DIVERSITY, TRAITS AND ECOSYSTEM SERVICES OF POLLINATORS ALONG CLIMATE AND LAND USE GRADIENTS ON MOUNT KILIMANJARO

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„Das schönste Glück des denkenden Menschen ist,
das Erforschliche erforscht zu haben und das Unerforschliche ruhig zu verehren.“

Johann Wolfgang von Goethe

TABLE OF CONTENTS

Ehrenwörtliche Erklärung 7

Summary 9

Zusammenfassung (German) 13

Chapter I: General Introduction 17

Chapter II: Temperature versus resource constraints: which factors determine bee diversity on Mt. Kilimanjaro, Tanzania? 27

Supplementary data to Chapter II 41

Chapter III: To be small and cold or large and hungry: trade-offs in bee body size along climatic gradients 47

Supplementary data to Chapter III 53

Chapter IV: Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields 59

Supplementary data to Chapter IV 71

Chapter V: General discussion 77

References 85

Author contributions 97

Acknowledgements 101

Publication list 103

Curriculum Vitae 105

EHRENWÖRTLICHE ERKLÄRUNG

Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation mit dem Titel “Diversity, traits and ecosystem services of pollinators along climate and land use gradients on Mount Kilimanjaro“ eigenständig, ohne Hilfe einer kommerziellen Promotionsberatung und unter der Anleitung und Betreuung durch Herrn Prof. Dr. Ingolf Steffan-Dewenter am Lehrstuhl für Tierökologie und Tropenbiologie (Zoologie III) der Julius-Maximilians-Universität Würzburg angefertigt habe und dabei keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet habe. Die vorliegende Dissertation hat weder in gleicher, noch in ähnlicher Form bereits in einem Prüfungsverfahren vorgelegen. Des Weiteren habe ich außer den mit dem Zulassungsantrag urkundlich vorgelegten Graden keine weiteren akademischen Grade erworben oder zu erwerben versucht.

Würzburg, den 29.07.2014

Alice Claßen

SUMMARY

Since more than two centuries naturalists are fascinated by the profound changes in biodiversity observed along climatic gradients. Although the theories explaining changes in the diversity and the shape of organisms along climatic gradients belong to the foundations of modern ecology, our picture on the spatial patterns and drivers of biodiversity is far from being complete. Ambiguities in theory and data are common and past work has been strongly concentrated on plants and vertebrates. In the last two decades, interest in the fundamental processes structuring diversity along climatic gradients gained new impetus as they are expected to improve our understanding about how ecosystems will respond to global environmental changes. Global temperatures are rising faster than ever before; natural habitats are transformed into agricultural land and existing land use systems get more and more intensified to meet the demands of growing human populations. The fundamental shifts in the abiotic and biotic environment are proclaimed to affect ecosystems all over the world; however, precise predictions about how ecosystems respond to global changes are still lacking. We investigated diversity, traits and ecosystem services of wild bees along climate and land use gradients on Mount Kilimanjaro (Tanzania, East Africa). Wild bees play a major role in ecosystems, as they contribute to the reproduction and performance of wild and crop plants. Their responsiveness to environmental changes is therefore of high ecological and economic importance.

Temperature and energy resources have often been suggested to be the main determinants of global and local species richness, but the mechanisms behind remain poorly understood. In the study described in chapter II we analyzed species richness patterns of wild bees along climate and land use gradients on Mount Kilimanjaro and disentangled the factors explaining most of the changes in bee richness. We found that floral resources had a weak but significant effect on pollinator abundance, which in turn was positively related to species richness. However, temperature was the strongest predictor of species richness, affecting species richness both directly and indirectly by positively influencing bee abundances. We observed higher levels of bee-flower-interactions at higher temperatures, independently of flower and bee abundances. This suggests that temperature restricts species richness by constraining the exploitation of resources by ectotherms. Current land use did not negatively affect species richness. We conclude that the richness of bees is explained by both temperature and resource availability, whereas temperature plays the dominant role as it limits the access of ectotherms to floral resources and may accelerate ecological and evolutionary processes that drive the maintenance and origination of diversity.

Not only species numbers, but also morphological traits like body size are expected to be shaped by both physiological and energetic constraints along elevational gradients. Paradoxically, Bergmann´s rule predicts increases of body sizes in cooler climates resulting from physiological constraints, while species-energy theory suggests declines in the mean body size of species caused by increased extinction probabilities for large-bodied species in low-energy habitats. In chapter III we confronted this ambiguity with field data by studying community-wide body size variation of wild bees on Mt. Kilimanjaro. We found that along a 3680 m elevational gradient bee individuals became on average larger within species, while large species were increasingly absent from high-elevational communities. This demonstrates, on the one hand, how well-established, but apparently contrasting ecological theories can be merged through the parallel consideration of different levels of biological organization. On the other hand it signals that the extinction risk in the course of environmental change is not equally distributed among species within a community.

Land use intensification is known to threaten biodiversity, but the consequences for ecosystem services are still a matter of debate. In chapter IV, we experimentally tested the single and combined contributions of pest predators and pollinators to coffee production along a land use intensification gradient on Mount Kilimanjaro. We found that pest predation increased fruit set by on average 9%, while pollination increased fruit weight of coffee by on average 7.4%. Land use had no significant effect on both ecosystem services. However, we found that in coffee plantations with most intensified land use, pollination services were virtually exclusively provided by the honey bee (*Apis mellifera*). The reliance on a single pollinator species is risky, as possible declines of that species may directly lower pollination services, resulting in yield losses. In contrast, pollination services in structurally complex homegardens were found to be provided by a diverse pollinator community, increasing the stability of pollination services in a long term.

We showed that on Mount Kilimanjaro pollinator communities changed along elevational gradients in terms of species richness (chapter II) and trait composition (chapter III). Temperature and the temperature-mediated accessibility of resources were identified as important predictors of these patterns, which contributes to our fundamental understanding about the factors that shape ectothermic insect communities along climatic gradients. The strong temperature-dependence of pollinators suggests that temperature shifts in the course of global change are likely to affect pollinator communities. Pollinators might either profit from rising temperatures, or shift to higher elevations, which could result in related biotic attrition in the lowland with consequences for the provision of ecosystem services in cropping systems. Up to now, land use intensification had no significant impact on the diversity of pollinator communities and their ecosystem services. Pollinators might profit from the strong landscape heterogeneity in the region and from the amount of flower resources in the understory of cropping systems. However,

progressing homogenization of the landscape and the pronounced application of pesticides could result in reduced diversity and dominance of single species, as we already found in sun coffee plantations. Such shifts in community compositions could threaten the stability of ecosystem services within cropping and natural systems in a long term.

ZUSAMMENFASSUNG (GERMAN)

Die Biodiversität auf der Erde ist nicht gleichmäßig verteilt, sondern verändert sich entlang klimatischer Gradienten – ein Phänomen, das Naturwissenschaftler schon seit mehr als zwei Jahrhunderten fasziniert. Über die Mechanismen, welche die Verteilung von Arten entlang von Klimazonen bestimmen, besteht nach wie vor keine Einigkeit, auch wenn viele der hier hervorgebrachten Theorien zu den Grundlagen der modernen Ökologie gehören. Ambivalenzen in den Erklärungsmodellen und erhobenen Daten sind häufig und bisherige Studien konzentrierten sich vorrangig auf Pflanzen und Vertebraten, während andere Taxa weniger Beachtung fanden. Die Unsicherheit über die Auswirkungen des globalen Wandels auf Ökosysteme und die Konsequenzen für Ökosystemdienstleistungen setzte neue Impulse im Bereich der Biodiversitätsforschung. Temperaturen steigen so schnell wie nie zuvor; natürliche Habitate werden zunehmend in Agrarflächen umgewandelt und bestehende Landwirtschaftssysteme werden intensiviert. Präzise Vorhersagen darüber, wie Ökosysteme auf solch drastische Umweltveränderungen reagieren, fehlen jedoch weitgehend.

In dieser Dissertation wird gezeigt, wie sich die Artenvielfalt, morphologische Merkmale und Ökosystemfunktionen von Bienen entlang von Klima- und Landnutzungsgradienten des Kilimandscharos (Tansania, Ostafrika) verändern. Bienen spielen eine wichtige Rolle in Ökosystemen, da sie als Bestäuber zur Reproduktion und Produktivität von Wild- und Nutzpflanzen beitragen. Die Veränderung ihres Artenreichtums, ihrer Merkmale und ihrer Ökosystemdienstleistungen entlang von Umweltgradienten ist somit von großer ökologischer und ökonomischer Relevanz.

Temperatur und die Verfügbarkeit von Ressourcen sind die Faktoren, mit denen globale und lokale Muster von Diversität am häufigsten erklärt werden. Die kausalen Zusammenhänge über welche die Temperatur und die Verfügbarkeit von Ressourcen eine Erhöhung der Artenvielfalt bewirken, sind jedoch nach wie vor unklar. Im zweiten Kapitel dieser Arbeit wurde untersucht, wie sich der Artenreichtum von Bienen entlang von Klima- und Landnutzungsgradienten des Kilimandscharos verändert und welche Faktoren für diese Veränderungen verantwortlich sind. Blühressourcen hatten einen schwachen, aber signifikanten Einfluss auf die Bestäuberabundanzen, welche wiederum einen Großteil des Artenreichtums erklärten. Insgesamt hatte die Temperatur jedoch einen deutlich stärken Einfluss auf die Artenvielfalt als die Verfügbarkeit von Blühressourcen: Die Temperatur wirkte sich direkt, möglicherweise über einen Erhöhung von Speziationsraten, und indirekt, über eine Erhöhung der Bienenabundanz, auf die Artenvielfalt von Bienen aus. Zusätzlich konnte beobachtet werden, dass die Blütenbesuche von Bienen unabhängig von der Blütendichte und der Bienenabundanz, mit einem Anstieg der

Temperatur zunahmen. Aus diesen Beobachtungen folgern wir, dass bei Ektothermen die Nutzbarkeit von Ressourcen durch die Temperatur gesteuert sein könnte.

Die Untersuchung morphologischer Merkmale entlang von Umweltgradienten erlaubt es, deterministische von stochastischen Prozessen bei der Zusammensetzung von Artengemeinschaften zu unterscheiden. Während bei stochastischen Prozessen Merkmale entlang von Umweltgradienten zufällig aus Artengemeinschaften ausscheiden sollten, wird im Falle deterministischer Prozesse ein gerichtetes Muster erwartet. Unter den deterministischen Prozessen konkurrieren bezüglich der Körpergröße zwei scheinbar konträre Theorien: Während die Bergmannsche Regel vorhersagt, dass große Tiere, aufgrund eines verbesserten Oberflächen-Volumen-Verhältnisses, einen Vorteil in kühlen Regionen haben, weist die Arten-Energie-Theorie größeren Arten eine erhöhte Aussterbewahrscheinlichkeit in energielimitierten, kühlen Gebieten zu, so dass die mittlere Körpergröße von Lebensgemeinschaften bei kälterer Temperatur sinken sollte. Im dritten Kapitel dieser Dissertation untersuchten wir, ob sich morphologische Merkmale von Wildbienen mit zunehmender Höhe verändern. Dabei betrachteten wir nicht nur Merkmalsveränderungen innerhalb von Artengemeinschaften, sondern auch innerartliche Veränderungen. Sowohl physiologische als auch energetische Restriktionen prägten die Merkmalskompositionen, allerding auf unterschiedlichen biologischen Ebenen. So nahm die Körpergröße innerhalb von Arten mit der Höhe im Durchschnitt zu (=Bergmannsche Regel), während auf Gemeinschaftsebene kleinere Arten die Hochgebirgsregionen dominierten (=energetische Restriktion). Die parallele Betrachtung der intra- und interspezifischen Ebene ermöglichte es uns, scheinbar konträre ökologische Theorien zusammenzuführen. Zudem konnten wir zeigen, dass Merkmale nicht zufällig, sondern gerichtet aus Artengemeinschaften gefiltert werden.

Landnutzungsintensivierung bedroht Biodiversität, aber die Konsequenzen für Ökosystemdienstleistungen sind nach wie vor ungewiss. Im vierten Kapitel dieser Arbeit prüften wir mit Hilfe von einzelnen und kombinierten Bestäuber- und Prädatorausschlussexperimenten, welchen Beitrag Bestäuber, Vögel und Fledermäuse in verschiedenen Anbausystemen zur Kaffeeproduktion am Kilimandscharo leisten. Wir zeigten, dass sich Bestäuber und Prädatoren in ihren Effekten ergänzten: Während Bestäuber eine Steigerung des Kaffeebohnengewichtes um durchschnittlich 7.4% bewirkten, konnte durch die Prädation von Schädlingen der Fruchtansatz des Kaffees um durchschnittlich 9% gesteigert werden. Landwirtschaftliche Intensivierung, von komplexen Waldwirtschaftssystemen, über beschattete Kaffeeplantagen, bis hin zu Sonnenplantagen hatte keinen negativen Effekt auf die Ökosystemdienstleistungen von Bestäubern und Prädatoren. Wir konnten jedoch nachweisen, dass in Waldwirtschaftssystemen eine diverse Bestäubergemeinschaft den Kaffee bestäubt, während in Sonnenplantagen fast ausschließlich die Honigbiene als Bestäuber fungiert. Eine solche Verschiebung der Bestäuberkomposition könnte die langfristige Stabilität intensiv genutzter Flächen gefährden.

In dieser Dissertation zeigten wir, wie sich Bestäubergemeinschaften am Kilimandscharo entlang von Höhengradienten bezüglich ihrer Artenvielfalt (Kapitel II) und ihrer Merkmale (Kapitel III) verändern. Temperatur und temperatur-gesteuerte Ressourcennutzbarkeit wurden als maßgebende Determinanten dieser Muster identifiziert. Damit wurde ein Beitrag zur Identifikation von Gesetzmäßigkeiten in der Verteilung ektothermer Insekten entlang von Klimagradienten geleistet. Unsere Ergebnisse weisen darauf hin, dass Klimaveränderungen im Zuge des globalen Wandels Konsequenzen für Bestäubergemeinschaften haben könnten. Eventuell könnten Bestäuber von den steigenden Temperaturen profitieren. Gleichsam könnte es aber auch zu einer Verschiebung von Bestäubern in höher gelegene Regionen und zu einem daran gekoppelten Einbruch der Bestäubungsleistungen in tiefliegenden Kulturlandschaften kommen. Im Hinblick auf die Konsequenzen anthropogener Landnutzung wurde festgestellt, dass die landwirtschaftliche Intensivierung am Kilimandscharo bisher keinen messbaren negativen Effekt auf die Ökosystemdienstleitungen von Bestäubern hatte. Die Bestäuber profitieren vermutlich von der starken Landschaftsheterogenität der Region und zahlreichen krautigen Blühressourcen im Unterwuchs von Agrarflächen. Eine zunehmende Homogenisierung der Landschaft und ein verstärkter Einsatz von Pestiziden könnten jedoch, wie auf Sonnenplantagen bereits zu finden, zu einer Dominanz von einigen wenigen Arten führen, welches zusammen mit der klimabedingten Artenverschiebung die langfristige Stabilität von Agrarsystemen und natürlichen Systemen gefährden könnte.

CHAPTER I: GENERAL INTRODUCTION

Biotic changes along climatic gradients

Since centuries it is known, that the number of species and species traits are not equally distributed on earth, but that they exhibit strong spatial variation (Bergmann, 1847; Allen, 1877; Wallace, 1878; Dobzhansky, 1950; Lomolino *et al.*, 2006). The latitudinal diversity decline from the tropics to the poles is one of the most striking patterns described in this context (Wallace, 1878; Dobzhansky, 1950; Pianka, 1966; Willig *et al.*, 2003). It is present in terrestrial, freshwater and marine ecosystems, and concerns plants, animals and microbes at nearly all levels of biological organization (Willig *et al.*, 2003). Numerous single and interacting evolutionary and ecological factors, such as evolutionary time, geographic area, biotic interactions, ambient energy or productivity have been forwarded and discussed as potential drivers of biodiversity (Krebs, 2009; Graham *et al.*, 2014), but there is still no general consensus. In the past, research was mainly focused on plants and vertebrates (Terborgh, 1977; Currie, 1991; Lomolino, 2001), which might have hampered the detection of general principles. Since two decades, the debate about the factors, shaping species and species traits along environmental gradients has gained new impetus. The world is changing and ecosystems are predicted to respond to these changes, as it can already be observed (Shaver *et al.*, 2000; Walther *et al.*, 2002). Global temperatures are rising faster than ever before; natural habitats are transformed into agricultural land, agricultural systems get more and more intensified. The identification of general principles behind species distribution patterns would improve our prediction capacities of how species and ecosystems may respond to such environmental changes in future.

On the search for principles underlying species distributions, the investigation of trait compositions within communities can be more efficient than the analysis of species numbers alone, because trait distributions require no species extinction to be responsive and can thus be used as “early-warning indicators” (Mouillot *et al.*, 2013). While random trait distributions signal simple stochastic processes determining species richness patterns, an accumulation of similar traits within communities points towards deterministic mechanisms shaping communities (Cornwell & Ackerly, 2009). A shift of trait dominances along environmental gradients can then identify potential factors shaping communities (Hoiss *et al.*, 2012) and signal which species might be most vulnerable in future (Conti *et al.*, 2013). Shifts in trait compositions can occur either through intraspecific trait shifts or through species turnover. So far, intraspecific trait shifts have either been ignored, because they were assumed to be negligible compared to interspecific trait shifts, or they were investigated within selected species, but not on a community level. However, many theoretical approaches have highlighted the importance of intraspecific variation within community ecology (Ackerly & Cornwell, 2007; Albert *et al.*, 2011; Bolnick *et al.*, 2011; Clark *et al.*, 2011; Violle *et al.*, 2012), asking for empirical proof. Indeed, few botanical studies, considering intra- and interspecific trait shifts in parallel, showed that intraspecific trait shifts can be highly relevant for understanding processes on a community level (Ashton, 2004; Kraft *et al.*, 2008; Jung *et al.*, 2010; Paine *et al.*, 2011; Hulshof *et al.*, 2013). Whether this holds also true for animals is currently unknown.

Elevational gradients – what can they tell us?

Elevational gradients are powerful tools to investigate biogeographic patterns or the impact of climate change. As each mountain is unique in its topography, climate, geology and history, potentially explanatory factors shaping species and traits can be statistically disentangled (Spehn & Körner, 2010). Elevational gradients can be used as model systems for global patterns, because many explanations for the relationship between latitude and species richness, such as the decline in temperature, hold true for both elevational and latitudinal gradients. Species range shifts over time provide interesting insights in ecosystem responses to climate change (Chen *et al.*, 2011). However, for many taxonomic groups and regions, especially in Africa, reliable and standardized baseline data are often lacking. Also, incomplete sampling along elevational gradients in combination with interpolation of species ranges, can bias species richness patterns, which has often been ignored (Grytnes & Vetaas, 2002).

Some prominent differences complicate the transferability between elevational and latitudinal gradients: Most obvious, along elevation temperature drops about thousand times stronger than along latitude (about 5.5°C per 1000 m in altitude), which makes upslope shifts of species in the course of global warming more likely than poleward shifts, because species are less limited by dispersal constraints. Also land area declines rapidly: Above the tree line the global land area is on average halved every further 167m of elevation (Körner, 2007), which can have strong impact on communities, as predicted by the species-area-relationship (MacArthur & Wilson, 1967; Lomolino, 2000). The length of daytime, affecting generation times and growth rates of many plants and animals is stable along elevation, but not along latitudes. Increased radiation with elevation pronounces the differences between surface and atmospheric temperature and thus promotes the presence of surprisingly warm microhabitats in high elevations compared to high latitudes (Mani, 1968). On mountains the atmospheric pressure decreases and with this the partial pressure of atmospheric gases, challenging the metabolic and growth rates of animals (Dillon, 2006). Reduced air density can negatively affect the flight performance of many insects or at least raise the energetically costs for flight (Dillon, 2006). Thus, elevational gradients can help us to understand which mechanisms shape species richness also on a global scale, but in some aspects they will create patterns that are unique for particular mountains.

The impact of land use and climate change on mountain biodiversity and the consequences for ecosystem functioning

Due to a high species turnover with elevation and high degrees of endemism, many mountains and especially many tropical mountains are unique biodiversity hotspots in their regions (Ricketts *et al.*, 2005). However, not least because of the reliable supply of fresh water, fertile soil and timber, mountains also became popular residential areas. Growing population densities, land use intensification and anthropogenic habitat destruction threaten biodiversity, particularly in species-rich lowlands (Soini, 2005; Nogués-Bravo *et al.*, 2008). The conversion of structurally complex natural habitats into structurally simplified farmland enhances erosion and reduces the number of stable food resources and nesting sites (Newton, 1994; Nicholls & Altieri, 2012). Habitat fragmentation and human activity disturbs mating and breeding activity of birds, reptiles and mammals. Frequent ploughing, mechanically tillage and the application of pesticides drastically reduce the number of food resources and interrupt the life cycles of many insects (Rodenhouse *et al.*, 1995). The negative impact of land use change can obfuscate natural species richness patterns along elevational gradients and complicate their interpretation (McCoy, 1990; Nogués-Bravo *et al.*, 2008). Also the distributions of organismic traits can be affected. It has been shown that species with certain morphological or life-history traits respond more vulnerable to land use change than other species (Larsen *et al.*, 2005). The parallel consideration of climatic and land use factors is thus highly valuable, but has often been ignored.

In addition, climate is changing and is predicted to change in future at rates that are unparalleled in human history. Within the last century, the global mean surface air temperature raised between 0.56°C and 0.92°C and is predicted to further increase by up to 0.2°C per decade, depending on the region and emission scenario (Cubasch *et al.*, 2013). Considering the responsiveness of species to previous climate changes (Walther *et al.*, 2002; Perry, 2005), it is likely that anthropogenic climate change will soon be the main driver of species range shifts, functionally altered community compositions and species extinctions.

A widely discussed and empirically approached question in ecology is, whether the loss of biodiversity due to land use and climate change affects ecosystem functioning (e.g. Chapin III, 1997; Cardinale *et al.*, 2012). During the last two decades unequivocal evidence has been established that the loss of biodiversity limits ecological communities in their capacity to recycle biologically essential nutrients, to produce biomass or to capture biologically relevant resources. These biodiversity effects have been shown to be stable across different ecosystems, study organisms and trophic levels (Worm *et al.*, 2002; Cadotte *et al.*, 2008; Cardinale *et al.*, 2011). Importantly, the effect of biodiversity on ecosystem functions has been shown to be not linear but saturating, i.e. the loss of ecosystem functions accelerates with the strength of biodiversity loss. One explanation for such relation is that diverse communities contain a combinatory set of functional traits that can complement each other (Naeem, 2008; Brittain *et al.*, 2013a). In even more diverse communities the number of functionally redundant species increases. Their presence might thus not increase ecosystem function anymore, but can act as an insurance against function loss in the course of species extinction (Naeem & Li, 1997). The functioning of ecosystems can be highly profitable for human beings. Ecosystems provide food and drinking water or support nutrient cycles or crop pollination. The investigations of how environmental change can affect such ecosystem functions and related ecosystem services is thus of both ecological and economic importance.

The KiLi-Project – concept and general study design

The project „Kilimanjaro ecosystems under global change: Linking biodiversity, biotic interactions and biogeochemical ecosystem processes”, in short, the “KiLi-Project” is a DFG-funded multidisciplinary research unit (FOR1246), that aims to understand the combined effects of climate and land use change on biodiversity, biotic and biogeochemical processes and related ecosystem services. The project was launched in February 2010 and is currently in its second approved phase. It consists of seven subprojects (SP) and two central projects. The first three subprojects concentrate on climate and biogeochemical processes, including water, carbon and nutrient cycles. Subproject four and five work on plant diversity, plant performance, functional traits and vegetation dynamics. The last two projects, from which also the presented thesis derived, investigates the single and combined effects of climate and land use change on the diversity of vertebrates (birds and bats (SP6)), and invertebrates (pollinators and decomposers (SP7)) and related ecosystem services. One particularity and strengths of this project is that all seven subprojects work on the same study sites. This provides the unique possibility of powerful data syntheses, aiming to understand the consequences of climate and land use change on mountain ecosystems.

The KiLi-Project conducts its research on the southern slopes of Mount Kilimanjaro, Tanzania. Mount Kilimanjaro, with 5895 m a.s.l. the highest free-standing mountain of the world, is a stratovolcano, located 300 km south of the equator. Temperature drops 6.1°C per 1000m a.s.l.. Precipitation shows a hump-shaped distribution, with annual rainfall of approximately 500-900 mm in the lowlands, >3000 mm in the forest belt and 200 mm in the alpine zone (Hemp, 2006a). On Mount Kilimanjaro land use and habitat fragmentation mainly concentrates on the area from the lowlands up to the border of the National Park (~1800m a.s.l.). In the lowlands the majority of natural savannahs were transformed into crop fields (mainly maize, sunflowers and beans). In elevations between 1000 – 1800m a.s.l., naturally occurring low land forests have been almost completely cut and replaced by small-scale traditional agroforestry systems (Chagga homegardens), shaded or unshaded coffee plantations, grasslands or human settlements. Inside the Kilimanjaro National Park, which was established in 1973, natural ecosystems are strongly impacted by illegal and selective logging and burning. The frequency and intensity of bush fires significantly increased within the last three decades, which was associated with the increasing dryness due to global warming. Logging and bush fires lead to a severe shift in the tall subalpine forest *Podocarpus*-composition, which is then replaced by the giant heather *Erica trimera*, which further enhances the fire risk, as it burns well. The shifts in tree compositions severely effects forest´s capacity to receive rainfall and fog interception water, which impacts mountain water fluxes much stronger than the shrinking glaciers on the top of Kilimanjaro, which have become a symbol for climate change and global warming (Hemp, 2005).

