Applying the effect-response framework in the tropics: Links between plant functional traits, the abiotic environment, and ecosystem functioning at Mount Kilimanjaro, Tanzania

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David Schellenberger Costa
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Gutachter: Prof. Dr. Michael Kleyer

Zweitgutachter: Prof. Dr. Gerhard Zotz

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All of a sudden the veil of mist was rent apart, and to our admiring gaze was revealed the snowy peak of Kilimanjaro, grand, majestic, more than earthly in the silver light of the morning.

Hans Meyer

Summary

The present work investigates the responses of plants to abiotic environmental conditions and their effects on ecosystem properties. It builds on the notion of the effect-response framework, which states that plants are linked with the abiotic environment on one hand and ecosystem functioning and services on the other. These links are provided by functional traits. The causal chain is not unidirectional. Plants can change abiotic conditions, e.g. through fixation of atmospheric CO_2, N_2, or water retention, and biotic components of ecosystems, e.g. herbivores, affect plants in turn. These feedback loops are out of the scope of the present work, as their analysis requires data with temporal resolution. This work focuses on the net effects of changes in abiotic conditions on functional traits and on ecosystem functioning, both directly and mediated by traits.

Mount Kilimanjaro in Tanzania served as a model for tropical ecosystems. The data presented were collected there. Along an elevation gradient of 3500 m, a precipitation gradient of 2500 mm, and a disturbance gradient from natural systems to intensively managed plantations, plant functional traits of the most abundant and widespread species were collected in sixty plots. Five plots were located in each of the twelve dominant ecosystem types at the mountain. Traits were selected to relate to plant functions as growth, persistence, and reproduction. For practical reasons, the focus was on above-ground traits, as trees constituted a substantial part of the vegetation of most ecosystem types. In total, about 2300 specimens from nearly 170 species were sampled. This included a wide range of life forms from alpine shrubs to annual weeds growing in maize fields, from 60 m tall rainforest trees to undergrowth ferns.

The introduction to this thesis gives an overview of the most important concepts of plant functional trait research applied in this work and characterizes the research area. The main part consists of three chapters to be published as research articles. These chapters highlight different aspects of the effect-response framework.

For the first of the main chapters, a large dataset of vegetation surveys collected by Andreas Hemp within the last 20 years was accessed in addition to plant functional traits. This data was used to investigate the niche breadths of plant species along environmental gradients and address the question whether plant functional traits can predict corresponding niche optima. Niche breadth sizes were mainly governed by ecosystem age and mean temperature - old and warm habitats harbored the species with the smallest niche breadths. This was predicted by theory, but to our knowledge this study is the first to show this pattern on three spatially related gradients simultaneously. The relationship is explained by increased competition with more time for speciation, which forces species to adapt to small parts of the environmental gradients. Optima positions were partly predicted by plant functional traits. A considerable part of variation remained unexplained, pointing to biotic interactions and historic events as important drivers of niche breadth size and optima positions.

The second study dealt with the variance of trait values within and between plant communities. While it is commonly assumed and has been confirmed in various studies that mean trait values of plant communities respond to changes in abiotic conditions, the role of the latter in shaping variation in trait values has seldom been addressed. The first hypothesis of this study was that many different plant life strategies would be found at benign environmental conditions, thus a wide range of trait expressions. In contrast, where environmental conditions pose challenges to plant survival, only a small range of trait values may allow species to thrive. The results corroborated this hypothesis. The second hypothesis was that between sites, comparable environmental conditions should result in trait similarity. If they did not, this would indicate neutral processes as drivers of species assembly. Comparisons revealed that within, but also between adjacent ecosystem types along natural gradients, trait similarity was relatively high, while along a disturbance gradient, strong shifts in trait expressions were observed. Very likely, this was due to gradual changes in conditions along the natural gradients and abrupt changes along the disturbance gradient. This suggested environmental filtering to play a prominent role in determining species composition. Nevertheless, species similarity was much lower than trait similarity, meaning that different species performing the same functions occurred. This may be an effect of neutral processes.

In the third main chapter, it was investigated whether plant functional traits, the abiotic environment, or both combined influence mean animal body mass in taxonomically defined groups or feeding guilds. This study presents a novel application of the effect-response framework towards understanding ecosystem functioning. The central question builds on Bergmann's rule of the negative correlation of temperature and body size and its exceptions, and the attempt to explain contradictions invoking resource availability. The latter was described with plant functional traits, which were in turn determined by the abiotic environment. The results did not reveal a single main cause of animal body mass, but showed partly idiosyncratic relationships of temperature and resource availability, i.e. plant functional traits, with mean animal body mass. This pointed towards variables not considered and assumptions in the overall model demonstrating the complexity of environment - animal body mass relationships.

After the main chapters, a synthesis arranges those in an ecosystem framework and highlights common assumptions and results across the three studies as well as limitations of the approaches applied. The outcomes of different analyses aiming at understanding plant-environment relationships are compared and the equivalence of the results is demonstrated. Metabolic theory of ecology is addressed, as it was used to explain patterns of both species and body mass distributions.

The outlook presents ongoing studies related to this work and suggests interesting goals for further research. This includes the relationship between functional traits and growth performance under climatic changes, the contribution of epiphytes to trait space, the links between functional traits across trophic levels, and the evaluation of ecosystem services with a special focus on carbon fixation and storage.

Zusammenfassung

Die vorliegende Arbeit untersucht die Wirkung abiotischer Umweltfaktoren auf Pflanzen und deren Einfluss auf Ökosystemeigenschaften. Die Grundlage dafür bildet das *effect-response framework*. Es beschreibt den Zusammhang zwischen Pflanzen und ihrer abiotischen Umwelt einerseits und Ökosystemfunktionen und -dienstleistungen andererseits. Die Herstellung dieses Zusammenhangs geschieht durch die funktionellen Eigenschaften von Pflanzen. Die Kausalität ist jedoch nicht linear. Pflanzen können die abiotische Umwelt verändern, z. B. durch die Fixierung von CO_2 und N_2 aus der Luft, oder durch Wasserspeicherung. Gleichzeitig beeinflussen biotische Ökosystemkomponenten, wie Herbivore, die Pflanzen selbst. Diese Wechselbeziehungen sind nicht Gegenstand dieser Arbeit, denn ihre Analyse setzt zeitlich aufgelöste Daten voraus. Der Schwerpunkt dieses Manuskripts liegt in der Auswirkung von Änderungen abiotischer Umweltbedingungen auf funktionelle Eigenschaften von Pflanzen und die Unterscheidung direkter und indirekter, durch jene Eigenschaften übertragenen Einflüsse der abiotischen Umwelt auf Ökosystemfunktionen.

Der Kilimandscharo in Tansania diente als Modellsystem für tropische Ökosysteme. Dort erfolgte die Sammlung der verwendeten Daten. Die funktionellen Eigenschaften der häufigsten und am weitesten verbreiteten Pflanzenarten wurden entlang eines Höhengradienten von 3500 m, eines Niederschlagsgradienten von 2500 mm und eines Störungsgradienten von natürlichen Habitaten bis hin zu intensiv genutzten Plantagen auf 60 Untersuchungsflächen gesammelt. Dabei befanden sich jeweils fünf Flächen in den wichtigsten Ökosystemen am Berg. Die Auswahl der funktionellen Eigenschaften richtete sich nach deren Bezug zu Funktionen wie Wachstum, Überleben und Fortpflanzung. Insgesamt wurden ungefähr 2300 Proben von fast 170 Arten gesammelt. Die Sammlung umfasst ein breites Spektrum von Lebensformen von alpinen Büschen über einjährige Unkräuter aus Maisfeldern hin zu 60 m hohen Regenwaldbäumen und Farnen aus der Krautschicht.

Die Einleitung dieser Arbeit gibt einen Überblick über die wichtigsten hier ver-

wendeten Konzepte der Forschung zu funktionellen Eigenschaften von Pflanzen sowie über das Untersuchungsgebiet. Der Hauptteil besteht aus drei Kapiteln, die als wissenschaftliche Abhandlungen veröffentlicht werden. Die Kapitel untersuchen einzelne Teile des *effect-response framework*.

Für das erste der drei Kapitel des Hauptteils konnte zusätzlich zu den funktionellen Eigenschaften auf Vegetationsaufnahmen von Andreas Hemp zurückgegriffen werden, die dieser in den letzten 20 Jahren aufgenommen hat. Der Datensatz wurde verwendet, um den Einfluss von Umweltfaktoren auf die Nischenbreite von Pflanzen zu untersuchen. Außerdem wurde geprüft, ob funktionelle Eigenschaften zur Vorhersage von Nischenoptima auf den entsprechenden Gradienten der Umweltfaktoren verwendet werden können. Die Nischenbreite wurde hauptsächlich durch das Alter eines Ökosystems und dessen Durschnittstemperatur bestimmt - alte und warme Lebensräume beherbergten die Arten mit den schmalsten Nischenbreiten. Das entsprach theoretischen Vorbetrachtungen, die vorliegende Arbeit ist unseres Wissens aber die erste, die dieses Muster anhand dreier Gradienten in einem Untersuchungsgebiet darstellt. Dieser Zusammenhang wird mit der Zunahme von Konkurrenz begründet. Diese ergibt sich aus einer größeren Artenvielfalt alter Ökosysteme, die einzelne Arten zwingt, sich an schmale Abschnitte von Umweltgradienten anzupassen. Die Lage von Optima entlang der Umweltgradienten konnte durch funktionelle Eigenschaften zum Teil vorhergesagt werden. Allerdings blieb ein bedeutender Teil der Streuung unerklärt, was auf Wechselwirkungen zwischen Arten und historische Ursachen als wichtige Einflussgrößen der Nischenbreiten und -optima schließen lässt.

Die zweite Studie beschäftigt sich mit der Streuung von Werten funktioneller Eigenschaften in und zwischen Pflanzengemeinschaften. Während allgemein vorausgesetzt wird und auch häufig nachgewiesen werden konnte, dass die Mittelwerte funktioneller Eigenschaften durch die abiotische Umwelt beeinflusst werden, wurde der Einfluss letzterer auf die Streuung der Werte funktioneller Eigenschaften nur selten untersucht. Die erste Annahme dieser Studie war, dass unter milden Umweltbedingungen für Pflanzen viele Lebensweisen möglich sind, und daher die funktionellen Eigenschaften eine Vielzahl von Werten annehmen. Im Gegensatz dazu sollten unter harten Bedingungen nur eine geringe Anzahl von Werten ein Überleben der Pflanzen ermöglichen. Die Ergebnisse bestätigten diese Vermutung. Die zweite Annahme bezog sich auf die Ähnlichkeit der funktionellen Eigenschaften zwischen Untersuchungsflächen. Vergleichbare Umeweltbedingungen sollten zu vergleichbaren Eigenschaften führen. Wäre das nicht so, würde das darauf hinweisen, dass neutrale Prozesse Artenzusammensetzungen bestimmen. Es zeigte sich, dass sowohl innerhalb von Ökosystemtypen, aber auch zwischen Ökosystemtypen entlang natürlicher Umweltgradienten die Ähnlichkeit funktioneller Eigenschaften hoch war. Entlang eines Störungsgradienten wurden dagegen große Unterschiede festgestellt. Das lag wahrscheinlich daran, dass sich entlang natürlicher Gradienten Umweltfaktoren langsam verändern, während entlang des Störungsgradienten plötzliche Sprünge stattfinden. Diese Ergebnisse legen nahe, dass die Artauswahl durch die vorherrschenden Umweltbedingungen einen wichtigen Einfluss auf die Pflanzengemeinschaften hat. Allerdings war die Ähnlichkeit der Artenzusammensetzungen wesentlich geringer als die der funktionellen Eigenschaften. Das bedeutet, dass in sich von den Umweltbedingungen entsprechenden Ökosystemen funktionell ähnliche, aber unterschiedliche Arten vorkommen. Das könnte auf neutrale Prozesse zurückzuführen sein.

Im dritten Kapitel des Hauptteils wurde untersucht, ob funktionelle Eigenschaften, die abiotische Umwelt, oder beide zusammen einen Einfluss auf die mittleren Körpergewichte von taxonomisch oder anhand der Ernährungsweise definierten Tiergruppen haben. Diese Studie stellt eine neue Anwendung des *effect-response framework* mit dem Ziel des Verstehens von Ökosystemfunktionaltät dar. Die zentrale Frage baut auf der Bergmannschen Regel über den negativen Zusammenhang von Temperatur und Körpergröße, deren Ausnahmen, und dem Versuch, diese mit der Nahrungsverfügbarkeit zu erklären, auf. Nahrung für Herbivore wurde mit funktionellen Eigenschaften von Pflanzen beschrieben. Diese hängen selbst von der abiotischen Umwelt ab. Die Ergebnisse ließen keine alleinige Hauptursache für das Körpergewicht erkennen, sondern zeigten zum Teil tiergruppenspezifische Beziehungen von Temperatur, Nahrungsverfügbarkeit, also funktionellen Eigenschaften, und dem Körpergewicht auf. Das deutete auf nicht berücksichtigte Variablen und Beziehungen im Grundmodell hin und unterstreicht die Vielschichtigkeit des Zusammenhangs zwischen der Umwelt und dem Körpergewicht von Tieren.

Auf den Hauptteil folgt eine Synthese, in der die einzelnen Kapitel in einem Ökosystemgerüst verortet werden. Außerdem werden gemeinsame Annahmen und Ergebnisse der drei Studien hervorgehoben. Die Ergebnisse der verschiedenen Analysen zum Zusammenhang zwischen Umwelt und funktionellen Eigenschaften werden verglichen und deren Äquivalenz gezeigt. Die *metabolic theory of ecology* wird ebenfalls besprochen, da sie zur Erklärung sowohl von Arten- als auch Körpergewichtsverteilungen herangezogen wurde.

Der Ausblick zeigt laufenden Studien im Zusammenhang mit dieser Arbeit und schlägt weitere interessante Fragestellungen vor. Dazu gehören der Zusammenhang von funktionellen Eigenschaften und Wachstumsleistung unter dem Einfluss des Klimawandels, der Beitrag von Epiphyten zur Vielfalt funktioneller Eigenschaften, die Zusammenhänge zwischen funktionellen Eigenschaften entlang der Nahrungskette, und die Bewertung von Ökosystemdienstleistungen mit besonderer Berücksichtigung der Kohlenstoffixierung und -speicherung.

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Contents

Chapter 1

Introduction

1.1 The effect-response framework

The classification of life forms based on functional characteristics as opposed to phylogeny dates back at least to ancient Greece (Weiher et al., 1999). Modern concepts were developed in the 1960s for animals, referring to species using the same resources as guilds (Root, 1967). Conceptual advances lead to the introduction of functional groups or types to describe species with similar resource requirements, or a common response to environmental changes (Gitav and Noble, 1997).

In this context, species were classified comparing morphological or physiological features thought or known to be linked to species' respective responses. These features were defined as *functional traits*, the "biological characteristics of plant species that respond to the dominant processes in an ecosystem" (Lavorel et al., 1997). A more species-centered definition of functional traits was given by Violle et al. (2007): "Functional traits are defined as morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction and survival, the three components of individual performance." This latter definition leaves open the way species interact with the environment. While in the beginning functional trait research focused on the responses of plants towards environmental variation, increasing interest arose into how species affect ecosystem processes (Díaz and Cabido, 2001). Functional traits are not only the result of the prevailing environmental conditions, but influence the functioning of ecosystems. A prominent example are plants' effects on element cycles through modifications in the uptake, retention and release of nutrients (Cornwell et al., 2008). This creates feedback loops with the abiotic environment and has consequences for ecosystem functioning and services (Díaz et al.,

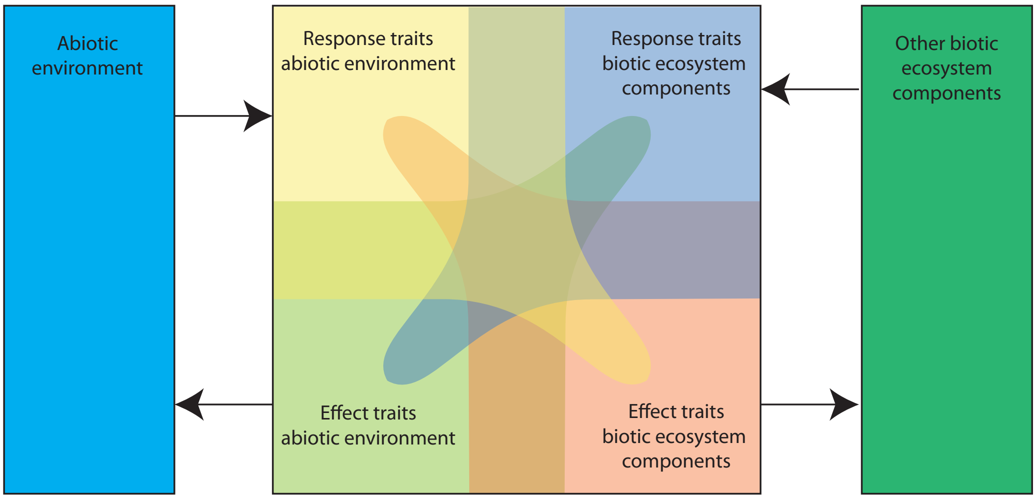

Figure 1.1: **The effect-response framework**
Response traits reflect adaptations of plant species to abiotic or biotic properties of ecosystems. Effect traits determine how plants shape other ecosystem components. Response and effect traits are not fixed. The inclusion of a specific trait depends on the context investigated. Theoretically, traits can be effect and response traits simultaneously. They may be affected by the abiotic environment and translate this effect to biotic ecosystem components, or *vice versa*.

2004).

Here, *ecosystem functioning* is defined as the sum of the storage capacities and processes involving fluxes of energy and matter in and between ecosystems (Naeem et al., 1999, 2012). *Ecosystem services* are closely linked to ecosystem functioning - they include the subset of ecosystem functioning directly relevant to humans, in addition to benefits that are not directly linked to fluxes of matter and energy, as recreational value (Díaz et al., 2005). The *effect-response framework* acknowledges the role of plant communities in mediating relationships between the abiotic environment and ecosystem functioning with traits reacting on environmental constraints and effect traits determining properties and processes, respectively (Lavorel and Garnier, 2002). This is displayed in Figure 1.1.

The classification of a certain trait into one of the four categories of response and effect traits depends on the abiotic environmental factors and other ecosystem components considered (Díaz et al., 2007). The effect-response framework has been applied to predict key aspects of ecosystem functioning such as productivity, nutrient cycling, carbon storage, and resilience (Díaz et al., 2004). Nevertheless, many aspects of ecosystem functioning have not been addressed using this concept yet, and a part of this thesis is dedicated to fill this gap.

1.2 Trade-offs and functional types

Plant functional traits do not exist independent of each other - plants have a limited amount of energy to invest in growth, persistence, and reproduction. Thick leaves will reduce available light for chloroplasts in the lower tissues. Increased metabolic activity comes together with higher respiration and susceptibility to drought. Short generation cycles are only possible for small herbaceous plants, but resistant woody tissues require perennial growth. The literature on trade-offs between traits is extensive (e.g. West et al., 2002; Reich et al., 2003; Cornwell et al., 2008). Most attention has been given to traits related to growth, as they are readily measurable in plants with vegetative tissue only. Additionally, growth performance directly influences carbon sequestration. This is expressed by the strong links between nitrogen content, photosynthetic activity, specific leaf area, and the primary productivity of ecosystems (Reich et al., 1992, 1994; Weiher et al., 1999). The trade-off exemplified is between fast growth with high turnover and slow growth with long persistence of plant organs. As this is expressed in leaf traits globally, it has been termed the *worldwide leaf economics spectrum* (Wright et al., 2004).

As differences in growth strategies involve all plant tissues, the trade-off seen in the leaf economics spectrum can be found in other traits, as such relating to plant structure or litter decomposition (Cornwell et al., 2008; Ishida et al., 2008). An example involving specific leaf area and stem specific density from the dataset collected for this work is shown in Figure 1.2. Further elaborating the trade-off concept, Grime et al. (1997) suggested a classification of plants along three axes: the first is related to growth or persistence, the second separates monocots and dicots on structural features, and the third relates to reproductive strategies opposing species with many small and few large seeds. Other trade-off axes exist, e.g. the leaf size-twig size spectrum proposed by Westoby et al. (2002).

