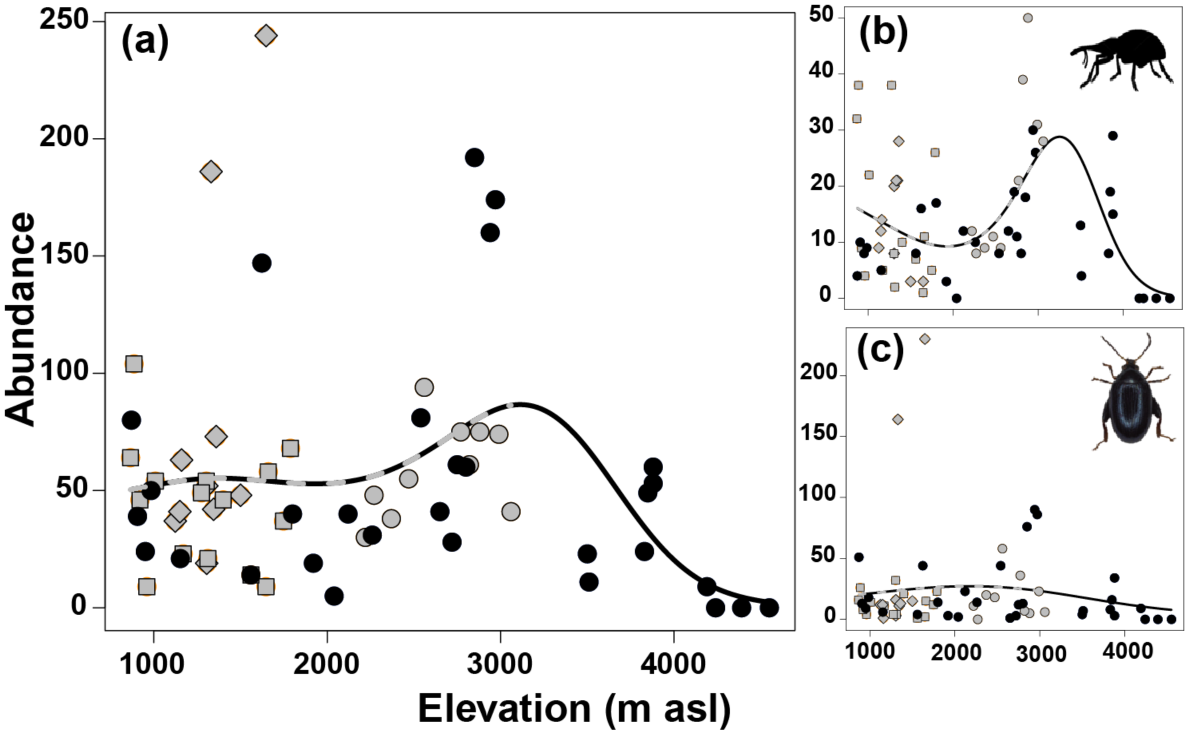
Conclusion

Our study reveals interesting species diversity patterns and uncovers strong predictors of species diversity along elevation gradients. Although the patterns detected in our study differ from the commonly reported patterns (i.e. a monotonic decline or a hump-shaped pattern), they provide valuable ecological insights. We associated unexpected decline of species diversity in lower montane forests with idiosyncratic climatic conditions of the forest microhabitats. This finding underscores the importance of taking into account unique microclimatic conditions of complex ecosystems (such as forest microhabitats in our study system) when developing an understanding of the mechanisms underlying macroecological patterns.

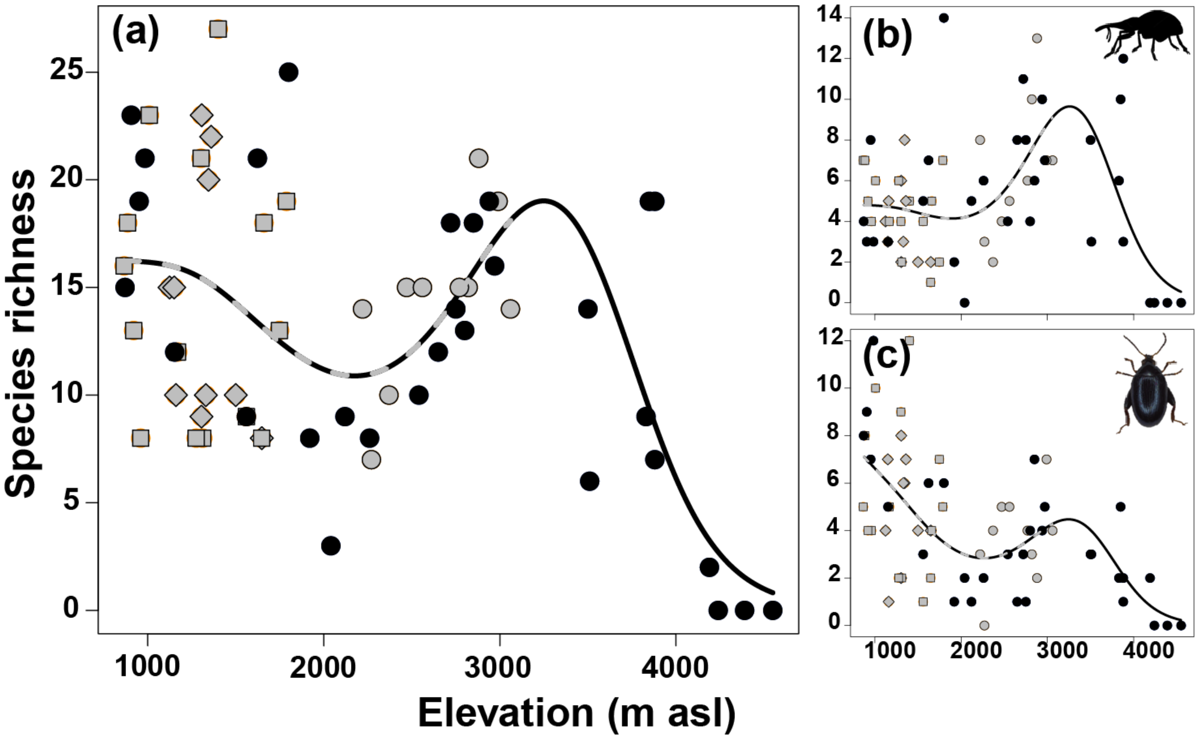
Furthermore, our findings elucidate how species diversity is linked to climate-mediated resource abundance (NPP) through herbivore abundance and resource diversity (FDis of plant communities). The lack of a direct pathway through which resource abundance affects species diversity suggests that indirect effects are key to understanding mechanisms underlying ecological relationships. Conversely, a strong positive relationship detected between species diversity of phytophagous beetles and plant resource diversity suggests that as ecosystems structural complexity is expected to shift towards structurally less complex ecosystems due to increased human influences, species diversity and ecological patterns are likely to follow a concordant decline and shift, respectively. In order to halt such decline and promote species diversity, efforts to restore and conserve ecosystem structural complexity and associated biodiversity within and outside protected areas are critical and such efforts need to be responsive to and integrate human dimensions.

As global climate is constantly changing, effects of climate-mediated factors (such as resource abundance) on species diversity detected today are also likely to change over the coming decades suggesting that our ability to conserve the biodiversity of the planet will increasingly be tied to our ability to manage global changes and biotic changes associated with it. Therefore, we recommend the adoption of conservation approaches which takes into account climate change scenarios when formulating conservation plans and policies. We are aware that the diversity of insect herbivores is strongly influenced by bottom-up and top-down controls and that climate change is shaping bottom-up and top-down controls in various ecosystems. However, in this study we only focused on bottom-up control and the top-down control was beyond our scope. Future studies which simultaneously address the effects of bottom-up and top-down controls along land use and elevation gradients are highly recommended.