The KiLi-Project works on sixty 0.25-ha study sites, with each five replicates of six natural habitat types, consisting of savannah (700 - 1100 m a.s.l.), lower montane forest (1100 - 1800 m a.s.l.), Camphor (*Ocotea*) forest (1800 - 2800 m a.s.l.), *Podocarpus* forest (2800-3200 m a.s.l.), *Erica* forest (3200 - 4000 m a.s.l.), and alpine *Helichrysum* vegetation (4000 - 4600 m a.s.l.); and six disturbed habitat types: maize fields (700-1100 m a.s.l.), traditional agroforestry systems (‘Chagga homegardens’), grasslands and shaded coffee plantations (1100 – 1800m as.), disturbed Camphor forest (1800-2800m a.s.l.), and disturbed *Podocarpus* forest (2800 – 3200m a.s.l.) (Fig. I.1, Plate I.2). For one subproject (see chapter IV) four additional study sites have been selected on sun coffee plantations (Fig. I.1).

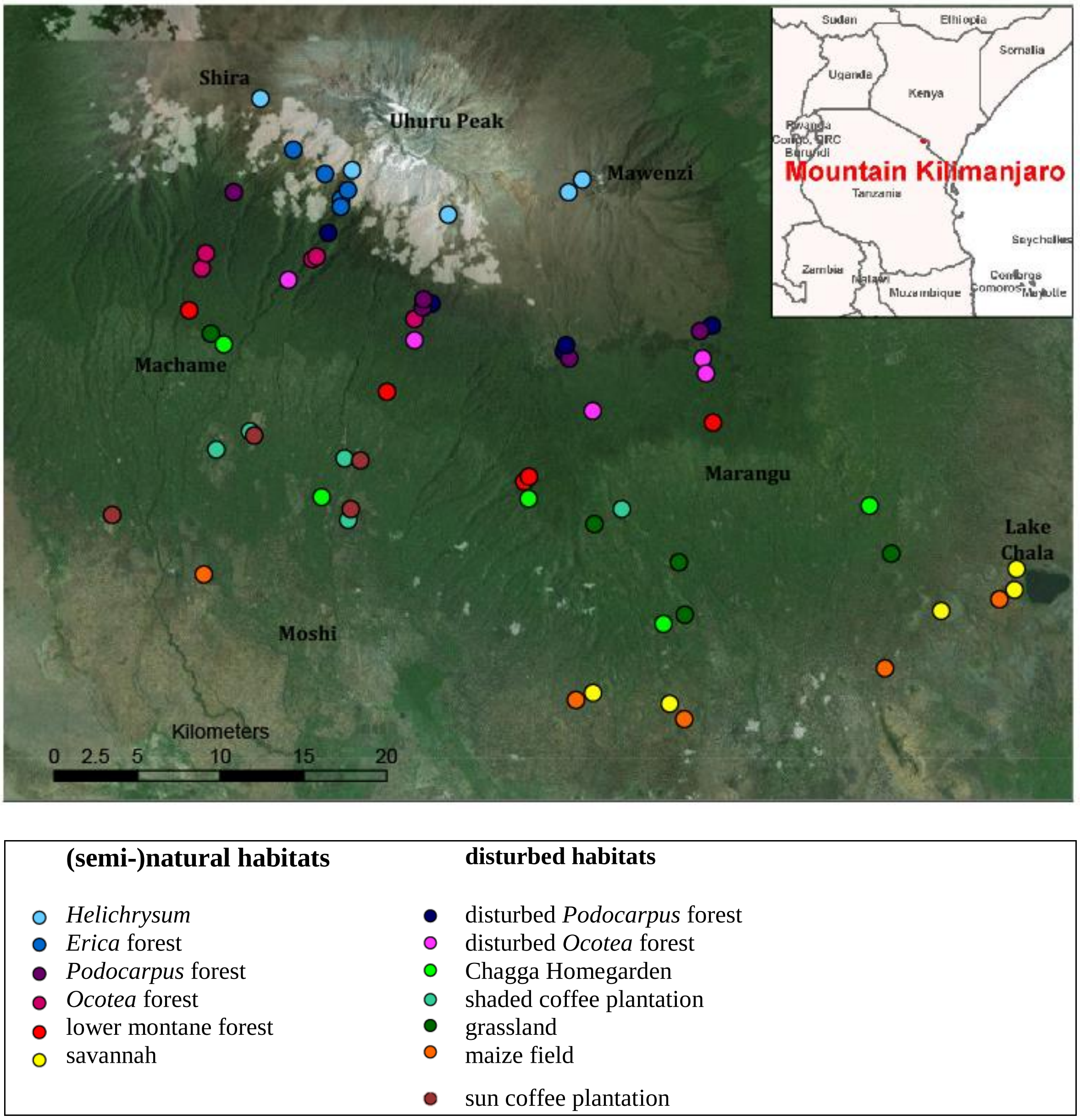


Figure I. 1 Study sites of the KiLi project. Mount Kilimanjaro is located in Tanzania, East Africa at the boarder to Kenya. Sixty 0.25-ha study sites of 12 different habitat types (+4 sun coffee plantations for a side project; see chapter IV)) were selected along an elevational gradients reaching from 870m to 4550m above sea level. Both natural (savannah, lower montane forest, *Ocotea* forest, *Podocarpus* forest, *Erica* forest, *Helichrysum*) and disturbed habitat types (maize field, coffee plantations, Chagga homegarden, grasslands, disturbed *Ocotea* forest, disturbed *Podocarpus* forest) were selected to investigate the combined effect of climate and land use change on species, traits and ecosystem functions. Background map from Bing Aearial BaseMaps®, 2014.

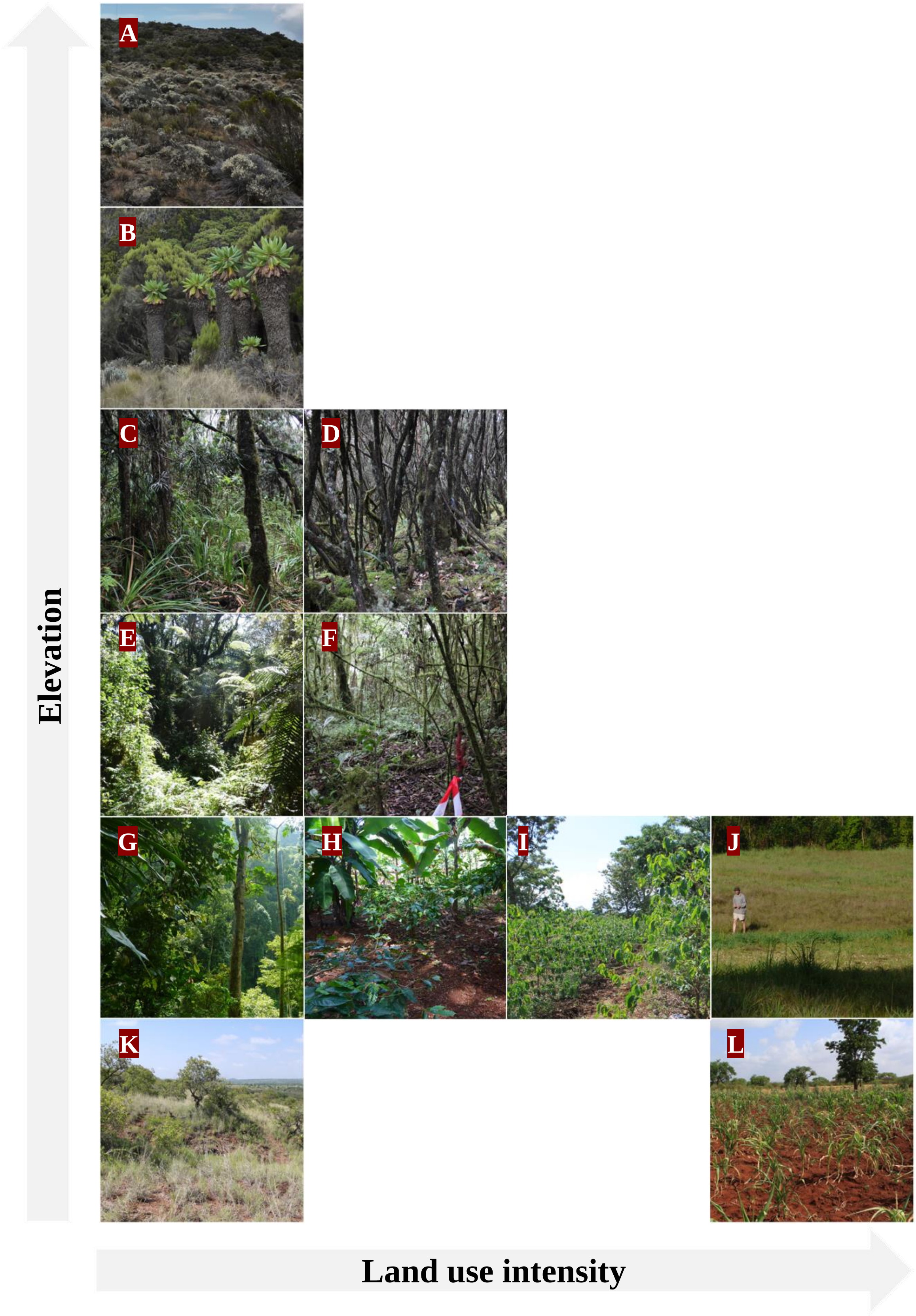
Study system

In subproject 7 of the KiLi project we investigated species richness, trait distributions and ecosystem services of pollinators along elevational and land use gradients on Mount Kilimanjaro. Around 80% of all wild plants and about two thirds of all crop species rely on - or benefit from – insect pollinators for successful reproduction, fruit quality and gene flow (Klein *et al.*, 2007). With this, pollinators do not only make an important contribution to the maintenance of plant biodiversity, fitness and their capacity to react to environmental changes, they also support crop production and maintain food security. An estimated 9.5% (i.e. 153 billion per year) of the total value of world agricultural production was assigned to pollination services (Potts *et al.*, 2010 and references in here), indicating the enormous economic impact of pollinators. Importantly, not only pollinator abundance but also pollinator diversity affects the efficiency of pollination services (Klein *et al.*, 2003). In a diverse pollinator community, different functional groups can interact with each other (Brittain *et al.*, 2013b) or spatially or temporally complement each other in their services (Hoehn *et al.*, 2008; Brittain *et al.*, 2013a; Garibaldi *et al.*, 2013), thereby increasing the pollination efficiency within an ecosystem. Climate and land use change have been reported to negatively affect pollinator diversity and pollinator vitality. Such declines threaten pollination services in both natural habitats and cropping systems. It has been shown that some pollinator species are more vulnerable to land use change than others. For instance, bumblebees with long tongues that are specialized on certain diets are stronger impacted by land use change than short-tongued bumblebees that are rather generalized (Goulson *et al.*, 2005). Understanding the mechanisms that shape pollinator communities and pollinator traits along environmental gradients is of high ecological and economic importance.

In this dissertation we assessed the diversity of important pollinators (wild bees) on the 60 study sites distributed along climatic and land use gradients. We attracted wild bees by installing pan trap clusters, each consisting of one blue, one yellow and one white UV-light reflecting trap, in different vegetation heights (Plate I.1). In chapter II we present how species richness of bees changed along climatic gradients and which factors predominantly caused these patterns. In chapter III we demonstrate how morphological trait distributions of these wild bees changed along elevational gradients on Mount Kilimanjaro. We thereby consider both inter- and intraspecific trait shifts, as physiological or energy constraints might both effect species but on a different level of biological organization. In chapter IV we present the results of a cooperation study that we conducted in close collaboration with subproject 6 of the KiLi project. Here, we analyzed how pollinators and pest predators (birds and bats) support coffee production on Mount Kilimanjaro and how their ecosystem services are effected by land use intensification.

Plate I.1 Pollinators were attracted with yellow, blue and white pan traps, which were installed in different vegetation heights. Left: Pan trap cluster installed in the canopy cover of a shaded coffee plantation (1306 m a.s.l.). Red circles mark the position in the tree, and the magnification of the trap respectively); right: Pan trap cluster installed in the herbal layer of a *Helichrysum* plot (4240 m a.s.l.).

Plate I.2 (right side) The twelve major habitat types on Mount Kilimanjaro: (A) alpine *Helichrysum* vegetation (4000 - 4600 m a.s.l.), (B) *Erica* forest (3200 - 4000 m a.s.l.), (C) *Podocarpus* forest, (D) (fire) disturbed *Podocarpus* forest (2800 – 3200m a.s.l.), (E) Camphor (*Ocotea*) forest, (F) disturbed (by former logging) Camphor forest (1800-2800m a.s.l.), (G) lower montane forest, (H) traditional agroforestry systems (‘Chagga homegardens’), (I) shaded coffee plantations, (J) grasslands, (K) savannah and (L) maize fields (700-1100 m a.s.l.).


A
B
C
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E
F
G
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Elevation
Land use intensity

CHAPTER II: TEMPERATURE VERSUS RESOURCE CONSTRAINTS: WHICH FACTORS DETERMINE BEE DIVERSITY ON MT. KILIMANJARO, TANZANIA?

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ABSTRACT

Aim *Understanding the mechanisms controlling variation in species richness along environmental gradients is one of the most important objectives in ecology. Resource availability is often considered as the major driver of animal diversity. However, in ectotherms, temperature might play a predominant role as it modulates metabolic rates and the access of animals to resources. Here, we investigate the relative importance of resource availability and temperature in determining diversity pattern of bees along a 3.6 km elevational gradient.*

Location *Mount Kilimanjaro, Tanzania.*

Methods *We assessed bee species richness and bee abundance with pan traps and floral resources with transect records on 60 study sites which were equally distributed over six near-natural and six disturbed habitat types along an elevational gradient from 870m to 4550m a.s.l. We used path analysis to disentangle the direct and indirect effects of temperature, precipitation, floral resource abundance, and bee abundance on bee species richness. In addition, we monitored flower visitation rates during transect walks at all elevations to evaluate the temperature-dependence of bee-plant interactions.*

Results *Bee species richness exponentially declined with elevation whereas bee abundance showed an inverse hump-shaped distribution along the elevational gradient. While the abundance of floral resources had a significant but only weak effect on species richness, the effect of temperature was strong. Temperature affected species richness both directly and indirectly via bee abundances. Furthermore, we observed higher levels of bee-plant-interactions at higher temperatures, independent of flower and bee abundances, supporting the hypothesis that temperature limits diversity by constraining the resource-exploitation in ectotherms.*

Main conclusions *Bee species richness is explained by both temperature and resource availability. Temperature plays the more important role, presumably by limiting access of* *ectotherms to resources and by accelerating ecological and evolutionary processes that drive the maintenance and origination of diversity.*

Key words: Apoidea, elevational gradients, productivity-hypothesis, physiological-tolerance hypothesis, energy-richness hypothesis, temperature-speciation hypothesis, pollination, climate change, land use change, macroecology

INTRODUCTION

Elevational gradients in species richness belong to the best described patterns in ecology, but the causal mechanisms behind the patterns remain poorly understood (Rahbek, 1995; Lomolino *et al.*, 2006; McCain & Grytnes, 2010). A variety of deterministic hypotheses have been forwarded emphasizing the impact of history, climatic factors and energy availability on global and regional biodiversity patterns (Dobzhansky, 1950; Pianka, 1966; Srivastava & Lawton, 1998; McCain, 2007; Brown, 2014). However, the operation modes of such environmental factors, influencing species richness patterns either directly or indirectly, are often unclear, hampering predictions about the impact of environmental changes on biodiversity.

One of the most frequently discussed predictors for species richness is resource availability (Brown & Maurer, 1989; Gillman & Wright, 2006; Ferger *et al.*, 2014; Hurlbert & Stegen, 2014). In highly productive ecosystems, resources are expected to be available in amounts that allow on average more and larger populations to persist. As the individual population’s probability of demographic extinction is a negative decelerating function of its abundance (Lande, 1993; Srivastava & Lawton, 1998), more and larger populations may persist under high than under low levels of resource availability. Primary productivity has often been used as a proxy for energy or resources, when explaining latitudinal and elevational animal diversity patterns (Hawkins *et al.*, 2003). Rarely, species richness patterns were directly related to the resources that are effectively used by the investigated organisms. Studies relating the species richness of endothermic taxa to the availability of resources repeatedly found strong positive relationships (Ferger et al. 2014, Price et al. 2014).

However, in ectothermic organisms the amount of potentially available resources in the environment does not necessarily correspond to the amount of energy accessible to organisms. Instead, ambient temperature may determine how much of the principally available resources can effectively be used (Kaspari *et al.*, 2000): Energy consumption of foraging honeybees has been shown to decrease by >80% over a temperature gradient of 25°C (Stabentheiner *et al.*, 2003). Consequently, assuming same levels of resource densities, the net-profit of foraging animals declines with decreasing temperatures. Ectothermic organisms respond to this by restricting foraging to temperatures above a certain threshold (Willmer, 1983), so that cumulative foraging times and the net energetic intake may be higher in warm than in cold environments. Such temperature-mediated resource-exploitation limitations should result in shrinking population densities and increasing the probabilities of species extinction in cooler climates.

Temperature is also known to have a direct effect on species richness (Sanders *et al.*, 2007). First, only a few species are expected to physiologically tolerate the harsh and cold climates of high-elevation or high-latitude habitats (Currie, 1991). Second, temperature may directly act on speciation rates, by e.g. curtailing generation times or increasing metabolic rates and related nucleotide substitutions (Laird *et al.*, 1969; Gillooly *et al.*, 2005).

Wild bees play a key role in natural and agricultural ecosystems as they maintain the reproduction, gene flow and diversity of wild plants, boost crop production and stabilize food security (Garibaldi *et al.*, 2011; Albrecht *et al.*, 2012; Brittain *et al.*, 2013a). Understanding the underlying mechanisms that shape bee richness is thus of high ecological and economic importance. We analyzed species richness of wild bees (Hymenoptera: Apoidea, “Apiformes”) and the potential drivers of species richness in natural and disturbed habitats along climatic gradients on Mount Kilimanjaro (Tanzania, East Africa). Using path analysis we separated the direct and indirect effects of temperature, floral resources and bee abundances on bee species richness. As precipitation, primary productivity and land use may alter the amount of floral resources, bee abundances and/or bee richness we included these variables in our path model and tested the following hypotheses (Fig. II.1):

1. *Resource-availability-hypothesis*: Resource availability is directly limiting to bee species richness as larger populations with lower extinction risk can be sustained in habitats with high amounts of resources. We therefore expect to find a positive effect of flower abundance on bee richness via a positive effect on bee abundance.

2. *Temperature-mediated-resource-exploitation-hypothesis*: In ectotherms, temperature is limiting to the amount of resources which can effectively be exploited. Under warm temperatures bee foraging activity and the net energy gain is higher than under cold temperatures, resulting in higher bee abundances. We therefore expect to find a positive effect of temperature on bee richness via a positive effect on bee abundances.

3. *Temperature-speciation-hypothesis*: Temperature limits the occurrences of species due to physiological constraints and/or by its impact on speciation rates. We therefore expect to find a direct effect of temperature on bee richness, which is not mediated by bee abundances.

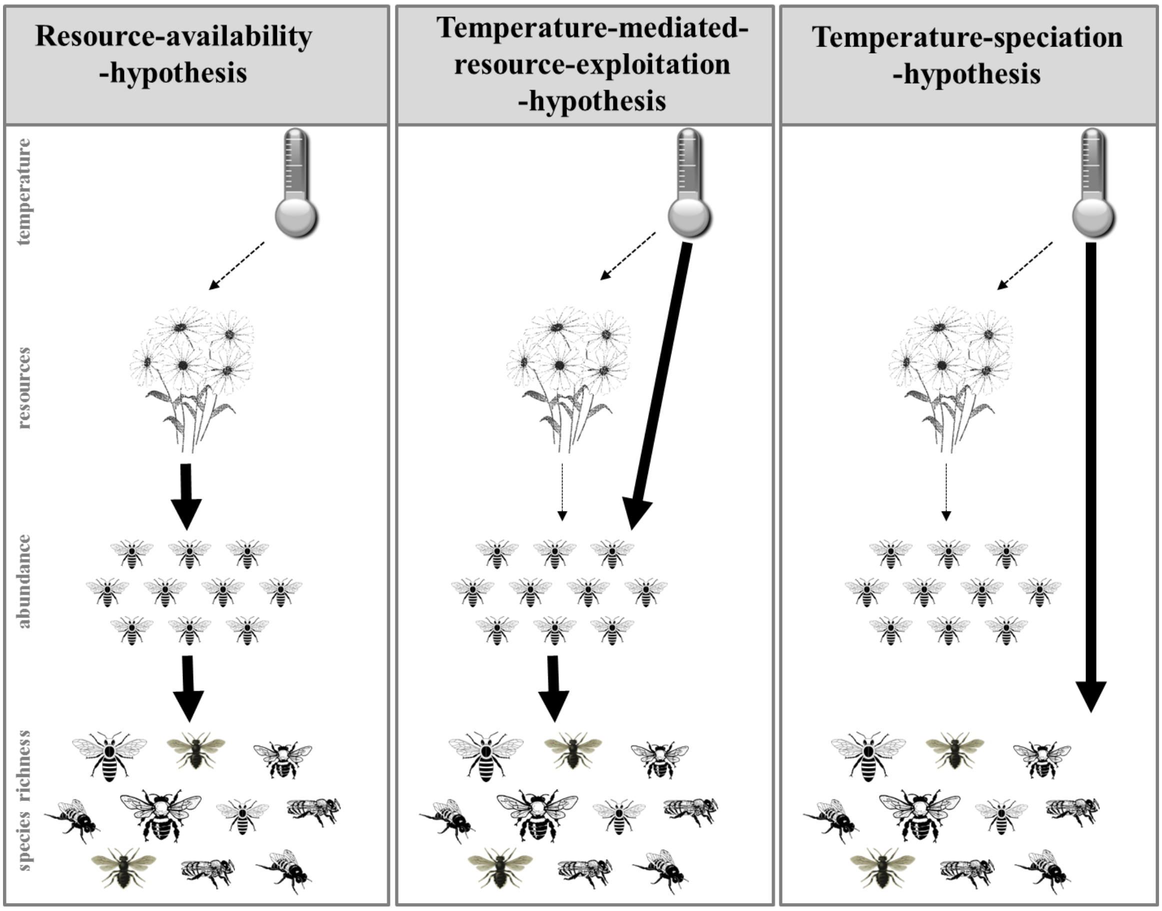


Figure II.1 Three alternative hypotheses explaining how temperature, resources and abundances explain species richness of ectotherms. Bolded arrows indicate basic effects, small arrows facultative effects within the respective hypothesis. The *resource-availability-hypothesis* predicts that the amount of resources directly limits the number of species, while the *temperature-mediated-resource-exploitation-hypothesis* predicts that temperature controls the accessibility of resources in ectotherms, and with this their capacity to maintain high abundances. Both hypotheses assume that high abundances reduce species extinction risks and fascilitate higher levels of species to coexist in equilibrium. In contrast, the *temperature-speciation-hypothesis* predicts that temperature, but not resources, shape species richness via physiological constraints and speciation processes.

METHODS

Study region and study design

The study was conducted at Mount Kilimanjaro (2° 45’ – 3°25’ S, 37°0’ – 37°43’ E) (Tanzania), the highest free standing mountain of the world (700 m a.s.l. – 5895 m a.s.l.). Temperature drops linearly around 6.1°C per 1 km elevational difference, while mean annual precipitation peaks in the forest belt at around 2200m a.s.l. (Hemp, 2006a). Human activity and land use is mainly concentrated in the lowlands of Kilimanjaro. We selected 60 study sites of 0.25 hectare size in 12 major ecosystem types on the southern slopes of Mt. Kilimanjaro, covering an elevational gradient from 866 m a.s.l. up to 4550 m a.s.l.. Investigated ecosystem types consisted of six natural habitats with no or only low human impact (savannah, lower montane forest, *Ocotea* (camphor) forest, *Podocarpus* forest, *Erica* forest, *Helichrysum* scrub vegetation) and six disturbed habitat types with moderate to strong human impact (maize fields, homegarden, commercial coffee plantations, grasslands, disturbed (by former logging) *Ocotea* forests and (fire) disturbed *Podocarpus* forests. The study followed the general study design of the research unit "Kilimanjaro ecosystems under global change: linking biodiversity, biotic interactions and biogeochemical ecosystem processes" (https://www.kilimanjaro.biozentrum.uni-wuerzburg.de).