Like phylogenetically unrelated animals may show convergent evolution due to exposure to similar environmental conditions, the same major trade-offs have evolved in plants. These functionally similar species have been called *functional types*, and they are thought to have similar functions in ecosystems, i.e. respond to the abiotic environment and influence biotic ecosystem components in the same way (Duckworth et al., 2000). The use of functional types has been promoted as a tool to generalize

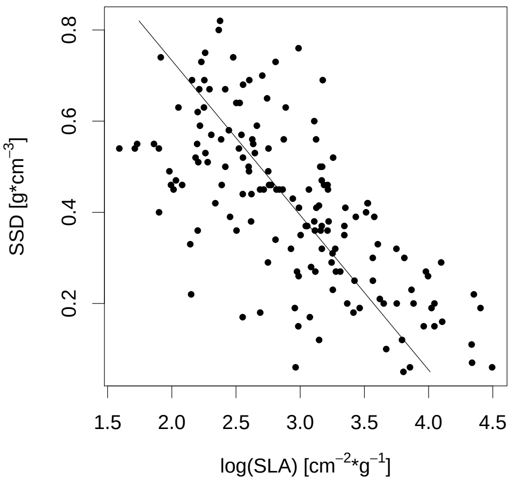

Figure 1.2: **Trade-off between specific leaf area (SLA) and stem specific density (SSD)**
The figure demonstrates the negative relationship between SLA and SSD for 157 species sampled at Mount Kilimanjaro. SLA values have been log-transformed. The line shows a ranged major axis (RMA) regression.

across ecosystems. It may also help to understand deterministic processes in species-rich communities as tropical rainforests, where many species are believed to be functionally nearly identical, and modeling each single species would not be feasible due to the computational complexity and interpretational difficulty associated with the results (Steffen et al., 1992; Bonan et al., 2002; Díaz et al., 2016). Still, the concept of trade-offs bears caveats: it may be apparent in some traits, but involve changes in a number of traits that may not all have been identified. An example is the seed size - seed number relationship. Although it certainly exists, other factors need to contribute to the performance of large-seeded species to be competitive (Moles and Westoby, 2004). Trying to describe plant communities using only single traits from trade-offs, e.g. seed size, will thus not capture the full variation inherent in this axis of plant differentiation.

Not all traits are linked through trade-offs. Traits relevant to regeneration appear to be only weakly coupled to vegetative traits (Díaz et al., 1998), and seed mass is larger in the tropics in general, independent of growth form and dispersal mode (Westoby et al., 1992). In a large neotropical tree dataset, the link between leaf and stem traits observed in this work has not been found (Fortunel et al., 2012). This demonstrates some trade-offs can only be found in spatially or taxonomically restricted groups.

In summary, selective pressure on one trait generally has consequences for a subset of the traits of an organism. This selective pressure may arise through dispersal of a species to novel habitats, or changes of environmental conditions or biotic interactions within an ecosystem. Other traits, however, may only respond to different environmental drivers. Additionally, the visibility of trade-offs may depend on the plant groups considered, e.g. trees only or all terrestrial vascular plants.

1.3 Fundamental and realized niche

Each species is limited in its endeavor to grow and disperse by the range of abiotic conditions it can persist at. These conditions can be seen as axes of an n-dimensional hypervolume, and the permissible part of this hyper-volume for a given species is called its *fundamental niche* (Hutchinson, 1978). It is defined by the physiological characteristics of a species. In the real world, virtually all species are involved in interactions with others. These interactions may have positive or negative effects on species' survival, and they may allow a species to grow at conditions where it would not occur because facilitation attenuates environmental stressors, or competition and predation may exclude species from physiologically viable conditions. Among plant species, facilitation will generally occur towards extreme environmental conditions, as in alpine environments, and competitive exclusion in nutrient-rich productive habitats (Austin, 1999). The resulting real distribution of a plant along the environmental axes of the n-dimensional hypervolume is termed its *realized niche*. Other definitions of the niche exist, e.g. some that view niches as habitat properties that can be filled by species (Grinnell, 1917). Nevertheless, in this work, the objective was to investigate changes in the extent of environmental space species occupy, so the Hutchinsonian definition was adopted.

1.4 Niche and neutral theory

In niche theory, abiotic conditions, e.g. the temperature regime and precipitation, are thought to act as a filter for species (Moles et al., 2014). Plants with trait expressions promoting survival at given conditions will pass the filter. Thus, plant functional traits are closely linked to this process called *environmental filtering* (Westoby and Wright, 2006; Lebrija-Trejos et al., 2010). This view has been widely accepted, as strong gradients evidently triggered the evolution of particular plant morphologies, as those of desert cacti and tiny cushion vegetation in cold alpine environments. But even within sites, species are often morphologically and phylogenetically different (Westoby and Wright, 2006). Passing the environmental filter but being sufficiently different from each other has been formulated as a condition for species co-occurrence, as similar species should out-compete each other (Ackerly and Cornwell, 2007; Bermudez and Retuerto, 2013). This mechanism has been termed *limiting similarity*.

Nevertheless, the high diversity of co-occurring species in tropical forest ecosystems has raised the question if this is correct, or if co-occurrence may be possible without strong differences in functional traits. The neutral theory brought forward by Hubbell (2001) formulates this notion: It posits that co-existence is not linked to traits, but to chance. Survival probabilities of species depend on their abundances, and traits have no effect on a plants' success or failure to grow at a certain site. This questions the concept of functional traits, as they are assumed to be of no relevance for species' interactions with the environment and other species. As chance is believed to be the only driver of changes in species composition, traits, and consequently species identities, may vary randomly, a process called *ecological drift*. Figure 1.3 shows a simulation comparing mean trait values of five communities assuming neutral processes and environmental filtering, respectively.

The contrasting views on the mechanisms by which species coexist at ecologically relevant timescales are extremes on a gradient of determinism to stochasticity. In general, it is assumed the truth lies in between (Leibold and McPeek, 2006). A series of studies have tried to reconcile niche and neutral theory in different ways (e.g. Gravel et al., 2006; Cadotte, 2007). The majority of research comes to the conclusion that processes are scale-dependent, environmental filtering making a preselection of species from regional species pools, and neutral processes allowing for the coexistence of similar species at small scales (Gaston and Chown, 2005; Jabot et al., 2008). Only species passing the environmental filter would share a given habitat. While species with different adaptations may coexist because they use resources differently and may even facilitate each other, functionally identical species, i.e. species with the same traits, may only coexist if sufficient space or resources are available to support several populations. Contrary to other species that may go extinct, too, species with functionally identical competitors would have a higher risk of local extinction, because dead individuals could be replaced by functionally identical individuals from other species.

An interesting view is presented by Wennekes et al. (2012) who argue that the distinction between niche and neutral theories is of philosophical nature. On large

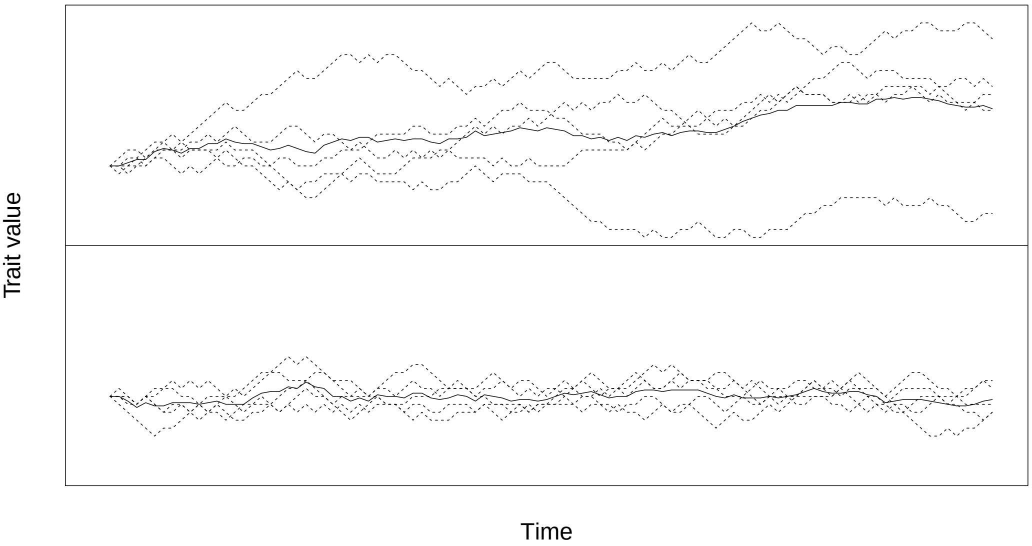

Figure 1.3: **Changes in mean trait values comparing neutral processes and environmental filtering**
The upper panel shows the mean values of a hypothetical trait over time for five communities assuming neutral processes are acting and changes driven by chance only. The lower panel displays the same trait in the presence of environmental filtering. Traits still change by chance, but deviations away from the optimal (initial) values become increasingly unlikely the more actual values differ from it. Dashed lines represent community means, solid lines are overall means.

scales with coarse data at hand, neutral processes seem to explain patterns. At small scales and with better data, evidence for niche processes will be found. This idea can be extended to the intraspecific scale: Even individuals of the same species are not completely equal in general, and it could be claimed that competition among conspecifics is a deterministic process. In essence, this barely changes the formulation of the initial question: Instead of asking whether niche or neutral processes shape species distributions, it would be asked which differences in species or individual traits are necessary to exceed environmental stochasticity, i.e. disturbance events affecting individuals randomly, and thus produce net deterministic effects.

1.5 Species and functional diversity

Contrary to neutral theory, the trait-based approach adopted throughout this work is based on the notion that ecosystem functioning does not depend on mere species numbers, but on species properties termed functional traits (McGill et al., 2006). Nevertheless, high species richness is of potential economic value (Lanzerath and Friele, 2014) and an insurance for ecosystem resilience under changing environmental conditions, as large numbers of different species with different trait compositions may sustain redundant processes compensating for the loss of some species from the system (Isbell et al., 2011). Another asset of high diversity is the likely occurrence of many different functional types that may optimally use available resources and foster productivity. In grasslands, high-diversity sites have been found to be more productive than monocultures (Tilman, 2001). The destruction of terrestrial habitat, especially rainforests, and the pollution of the seas are continuing at high velocity and have detrimental effects on biodiversity and ecosystem services, as they exceed ecosystem resilience (Hooper et al., 2005). Although the protection of biodiversity has been formulated as a main objective of international efforts for a sustainable use of the resources on earth (Balmford et al., 2005), a better mechanistic understanding of the effects of environmental change on ecosystems may help to convince stakeholders and society to put more efforts into their protection.

1.6 Community-weighed means and trait variance

Based on the premise that environmental filtering structures species assemblages, limiting similarity prevents species from becoming very similar, i.e. choose the most profitable trait combinations: Competition will restrict the similarity of species,

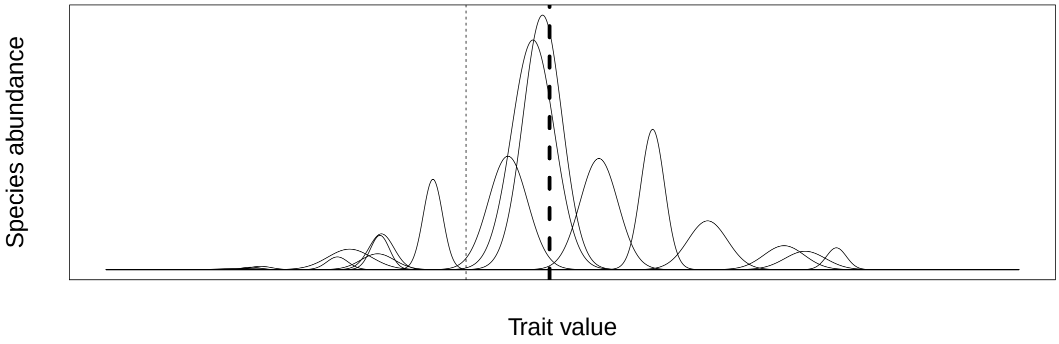

Figure 1.4: **The community-weighed mean (CWM)**
Species co-occurring in communities often differ in their trait values owing to different life strategies. The underlying causes may be recent processes, e.g. competition or predation, or the evolutionary history of those species. To characterize communities and investigate general relationships between plants traits and the environment, CWMs are used. Because of weighing traits by abundance, CWMs generally represent trait values close to those of the dominant species in a community, which are expected to be optimally adapted to the environment. Curves show individual species, the bold dashed line marks the CWM, and the thin dashed line the unweighed mean for comparison.

creating a mixture of trait expressions at a given site (Westoby et al., 2002). This implies that under given environmental conditions, more than one value for each trait exists. The question is how to determine if environmental conditions provoke changes in trait values or if trait values have an influence on ecosystem functioning. An obvious solution is to take the mean of the trait values at a given site, and to relate this mean to environmental conditions or ecosystem functioning. Still, abundant and rare species would contribute equally to this mean, although rare species are more likely to be exceptional in their trait combinations, meaning they may be specialists that were pushed to the margins of the possible trait value range, while dominant species are likely to center at the optimal trait combinations of a given site (Grime, 1998). Thus, trait values should be weighed by species abundance, resulting in the *community-weighed mean* (CWM, Fig. 1.4).

In the case of plants, abundance is often expressed as percent cover. This approach was followed in this work. To calculate the CWM, all cover values of a community were summed to get the total cover. Then, individual covers were divided by total cover and multiplied by the respective trait values. For a trait x, the CWM was calculated as

$$CWM_x = \sum_{i=1}^{\#species} \frac{cover_i}{cover_{total}} * x_i$$

The x_i denote species' trait values. For animals, cover cannot be measured. Thus, if traps are used, traits may be weighed by the fraction of a certain species within the total of specimens collected. Another possibility is to derive abundance as the number of sightings within a specified time frame.

Apart from the CWM, the spread of trait values in a community, i.e. trait variance, can have a strong influence on ecosystem functioning and services (Díaz and Cabido, 2001). The (weighed) variance of a single trait x in a community could be measured simply as

$$Var_x = \sum_{i=1}^{\#species} \frac{cover_i}{cover_{total}} * (x_i - \overline{x})^2$$

where $\overline{x}$ is the community-weighed mean. Laliberté and Legendre (2010) introduced *functional dispersion* calculated as

$$FDis_x = \sum_{i=1}^{\#species} \frac{cover_i}{cover_{total}} * |x_i - \overline{x}|$$

For comparability with other studies, we adopted this measure. In the multivariate context, this expands to

$$FDis = \sum_{i=1}^{\#species} \frac{cover_i}{cover_{total}} * \sqrt{\sum_{j=1}^{\#traits} (x_{i,j} - \overline{x_j})^2}$$

$x_{i,j}$ denote species trait values, and $\overline{x_j}$ are community-weighed means. The practical difference between FDis and the ordinary variance is the square root taken from the quadratic terms in FDis. This means ordinary variance gives more weight to species which differ strongly from the community mean compared to such that are close, while FDis gives the same weight to all species.

Nevertheless, both FDis and the ordinary variance describe the spread of trait values, thus functional diversity. In Chapter 3, FDis has been used and named as such. In the synthesis chapter, I preferred the term variance because it can be used in a broad sense to describe any related measure.

1.7 Mountain ecosystems and environmental gradients

Testing theories about plant functional traits requires differences in environmental conditions. Research on plant distributions has identified temperature and precipitation as the main drivers shaping plant communities (Gentry, 1988; Hawkins et al., 2003; McCain and Grytnes, 2010; Storch, 2012). Temperature is intimately linked elevation. Additionally, soil nutrient levels have been shown to affect species composition (John et al., 2007).

In an experimental setting, effects of changes in environmental conditions would be investigated using a factorial design, i.e. replicating experiments changing single factors and all possible combinations separately. Unfortunately, when ecosystem functioning is being investigated, the size of the research units and the time needed to understand effects of changes makes such an approach impractical. Thus, natural systems have to be used to test hypotheses concerning the response of ecosystems to changes in environmental conditions. As co-variations in environmental conditions become more likely with increasing scale, relatively small systems with strong gradients in the desired factors and little co-variation are preferable. While no natural system will strictly meet these conditions, mountains come close: Large elevation gradients of small spatial extent offer the possibility to test temperature predictions, and at least in natural systems, edaphic conditions are often homogeneous (Beck et al., 2008; Gradstein et al., 2008). Precipitation regimes are highly variable between mountains, but research at different localities with differing rainfall may elucidate its role in determining properties of plant communities. Often, anthropogenic disturbance in mountainous regions is less than in the lowlands because of the more difficult accessibility (Lomolino, 2001). Finally, mountain ecosystems may, depending on the geologic history of the surrounding landscape, be comparable to islands or restricted microcosms of laboratories if distances to other mountain systems are large (Assefa et al., 2007). Isolation is an important factor to be considered, because contrary to laboratory experiments, energy and matter fluxes between ecosystems may foster or mitigate the effects of environmental changes (Staddon et al., 2010).

1.8 Mount Kilimanjaro as a model system for tropical habitats

The data presented here was collected at Mount Kilimanjaro, the highest free-standing mountain in the world. Mount Kilimanjaro is located in Northern Tanzania at 3.1 °S 37.4 °E. It is a dormant volcano and was created by three major eruptions the youngest of which formed the highest peak Kibo around 150000 yrs ago. It features a large elevation gradient from the savanna plains at 1000 m a.s.l. to the top at 5892 m a.s.l. and is thus well-suited to study influences of environmental changes on plant functional traits and ecosystem functioning. Mount Kilimanjaro serves as a model system for tropical habitats, especially for other regions in East Africa that are characterized by high mountains interspersed within a savanna matrix.

The climate of the lowlands is arid, with long and short rain seasons from March to July and November to December, respectively. On the upper slopes, the climate of the northern and southern parts of Mount Kilimanjaro differs strongly. This study focused on the southern parts, which receive considerably more rainfall than the North. They are heavily populated at lower elevations. The high water availability sustains a large rainforest belt above the populated areas. Farmers at Mount Kilimanjaro benefit from the year-round water supply allowing for permanent growth of food and cash crops. Climatic and land-use changes in this region will thus have strong effects on rural societies.

The following description of the abiotic environment and the vegetation refers to the southern slopes of Mount Kilimanjaro. Abbreviations in brackets refer to the dominant ecosystem types at the mountain. Representative images can be found in Appendix A.

The lowest part of the elevation gradient (800 - 1100 m a.s.l.) is characterized by annual grasses and trees adapted to low levels of precipitation (700 mm*a^{-1}) and pronounced seasonality. The natural vegetation is a savanna landscape with many different grasses and drought-adapted trees (SAV). In agricultural areas, dicotyledonous weeds, especially Asteraceae, constitute the undergrowth of crop fields (MAI). Areas located at 1100 - 2100 m a.s.l. receive considerably more rainfall and have been populated by humans for at least 2000 yrs (Odner, 1971). Traditional agroforestry systems (HOM) have an upper canopy of forest trees, an understory of bananas and coffee trees, and a ground layer of taro plants and annual weeds of cultivation (Hemp, 2006). Shade trees at this elevation host epiphytic ferns. Interspersed between homegardens, grasslands (GRA) are kept open by farmers regularly cutting grass and herbs for their livestock. Coffee plantations (COF) have displaced small-scale farming to a considerable extent. Submontane and lower montane forest (FLM) remains in deep valleys adjacent to and within the limits of Kilimanjaro national park. The camphorwood *Ocotea usambarensis* Engl. dominated these forests but has declined through logging in the past. The middle montane forest

(FOC and FOD) at 2100 - 2800 m a.s.l. receives rainfall up to 3500 mm*a^{-1} and hosts large numbers of terrestrial and epiphytic ferns. The upper canopy is nearly exclusively formed by *Ocotea usambarensis*, the understory consists of the tree fern *Cyathea manniana* HOOK. and several Rubiaceae species. In the upper montane forest (FPO and FPD) at 2800 - 3000 m a.s.l. *Ocotea usambarensis* is substituted by *Podocarpus latifolius* (THUNB.) R. BR. EX MIRB. and *Schefflera volkensii* (HARMS) HARMS. Precipitation decreases steadily with elevation reaching amounts similar to the savanna plains at 4500 m a.s.l. The cloud forest (FER) extends between 3000 and 4000 m a.s.l. *Erica rossii* DORR dominates adjacent to the upper montane forest and is replaced by *Erica trimera* (ENGL.) BEENTJE from 3400 m a.s.l. on upwards. The giant heather *Dendrosenecio kilimanjari* (HUTCH. & TAYL.) E. B. KNOX grows in the upper cloud forest and continues to occur in the lower parts of the alpine shrubland (HEL) dominated by *Helichrysum* spp. MILL., which forms the last considerable plant cover ranging from 4000 to 4500 m a.s.l.

Sixty research plots were established in the twelve dominant vegetation types along the mountain, five plots in each ecosystem type. Vegetation surveys were conducted and the 169 most abundant and widespread species identified within our plots (Appendix B). The traits sampled from those species are given in Appendix C. Species-level traits, i.e. traits that do not vary among conspecifics, were collected both in the field and extracted from the Flora of Tropical East Africa (Turrill and Milne-Redhead, 1952). Individual-level traits that exhibit intraspecific variation were sampled from 15 specimens distributed as widespread as possible along the mountain. In total, 2279 samples were collected. For the first study presented in this thesis, roughly 1000 vegetation surveys including species abundances collected by Andreas Hemp within the last 20 years were used. This allowed for an assessment of species' niches and their comparison with plant functional traits collected in the sixty new plots. In the second and third study, functional traits were linked to data on abiotic and biotic components of ecosystems gathered by coworkers.

The environmental factors considered in this work comprise elevation, precipitation, soil nutrients, and temperature. Gradients of the latter are known to feature the strong species turnover and are probably the main determinants of the fundamental niche (Moles et al., 2014; Gentry, 1988; Van Der Heijden et al., 2008; Sanders and Rahbek, 2012).