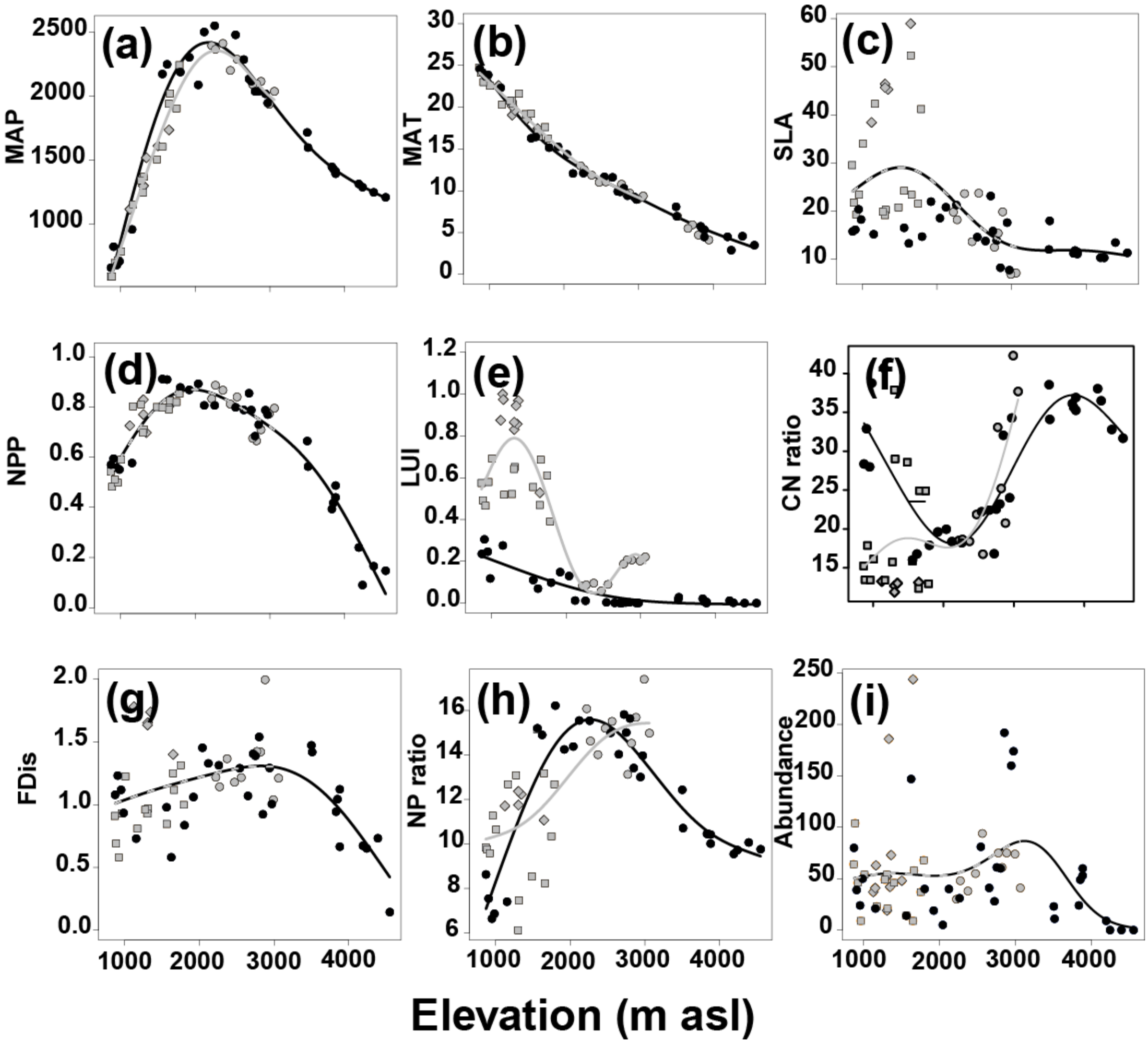
Supplementary information



Supplementary FIG. III. 1. Patterns of phytophagous beetles' abundance as described in natural and anthropogenic habitats along the elevation gradient of Mt. Kilimanjaro. Filled (black) and broken (gray) trend lines indicate beetles abundance richness in natural and anthropogenic habitats, respectively. (a) Represents patterns of abundance described by all phytophagous beetles; (b) represents patterns of abundance described by weevils; (c) represents patterns of abundance described by leaf beetles. We used generalized additive models (GAMs) with a basis dimension of k = 5 to calculate the trend lines.



Supplementary FIG. III. 2. Patterns of elevational observed (actual) species richness of phytophagous beetles in natural and anthropogenic habitats along the elevation gradient of Mt. Kilimanjaro. Filled (black) and broken (gray) trend lines indicate patterns of elevational species richness in natural and anthropogenic habitats, respectively. (a) Represents patterns of species richness as described by all phytophagous beetles; (b) represents patterns of species richness as described by weevils; (c) represents patterns of species richness as described by leaf beetles. We used generalized additive models (GAMs) with a basis dimension of k = 5 to calculate the trend lines.



Supplementary FIG. III. 3. Distribution of predictor variables of species diversity (a) MAP (b), MAT, (c) SLA, (d) NPP, (e) LUI, (f) CN ratio, (g) FDis, (h) NP ratio, and (i) herbivore abundance along the elevation gradient. Symbols denote study sites in natural (filled dots) and anthropogenic (filled squares) habitats. Black trend lines describe the distribution of predictor variables in natural habitats and grey trend lines describe the distribution of predictor variables in anthropogenic habitats. Where no significant land use effect (interaction nor additive) was detected, one interrupted black-gray trend line was drawn (Fig. III. 3c, d, g & i).

Chapter IV: Primary productivity and habitat protection predict species richness and community biomass of large mammals on Mt. Kilimanjaro.

Summary

Aim: Despite their large functional and cultural importance, the patterns and drivers of large mammal diversity along elevational gradients of tropical mountains remain poorly understood. Here, we evaluate the importance of climate, resources and human impact for the distribution, species richness and community biomass of wild mammals along a 3600 m elevational gradient on Mt. Kilimanjaro, Tanzania.

Location: Mt. Kilimanjaro, Tanzania

Methods: Mammal species richness was explored with camera traps on 66 study sites spread over six natural and seven disturbed habitats along an elevational gradient from 870 to 4550 m asl. We applied path analysis to unravel the direct and indirect effects of temperature and precipitation, primary productivity, land use, land area, the protection of habitats and the occurrence of domestic mammals on the species richness and community biomass of wild mammals.

Results: Both species richness and community biomass of wild mammals showed a unimodal distribution with elevation and peaked in the montane zone of Kilimanjaro. However, the peak shifted significantly to lower elevations when only protected habitats were considered. Path analyses revealed that wild mammal species richness and community biomass were mainly driven by variation in net primary productivity, land area and the protection of habitats whereas a direct temperature effect was less important.

Main conclusions: Our study underscores the importance of food resources for the establishment of diversity gradients in large mammals. While temperature has been revealed as an important direct driver of diversity in several ectothermic taxa, its effect on endothermic organisms appears to be indirect, via a modulation of resources. Moreover, our study reveals the sensitivity of large mammals to human impact and points to the pivotal role of protected areas for their long-term conservation on tropical mountains.

Keywords altitudinal gradients, biomass, diversity gradients, energy-richness hypothesis, food resources, land use, Mammalia, nature conservation, species-area hypothesis, temperature-richness hypothesis

Introduction

Elevational gradients in species richness are well depicted in ecology, yet there is no consensus about the major drivers (Rahbek 1995, Peters et al. 2016, Beck et al. 2017). A range of deterministic hypotheses have been suggested that highlight the influence of energy availability, climatic factors, and history on biodiversity gradients (Pianka 1966, McCain 2004, 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 (Allen et al. 2002, Mittelbach et al. 2007, Hurlbert and Stegen 2014). The 'temperature-richness hypothesis' predicts that temperature restricts species' occurrence by imposing physiological constraints and by influencing ecological and evolutionary processes (Belmaker and 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 (Allen et al. 2002, Beck et al. 2017). 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, Hawkins et al. 2003, Romdal and Grytnes 2007).

Despite their large functional and cultural importance, little is known about the patterns and drivers of large mammal diversity along elevations. 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 2004, Rowe et al. 2014, 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 (McNaughton et al. 1988, 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, 22% have been categorized as threatened or extinct by the 2008 IUCN Red List (IUCN, 2016).

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 the Mt. Kilimanjaro, Tanzania. 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.

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 drivers of diversity and of the changes in mammal-mediated ecosystem functions. 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, Schipper et al. 2008).

By using path analysis, we unraveled 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 large mammals is constrained by energy availability (Buckley et al. 2012). 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). We, therefore, expect that species richness and biomass of wild mammals is positively correlated to the net primary productivity of ecosystems along elevation and land use gradients on Mt. Kilimanjaro.