Bee diversity assessment

Species richness and the abundance of bees were assessed by installing eight pan trap clusters, each consisting of one UV-bright blue, one yellow and one white pan (Campbell & Hanula, 2007; Westphal *et al.*, 2008). Pan trap clusters were installed along two 50m transects on each study site with a minimal distance of 15m between them. We sampled pollinators in different vegetation heights, i.e. at ~35 cm (herbal layer) and ~120 cm (shrub layer) above ground. In forest sites we installed a subset of trap clusters in the canopy of trees (up to a mid-canopy layer of ~25m). Pan traps were filled with water and a drop of liquid soap to break water surface tension, and were emptied after 48 hours. We conducted three sampling rounds. Destroyed traps were replaced by pan trap samples from a fourth sampling round. Species were sorted to morphospecies level and, wherever possible, identified to species level. Because bee catches per individual sampling round were rather low we pooled species and abundance data of sampling rounds per study site for all analyses.

Floral resources assessment

During each sampling round (pan traps, transect walks) floral resources were estimated on ten 4m x 5m subplots that were evenly distributed along the two 50m transects, where pan traps were installed. In each subplot we counted the number of flower units, including flowers of the lower canopy. We defined a flower unit as a patch of flowers that a small pollinator of about 1 cm length would exploit by walking, instead of flying (e.g. the inflorescences of Asteraceae were counted as distinct flower units) (Carvalheiro *et al.*, 2008). Flower resources were then extrapolated for the study site and averaged for the different surveys per study site.

Primary productivity

We used the normalized difference vegetation index (NDVI) as a proxy for primary productivity (Kerr & Ostrovsky, 2003). In the light of the well-known negative biases due to sensor degradation of MODIS Terra (Wang *et al.*, 2012), NDVI estimations used in this study were based exclusively on MODIS Aqua product MYD13Q1 with a horizontal resolution of 250 m x 250 m. Cloud contamination was a very prominent feature on Mt. Kilimanjaro and problematic with regard to realistic estimations of NDVI. To address this issue we first identified all pixels with a MYD13Q1 quality flag of three and deleted these together with the eight adjacent surrounding pixels. Afterwards, we followed the approach proposed by (Atzberger & Eilers, 2011) using the 'Whittaker smoother' based on three iterations with a lambda of 6000. We then calculated the overall mean NDVI for the ten year period 2003 – 2012 and extracted the pixel values corresponding to the locations of our study sites.

Land use and disturbance index

Types of local land use are variable along the elevational gradient of Mt. Kilimanjaro. To deal with this complexity we used a hierarchical approach incorporating four different equally weighted indicators of land use intensity, which were measured on each study site: (a) annual removal of plant biomass, (b) chemical inputs to the ecosystem, (c) vegetation structure in comparison to sites with natural vegetation, and (d) the proportion of managed habitats in the surrounding landscape. The single components were processed to generate a synthesis indicator for human land use in ecosystems. Further details about the single components of the index and its computation are given in the supplement II.S1.

Climate data

All study sites were equipped with temperature sensors that were installed approximately 2m above the ground. Coated plastic funnels were used for radiation shielding. For approximately two years, temperature was recorded in five minutes intervals. Mean annual temperature was calculated by averaging all individual measurements per study site. Because on seven study sites temperature loggers were repeatedly stolen, we used a linear model, with temperature as response variable and elevation and habitat type as additive explaining variables to interpolate mean annual temperature values for the seven missing study sites ($R^2 = 0.99$, $n = 53$, $p < 0.01$). Precipitation data were interpolated for each study site, using about 70 rain gauges spread in different elevations on Mount Kilimanjaro (Hemp, 2006a, b).

Bee-flower interactions

Flower visitors were recorded during 79 variable transect walks that were conducted on a subset of 20 study sites from 984 to 4390m a.s.l. To minimize trampling effects on the vegetation, study sites were extended from 0.25 to one ha. For four hours we slowly moved along variable transect corridors and recorded each pollinator that touched the reproductive parts of a flower. We then counted the number of flower visits conducted by bees within the four hours and calculated the mean number of bee-flower interactions per hour. We additionally estimated the number of flowers on the study sites as described above (one estimation per transect walk).

Statistical analyses

The distribution of bee species richness and bee abundance was analyzed with generalized linear models assuming a poisson distribution of errors. We fitted the models with a linear term of elevation, and with a linear plus quadratic term of elevation.

We used path analyses to disentangle the direct and indirect effect of climate (temperature and precipitation), land use, primary productivity, flower abundance and bee abundances on bee species richness on Mount Kilimanjaro (Mitchell, 2001). Prior to analyses, we log-transformed flower counts to improve normality of residuals. All explaining variables were standardized by z-transformation using the ‘scale’ function in R. Based on our ecological understanding of bees, we hypothesized that temperature, precipitation, and land use predict species richness and abundance directly and indirectly via their combined effect on primary production and the amount of floral resources. We also assumed that primary productivity would be a predictor of flower abundance, and both would affect bee species richness and abundance. Therefore, we pre-selected possible path combinations, by analyzing the four response variables of our path model (bee species richness, bee abundance, flower abundance, primary productivity) with all explaining variables, i.e. temperature, precipitation, land use (+flower abundance and primary productivity in the case of species richness and abundance; +primary productivity in the case of flower abundance) with linear models. For each model we used the dredge’ function of the R package ‘MuMIn’ to evaluate models defined by all possible variable combinations and ranked them by their AIC-based model weight. As our sample size was relatively low compared to the number of estimated parameters, we used the AIC with a second-order bias correction (AICc) for inferring the support of individual models. For the best supported models (Δ AICc < 2) we calculated the relative variable importance (RVI), i.e. the sum of AICc weights across all models including the explanatory variable. The relative variable importance thus mirrors the statistical certainty with which a variable is included into competitive models, a measure, which has often been ignored, although the number of competitive models is generally high in ecology (Conroy *et al.*, 1995; Wintle *et al.*, 2003). We then set up all remaining path model combinations and ranked them based on their AICc, using the R package ‘lavaan’. For all competitive path models (Δ AICc < 2) we calculated path coefficients, their statistical significance and multiple coefficients of determination (R^2) of explanatory variables. The total effect of primary productivity on bee richness was calculated by adding the direct path coefficient to the product of the indirect path coefficients of that link (Mitchell, 2001).

To analyze the effect of temperature on resource use by bees we related the number of bee-flower interactions counted during each transect walk survey to the mean temperatures measured on study sites. We added flower and bee abundance as covariables in the model to control for an expected positive influence of both variables on the number of bee-flower interactions. Bee abundance data were derived from pan trap catches (total abundance across three sampling rounds). All explaining variables were z-transformed for comparability. We fitted linear mixed effects models with temperature, (log-transformed) flower abundance, (log-transformed) bee abundance and all possible interactions as fixed factors and included study site as a random factor to avoid pseudo-replication. Using the 'dredge' function we ranked all models by their AICc-values and present the summary output of all models with ΔAICc<2 (Tab. II.S3a).

RESULTS

In total we caught 4899 bees and sorted them into 129 morphospecies (32 genera). Species richness exponentially declined with elevation (Fig. II.2). Bee abundance, in contrast, showed an inverse hump-shaped distribution along the elevation gradient, with maximal bee abundance in *Erica* forests and *Helichrysum* shrubs, (3500 and 4550m a.s.l.) (Fig. II.2). Interestingly, one morphospecies of the widespread genus *Lasioglossum*, dominated the higher elevation habitats and accounted for 59 % of all bee individuals sampled on Mount Kilimanjaro.

Path analyses indicated that all three mechanisms of our hypotheses (Fig. II.1) simultaneously explain bee species richness on Mount Kilimanjaro, whereby the effect of temperature outweighed the effect of resources. As predicted by the *resource-availability-hypothesis,* the amount of floral resources had a weak but significant effect on bee abundance in all competitive models (standardized path coefficient = 0.23, p=0.011), while bee abundance was a strong predictor of bee richness (standardized path coefficient = 0.54, p < 0.001) (Fig. II.3). In accordance with the *temperature-mediated resource-exploitation-hypothesis* temperature had a moderately strong direct effect on bee abundances (standardized path coefficient = 0.40, p<0.001) (Fig. II.3). Importantly, and in accordance with the *temperature-speciation-hypothesis,* temperature also had a strong direct effect on species richness that was not mediated by bee abundance (standardized path coefficient = 0.68, p < 0.001) (Fig. II.3). The best supported path model explained 88% of the total variance in species richness and 54% of the total variance in bee abundance (Fig. II.3). Relative variable importance was maximal (i.e. 1) between all remaining links, except for one (flower abundance → bee abundance; RVI: 0.3).

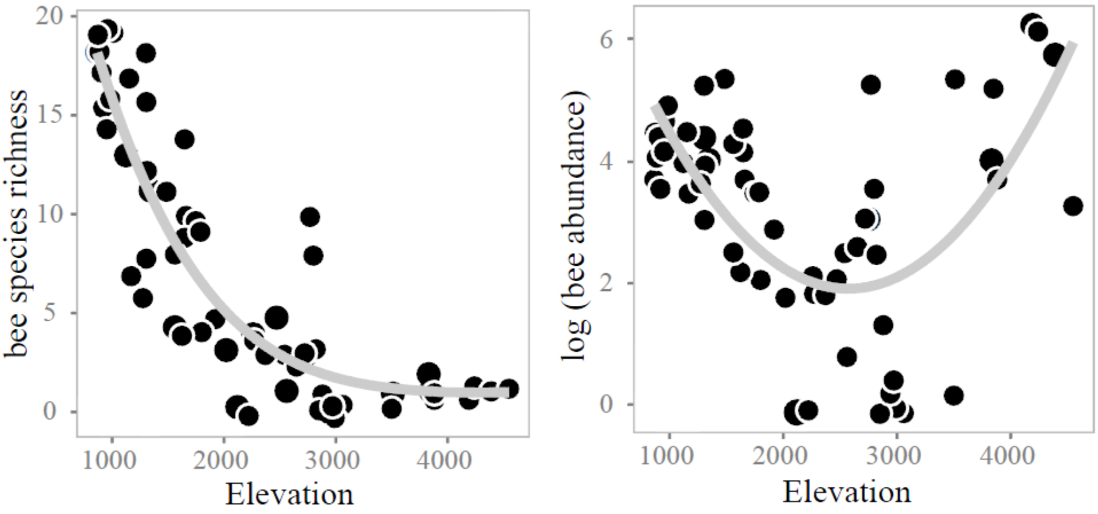


Figure II.2 Species richness and abundance of wild bees change along climatic gradients on Mount Kilimanjaro. Species richness strongly declined with elevation (left figure), while (log-transformed) abundances showed an inverse hump-shaped distribution (right figure).

Precipitation and temperature had a strong positive effect on primary productivity. However, primary productivity was not positively related to flower abundance as expected. Instead, primary productivity had either no, or even a negative effect on flower abundance (Fig. II.3 and Fig. II.S2). Also, primary productivity had a strong negative effect on bee abundance and thus a negative *total* effect on bee richness (i.e. indirect (negative) effect, via abundance + direct (positive) effect of primary productivity on bee richness = -0.20). Land use, in contrast, had a positive effect on flower abundance and did not negatively affect bee abundance or richness.

In support of the resource-exploitation hypothesis, the number of bee-flower interactions increased with increasing temperature (Fig. II.4): The best model, describing the number of bee-flower interactions contained temperature and the amount of flowers as explaining variables, while bee abundance appeared not to be strongly correlated to the number of flower visits by bees. The presented additive model (Fig. II.4) had the highest model weight, but was statistically not distinguishable from the model including the interaction term (flower abundance x temperature) (Δ AICc < 2) (Tab. II.S3a). Nevertheless, in both competing models the number of bee-flower interactions increased with increasing mean annual temperatures (t = 2.69, d.f. 18, p=0.015) and the amount of floral resources (t-value=5.05, d.f.=58, p<0.001) (Fig. II.4).

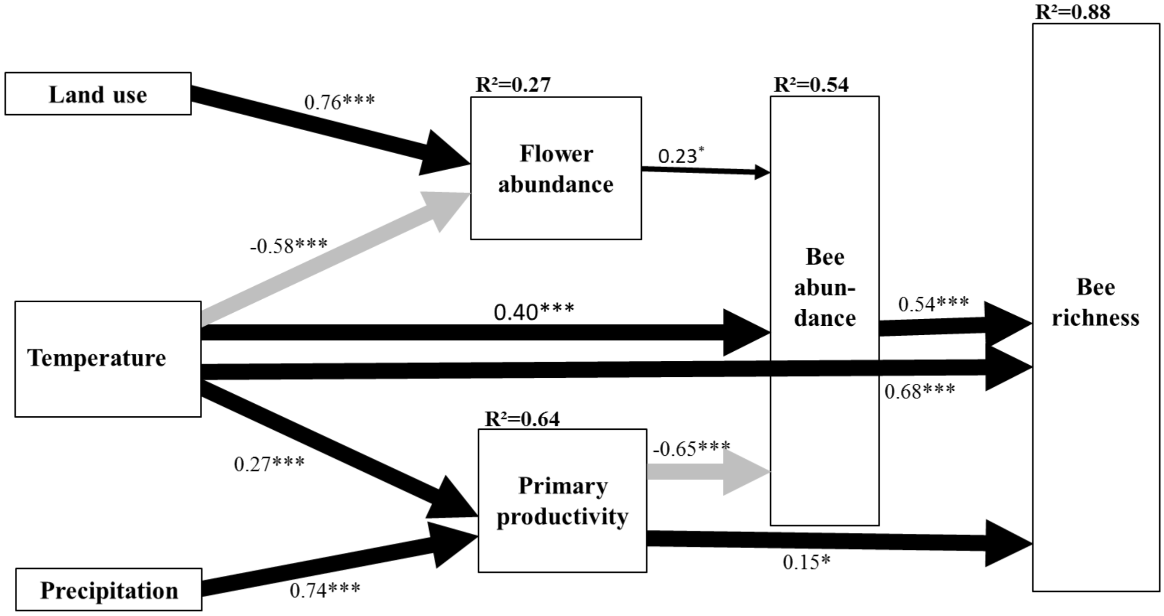


Figure II.3 Direct and indirect predictors of bee abundance and bee species richness on Mount Kilimanjaro. The path model with the lowest Akaike information criterion, corrected for small sample size (AICc) is presented. Bee species richness, bee abundance and flower abundance were log-transformed prior to analysis. Arrow widths indicates relative variable importance in all competitive linear models with ΔAICc<2 derived from multi-model inference. Grey colors indicate negative effects. The relative amount of explained variance (R^2, derived from the best supported model including bee species richness as the response), standardized path coefficients and their statistical significance (*P<0.05, **P<0.01, ***P<0.001) are given. Competitive models (ΔAICc<2) propose a positive effect of precipitation on bee abundance, a positive effect of land use on bee abundance, and a negative effect of primary productivity on flower abundance (see II.S2).

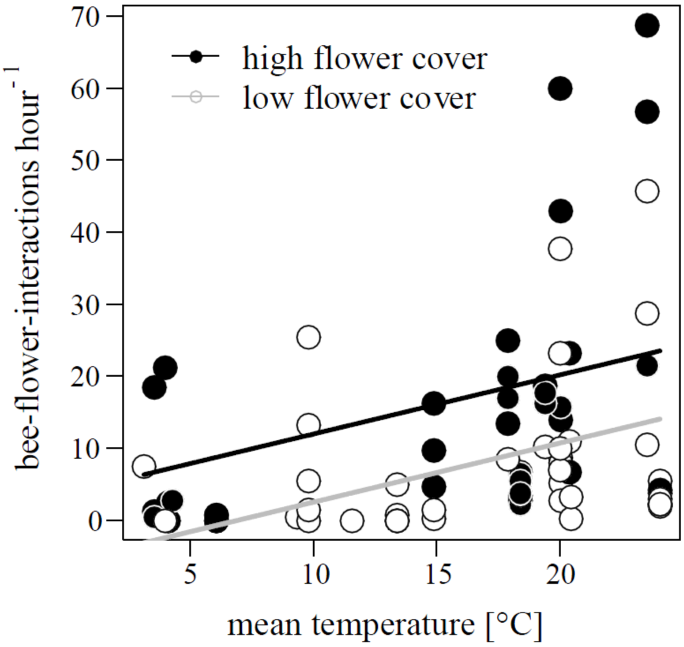


Figure II.4 Mean annual temperature and (log-transformed) flower cover predicted the number of bee-flower interactions per hour. The number of interactions increased with increasing temperature. The effect levels were dependent on the flower cover. Model predictions are shown for groups fixed at the lower (25%) (grey line) and the upper (75%) quartile (black line) value of flower cover. Statistical analysis based on linear mixed effects models with study site as a random factor. Marginal R^2=0.31, conditional R^2=0.62.

DISCUSSION

On Mount Kilimanjaro, bee species richness declined with elevation, which appears to be a general pattern of bee communities of both temperate and tropical ecosystems (Arroyo *et al.*, 1982; Hoiss *et al.*, 2012). Our study suggests that temperature rather than resource abundance determined species richness as temperature governs the access of pollinators to food resources and accelerates ecological and evolutionary processes leading to the origination and maintenance of diversity.

The idea that resources or ultimately the total productivity of ecosystems limits the number of species that coexist in ecosystems goes back to the roots of quantitative ecology. It is here further strengthened by theoretical developments and empirical evidence from the field (Pianka, 1966; Ferger *et al.*, 2014). In accordance with the resource hypothesis we found that the availability of floral resources had a positive effect on bee abundance, a result also found by Hoiss et al. (2012). However, the effect of flower availability on bee abundance was weak compared to the direct effect of temperature on bee abundance. We conclude that the resource-exploitation-hypothesis explains this difference: as energy consumption of active bees drastically declines with increasing temperature (Stabentheiner *et al.*, 2003), bees might restrict foraging activity to temperatures where the energy gain through collected nectar or pollen exceeds the energy costs of the foraging flight. Accordingly, we found that the number of bee-flower-interactions equally decreased with dropping temperatures (also detected by Arroyo *et al.*, 1985). This facilitates the maintenance of more and larger populations and higher species richness in ectotherms in warmer habitats, even when resource availability is stable across habitats. In contrast, resource exploitation of endotherms is expected to be much less affected by temperature. Indeed, it was found that the species richness of (endothermic) frugivore and insectivore birds on the same study sites on Mount Kilimanjaro was better explained by the availability of food resources (fruits and insects respectively) and vegetation structure, than by temperature (Ferger *et al.*, 2014). The availability and constant usability of food resources likely outweigh physiological costs of keeping body temperature in cooler climates in endotherms.

In accordance with the temperature-speciation-hypothesis we also detected a strong direct effect of temperature on species richness, which was not mediated by high bee abundances. Because temperature controls the speed of chemical reactions, all kinds of biological processes that shape species richness, such as species-interactions, mutations, adaptive evolution or speciation, depend on temperature (Brown *et al.*, 2004). Nevertheless, a detailed mechanistic understanding of how temperature affects species richness is currently lacking. We assume, that evolutionary processes like temperature-mediated speciation rates (Allen *et al.*, 2006) are complemented by ecological mechanisms, like e.g. temperature-dependent negative-density mortality rates (de Sassi *et al.*, 2012; Johnson *et al.*, 2012; Bagchi *et al.*, 2014; Brown, 2014). For instance, abundant bee and wasps species have been shown to be preferentially attacked by parasitoids and predators (Steffan-Dewenter, 2003), allowing more species to coexist (Paine, 1974). It seems likely that due to increased species-interaction rates, these effects are more pronounced under warm temperatures. This requires further investigation.

Primary productivity has often been used to explain biodiversity patterns of narrowly defined animal taxa. This assumes that the fraction of total primary production secured by these taxa varies little with primary production. However, this assumption is unlikely to hold as narrowly defined taxa are often only capable of exploiting resources over a restricted part of a full environmental gradient and high-level taxonomic turnover within functional guilds along environmental gradients is a well-documented pattern (e.g. decomposer: termites-fungi; pollinators: bees-diptera). In this respect, we showed that floral resources influenced bee richness, via abundance, stronger than primary productivity. High levels of primary productivity had a negative impact on bee abundance, which overweighed the slight positive impact on bee richness. On Mount Kilimanjaro, primary productivity peaks in the lower forest belt around 2500m a.s.l. Dense canopy covers restrict the amount of flowering plants in the herbal and shrub layer, up to the lower canopy cover (Fig. II.S2). We are aware of the fact that high levels of primary productivity, which are linked to dense vegetation covers, could either reduce the effective survey area (Hurlbert, 2004), reduce sample efficiency of pan traps, or shift pollinator activity to the highest canopy cover. However, as transect walks and canopy observations in the forest revealed similarly low bee species richness and abundance in forests (in the forests 96% of all flower visiting bees belonged to the same species - *Apis mellifera*!) we assume that such sampling artifacts are rather negligible. Instead, we suggest that the clumped distribution of floral resources in tropical forests, with few mass-flowering trees per km² support few social and long-distance foraging species, but to much lesser degree small solitary bees, which often have foraging ranges of less than 600m (Greenleaf *et al.*, 2007) and make up the largest part of the species communities on Mt. Kilimanjaro. A similar negative correlation between primary productivity and species abundance/ richness was found for birds within forests (but not grasslands) (Hurlbert, 2004) and ants (Sanders *et al.*, 2007). The authors suggested that forest communities respond differently to primary productivity than communities from more open habitats, or that other factors than productivity might limit species in habitats where primary productivity is very high, which is closely related to our suggestions. Further experiments, that consider other parameters like e.g. vegetation structure, are required to fully understand these relationships.

Surprisingly, land use and habitat disturbance had no negative impact on bee richness on Mount Kilimanjaro. In contrast, increased flower abundance in more open (disturbed) habitats even supported high bee diversity (Gikungu *et al.*, 2011). Species richness was either comparable with natural systems in equal elevations (e.g. savannahs vs. maize fields), or even higher (e.g. lower montane forest vs. coffee plantations, grasslands or homegarden). However, land use and the human impact on ecosystems are currently only moderate on Mount Kilimanjaro. Subsistence farming is the dominating agricultural system which is of small scale (field sizes are mostly considerably less than 1 ha) and sustains rather high levels of semi-natural habitats on or around crop fields. The small size of fields and the diversity of different cropping systems shape a mosaic-like heterogeneous landscape. Agricultural lands are mainly weeded manually, which restricts the impact of soil compaction on soil-nesting species. Stem-nesting bees have been observed to profit from maize stems that partly remained on the fields a long time after harvest. In general small-scale farming in its current form still supports a high diversity of bees on Mount Kilimanjaro, which is rewarded by stable pollination services across agricultural landscapes (Classen *et al.*, 2014). Accelerating land use intensification and the increased use of pesticides and machines, however, might strongly impact pollinator diversity and pollination services, as reported from the western world, where pollinator community declines due to land use intensification are alarming (e.g. Biesmeijer, 2006; Potts *et al.*, 2010).

We identified temperature as the most important predictor of bee species richness, as it controls both resource-exploitation and general speciation rates. Rising temperatures in the course of climate change are thus expected to have impact on bee species richness. However, even though we found positive effects of temperature on species richness, predictions of whether bees will profit from global warming or not are tenuous. Especially in the lowlands of Mount Kilimanjaro, bees and other ectotherms might live close to their thermal maximum (Deutsch *et al.*, 2008) and further warming may lead to a biotic attrition in lowlands. When temperature rises, species are predicted to go extinct or to adapt by moving upslope (or polewards) aiming to remain in their preferred temperature range. Extinction is expected to particularly affect specialists and narrow-ranged species, which may not find suitable habitat corridors to move up (Parmesan, 2006), especially if land use changes accelerate habitat loss. Range-shifts, especially from the tropical lowlands, can result in additionally impoverished biotas, as moving species cannot be replaced by species of even warmer places (Colwell *et al.*, 2008). On the other end of the gradient, so-called "mountaintop-extinction" may occur, which should not only result from rising temperature (bees are expected to live below their thermal optimum here), but also from shifted levels of density-dependent processes, like interspecific competition, or host-parasite interactions (Romo & Tylianakis, 2013).

CONCLUSIONS

On Mount Kilimanjaro, bee species richness was explained by both temperature and food resources, whereas temperature, controlling both the usability of resources and speciation-related processes, played a predominant role. The optimal foraging temperature range of ectotherms is narrower than their thermal range, which has often been ignored when disentangling the effects of resources and temperature on species richness. We conclude that the consideration of temperature-mediated resource use improves our understanding of how animals, and in particular ectotherms, respond to environmental changes on local and global scales.