Disturbance was included in the analyses, because disturbance events can have profound consequences for both individual species' distributions as well as ecosystem functioning as a whole (Sagar et al., 2003; Lozada et al., 2008). In general, disturbance cannot simply be treated as a part of the abiotic environment, as it includes both abiotic and biotic alterations of ecosystems. A definition is given by Rykiel (1985): "[Disturbance is] a physical force, agent, or process, either abiotic or biotic, causing a perturbation (which includes stress) in an ecological component or system; relative to a specified reference state and system; defined by specific characteristics". Examples include the devastation of savanna habitats by large numbers of crickets or elephants, but also pollution of water sources or fires. In this work, natural biotic interactions causing disturbance have not been addressed.

The focus of this work was on anthropogenic disturbance, expressed by the extraction or destruction of plant biomass, including intentional and unintentional burning, the use of herbicides, but also fertilization, irrigation, and livestock grazing. Cultivation, i.e. the conversion of natural habitats to used lands, is often expressed by a chain of disturbance events, like burning followed by regular herbicide and fertilizer application in maize fields.

For better readability, the term abiotic environment includes disturbance. Figure 1.5 gives an overview of the locations, precipitation, and disturbance data of the research sites.

For the large number of vegetation surveys done by Andreas Hemp and used in Chapter 2, detailed information was not available and we relied on the subjective estimation of disturbance on a scale from 0 (natural conditions) to 10 (strongly anthropogenic). The sixty newly established plots were more thoroughly investigated and an elaborated disturbance index was developed. It included biomass removal, fertilizer application, and the degree of alteration of the vegetation structure in the vicinity of the plots. As with the index used for the other vegetation surveys, only anthropogenic alterations of ecosystems were counted. The appendices of Chapters 3 and 4 include information on the calculation of the disturbance index (pages 104 and 131, respectively).

1.9 The KiLi project

This work was done as part of the KiLi project "KiLi - Kilimanjaro ecosystems under global change - Linking biodiversity, biotic interactions and biogeochemical ecosystem processes". This collaborative effort involved scientists from different disciplines investigating climate, soil, plants, and animals at common plots. The effect-response framework explains the central position of plant functional traits in ecosystem functioning, as plants are dependent on climate and soil properties and

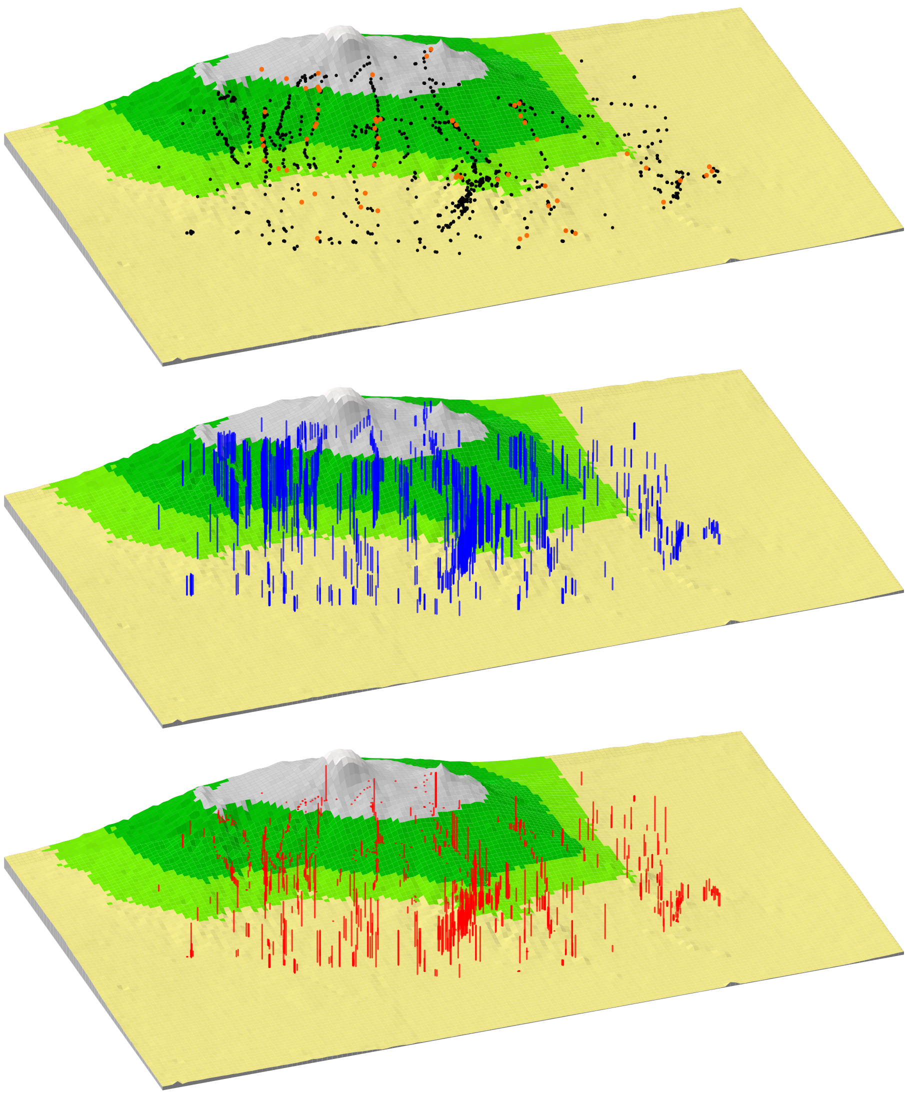

Figure 1.5: **Research sites and the abiotic environment**
The panels represent a part of grid cell 37M of the UTM coordinate system. The upper left corner is at 3 °S 37 °E, the lower right corner at 3.5 °S 37.8 °E. The left and right borders run in North-South direction and the upper and lower borders in East-West direction. The upper panel shows the approx. 1000 vegetation surveys performed by Andreas Hemp (black dots) and the location of the sixty new research sites (orange circles). The middle panel shows annual precipitation. Bars represent a rainfall gradient from about 500 to 3600 mm*a^{-1}. The lower panel gives disturbance values for all sites. The definition of disturbance varied between the vegetation surveys and the new sites, but values were transformed so that dots denote natural conditions, while bars show the degree of anthropogenic impact. These figures were created using topographical data from ASTER GDEM, a product of METI and NASA.

offer the habitat and food resources for animals. The strength of the KiLi project lies in the synchronous data collection at common research sites allowing for better inferences through the reduction of errors introduced by variations in co-variables inherent to studies combining data from different collection times or localities.

Additionally, long-term climatic and vegetation records allow for an understanding of vegetation dynamics in time. A baseline hypothesis of the KiLi project is that climatic and land-use changes will mostly be expressed in shifts of existing vegetation zones and land-use types. Thus, if data can be extrapolated into the area of the respective vegetation units, the effects of changes in the extent of those units for ecosystem functioning and services can be predicted. This is urgently needed because it may allow stakeholders and politicians to base management decisions on reliable long-term predictions instead of immediate revenue only.

1.10 Outlook on the three main chapters

The second chapter of this work deals with the primary determinants of plant species distributions: It investigates how the abiotic environment shapes the niche of a given species. To this end, we explored the relationship between plant niche breadth and position along environmental gradients. Additionally, Chapter 2 shows the relationships between those niche parameters, and niche volume, i.e. the environmental space populated by a certain species, with its functional traits. This presents an application of the response part of the effect-response framework described earlier.

The third chapter elaborates on the hypotheses of environmental filtering and neutral theory. As a baseline expectation, we assumed that along the elevation and disturbance gradients at Mount Kilimanjaro, environmental filtering would be strong because of the changes in the abiotic environment. In contrast, within ecosystem types, relatively similar conditions may have created a common species pool from which species are selected by chance. This would imply a shift from neutral processes at small (plot) scales to environment filtering at larger scales, when environmental conditions differ strongly between sites. As in the preceding chapter, the response part of the effect-response framework was the objective of this investigation. Nevertheless, the focus shifted from species distributions and niche breadths towards the relationship of community-weighed means and trait variance with the environment and relative changes in trait composition between ecosystem types.

In the forth chapter, plant functional traits shaped by the abiotic environment are used to predict a part of ecosystem functioning - the mean body mass of animal taxonomic groups or feeding guilds. The strength of the influence of those traits was compared to the well-known effect of temperature expressed in Bergmann's rule (Bergmann, 1848). This work is one of the few trying to predict the effects of plant functional traits on the properties of animal communities, and novel in the use of animal body mass as a response variable.

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Chapter 2

Plant niche breadth along environmental gradients and its relationship to plant functional traits

David Schellenberger Costa[1]*, Michael Kleyer[1], Friederike Gerschlauer[2], Ralf Kiese[2], Markus Fischer[3,4], Andreas Hemp[5]

[1]Department of Biology and Environmental Sciences, University of Oldenburg, 26111 Oldenburg, Germany

[2]Institute for Meteorology and Climate Research, Karlsruhe Institute of Technology, 82467 Garmisch-Partenkirchen, Germany

[3]Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland

[4]Senckenberg Gesellschaft für Naturforschung, Biodiversity and Climate Research Center, 60325 Frankfurt, Germany

[5]Department of Plant Systematics, University of Bayreuth, Universitätsstrasse 30, 95440 Bayreuth, Germany

*Corresponding author

Abstract

Aim We tested whether the relationships of different niche parameters with gradients in elevation, precipitation and anthropogenic disturbance, and with community diversity, support predictions from metabolic theory and a competition-based hypothesis of an inverse niche breadth-diversity relationship. Moreover, we explored the predictive potential of plant functional traits on niche parameters.

Location Southern slopes of Mount Kilimanjaro, Tanzania

Methods We derived species distribution models for 1492 plant species based on presence/absence data using generalized linear models. Parameter estimates were tested with bootstrapping. We investigated the relationship between plant functional traits and niche parameters with principal components regression to account for high trait correlations.

Results Niche breadth increased with optima position on elevation, precipitation, and disturbance gradients. Elevation niche breadth and volume decreased with increasing community diversity. However, precipitation and disturbance niche breadth were rather constant along the diversity gradient. Plant functional traits explained about 40% of the variation in optima positions on all gradients, but niche volume was only moderately related to traits.

Main conclusions Niche breadths showed the same patterns on the three gradients considered indicating temperature and habitat age may be the main driving factors determining niche breadth distributions. Still, high variability in niche breadths along the upper gradient parts suggests other strong influences, such as niche overlap and physiological barriers. Niche breadth and volume patterns along the diversity gradient were more complex than expected from our hypotheses. Historic factors such as different colonization times and initial niche breadths of colonizing species as well as different habitat connectivities and dispersal limitations are possible reasons. Niche optima were reliably predicted by functional traits, but this was not the case for niche volume, implying that intraspecific variability may be more important than absolute trait values.

Keywords niche size, species richness, competition, metabolic theory, temperature, elevation, precipitation, disturbance, species distribution model

Introduction

Species' distributions are the outcome of environmental requirements, dispersal limitations and competitive interactions. Since Grinnell (1917) ecologists have employed the niche concept to describe these distributions. Different meanings were attributed to the term (e.g. Grinnell, 1917; Hutchinson, 1978), and a definition is essential to avoid misinterpretations (McInerny and Etienne, 2012). Here, we adopt a Hutchinsonian framework defining the niche as a multidimensional volume in environmental space describing the conditions a given species occurs at. This implies the use of the realized as opposed to the fundamental niche, as the latter is hardly measurable in multi-species assemblages (Malanson et al., 1992; Tokeshi, 1993; Monahan, 2009). Species' tolerances towards environmental factors are described by the extent of their occurrence along environmental axes. We refer to these ranges as a species' niche breadths.

In this study, we focused on vascular plants, as they are the main primary producers in most terrestrial ecosystems. As the high dimensionality of the niche makes its exact measurement impossible, it is necessary to choose a set of relevant axes. We selected temperature, annual precipitation, and the strength of anthropogenic biomass removal - here termed disturbance for simplicity. Temperature and precipitation are the most influential factors driving diversity patterns (Gentry, 1988; Hawkins et al., 2003; McCain and Grytnes, 2010; Storch, 2012). We used elevation as a proxy for temperature, as their correlation is high at local scales. Anthropogenic disturbance, expressed by the removal of plant biomass, can profoundly alter ecosystems (Sagar et al., 2003; Lozada et al., 2008), and has strong impacts on individual species distributions (Clavel et al., 2010). As species distributions vary on all three gradients, the collective range of a species on these gradients will be called its niche volume, which is a simplified three-dimensional version of the n-dimensional hypervolume (Hutchinson, 1978).

Due to competition, species are supposed to replace each other along environmental gradients in a way that each species occupies the section providing its optimum requirements. Therefore, with increasing species richness, niches should become narrower (Whittaker, 1967; MacArthur, 1972; Pianka, 1974; Fox, 1981; Vázquez and Stevens, 2004). We used this concept as a working hypothesis for our study (competition hypothesis, COH). However, species with high competitive ability may monopolize benign habitats and relegate inferior species to stressful habitats (Scholten et al., 1987), where positive species interactions and therefore increased niche breadths may be more important than competition (Bertness and Callaway, 1994). Alternatively, if niches overlap rather than replace each other, i.e. species with small distributions are nested within species with large distributions, then variation in niche breadths should increase with species richness (Whittaker, 1967; Chase and Leibold, 2003).

Species richness itself may stochastically vary around a mean determined by resource availability (Harmon and Harrison (2015), but see Rabosky and Hurlbert (2015) for a contrasting view). In addition, the metabolic theory of ecology (MTE) predicts that species richness is positively related to temperature and productivity, because productivity will enhance the total number of populations and temperature should increase diversification rates (Allen and Gillooly, 2007; Storch, 2012) and other temperature-depending processes creating diversity (Brown et al., 2004; Enquist and Bentley, 2012; Brown, 2014). Increasing diversity will result in more competitive interactions, which in turn should lead to decreasing niche breadths (MacArthur, 1972; Clavel et al., 2010).

Niche breadth can also be seen as a compound property summarizing the effects of functional traits. Plants from alpine environments should be characterized by relatively small and dense growth, a low canopy height, and high stem specific density (SSD), dense leaves with a low specific leaf area (SLA), high leaf dry matter content (LDMC), and leaf pubescence to protect from UV radiation and slow heat loss (Körner, 2003; Ma et al., 2010). In low-precipitation environments leaves will have to be tough with a low SLA, high LDMC, and high SSD. Disturbed habitats should be characterized by fast-growing plants with high SLA values, high seed numbers, and short life cycles (Lienin and Kleyer, 2011). Trait-environment relationships should provide a functional explanation of points of highest occurrence probability, i.e. niche optima, on the temperature, precipitation, and disturbance gradients.

Although many studies deal with niche breadths on latitudinal gradients (e.g. MacArthur, 1972; Rohde, 1992; Vázquez and Stevens, 2004), at the landscape scale (Fox, 1981), and theoretically (e.g. Soberón and Nakamura, 2009; Blonder et al., 2014), very few investigated niche breadth distributions on elevation gradients (but see Saupe et al., 2015). To our knowledge, this study is the first to investigate niche breadths along different environmental gradients integrating data on functional traits to predict niche parameters.

We used Mount Kilimanjaro in Tanzania as a model system, as tropical mountains featuring large environmental gradients on a small spatial scale are well-suited to test hypotheses regarding niche breadths (e.g. Beck et al., 2008; Gradstein et al., 2008). The precipitation gradient along the mountain is related to productivity

(Ensslin et al., 2015) while the elevation gradient represented temperature. By assembling distribution models for approx. 1500 species, our study relies on a unique dataset to test the following predictions of the COH and MTE concepts: COH related to productivity assumes that niche breadths decrease with increasing species richness, which should be highest at the highest precipitation. COH related to temperature assumes that niche breadths decrease with increasing species richness, which should be highest at sites with the highest temperature. Finally, time may increase diversity, therefore different habitat ages may contribute to niche breadth differences, with the smallest niche breadths occurring in the oldest habitats.

Materials and Methods

Study region Mount Kilimanjaro is located in Northern Tanzania at 3.1 °S 37.4 °E. It is the highest free-standing mountain in the world, covering an area of approx. 4000 km^2. Mount Kilimanjaro is a stratovolcano that last erupted about 150 ka BP (Nonnotte et al., 2008). A period known as the East African megadroughts affected the area from 135 to 75 ka BP (Scholz et al., 2007). This was followed by fluctuating but more humid conditions until the present time, species depending on high precipitation levels probably establishing after the megadroughts period (Thompson et al., 2002). Permanent human settlements and land-use conversion affect the area since 2000 years (Odner, 1971).

The elevation gradient reaches from the lowlands at 800 m a.s.l. to the peak at 5892 m a.s.l. This corresponds to a gradient of mean annual temperature from 25 °C in the plains to 1 °C at 4500 m a.s.l., the limit of significant vegetation cover. Main soil types in the area are highly weathered andosols, being replaced mostly by vertisols at lower elevations. Table 2.1 gives on overview of the six elevation belts, annual precipitation, major disturbance types, and the dominant ecosystems. Variability in rainfall is strongest in the savanna region and gradually decreases towards the top of Mount Kilimanjaro (Mwangomo et al., 2014). Disturbance variability is strongest at lowermost elevations, low at middle elevations and increases again in the alpine zone, where occasional fires occur.

Vegetation surveys and environmental data Vegetation surveys were done by Andreas Hemp within the last 20 years at 969 plots on several transects along the southern parts of the mountain (Fig. 2.1, Hemp, 2009) spanning an elevation gradient of approx. 3700 m including 1492 plant species. To account for different

Table 2.1: **Elevation belts, precipitation, disturbance types, and dominant ecosystem types at Mount Kilimanjaro**
Disturbance was measured on a scale from 0 (no disturbance) to 10 (heavily disturbed) based on the frequency, extent, and type of disturbance.

Elevation Belt	Elevation Range [m a.s.l.]	Mean Precipitation [mm*a^{-1}]	Disturbance Types	Mean Disturbance	Dominant Ecosystem Types
Alpine scrub	4000 - 4500	700	-	0	*Helichrysum* scrub
Cloud forest	3000 - 4000	1100	Trampling (tourists), fire	1.2	*Erica* forest
Upper montane forest	2800 - 3000	1500	Fire	1	Disturbed and undisturbed *Podocarpus* forest
Middle montane forest	2100 - 2800	2200	Logging	1	Disturbed and undisturbed *Ocotea* forest
Submontane and lower montane forest	1100 - 2100	1900	Logging, farming, herbicides, grazing	3.5	Disturbed forest, agroforestry, grasslands, coffee plantations
Colline savanna zone	800 - 1100	900	Farming, grazing	3.9	Savanna, woodlands, maize fields

plant sizes and minimum areas of communities, plot areas were 1000 m^2 in forests, 100 m^2 in clearings, grasslands, and heathlands, 25 m^2 in salt marshes, swamps, and ruderal vegetation, and 5 m^2 in rocky habitats. Elevation was measured using hand-held GPS units (Garmin Ltd.) and cross-checked with 1:50000 scale maps (Tanzanian Government, 1964). Correlation of elevation and temperature for a subset of plots equipped with automated temperature loggers for several years was high (r = -0.98, Mwangomo et al., 2014). Precipitation data was extracted from the Kilimanjaro precipitation model (Hemp, 2009). Human disturbance was quantified as a single number on an ordinal scale reflecting natural biomass removal from the system for each vegetation survey. Values ranged from 0 (no human disturbance/ biomass removal) to 10 (heavily disturbed/ nearly complete removal of naturally grown biomass).

Plant functional trait collection Plant functional traits were collected for a subset of 133 species representative of the dominant ecosystem types within the research area (Tab. 2.1). Fifteen plant individuals were sampled for each species on the largest possible range of abiotic environmental conditions to capture intraspecific variability. For some locally dominant but regionally rare tree species, only five individuals were sampled. Functional traits measured are described in Table 2.2.

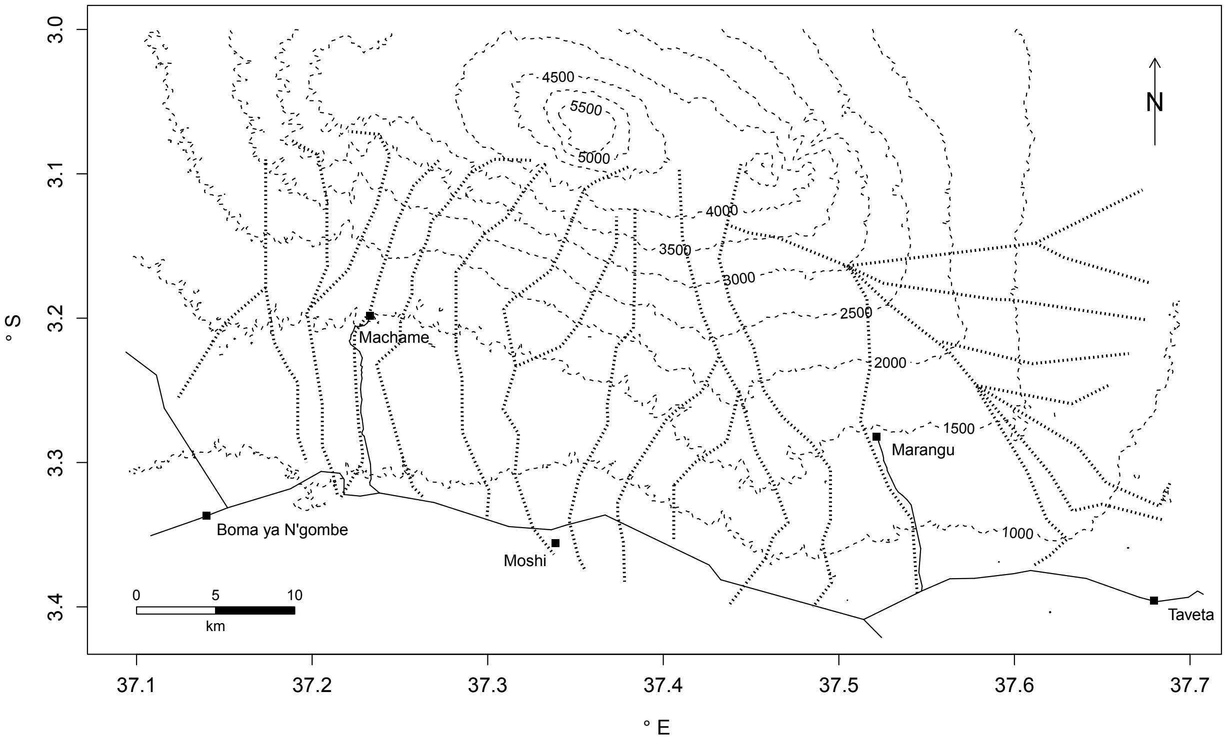

Figure 2.1: **Contour map of the southern slopes of Mount Kilimanjaro, Tanzania**
Dotted lines represent transects where vegetation records were taken. The unit of contour line elevation is [m a.s.l.]. This map was created using topographical data from ASTER GDEM, a product of the Japanese Ministry of Economy, Trade and Industry (METI) and the US National Aeronautics and Space Administration (NASA).