2. Elevational 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).

3. 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). We therefore expect that the decrease in land area with increasing elevation is correlated with a loss of mammal species richness.

4. 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).

Methods

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 asl. 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 asl to -8°C at the summit. Mean annual precipitation is unimodally distributed with a peak of ~2700 mm at around 2200 m asl (Appelhans et al. 2016).

Research was conducted on 66 study plots established in the framework of the KiLi project (DFG research unit FOR 1246) on the southern slopes of Mt. Kilimanjaro (Peters et al. 2016). The study plots ranged from 870 to 4550 m asl 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 asl), lower montane forest (1560 – 2020 m asl), *Ocotea* forest (2120 – 2750 m asl), *Podocarpus* forest (2800 – 2970 m asl), *Erica* forest (3500 – 3900 m asl) and alpine *Helichrysum* scrub vegetation (3880 – 4550 m asl). Anthropogenic habitats consisted of maize fields (866 – 1009 m asl), grasslands (regularly cut by hand for cattle feeding, 1303 – 1748 m asl), commercial coffee plantations (1124 – 1648 m asl) and Chagga agroforestry (1169 – 1788 m asl), selectively logged *Ocotea* forest (2220 – 2560 m asl) and burned *Podocarpus* (2770 – 3060 m asl) and *Erica* forests (3500 – 3880 m asl). The five study plots per habitat type were distributed in a way to reflect a within-habitat type elevation gradient to detect fine-scale changes in biodiversity with changing elevation. Spatial distances among study sites were larger than 300 m in all cases. If possible, study sites were established in core zones of larger areas of the respective habitat type, so that effects of transition zones were minimized. Anthropogenic habitats were classified as either ‘low land use intensity’ or ‘high land use intensity’ habitats based on their level of disturbance (see Supplementary Table IV. 1). All study sites above 1800 m asl, which were situated inside Mt. Kilimanjaro National Park, and additionally two lowland savanna sites, which were situated in wildlife conservation areas, were classified as ‘protected’. All other study sites were classified as ‘unprotected’.

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 site (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). Since precipitation data was not available for all study plots, mean annual precipitation was regionally interpolated using a co-kringing approach (Appelhans et al. 2016). We used the normalized difference vegetation index (NDVI) as a surrogate for net primary productivity (Detsch et al. 2016, 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 Appelhans et al. (2016), Detsch et al. (2016), and Peters et al. (2016).

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 on or in the direct vicinity (within a distance of 50 m) of each of the 66 study plots. Cameras were placed along trails or at animal latrine sites to increase the chance of mammal detection and were fastened to trees or poles at a height of 70 - 140 cm above the ground depending on local topography. 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 approach is called hourly event count and 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 on each plot 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. Faeces were identified using Stuart and 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 the body weight of males and females was listed, we always calculated the average body weight across sexes. On each study plot, species richness was calculated by counting the number of all species recorded by the five camera traps and by the systematic monitoring of mammalian faeces. Community biomass was computed by summing up the body weight of the individuals of all species across hourly event counts. For calculating the biomass of the mammal community, only camera trap samples were taken into account. 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 mammal community biomass.

Statistical analysis

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 were 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 predictor 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 and land use type as explanatory variables (factorial: natural versus anthropogenic habitat) which models individual trend lines for each land use type. If the interaction term showed a significance level of $P > 0.1$, we deleted it and used a simple additive effect model (y ~ elevation + land use). In this case, the model would have the same trend line in natural and anthropogenic habitats but the intercepts are allowed to vary. We successively deleted elevation, land use or both explanatory variables from the model in case their significance level exceeded $P > 0.1$. As we detected a significant effect of protected 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 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. 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. In addition, we assumed that NPP along the elevational gradient is driven by changes in mean annual temperature and mean annual precipitation (Peters et al. 2016). Finally, we assumed that the species richness of domestic mammals is determined by land use, the protection status of plots and NPP.

For the community biomass of wild mammals as the final endogenous variable, the same response and predictor variables as for species richness were used, with the exception that instead of species richness of domestic mammals, community biomass of domestic mammals was used as an explanatory variable. Both the community biomass of domestic mammals and the community biomass of wild mammals was log-transformed [log (x+1)] prior to analyses.

Potential path combinations were pre-selected by defining a set of competitive explanatory models for each endogenous variable 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 $\Delta AIC_C < 2$ were considered for path analyses.

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 with the *'sem.fit'* function of the R package *'piecewiseSEM'* (Shipley 2009, 2013, Lefcheck 2016). 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). To assess whether path coefficients were significant and positive or negative, the *‘sem.coefs’* function was employed. R^2- values were allocated to endogenous variables with the *‘sem.model.fits’* function.

Results

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 (Fig. IV. 1; Table IV. 1). Thirty-three species were wild mammals while the

FIG. IV. 1. Screenshots of wild mammals trapped with cameras on Mt. Kilimanjaro (a): Zanzibar Syke's Monkey (*Cercopithecus nicticans albogularis*); (b): Crested Porcupine (*Hystrix cristata*), (c): Serval (*Leptailurus serval*); (d): African Civet (*Civettictis civetta*); (e): Ratel (*Mellivora capensis*); (f): Bushpig (*Potamochoerus larvatus daemonis*); (g): Abbott's Duiker (*Cephalophus spadix*); (h): Lesser Kudu (*Tragelaphus imberbis*).

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*), Fig. IV. 2g) was listed as "endangered" (IUCN, 2016). The most common species was the Common Duiker (*Sylvicapra grimmia hindei*), which was recorded at 31 of 66 study sites (Fig. IV. 2), followed by the Zanzibar Syke's Monkey (*Cercopithecus nicticans albogularis*, Fig. IV. 1a, Fig. IV. 2) and the Abbott's Duiker, which occurred on 19 and 13 plots, respectively (Fig. IV. 1g, Fig. IV. 2).

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 (Fig. IV. 3a, black and grey dotted line, explained deviance (ED) = 18.1%, $P_{elevation} < 0.001$). However, if only study sites in protected areas were considered, the peak of the elevational diversity distribution shifted from elevations of ca. 2500 m to ca. 1500 m asl, forming a low-elevation plateau pattern

A unimodal pattern similar to that of the species richness of all mammals was found for omnivores (Fig. IV. 3c, ED = 44.3%, $P_{elevation} < 0.05$). In herbivores, species richness monotonically decreased with elevation in natural habitats but increased in anthropogenic

TABLE IV. 1. Recorded mammal species on Mt. Kilimanjaro. Animal body weight is shown in kg, elevation in m asl

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	1647
		Sciuridae sp. 2	Rodentia sp. 2*	omnivore	0.1	95; 3	14	1124-2880
	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	2120-3880
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.

[*] 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.

habitats (Fig. IV. 3b, ED = 34.8%, $P_{interaction} < 0.05$). For carnivores, no significant species richness trend with elevation could be detected (Fig. IV. 3d: $P_{elevation\ ,\ interaction} > 0.1$).