Supplementary data to Chapter II

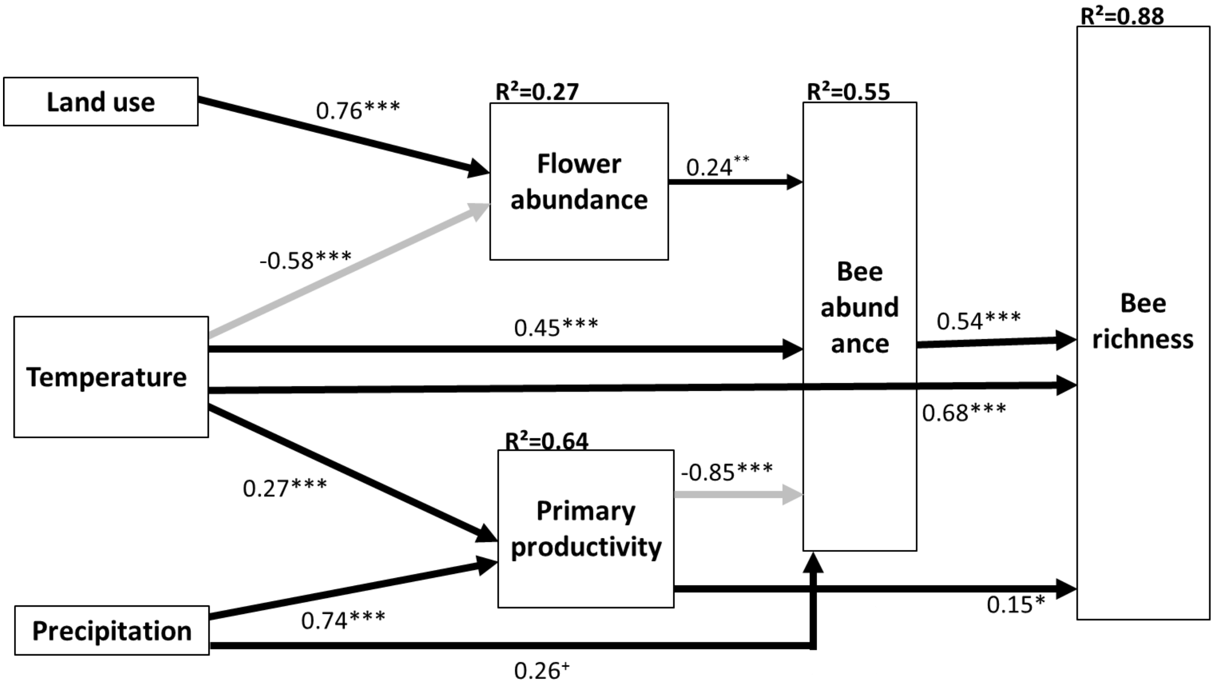
II.S1. Calculation of the land use disturbance index

a) Annual removal of plant biomass was calculated by averaging standardized expert estimates of plant biomass removal on study sites. This included estimates of biomass removal by mowing, cattle grazing, ploughing, fire events, logging and firewood collection. With the exception of ploughing which was estimated on an ordinal scale (no ploughing, ploughing by hand, ploughing with a tractor), all estimates were calculated in percentage of the standing biomass removed per year. (b) Chemical inputs were calculated by averaging standardized expert estimates of irrigation, fertilization, insecticide, fungicide, and herbicide treatments. Estimates were done on an ordinal scale (no or very low input, medium input, high input). (c) Structural characteristics describing the dissimilarity to natural habitats are often used as an indicator of human land use. For describing the vegetation structure we measured the canopy closure using a canopy densiometer, for canopy height we used a range finder. Vegetation heterogeneity was defined as the Shannon-Wiener diversity of canopy cover values estimated by an observer in the field at height levels of 1, 2, 4, 8, 16, 32, 64 m. All measurements of canopy closure, canopy height and vegetation heterogeneity were conducted at nine points which were equally dispersed over the 50 x 50 m study site. As the natural vegetation strongly changes along elevational gradients, we could not use the raw data as a measure of land use. Raw canopy closure would be a good measure of human land use e.g. in submontane sites where the natural vegetation, forest, has a canopy closure of 100% and managed ecosystems values of <100 %. However, it is not suitable for ecosystems in the colline savannah zone were even the natural vegetation has a canopy closure of ~10 %. Therefore, we calculated the mean Euclidian dissimilarity of vegetation structure measures of the respective study site to the average vegetation structure that was measured for study sites holding natural vegetation for which, by definition, the dissimilarity to natural vegetation was assumed to be 0. (d) As it is well established that land use intensification at the landscape scale influences ecosystem properties at a local scale (see e.g. Tscharntke *et al.*, 2012) we included a variable describing the landscape composition, i.e. the proportion of areas with managed habitats in the surrounding landscape (radius = 1500 m), as a fourth indicator of human land use. The calculation of the relative proportion of natural versus managed habitats was based on a land-cover classification of the Kilimanjaro region (unpublished) that identified 27 different habitat types (18 natural and 9 managed habitat types) in the study area. Briefly, this product is based on a maximum likelihood classification applied to four almost cloud-free Terra-ASTER scenes from 11/02/2005, 02/11/2008, 28/02/2011, and 24/02/2013. All four components of the land use index were standardized before averaging them to a final composite index of human land use. All standardizations were done by calculating the difference of individual measures to the mean of all measures divided by the range of all measures $(y_i - \bar{y})/(\max(y)-\min(y))$, producing land use intensity values of between 0 (lowest land use) and 1 (highest land use).

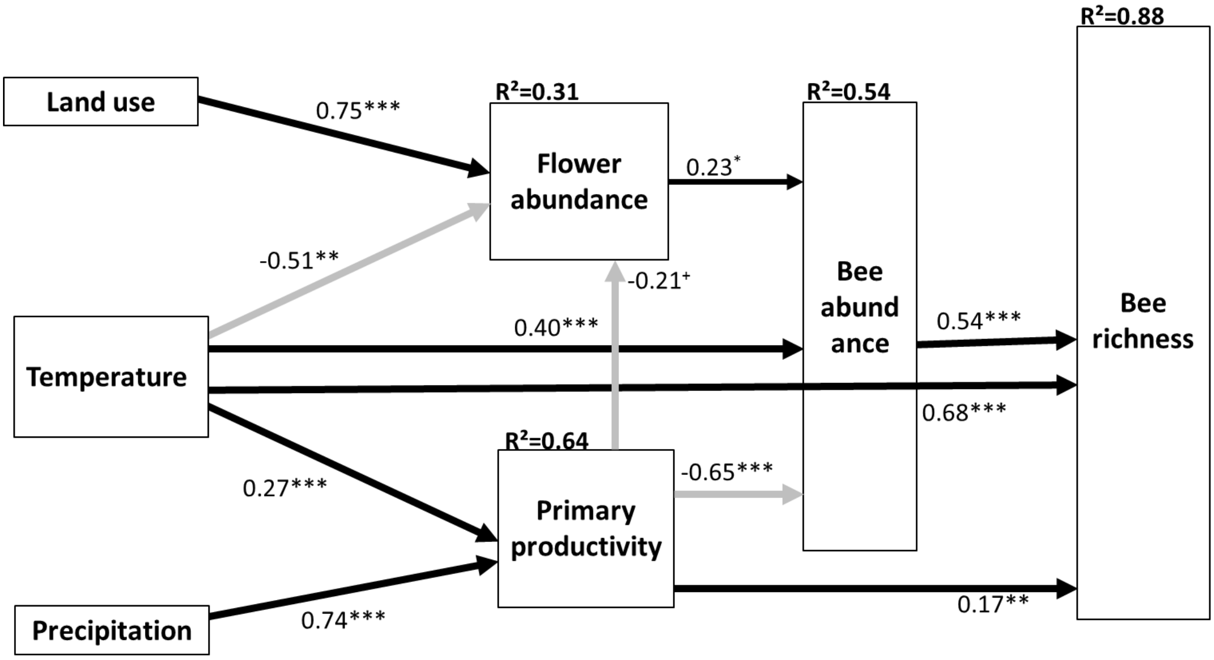
II.S2 – Alternative path models and their test statistics

In Fig. II.3 we present the path model with the lowest AICc value. However, the four alternative models presented here were statistically not distinguishable from the presented model:

ΔAICc = 0.49



ΔAICc = 0.51



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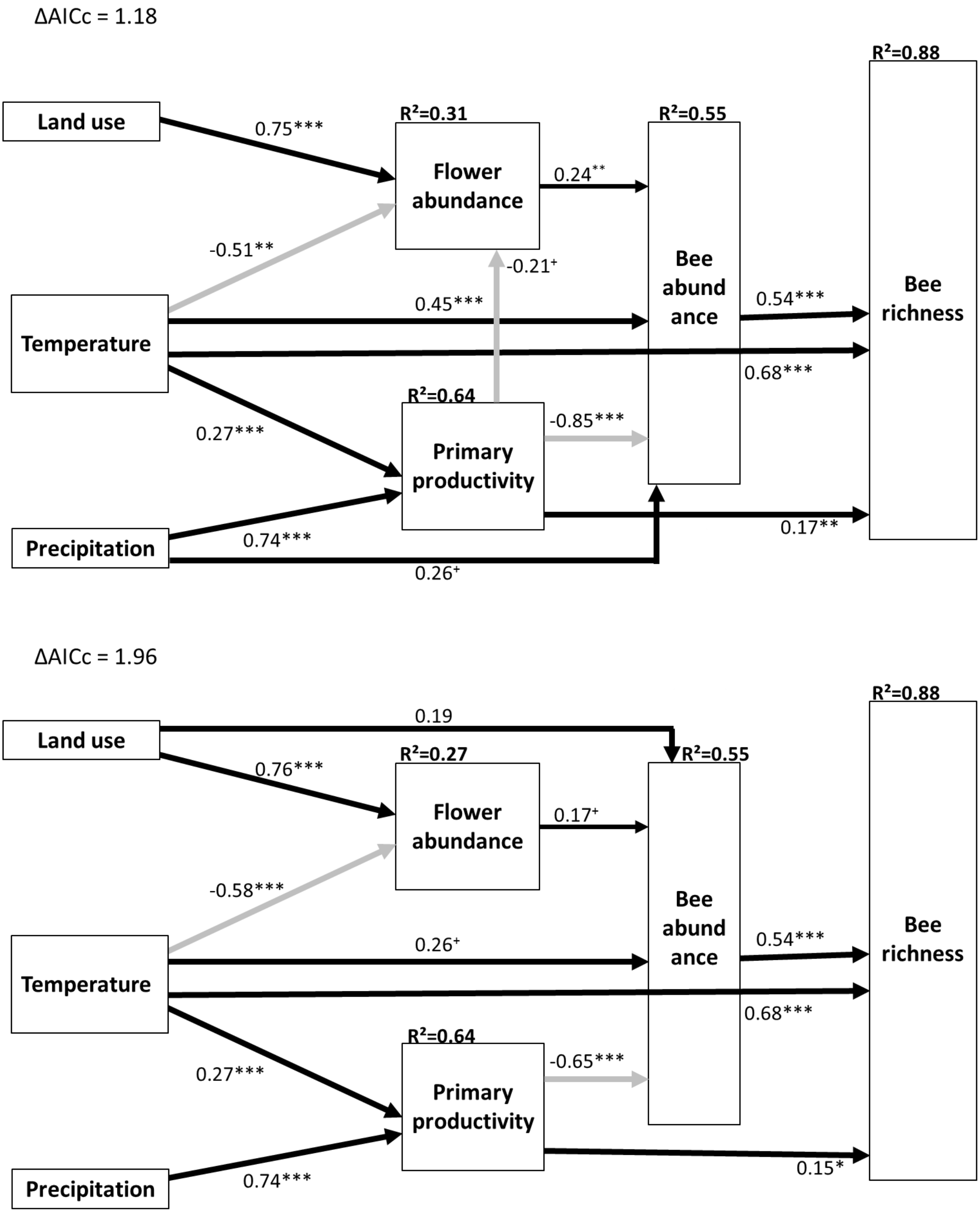

Figure II.S2 Direct and indirect predictors of bee abundance and bee species richness on Mount Kilimanjaro. These alternative path models were statistically not distinguishable from the best model presented in Fig. II.3 (ΔAICc<2). Bee species richness, bee abundance and flower abundance were log-transformed prior to analysis. Grey colors indicate negative effects. The relative amount of explained variance (R^2), standardized path coefficients and their statistical significance ($^+P<0.1$, $*P<0.05$, $**P<0.01$, $***P<0.001$) are given. Alternative models propose a positive effect of precipitation on bee abundance, a positive effect of land use on bee abundance, and a negative effect of primary productivity on flower abundance in different compositions. Note that the figure starts on the previous page.

II.S3- Analysis of bee-plant interactions

Table II.S3a Model selection table (delta AIC < 4), for linear mixed effects models analyzing the effect of temperature (T), (log-transformed) bee abundances (# bees) and (log-transformed) flower abundances (# flowers) on the number of bee-plant interactions per hour. Study site was included as a random term in all models. Note that all explaining variables were z-transformed prior to analysis.

Inter-cept	T	# bees	# flowers	T x # bees	T x # flowers	d.f.	AICc	delta	weight
11.42	5.54		6.50			5	606.4	0.00	0.45
11.49	5.29		6.33		1.25	6	608.0	1.54	0.21
11.45	5.52	-0.46	6.56			6	608.7	2.29	0.14
12.05	8.94	-5.47	6.60	-5.67		7	608.8	2.36	0.14
11.49	5.29	-0.06	6.34		1.24	7	610.4	3.95	0.06

Table II.S3b Output of linear mixed effects model (best model), analyzing the influence of temperature and flower abundance on the number of bee-plant interactions. Note that all explaining variables were z-transformed prior to analysis. Study site was included as a random term.

	Value	SE	d.f.	t-value	*p*
Intercept	11.43	2.22	58	5.15	<0.001
log (flower abundance)	6.50	1.29	58	5.05	<0.001
temperature	5.54	2.06	18	2.69	0.015

CHAPTER III: TO BE SMALL AND COLD OR LARGE AND HUNGRY: TRADE-OFFS IN BEE BODY SIZE ALONG CLIMATIC GRADIENTS

This chapter is in preparation for publication as: Classen A, Steffan-Dewenter I, Kindeketa WJ, and Peters MK. To be small and cold or large and hungry: trade-offs in bee body size along climatic gradients.

ABSTRACT

Species traits do not assemble randomly along climatic gradients, but follow principles, whose identification has challenged ecologists for centuries. Physiological mechanisms and community assembly rules have been proposed to explain trends in the body size of organisms, but with conflicting results and interpretations: While Bergmann´s rule predicts increases of body sizes in cooler climates resulting from physiological constraints, species-energy theory suggests declines in the mean body size of species caused by increased extinction probabilities for large-bodied species in low-energy habitats. We studied community-wide body size variation of wild bees at Mt. Kilimanjaro and found that along a 3680 m elevational gradient bee individuals became on average larger within species, while large species were increasingly absent from high-elevational communities. This demonstrates how well-established, but apparently contrasting ecological theories can be merged through the parallel consideration of different levels of biological organization.

Key words: body size, Bergmann´s rule, community ecology, intraspecific variation, interspecific variation, niche breadth, Mount Kilimanjaro, bees, competition, environmental filtering, community assemblages, species coexistence, functional traits

INTRODUCTION

Understanding the causes of morphological variation in animals along climatic gradients is one of the most enduring questions in ecology (Humboldt & Bonpland, 1807; Bergmann, 1847; Allen, 1877; Brown, 1995; Ashton, 2002; Hoiss *et al.*, 2012) . Mechanisms regarding physiological constraints of species (e.g. Bergmann's rule (Bergmann, 1847), Allen´s rule (Allen, 1877)) and mechanisms characterizing the availability and allocation of food among species in local species assemblages (e.g. species-energy-theory (Brown & Maurer, 1989), character displacement (Brown & Wilson, 1956)) are used to explain the distribution of organismic traits along gradients of latitude and elevation. Even though these mechanisms are non-exclusive, they make different predictions concerning trends in organismic traits and find conflicting evidence from the field (Blanckenhorn, 2004).

Physiology-based theories are built upon the assumption that the rapid changes in the physical environment along elevational gradients profoundly impact the distribution and evolution of organisms due to physiological constraints, with consequences for morphological trait distributions. Averaged body-size is predicted to increase with decreasing temperatures (Bergmann, 1847), which has been suggested to result, *inter alia,* from lower developmental temperatures in ectotherms (Van Voorhies, 1996), or increased heat conservation through higher surface to volume ratios (Blackburn *et al.*, 1999). In contrast, energetic constraints considering the allocation of energy among size-structured species populations, predict mean body sizes on average to decrease with elevation, due to higher extinction risks of large compared to small organisms in energy-limited habitats (Brown & Maurer, 1989): Everything else being equal, large-bodied species have higher per capita energy requirements and consequently lower population sizes when having access to the same amount of resources (Damuth, 1981; Brown *et al.*, 2004). With extinction probabilities on average increasing with decreases in population size, in energy- and area-restricted high elevational habitats, the extinction probability of large-bodied species is predicted to be higher than that of small-bodied species (Brown & Maurer, 1989), resulting in an overall decline of mean body sizes and interspecific variances within species communities. Although the predicted impact of physiological and energetic constraints on species trait distributions are contradicting, the mechanisms could act simultaneously structuring traits at different levels of organismic organization, i.e. at the inter- and intraspecific level, resulting in either intraspecific trait shifts or species turnover. Intraspecific variances are expected to be increased in high-elevational habitats, where competition is lowered due to successive extinction of competing species (‘character release’) (Lomolino *et al.*, 2012) (Fig. III.1).

METHODS IN BRIEF

Here we used the unique elevational gradient on Mount Kilimanjaro to analyze how morphological traits of wild bees (Hymenoptera: Apoidea) shift along climatic gradients within and across species and whether these patterns are predicted by physiological constraints or energetic constraints. We focused on three morphological traits: body mass, measured by the intertegular distance (ITD) (Cane, 1987), glossa length (GL), which can be associated with diet breadth (Goulson *et al.*, 2005) or flower diversity, and the ratio of forewing length to intertegular distance, in the following called “relative forewing length” (rFL). The selected traits are of high ecological importance due to their connectedness to metabolism, resource use, dispersal capacity and pollination function, and have been shown to be sensitive to abiotic and biotic changes (Hoiss *et al.*, 2012; Pellissier *et al.*, 2013). We analyzed both trait means and trait variances, each on an intra- and interspecific level.

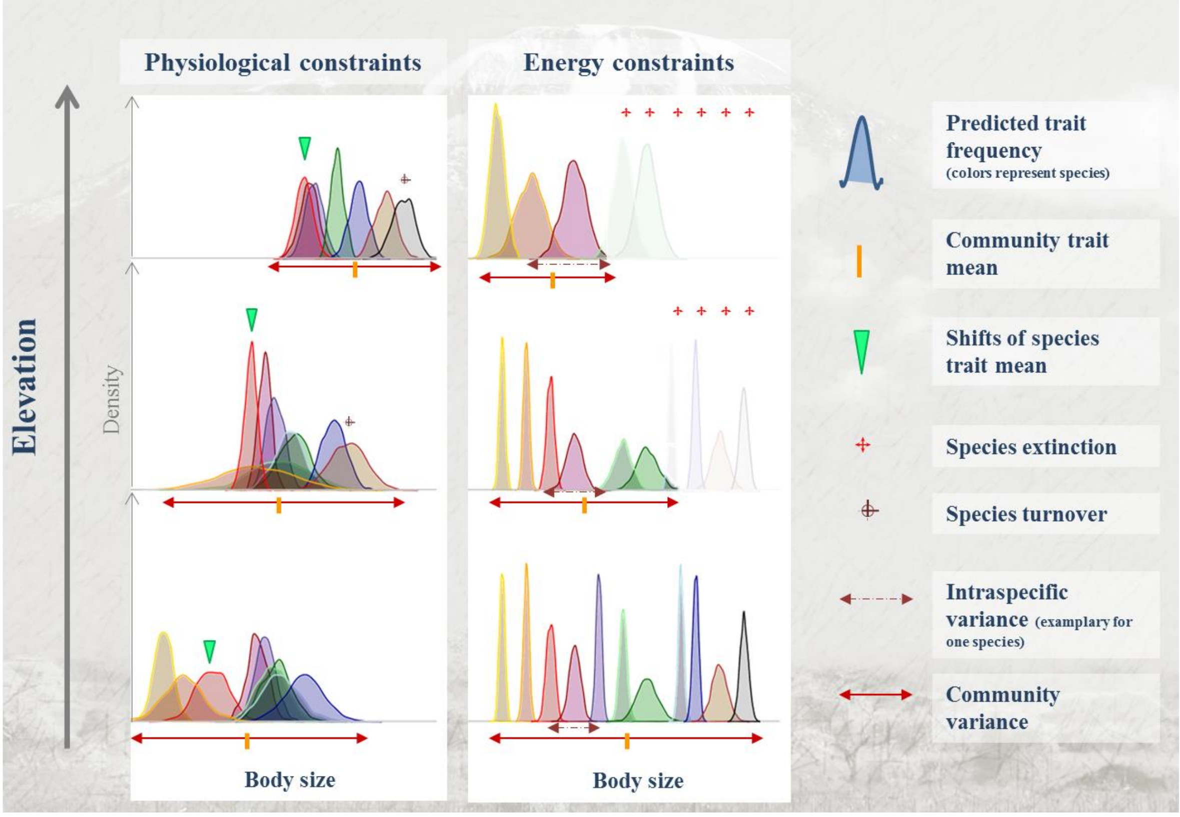

Figure III.1 Predicted effects of physiological and energy constraints on distributions of body sizes along elevational gradients. According to physiological-based theories (here: Bergmann´s rule), body size is predicted to increase with elevation (through intraspecific trait shifts or species turnover). In contrast, energetic limitations may cause mean body size to decrease on community levels, due to increased extinction probabilities of large species in energy-restricted high-elevational habitats. Community variances of body size are predicted to decrease by this non-random directed species loss. Reduced competition due to species loss and declining interaction rates along the elevational gradient is expected to increase intraspecific niche breadths.

RESULTS AND DISCUSSION

In total, we caught 3630 bee individuals of 66 species. Species richness declined with elevation (GLM, z = -9.01, *p*<0.001) (Fig. III.S1). Species trait means shifted conditionally on the level of biological organization: At the community level, body size and glossa length decreased with increasing elevation (Fig. III.2a, b) (ITD: $R^2 = 0.52$, t = -5.60, *p*<0.001; GL: $R^2 = 0.54$, t = -5.80, *p*<0.001, the same pattern was found for relative GL = GL/ITD), while relative forewing lengths increased with elevation (Fig. III.2c) (rFL: $R^2 = 0.42$, t = 4.54, *p*<0.001). Community trait patterns were consistent for abundance-weighted and species weighted means (III.S2) and were shaped by the loss and turnover of species. Within species, individuals were on average larger in colder habitats, as predicted by physiological-based theory (Fig. III.2d) ($t = 3.43$, $p<0.001$). Glossa lengths decreased with elevation within species (Fig. III.2e) ($t = -2.18$, $p = 0.033$), while relative wing-lengths stayed constant along the elevational gradient (Fig. III.2f) ($t = 1.16$, $p = 0.250$) (Tab. III.S3). Thus, our data suggests that while individuals within species increasingly become larger, large, long-tongued and small-winged species are increasingly absent from high-elevation habitats.

In addition to trait means, trait variance also changed with elevation at both the inter- and intraspecific level: Interspecific variation of all traits decreased with increasing elevation, which was mainly explained by an increasing non-random absence of large-bodied, large-winged and long-tongued species along the elevational gradient (σ^2 ITD: $R^2 = 0.45$, $t = -4.88$, $p<0.001$; σ^2 GL: $R^2 = 0.53$, $t = -5.72$, $p<0.001$; rFL: $R^2 = 0.13$, $t = -2.06$, $p = 0.048$) (Fig. III.3 a-c). However, the loss of interspecific trait variation was paralleled by weak declines of intraspecific variation, found for both body size and glossa length (σ^2 ITD: $R^2 = 0.13$, $t = 2.09$, $p = 0.045$ (Fig. III.3d), σ^2 GL: $R^2 = 0.27$, $t = -3.27$, $p = 0.003$) (Fig. III.3e), providing no evidence for the prediction that a drop of interspecific competition results in intraspecific character release. Probably, habitat heterogeneity in warmer lowlands maintains higher trait variability, while in high elevations only few phenotypes are selected. Only the intraspecific variation of standardized forewing lengths which increased with elevation, weakly indicated the predicted character release (σ^2 rFL: $R^2 = 0.31$, $t = 3.57$, $p = 0.001$) (Fig. III.3f) (Tab. III.S4).

The distribution of morphological traits within and across species in bee communities along elevational gradients at Mount Kilimanjaro suggests that physiological- and energy-based mechanisms simultaneously constrain the size and shape of organisms - reflected in contrasting trait-elevation patterns identified at the species versus community level. We found that on a population level, body sizes followed predictions of Bergmann´s rule, i.e. individuals of species were on average larger at high elevations, while the number of large-bodied species drastically declined with elevation, as predicted by community assembly rules considering differential energy requirements within size-structured species communities. This demonstrates how well-established, but apparently contrasting ecological rules and predictions concerning organism´s body sizes can be merged through the parallel consideration of different levels of biotic organization. The trait distributions of glossa and relative forewing lengths supported these findings. For example, increases of relative forewing lengths, a strategy to maintain flight capacities under dropping air density (Dillon, 2006), was caused by species loss and turnover, rather than by intraspecific adaptation (i.e. physiological constraints acting on communities). In contrast, the decrease in glossa lengths, possibly indicating the dominance of species with a generalist diet in high elevations, was found at both inter- and intraspecific levels. It is suggested to result from energy constraints, forcing species to expand diet breadth in high elevational habitats (Ramos-Jiliberto *et al.*, 2010; Green *et al.*, 2013).