Sampling and processing of plant material followed Kleyer et al. (2008). Leaf δ^{13}C was measured with a Costech Elemental Analyzer (Costech International S.p.A., Milano, Italy) at the Center for Stable Isotopes, Karlsruhe Institute of Technology (KIT), Garmisch-Partenkirchen according to Balesdent et al. (1993).

Data analysis Species distribution models (SDM) yielding niche breadths and optima of individual species on the three environmental gradients were calculated using generalized linear models (GLM) with a logit link and binomial error structure (Nelder and Baker, 1972). The explanatory variables elevation, precipitation, and disturbance entered with a linear and a quadratic term each into initial models. SDMs were obtained by model averaging with corrected AIC (AICc) weights and shrinkage coefficients using the dredge function in the R package MuMIn (Bartoń, 2013). As occurrence probabilities of logit link GLMs are between 0 and 1 by definition, a threshold is needed to define a species' niche breadth. We used Cohen's Kappa (κ), which has been shown to lead to accurate predictions (Peppler-Lisbach, 2008). Cohen's Kappa is defined as the value in the range between zero and one which leads to the highest concordance between observation and prediction if converting the values of the occurrence probability curve of the SDM to one if above and to zero if below κ. Thus, the intercepts between the SDM curve and the constant $y = \kappa$ defined a species' niche breadth on the respective gradient (see Appendix S1(a) at page 71 in Supporting Information).

Species' optima along a gradient were defined as the point of maximum occurrence probability predicted by the SDM. Niche volume was calculated accordingly (see App. S1(b) at page 71): We divided each of the three gradients into 99 equal-sized intervals, resulting in the division of environmental space into 99^3 cubes. We evaluated a species' occurrence probability in each cube using the SDM. Niche volume was the fraction of cubes with an occurrence probability greater than κ. This approach may overestimate niche volume if distributions have several holes or parts of environmental space are not present in the natural habitat (Blonder et al., 2014), but interpolation properties of GLM also have the advantage of reducing possible bias through incomplete sampling.

To assess model quality, we performed a bootstrapping approach. Bootstrapping is a resampling procedure randomly drawing with replacement from the original data. This generates a new dataset with an equal number of occurrences, but a subset of the environmental conditions a species was found in. The SDM is then calculated on this data. This was repeated 10000 times. We calculated confidence

Table 2.2: **Plant functional traits used to predict the distribution optima of plants on the elevation, precipitation and disturbance gradients as well as their niche volumes**

Trait collection was according to the standards described in Kleyer et al. (2008). Abbreviations: SE Spatial expansion, GI Growth investment, RS Reproductive strategy, SA Stress adaptations.

Group	Trait	Unit	Value Range	Description
SE	Leaf area	cm^2	Numeric	One-sided leaf area
SE	Canopy height	cm	Numeric	Height of highest photosynthetic tissue
GI	Specific leaf area (SLA)	cm^2*g^{-1}	Numeric	Leaf area per g leaf dry weight
GI	Leaf dry matter content (LDMC)	$mg*g^{-1}$	Numeric	Leaf dry matter per g fresh leaf tissue
GI	Stem specific density (SSD)	$g*cm^{-3}$	Numeric	Dry weight per unit volume
GI	Leaf C_{mass}	$mg*g^{-1}$	Numeric	Leaf carbon content per g dry tissue
GI	Leaf N_{mass}	$mg*g^{-1}$	Numeric	Leaf nitrogen content per g dry tissue
GI	Leaf P_{mass}	$mg*g^{-1}$	Numeric	Leaf phosphorus content per g dry tissue
GI	Perennial	-	Boolean	Plant lifespan, annual or perennial
RS	Relative seed number	cm^{-1}	Numeric	Number of seeds per m canopy height
RS	Seed crop frequency	a^{-1}	Numeric	Number of seed productions per year
SA	Liana	-	Boolean	Liana or self-supporting
SA	Shoot growth form	-	0, 1, 2	0 = prostrate, 1 = ascending, 2 = erect
SA	Leaf pubescence	-	0, 1, 2	Density of leaf hairs (0 = no or few hairs, 1 = hairy, 2 = densely covered with hairs)
SA	Spinescence	-	0, 1, 2, 3, 4	Size and density of spines (0 = no spines, ..., 4 = medium density of large spines)
SA	Leaf $\delta^{13}C$	-	Numeric	Ratio of stable carbon isotopes, allows distinction between plants with C_3 and C_4 photosynthesis
SA	Endozoochory	-	Boolean	With or without digestible fruits

intervals for niche optima and breadths. We only included species in the analyses whose confidence intervals ($\alpha = 0.05$) for optima and niche breadths were smaller than $\frac{1}{4}$ of the respective gradient length. We chose this threshold as it proved to be an acceptable compromise excluding species with data too scarce to obtain reliable SDMs while keeping rare species with small distributions and thus few data points but good models in the dataset. By this criterion, we included 67 %, 32 % and 26 % of the 1492 species in our optima and niche breadth analyses for elevation, precipitation, and disturbance, respectively. For niche volume, niche breadth confidence intervals on the three gradients were evaluated, which resulted in 13 % of the species being used in the analysis.

Species occurring once in the whole dataset were fitted differently using a unimodal curve with highest occurrence probability at the (sole) observed occurrence conditions and a maximal occurrence probability of 0.01 at any other plot. We performed calculations both including and excluding these rare species, as they made up a high proportion of the total species number in the initial dataset (19 %), which could significantly bias the analyses. As differences in the results were negligible, only results excluding these singleton species are presented.

Niche breadths and volume along the environmental and diversity gradients The linear trends between niche optima and breadths were analyzed with ordinary linear least squares (OLS) regression (R base package, Team, 2014). We favored this method over a weighed regression on the individual species' niche breadths because we were interested in the trend of niche breadth change over the whole gradient, which would have been strongly influenced by the unequal species numbers along the gradient. Mean niche breadths were calculated depending on niche optima for 14 equal-sized intervals along the three environmental gradients.

We calculated mean niche breadths and volumes per plot and contrasted them with community species richness. We will refer to those means as community niche breadth and volume in the following. We also calculated average niche breadth and volume using all species, but differences were not changing the results qualitatively and are thus not shown. We refrained from using a regression technique here as data did not indicate a single functional relationship between community niche breadth and diversity.

Relationships of niche optima and volume with plant functional traits We assessed the potential of plant functional traits to predict niche optima and niche volume with principal components regression (PCR, pls package, Mevik and Wehrens, 2007). We applied PCR instead of ordinary multiple regression as it can deal with correlated predictors, which is often the case for functional traits. PCR was done using singular value decomposition extracting the first four components and investigating all four response variables (elevation, precipitation, and disturbance optima, niche volume) separately. Predictors and response variables were standardized prior to analysis. Standard errors for coefficient estimates were calculated with leave-one-out cross validation using the var.jack function (pls package). For clarity, plant functional traits were divided into four groups (Tab. 2.2): Spatial expansion traits describe the degree to which a plant invests in the occupation of space in its environment. Growth investment traits include traits of the leaf economics spectrum (Wright et al., 2004) and mirror plant growth strategies: to grow fast with short-lived tissue or grow slowly with a stronger overall structure. Reproductive investment traits characterize plants' reproductive strategies. Stress adaptations traits contain adaptations that enhance a plant's survival ability under extreme environmental conditions.

Results

Species richness decreased monotonically with elevation. Mean relative niche breadths were 0.14, 0.27, and 0.37 for elevation, precipitation, and disturbance, respectively, indicating that niche breadths were more strongly limited by elevation than by precipitation and disturbance (for models of all species, see Appendix S2 in Supporting Information). The mean generalized R^2 value of the SDMs was 0.53. There was no correlation between the number of occurrences per species and the generalized R^2 of its SDM ($r = -0.05$). Correlations between the number of occurrences and niche breadth were 0.52, 0.71, and 0.37 for elevation, precipitation, and disturbance, respectively.

Niche breadths along the environmental gradients

On the three gradients, mean niche breadth and niche breadth variability increased towards the upper ends of the gradients (Fig. 2.2). Larger niche breadths were thus found at high elevation, high annual rainfall and high disturbance. A slightly hump-shaped pattern characterized the lower to intermediate parts of the elevation and precipitation gradients, and variability increased strongly towards the upper gradient ends. At the disturbance gradient, niche breadth variability was similar on the whole gradient. Explained variance was highest on the elevation gradient ($R^2 = 0.80$), followed by the disturbance and precipitation gradients ($R^2 = 0.56$ and 0.46, respectively).

Niche breadths and volume along the diversity gradient

Community niche breadth was not related to diversity in a functional one-to-one relationship. Rather, for a given community species richness, large differences in community niche breadths and volumes were observed (Fig. 2.3). While overall patterns of elevation niche breadth and niche volume were as expected by the competition hypothesis, precipitation and disturbance niche breadth patterns deviated from our prediction.

Elevation niche breadths were highly variable at low diversities; variability decreased with diversity and was high again at the upper gradient end. Average community niche breadth (Fig. 2.3, triangles) decreased slightly with diversity.

Precipitation niche breadths were highly variable at low diversities, plots clustered in a large and small niche breadth group at intermediate diversity levels. These groups represented plots with higher and lower annual precipitation levels (precipitation data not shown), plots with higher annual precipitation harboring species with larger precipitation niches. Average community niche breadth had a hump-shaped relationship with diversity, but large variability at the gradient extremes may have obscured a rather constant pattern.

Disturbance niche breadth also showed a high variability along the whole diversity gradient. A separation of plots was visible as for precipitation, but plots clustered by elevation such that upper elevation forest plots had lower mean disturbance niche breadths than plots from lower elevations (elevation data not shown). The overall pattern displayed no pronounced trend, average community niche breadth being rather constant throughout the gradient. Average community niche volume decreased with diversity. The pattern was very similar to the elevation pattern, reflecting the strength of correlations between niche breadths and niche volume: They were 0.76, 0.64 and 0.48 for elevation, precipitation and disturbance, respectively.

Relationships of niche optima and volume with plant functional traits

Table 2.3 summarizes the effect of plant functional traits on the positions of the individual species' elevation, precipitation, and disturbance optima as well as on

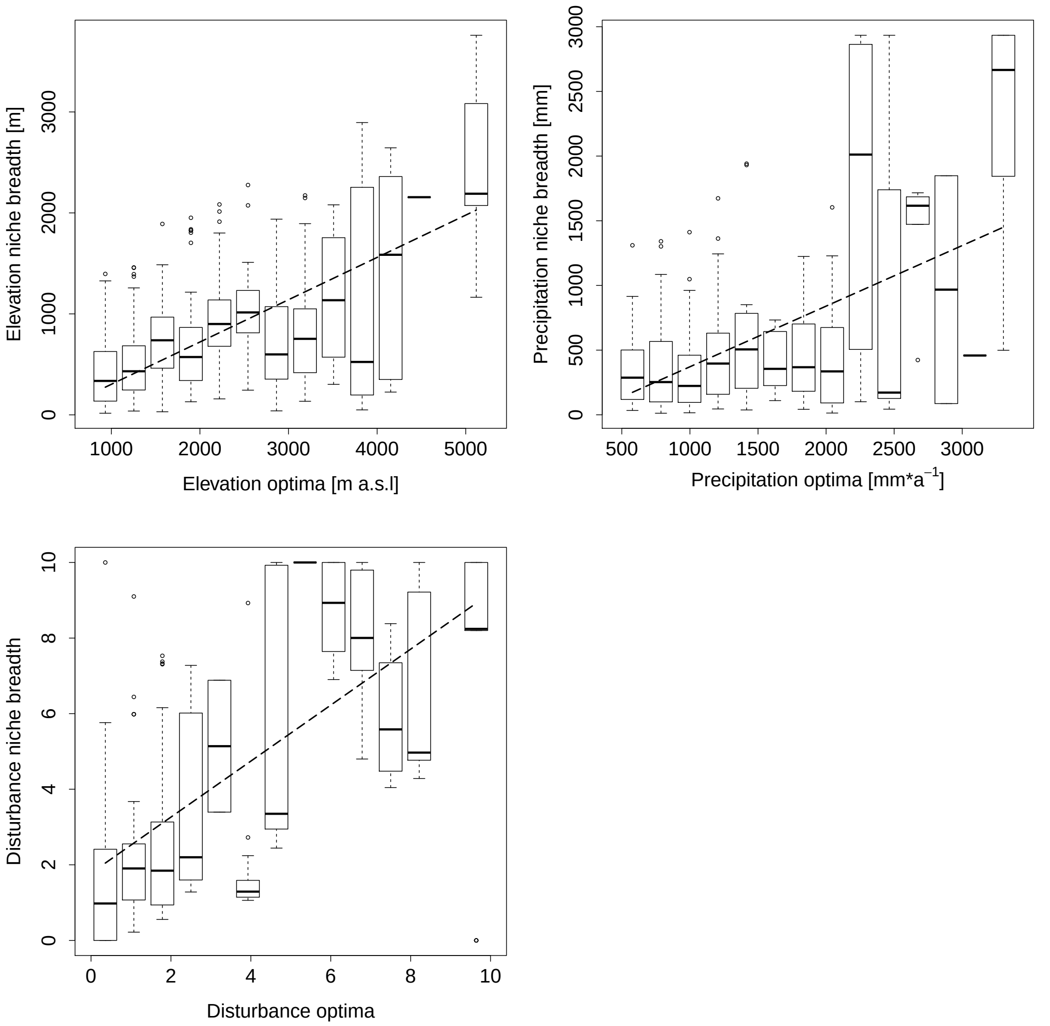

Figure 2.2: **Relationship of niche optima position and niche breadth along the three environmental gradients**

Regression lines are ordinary least squares regressions of group means. Horizontal bold lines in the boxes are medians. Slopes are 0.38, 0.44, and 0.71, p values are 3.1E-04, 8.4E-03, and 5.3E-03 for elevation, precipitation, and disturbance, respectively.

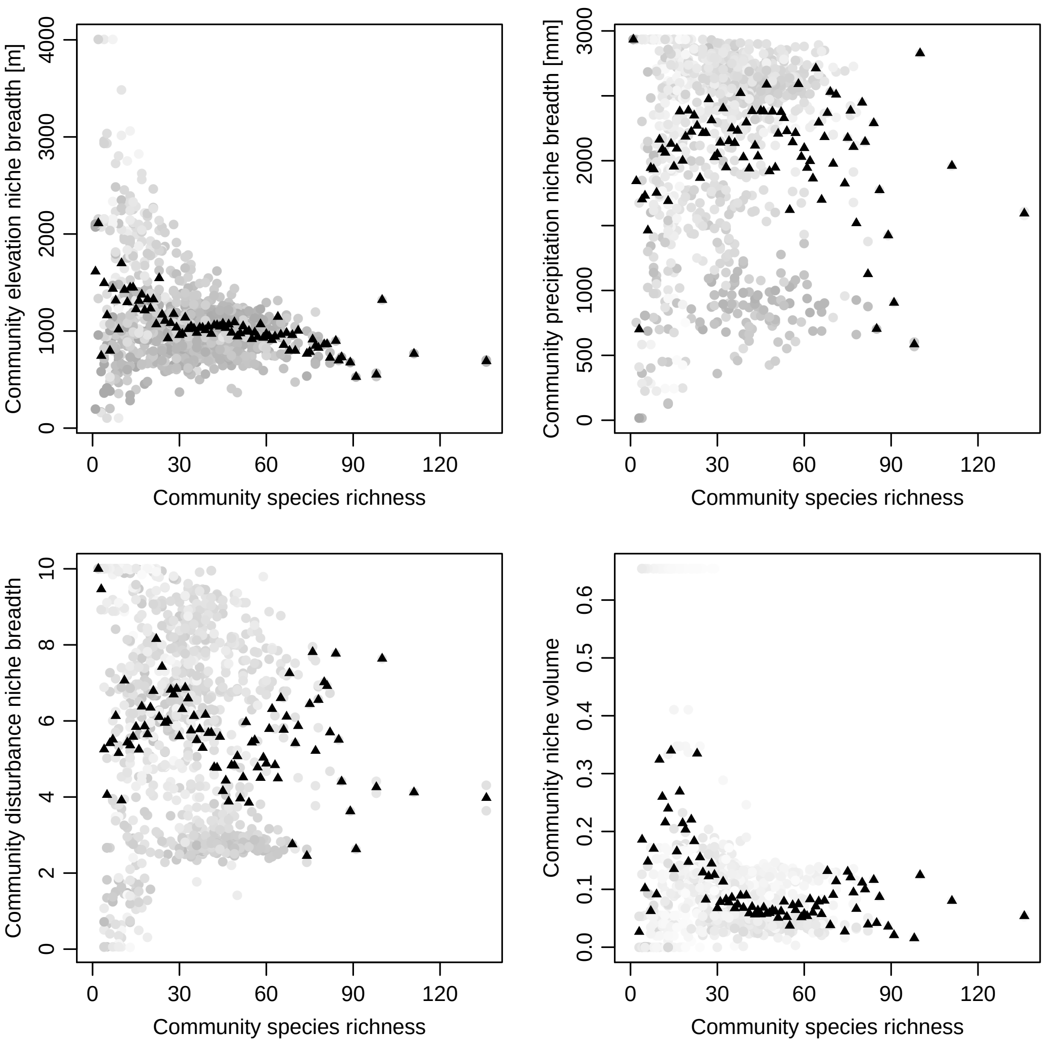

Figure 2.3: **Relationship of community species richness and community niche breadth and volume**
Shading of circles indicates the fraction of species included in community niche breadth calculation as judged from bootstrapping (see Methods). Black triangles represent averages of community niche breadth. Note that numbers of species included in elevation, precipitation, and disturbance as well as niche volume analyses varied.

niche volumes. Explained variance was comparable for elevation, precipitation and disturbance optima ($R^2 = 0.4$, 0.4, and 0.36, respectively). Interestingly, niche volumes were also quite well explained by traits ($R^2 = 0.36$).

However, traits could only be unambiguously related to optima and niche volume if standard errors of coefficients were smaller than the coefficients themselves (Tab. 2.3, standard errors in parentheses). This was the case for a subset of traits only.

Elevation optima were predicted by leaf size, all growth investment traits except LDMC and leaf N_{mass}, leaf pubescence, leaf $\delta^{13}C$, and endozoochory. Leaf $\delta^{13}C$ and leaf pubescence had the largest influences on elevation optima, the first with a negative and the second with a positive coefficient.

Optima on the precipitation gradient were explained by spatial expansion traits, all growth investment traits except leaf C_{mass} and P_{mass}, seed crop frequency, “liana”, shoot growth form, leaf $\delta^{13}C$, and endozoochory. The strongest predictors of precipitation optima were leaf N_{mass}, leaf size, LDMC, and leaf $\delta^{13}C$, the former two positively and the others negatively related to it.

Disturbance gradient optima were related to spatial expansion traits, growth investment traits except LDMC and leaf N_{mass}, shoot growth form, leaf $\delta^{13}C$, and endozoochory. The strongest predictors were canopy height, “perennial”, and endozoochory, all with negative coefficients. Although explained variance was similar to optima positions, coefficients of the trait - niche volume were not stable under cross validation. Nevertheless, canopy height and endozoochory had coefficients of the same magnitude as the confidence intervals, suggesting that widespread species were small and relied on other dispersal mechanisms than endozoochory.

Discussion

Niche breadths and volume along the environmental and diversity gradients

The competition hypothesis (COH) assumes that increasing richness leads to higher competition, followed by species replacements on gradients and thus narrower niches (Whittaker, 1967; MacArthur, 1972; Fox, 1981). According to the metabolic theory of ecology, species richness increases with temperature and habitat age, among other processes (Brown, 2014). Consequently, niche breadths should be narrower at lower elevations where temperature is high and in habitats representing ancient conditions.