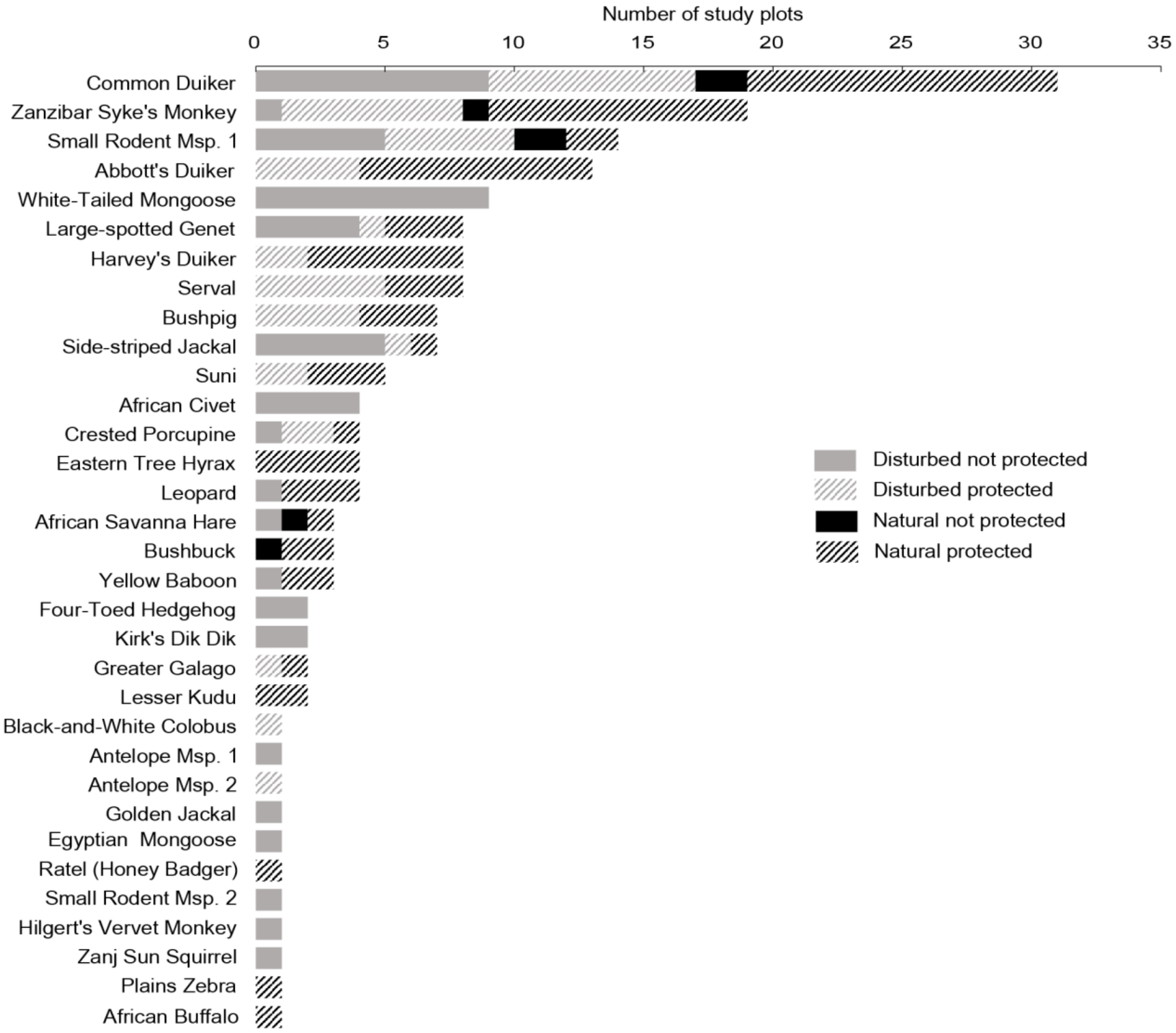


FIG. IV. **2.** Occurrence of wild mammals on the study plots on Mt Kilimanjaro recorded with camera traps and transect walks. Study plots are subdivided into natural and disturbed sites that are either classified as protected or not protected.

The community biomass of wild mammals exhibited a unimodal distribution along the elevational gradient with no difference between natural and anthropogenic habitats (Fig. IV. 4a, ED = 19%, $P_{elevation} < 0.05$). In herbivores, the pattern of community biomass along the

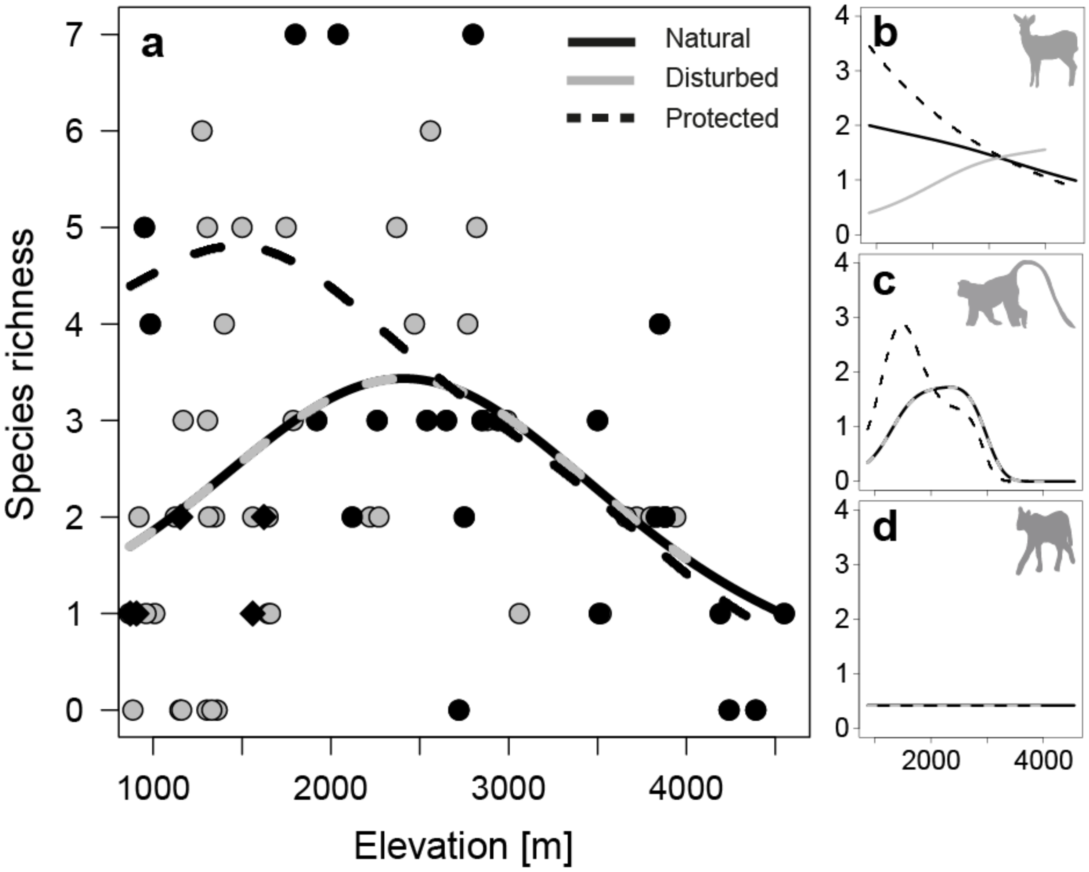


FIG. IV. 3. Elevational patterns of species richness of large mammals on Mt. Kilimanjaro (a) and patterns for individual trophic guilds: herbivores (b), omnivores (c) and carnivores (d). In (a), dots and diamonds depict original measurements on study sites. Natural habitats are displayed in black whilst anthropogenic habitats are shown in grey. Natural sites are subdivided into protected habitats (dots) and non-protected habitats (diamonds). Trend lines were computed by applying generalized additive models [Poisson family, basis dimension (k) = 5]. Black lines represent trends for natural habitats, grey lines trends for anthropogenic habitats. Dashed black lines depict trends for natural and disturbed forest habitats that were additionally situated in protected areas.

elevation gradient mirrored the pattern of species richness with a higher biomass in natural habitats at low and mid elevations than in anthropogenic habitats (Fig. IV. 4b, ED = 30.9%,

$P_{interaction} < 0.001$). For omnivores, community biomass declined with elevation in natural habitats while there was a hump-shaped pattern in anthropogenic habitats (Fig. IV. 4c, ED = 30.6%, $P_{interaction} < 0.05$).