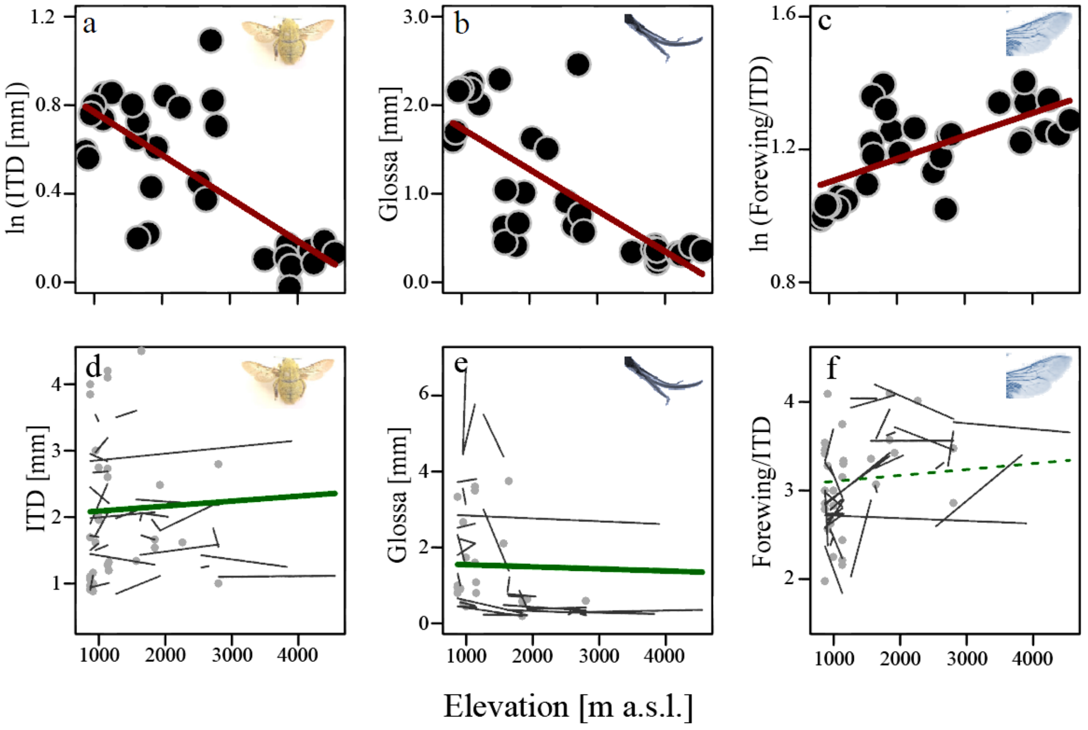

Figure III.2 Change of trait means with elevation on a community level (a-c) and within species (d-f). Black circles represent community weighted means of the respective traits (a-c). On a community level (a) intertegular distance (ITD), and (b) glossa length decreased with elevation, while (c) the relative forewing length increased. Within species, (d) ITD on average increased, with species level responses (grey lines) varying, (e) glossa length slightly decreased with increasing elevation, and (f) relative forewing length did on average not change along elevation. Solid lines indicate statistical significance on a level of p<0.05 (p>0.10: dashed line). Grey dots represent single finds.

We showed that morphological traits of communities at Mt. Kilimanjaro were predicted by both physiological- and energy-based constraints structuring trait expression simultaneously at different levels of biological organization. Further work will have to determine the transferability to other taxa and latitudinal gradients, but the parallel analysis of species and community traits, it seems, may sharp our understanding about trait-related species and community responses to climatic change.

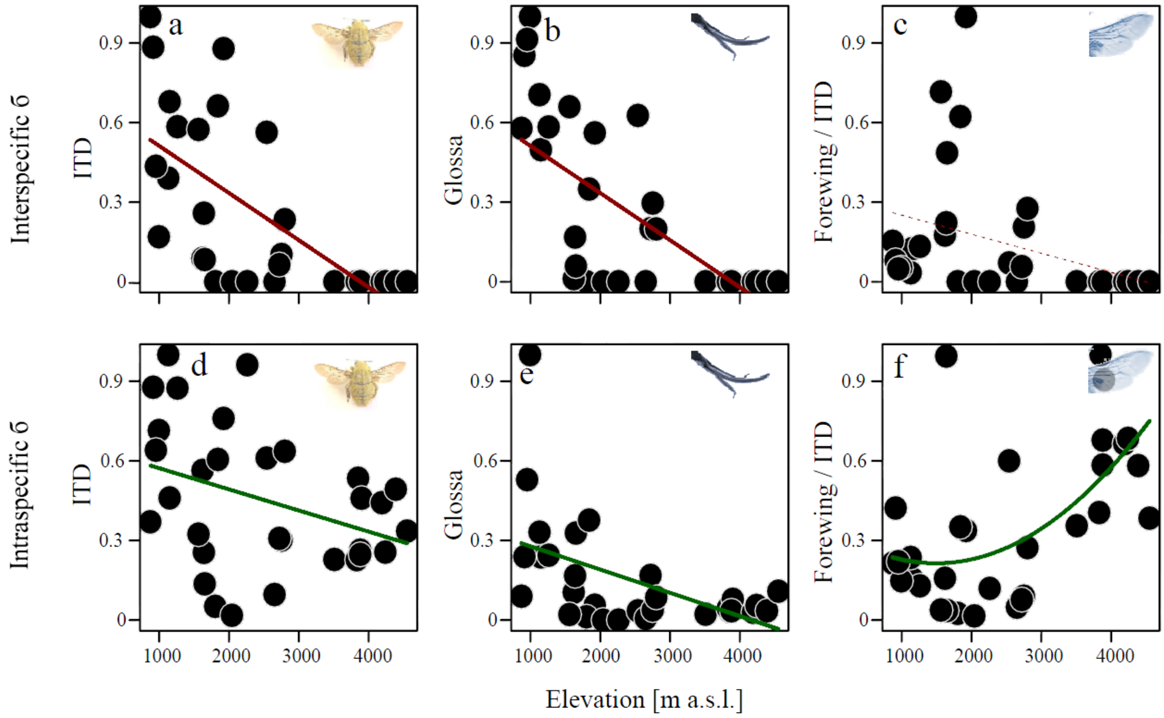

Figure III.3 Change of interspecific trait variances (a-c) and intraspecific trait variances (d-f) with increasing elevation. Black circles represent interspecific trait variances per study site (a-c) or intraspecific trait variances averaged per study site (d-f). For standardization, variances were related to the maximum variance detected for the respective trait in the region. Interspecific variances of (a) intertegular distance (ITD), (b) glossa length, and (c) relative forewing length decreased with elevation. The decline of interspecific variances was paralleled with a decrease of averaged intraspecific variances in (d) ITD and (e) glossa. Intraspecific variances of (f) relative forewing length increased with elevation.

Supplementary data to Chapter III

Supplementary Materials and Methods

The study was conducted on the south-eastern slopes of Mount Kilimanjaro (Tanzania, East Africa, 2°45’-3°25’S, 37°00’-37°43’E) between 2011 and 2012. We selected thirty-five 50 x 50m study sites covering natural and seminatural habitats in seven elevational belts ranging from savannah (871 – 1130m a.s.l.), homegarden (1150 – 1840m a.s.l.), low montane forest (1620 – 2040m a.s.l.), *Ocotea* forest (2260 – 2750m a.s.l.), *Podocarpus* forest (2720 – 2800m a.s.l.) and *Erica* forest (3510 – 3900m a.s.l.) to alpine *Helichrysum* zones (3880 – 4550m a.s.l.). Bees were captured with pan traps that were installed close to the ground and in the canopy. We conducted three sampling rounds, pooled species plotwise and sorted them to morphospecies. For all individuals, we measured intertegular distances, glossa lengths and relative forewing lengths and calculated means and standard deviations. We measured maximal ten individuals of one species per plot. On plots were we found more than ten individuals per species, we randomly sampled the remaining individuals from a Gaussian probability distribution of trait values, which was defined by the mean and standard deviation (SD) of the ten measured individuals (Albert *et al.*, 2011).

Species richness patterns along elevation were analyzed with generalized linear models assuming poisson error distributions. With linear models we examined shifts of community level trait means along elevation. The responses of mean trait values and trait variation to elevation were analyzed with generalized linear mixed effect models (fixed effect: elevation, crossed random effects: species, study site) (Bates *et al.*, 2013; Kuznetsova *et al.*, 2013) (III.S3). An ANOVA-based approach was used to separate within- and between-group variance components (Violle *et al.*, 2012) (III.S5). Trait measures of singleton species were excluded from these analyzes as these were assumed to be transient species and intraspecific variation cannot be calculated.

III.S1 – Species richness along elevation

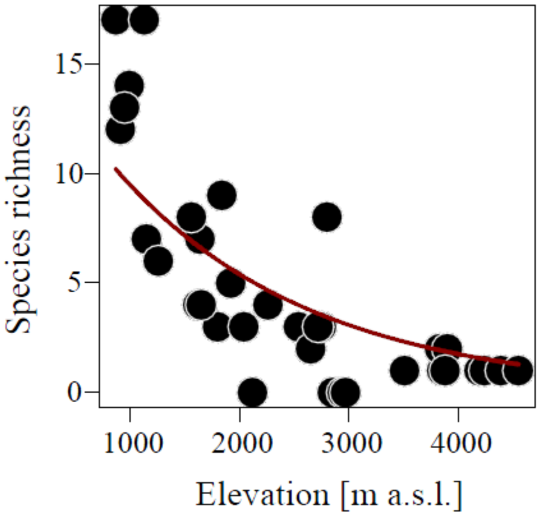

Figure III.S1 Elevation predicts species richness of wild bees at Mount Kilimanjaro.

III.S2 – Abundance-weighted means versus species-weighted means

Table III.S2 Relationship between (a) abundance-weighted or (b) species-weighted community trait means and elevation.

Trait		Estimate	SE	t-value	p
(a) abundance-weighted means					
ITD	Intercept	0.96	0.01	10.06	<0.001
	elevation	-1.94e-04	3.46e-05	-5.60	<0.001
GL	Intercept	2.20	0.22	9.98	<0.001
	elevation	-4.63e-04	7.99e-05	-5.80	<0.001
rFL	Intercept	1.03	0.04	24.55	<0.001
	elevation	6.91e-05	1.52e-05	4.54	<0.001
(b) species-weighted means					
ITD	Intercept	1.03	0.09	11.18	<0.001
	elevation	-1.93e-04	3.33e-05	-5.80	<0.001
GL	Intercept	2.17	0.18	12.09	<0.001
	elevation	-4.33e-04	6.50e-05	-6.66	<0.001
rFL	Intercept	1.06	0.04	27.27	<0.001
	elevation	6.00e-05	1.4e-05	3.98	<0.001

We compared two different community trait means. One is calculated by averaging across all individuals within a community (=abundance-weighted means; see Fig. III.2). Here dominant species (and their traits) shape mean values more than rare species do. In contrast, the species-weighted mean is calculated by averaging across the species within a community independent of their abundance. The trait mean distribution patterns along elevation were consistent for both types of community trait means.

S3 – Intraspecific trait mean shifts with increasing elevation

Intraspecific mean shifts with increasing elevation were analyzed with generalized linear mixed effect models (lmer-function within the R-package lme4 (Bates et al. 2013)). P-values were calculated based on Satterthwaite´s approximations (summary function within the R-package lmerTest (Kuznetsova et al. 2013)).

Table III.S3 Effects of elevation on intraspecific trait means. Output of generalized mixed effect models with individual based trait values as response, elevation as explaining variable and species and plot as crossed random terms. Within species, body size (represented by intertegular distance ITD) on average significantly increased with increasing elevation, while glossa length (GL) decreased, and relative forewing length (rFL) stayed on constant levels.

Trait		Estimate	SE	t-value	p
ITD	Intercept	2.02	0.17	12.18	<0.001
	elevation	7.5*e-05	2.2*e-05	3.43	<0.001
GL	Intercept	1.6	0.92	8.35	<0.001
	elevation	-5.5*e-05	2.5*e-05	-2.18	0.033
rFL	Intercept	3.04	0.12	24.71	<0.001
	elevation	6.7*e-05	5.7*e-05	1.16	0.250

III.S4 – Intraspecific variance declines with increasing elevation

There are two non-exclusive explanations for the detected change of intraspecific variances along elevation (Fig. III.3d-f, main document): Either the shifts are due to changes of variation within species (e.g. individuals occurring in the lowlands having higher phenotypic variability than individuals of the same species from the higher regions), or the shifts are explained by changes in species composition, with communities in lowlands holding more species with higher phenotypic variability than communities in higher elevations. To disentangle these effects we calculated intraspecific variance for all species at a plot level. We then used linear mixed effect models to analyze the influence of elevation on this intraspecific variance, while controlling for species in the random term. A significant result indicates that intraspecific variance is at least partly determined by changes of variance within species.

Table III.S4 Output of linear mixed effect model with the intraspecific variance of single traits (averaged for each species on a plot-level) as response variable, elevation as a predictor variable and species as random term. Significant effects of elevation on intraspecific variance indicate that the decline of intraspecific variance along elevation is caused by variance declines within species.

Trait		denDF	F-value	p-value	Direction
ITD	Intercept	58	57.57	<0.0001	
	Elevation	58	0.43	0.5156	-
GL	Intercept	57	4.03	0.0494	
	Elevation	57	0.01	0.9145	-
rFL	Intercept	58	45.04	<0.0001	
	Elevation	58	7.37	**0.0087**	↗

Only the intraspecific variation of relative forewing lengths was partly explained by an increase of variances within species and not solely by species turnover.

III.S5 Calculation of inter- and intraspecific variances

Interspecific (= between-species) trait variance was calculated for each study site and trait by

$$\sigma^2{}_{INTER} = \sum_{k=1}^{n} \sum_{i=1}^{m} \frac{(\hat{y}_k - \bar{y})^2}{N}$$

with $\hat{y}_k$ being the species mean of one respective trait within a community of species k = 1 to species n, $\bar{y}$ being the abundance weighted mean of the trait across the whole species community, N being the total number of individuals in a community, and i = 1 to m being the individuals within each species.

Intraspecific (within-species) trait variance was calculated for each study site and trait by

$$\sigma^2{}_{INTRA} = \sum_{k=1}^{n} \sum_{i=1}^{m} \frac{(y_i - \hat{y}_k)^2}{N}$$

with y_i being the respective trait value of individual i=1 to individual m of species k=1 to species n, $\hat{y}_k$ being the mean of species k, and N being the total number of individuals of the community (N).

Both inter- and intraspecific trait variances were standardized by dividing study site-based variances by the maximally observed inter- or intraspecific variance, respectively; in consequence variance values range from zero to one.

CHAPTER IV: COMPLEMENTARY ECOSYSTEM SERVICES PROVIDED BY PEST PREDATORS AND POLLINATORS INCREASE QUANTITY AND QUALITY OF COFFEE YIELDS

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ABSTRACT

Wild animals substantially support crop production by providing ecosystem services like pollination and natural pest control. However, the strengths of synergies between ecosystem services and their dependencies on land use management are largely unknown. Here we took an experimental approach to test the impact of land use intensification on both individual and combined pollination and pest control services in coffee production systems at Mount Kilimanjaro. We established a full-factorial pollinator and vertebrate exclosure experiment along a land use gradient from traditional homegardens (agroforestry systems), shaded coffee plantations to sun coffee plantations (total sample size = 180 coffee bushes). The exclusion of vertebrates led to a reduction of fruit set of circa 9%. Pollinators did not affect fruit set, but significantly increased fruit weight of coffee by an average of 7.4%. We found no significant decline of these ecosystem services along the land use gradient. Pest control and pollination service were thus complementary contributing to coffee production by affecting the quantity and quality of a major tropical cash crop across different coffee production systems at Mount Kilimanjaro.

Key words: land use change, agroforestry, pollination, *Coffea arabica*, biological pest control, Mount Kilimanjaro

INTRODUCTION

The productivity of crops depends on an intricate interplay of farming practices, abiotic conditions, and ecosystem services provided by natural species communities (Boreux *et al.*, 2013). However, in agricultural practice, the different components of such interplay still receive unequal attention. While the cost-benefit analyses of human inputs into cropping systems are easily assessable, the valuations of ecosystem services are less obvious and often neglected when new farming strategies are adopted (Fisher *et al.*, 2008). Indeed, intensification of land use is often considered as the only possibility to meet the food demands of growing human populations. However, an impoverishment of biotic communities in the course of local land use intensification may reduce the natural functionality of agricultural systems. Such decline requires costly human interventions which can further accelerate the loss of animal-mediated ecosystem services (Dale & Polasky, 2007; Bommarco *et al.*, 2013).

Two important ecosystem services that contribute to crop productivity and food security are pollination and natural pest control (Naylor & Ehrlich, 1997; Klein *et al.*, 2007). About two thirds of all crop species benefit from cross-pollination by developing higher fruit sets and/or higher fruit quality (Klein *et al.*, 2007; Aizen *et al.*, 2009). Pollination also increases yield stability and maintains genetic variability of crops, which counteracts inbreeding depression and facilitates resistance to environmental changes (Garibaldi *et al.*, 2011) . Pest predation, in contrast, enhances crop productivity indirectly: approximately 35 to 40 percent of potential crop yields worldwide are destroyed by pests, including herbivorous insects (Oerke, 2005; Pimentel, 2009). Herbivores either damage the utilized parts of crops directly, or induce resource allocations in plants. For example, leaf damage by herbivorous pests may result in reduced fruit and seed set (Strauss *et al.*, 2002). Birds and bats, preying upon herbivorous pests, can directly reduce pest infestation rates and thus indirectly increase crop productivity (Mols & Visser, 2002; Kalka *et al.*, 2008; Kellermann *et al.*, 2008).

Ecosystem services provided by pollinators and pest predators in agricultural production systems can be either additive or synergistic (Lundin *et al.*, 2012). In case of additive effects, pollinators and pest predators affect the same yield parameter (e.g. fruit set), but independently of each other, or they affect different yield parameters (e. g. fruit set and fruit quality), resulting in complementary effects of both guilds on crop production. However, there may also be interacting effects between pollinators and predators. Low levels of pest control can reduce pollination services due to altered floral displays or herbivore-induced changes in plant volatile components that are avoided by pollinators (Kessler *et al.*, 2011). Likewise, some seed predators preferentially attack cross-pollinated ovules, counteracting positive pollinator effects. Therefore, the top-down control of seed predators can stabilize positive pollination effects (Lundin *et al.*, 2012). Such scenarios can lead to combined effects of multiple ecosystem services that are different from those of individual services.

Ecosystem services provided by pollinators and pest predators are known to be negatively affected by local land use intensification (Naeem *et al.*, 1995; Cardinale *et al.*, 2012). For instance, loss of habitat structure by tree removal or frequent ploughing reduces the number of suitable nesting sites for animals (Newton, 1994). Herbicides diminish plant diversity and thus the resource diversity for bees (Nicholls & Altieri, 2012). Regular insecticide application affects abundances of insect pollinators (Johansen, 1977) and decreases the amount and temporal stability of food resources for insect predators such as birds and bats. Also, mass-flowering events or high biomass turnover rates that are characteristic of intensively managed cropping systems, provide temporally unstable food and nesting resources (Peters *et al.*, 2013), while the use of machines and increased human activity on these farms disturb mating, breeding and foraging activities (Rodenhouse *et al.*, 1995). The consequent loss of diversity poses serious threats to ecosystem services, as modified animal communities may be functionally impoverished (Canaday, 1996; Larsen *et al.*, 2005).

While the effects of both pollinators and insect predators on crop performance are comparatively well understood, very few studies investigate ecosystem service synergies, i.e. interactions between functional groups and consequences for yield quantity and quality in a land use context (Lundin *et al.*, 2012; Maas *et al.*, 2013; Martin *et al.*, 2013). In this study, we investigated the impact of increased management intensity on single and combined contributions of pollinators and vertebrate pest predators to the productivity of coffee in three farming systems on Mount Kilimanjaro, (Tanzania). *Coffea arabica* is a self-pollinating crop that can benefit from insect pollination by developing higher fruit set, heavier fruits and fewer seed aberrations (Ricketts, 2004a). The most important flower visitors are social bees (*Apis mellifera* and stingless bees), followed by solitary bees, syrphids and butterflies (Ngo *et al.*, 2011). Birds and bats have been shown to reduce herbivore numbers and herbivory rates in natural systems (Kalka *et al.*, 2008), as well as coffee-specific pest species (Greenberg *et al.*, 2000; Perfecto *et al.*, 2004; Kellermann *et al.*, 2008), but the consequences for fruit set and fruit quality of coffee are still a matter of debate (but see (Kellermann *et al.*, 2008)). Ecosystem services provided by pollinators and vertebrates are threatened by the local intensification of farming practices on Mount Kilimanjaro. The cash crop coffee, which was traditionally planted in complex agroforestry systems (Chagga homegardens), is now mainly produced in simplified monocultures under shade trees or at full sunlight exposure. Such habitat changes could affect pollinator and pest predator populations with consequences for the stability of single and combined ecosystem services. Against this background, we address the following questions:

(1) What are the single and combined effects of pest control agents and pollinators on coffee production?

(2) How do differently managed coffee production systems influence the magnitude of ecosystem services provided by insect predators and pollinators?

METHODS

Study area and study sites

The study was conducted from September 2011 to November 2012 on the southern slopes of Mount Kilimanjaro, Tanzania, at elevations between 1120 m and 1660 m above sea level. We selected four 50 m x 50 m study sites for each of three coffee (*Coffea arabica*) production systems: traditionally managed homegardens (HOM), shaded coffee plantations (SHA) and sun coffee plantations (SUN). The distance between study sites ranged from 0.48km to 45.56km (2.96 km to 40.05 km between study sites of the same production system). Homegardens are agroforestry systems with a diverse mixture of forest vestiges and fruit trees covering the most important cash crops coffee and banana (*Musa spp.*), which are planted within a variety of intercrops. Canopy cover averages 80% in these systems. On shaded coffee plantations, coffee is planted in monocultures under shade trees, with a canopy cover of around 30%, while in sun coffee plantations coffee is grown in monoculture at full sunlight exposure.

In all management systems, farmers were requested to continue their usual farming practice during the study period: Pruning was conducted once per harvest season in all systems. In homegardens, insecticides and fungicides were irregularly applied depending on infestation rate and income level of farmers. Weeds were removed manually. On shaded and sun coffee plantations regular, intensive pesticide and fungicide spraying was applied on the whole farm. Weeds were either controlled by herbicides (on two SHA sites and on three SUN sites), grass cutting (one SHA, one SUN) or manual weeding (one SHA). During the dry seasons (Dec – March, June – Oct) all plantations were frequently irrigated with sprinklers, while homegardens were supplied by traditional water channel systems.

Study design

On each study site we selected three clusters of four coffee bushes (minimum distance between clusters: approximately 15-20m) (Fig. IV.S1). Within clusters, we selected four bushes of similar size and with comparable bud status and applied to each bush one of the following treatments: (a) open control (b) pollinator exclosure, (c) vertebrate exclosure, and (d) combined pollinator and vertebrate exclosure (Fig. IV.1). As pre-experiments revealed that the less conspicuous pollinator exclosures got often damaged during pruning, harvest or pesticide treatments by farmers, we selected three additional coffee bushes per study site outside of clusters and installed pollinator exclosure treatments and control twigs to supplement pollinator treatment bushes within clusters (Fig. IV.S1). To exclude pollinators we used transparent gauze bags (mesh size: 0.39 x 0.77 mm) that were pulled over two randomly selected twigs with closed flower buds. Gauze bags were stretched with strings to avoid insect pollination from outside the nets and waterlogging. Two twigs served as open controls to directly contrast them to the pollinator exclosure treatment on the hierarchical level of the coffee bush (Fig. IV.S1).

Vertebrates were excluded from two whole coffee bushes by cultivation guard net cubes (~2 m x 2 m x 2m, mesh size 30 mm x 30 mm). One of the vertebrate exclosures was combined with one pollinator exclosure treatment (combined exclosure). Vertebrate exclosure nets were checked at least every two weeks and repaired or replaced if necessary. One coffee bush per cluster without any treatment was selected as an open control (Fig. IV.1). On both vertebrate exclosures and controls, we marked two twigs for fruit parameter assessment. A more detailed description of the experimental set up is illustrated in Fig. IV.S1 and Plate IV.S1.

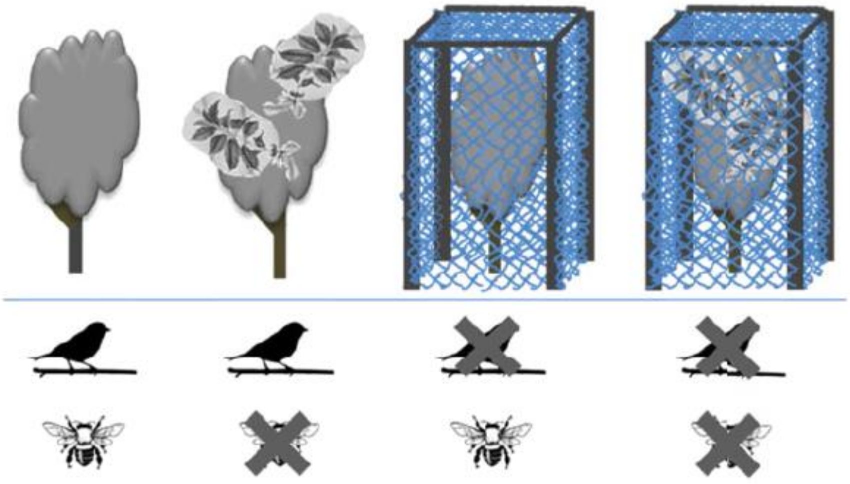

Figure IV.1 Experimental set up. From the left to the right: open control, pollinator exclosure, vertebrate exclosure, combined pollinator and vertebrate exclosure (see figure S1a for more details).