Table 2.3: **Estimates and R^2 for a principal components regression of elevation, precipitation, and disturbance optima as well as niche volume on plant functional traits**

Predictors and responses were standardized prior to the analysis. Thus, coefficients are comparable across predictors and responses, respectively. Standard errors of the coefficient estimates obtained by jackknifing are given in parentheses. For trait descriptions see Table 2.2. For disturbance niche breadth, spinescence and "liana" could not be included in the analysis because variation was too low among the selected species. Coefficients with absolute values larger than standard errors are printed in bold.

Group	Predictor	Elevation Optima	Precipitation Optima	Disturbance Optima	Niche Volume
Spatial expansion	Leaf area	**-0.12** (±0.09)	**0.14** (±0.04)	**-0.05** (±0.03)	-0.14 (±0.19)
	Canopy height	-0.01 (±0.06)	**0.07** (±0.04)	**-0.11** (±0.02)	-0.09 (±0.09)
Growth investment	SLA	**-0.06** (±0.05)	**0.05** (±0.04)	**0.08** (±0.03)	0.07 (±0.08)
	LDMC	0.01 (±0.06)	**-0.14** (±0.05)	-0.02 (±0.03)	-0.04 (±0.05)
	SSD	**0.06** (±0.04)	**-0.07** (±0.04)	**-0.08** (±0.04)	-0.01 (±0.09)
	Leaf C_{mass}	**0.15** (±0.05)	0.02 (±0.03)	**-0.09** (±0.04)	-0.01 (±0.12)
	Leaf N_{mass}	-0.01 (±0.03)	**0.17** (±0.05)	0.02 (±0.03)	0.03 (±0.05)
	Leaf P_{mass}	**-0.11** (±0.05)	0.04 (±0.04)	**0.08** (±0.04)	-0.04 (±0.16)
	Perennial	**0.14** (±0.03)	**0.06** (±0.03)	**-0.12** (±0.03)	0.04 (±0.08)
Reproductive strategy	Relative seed number	0.12 (±0.13)	0.04 (±0.06)	0.05 (±0.06)	0.17 (±0.18)
	Seed crop frequency	-0.04 (±0.18)	**0.08** (±0.05)	0.07 (±0.07)	-0.08 (±0.17)
Stress adaptations	Liana	-0.05 (±0.19)	**0.13** (±0.05)	-0.02 (±0.07)	NA NA
	Shoot growth form	-0.07 (±0.11)	**-0.07** (±0.04)	**-0.04** (±0.03)	0.11 (±0.21)
	Leaf pubescence	**0.23** (±0.15)	-0.01 (±0.07)	-0.01 (±0.03)	0.23 (±0.27)
	Spinescence	-0.1 (±0.14)	0.01 (±0.05)	0.01 (±0.09)	NA NA
	Leaf $\delta^{13}C$	**-0.18** (±0.09)	**-0.14** (±0.06)	**0.08** (±0.05)	-0.2 (±0.21)
	Endozoochory	**-0.06** (±0.03)	**0.09** (±0.05)	**-0.1** (±0.02)	-0.09 (±0.09)
R^2		0.4	0.4	0.36	0.36

We found that (i) elevation niche breadths were indeed narrower at lower elevations, (ii) elevation niche breadths decreased with species richness together with overall niche volume, and (iii) undisturbed savanna had the smallest niche breadths on all environmental gradients with monotonic increases towards historically younger habitats, which rendered some support to this hypothesis. Also, C_4 photosynthetic pathways indicating higher metabolic activity were more common at lower elevations, as indicated by leaf $\delta^{13}C$.

Community elevation niche breadths and niche volume were both decreasing with higher diversity, but showed strong variability at low diversity levels. While an inverse niche breadth and volume – diversity relationship has been found in many tropical habitats (Vázquez and Stevens, 2004; Lamanna et al., 2014), high variability at low diversities in our system was due to communities composed of species with very small niche breadths. For instance, swamp communities harbored only few (< 5) species, which did not occur elsewhere. These specialist species may be weak competitors, but are adapted to a habitat unsuitable for others (Boulangeat et al., 2012). Therefore, their niche breadths were very small, and so was their niche volume. We also found considerable niche breadth variation at higher elevations. At 3000 – 4000 m a.s.l., frost constituted a strong niche boundary for all tropical species without frost resistance, as freezing cell water results in irreparable tissue damage (Beck et al., 1984; Davis et al., 1999). Frost could lead to narrow niche breadths as species would not be able to escape the competitive pressure at the more benign side of the temperature gradient by occupying sites further up the mountain. This may explain the slightly humped-shaped pattern on the elevation gradient between 1000 – 4000 m a.s.l. Conversely, distributions of species with frost resistance would be unconstrained by frost and, although considered specialists in a tropical environment, they might have large elevation niche breadths.

The COH related to productivity assumes that niche breadth decreases with increasing productivity or resources (Wright, 1983). However, precipitation niche breadths did not respond to diversity in a uniform manner, but were separated in two clumps of narrow and broad niches. Additionally, niche breadths and, more pronouncedly, variability in niche breadths, increased with precipitation. Likewise, the precipitation niche breadth-richness relationship showed considerable variation. Thus, support for this hypothesis is relatively low. Niche breadth variation on the precipitation gradient points to niche overlap rather than niche replacement, particularly at the wettest conditions (McCain and Grytnes, 2010), where lianas, tree ferns and epiphytes occurred. For these growth forms, niche separation is not based on direct competition for the same resources as assumed by the COH, but on occupying different structural niches. For epiphytes, which constitute a large part of the vascular plant diversity in the forest habitats of Mount Kilimanjaro (Hemp, 2001), niche breadths on the precipitation gradient additionally depend on relative humidity (Gessner, 1956) and host tree availability. Altogether, niche overlap rather than niche replacement (Whittaker, 1967; Chase and Leibold, 2003) may have created the high variability at higher precipitation. A decrease in niche breadths on the precipitation gradient at around 2000 mm*a^{-1} is probably caused by the exclusion of rainforest species under the disturbed conditions of agroforestry and plantation habitats limiting their downward distributions (Morin and Chuine, 2006).

We found that niche breadths increased with disturbance. Disturbance often restricts the occurrence of strong competitors thereby increasing niche breadths of inferior species. For instance, the lowest elevations are characterized by extended dry seasons limiting tree productivity and facilitating rich herbaceous vegetation. With conversion to grasslands or maize fields, trees are excluded, whereas herbaceous species persist and weeds increase in abundance. Between the lowest elevations and the rainforest at higher elevations, agroforestry is practiced since centuries (Odner, 1971). Natural forests prevail only at the steepest slopes of river gorges (Hemp, 2006). Release from competition by trees and the diversity of disturbance regimes (grazing, tilling, cultivation) may have increased niche breadths of herbaceous species on the disturbance gradient.

While high variation in niche breadths at a given point on the environmental gradients is due to ecological reasons, variation between adjacent points exemplified by extreme differences between group medians and quartiles on the precipitation and disturbance gradients is due to stochasticity given the exclusion of a considerable amount of species through the bootstrapping filter. Nevertheless, the increasing niche breadth patterns remained stable even if all species regardless of model quality were included into the analyses (data not shown).

A reservation on the validity of our interpretation may be that the elevation and precipitation gradients do not extend to the absolute minima. In consequence, the true overall patterns may differ somewhat from those observed. It is reasonable to assume that the niches of some species with distributions centered at the lower sampled gradient ends extend into lower parts not investigated in our study. This means that elevation and precipitation niche breadths at the lower gradient ends might be underestimated. Still, as other species not sampled are to be expected at the lower gradient ends, sampling the entire gradients would likely result in similar patterns. Many studies have investigated geometric constraints as an explanation for diversity patterns of geographic domains and continue to test for the mid-domain effect (e.g. Colwell et al., 2004; Storch et al., 2006; Grytnes et al., 2008), whose existence is a matter of debate (Currie and Kerr, 2008). The elevation gradient in our study can be seen as a geographic domain. Under the assumptions of the mid-domain effect, niche breadth should be highest in the middle of the gradient decreasing towards the extremes through the restriction of large niche breadth-species to the domain center. Although the elevation gradient sampled is incomplete in the lowlands, the strong deviations from mid-domain expectations at its upper end make a strong influence of geometric constraints on the species distributions in our study system unlikely.

Two important drivers of species distributions not considered explicitly in this study are area and colonization history (McCain and Grytnes, 2010; Fritz et al., 2013). Decreasing area could potentially increase the minimal possible niche breadth along the elevation gradient, if seen as a geographical domain, as each species needs a minimum area to sustain viable populations. Still, even at the highest elevations, plant populations are large as habitat sizes are in the range of square kilometers rather than few hectares. Frequent patches of bare soil within the vegetation (DSC, pers. obs.) suggest species are rather limited by abiotic stress than by area constraints. Colonization history has implicitly been invoked in the MTE hypothesis, as habitats at low elevations, with low annual precipitation, and a low level of disturbance represent ancient conditions in the area. Montane rainforest had already formed in the Eastern Arc mountains when Mount Kilimanjaro last erupted (Marchant et al., 2005), and pollen records suggest the mountain served as a glacial refuge thereafter (Schüler et al., 2012). The flora above 3000 m a.s.l. of Mount Kilimanjaro partly resembles that of other African high-mountain systems, but long-distance dispersal between those is rather rare, and a high degree of single-mountain endemism (64 % for vascular plants, Hedberg, 1969) confirms that rare dispersal events and large speciation time may indeed be key factors leading to the observed niche breadth distribution.

In summary, considering niche breadths, COH-temperature predictions were partly supported whereas COH-productivity predictions were not supported. Relationships between diversity, competition, and niche breadth were more complex then assumed by our hypotheses.

Relationships of niche optima and volume with plant functional traits

We assumed environmental conditions to act as a filter on species co-existence and traits to be an expression of the selection by this filter (Kleyer et al., 2012). In most cases, several traits explained optima, as functional traits are often correlated due to coordinated biological functions (Kleyer and Minden, 2015). Our results linking traits to gradient optima mostly confirm findings from previous studies in the Neotropics and temperate regions (Cornwell and Ackerly, 2009; Lebrija-Trejos et al., 2010; Minden et al., 2012; Lasky et al., 2013; Lohbeck et al., 2013). Differences for particular traits may arise through regional or site-specific influences. A global analysis by Moles et al. (2014) linking traits to temperature and precipitation found relatively weak relationships, especially for precipitation, which may be due to the global scale of their work. In our study, traits explained between a third and half of the variance associated with optima position and niche volume. As both trait measurement errors and model inaccuracy are likely to obscure patterns, we expect the true relationship between traits and environmental optima to be even stronger.

The traits linked to elevation optima characterize functional types: perennial, robust plants with leaf hairs at high elevations and annual, fast growing C_4 plants (indicated by leaf δ^{13}C) at low elevation. Spatial expansion and growth investment traits indicating fast nutrient acquisition and turnover characterized plants with optima at high precipitation levels. C_4 plants were strongly associated with low precipitation levels, as is expected from this adaptation. Lianas and endozoochorous plants were positively related to precipitation optima as a complex vegetation structure and water availability make liana growth and investment in fleshy fruits possible or less costly (Howe and Smallwood, 1982). With increasing disturbance, plants were mostly annual, with higher SLA and leaf P_{mass}, lower SSD and less zoochorous, as found in other studies (e.g. Kühner and Kleyer, 2008; Elser et al., 2010; Ordonez et al., 2010; Lienin and Kleyer, 2011), reflecting fast growth and dispersal strategies. We expected large seed numbers and high seed crop frequencies to be strong predictors of disturbance optima (Lippok et al., 2013). The weak evidence in our study may be caused by the inclusion of few dominant fern species in undisturbed forest ecosystems, which had high spore numbers compared to other plants. Traits indicating conservation of resources (small plant and leaf size, low SLA, high LDMC), investments in structural tissue (leaf C_{mass}) and protection (leaf pubescence) increased with elevation (Moles et al., 2014). The explained variance of the trait – niche volume regression was similar to optima analyses, but confidence intervals for all traits were at least as large as their coefficients, meaning that the relationship indicated by the coefficients was only weakly supported by the data. Traits associated most strongly with niche volume indicated that widespread species were characterized by low height and dispersal mechanisms other than endozoochory. A similar pattern has been found for climatic niches of woody and non-woody plant lineages, in which the latter had a larger niche volume (Smith and Beaulieu, 2009). A possible reason for the weak association of most traits with niche volume is pointed out by Violle and Jiang (2009): They suggest that niche breadth, and thus its multi-dimensional analogue niche volume, should mainly be determined by the intraspecific variability in trait expressions. It will be interesting to test this hypothesis in the future.

Conclusions

The competition hypothesis stating niche breadth decreases with diversity in combination with the metabolic theory of ecology allowed to explain a considerable part of the niche breadth distributions of plants along both environmental and diversity gradients. Niche breadths were narrowest at hot, dry, and undisturbed sites, which also represent the oldest habitats in the area. Nevertheless, there was large variation in the relationship of niche breadth and community diversity, which is not surprising, given the necessary simplification inherent in the competition hypothesis. Niche replacement, i.e. the compression of niche breadths with increasing species richness in a community, will not necessarily take place in case of new colonizers exhibiting different life strategies with regard to the existing species. Additionally, both historic factors and recent dispersal limitations are likely to have shaped present-day species distributions. Plant functional traits strongly influenced species positions on the environmental gradients. Elevation, precipitation and disturbance optima were equally well predicted by trait syndromes in concordance with current theory, indicating species sorting in response to these gradients.

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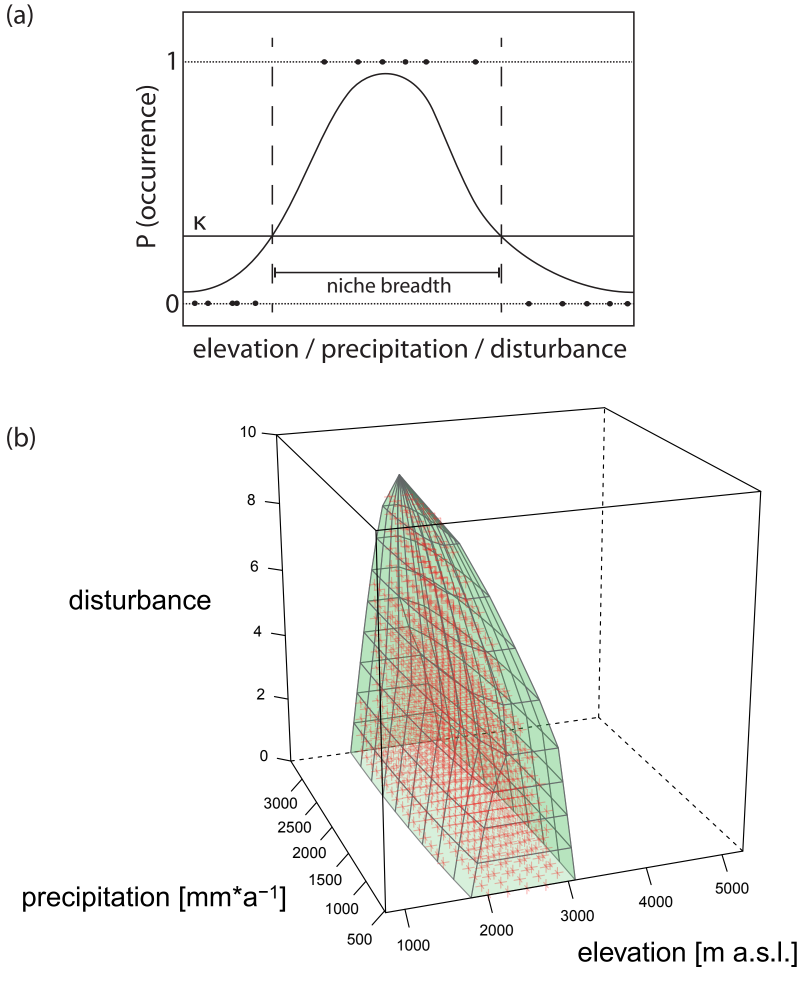
Appendices

Appendix S1: Illustration of niche breadth and niche volume calculations
(a) Niche breadth calculation. As the GLM curves obtained are bounded between 0 and 1 by definition, niche breadth had to be defined. We used Cohen's κ: The GLM curve was cut subsequently at values from 1 to 0, defining the part of the curve above the cut as the range of a species' occurrence and the part below as where it does not occur. We then calculated the number of correct predictions of presence and absence by the model given the observations (black dots). The cut value with the highest number of correct predictions was κ, and the extent of the range of the GLM curve above κ was a species' niche breadth on the respective gradient. (b) Niche volume. Occurrence probabilities were calculated on a regular grid in environmental space. Probabilities above κ (red crosses) defined a species' niche volume. The maximum extent of the niche volume corresponds to the niche breadth length on the respective axes.



Appendix S2: Parameter confidence intervals and distribution models of all species
Given are niche breadth predictions (P), lower confidence interval limits (L), upper confidence interval limits (U), and generalized R^2 values. Species are ordered by decreasing numbers of prevalences in the data set. Scientific names are according to Tropicos.org. Missouri Botanical Garden. 2015.

This content has not been included in the thesis because it is about 500 pages long. It is available digitally from the authors on request.

Chapter 3

Convergence and divergence of plant functional traits along environmental gradients

David Schellenberger Costa[1]*, Friederike Gerschlauer[2,†], Bernd Huwe[3,†], Ralf Kiese[2,†], Anna Kühnel[3,†], Yakov Kuzyakov[4,†], Holger Papst[4,†], Michael Kleyer[1]

[1]Department of Biology and Environmental Sciences, University of Oldenburg, 26111 Oldenburg, Germany

[2]Institute for Meteorology and Climate Research, Karlsruhe Institute of Technology, 82467 Garmisch-Partenkirchen, Germany

[3]Bayreuth Center of Ecology and Environmental Research, University of Bayreuth, 95440 Bayreuth, Germany

[4]Department of Agricultural Soil Science, University of Göttingen, 37077 Göttingen, Germany

*Corresponding author

†These coauthors provided data but did not yet contribute to this version of the manuscript.

Abstract

Variability in functional traits has mainly been investigated in studies dealing with convergence and limiting similarity comparing communities within an ecosystem. We present a comparison of changes in community-weighed means (CWMs) and functional dispersion (FDis), a measure of functional diversity, along four environmental gradients and between ecosystems experiencing similar environmental conditions. We investigated whether deterministic environmental filtering or stochastic processes as advocated by neutral theory determine species composition. Temperature, precipitation, disturbance, and soil nutrients not only governed changes in CWMs as expected from previous studies, but also affected FDis, although explained variance was lower.

Comparing communities at different positions along the gradients, trait similarity was generally higher at proximate than distant sites, pointing to environmental filtering. Nevertheless, traits responded differently to environmental conditions, with some being more affected than others. Especially traits related to plant-animal interactions, e.g. dispersal syndrome and diaspore color, seemed to be rather uncoupled from the environment and exhibited moderate differences between sites regardless of environmental conditions, indicating neutral processes may be drivers of those traits' expressions. Differences in species composition, i.e. species β diversity, increased faster than trait β diversity regarding more distant plots along the environmental gradients, since species distributions are affected by present and historic factors, while traits respond to the present environment only.

Keywords environmental filtering, limiting similarity, neutral theory, temperature, elevation, precipitation, disturbance, soil nutrients, community-weighed mean, FDis, null model

Introduction

Traditionally, local species composition has been explained from habitat preferences of species following assembly rules based on gradients of competition and physiological stress (Austin, 1999; Dale, 1999; Chase and Leibold, 2003). Species are assumed to be trait-filtered along these gradients, reflecting the selective pressure of the environment, which restricts trait expressions to a subset of the those available in the regional species pool (Kleyer et al., 2012). This process is often called convergence

(Grime, 2006). Convergence towards non-phanerophytic life forms above the tree line is only one prominent example (Tranquillini, 1979; Wielgolaski and Karlsen, 2007). Conversely, if there are many viable life strategies in a given environment in relation to the regional species pool, the trait composition of a community will be divergent (Weiher and Keddy, 1995; Weiher et al., 2011). In dry grasslands, for example, co-occurrence of ephemerals and scleromorphic perennials may result in divergence in growth and reproduction traits (Schleicher et al., 2011b).

The definition of the species pool is crucial and different choices are being advocated depending on the research objective (Grime, 2006; de Bello, 2012). It is likely that any community's trait composition will shift from divergence to convergence as the species pool is extended from the species present at a single site to larger scales (Weiher and Keddy, 1995; de Bello, 2012). Divergence will occur at small scales, where alternative functional pathways to survival exist in a given environment, while convergence takes over as soon as environmental conditions differ strongly among sites. Across sites with similar environmental conditions without differences in selective pressure, variations in species occurrences should mostly be trait-independent, i.e. while species identities may vary, trait expressions should not.

In contrast to theories relying on functional traits and environmental filters, neutral theory states that the main driver of biodiversity patterns is stochasticity (Hubbell, 2001). Dispersal and speciation rates together with initial species abundances are assumed to be the factors determining the starting point of ecological drift, i.e. random walks of species' abundances in time. Recent work suggests that environmental filtering and neutral mechanisms affect community assembly simultaneously (Leibold and McPeek, 2006). However, the relative importance of either mechanism should vary among ecosystems and even different stages of community succession (Cottenie, 2005; Leibold et al., 2004).