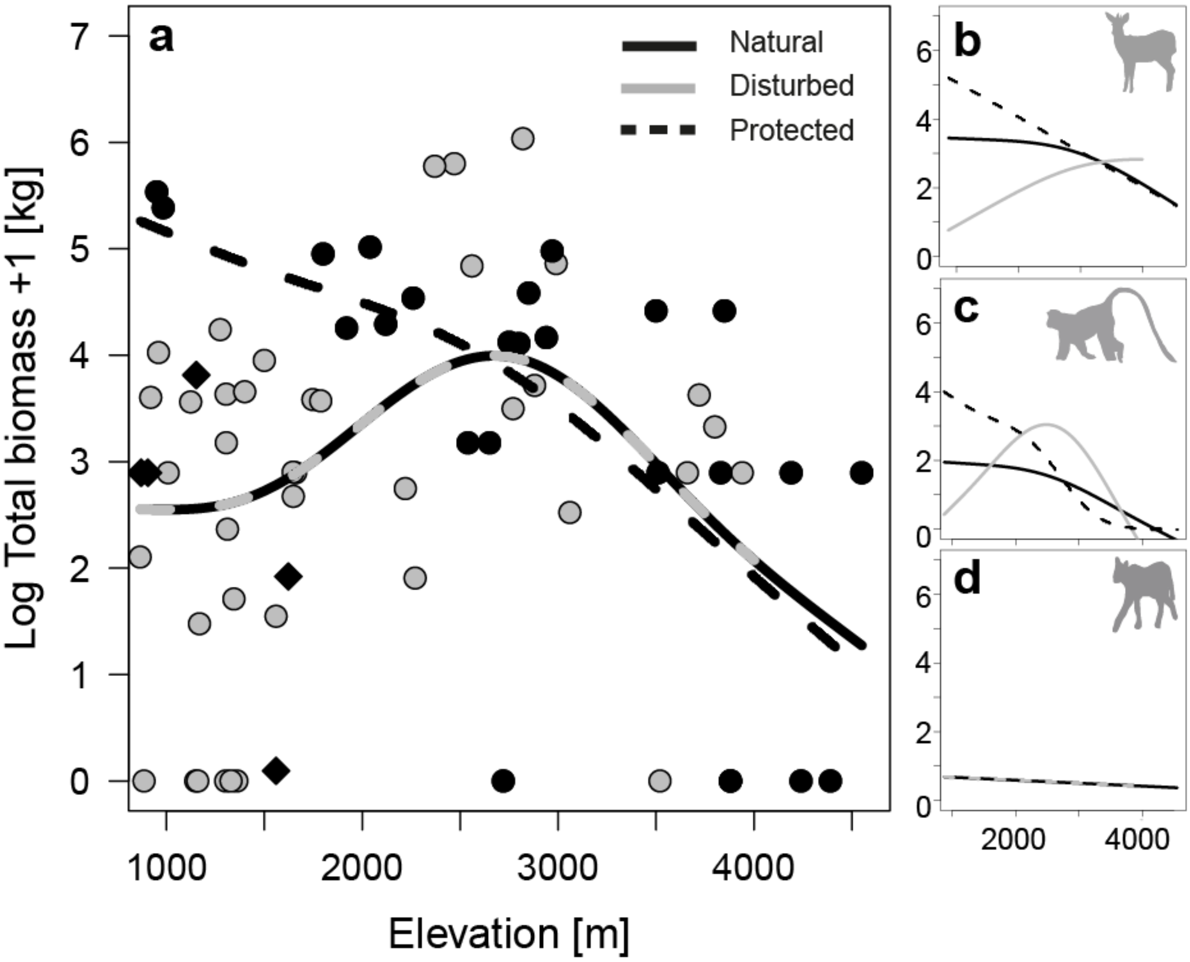


FIG. IV. 4. Distribution of community biomass of wild mammals along the elevational gradient on Mt. Kilimanjaro (a) and separated into the trophic guilds herbivores (b), omnivores (c) and carnivores (d). In (a), dots (black: natural habitat, protected; grey: anthropogenic/disturbed habitat) and diamonds (natural habitat, unprotected) depict original measurements on study sites. Trend lines were computed by 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 and disturbed forest habitats that were additionally situated in protected areas.

Protected areas showed a significantly higher community biomass at low and mid elevations than unprotected areas (all mammals: Fig. IV. 4a: ED = 27.7 %, $P_{interaction} < 0.05$; herbivores: b: ED = 30.9%, $P_{interaction} < 0.001$; omnivores: c: ED = 47.3 %, $P_{interaction} < 0.001$). This result was largely driven by the mammal species with large body weight, which were regularly present in natural protected areas but absent from unprotected areas (see Supplementary Fig. IV. 2). In carnivores, no pattern of community biomass with elevation was observed (Fig. IV. 4d, ED = 0.9%, $P_{interaction} = 0.44$)

Drivers of species richness and community biomass

For both, species richness and community biomass of wild mammals, energy and protection status were the most important explanatory variables in path analysis (Fig. IV. 5). The best-supported model suggested that the species richness of wild mammals increased with net primary productivity (NPP) and was higher in protected areas than in unprotected habitats. Additionally, we found a positive effect of land area on wild mammal species richness (Fig. IV. 5b). Competing path models included a positive relationship between the species richness of domestic and wild mammals. There was also a positive effect of mean annual temperature on wild mammal species richness. Both relationships were, however, not significant ($p = 0.32$; $P = 0.45$, respectively). The community biomass of wild mammals increased with increasing NPP and was higher in protected than in unprotected areas.

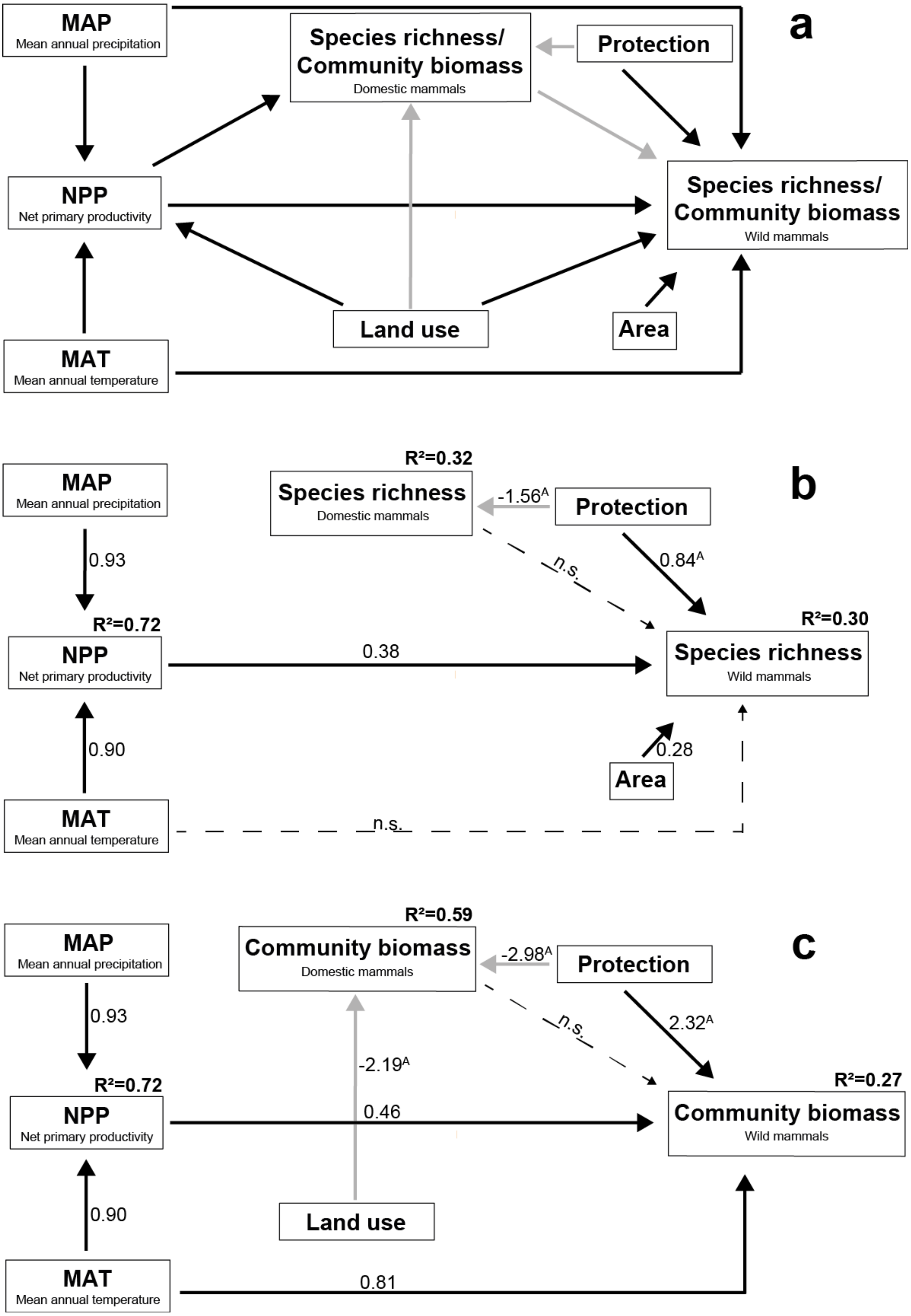


FIG. IV. 5. Predictors of species richness and community biomass of wild mammals on Mt. Kilimanjaro. Black and grey lines represent positive and negative effects, respectively, while dashed lines indicate a non-significant effect. (a) Expected path model showing anticipated effects of predictor variables on species richness and community biomass of wild mammals. (b) Predictors of wild mammal species richness. The best path model with the lowest (AICc = 33.96) is displayed with solid lines. The relative amount of explained variance (R^2, deduced from the best-supported path model) is shown. Dashed lines depict potential paths included in competing paths models (all path models with $\Delta AIC_C < 2$ determined by multi-model inference) but eliminated from the final path model. (**c**) Predictors of community biomass of wild mammals (best path model: AICc = 38.60). Species richness of domestic mammals was lower in protected than in unprotected areas. For land use, the levels agricultural, disturbed and natural were used. Numbers above paths represent standardized path coefficients. A Predictor variable (protection, land use) is a factor, therefore path coefficients are not standardized.