Pollinator visitation rates

During coffee blossom we selected coffee twigs with open coffee flowers (mean±SE number of coffee flowers per twig = 66±2.9) and recorded in ten minute observation intervals all flower visitations of honey bees (*Apis mellifera*) and "other pollinators", including wild bees, syrphid flies and butterflies. We repeated observations on at least 16 coffee bushes per study site, including bushes of all treatments. Pollinator visitation rates were calculated by dividing the number of visits of honey bees and other pollinators respectively by the number of observed flowers. Neither vertebrate exclosure cubes, nor the presence of pollinator exclosures on a tree negatively affected flower visitation rates on open twigs (Tab. IV.S2a).

Fruit parameter and herbivory assessment

One week after coffee blossom pollinator exclosures were removed to avoid exclusions of leaf and fruit herbivores that oviposite during early fruit set on the respective twigs. We counted the number of flowers with withered petals on all marked twigs. Buds which were not open by that time were manually removed and not counted. Six weeks after coffee blossom, we counted the number of early fruits per marked twig and related it to the number of flowers (hereafter early fruit set). Fruits were counted again 6 months after the coffee blossom, as by that time fruits were harvestable on a the first plots. The chance of further fruit loss on other plots was low, as fruit drop in Arabica coffee takes place in the first three months after blossoming (DaMatta *et al.*, 2007). Fruits of the same bush and twig treatment were pooled and related to both the corresponding numbers of flowers (hereafter late fruit set) and number of early fruits (hereafter fruit retention rate), respectively (see statistics for more details). After fruit ripening, coffee berries of all treatments were harvested. For 15 randomly selected fruits per bush and twig treatment, we assessed fruit weight and infestation rates with the coffee berry borer (*Hypothenemus hampei*), a pest insect which drills ripening seeds for mating and oviposition (Tab. IV.S3). Herbivory rates were determined for each coffee bush by estimating the proportion of leaf damage of 30 randomly selected leaves of different age classes before the installation of vertebrate exclosures and six months later.

Statistical analyses

We analysed the effect of exclosure treatments on early fruit set, late fruit set and fruit retention rate with generalized linear mixed effects models ('lmer' function in package 'lme4'). The total number of flowers (and fruits) differed enormously between study sites. Therefore, we used a two-vector response variable for fruit set and retention rate, consisting of the number of harvestable fruits (success) and the number of “dropped fruits” (failures, i.e. number of flowers (or early fruits) – number of harvestable fruits) for which we assumed a binomial error distribution (Crawley, 2007). We tested treatment and coffee production system effects on early and late fruit set and retention rate with pollinator exclosure (PollEx), vertebrate exclosure (VertEx) and production system (HOM, SHA, SUN) and all possible interactions as fixed factors. To meet the hierarchical structure of the study design, we added study site, cluster, bush and twig as nested random effects. Overdispersion of the data was corrected by adding an observation-level random effect (Bates *et al.*, 2013). Presence/absence of the coffee berry borer was analysed in the same way (IV.S3). Impacts of VertEx, PollEx, production system and all possible interactions on fruit weight were investigated with linear mixed effects models, because the error distribution of this response variable followed a normal distribution. To meet the nested study design, we averaged fruit weight per treatment and included study site, cluster and bush as nested random

effects ('lme' function in package 'nlme'). For model simplification we performed likelihood ratio tests and removed all terms that were not statistically significant (Crawley, 2007).
We tested if the exclusion of vertebrates influenced coffee production via altered herbivory levels on coffee bushes by fitting two linear mixed effects models with vertebrate exclosure, production system and its interaction as fixed factors, study site and cluster as a random factors and averaged herbivory per tree before and six months after the exclosures as response variables (IV.S4). The influences of production system on visitation rates of “honey bees” and “other pollinators” were analysed with linear mixed effect models, with study site as a random factor. Models were simplified using likelihood ratio tests. All statistical analyses were conducted with the software R 2.14.2 for Windows (R Development Core Team, 2012).

RESULTS

Pollinators and vertebrates increased coffee productivity complementarily by affecting different fruit parameters. Vertebrate exclosure had an effect on fruit quantity: early fruit set, fruit retention rate (Tab. IV.S5) and late fruit set were significantly higher on bushes, that were accessible to flying vertebrates, than on vertebrate exclosures (Tab. IV.1, Fig. IV.2). In contrast, pollinators had no effect on fruit quantity parameters (Tab. IV.1). Both the three-fold interaction between treatments and production system, and the two-fold interaction effects (PollEx x VertEx and VertEx x production system) on fruit set were not significant and thus not included in the minimal adequate model (Tab. IV.1).

We measured late fruit set reductions by an average of 9.0% under vertebrate exclosures. Also herbivory rates were affected by the six-month vertebrate exclosure: Before the exclosure treatment, herbivory rates did not differ between coffee bushes (Tab. IV.S4a). However, six months after exclosure installation, leaf herbivory rates were significantly higher under vertebrate exclosures in homegardens and unshaded plantations than on control bushes to which vertebrates had access (Fig. IV.3, Tab. IV.S4b). The infestation of berries with the fruit borer *Hypothenemus hampei* was not affected by treatments and production system (Tab. IV.S3) (averaged infestation rates 1.53%).

Fruit quality was affected by pollinator exclosure, but not by vertebrate exclosure: Fruit weight decreased on average by 7.4 % when pollinating insects were excluded from coffee flowers (Tab. IV.1, Fig. IV.2). Both threefold and twofold interaction effects (VertEx x PollEx, PollEx x production system) on fruit weight were not significant (table IV.1).

Table IV.1 Production system-dependent influence of pest control and pollination on *C. arabica* fruit set and fruit weight, respectively. Output of (generalized) mixed effects models with fruit set and fruit weight as response variables and vertebrate exclosure (VertEx), pollinator exclosure (PollEx), production system and their interactions as explanatory variables (full models). After model simplification, VertEx (in case of fruit set) or PollEx (in case of fruit weight) remained the only explaining variables in the models (simplified models). Significance codes: **p < 0.01; *p < 0.05.

	full model					**simplified model**				
Fixed effects	nDF	dDF	Test statistics	*p*		nDF	dDF	Test statistics	*p*	
Late fruit set			χ^2					χ^2		
VertEx	1	–	4.73	0.030	*	1	–	4.89	0.027	*
PollEx	1	–	0.17	0.682						
Production system	2	–	6.04	0.049	*					
VertEx x PollEx	1	–	0.34	0.557						
VertEx x Production system	2	–	3.91	0.142						
PollEx x Production system	2	–	1.51	0.470						
VertEx x PollEx x Prod. syst.	2	–	1.00	0.608						
Fruit weight			F					F		
VertEx	1	90	0.13	0.724						
PollEx	1	78	8.84	0.004	**	1	83	8.93	0.004	**
Production system	2	9	0.48	0.636						
VertEx x PollEx	1	78	1.55	0.217						
VertEx x Production system	2	90	0.84	0.434						
PollEx x Production system	2	78	0.63	0.534						
VertEx x PollEx x Prod. syst.	2	78	1.13	0.329						

The composition of flower visitors shifted along the land use gradient: visitation rates of honey bees (*Apis mellifera*) drastically increased with land use intensity, resulting in 3.4 times higher honey bee visitation rates on sun plantations than in homegardens. Interestingly, in homegardens more than one third of flower visitations were by other pollinators than *Apis mellifera*. In total flower visitation rates by other pollinators were 8.2 times higher in homegardens than in sun plantations (Fig. IV.3, Tab. IV.S2b).

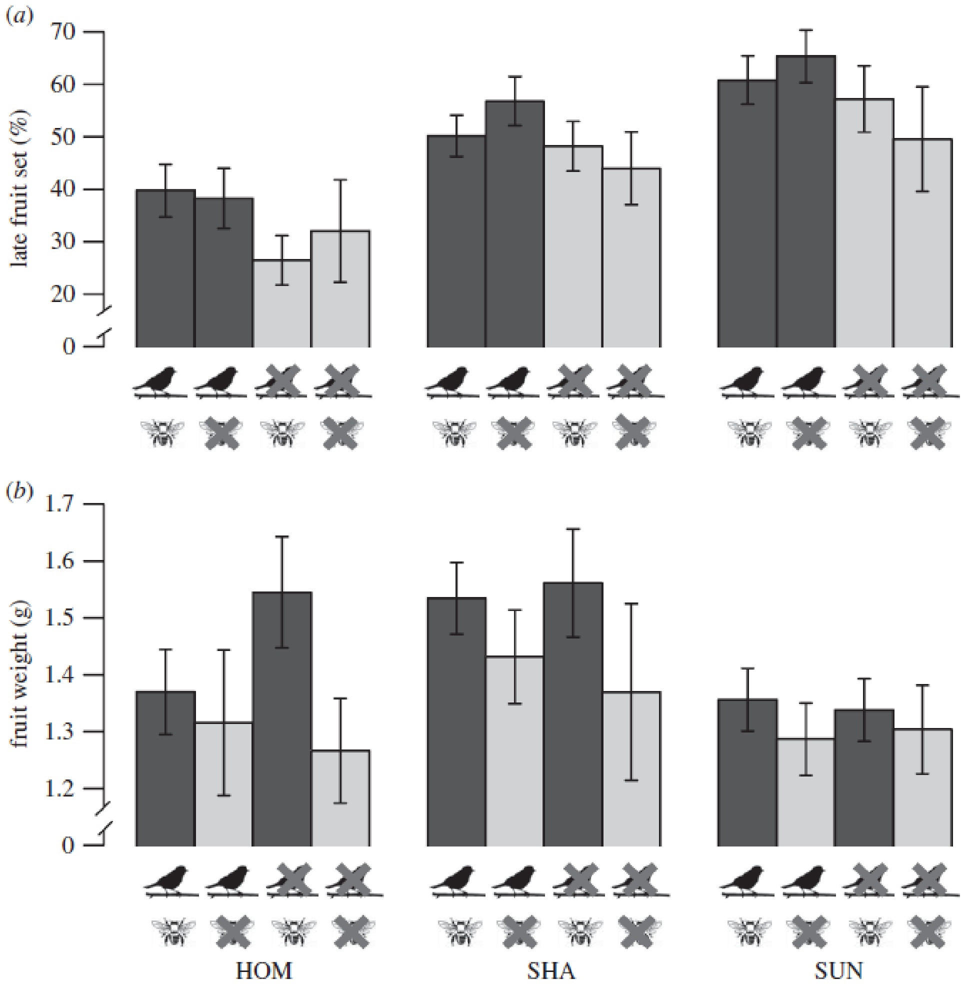

Figure IV.2 Effects of single and combined vertebrate and pollinator exclosures on late fruit set (a) and fruit weight (b) of *Coffea arabica* in different production systems (homegardens (HOM), shaded plantations (SHA), sun plantations (SUN)). Statistics are presented in Tab. IV.1 and Tab. IV.S6. Vertebrate pest predation, but not pollination, positively influenced fruit set. In contrast pollination, but not pest predation resulted in increased fruit weights. Bar colors in each panel indicate which treatments were lumped in the course of model simplification. Please note that fissures were applied to y-axes for better effect resolutions.

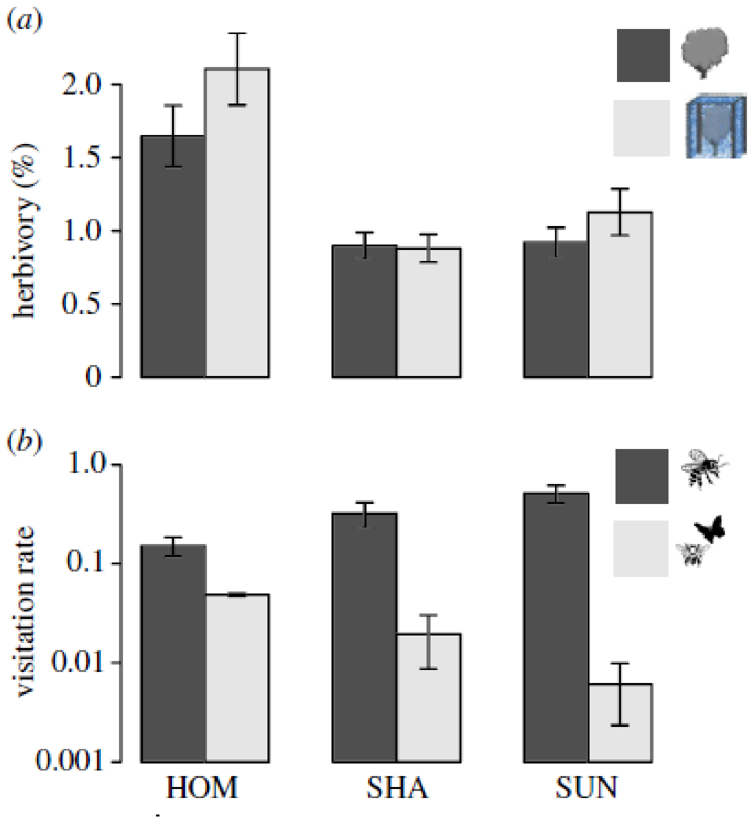

Figure IV.3 Herbivory and pollinator visitation rates at Arabica coffee in different production systems. The upper panel shows averaged leaf herbivory (%) on open controls (dark bars) and under vertebrate exclosures (light bars) six months after exclosure installation. The lower panel presents averaged coffee flower visitation rates (i.e. averaged number of pollinator visits per flower) of honey bees (*Apis mellifera*) (dark bars) and “other pollinators”, including wild bees, butterflies and syrphid flies (light bars) during ten minute observation intervals. Statistics are presented in Tab. IV.S4b (herbivory) and Tab. IV.S2b (visitation rates). Note log-transformation of the y-axis in the lower panel.

DISCUSSION

Complementary contribution of pest control agents and pollinators to coffee production

We showed that both vertebrate pest predators and pollinators contribute to coffee production at Mount Kilimanjaro by affecting different yield parameters, i.e. fruit quantity (fruit set) and fruit quality (fruit weight), respectively. As both fruit set and fruit weight increase the total yield of coffee farmers, the conservation of ecosystem services provided by pollinators and flying vertebrates may be of considerable economic importance. The exclusion of birds and bats resulted in an increase of herbivory and, importantly, also in a reduction of fruit set by an average of 9.0%. The effectiveness of birds and bats in controlling arthropod abundances, pest infestation rates and herbivory has been shown on coffee farms (Greenberg *et al.*, 2000; Perfecto *et al.*, 2004; Kalka *et* *al.*, 2008; Kellermann *et al.*, 2008), however, the consequences of such changes for economically relevant fruit parameters are rarely documented (but see Kellermann *et al.*, 2008). We suggest that the increase of herbivory rates under the exclosures partly explained the reduction of fruit set, as herbivory pressure can trigger resource allocation from reproductive to vegetative organs of plants (Hendrix, 1988). However, as the increase of herbivory was only weak, we assume that changes in arthropod assemblages (e.g. an increase of leaf sucking insects (Maas *et al.*, 2013)) under vertebrate exclosures additionally affected fruit set. In addition to vertebrates, parasitoid wasps are known as important agents controlling herbivores on coffee plants (Infante *et al.*, 2008) whose contribution to coffee production could not be analyzed in this study. Future studies should incorporate this important group in experiments to assess the total benefit of natural biota for agricultural production.

Self-compatible *Coffea arabica* profited from insect cross-pollination, by developing on average 7.4% heavier fruits on open pollinated twigs than on self-pollinated twigs. An effect of cross-pollination of similar order of magnitude has been shown in the few other studies that considered not only fruit set but also fruit weight of coffee in their analyses (Roubik, 2002; Philpott *et al.*, 2006). Increased pollen loads and higher genetic pollen diversity have been proposed to influence the seed weight of self-compatible plants, but detailed information about the physiological mechanisms are still missing (Philpott *et al.*, 2006). Seed size (which is correlated with seed weight) is of special economic interest as it does not only increase the total yield but also has a crucial impact on the quality and price of coffee. To our surprise, pollinators did not affect fruit set, which is inconsistent with the results of other studies investigating pollinator dependencies of coffee (Roubik, 2002; Klein *et al.*, 2003), though not uncommon for self-compatible plants like *Coffea arabica* (Free, 1993). Ngo et al. (2011) proposed that effects of pollinator exclosures differ between locations or coffee varieties (Ngo *et al.*, 2011). Indeed, most previous studies were conducted in the Neotropics or Asia, but not in Africa, where coffee originates from (DaMatta *et al.*, 2007).

We did not find interaction effects between pollination and pest control. These results suggest that in *Coffea arabica* the effect of pollination on fruit weight is independent of the pest control level and, *vice versa*, cross-pollination does not alter the effect of pest control on fruit set. We suggest that in coffee physiological mechanisms triggered by herbivory (e.g. resource allocations) are not linked to the pollination-dependent physiological pathways affecting fruit quality, which might explain independencies. However, by installing vertebrate and pollinator exclosures only shortly before flowering, we a priori excluded some interaction mechanisms that are explained by increased herbivory immediately before or during flowering (e.g. floral tissue damage diminishing the attractiveness of flowers to pollinators) (Kessler *et al.*, 2011). Furthermore, unconsidered pest control agents (like e.g. parasitoids) could interact with pollination services.

Effects of local land use intensity on ecosystem services

Against expectations, we found no significant effect of land use intensity on the ecosystem services provided by pollinators and pest predators. Sun coffee plantations are currently embedded in a tessellated and still diverse landscape at Mount Kilimanjaro, and may benefit from high connectivity to structurally more complex habitats like homegardens, shaded plantations, and forests, which provide nesting sites and stable food resources for pest predators and pollinators (Ricketts, 2004a). Mobile animals have been proposed to increase their foraging ranges in intensified systems, which can additionally buffer potential ecosystem service declines (Breitbach *et al.*, 2010). Interestingly, we detected a shift in the composition of flower visitors along the land use gradient: mass-flowering events on sun plantations attracted only very few other coffee flower visitors than *Apis mellifera*, while in homegardens more than one third of flower visitations were from wild pollinators. Despite variable total flower visitation rates pollination services were stable in all production systems. Either there is no pollinator-limitation along the land use gradient, or the services provided by a few wild pollinators can fully replace pollination service by more abundant honey bees (Garibaldi *et al.*, 2013). This suggests that management forms that support wild pollinators are both productive and less sensitive than systems relying on single managed pollinator species (honey bees), as pollination services are stabilized under varying environmental conditions (Garibaldi *et al.*, 2011). This is supported by Ricketts, who showed that wild pollinators can compensate drastic *Apis* declines by stabilizing visitation rates on coffee farms that are near to tropical forest fragments, but not on isolated farms (Ricketts, 2004b). Further expansions of sun coffee plantations that isolate intensified systems from more natural systems may therefore reduce the stability of ecosystem services, with potential negative effects for crop productivity.

We showed that the ecosystem services of both pest predators and pollinators complementary support productivity of a major tropical cash crop, *Coffea arabica*. Land use intensification does not influence these ecosystem services at Mount Kilimanjaro; however, shifts in the composition of pollinator visitors raise concern about the stability of ecosystem services in intensified systems. Optimization of ecosystem services in agricultural landscapes thus requires both the knowledge of multiple ecosystem services operating in parallel, but also of management strategies that reliably match the demands of wild animals providing these services.

Supplementary data to Chapter IV

IV.S1a – Cluster arrangement and experimental set up

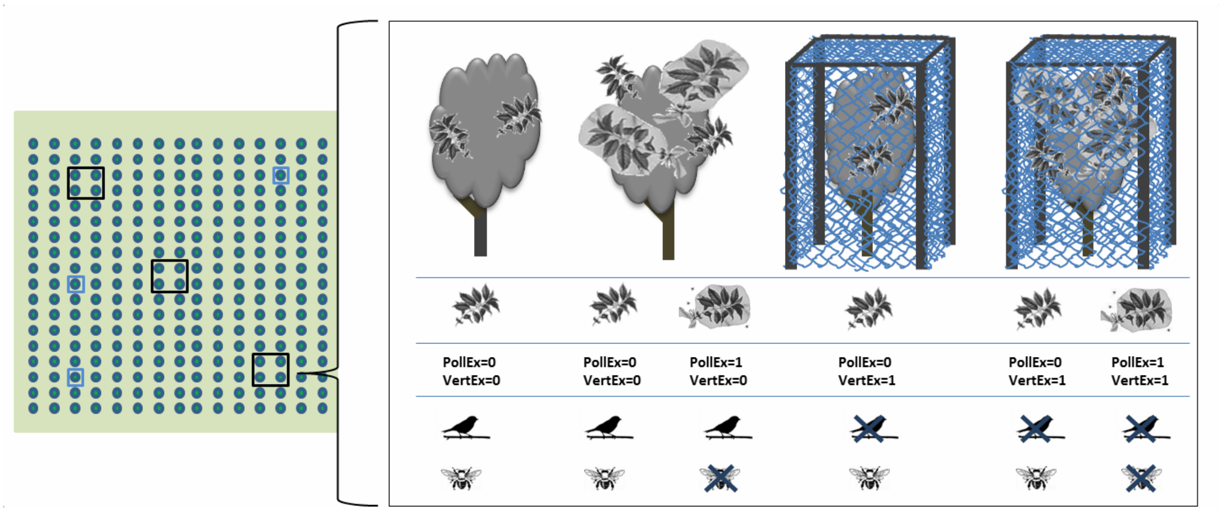

Figure IV.S1 Schematic illustration of cluster arrangements on coffee farms (left side) and extended version of the experimental set up (right side). Black rectangles mark the position of selected clusters. Blue squares mark the position of additional pollinator exclosure trees. The additional pollinator exclosures were installed to supplement losses inside the clusters. During the experiment treatment losses were high and treatment effect sizes were comparatively small. Therefore, we included supplementary bushes in all analyses (extra pollinator exclosures got separate cluster numbers in statistical models). The four different treatments (control, pollinator exclosure, vertebrate exclosure and combined exclosure) are described by two variables, i.e. pollinator exclosure “PollEx” and vertebrate exclosure “VertEx” in the models. Note that control branches on a coffee bush with pollinator exclosures are treated as open control in all models, whereas control branches on coffee bushes with combined pollinator vertebrate exclosures are treated as VertEx in all models. For fruit parameter assessment (fruit set, fruit weight), we pooled two pollinator exclosure twigs per tree and two control twigs respectively.

Plate IV.S1 Left: Picture of single vertebrate exclosure (in the front) and combined vertebrate pollinator exclosure (in the back) on shaded coffee plantation. Right: Single pollinator exclosure during coffee blossom.

IV.S2- Influence of all exclosure treatments on visitation rates

To check whether a vertebrate exclosures or the presence of pollinator exclosures on a coffee bush negatively affects pollinator visitation rates, we conducted observations on 107 trees with different treatments.

We analyzed data with a linear mixed effect model (response variable: Visitation rate, fixed factor: Treatment of the tree (levels: open control, pollinator exclosure tree, vertebrate exclosure, combined pollinator- vertebrate exclosure), random term: study site). Note that the treatment “pollinator exclosure” refers this time to observations on open control twigs on a pollinator exclosure tree. On true pollinator exclosures twigs we did not observe any pollinators.

Table IV.S2a Effect of exclosure treatments on insect pollinator visitation rates.

	numDF	denDF	F-value	p-value
Intercept	1	93	26.55	<0.0001
Treatment	3	93	1.30	**0.279**

To compare visitation rates along the land use gradient we conducted observations on in total 204 coffee bushes (97 of them did not belong to our selected trees). During observations we distinguished between honey bee visitors (*Apis mellifera*) and other pollinators (including wild bees, syrphid flies, and butterflies). We used linear mixed effect models to analyse whether visitation rates of different pollinators change along the land use gradient (response: visitation rate, fixed factor: land use type, random factor: study site).

Table IV.S2b Effect of land use type on pollinator visitation rates of honey bees (*Apis mellifera*) and other pollinators

Fixed effects	Estimate	SE	t-value	p	
Visitation rate of honey bee					
Intercept (HOM)	0.153	0.099	1.541	0.125	
Shaded plantation	0.170	0.132	1.285	0.234	
Sun plantation	0.360	0.132	2.727	0.026	*
Visitation rate of other pollinators					
Intercept (HOM)	0.049	0.008	6.295	<0.001	
Shaded plantation	-0.029	0.010	-2.814	0.022	*
Sun plantation	-0.043	0.010	-4.100	0.0034	**

IV.S3 – Influence of all exclosure treatments on the infestation rates with the coffee berry borer

The coffee berry borer (CBB) *Hypothenemus hampei* (Coleoptera) is a fruit herbivore that attacks coffee berries for oviposition, development and mating. The losses in coffee production through this pest insect can be enormous. We tested whether our exclosure treatments had an effect on the infestation rates with the coffee berry borer. We opened all harvested berries (all, but maximal 15 berries per treatment branch) and checked for coffee berry borer damages (presence/absence).