In general, strong environmental gradients should filter species by traits, and ecosystems experiencing similar environmental conditions should thus have similar trait suites. Nevertheless, filtering strength may be variable, and sites with weaker environmental filtering could differ in their species and trait composition in a stochastic manner, reflecting ecological drift. Testing neutral theory requires detailed species- and metacommunity information, which is difficult to obtain (Gotelli and McGill, 2006; Nee and Stone, 2003). Alternatively, null models can be used to investigate the deviation of the community trait composition from random samples based on a metacommunity species pool. Convergence and divergence, and thus environmental filtering and competition, are indicated by lower or higher variance in trait expressions relative to the null model distribution of random samples (Mason et al., 2007; Grime, 2006). Neutral processes are expected if traits expressions do not vary significantly from the null model distribution.

Many studies investigating plant functional trait distributions have found support for both trait-filtering and neutral processes (e.g. Thompson et al., 2010; Schleicher et al., 2011a; Spasojevic and Suding, 2012; Swenson et al., 2012b). Still, while the environment is incorporated in some of these approaches, the environmental gradients considered are often few. Here, we investigated trait expression and species distributions at Mount Kilimanjaro, East Africa. This mountain and its surrounding plains feature large environmental gradients of temperature, precipitation, and anthropogenic disturbance.

We hypothesized that variation in plant functional traits decreases with extreme environmental conditions, which reduce the number of viable plant life strategies, thus trait expressions (Weiher and Keddy, 1995; Cornwell et al., 2006). Examples of such conditions are alpine habitats with daily temperature ranges from -10 °C to +20 °C, or coffee plantations with regular herbicide application. We assumed convergence to be associated with changes in trait means along environmental gradients, too. Traits indicating rapid growth and resource acquisition should increase with resource availability, i.e. precipitation and soil nutrients, as well as with disturbance intensity (Lienin and Kleyer, 2011). Plant size should decrease and generative reproduction increase with disturbance, whereas traits related to the photosynthetic pathway should respond to temperature (Ehleringer et al., 1997).

Considering the occurrence of neutral processes, we wanted to know if sites belonging to the same ecosystem type sharing the same environmental conditions were more similar to each other in terms of functional traits than compared to other sites. If yes, this would point to environmental filtering. If no, differences in trait and species composition among sites could not be explained by filtering for growth, persistence or reproductive traits. This would suggest neutral processes to determine community composition (Hubbell, 2001).

In addition, within or between environmentally close ecosystem types, neutral processes are indicated if large variation in species composition is contrasted by small differences in functional traits. Although sites belonging to the same ecosystem type should be more similar to each other in terms of species and traits, within elevation belts and at similar levels of disturbance, we expected to find stronger differences in species composition than in functional traits indicating neutral processes.

Materials and Methods

Study site and data collection Data collection took place at Mount Kilimanjaro, Northern Tanzania. We investigated the twelve major ecosystem types at the southern slopes of the mountain (see Appendix S1 at page 103 for data on elevation, temperature, precipitation, and disturbance) and established five plots in each of them. The average distance between plots of the same ecosystem type was 14 km. The highest sites were situated in alpine *Helichrysum* shrubland (HEL). Descending, plots were located in *Erica* cloud forest (FER), joined by upper montane *Podocarpus* (FPO) and *Ocotea* forest (FOC) at lower elevations. Besides these undisturbed sites, plots were also established in fire-disturbed *Podocarpus* (FPD) and selectively logged *Ocotea* forests (FOD) covering substantial parts of the mountain. The lowest forest belt is formed by lower montane forest (FLM), characterized by its high heterogeneity due to its disturbance history. In populated areas, forest has been replaced by homegardens (HOM), the traditional agroforestry systems of the local Chagga people. Grasslands (GRA) and coffee plantations (COF) were the most disturbed habitats at these elevations. In the lowlands, savanna fragments (SAV) were selected together with maize fields (MAI). Natural savanna has become sparse in the last decades because of human population growth. For the total of 60 plots, continuous temperature and humidity measurements were made from 2010 to 2014 and combined with long-term precipitation measurements (Mwangomo et al., 2014). Disturbance was measured as a compound variable including the combined effects of fertilization, biomass removal, and differences in the surrounding habitat matrix (see Appendix S2 at page 104 for details).

Soil and plant samples were taken between 2010 and 2012. Plant functional trait measurement followed the LEDA protocols (Kleyer et al., 2008, www.leda-traitbase.org). Vegetation surveys were performed at all plots using the Braun-Blanquet-scale (Braun-Blanquet and Schoenichen, 1964). Resulting abundance class values were converted to percentage cover for all species. As plant diversity was too high to make a complete sampling feasible, the dominant species representing 80 % of the plant biomass at a certain plot were selected for trait measurements. For practical reasons, we did not include epiphytes in this study, as accessing the canopy of rainforest habitats was not possible because of time constraints. We collected 15 samples of each species and chose individuals from the widest possible range of environmental conditions to account for intraspecific variability. Table 3.1 shows the 16 plant functional traits collected. Traits were selected to mirror plant life strategies with their respective expressions. Growth investment traits relate to the worldwide leaf economics spectrum (Wright et al., 2004) describing fast versus slow growth and nutrient turnover. Reproductive investment traits separate plants with fast generation cycles and high seed numbers from such with slow reproduction and reliance on few, often large seeds. Under specific abiotic conditions, as cold or high UV radiation, plants have developed particular adaptations classified in the third trait group. Finally, plant-animal interaction traits describe adaptations of plants both to avoid predation by herbivores and to enhance pollen and seed dispersal, which may involve animals.

Laboratory analyses for leaf C, N, and P contents were done at Oldenburg University, Germany. Leaf stable carbon isotopes were analyzed at the Karlsruhe Institute of Technology in Garmisch-Patenkirchen, Germany. We collected soil samples and measured plant-available Ca^{2+}, K^{+}, Na^{+}, N, and P concentrations at Sokoine University in Morogoro, Tanzania. The results were summarized in a PCA. The first axis, which contained 73 % of soil nutrient variation, was termed "soil nutrients" and reflected the overall soil nutrient availability for plants, high values indicating high nutrient availability.

Statistical analyses We chose functional dispersion (FDis, Laliberté and Legendre, 2010) to compare different communities' trait compositions. FDis is unaffected by the number of species present in a community. It is a measure of functional divergence following Mason et al. (2005). According to Butterfield and Suding (2013), single trait diversity indices can outperform those calculated from multiple traits. We therefore calculated FDis for each plant functional trait on the 60 plots separately as well as for all traits together ("multivariate FDis") using the dbFD function in the R package FD (Laliberté and Legendre, 2010).

Along environmental gradients, we analyzed differences in FDis and related those to environmental conditions using a partial least squares (PLS) approach. PLS can deal with correlated predictors, which was the case in our study system (Tab. 3.2). As PLS is an ordination method, no p values are given. Explained variance and the signs of coefficients indicate the strength and directionality of relationships. Calculations were done using the plsr function in the R package pls (Mavik et al., 2013). Standard errors for coefficient estimates were calculated with leave-one-out cross validation using the var.jack function (pls package).

Trait similarity between plots was assessed comparing community-weighed means (CWM, Garnier et al., 2007) and FDis values. In a null-model approach, we per-

Table 3.1: **Plant functional traits selected to mirror plant life strategies** Sampling and measurements followed the LEDA protocols (Kleyer et al., 2008). Means are given for all traits except for leaf pubescence and spinescence, where medians are given, and categorical traits. Specific leaf area, canopy height, relative seed number, and leaf area values were log-transformed prior to analyses. Abbreviations: GI Growth investment, RI Reproductive investment, AAC Adaptations to specific abiotic conditions, PIA Plant-animal interactions.

Group	Trait	Unit	Mean (Range)	Description
GI	Specific leaf area (SLA)	cm^2*g^{-1}	18.9 (4.9 - 89.1)	Leaf area per g leaf dry weight
GI	Leaf dry matter content (LDMC)	$mg*g^{-1}$	0.31 (0.06 - 0.61)	Leaf dry matter per g fresh leaf tissue
GI	Stem specific density (SSD)	$g*cm^{-3}$	0.41 (0.05 - 0.82)	Dry weight per unit volume
GI	Leaf N_{mass}	$mg*g^{-1}$	22 (6.2 - 47.9)	Leaf nitrogen content per g dry tissue
GI	Leaf C_{mass}	$mg*g^{-1}$	441.7 (362.1 - 551)	Leaf carbon content per g dry tissue
GI	Leaf P_{mass}	$mg*g^{-1}$	2 (0.5 - 7.5)	Leaf phosphorus content per g dry tissue
GI	Canopy height	m	1.03 (0.05 - 44.92)	Height of highest leaves
RI	Relative seed number	cm^{-1}	8.08 (0.04 - 99707)	Number of seeds per m canopy height
RI	Seed crop frequency	a^{-1}	1.57 (0.2 - 12)	Number of seed production events per year
AAC	Leaf area	cm^2	10.28 (0.02 - 10097)	One-sided leaf area
AAC	Leaf pubescence	-	0 (0 - 2)	Density of leaf hairs (0 = no or few hairs, 1 = hairy, 2 = densely covered with hairs)
AAC	Leaf $\delta^{13}C$	-	-26.2 (-35 - -10.7)	Ratio of carbon isotopes relative to a standard
AAC	Spinescence	-	0 (0 - 4)	Size and density of spines (0 = no spines, . . . , 4 = medium density of large spines)
PAI	Dispersal syndrome	-	Categorical (5)	Type of transport of dispersal unit
PAI	Diaspore color	-	Categorical (14)	Color of fleshy or dry fruit or spore
PAI	Flower color	-	Categorical (9)	Color of flower petals, if existent

Table 3.2: **Pearson correlations between environmental factors and plant functional traits**
Precipitation has a hump-shaped distribution along the temperature gradient, while both disturbance and soil nutrients increase with temperature. Abbreviations: Temp temperature, Prec precipitation, Dist disturbance, Nut soil nutrients, SLA specific leaf area, LDMC leaf dry matter content, SSD stem specific density, CH canopy height, RSN relative seed number, SCF seed crop frequency, LP leaf pubescence, Spin spinescence.

	Temp	Prec	Dist	SLA	LDMC	SSD	Leaf N_{mass}	Leaf C_{mass}	Leaf P_{mass}	CH	RSN	SCF	Leaf area	LP	Leaf $\delta^{13}C$
Prec	-0.51														
Dist	0.76	-0.5													
Nut	0.78	-0.66	0.7												
LDMC				-0.61											
SSD				-0.68	0.61										
Leaf N_{mass}				0.61	-0.67	-0.53									
Leaf C_{mass}				-0.6	0.35	0.47	-0.24								
Leaf P_{mass}				0.5	-0.42	-0.34	0.31	-0.44							
CH				-0.57	0.2	0.38	-0.01	0.55	-0.37						
RSN				0.16	-0.11	-0.29	0.09	0.03	0.14	-0.29					
SCF				0.22	-0.19	-0.27	0.24	-0.12	0.18	-0.16	0.45				
Leaf area				-0.13	-0.24	-0.08	0.28	0	0	0.56	-0.2	0.13			
LP				-0.11	0.04	0.12	-0.15	0.09	-0.08	-0.17	0.15	-0.09	-0.24		
Leaf $\delta^{13}C$				0.04	0.27	-0.07	-0.35	-0.29	0.2	-0.27	0.03	-0.07	-0.2	-0.11	
Spin				-0.16	0.06	0.21	-0.11	0.1	-0.06	0.07	-0.08	-0.02	0.07	-0.06	-0.06

formed a pairwise comparison of the 60 plots.

First, we defined the species pool of each plot pair as the species occurring in both plots that had been sampled for traits. These small species pools avoided small-scale patterns of convergence or divergence to be overridden by differences along strong environmental gradients and different null models to converge to the same values (de Bello, 2012).

Second, the species pool was split into three abundance classes according to the observed species abundances. This method ensured comparisons of similar plots in terms of functional traits would lead to null models encompassing the observed data within confidence intervals as would be expected (for a similar approach, see Thompson et al., 2010). Otherwise, rare species could influence results in a way that even comparing identical plots observed data would fall outside confidence limits of null model distributions.

Third, null models were constructed for each plot separately to account for different species numbers and abundances in each plot. To this end, species were drawn randomly from the species pool considering their abundance class and leaving the number of species in each class as in the observed data. Null model draws were performed 1000 times for each trait.

Fourth, the two CWMs and FDis values (one from each of the two plots) were compared to the null model distributions. Similarity between plots was rated on a scale from 0 to 4 (0 to 64 for the multivariate FDis including all 16 traits), depending on whether both observed CWMs fell into null model confidence intervals, and if so, if FDis values did, too. As an example, if the first plot's CWM and FDis fell into confidence limits, this would add two to the similarity value. If the second plot's CWM was outside confidence limits, the similarity of both plots would be two irrespective of its FDis value, because FDis would only be compared if the CWM lay within confidence limits. This was done because CWMs inform about the mean of trait values, which are related to ecosystem functioning and whose overlap indicates functional similarity. On the contrary, FDis describes the spread of values. Communities with identical FDis might be completely dissimilar functionally because of no overlap in trait values at all.

The relationship between trait and species β diversity was investigated using the exponential Shannon index as a measure of species β diversity following (Jost, 2007). It has the property of weighting rare and abundant species proportionally (R package vegetarian, Charney and Record, 2012). Trait β diversity was calculated as 64 - trait similarity (see above) and scaled to the same range as species β diversity.

Results

Functional dispersion and community-weighed means along environmental gradients

Functional dispersion (FDis) was moderately well and community-weighed means (CWMs) were very well explained by temperature, precipitation, disturbance, and soil nutrients (Tab. 3.3 and App. S2 at page 104). For FDis, explained variance of specific adaptation traits was higher on average than for other trait groups. Individual R^2 values ranged from 0.13 to 0.56. The multivariate FDis had a R^2 value of 0.08 only. Considering CWMs, growth investment and specific adaptations traits were equally well explained (mean $R^2 = 0.62$). Reproductive investment and plant-animal interaction traits had lower R^2 values (mean $R^2 = 0.51$). R^2 values ranged from 0.42 to 0.72.

Figure 3.1 shows values of significant coefficients for both trait FDis and CWMs. It reveals that on environmental gradients (i) trait means change without significant

Table 3.3: **Functional dispersion (FDis) along the environmental gradients** Predictors and responses were standardized prior to the analysis. Thus, coefficients are comparable across predictors and responses, respectively. Standard errors of the coefficient estimates obtained by jackknifing are given in parentheses. Coefficients larger than standard errors are printed in bold. FDis was calculated as a multivariate index (first line "All traits") and as a univariate index for each trait separately.

Function	Traits	Temperature	Precipitation	Disturbance	Soil Nutrients	R^2
	All traits	**0.3** (±0.27)	**0.29** (±0.18)	-0.1 (±0.18)	0.07 (±0.22)	0.08
Growth investment	SLA	-0.03 (±0.2)	**0.42** (±0.15)	-0.16 (±0.2)	0.25 (±0.25)	0.15
	LDMC	**0.57** (±0.23)	**0.17** (±0.16)	**-0.53** (±0.2)	**-0.29** (±0.25)	0.28
	SSD	**0.43** (±0.21)	**0.41** (±0.17)	**-0.54** (±0.17)	**0.26** (±0.25)	0.24
	Leaf N_{mass}	**0.4** (±0.21)	**0.58** (±0.14)	0.18 (±0.18)	-0.12 (±0.23)	0.30
	Leaf C_{mass}	0.02 (±0.24)	-0.01 (±0.17)	**-0.44** (±0.16)	-0.01 (±0.17)	0.18
	Leaf P_{mass}	**0.53** (±0.22)	0.1 (±0.14)	**-0.45** (±0.28)	**0.58** (±0.42)	0.51
	Canopy height	0.08 (±0.19)	**0.37** (±0.14)	**-0.43** (±0.15)	0.12 (±0.17)	0.30
Reproductive investment	Relative seed number	**0.33** (±0.17)	**0.57** (±0.14)	**-0.17** (±0.13)	0.11 (±0.13)	0.25
	Seed crop frequency	**0.2** (±0.15)	**0.47** (±0.16)	**0.43** (±0.15)	0.14 (±0.2)	0.34
Adaptations to specific abiotic conditions	Leaf area	**-0.62** (±0.2)	**0.23** (±0.12)	**0.22** (±0.16)	**0.16** (±0.13)	0.24
	Leaf pubescence	**-0.85** (±0.15)	**-0.74** (±0.1)	**0.33** (±0.13)	-0.15 (±0.15)	0.56
	Leaf $\delta^{13}C$	**0.9** (±0.15)	**-0.15** (±0.09)	-0.15 (±0.21)	**-0.31** (±0.22)	0.42
Plant - animal interactions	Spinescence	**0.48** (±0.32)	-0.06 (±0.2)	**-0.72** (±0.29)	**0.6** (±0.48)	0.47
	Dispersal syndrome	0.24 (±0.24)	0.09 (±0.18)	**0.3** (±0.19)	-0.13 (±0.17)	0.14
	Diaspore color	**0.63** (±0.27)	**0.35** (±0.18)	**-0.42** (±0.15)	0.12 (±0.27)	0.23
	Flower color	0.14 (±0.15)	**-0.25** (±0.14)	**0.29** (±0.15)	**-0.35** (±0.25)	0.13

changes in within-plot trait variability (only white bars), (ii) within-plot variability changes without significant changes in trait means (only grey bars), (iii) trait means change in same direction as within-plot dispersion, (iv) trait means and within-plot dispersion change in opposite directions.

Temperature, precipitation, and disturbance had stronger effects on trait FDis and CWM than soil nutrients, as evidenced by the numbers of significant coefficients (printed in bold in Tab. 3.3 and App. S2). The effects of temperature and disturbance were mostly opposed, i.e. trait CWM or FDis values increasing with temperature decreased with disturbance. Relationships of precipitation, temperature and soil nutrients with CWMs and FDis were mostly similar.

Low temperatures favored high leaf C_{mass}, leaf pubescence, and relative seed numbers, whereas canopy height, leaf area, spinescence, and leaf δ^{13}C as an indicator of the C_4 photosynthetic pathway increased with temperature. FDis decreased or increased in the same direction as CWMs for leaf pubescence and leaf δ^{13}C, but in opposite directions for relative seed number and leaf area. This means that the leaf area of the most dominant species increases with temperature, but low temperature favored both large and small leaves within a plot. FDis of other growth traits and diaspore color increased with temperature. Overall trait space measured by the multivariate FDis also increased with temperature.

At high precipitation values, we found high SLA, leaf N_{mass}, canopy height, and leaf area together with low LDMC, SSD, leaf δ^{13}C, and leaf pubescence. FDis of almost all traits including multivariate FDis increased with precipitation, indicating a larger variability of life history strategies. Exceptions were spinescence and flower color, which showed the opposite pattern.

Disturbance favored high values of traits indicating rapid growth and reproduction (SLA, leaf N_{mass}, leaf P_{mass}, relative seed number), whereas canopy height, leaf area, LDMC and SSD decreased. In contrast to the precipitation gradient, FDis of many traits decreased with increasing disturbance, indicating fewer alternative life history strategies within a plot. This was not the case for dispersal syndrome, meaning plants employed a larger range of dispersal strategies in disturbed environments.

As would be expected, leaf N_{mass} and leaf P_{mass} increased with soil nutrients. For leaf P_{mass}, FDis increased as well. LDMC and leaf δ^{13}C decreased while spinescence increased both in CWMs and FDis with increasing soil nutrients. Flower color variability decreased at high soil nutrient concentrations, as evidenced by low FDis.