Furthermore, community biomass significantly increased with temperature (Fig. IV. 5c). The best competing path model included a non-significant negative effect of community biomass of domestic mammals on the community biomass of wild mammals ($P = 0.25$). The species richness of wild mammals was positively correlated to the community biomass ($r = 0.56$) and abundance of wild mammals ($r = 0.90$).

Discussion

In this study, we present a detailed analysis of both the patterns and drivers of large mammal elevational diversity. To our knowledge, this is the first study which combines data on the elevational diversity of large mammals with detailed tests of multiple macroecological hypotheses for explaining diversity gradients. Wild mammal species richness and community biomass showed 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 (Nor 2001, Rickart 2001, SÁnchez-Cordero 2001, Chen et al. 2017). However, our data suggests that the unimodal distribution of wild mammals is largely influenced by human impact at low elevations as in protected habitats mammal diversity was high even in the lowlands and the pattern of elevational diversity consequently more strongly resembled a lower plateau pattern (McCain and Grytnes 2010).

Net primary productivity and area as major drivers for endothermic species richness

Species richness and community biomass of wild mammals were determined by net primary productivity (NPP) and the protection status of study plots, the former being additionally positively regulated by area and the latter by temperature. In accordance with the energy-richness hypothesis (Currie et al. 2004), both wild mammal species richness and community biomass peaked at around 2500 m asl 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 confirms 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), 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 is also supported by a strong correlation between species richness and biomass/abundance of wild mammals in our study (Currie et al. 2004, Storch 2012).

In addition to NPP, we detected a positive effect of land area, a second energy-related factor, on wild mammal species richness. Larger areas of land can sustain larger populations of animals, which reduces the extinction risk of individual species and increases, on average, the number of species in an area. The species-area relationship has been identified as an important factor driving mammal species richness (Chen et al. 2017) and has been conceptually fused with the energy-richness hypothesis in the so-called ‘species-energy hypothesis’. To sum up, the significant effects of both NPP and land area give support to the view that food resources are limiting the number of coexisting large mammal species along tropical elevation gradients.

The importance of temperature

In addition to the effect of NPP, we found a positive effect of temperature on wild mammal community biomass. Temperature is a critical factor for endotherms, setting limits of species’ distributional ranges (Fernández and Vrba 2005). At low temperatures, there are increased metabolic costs for endotherms which may result in reduced population densities (Buckley et al. 2012). Furthermore, temperature has also been identified as an important driver of diversification in mammals, with higher levels of species diversity and rates of diversification observed at higher temperatures (Owen 1990, Brown 2001, Rolland et al. 2014). Very high or low temperatures have been shown to be a more important factor for species of large mammals compared to small mammals (Andrews and O’Brien 2000). One reason for this apparent paradox might be that small mammals can find better shelter from extreme temperatures in dense ground vegetation or by burrowing underground while large mammals are characterized by greater mobility. For small mammals, NPP and precipitation are of greater importance than temperature (Andrews and O’Brien 2000).

We did not find a positive effect of precipitation, neither on mammal species richness nor on mammal community biomass. Presumably, water availability is more relevant in drier ecosystems than the Mt. Kilimanjaro region, and this trend was mainly shown for small mammals (Nor 2001, SÁnchez-Cordero 2001). In contrast to small mammals, large mammals have been found to be less dependent on precipitation (Andrews and O’Brien 2000). 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, neither species richness nor community biomass of wild mammals was impacted by domestic mammals, probably due to the absence of intensive grazing regimes on Mt. Kilimanjaro

Implications for conservation

In protected habitats, both species richness and community biomass of wild mammals were higher than in unprotected areas. Large herbivores like Lesser Kudu and Plains Zebra and large omnivores like Yellow Baboon were only found in protected areas but were absent from unprotected areas, even if natural vegetation was still intact. In unprotected habitats, large mammals are particularly vulnerable to losses through hunting, either through bushmeat hunting or retaliatory killing for crop losses (Schipper et al. 2008, Kinnaird and O’brien 2012). In addition, the presence of domestic mammals might have a negative impact on wild mammals (Di Bitetti et al. 2013). As a result, the species richness, abundance, and body size of wild mammals are often lower in unprotected than in protected habitats (Kinnaird and 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 in our study all plots above 1800 m asl were located inside the boundaries of Mt. Kilimanjaro National Park. Furthermore, at low elevations, the landscape on the mountain is characterized by a 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). In its current form, the heterogeneous landscape on Mt. Kilimanjaro can sustain high levels of biodiversity. However, increasing agricultural intensification 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). 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 and 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 low species diversity and small body sizes in anthropogenically modified landscapes (Kinnaird and O'brien 2012). A reason for this discrepancy could be that the monitoring applied here 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 sites, reduced variation and clearer trends along gradients of elevation and human impact.

We recorded 27 (66%) of the 41 large mammal species that had been reported to occur on the southern slopes of Mt. Kilimanjaro in 1995 (Grimshaw et al. 1995). Only the African savanna Hare, which we encountered at low elevations, does not appear in Grimshaw's species list. 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, a second population stronghold of this species (Bowkett et al. 2014).