We analyzed data with generalized mixed effect models, assuming binomial error structures. We fitted the model with pollinator exclosure (PollEx), vertebrate exclosure (VertEx), land use type and all possible interactions as fixed factors and study site, cluster, tree and branch as nested random terms. Model simplification was based on likelihood ratio tests.

The null model was not significantly different from the most simplified model with one remaining fixed factor (Tab. IV.S3). Thus, neither pollinator exclosure, nor vertebrate exclosure, nor any interaction between treatments and land use type had an effect on the infestation rate with *Hypothenemus hampei*.

Table IV.S3 Modell comparison based on likelihood ratio tests. The null model (~1) did not significantly differ from the most simplified model with PollEx as last remaining explaining variable. Infestation rates of the Coffee berry borer (CBB) were thus not explained by exclosure treatments.

Modell	DF	logLik	Pr(>Chisq)
CBB~1	5	-612.67	
CBB~PollEx	6	-611.38	**0.107**

IV.S4- Herbivory rates before and after vertebrate exclosure treatments

To exclude herbivory rate differences between our selected bushes immediately before vertebrate exclosure installation, we estimated herbivory rates on 30 randomly selected leaves of all age classes per tree (exclusive additional pollinator exclosures (see IV.S1)). Averaged herbivory rates were analyzed with linear mixed effect models, which were fitted with VertEx, land use type and their interaction as fixed factors and study site and cluster as nested random terms. Model simplification was based on likelihood ratio tests.

Before exclosure

Table IV.S4a Modell comparison based on likelihood ratio tests. The null model (~1) did not significantly differ from the most simplified model with VertEx as last remaining explaining variable. Thus, herbivory rates did not differ between the selected trees before the vertebrate exclosure set up.

Modell	DF	logLik	Pr(>Chisq)
Herbivory~VertEx	1	-181.00	
Herbivory~1	2	-181.01	**0.887**

After exclosure

Six months after the vertebrate exclosure set up, we measured herbivory rates again and found an increase of averaged herbivory rates under vertebrate exclosures in homegarden and sun plantations (but not in shaded coffee plantations). The best model was the most complex model, with VertEx, land use type and their interaction as fixed factors.

Table IV.S4b Effect of vertebrate exclosure, land use type and their interaction on averaged herbivory rates, 6 months after exclosure installation.

	numDF	denDF	F-value	p-value
Intercept	1	105	53.44	<0.0001
VertEx	1	105	7.61	**0.007**
Land use type	2	9	3.20	**0.089**
VertEx x Land use type	2	105	3.10	**0.049**

IV.S5- Early frut set and fruit retention rate

We analyzed early fruit set (i.e. fruits set six weeks after coffee blossom) and fruit retention rates with the same model as presented for late fruit set: We created a two-vector response variable (fruit (success), no fruit (failure)) and fitted it with VertEx, PollEx, land use type and all possible interactions as fixed factors, and study site, cluster and coffee bush as random term. We then simplified the model based on likelihood ratio tests.

The best model explaining *early fruit set* included VertEx and land use type as explaining variables. Early fruit set was reduced under vertebrate exclosures and higher in sun plantations than in homegardens. There was no significant interaction between vertebrate exclosure and land use type. Pollinators did not affect early fruit set.

The best model explaining *fruit retention rate* included VertEx as only explaining variables. Fruit retention rates were lower under vertebrate exclosures than on open controls. Land use type did not affect fruit retention rates.

Table IV.S5 Influence of pest control and land use type on early fruit set and fruit retention rate in *Coffea arabica*. Output of generalized mixed effect models that were simplified based on likelihood ratio tests (best model presented).

	DF	χ^2	p-value
Early fruit set			
VertEx	1	5.91	**0.015**
Land use type	2	7.61	**0.018**
Fruit retention rate			
VertEx	1	4.91	**0.027**

IV.S6 – Late fruit set and fruit weight

Table IV.S6 Influence of vertebrate exclosures (VertEx) on late fruit set (a) and effect of pollinator exclosures (PollEx) on averaged fruit weight (b). Output of minimal adequate models (see table IV.1), showing the estimates. On twigs that were accessible for flying vertebrates 49.8% of all open flowers developed into harvestable fruits (1/(1+(1/exp(Estimate))), while under vertebrate exclosures 40.8% of all open flowers developed into fruits.

Fixed effects	Estimate	SE	DF	Test-statistics	*p*	
(a) Late fruit set				*z-value*		
Intercept (Control)	-0.0055	0.289	–	-0.019	0.985	
VertEx	-0.3677	0.166	–	-2.211	**0.027**	*
(b) Fruit weight [g]				*t-value*		
Intercept (Control)	1.4353	0.066	93	21.841	0.000	
PollEx	-0.1058	0.035	83	-2.989	**0.004**	**

CHAPTER V: GENERAL DISCUSSION

Predictors of bee richness along environmental gradients

In this dissertation we disentangled the factors which shape bee diversity, morphological traits and pollination services along climate and land use gradients on Mount Kilimanjaro. Temperature and resources have been widely recognized as the major predictors of species diversity along large-scale environmental gradients (Brown & Maurer, 1989; Brown, 2014). Recent studies found high support for limitations of diversity by resources, however, the mechanisms behind are still a matter of debate and have largely been analysed for vertebrate taxa (Ferger *et al.*, 2014; Price *et al.*, 2014). We showed that in ectothermic bees temperature-limitations were of considerably higher importance than resource-limitations, because temperature modulated the access of bees to floral resources. This aspect, which has mostly been ignored in literature, contributes to our understanding about the combined effects of resources and temperature on ectothermic organisms. When temperature is below the foraging temperature of ectotherms, species richness can be low despite high resource availability (like in the *Helichrysum* zone of Mount Kilimanjaro). In warm areas where temperature does not restrict foraging activity, resources could become limiting to species richness. On Mount Kilimanjaro, we found no evidence for such resource limitation in the lowlands. Here, the amount of floral resources was sufficient to support high bee diversities, resulting in exponential species richness declines with increasing elevation. Resource limitations in the lowlands and temperature-mediated resource-accessibility constraints in the highlands would result in hump-shaped distribution patterns, which are found in many other ectothermic organisms (e.g. Sanders, 2002; Brehm *et al.*, 2007).

We also detected a strong direct effect of temperature on bee richness, demonstrating that temperature controls evolutionary and ecological processes that drive the maintenance and origination of diversity. Under warm temperatures, generation times are usually shortened, which means that the number of mutation-prone DNA-replication processes is increased. Also the amount of mutagen free radicals, causing nucleotid substitutions, is increased under elevated temperatures and consequently increased metabolism rates. Both processes may accelerate speciation rates (Laird *et al.*, 1969; Martin & Palumbi, 1993; Gillooly *et al.*, 2005; Clarke & Gaston, 2006). Especially on Mount Kilimanjaro, which is from an evolutionary point of view relatively young, such evolutionary processes are likely complemented by ecological mechanisms, such as temperature-dependent negative-density mortality rates (de Sassi *et al.*, 2012; Johnson *et al.*, 2012; Bagchi *et al.*, 2014; Brown, 2014). Parasitoids and predators have been shown to preferentially attack abundant bee and wasp species (Steffan-Dewenter, 2003), allowing more species to coexist (Paine, 1974). These effects are predicted to be more pronounced under warm temperatures, as temperature increases species interaction rates (Tylianakis *et al.*, 2008). However, knowledge about such temperature-dependent negative-density dependent effects is still restricted and requires further experimental investigation.

In addition to temperature, the number of floral resources was found to be indirectly limiting to bee species richness, via bee abundances. Positive effects of flower abundances on bee abundances have also been found on local scales in temperate regions (Hoiss *et al.*, 2012), and on landscape scales when considering floral resources from mass-flowering crops (Westphal *et al.*, 2003). On Mount Kilimanjaro, the number of flowers was higher in managed habitats than in natural habitats. This may partly explain the finding that land use change did currently not negatively affect bee species richness in that region (also detected by e.g. Klein *et al.*, 2002). Therefore, preserving floral resources could be a comparatively simple management strategy in areas where pollinator diversity is threatened. However, we assume that on Mount Kilimanjaro also other factors than flower densities contribute to the high bee species richness in managed habitats. For example, insect pollinators may benefit from low application rates of pesticides, which are simply not financeable for many local farmers. Also, the small size of fields and the diversity of different cropping systems shape a mosaic-like heterogeneous landscape. Thus, the distances from open habitats to forested plots are generally short, guaranteeing good-quality nesting sites for many tree-nesting species in immediate vicinity (Ricketts, 2004b). Manual weeding, instead of mechanically ploughing may allow many ground nesting species to persist. Stem-nesting bees could profit from maize stems that usually remain on the field several months after harvest (Kim *et al.*, 2006). Although we did not explicitly test, whether the number of nesting sites is limiting to bee species on Mount Kilimanjaro, we know from other studies that such nesting limitation can be strong (Potts *et al.*, 2005; Steffan-Dewenter & Schiele, 2008).

The direct and indirect effects of temperature on pollinator diversity were stronger than the resource effect, signaling pollinators' sensitivity to temperature increases in the course of climate change. The loss of thermo-microhabitats due to habitat degradation may even increase this sensitivity. Our data suggest, that pollinator diversity might profit from global warming, either because temperature promotes the accessibility to floral resources, and/or because of facilitated speciation processes. However, such predictions need to be treated with caution. Bees in the lowlands might live close to their maximal thermal tolerance limit (Deutsch *et al.*, 2008), suggesting that communities that are now found in the lowlands shift upslopes, or polewards with ongoing global warming, to stay in their preferred temperature range. Upslope shifts along elevational gradients are suggested to be more likely, as the distances between climatic zones are much shorter than on latitudinal gradients (Colwell *et al.*, 2008). Species range shifts have already been detected in many plants and animal species (Parmesan *et al.*, 1999; Root *et al.*, 2003). However, especially in the tropical lowlands, which belong to the hottest places in the world, such shifts can result in biotic impoverishments of species-rich lowland communities, because no species move up behind them (Colwell *et al.*, 2008). On the top of the mountain, species might then be faced with shifted levels of density-dependent processes, like interspecific competition, or host-parasite interactions (Romo & Tylianakis, 2013), which could result in mountain-top extinctions. Specialists and narrow-ranged species, which may not find suitable habitat corridors to move up, due to progressing land use change and habitat degradation, may be especially extinction-prone (Parmesan, 2006). Species loss and shifts in pollinator communities might have drastic consequences for the plant communities that rely on their pollinators. Range-shifts of plants might not parallel with the range-shifts of pollinators, causing spatial mismatches between plants and pollinators. As temperature increases has also been shown to affect the phenology of plants and pollinators, temporal mismatches can additionally destabilize plant-pollinator-networks (Gordo & Sanz, 2005; Hegland *et al.*, 2009). With this dissertation we provide first quantitative baseline data for wild bee populations on Mount Kilimanjaro. Currently, we can solely use the space-for-time approach to predict the impact of climate change on wild bee communities. Any data collected in future, can draw on our baseline data, which will sharpen, verify or deny any predictions of how wild bees respond to environmental changes.

Evidence for directive trait loss along elevational gradients

Energy-limitations and temperature-constraints in high-elevations are also suggested to explain the shift in morphological traits. In chapter III we showed that morphological pollinator traits shifted along elevation, however, the direction of the shift was partly dependent on the level of biological organization. On a community level, the number of small-bodied and large-winged bees, with on average shorter tongues increased with elevation, while on an intraspecific level bees became on average larger, with shorter glossae and stable wing:body-size ratios. We suggest, that individuals within species respond to physiological constraints, as predicted by Bergmann´s rule (Bergmann, 1847; Ashton, 2002), while species within communities are rather shaped by energy-limitations, as predicted by community assembly rules (Brown & Maurer, 1989). We assume that larger body sizes are favored in cold environments (as proofed on an intraspecific level); however, energy-restrictions can be so strong in high elevations that large bee species cannot maintain large population densities, which increases the chance of local extinction (Srivastava & Lawton, 1998). With this, two apparently contradicting theories of ecology can be merged.

Generally, the functional approach we used in chapter III allowed us to differentiate between niche and neutral assembly processes, which can both shape species along environmental gradients. Such differentiation cannot be achieved, when looking at species numbers alone (chapter II). Neutral theory predicts that species respond identically to environmental disturbance, proclaiming that traits are randomly disappearing along environmental gradients (Suding *et al.*, 2005). In contrast, directive trait shifts or trait losses are expected to be present, when non-neutral processes act on communities, diminishing the abundance of particular traits (Suding *et al.*, 2005; Mouillot *et al.*, 2013). We found that bee species did not randomly disappear from communities; instead temperature-mediated resource usability limitations seem to select for small organisms with lower energy requirements. Although large-bodied organisms with energetically favorable surface:volume ratios require less energy per gram body mass than small-bodied organisms, the total energy-requirements are increased. Also, the enlargement of forewings in relation to body size has been detected as a powerful adaption for energy-saving flights in habitats with reduced air densities (Dillon, 2006). Species with small wings compared to body size might thus not be able to efficiently forage in higher elevations. Similarly, long glossa lengths in bees have sometimes been associated with greater specialization (Goulson *et al.*, 2005) which could be a risky foraging strategy when resource accessibility is already restricted. In summary, the directive trait shifts strongly suggest that not neutral, but selective forces like energy-constraints shape species communities along elevation.

Quantitative and qualitative shifts in trait composition, do not only allow us to investigate the underlying mechanisms shaping species communities, they can also act as “early-warning-systems”, as they do not require species extinction to be reactive (Mouillot *et al.*, 2013). Large-bodied bee species were increasingly excluded from high-elevational bee communities. In turn, this indicates, that rising temperatures in the course of climate change might restructure ecological communities, leading to an increasing number of large-bodied species in habitats which are currently dominated by small-bodied species. For the habitats at lowest elevations, i.e. the savannah, predictions on the composition of species communities under elevated temperatures are only speculative: If temperature increases and precipitation patterns stay constant, severe drought events might negatively impact the abundance or quality of floral resources (Galen, 2000; Sangtarash *et al.*, 2009). Limited resource abundance due to aridity may thus especially affect large-bodied bee species with higher energy requirements, which either become extinct or which move up to higher elevations. As ecosystem function and species richness has been proclaimed to be a non-linear function, in which the loss of certain keystone species can result in stronger ecosystem service losses than expected under random species loss (Larsen *et al.*, 2005), the loss of large-bodied pollinators in the lowlands would be extremely alarming. Large-bodied bees have been shown to be more effective pollinators, as they generally have larger foraging ranges and have been associated with higher seed sets (Sahli & Conner, 2007). That means that their “response traits” (i.e. the trait that directly responses to environmental changes, e.g. body size) are coupled with so-called “effect traits” (i.e. traits that determine functional contributions of species, e.g. scopa length) (Lavorel & Garnier, 2002; Naeem & Wright, 2003). As land use and cropping activities are mainly concentrated in the lowlands, the loss of large-bodied bees due to climate change may lead to severe pollination declines with strong economic impact. A similar effect was found in bees in California and in dung beetles from Venezuela. Here, not climate but land use change altered the extinction order of species, with large-bodied species being most extinction-prone and (simulated) ecosystem services declining stronger than expected under random species loss (Larsen *et al.*, 2005).

Interestingly, our finding that bee body sizes decrease on a community level with increasing elevation does not seem to be ubiquitous. Instead, the exact opposite was found in the temperate Alps in Germany. Here, both abundance- and species-weighted bee body size increased on a community level with increasing elevation (Hoiss *et al.*, 2012). The increase in body size on a community level was predominantly caused by the dominance of the genus *Bombus* in high-elevational habitats of the German Alps – a genus that does not occur in subsaharan Africa. The contrasting pattern signals, that there is more than one solution how to respond to energy constraints. Due to their body size, bumblebees are able to fly large distances. Foraging habitats in the Alps might be better connected than on Mount Kilimanjaro, where the forest belt is broad and due to its patchy flower distribution assumed to be not very attractive for pollinators. We thus assume that bees foraging in the highlands of Mount Kilimanjaro do also nest in the highlands to avoid energy-consuming flights across the forest belt. This could be different in the Alps. Pollinator competition in the lowlands has been shown to be high in the Alps (Hoiss *et al.*, 2012), so that it might be energetically advantageous to forage in the highlands, but to nest in the lowlands where nesting seasons are much longer due to advanced snow-melts. Large bee body sizes have been associated with large foraging distances. As the relative energy-consumption is reduced in large species, the foraging flight might be energetically worthwhile. The finding, that on an intraspecific level, bees on Mount Kilimanjaro became on average bigger in the highlands supports the idea that larger bees have an advantage under cold temperatures. Alternatively, the large body size of bumblebees could be connected with other morphological traits that make them less prone to cold temperatures. The dense coat of bumblebees could be one adaptation that allows bumblebees to forage even under unfavorable weather conditions (Lundberg, 1980). On Mount Kilimanjaro, the restricted diversity of flower types (mainly short-tubed Asteraceae) and the limitation of nesting sites above the tree-line might prevent genera that resemble bumblebees in morphology and ecotype (e.g. *Tetralonia, Amegilla, Xylocopa*) to persist in the highlands. Though admittedly unsatisfying, such case-sensitive argumentations show how complicate it can be to detect general patterns in ecology and motivate further studies in different latitudes with phylogenetically independent species communities (Lawton, 1999; Simberloff, 2004).

Endangered stability of ecosystem services along land use gradients

In chapter IV we used an experimental approach to investigate the single and combined contributions of pollinators and pest predators to coffee production and tested whether these services are affected by land use intensification. We found that pollinators effectively contributed to coffee production by increasing fruit weight by on average 7.4%. Birds and bats reduced herbivore pressure and were related to fruit set increases of on average 9%. As both fruit quantity and fruit quality was affected, the services of pollinators and pest predators were not simple additive, but complemented each other. Land use intensification on coffee farms had currently no detectable effect on the services provided. However, we detected a shift in the coffee-flower visiting pollinator community along the land use gradient: While in homegarden flower-visitors were diverse, consisting of wild bees, butterflies and syrphid flies, sun-coffee plantations were almost exclusively pollinated by the honeybee *Apis mellifera*. Interestingly, we did not find a diversity decline in pollinator communities when looking at pan trap catches along the coffee management intensification gradient (G. Maaßen, unpublished), which coincides with the results presented in chaper II showing that land use does not affect pollinator diversity on Mount Kilimanjaro. However, in sun-coffee plantations, wild bees were observed to forage preferentially in the herbal layer, although coffee flowers are very attractive for wild pollinators, as we observed in homegardens where the honeybee was not so dominant. Although we found currently no significant decline of pollination services in sun-coffee plantations, we know from meta-analyses that honey bees cannot fully substitute the services of wild pollinators (Garibaldi *et al.*, 2013). Also, the drastic decline of honey bee populations, known under the term *colony collapse disorder*, asks for a stronger inclusion of wild pollinators into natural and agricultural systems, as they can act like an insurance against honey bee losses (Winfree *et al.*, 2007). Currently, pollination limitation detected in cropping systems is usually compensated by the addition of domesticated honey bees. However, the promotion of one species can shift the foraging behavior of wild pollinators to alternative food resources, as we observed in sun-coffee plantations. The provision of flower resources, the establishment of connecting corridors to habitats with suitable nesting resources and a reduction of pesticide application could thus be better alternatives to ensure ecosystem services, as these measures are predicted to attract a diverse pollinator community, whose ecosystem services can complement ecosystem services of honey bees (Garibaldi *et al.*, 2013), and whose pollination services assure the stability of pollination in a long term.

CONCLUSIONS

On Mount Kilimanjaro, bee species richness declined with increasing elevation. Temperature was identified as the main predictor of bee richness. It controlled both evolutionary and ecological speciation rates, and the access to floral resources. Also morphological traits of wild bees shifted along the elevational gradient. The parallel consideration of intra- and interspecific trait shifts revealed that physiological temperature constraints and energy-limitations in the highlands can shape pollinator communities simultaneously, but in different directions depending on the level of biological organization. This allowed us to unify the contrasting predictions of Bergmann´s rule and community assembly rules in the same organismic system. Furthermore, trait distribution shifts revealed that community assembly processes are directional, but not neutral, as sometimes suggested (Bell, 2001; Hubbell, 2001). We conclude that temperature shifts in the course of global change are likely to affect the pollinator communities on Mount Kilimanjaro with regard to species and trait compositions, which could threaten pollination function. If pollinators live close to their maximal thermal tolerance limit, we expect that under rising temperatures pollinators will shift to higher elevations, which may result in biodiversity and related ecosystem service losses in cropping systems of the lowlands. Our data provide important baseline data that will allow scientists to revise these predictions in future. Up to now, land use intensification had no significant impact on pollinator communities and their ecosystem services. Pollinators are suggested to profit from the strong landscape heterogeneity in that region and from the amount of flower resources in the understory of cropping systems. However, progressing homogenization of the landscape and the pronounced application of pesticides could result in reduced diversity and/or dominance of single species, as we already found in sun coffee plantations. Such shifts in community compositions could threaten the stability of ecosystem services within cropping and natural systems in a long term.

REFERENCES

Ackerly, D.D. & Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters*, 135–145.

Aizen, M.A., Garibaldi, L.A., Cunningham, S.A. & Klein, A.M. (2009) How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Annals of Botany*, **103**, 1579–1588.

Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G. & Violle, C. (2011) When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 217–225.

Albrecht, M., Schmid, B., Hautier, Y. & Muller, C.B. (2012) Diverse pollinator communities enhance plant reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4845–4852.

Allen, A.P., Gillooly, J.F., Savage, V.M. & Brown, J.H. (2006) Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences*, **103**, 9130–9135.

Allen, J. (1877) The influence of physical conditions in the genesis of species. *Radical Review*, 108–140.

Arroyo, M.T.K., Armesto, J.J. & Primack, R.B. (1985) Community Studies in Pollination Ecology in the High Temperature Andes of Central Chile II. Effect of Temperature on Visitation Rates and Pollination Possibilities. *Plant Systematics and Evolution*, **149**, 187 – 203.

Arroyo, M.T.K., Primack, R.B. & Armesto, J. (1982) Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. *American Journal of Botany*, **69**, 82–97.

Ashton, K.G. (2004) Comparing phylogenetic signal in intraspecific and interspecific body size datasets: Phylogenetic signal of intraspecific data. *Journal of Evolutionary Biology*, **17**, 1157–1161.

Ashton, K.G. (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, **11**, 505–523.

Atzberger, C. & Eilers, P.H.C. (2011) Evaluating the effectiveness of smoothing algorithms in the absence of ground reference measurements. *International Journal of Remote Sensing*, **32**, 3689–3709.

Bagchi, R., Gallery, R.E., Gripenberg, S., Gurr, S.J., Narayan, L., Addis, C.E., Freckleton, R.P. & Lewis, O.T. (2014) Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, **506**, 85–88.

Bates, D., Maechler, M. & Bolker, B. (2013) Linear mixed-effect models using S4 classes. R-package version 0.999999-2.

Bell, G. (2001) Neutral Macroecology. *Science*, **293**, 2413–2418.

Bergmann, C. (1847) *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Größe*. Vandenhoeck und Ruprecht, Göttingen.

Biesmeijer, J.C. (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science*, **313**, 351–354.

Blackburn, T.M., Gaston, K.J. & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann’s rule. *Diversity and Distribution*, **5**, 165–174.

Blanckenhorn, W.U. (2004) Bergmann and Converse Bergmann Latitudinal Clines in Arthropods: Two Ends of a Continuum? *Integrative and Comparative Biology*, **44**, 413–424.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D.A. (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, **26**, 183–192.

Bommarco, R., Kleijn, D. & Potts, S.G. (2013) Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, **28**, 230–238.

Boreux, V., Kushalappa, C.G., Vaast, P. & Ghazoul, J. (2013) Interactive effects among ecosystem services and management practices on crop production: Pollination in coffee agroforestry systems. *Proceedings of the National Academy of Sciences*, **110**, 8387–8392.

Brehm, G., Colwell, R.K. & Kluge, J. (2007) The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and Biogeography*, **16**, 205–219.

Breitbach, N., Laube, I., Steffan-Dewenter, I. & Böhning-Gaese, K. (2010) Bird diversity and seed dispersal along a human land-use gradient: high seed removal in structurally simple farmland. *Oecologia*, **162**, 965–976.

Brittain, C., Kremen, C. & Klein, A.-M. (2013a) Biodiversity buffers pollination from changes in environmental conditions. *Global Change Biology*, **19**, 540–547.

Brittain, C., Williams, N., Kremen, C. & Klein, A.-M. (2013b) Synergistic effects of non-Apis bees and honey bees for pollination services. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122767.

Brown, J. (1995) *Macroecology*, 1st edn. The University of Chicago Press, Chicago and London.

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

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

Brown, J.H. & Maurer, B.A. (1989) Macroecology: The Division of Food and Space Among Species on Continents. *Science*, **243**, 1145–1150.

Brown, W.L. & Wilson, E.O. (1956) Character displacement. *Systematic Zoology*, **5**, 49–64.