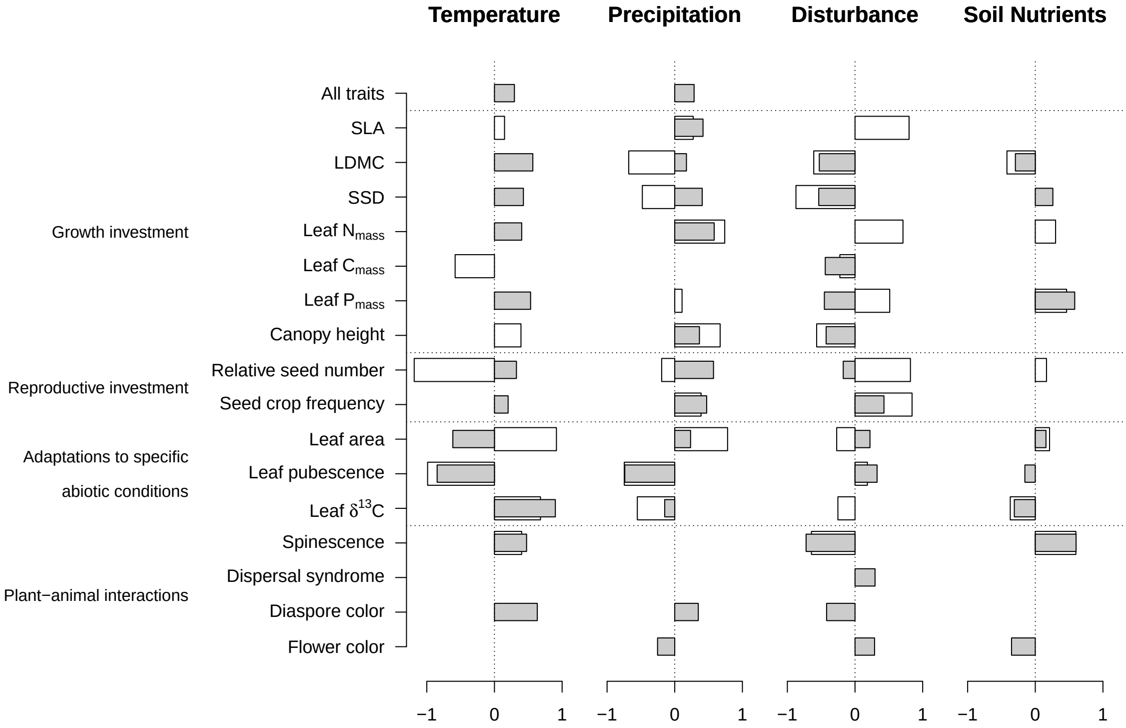


Figure 3.1: **Relationship of plant functional trait CWMs and FDis with environmental factors**
Bars represent coefficients of a multivariate PLS regression. Both environmental factors and plant functional traits were standardized. Coefficients are thus comparable between traits and environmental factors. Grey bars are FDis values, white bars are CWMs. Only values of coefficients larger than their corresponding standard errors were drawn. No CWM could be calculated for categorical traits and in a multivariate way (“All traits”).

Trait similarity and convergence

To detect similarities in trait expressions within and between vegetation types, we did pairwise plot comparisons (Fig. 3.2). We found pronounced differences separating the ecosystem types. Growth investment traits showed similar patterns, while other trait groups were variable. As hypothesized, similarity was generally higher within than between ecosystem types. Nevertheless, forest stands with tall trees, i.e. *Podocarpus* (FPO, FPD), *Ocotea* (FOC, FOD), and lower montane forests (FLM) formed a cluster that did not separate in terms of most traits. This was also the case for alpine *Helichrysum* shrubland (HEL) and *Erica* forest (FER). Savanna plots (SAV) and a part of the homegardens (HOM) were close to forests considering growth investment traits. On the contrary, grasslands (GRA) showed strong differences to all other ecosystem types. Maize fields (MAI) were most similar to coffee plantations (COF), but for some growth investment traits, they resembled forest ecosystems. The multivariate FDis pattern resembled that of growth investment traits, with three ecosystem type-clusters: HEL and FER; other forests, HOM, and SAV; and COF and MAI.

Differences in FDis from the null model distributions were mostly due to convergence, as would be expected through adaptations to different environmental conditions. Still, for all traits, within tall forest stands, i.e. FPD, FPO, FOC, FOD, and FLM, divergence was generally observed. Diaspore color and dispersal syndrome showed the opposite pattern: Differences among forest plots were mainly due to convergence, while between and among other ecosystems, they were due to divergence.

Relationship of trait and species β diversity

As expected, species β diversity was lowest within ecosystem types (Fig. 3.3, diagonal elements). Both trait and species β diversity increased with distance of plots on the elevation and disturbance gradients. Increases were stronger for species than for traits. Largest trait and species β diversities were observed comparing HEL and FER with COF and MAI plots, representing strong differences in both elevation and disturbance.

In contrast, trait and species β diversity were low between HEL and FER as well as between FPO, FPD, FOC, FOD, and FLM, indicating trait-independent species turnover among local communities. In the forest ecosystems, trait-independent species turnover, i.e. species β diversity higher than trait β diversity, occurred

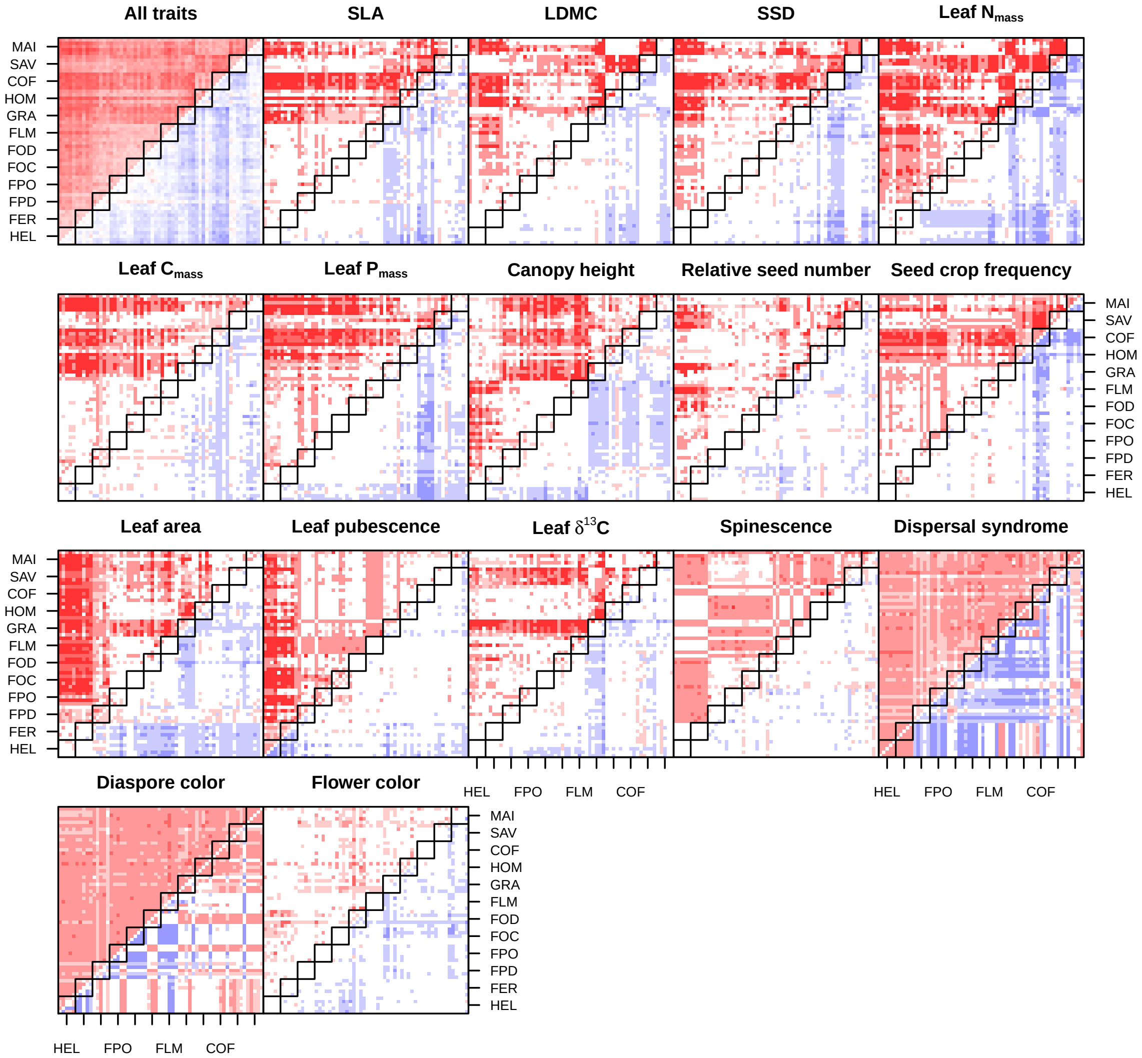


Figure 3.2: **Trait similarity within and between ecosystem types**
Ecosystem types are arranged according to their elevational distribution (see Tab. 3.1), with elevation increasing from left to right and bottom to top. Upper triangular: White areas represent complete trait similarity, i.e. both CWM and FDis of the respective plot pairs lie within null model confidence intervals, while red shading indicates CWM, FDis, or both being outside null model confidence intervals. Lower triangular: The color scale shows trait convergence and divergence. FDis values below null model distribution confidence intervals are blue (convergence), while those above are red (divergence). Dark colors show both plots' FDis values were below or above confidence limits, respectively, while light colors represent pairs where one plot was within FDis confidence limits. Note that upper and lower triangular are no mirror images: Plots may be different in terms of CWMs, but with similar FDis values. In this case, the lower triangular would be white while the upper triangular would be red. Black squares frame within-ecosystem type comparisons.

mainly between FPD and FPO, whereas FOD and FOC neither differed in species nor traits. In contrast, FLM differed strongly from other forests in terms of species, but not traits. Regarding communities at the footslopes of Mount Kilimanjaro, COF shared species and traits with HOM, and GRA with SAV, but were otherwise unique in their species and functional composition. In contrast, HOM shared traits with forests, in particular FOD, whereas species composition was different. Likewise, SAV shared traits, but not species, with FPD. This was probably due to similar tree height and similar growth forms in the understory vegetation, although the elevational distance between these communities is about 2000 m.

Discussion

Our study compares the responses of a broad range of plant functional traits related to main plant functions in terms of both community-weighed means (CWMs) and community variability in trait expressions along four gradients of major importance for plant life. Although CWMs have been in the focus of ecological research for decades and functional diversity is receiving increasing interest, the unique dataset presented here offers the possibility to address general questions of functional trait variability without the errors introduced by co-variables not accounted for and differences in data collection and processing inherent to meta-analyses of case studies.

Functional dispersion and community-weighed means along environmental gradients

Patterns of functional dispersion (FDis) along the environmental gradients confirmed our hypotheses: For most traits, low temperatures, low precipitation, and high disturbance were associated with low FDis values, indicating convergence in trait values, i.e. fewer viable plant life strategies under environmentally extreme conditions (Weiher and Keddy, 1995). Evidence was weaker for soil nutrients than for the other environmental factors, which may be due to a minor role of soil nutrients as an environmental filter compared to the others. Nevertheless, soil nutrients are known to be important drivers of species distributions in tropical ecosystems (Swaine, 1996; John et al., 2007). Thus, an alternative explanation could be that the nutrient gradient of the volcanic soils of Mount Kilimanjaro is relatively weak in relation to those of temperature, precipitation, and disturbance. Tropical mountain soils are typically N-limited (Tanner et al., 1998). This seems not to be the case at Mount Kilimanjaro

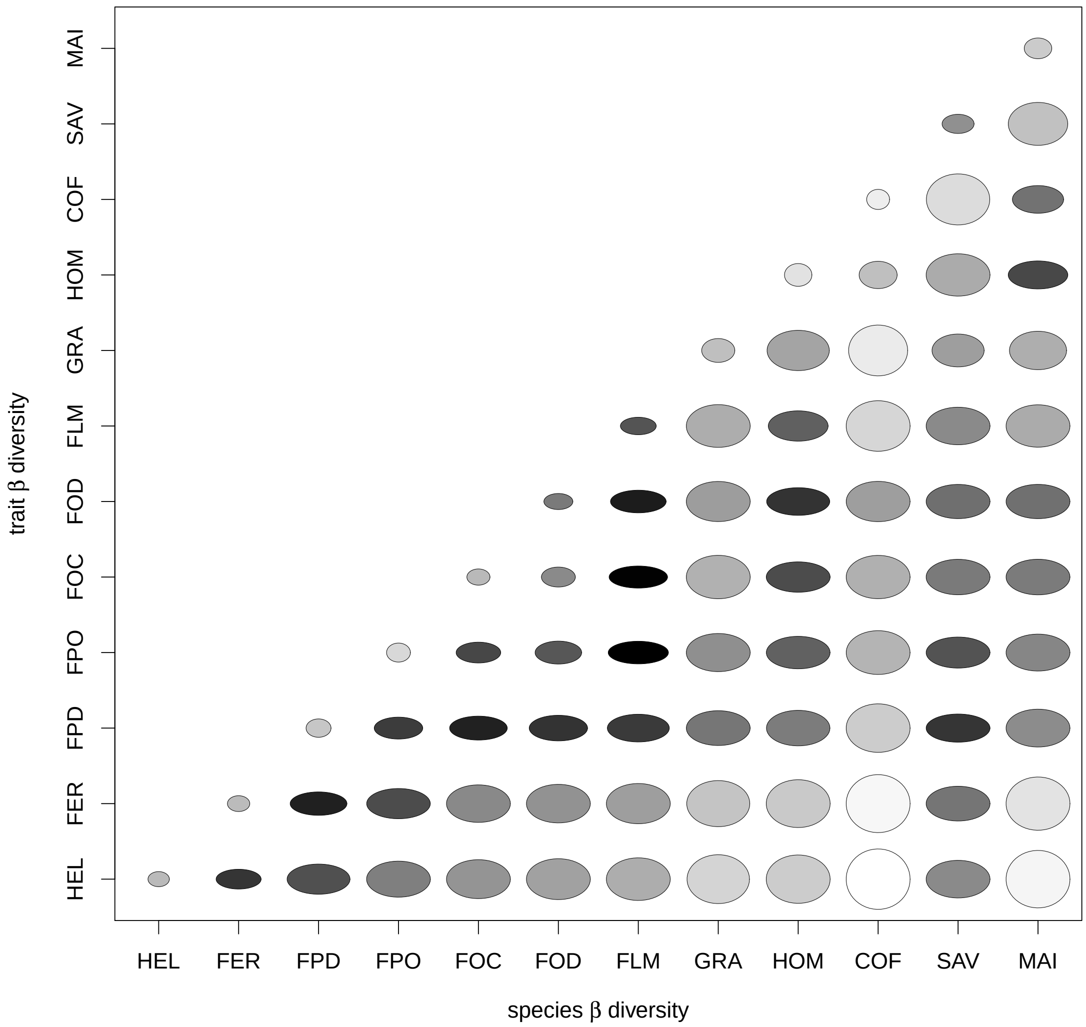


Figure 3.3: **Trait vs species β diversity**
Ecosystem types are arranged according to their elevational distribution (see Tab. 3.1), with elevation increasing from left to right and bottom to top. Horizontal ellipse diameters represent species β diversity (Jost, 2007). Vertical ellipse diameters show trait β diversity, the inverse of trait similarity. Both variables were scaled to [1,2]. Ellipse filling mirrors the ratio between species and trait β diversity, dark shading indicating relatively higher species β diversity than trait β diversity, showing trait-independent species turnover.

(Schrumpf et al., 2006), which suggests a lesser importance of nutrient limitation in contrast to other mountain areas.

Because of the weighing by abundance, CWMs reflect trait values of dominant species that exhibit life strategies allowing for optimal resource exploitation (Grime, 1998). Community-weighed means (CWMs) of traits were in the range of comparable studies (e.g. Ackerly et al., 2002; Spasojevic and Suding, 2012; Schöb et al., 2013). FDis explained variance under 0.5 for most traits shows the influence of other environmental and historic factors, e.g. colonization history, and possibly neutral processes (Schleicher et al., 2011a; Fritz et al., 2013). Although environmental constraints should limit the ranges of possible trait values, limiting similarity, i.e. competition among species in a given community, could influence the spread of trait values independently of the former.

Multivariate FDis, i.e. whole trait space, increased with temperature and precipitation, as expected by environmental filtering theory (Klopfer and MacArthur, 1961). Other studies reported different results, as bowl-shaped trait spaces or largest trait space at mid-latitudes (Spasojevic and Suding, 2012; Lamanna et al., 2014). Nevertheless, Lamanna et al. (2014) corrected trait space for species richness, while Spasojevic and Suding (2012) investigated growth investment traits exclusively. As community trait space is dependent on both traits and species considered, those contrasting results are not surprising. Here, we wanted to quantify absolute trait space. Through a broad choice of plant functional traits and the measurement of a large part of the species occurring in the communities, we are confident trait space was approximated sufficiently well to predict functional diversification on the environmental gradients.

Single-gradient changes in CWMs and FDis mostly supported previous studies (e.g. Mayfield et al., 2005; Swenson and Enquist, 2007; Lienin and Kleyer, 2012; Moles et al., 2014), but exceptions occurred and are discussed in the following. Generally, moderately high temperatures should allow for more viable plant life strategies than cold ones. While this is supported for most traits by our results, leaf area FDis decreased with temperature. It is often stated that leaf area should be small under cold and dry conditions because small leaves have lower transpiration rates (Peppe et al., 2011). Still, the growth of large-leaved giant groundsel (*Lobelia* spp. L.) and *Dendrosenecio* spp. B. NORD. in many African high-elevation ecosystems (Hedberg, 1969) shows that combinations of trait expressions exist that render large leaves successful even if regular night frost events occur. As Geller and Smith (1982) have shown, a set of structural adaptations involving the orientation of leaves and the arrangement along the plant axis allow for exceptionally low transpiration rates of large leaves.

Increases in growth investment trait CWMs with precipitation have been confirmed in previous studies (Fonseca et al., 2000). Plots with regular rainfall should have a larger trait space, as more life strategies, i.e. epiphytic and liana growth forms, are supported. The results of our study for FDis support this theory and are in line with a study along a precipitation gradient in California, which showed the same directionality of trait variability (Cornwell and Ackerly, 2009).

Increasing variability in reproductive traits with disturbance is a common pattern (Grime, 2006). Relative seed number did not conform to this, which may be due to the comparison of forest and grasslands on the exceptionally large disturbance gradient in our study, in contrast to comparisons of different grassland communities. Seed crop frequency CWMs increased with disturbance, as plants need to reproduce fast enough to survive disturbance as seeds (Jakobsson and Eriksson, 2000; Schippers et al., 2001; Lehsten and Kleyer, 2007). Still, if disturbance acts heterogeneously in habitats, as is the case in manual herbicide application and tilling, several reproductive strategies including different lengths of life cycles can coexist (Grime, 2006).

At the lower end of the soil nutrient gradient, divergence in leaf pubescence is probably a result of the correlation of soil nutrients with elevation, as alpine environments have the lowest nutrient concentrations of all ecosystem types at Mount Kilimanjaro (App. S1). Leaf pubescence helps to avoid heat loss and tissue damage by intense UV light and is therefore strongly linked to elevation. Along the upper end of the nutrient gradient, strong differences in nutrient availability were found between SAV rich in C_4 grasses and MAI dominated by dicotyledonous weeds, which are better adapted to disturbed environments through shorter generation times. This lead to a decrease in the leaf δ^{13}C CWM and a parallel convergence in leaf δ^{13}C values with increasing nutrient levels. LDMC convergence with increasing soil nutrients could be due to water storage in leaf tissues in the arid SAV and MAI ecosystems.

Plant-animal interaction traits showed idiosyncratic responses on the environmental gradients, probably due to co-evolution with pollinators, seed dispersers, and herbivores (Schaefer et al., 2004). Avoiding herbivory using spines is a common feature in hot and dry savanna habitats, where large herbivores have detrimental effects on vegetation (Hanley et al., 2007). Thus, numbers of spiny taxa increased in the relatively nutrient-rich and high-temperature SAV and the disturbed MAI ecosystems.

Trait similarity and convergence

Differences in trait expressions were smaller within than between ecosystem types, i.e. ecosystem type classification was supported by traits, as in other studies (Shipley, 2010; Swenson et al., 2012a). Spatial continuity and gradual changes in the abiotic environment could be responsible for the high similarity among tall forest stands (FPD, FPO, FOC, FOD, and FLM). HEL and FER also had many trait expressions in common. The separation of FER from the adjacent forests at lower elevations may be due to effects of freezing events representing a strong physiological boundary for many plant species (Beck et al., 1984; Sakai and Larcher, 1987). Interestingly, our approach revealed a more complex pattern of trait similarity than the one found for a subset of the traits investigated in this study by Swenson et al. (2011). The reason may be the inclusion of disturbance as a strong driver of trait expressions. At the lower forest border, strong differences in the intensities and land uses of the lower elevation ecosystem types forced a strong shift in trait compositions (Pakeman et al., 2011; Ding et al., 2012; Guedo and Lamb, 2013).

While convergence was the main reason for differences in FDis between ecosystems indicating trait differences resulting from trait filtering through the abiotic environment (Mason et al., 2007), among forest ecosystems, divergence was often found. This points towards alternative life history strategies resulting in a broad range of trait expression in forest communities. For instance, montane *Ocotea* forests (FOC) consisted of a tough-leaved upper canopy of *Ocotea usambarensis* ENGL., lianas of various genera, some equally tough-leaved understory trees with much denser wood, tree ferns with soft leaves and stems, a variety of Rubiaceae species with a high fruit number : stem biomass ratio, and a herbaceous community of grasses and weeds, but also members of the Piperaceae with thick leaves for water storage.

Influences of environmental factors and competition were mirrored by trait convergence and divergence within and between ecosystem types and changes of both CWMs and FDis along the environmental gradients, but neutral processes were less apparent. Ecological drift, i.e. the stochastic change of species identities within communities assumed by neutral processes, might result in convergence, divergence, or no differences in ecosystem trait composition, as traits are not expected to influence community assembly (Hubbell, 2001).

The number of plots per ecosystem type in our study and differences in environmental conditions within those limit possible inferences. Still, comparable differences in trait compositions between environmentally distant plots as seen especially in plant-animal interaction traits and co-occurrence of both divergence and convergence in the comparison of the same ecosystem types both indicate neutral processes. This is contrasted by many growth investment traits, which showed differences between ecosystem types resulting from trait convergence. Neutral processes may also shape trait distributions of these traits, but varying strengths of environmental filtering and stochasticity on trait expressions are likely (Shipley et al., 2011), and for growth investment traits, environmental filtering seems to be relatively strong.