Concluding remarks

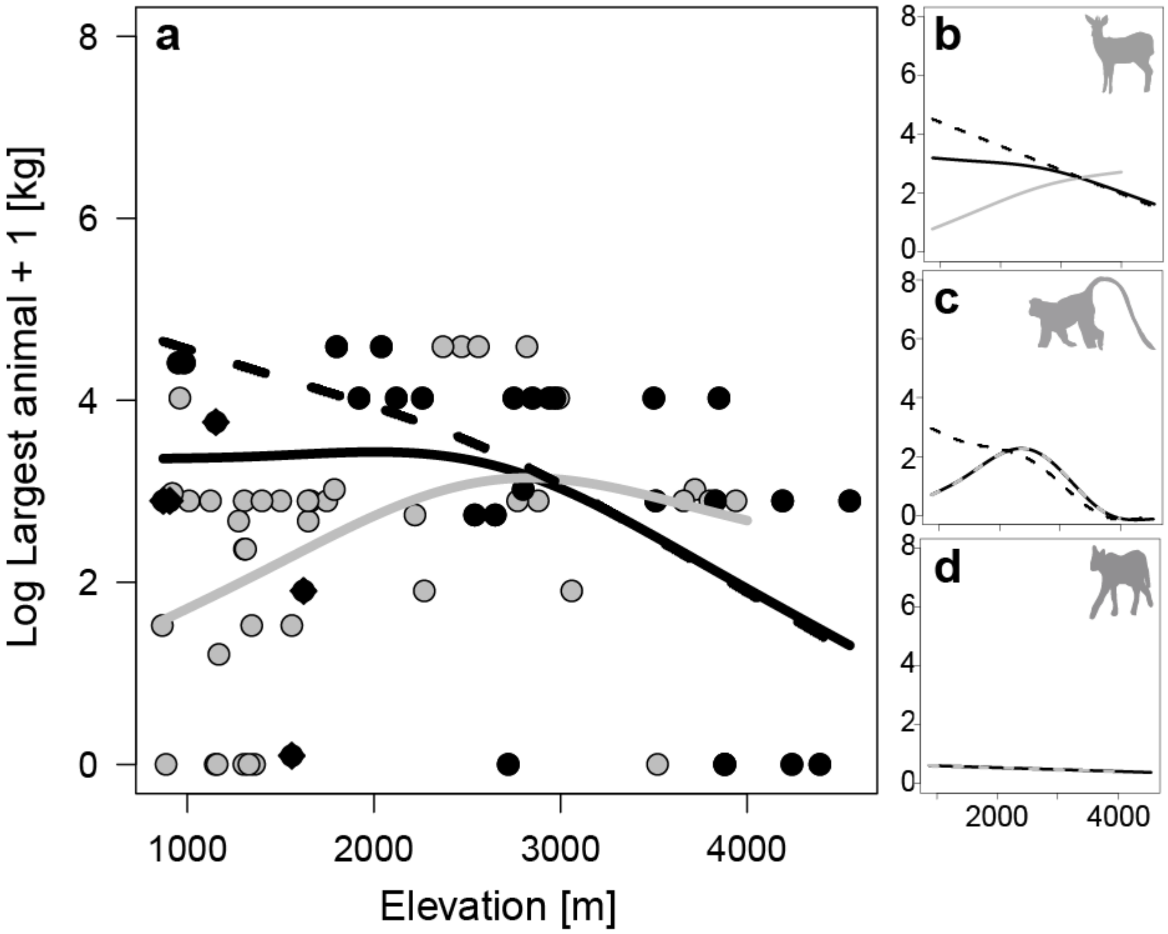
A fundamental purpose of ecology is to explain the disparate distribution of species richness around the globe. Elevational gradients, in particular, can help us to learn more about patterns in biodiversity and to locate priority areas for conservation, particularly in times of climate change and intense human land use. Our study shows that there is not a single factor influencing mammal diversity and community biomass along an elevational gradient. Rather, there are several not mutually exclusive factors, i.e. net primary productivity and, to a lesser degree, land area and temperature, which determine elevational diversity of large mammals in natural habitat on tropical mountains. Our study also emphasizes the importance of protected areas for the preservation of large mammals. 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.

Supplementary information

Supplementary Table IV. 1: 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* forest	5	anthropogenic	2270-3060	low
Erica forest	5	natural	3500-3900	none
burned *Erica* forest	5	anthropogenic	3500-3880	low
Helichrysum vegetation	5	natural	3880-4550	none

[1] Elevation is shown in m asl.



Supplementary FIG. IV. 1: 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 ($P_{interaction} < 0.05$, ED = 23.8%). When only protected areas were considered, the size of animals increased at low elevation sites ($P_{interaction} < 0.05$, ED = 25.3%). **(b)** Likewise, herbivores were larger in natural than in anthropogenic habitats ($P_{interaction} < 0.05$, ED = 24.7%). Again, animals were larger at low elevations when only protected habitats were taken into consideration ($P_{interaction} < 0.001$, ED =

27%). **(c)** The largest omnivores showed the same unimodal distribution for both natural and anthropogenic habitats ($P_{elevation} < 0.001$, ED = 28.5%). In protected areas, the size of omnivores increased at low elevation sites. ($P_{interaction} < 0.05$, ED = 40.3%). **(d)** Regarding carnivores, there was no relationship between the distribution of the largest mammals and elevation ($P_{interaction} = 0.54$, ED = 0.6 %).

Chapter V: General Discussion

This thesis comprises the study of invertebrate (Chapter III) and vertebrate herbivore (Chapter IV) taxa and the related ecosystem function [i.e. herbivory; (Chapter II)] conducted along a large elevational gradient on a tropical mountain (Mt. Kilimanjaro).

Patterns and drivers of community-level invertebrate herbivory (Chapter II)

Findings revealed an unimodal pattern of the total community-level invertebrate herbivory in natural habitats and the pattern strongly contrasted with the pattern detected in anthropogenic habitats. The unimodal pattern of total herbivory detected in natural habitat is congruent with our hypothesis suggesting that herbivory peaks at mid-elevations due to high levels of net primary productivity. Most of the East African Mountains experience the highest rainfall and most stable environmental conditions at mid-elevations and not at lower elevations as it may be the case in other regions (Garibaldi et al. 2011, Galmán et al. 2018). It is further stated that, at mid-elevations where resource-rich habitats (i.e. lower montane forests) are found at Mt. Kilimanjaro, it is likely that high plant growth rates and low investments in plant defense promote leaf herbivory (Coley et al. 1985). Alternatively, in resource-poor habitats where plants nutritional quality is lower (e.g. at higher elevations) due to lower nitrogen content and higher concentrations of plant defense compounds (e.g. at low elevations) herbivory is low (Coley et al. 1985, Pellissier et al. 2016, Abdala-Roberts et al. 2016).

Interestingly, in anthropogenic habitats we detected a bimodal pattern of leaf herbivory along the elevation gradient which was strongly contrasting to the patterns found in natural habitats; the first peak was detected at lower elevations, in the elevational zone dominated by maize fields and the second peak at mid-elevations in selectively logged *Ocotea* forests. The first peak and a subsequent decline in total herbivory (and for leaf chewers) at lower elevations in anthropogenic habitats could be connected to applications of N and P-rich fertilizers in the maize fields which could have increased leaf nitrogen concentration thus reduce CN ratio and increase NP ratio. Additionally, we found that the second peak which was detected at mid-elevations in anthropogenic habitats slightly shifted towards higher elevations relative to the peak in natural habitats. The finding of contrasting patterns in ecosystem functions in anthropogenic versus natural habitats demonstrates empirically the significance of anthropogenic effects in shaping the structure and functioning of mountain ecosystems and calls for conservation measures which are responsive to and incorporate human dimensions. As anthropogenic pressure on resources found in mountain ecosystems is increasing (Nogués-Bravo et al. 2008), this interdependence might limit our ability to detect macroecological patterns in the future.

On the other hand, findings also show that levels of herbivory were consistently lower (except for leaf miners) in anthropogenic habitats than in natural habitats. Variation in the patterns and levels of herbivory between natural and anthropogenic habitats not only provides useful insights which deepen our understanding of the ecological patterns but also underscores the need for future studies to take into account such differences in order to provide precise recommendations for policy formulation. Among feeding guilds, leaf chewers showed a disproportionally higher herbivory than leaf miners and leaf gallers finding which is consistent with other studies (Garibaldi et al. 2011, Andrew et al. 2012, Souza et al. 2013). However, most of these studies measured herbivory from a single host plant species rather than that of plant communities (Garibaldi et al. 2011, Souza et al. 2013).

Path analysis revealed that leaf traits (NP and CN ratios) were the strongest predictors of leaf herbivory in natural and anthropogenic habitats. However, the strength of their effect was diluted by the addition of a dataset from anthropogenic habitats. Rooted from this finding, it can be concluded that the increased human dependence on natural ecosystems is likely to alter concentration and composition of phytochemical traits and consequently alter biotic interactions and ecological patterns. Several studies have also shown the importance of leaf traits in determining herbivory (Poorter et al. 2004, Garnier et al. 2007, Galmán et al. 2018). However, these studies did not demonstrate simultaneously variation in the effect of phytochemical traits on community-level herbivory between natural and anthropogenic habitats. Here we have clearly shown that treating anthropogenic and natural habitats separately is critical for improving our understanding of the ecological phenomenon and formulating effective conservation and land use measures.

On the other hand, findings also revealed a strong influence climate has in mediating the effect of leaf traits on herbivory through NPP. Studies conducted in the similar ecosystem on other ecological functions have also the influence of climate in mediating biotic interactions other than herbivory (Classen et al. 2015, Peters et al. 2016). The detected strong interdependence between leaf herbivory and climate suggest that biotic interactions, energy and nutrient fluxes in terrestrial ecosystems are likely to be altered as a global climate is changing. We found that climate had a rather stronger effect in mediating leaf herbivory when we used a dataset from natural habitats than when we used a dataset combining data from natural and anthropogenic habitats. This finding provides an important insight that conducting studies without considering idiosyncrasy of the study system (e.g. using a dataset combining data from anthropogenic and natural habitats) may impede our ability to understand mechanisms underlying macroecological patterns and provide effective recommendations. Furthermore, findings highlight the expected climatic changes will likely have a more ecological effect on natural ecosystems than on human-dominated ecosystems.