Cadotte, M.W., Cardinale, B.J. & Oakley, T.H. (2008) Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences*, **105**, 17012–17017.

Campbell, J.W. & Hanula, J.L. (2007) Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems. *Journal of Insect Conservation*, **11**, 399–408.

Canaday, C. (1996) Loss of insectivorous birds along a gradient of human impact in Amazonia. *Biological Conservation*, **77**, 63–77.

Cane, J.H. (1987) Estimation of bee size using intertegular span (Apoidea). *Journal of the Kansas Entomological Society*, **60**, 145–147.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.

Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M.I. & Gonzalez, A. (2011) The functional role of producer diversity in ecosystems. *American Journal of Botany*, **98**, 572–592.

Carvalheiro, L.G., Barbosa, E.R.M. & Memmott, J. (2008) Pollinator networks, alien species and the conservation of rare plants: *Trinia glauca* as a case study. *Journal of Applied Ecology*, **45**, 1419–1427.

Chapin III, F.S. (1997) Biotic Control over the Functioning of Ecosystems. *Science*, **277**, 500–504.

Chen, I.-C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, **333**, 1024–1026.

Clark, J.S., Bell, D.M., Hersh, M.H., Kwit, M.C., Moran, E., Salk, C., Stine, A., Valle, D. & Zhu, K. (2011) Individual-scale variation, species-scale differences: inference needed to understand diversity. *Ecology Letters*, **14**, 1273–1287.

Clarke, A. & Gaston, K.J. (2006) Climate, energy and diversity. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2257–2266.

Classen, A., Peters, M.K., Ferger, S.W., Helbig-Bonitz, M., Schmack, J.M., Maassen, G., Schleuning, M., Kalko, E.K.V., Bohning-Gaese, K. & Steffan-Dewenter, I. (2014) Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20133148.

Colwell, R.K., Brehm, G., Cardelus, C.L., Gilman, A.C. & Longino, J.T. (2008) Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. *Science*, **322**, 258–261.

Conroy, M.J., Cohen, Y., James, F.C., Matsinos, Y.G. & Maurer, B.A. (1995) Parameter Estimation, Reliability, and Model Improvement for Spatially Explicit Models of Animal Populations. *Ecological Applications*, **5**, 17.

Conti, L., Schmidt-Kloiber, A., Grenouillet, G. & Graf, W. (2013) A trait-based approach to assess the vulnerability of European aquatic insects to climate change. *Hydrobiologia*, **721**, 297–315.

Cornwell, W.K. & Ackerly, D.D. (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, **79**, 109–126.

Crawley, M.J. (2007) *The R book*, John Wiley & Sons, Ltd.

Cubasch, U., Wuebbles, D., Chen, D., Facchini, M.C., Frame, D., Mahowald, N. & Winther, J.-G. (2013) *Introduction. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, pp. 119–158. Cambridge University Press, Cambridge, United Kingdom, New York.

Currie, D.J. (1991) Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, **137**, 27–49.

Dale, V.H. & Polasky, S. (2007) Measures of the effects of agricultural practices on ecosystem services. *Ecological Economics*, **64**, 286–296.

DaMatta, F.M., Ronchi, C.P., Maestri, M. & Barros, R.S. (2007) Ecophysiology of coffee growth and production. *Brazilian Journal of Plant Physiology*, **19**, 485–510.

Damuth, J. (1981) Population density and body size in mammals. *Nature*, **290**, 699–700.

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

Dillon, M.E. (2006) Into thin air: Physiology and evolution of alpine insects. *Integrative and Comparative Biology*, **46**, 49–61.

Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*, **38**, 209–221.

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

Fisher, B., Turner, K., Zylstra, M., Brouwer, R., Groot, R. de, Farber, S., Ferraro, P., Green, R., Hadley, D., Harlow, J., Jefferiss, P., Kirkby, C., Morling, P., Mowatt, S., Naidoo, R., Paavola, J., Strassburg, B., Yu, D. & Balmford, A. (2008) Ecosystem services and economic theory: Intergration for policy-relevant research. *Ecological Applications*, **18**, 2050–2067.

Free, J.B. (1993) *Insect Pollination of Crops.*, Academic Press, London.

Galen, C. (2000) High and Dry: Drought Stress, Sex-Allocation Trade-offs, and Selection on Flower Size in the Alpine Wildflower *Polemonium viscosum* (Polemoniaceae). *The American Naturalist*, **156**, 72–83.

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R. & Klein, A.M. (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits: Habitat isolation and pollination stability. *Ecology Letters*, **14**, 1062–1072.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhoffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipolito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlof, M., Seymour, C.L., Schuepp, C., Szentgyorgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N. & Klein, A.M. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, **339**, 1608–1611.

Gikungu, M., Wittmann, D., Irungu, D. & Kraemer, M. (2011) Bee diversity along a forest regeneration gradient in Western Kenya. *Journal of Apicultural Research*, **50**, 22–34.

Gillman, L.N. & Wright, S.D. (2006) The influence of productivity on the species richness of plants: a critical assessment. *Ecology*, **87**, 1234–1243.

Gillooly, J.F., Allen, A.P., West, G.B. & Brown, J.H. (2005) The rate of DNA evolution: Effects of body size and temperature on the molecular clock. *Proceedings of the National Academy of Sciences*, **102**, 140–145.

Gordo, O. & Sanz, J.J. (2005) Phenology and climate change: a long-term study in a Mediterranean locality. *Oecologia*, **146**, 484–495.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. & Knight, M.E. (2005) Causes of rarity in bumblebees. *Biological Conservation*, **122**, 1–8.

Graham, C.H., Carnaval, A.C., Cadena, C.D., Zamudio, K.R., Roberts, T.E., Parra, J.L., McCain, C.M., Bowie, R.C.K., Moritz, C., Baines, S.B., Schneider, C.J., VanDerWal, J., Rahbek, C., Kozak, K.H. & Sanders, N.J. (2014) The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. *Ecography*, 001-009 (early online).

Green, K., Davis, N.E., Robinson, W.A., McAuliffe, J. & Good, R.B. (2013) Diet selection by European hares (*Lepus europaeus*) in the alpine zone of the Snowy Mountains, Australia. *European Journal of Wildlife Research*, **59**, 693–703.

Greenberg, R., Bichier, P., Angon, A.C., MacVean, C., Perez, R. & Cano, E. (2000) The impact of avian insectivory and arthropods and leaf damage in some Guatemalan Coffee plantations. *Ecology*, **81**, 1750–1755.

Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia*, **153**, 589–596.

Grytnes, J.A. & Vetaas, O.R. (2002) Species Richness and Altitude: A Comparison between Null Models and Interpolated Plant Species Richness along the Himalayan Altitudinal Gradient, Nepal. *The American Naturalist*, **159**, 294–304.

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

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. (2009) How does climate warming affect plant-pollinator interactions? *Ecology Letters*, **12**, 184–195.

Hemp, A. (2005) Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. *Global Change Biology*, **11**, 1013–1023.

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

Hemp, A. (2006b) Vegetation of Kilimanjaro: hidden endemics and missing bamboo. *African Journal of Ecology*, **44**, 305–328.

Hendrix, S.D. (1988) *Herbivory and its impact on plant reproduction. Plant Reproductive Ecology - Patterns and Strategies*, pp. 246–263. Oxford University Press, Oxford.

Hoehn, P., Tscharntke, T., Tylianakis, J.M. & Steffan-Dewenter, I. (2008) Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2283–2291.

Hoiss, B., Krauss, J., Potts, S.G., Roberts, S. & Steffan-Dewenter, I. (2012) Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4447–4456.

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography.*, Princeton University Press, Princeton, NJ.

Hulshof, C.M., Violle, C., Spasojevic, M.J., McGill, B., Damschen, E., Harrison, S. & Enquist, B.J. (2013) Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. *Journal of Vegetation Science*, **24**, 921–931.

Humboldt, A. v. & Bonpland, A. (1807) *Essaie sur la géographie des plantes – accompagné d'un tableau physique des régions équinoxiales, fondé sur des mesures executées, depuis le dixième degré de latitude boréale jusqu'au dixième degré de latitude australe, pendant les années 1799, 1800, 1801, 1802 et 1803.*, Paris: Levrault, Schoell et Compagnie, Libraires.

Hurlbert, A.H. (2004) Species-energy relationships and habitat complexity in bird communities. *Ecology Letters*, **7**, 714–720.

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

Infante, F., Mumford, J., Baker, P., Barrera, J. & Fowler, S. (2008) Interspecific competition between Cephalonomia stephanoderis and Prorops nasuta (Hym.,Bethylidae), parasitoids of the coffee berry borer, Hypothenemus hampei (Col., Scolytidae). *Journal of Applied Entomology*, **125**, 63–70.

Johansen, C.A. (1977) Pesticides and Pollinators. *Annual Review of Entomology*, **22**, 177–192.

Johnson, D.J., Beaulieu, W.T., Bever, J.D. & Clay, K. (2012) Conspecific Negative Density Dependence and Forest Diversity. *Science*, **336**, 904–907.

Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. (2010) Intraspecific variability and trait-based community assembly. *Journal of Ecology*, **98**, 1134–1140.

Kalka, M.B., Smith, A.R. & Kalko, E.K.V. (2008) Bats Limit Arthropods and Herbivory in a Tropical Forest. *Science*, **320**, 71–71.

Kaspari, M., Alonso, L. & O'Donnell, S. (2000) Three energy variables predict ant abundance at a geographical scale. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 485–489.

Kellermann, J.L., Johnson, M.D., Stercho, A.M. & Hackett, S.C. (2008) Ecological and Economic Services Provided by Birds on Jamaican Blue Mountain Coffee Farms. *Conservation Biology*, **22**, 1177–1185.

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

Kessler, A., Halitschke, R. & Poveda, K. (2011) Herbivory-mediated pollinator limitation: negative impacts of induced volatiles on plant–pollinator interactions. *Ecology*, **92**, 1769–1780.

Kim, J., Williams, N. & Kremen, C. (2006) Effects of Cultivation and Proximity to Natural Habitat on Ground-nesting Native Bees in California Sunflower Fields. *Journal of the Kansas Entomological Society*, **79**, 309–320.

Klein, A.-M., Steffan-Dewenter, I., Buchori, D. & Tscharntke, T. (2002) Effects of Land-Use Intensity in Tropical Agroforestry Systems on Coffee Flower-Visiting and Trap-Nesting Bees and Wasps. *Conservation Biology*, **16**, 1003–1014.

Klein, A.M., Steffan-Dewenter, Ingolf & Tscharntke, Teja (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 955–961.

Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 303–313.

Körner, C. (2007) Climatic treelines: Conventions, global patterns, causes. *Erdkunde*, **61**, 316–324.

Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008) Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest. *Science*, **322**, 580–582.

Krebs, C.J. (2009) *Ecology: the experimental analysis of distribution and abundance*, 6th ed. Pearson Benjamin Cummings, San Francisco, CA.

Kuznetsova, A., Brockhoff, P.B. & Bojesen, R.H. (2013) lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-3.

Laird, C.D., McConaughy, B.L. & McCarthy, B.J. (1969) Rate of Fixation of Nucleotide Substitutions in Evolution. *Nature*, **224**, 149–154.

Lande, R. (1993) Risk of population extrinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, **142**, 911–927.

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

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177–192.

Lomolino, M.V. (2000) Ecology's most general, yet protean 1 pattern: the species-area relationship. *Journal of Biogeography*, **27**, 17–26.

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

Lomolino, M.V., Riddle, B.R. & Brown, J.H. (2006) *Biogeography*, 3rd edn. Sinauer Associates, Inc., Sunderland, Massachusetts.

Lomolino, M.V., Sax, D.F., Palombo, M.R. & van der Geer, A.A. (2012) Of mice and mammoths: evaluations of causal explanations for body size evolution in insular mammals: Body size evolution in insular mammals. *Journal of Biogeography*, **39**, 842–854.

Lundberg, H. (1980) Effects of weather on foraging-flights of bumblebees (Hymenoptera, Apidae) in a subalpine/alpine area. *Ecography*, **3**, 104–110.

Lundin, O., Smith, H.G., Rundlof, M. & Bommarco, R. (2012) When ecosystem services interact: crop pollination benefits depend on the level of pest control. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122243.

Maas, B., Clough, Y. & Tscharntke, T. (2013) Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecology Letters*, 1480–1487.

Maaßen, G. (2012) Effects of land use intensification on pollinator diversity and its consequences on pollination service in Coffea arabica at Mount Kilimanjaro. *Bachelor thesis, unpublished.*

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*, Princeton University Press, Princeton.

Mani, M.. (1968) *Ecology and biogeography of high altitude insects*, Junk, The Hague.

Martin, A.P. & Palumbi, S.R. (1993) Body size, metabolic rate, generation time, and the molecular clock. *Proceedings of the National Academy of Sciences*, **90**, 4087–4091.

Martin, E.A., Reineking, B., Seo, B. & Steffan-Dewenter, I. (2013) Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences*, **110**, 5534–5539.

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

McCain, C.M. & Grytnes, J.-A. (2010) *Elevational Gradients in Species Richness*. *Encyclopedia of Life Sciences* (ed. by John Wiley & Sons, Ltd), John Wiley & Sons, Ltd, Chichester, UK.

McCoy, E.D. (1990) The distribution of insects along elevational gradients. *OIKOS*, 313–322.

Mitchell, R.J. (2001) *Path Analysis*. *Design and analysis of ecological experiments* (ed. by S.M. Scheiner and J. Gurevitch), pp. 217–234. Oxford University Press, Oxford ; New York.

Mols, C.M.M. & Visser, M.E. (2002) Great tits can reduce caterpillar damage in apple orchards. *Journal of Applied Ecology*, **39**, 888–899.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, **28**, 167–177.

Naeem, S. (2008) Species Redundancy and Ecosystem Reliability. *Conservation Biology*, **12**, 39–45.

Naeem, S. & Li, S. (1997) Biodiversity enhances ecosystem reliability. *Nature*, **390**, 507–509.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1995) Empirical Evidence that Declining Species Diversity May Alter the Performance of Terrestrial Ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **347**, 249–262.

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

Naylor, R.L. & Ehrlich, P.R. (1997) *Natural pest control services and agriculture. Nature's services.*, pp. 151–174. Island Press, Washington.

Newton, I. (1994) The role of nest sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation*, **70**, 265–276.

Ngo, H.T., Mojica, A.C. & Packer, L. (2011) Coffee plant – pollinator interactions: a review. *Canadian Journal of Zoology*, **89**, 647–660.

Nicholls, C.I. & Altieri, M.A. (2012) Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable Development*, **33**, 257–274.

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

Oerke, E.-C. (2005) Crop losses to pests. *The Journal of Agricultural Science*, **144**, 31.

Paine, C.E.T., Baraloto, C., Chave, J. & Hérault, B. (2011) Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos*, **120**, 720–727.

Paine, R.T. (1974) Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, **15**, 93–120.

Parmesan, C. (2006) Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Pellissier, L., Pradervand, J.-N., Williams, P.H., Litsios, G., Cherix, D. & Guisan, A. (2013) Phylogenetic relatedness and proboscis length contribute to structuring bumblebee communities in the extremes of abiotic and biotic gradients: Assembly of bumblebee communities. *Global Ecology and Biogeography*, **22**, 577–585.

Perfecto, I., Vandermeer, J.H., Bautista, G.L., Nuñez, G.I., Greenberg, R., Bichier, P. & Langridge, S. (2004) Greater predation in shaded coffee farms: The role of resident neotropical birds. *Ecology*, **85**, 2677–2681.

Perry, A.L. (2005) Climate Change and Distribution Shifts in Marine Fishes. *Science*, **308**, 1912–1915.

Peters, V.E., Carroll, C.R., Cooper, R.J., Greenberg, R. & Solis, M. (2013) The contribution of plant species with a steady-state flowering phenology to native bee conservation and bee pollination services. *Insect Conservation and Diversity*, **6**, 45–56.

Philpott, S.M., Uno, S. & Maldonado, J. (2006) The Importance of Ants and High-Shade Management to Coffee Pollination and Fruit Weight in Chiapas, Mexico. *Biodiversity and Conservation*, **15**, 487–501.

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

Pimentel, D. (2009) *Pesticides and Pest Control. Integrated Pest Management: Innovation-Development Process* (ed. by R. Peshin and A.K. Dhawan), pp. 83–87. Springer Netherlands, Dordrecht.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, **25**, 345–353.

Potts, S.G., Vulliamy, B., Roberts, S., O’Toole, C., Dafni, A., Ne’eman, G. & Willmer, P. (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, **30**, 78–85.

Price, T.D., Hooper, D.M., Buchanan, C.D., Johansson, U.S., Tietze, D.T., Alström, P., Olsson, U., Ghosh-Harihar, M., Ishtiaq, F., Gupta, S.K., Martens, J., Harr, B., Singh, P. & Mohan, D. (2014) Niche filling slows the diversification of Himalayan songbirds. *Nature*, **509**, 222–225.

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Ramos-Jiliberto, R., Domínguez, D., Espinoza, C., López, G., Valdovinos, F.S., Bustamante, R.O. & Medel, R. (2010) Topological change of Andean plant–pollinator networks along an altitudinal gradient. *Ecological Complexity*, **7**, 86–90.

Ricketts, T.H. (2004a) Economic value of tropical forest to coffee production. *Proceedings of the National Academy of Sciences*, **101**, 12579–12582.

Ricketts, T.H. (2004b) Tropical Forest Fragments Enhance Pollinator Activity in Nearby Coffee Crops. *Conservation Biology*, **18**, 1262–1271.

Ricketts, T.H., Dinerstein, E., Boucher, T., Brooks, T.M., Butchart, S.H.M., Hoffmann, M., Lamoreux, J.F., Morrison, J., Parr, M., Pilgrim, J.D., Rodrigues, A.S.L., Sechrest, W., Wallace, G.E., Berlin, K., Bielby, J., Burgess, N.D., Church, D.R., Cox, N., Knox, D., Loucks, C., Luck, G.W., Master, L.L., Moore, R., Naidoo, R., Ridgely, R., Schatz, G.E., Shire, G., Strand, H., Wettengel, W. & Wikramanayake, E. (2005) Pinpointing and preventing imminent extinctions. *Proceedings of the National Academy of Sciences*, **102**, 18497–18501.

Rodenhouse, N.L., Best, L.B., O’Connor, R.J. & Bollinger, E.K. (1995) *Effects of agricultural practices and farmland structures. Ecology and management of migratory birs: a synthesis and review of critical issues.*, pp. 269–293. Oxford University Press, Oxford, England.

Romo, C.M. & Tylianakis, J.M. (2013) Elevated Temperature and Drought Interact to Reduce Parasitoid Effectiveness in Suppressing Hosts. *PLoS ONE*, **8**, e58136.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Roubik, D.W. (2002) Tropical agriculture: The value of bees to the coffee harvest. *Nature*, **417**, 708–708.

Sahli, H.F. & Conner, J.K. (2007) Visitation, effectiveness, and efficiency of 15 genera of visitors to wild radish, Raphanus raphanistrum (Brassicaceae). *American Journal of Botany*, **94**, 203–209.

Sanders, N.J. (2002) Elevational gradients in ant species richness: area, geometry, and Rapoport’s rule. *Ecography*, **25**, 25–32.

Sanders, N.J., Lessard, J.-P., Fitzpatrick, M.C. & Dunn, R.R. (2007) Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography*, **16**, 640–649.

Sangtarash, M.H., Qaderi, M.M., Chinnappa, C.C. & Reid, D.M. (2009) Differential responses of two Stellaria longipes ecotypes to ultraviolet-B radiation and drought stress. *Flora - Morphology, Distribution, Functional Ecology of Plants*, **204**, 593–603.

De Sassi, C., Staniczenko, P.P.A. & Tylianakis, J.M. (2012) Warming and nitrogen affect size structuring and density dependence in a host-parasitoid food web. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 3033–3041.

Shaver, G.R., Canadell, J., Chapin, F.S., Gurevitch, J., Harte, J., Henry, G., Ineson, P., Jonasson, S., Melillo, J., Pitelka, L. & Rustad, L. (2000) Global Warming and Terrestrial Ecosystems: A Conceptual Framework for Analysis. *BioScience*, **50**, 871.

Simberloff, D. (2004) Community Ecology: Is It Time to Move On?: (An American Society of Naturalists Presidential Address)*. *The American Naturalist*, **163**, 787–799.

Soini, E. (2005) Land use change patterns and livelihood dynamics on the slopes of Mt. Kilimanjaro, Tanzania. *Agricultural Systems*, **85**, 306–323.

Spehn, E.M. & Körner, C. eds. (2010) *Data mining for global trends in mountain biodiversity*, CRC Press, Boca Raton.

Srivastava, D.S. & Lawton, J.H. (1998) Why More Productive Sites Have More Species: An Experimental Test of Theory Using Tree-Hole Communities. *The American Naturalist*, **152**, 510–529.

Stabentheiner, A., Vollmann, J., Kovac, H. & Crailsheim, K. (2003) Oxygen consumption and body temperature of active and resting honeybees. *Journal of Insect Physiology*, **49**, 881–889.

Steffan-Dewenter, I. (2003) Importance of Habitat Area and Landscape Context for Species Richness of Bees and Wasps in Fragmented Orchard Meadows. *Conservation Biology*, **17**, 1036–1044.

Steffan-Dewenter, I. & Schiele, S. (2008) Do resources or natural enemies drive bee population dynamics in fragmented habitats. *Ecology*, **89**, 1375–1387.

Strauss, S.Y., Rudgers, J.A., Lau, J.A. & Irwin, R.E. (2002) Direct and ecological costs of resistance to herbivory. *Trends in Ecology & Evolution*, **17**, 278–285.

Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., Milchunas, D.G. & Pennings, S. (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences*, **102**, 4387–4392.

Terborgh, J. (1977) Bird Species Diversity on an Andean Elevational Gradient. *Ecology*, **58**, 1007.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H. & Westphal, C. (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, **87**, 661–685.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V. & Messier, J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, **27**, 244–252.

Van Voorhies, W.A. (1996) Bergmann size clines: a simple explanation for their occurrence in ectotherms. *Ecology*, **50**, 1259–1264.

Wallace, A. (1878) *Tropical Nature and Other Essays.*, New York: Macmillan.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wang, D., Morton, D., Masek, J., Wu, A., Nagol, J., Xiong, X., Levy, R., Vermote, E. & Wolfe, R. (2012) Impact of sensor degradation on the MODIS NDVI time series. *Remote Sensing of Environment*, **119**, 55–61.

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J. & Steffan-Dewenter, I. (2008) Measuring bee diversity in different european habitats and biogeographical regions. *Ecological Monographs*, **78**, 653–671.

Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2003) Mass flowering crops enhance pollinator densities at a landscape scale: Flowering crops enhance pollinator densities. *Ecology Letters*, **6**, 961–965.

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

Willmer, P.G. (1983) Thermal constraints on activity patterns in nectar-feeding insects. *Ecological Entomology*, **8**, 455–469.

Winfree, R., Williams, N.M., Dushoff, J. & Kremen, C. (2007) Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, **10**, 1105–1113.

Wintle, B.A., McCarthy, M.A., Volinsky, C.T. & Kavanagh, R.P. (2003) The Use of Bayesian Model Averaging to Better Represent Uncertainty in Ecological Models. *Conservation Biology*, **17**, 1579–1590.

Worm, B., Lotze, H., K., Hillebrand, H. & Sommer, U. (2002) Consumer versus resource control of species diversity and ecosystem functioning. *Nature*, **417**, 848–851.

Author contributions

Chapter II

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Alice Classen, Marcell K. Peters, William J. Kindeketa, Tim Appelhans, Connal D. Eardley, Mary W. Gikungu, Andreas Hemp, Thomas Nauss and Ingolf Steffan-Dewenter. Temperature versus resource constraints: which factors determine bee diversity on Mt. Kilimanjaro, Tanzania?

Author contribution: ISD, MKP and AC designed the study, AC and WJK conducted the field word, MKP developed the land use disturbance index, TA and TN contributed the temperature, land cover and primary productivity data; AC, CDE and MWG sorted and identified bee species, AH selected the study sites, delivered precipitation data and contributed to the flower counts. AC compiled and analyzed the data, and wrote the first draft of the manuscript. All authors contributed to the final version of the manuscript.

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Groot AT, **Classen A**, Inglis O, Blanco CA, Lopez J Jr, Teran Vargas A, Schal C, Heckel DG, Schoefl G. (2012). Genetic differentiation across North America in the generalist moth *Heliothis virescens* and the specialist *H. subflexa*. Molecular Ecology **20**:2676-2692.

Groot AT, **Classen A**, Staudacher H, Schal C, Heckel DG (2010). Phenotypic plasticity in sexual communication signal of a noctuid moth. Journal of Evolutionary Biology **23**:2731-2738.

Groot AT, Blanco CA, **Classen A**, Inglis O, Santangelo RG, Lopez J, Heckel DG, Schal C (2010). Variation in sexual communication of the Tobacco Budworm, *Heliothis virescens*. Southwestern Entomologist **35**:367-372.

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07/2011	Poster: Effects of climate and land use change on biodiversity and ecosystem functioning of pollinators and decomposers. **48. ATBC convention**, Arusha, Tanzania.
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