Patterns and drivers of species diversity of phytophagous beetles (Chapter III)

Findings revealed that species diversity of the overall phytophagous beetles depicted a bimodal pattern which tendentially declined along the elevation gradient. A similar pattern was also detected by the most dominant beetle group in our study, the leaf beetles (Chrysomelidae).

Similar patterns exhibited by the phytophagous beetles have also been detected in spiders and some plant groups along the same elevation gradient (Peters et al. 2016). Interestingly, a pattern exhibited by weevils (Curculionidae) – the second largest group in our study was dissimilar to the patterns exhibited by leaf beetles. Based on the findings, it can be concluded that patterns and so the drivers of species diversity may vary within and between families. The patterns we detected were largely associated with high resource abundance and high resource diversity at mid-elevations. However, findings revealed some unique modification on the hump-shaped pattern which is associated with microclimatic conditions of the lower montane forests. Some studies have shown that modifications to the widely documented species diversity patterns are possible (Rahbek 2005, Nogués-Bravo et al. 2008), however, these studies focused on the scale effect rather than the effect of microhabitats (and associated microclimates) in shaping macroecological patterns. This finding underscores the importance of microclimatic conditions of microhabitats in determining species diversity and macroecological patterns in complex ecosystems.

Apart from species diversity patterns, path analysis revealed that temperature and climate-mediated changes in food resources abundance and diversity were the strongest predictors of species diversity of phytophagous beetles. Several studies have also shown the relevance of resources abundance and temperature in determining species diversity. Furthermore, reports have shown that there is a strong relationship between resource availability and species diversity (Mittelbach et al. 2001, Šímová et al. 2013, Brown 2014), however, mechanisms through which food resources influence species diversity are still unclear (Rosenzweig 1992, Mittelbach et al. 2001). Unlike many studies investigating this relationship, we have disentangled mechanisms through which food resources can affect species diversity, i.e. through food resource diversity and food resource abundance rather than by food quality. This approach and the finding thereof are of importance in improving our understanding of the mechanisms determining biodiversity patterns. Available evidence also suggests that it is possible to have a high abundance of resources but low species diversity (Rosenzweig 1992, Brown 2014, Classen et al. 2015), suggesting that high resource abundance by itself is not a sufficient explanation to account for species diversity in every scenario. Conversely, accumulating evidence suggests that temperature is also an important predictor of species diversity through its effect on speciation and evolution (Classen et al. 2015, Rabosky et al. 2018), resource production (Brown 2014) and biotic interactions (Schemske et al. 2009). Evidence suggests that temperature can also influence species diversity by regulating resources consumption (Classen et al. 2015).

Patterns and drivers of species richness and community biomass of large wild mammals (Chapter IV)

Findings revealed that overall wild mammals depicted the unimodal pattern of species richness and community biomass along elevation gradients and no significant variation in the pattern was detected between natural and anthropogenic habitats. We associated the unimodal pattern of species richness and community biomass of large mammals with high resource abundance on the montane forest (at. ca. 2500m asl). On the other hand, path analysis revealed that resource abundance and level of habitat protection were the strongest predators of species richness and community biomass patterns of large wild mammals. Our findings suggest that overall species richness and community biomass are likely driven by anthropogenic pressure on wildlife resources particularly, at lower elevations.

However, patterns depicted by individual guilds showed clearly that impact of human pressure among guilds is non-uniform as reported in other studies (Helbig-Bonitz et al. 2015). Unlike omnivores (arboreal) most of which find a suitable habitat and food resources in the lower mountain forests, herbivores species richness and community biomass were higher in natural and protected areas located at lower elevations where savanna ecosystem is found. Higher herbivore richness at lower elevations (despite high poaching risk) is possibly due to higher high resource abundance particularly for large-bodied herbivores per unit area in savannah ecosystem than in montane forest ecosystems. Conversely, lack of clear patterns for carnivores' species richness and community biomass in all habitats is probably due to their behavior (i.e. feeding habit, relatively large home ranges and nocturnal lifestyle in which their peak active time mismatch that of humans) and thus face a limited direct risk through illegal hunting. It is also important to note that traditionally local communities around Mt. Kilimanjaro do not eat meat from carnivorous animals unlike other regions in Tanzania or Africa, suggesting that culture and traditions might play an important role in shaping species richness and community biomass patterns of carnivore guild.

As anthropogenic pressure (through illegal hunting and logging, livestock grazing, habitat conversion through agriculture) on mountain ecosystems is mounting towards higher elevations (Nogués-Bravo et al. 2008), it is likely that patterns of species richness and community biomass are likely to be modified in the future. Evidence from other studies suggests that increased human pressure on mountain ecosystems is becoming a global trend (Körner 2004, Nogués-Bravo et al. 2008). Our findings have clearly demonstrated that anthropogenic activities pose a great threat to biodiversity and associated ecosystem functions; however, it appears that sensitivity to these threats varies between feeding guilds. We call for conservation action which promotes the protection of species-rich lowland habitats

General conclusions

Altitudinal gradients represent a robust model system through which several ecological phenomena and hypotheses can be learned and tested, respectively. Unlike latitudinal gradients, elevational gradient studies allow the use of standardized methods and only one observer can work in different climates; a situation which ensures high data quality. Our study demonstrated the importance of elevational gradients in developing our understanding of the mechanisms underlying patterns of species diversity and ecosystem functions such as herbivory. Generally, our findings concur with a view that establishing an overall pattern for macroecological patterns along elevation gradient is a challenge (Andrew et al. 2012, Galmán et al. 2018). Findings showed empirically that patterns exhibited by ectotherms or by individual guilds rarely predict patterns exhibited by endotherms or by overall macroecological patterns, respectively. Similarly, I have demonstrated that patterns exhibited in natural (or protected) habitat seldom mirror patterns exhibited in anthropogenic (or unprotected) habitat and that, mixing of the two datasets diluted the predictability of models. I recommend treating idiosyncratic study systems separately in order to improve our understanding of the mechanisms driving macroecological patterns and provide well-defined recommendations for policy formulation. Findings from path analysis demonstrated that herbivore diversity, community biomass, and herbivory are strongly influenced by climate (either directly or indirectly). Therefore, predicted climatic changes are expected to strongly modify ecological patterns, biotic interactions, and energy and nutrient fluxes in terrestrial ecosystems in the coming decades with more impacts probably felt by natural ecosystems. On the other hand, this analytical method has enabled us to improve our understanding by disentangling and unearthing some indirect mechanisms driving ecological relationships which would otherwise not detected.

It is now evident that humans have strongly modified the tropical mountains in nearly all parts of the world and their pressure is advancing towards more intact habitats at higher elevations. Our findings indicate that this may have strong impacts on ecosystem functions and diversity, particularly of large mammals. I recommend conservation measures which will increase protection in species-rich areas and those measures should be responsive to and incorporate human dimensions to curb the situation. Despite some ecological challenges, it appears that Mt. Kilimanjaro ecosystem remains to be one of the world's strongholds of biodiversity and important refuge area for many species. Therefore, its conservation is of paramount importance and conservation measures should not only focus on protected habitats but also extend to conserving species-rich habitats in the lowland unprotected habitats with attention given to guild-specific requirements.

Although findings emanate from observational studies which have to take into account several confounding factors, they have managed to reveal patterns and drivers in real-world near-natural settings and ecosystems with fully established organisms' communities and a wide range of biotic interactions which are unlikely to be captured in artificial experiments. Elevational studies in more areas of the world, combined with experiments, to better understand natural processes operating on mountains and their sensitivity to the on-going global changes. Future studies addressing the effects of top-down forces by natural enemies (predators) on herbivore diversity and invertebrate herbivory would deepen our understanding of the mechanisms behind macroecological patterns along elevation gradients.

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Authors' contributions

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Publication list

Articles connected to the thesis

Henry K. Njovu, Marcell K. Peters, David Schellenberger Costa, Roland Brandl, Michael Kleyer, Ingolf Steffan-Dewenter. Leaf traits mediate changes in invertebrate herbivory along broad environmental gradients on Mt. Kilimanjaro, Tanzania. ***Submitted to the Journal of Animal Ecology: Ref # JAE-2018-00420***

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Other articles

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Curriculum Vitae