A shortcoming of our study could be the limitation of our trait collection to a subset of all species. Vegetation surveys at Mount Kilimanjaro suggest about 1500 species of vascular plants occur at the southern slopes (Andreas Hemp, unpublished data), ten times as many as were sampled. Nevertheless, as we collected the most abundant species constituting 80 % of the total plant biomass, the remaining species had very low abundances, and their influence on both CWMs and FDis should be negligible.

Another critic could be the restriction to terrestrial plants. Epiphytes are occupying parts of trait space not covered by terrestrial plants (Benzing, 2008; Petter et al., 2015). Still, considering their abundance at Mount Kilimanjaro, their contribution to total biomass would probably influence results quantitatively, but not qualitatively (DSC, pers. obs.).

While the interpretation of single trait patterns is valid in its own respect, the question remains in how far the full trait set covered a substantial part of plant life strategies, therefore approximating well overall trait space. Although many suggestions to which traits to use exist, three prominent axes of trait variation are defined by specific leaf area, canopy height, and seed mass (Westoby, 1998). Seed mass has not been included in our study, but seed number, and those traits are connected by a strong trade-off (Rees and Westoby, 1997).

Relationship of trait and species β diversity

The comparison of any measure of functional diversity with species diversity is inherently difficult, because while species diversity depends on the measure selected, e.g. species richness or Shannon entropy, functional diversity is additionally influenced by the number and kinds of trait incorporated in any index (Leps et al., 2006). Here, we selected many traits, as we were interested in testing if differences in species identities between plots, i.e. species β diversities, were mirrored by differences in trait space, i.e. trait β diversities, or whether we would find indications of trait-independent species turnover, thus neutral processes.

The stronger increases in species β diversity compared to trait β diversity with environmental distance were expected given that additionally to neutral processes, dispersal limitation, and historic factors may have shaped species diversity. The overall increases of trait β diversity are in line with the findings of Swenson et al. (2011). That study investigated single traits, but except for stem specific density, which had a hump-shaped pattern, all trait β diversities increased with environmental distance.

Although forest ecosystem types spanned an elevation gradient of about 1100 m with simultaneous considerable changes in precipitation (Tab. 3.1), trait syndromes were only weakly affected. Rather, the freezing line around 3200 m a.s.l. and strong disturbances in the lowlands marked pronounced differences in traits. Types of disturbance mattered: While GRA was characterized by mowing only, COF, HOM, and MAI were also affected by fertilization, and COF by herbicide application. This is expressed by large differences of GRA both compared to disturbed and undisturbed systems, and the gradual increases in trait β diversity from HOM to MAI to COF compared to natural systems.

Thus, while both temperature and disturbance varied between ecosystem types with associated changes in precipitation and soil nutrients, differences in disturbance regimes affected species and trait β diversity stronger than gradual changes of temperature. Nevertheless, this cannot be generalized, as the relative strength of those environmental factors may vary between systems (see e.g. Toledo et al., 2011).

The stronger changes in species β diversity compared to trait β diversity suggests neutral processes as drivers of species composition across the respective communities, but additional research is necessary to investigate the contribution of dispersal limitation or historic factors to the patterns observed.

Conclusions

This work showed the influence of four environmental gradients on community-weighed means (CWMs) and functional dispersion (FDis) of plant functional traits. Additionally, it investigated trait similarity in relation to distance in environmental space and whether convergence or divergence in trait values were responsible for differences in traits between sites. As expected, relationships of temperature, precipitation, disturbance, and soil nutrients with FDis explained a part of the within-community spread in trait values, but remained behind the magnitude of explained variance for CWMs. Lower FDis, i.e. convergence in trait values, was mostly observed in environmentally extreme conditions, i.e. cold, dry, disturbed, and nutrient-poor environments. Although individual traits differed in their responses to the environment, higher similarity within ecosystem types was generally confirmed. Differences in FDis between sites were mostly due to convergence, but divergence was also present, especially in traits relating to plant-animal interactions. This implicates environmental filtering and limiting similarity are shaping plant communities. Neutral processes were indicated by comparable differences in trait syndromes between and among ecosystem types. Species β diversity increased faster than trait β diversity with environmental distance. This was expected, as species identities depend on present and historic processes limiting their distributions, while traits respond to the present environment. Nevertheless, the latter pattern could also be driven by neutral processes.

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Appendices

Appendix S1: Dominant ecosystem types at Mount Kilimanjaro and abiotic environmental conditions

Mean values for each ecosystem type are given together with the value range in parentheses. Disturbance was calculated following the procedure described in Appendix S2. Soil nutrients is the value of the first axis of a PCA including plant available Ca^{2+}, K^{+}, Na^{+}, N and P. Larger values indicate higher nutrient availability.

Ecosystem Type	Elevation [m a.s.l.]	Precipitation [mm*a^{-1}]	Temperature [°C]	Disturbance	Soil Nutrients
Helichrysum shrubland (HEL)	4250 (3880 - 4550)	1293 (1208 - 1411)	4.2 (2.9 - 5.3)	0 (0 - 0.02)	-1.45 (-1.65 - -1.36)
Erica forest (FER)	3716 (3500 - 3890)	1517 (1393 - 1716)	6.2 (4.5 - 8.1)	0.02 (0.01 - 0.04)	-1.41 (-1.54 - -1.3)
Disturbed *Podocarpus* forest (FPD)	2904 (2770 - 3060)	2056 (1936 - 2116)	9.7 (9 - 10.8)	0.23 (0.15 - 0.26)	-1.2 (-1.35 - -0.83)
Podocarpus forest (FPO)	2856 (2720 - 2970)	2036 (1946 - 2136)	9.6 (9 - 10.3)	0 (0 - 0)	-1.25 (-1.31 - -1.17)
Ocotea forest (FOC)	2464 (2120 - 2750)	2388 (2117 - 2552)	11.5 (9.9 - 12.1)	0.01 (0 - 0.02)	-1.15 (-1.33 - -0.92)
Disturbed *Ocotea* forest (FOD)	2378 (2220 - 2560)	2334 (2202 - 2413)	11.9 (11 - 13)	0.08 (0.07 - 0.1)	-1.19 (-1.33 - -1.05)
Lower montane forest (FLM)	1806 (1620 - 2040)	2201 (2089 - 2305)	15.5 (14.4 - 16.5)	0.16 (0.1 - 0.21)	-0.67 (-1.04 - -0.18)
Grasslands (GRA)	1500 (1300 - 1750)	1610 (1248 - 2022)	18.9 (16.5 - 20.8)	0.53 (0.49 - 0.57)	0.47 (-0.57 - 1.49)
Homegardens (HOM)	1490 (1150 - 1840)	1656 (1152 - 2244)	18.7 (16.2 - 20.8)	0.57 (0.41 - 0.63)	1.07 (-0.42 - 2.63)
Coffee plantations (COF)	1349 (1120 - 1660)	1393 (1115 - 1736)	19.8 (17.4 - 22.6)	0.92 (0.59 - 1)	1.72 (-0.16 - 3.24)
Savanna (SAV)	971 (871 - 1130)	764 (657 - 957)	23.7 (22.3 - 24.6)	0.32 (0.16 - 0.42)	1.99 (-0.57 - 6.15)
Maize fields (MAI)	938 (860 - 1020)	674 (588 - 785)	23.6 (22.6 - 24.8)	0.71 (0.54 - 0.91)	3.06 (-0.4 - 5.25)

Appendix S2: Disturbance index calculation

Disturbance is a broad term including many distinct and sometimes habitat-specific alterations in ecosystems (White and Jentsch, 2001). By recording a large range of possible perturbations in our plots, we derived a meaningful classification of the degree of disturbance. Our index was calculated as a composite metric including the effects of biomass removal, input of chemicals and overall landscape structure in the vicinity of the research plots (1500 m radius). Biomass removal has a strong impact on vegetation structure and biodiversity by impeding slow-growing species from reproducing (Lambers et al., 2008). Chemicals strongly alter soil nutrient availability in the case of fertilizers and kill weeds and natural enemies as fungi or insects. A strongly disturbed landscape matrix can influence plants and animals through edge effects (Murcia, 1995). See Kleyer (1999) for similar composite indices in temperate landscapes. All terms in the summary formula and the sub-formulas were linearly standardized to [0,1].

Summary formula:

$$\text{disturbance} = \text{biomass removal} + \text{input of chemicals} + \text{disturbance of the surrounding landscape matrix}$$

Biomass removal:

$$\text{biomass removal} = \text{current timber harvest} + \text{historic timber harvest} + \text{mowing+grazing} + \text{ploughing} + \text{fire (last 30 yrs)}$$

Input of chemicals:

$$\text{input of chemicals} = \text{pesticide application} + \text{fungicide application} + \text{herbicide application} + \text{fertilizer} + \text{irrigation}$$

Disturbance of the surrounding landscape matrix:

$$\text{disturbance of the surrounding landscape matrix} = \text{overall NDVI difference of research plot vicinity to natural habitat}$$

Appendix S3: Trait community-weighed means (CWMs) along environmental gradients

Predictors and responses were standardized prior to the analysis. Thus, coefficients are comparable across predictors and responses, respectively. Standard errors of the coefficient estimates obtained by jackknifing are given in parentheses. Coefficients larger than standard errors are printed in bold. CWMs could not be calculated for categorical traits and in a multivariate way (“All traits”).

Function	Traits	Temperature	Precipitation	Disturbance	Soil Nutrients	R^2
	All traits	NA NA	NA NA	NA NA	NA NA	NA
Growth investment	SLA	**0.15** (±0.12)	**0.27** (±0.09)	**0.8** (±0.16)	0 (±0.12)	0.65
	LDMC	0.06 (±0.15)	**-0.68** (±0.11)	**-0.61** (±0.17)	**-0.42** (±0.25)	0.52
	SSD	-0.07 (±0.12)	**-0.48** (±0.09)	**-0.87** (±0.16)	-0.05 (±0.18)	0.68
	Leaf N_{mass}	-0.11 (±0.14)	**0.74** (±0.1)	**0.71** (±0.17)	**0.3** (±0.19)	0.54
	Leaf C_{mass}	**-0.58** (±0.16)	0.1 (±0.11)	**-0.22** (±0.11)	0.01 (±0.13)	0.67
	Leaf P_{mass}	0.02 (±0.15)	**0.11** (±0.1)	**0.51** (±0.17)	**0.46** (±0.26)	0.72
	Canopy height	**0.39** (±0.14)	**0.67** (±0.09)	**-0.57** (±0.12)	0.09 (±0.12)	0.62
Reproductive investment	Relative seed number	**-1.19** (±0.17)	**-0.19** (±0.12)	**0.82** (±0.11)	**0.17** (±0.12)	0.51
	Seed crop frequency	-0.07 (±0.12)	**0.39** (±0.12)	**0.84** (±0.16)	0.1 (±0.13)	0.54
Adaptations to specific abiotic conditions	Leaf area	**0.92** (±0.11)	**0.78** (±0.09)	**-0.27** (±0.12)	**0.21** (±0.15)	0.68
	Leaf pubescence	**-0.99** (±0.16)	**-0.75** (±0.09)	**0.18** (±0.1)	-0.06 (±0.11)	0.70
	Leaf δ^{13}C	**0.68** (±0.2)	**-0.55** (±0.14)	**-0.25** (±0.22)	**-0.37** (±0.33)	0.42
Plant - animal interactions	Spinescence	**0.4** (±0.27)	-0.1 (±0.18)	**-0.64** (±0.23)	**0.6** (±0.38)	0.45
	Dispersal syndrome	NA NA	NA NA	NA NA	NA NA	NA
	Diaspore color	NA NA	NA NA	NA NA	NA NA	NA
	Flower color	NA NA	NA NA	NA NA	NA NA	NA

Chapter 4

Do plant functional traits predict animal body mass?

David Schellenberger Costa[1]*, Alice Classen[2,†], Stefan Ferger[3,†], Marcell Peters[2,†], Katrin Böhning-Gaese[3,†], Ingolf Steffan-Dewenter[2,†], Michael Kleyer[1]

[1]Department of Biology and Environmental Sciences, University of Oldenburg, 26111 Oldenburg, Germany

[2]Department of Animal Ecology and Tropical Biology, University of Würzburg, 97074 Würzburg, Germany

[3]Senckenberg Gesellschaft für Naturforschung, Biodiversity and Climate Research Center, 60325 Frankfurt, Germany

*Corresponding author

†These coauthors provided data but did not yet contribute to this version of the manuscript.

Abstract

Body size in animals spans an enormous range from unicellular organisms to large aquatic mammals. In a functional context, body size can be seen as a species trait reacting on environmental filters and allowing for access to particular food resources. Since centuries, ecologists and evolutionary biologists investigate the factors governing body size distributions in animals. Among the most prominent explanations is Bergmann's rule that states that body mass is mainly controlled by temperature, as large animals can regulate their body temperature more efficiently. Many taxa conform to the rule, and even some cold-blooded ectotherms follow it, although for different reasons. Nevertheless, remarkable exceptions to Bergmann's rule and its adaptation for cold-blooded taxa exist, and it has been argued that other forces govern body size in animals. Here, we test whether food resources constrain body size in both warm- and cold-blooded animals. We investigate the effect of plant functional traits representing direct resources for herbivores and indirect resources for secondary consumers. We also tested whether environmental complexity drives animal body mass, as the size of animals is linked to how they perceive the environment. As an alternative to the food resources and environmental complexity hypotheses, we included temperature as proposed by Bergmann's rule in our analyses. Our results revealed that temperature was a more influential driver of animal body mass patterns than food resources or environmental complexity, although relationships were not always as expected. Some taxa were equally well predicted by both temperature and traits. However, resource availability is difficult to measure and more accurate data may reveal a stronger effect of food resources on animal body mass.

Keywords Bergmann's rule, body size, net primary production, food resources, temperature, elevation, precipitation, disturbance, insects, birds, community-weighed mean, structural equation model

Introduction

Animal body size attracted scientific attention long before the theory of evolution provided a framework to explain the existing variability. The observation of differences in body size among closely related species inspired Bergmann to formulate his classic rule (Bergmann, 1848). It states that body size of sister species is larger in colder climates for energetic reasons. For cold-blooded animals, higher frost resistance, larger energy reserves for surviving starvation periods and longer growth and development time through low temperatures have been brought forward to explain negative relationships of temperature and size (Marcondes et al., 1999; Atkinson, 1994; Shelomi, 2012). Although plausible, many exceptions to the rule suggest other factors to be relevant in determining body size, too (McNab, 1971; Geist, 1987).

Recently, Huston and Wolverton (2011) argued that body size is mostly correlated with food availability approximated by NPP ("ecologically and evolutionary relevant net primary production"). Studies on carnivores have shown that food availability is positively correlated to body size (Boyce, 1978; Hilderbrand et al., 1999; Smith and Lyons, 2011), and a decrease in body size through resource limitation has been brought forward as an explanation of different body sizes of island and mainland forms of related species ("island rule", Foster, 1964). Here, we investigated if high resource availability has a positive effect on animal body mass in tropical environments ("more food hypothesis", see Geist, 1987, for temperate regions, see Wolverton et al., 2009). Plants as the main terrestrial primary producers provide food resources for animals. Thus, plant functional traits describing food quality and quantity should affect body mass. Depending on the trophic position of an animal, this relationship may be direct or indirect. Plant functional traits can be proxies for resource availability in various aspects: fruit sizes and numbers indicate food availability for frugivores, leaf structure and nutrient contents reflect palatability for leaf-consuming herbivores and flower attributes are relevant for animals depending on nectar.

Besides resources, changes in the three-dimensional structure of habitats have been brought forward to explain variability in body mass, too (Allen et al., 2006). Increased structural complexity in habitats may offer niches for more species. Depending on the average size of a taxonomic group or guild, this may lead to increases in average body mass. Large or coarse-grained structured habitats with more patchily distributed resources should harbor larger animals than small or fine structured ones because the spatial resolution at which animals perceive and forage resources is supposed to be a function of their size (Nash et al., 2014a,b). Total plant biomass can be a proxy of structural complexity (Ensslin et al., 2015). Precipitation has been identified as the main driver of changes in plant biomass across ecosystems (Stegen et al., 2011), and it plays a key role in filtering plant functional traits, too (Wright et al., 2004). Additionally, disturbance events can induce severe changes in plant traits and biomass (Lienin and Kleyer, 2011). Thus, precipitation and disturbance may influence animal body mass indirectly.

In summary, temperature, resource availability, and resource distribution may influence species' body masses. If animals with similar ecological requirements react canonically to these factors, it may be possible to trace direct and indirect influences on an integrated measure of their body mass distribution, the community-weighed mean (CWM), which allows for comparing systems with different species and phylogenetic histories. We predicted the body mass CWMs of moths, bees, frugivorous birds, and insectivorous birds in a tropical mountain ecosystem featuring large gradients in temperature, precipitation, and disturbance. As plant traits and biomass also respond to these abiotic factors, animal body mass may be directly or indirectly controlled by those. We therefore used a effect-response framework (Suding et al., 2008) to link abiotic environment, plant functional traits, and animal CWMs. This concept was expressed in detailed box-and-arrow diagrams, which formed initial models. The specific hypotheses connected with expected relationships are listed in Table 4.3. The initial models were tested with structural equation modeling. We confirmed previous studies showing a strong link between precipitation, disturbance, plant traits, and total plant biomass and tested whether temperature, food resources, structural complexity, or a combination of these factors explained differences between animal CWMs in different ecosystems.

Materials and Methods

Study region We chose Mount Kilimanjaro as our study system. Mount Kilimanjaro is located in Northern Tanzania at 3.1 °S 37.4 °E. Being the highest free-standing mountain in the world, it covers an area of approx. 4000 km^2. The elevation gradient spans from the lowlands at 800 m a.s.l. to the peak at 5892 m a.s.l. Precipitation values range from 550 mm*a^{-1} to 3600 mm*a^{-1}, with the highest amount of rainfall occurring at mid-elevations in the forest belt and the lowest amounts in the alpine zone and the plains surrounding the mountain (Hemp, 2001). Anthropogenic disturbance is expressed differently along the mountain. Fires and occasional timber extraction affect higher elevations, while agriculture with herbicide application is practiced in lowland areas.

Data collection Collection of plant functional traits and data on animal taxa took place on 60 plots in the twelve ecosystem types of major importance at the mountain between August 2010 and November 2012. Plot size was 50 x 50 m. Plots

Table 4.1: **Temperature, precipitation and disturbance ranges of the principal ecosystem types at Mount Kilimanjaro**
The twelve ecosystem types investigated in this study represent a large part of the habitats present at the southern slopes of Mount Kilimanjaro, Tanzania. Middle and high elevation vegetation are named after the dominant tree species *Ocotea usambarensis* Engl., *Podocarpus latifolius* (Thunb.) R. Br. ex Mirb., *Erica* spp. L., and the shrubby *Helichrysum* spp. Mill., respectively. Disturbance was calculated including various aspects of anthropogenic changes to the environment described in Appendix S1 (page 131).

Ecosystem Type	Mean Temperature [°C]	Annual Precipitation [mm*a^{-1}]	Disturbance	Main Disturbance Type
Helichrysum shrubland	4.2 (2.9 - 5.3)	624 (573 - 775)	0 (0 - 0.02)	-
Erica forest	6.2 (4.5 - 8.1)	858 (679 - 1148)	0.02 (0.01 - 0.04)	Fire
Podocarpus forest	9.6 (9 - 10.3)	1612 (1305 - 1984)	0 (0 - 0)	-
Disturbed *Podocarpus* forest	9.7 (9 - 10.8)	1539 (1332 - 1803)	0.23 (0.15 - 0.26)	Fire
Ocotea forest	11.5 (9.9 - 12.1)	2182 (1629 - 2678)	0.01 (0 - 0.02)	Logging
Disturbed *Ocotea* forest	11.9 (11 - 13)	2038 (1884 - 2290)	0.08 (0.07 - 0.1)	Logging
Lower montane forest	15.5 (14.4 - 16.5)	2495 (1973 - 2820)	0.16 (0.1 - 0.21)	Logging
Homegardens	18.7 (16.2 - 20.8)	1954 (1360 - 2650)	0.57 (0.41 - 0.63)	Weed removal
Grasslands	18.9 (16.5 - 20.8)	1794 (1090 - 2750)	0.53 (0.49 - 0.57)	Herbicides
Coffee plantations	19.8 (17.4 - 22.6)	1662 (1250 - 2000)	0.92 (0.59 - 1)	Mowing
Savanna	23.7 (22.3 - 24.6)	776 (600 - 1020)	0.32 (0.16 - 0.42)	Cattle grazing
Maize fields	23.6 (22.6 - 24.8)	790 (610 - 880)	0.71 (0.54 - 0.91)	Weed removal

were distributed equally among ecosystems types, five plots belonging to each type (Tab. 4.1).

Temperature was measured continuously for several years with automatic data loggers covering the data collection time frame (Mwangomo et al., 2014). Precipitation data was derived from the Kilimanjaro rainfall model (Hemp, 2009). Disturbance was calculated as a composite metric including the effects of land use and landscape structure (see Appendix S1 in Supporting Information at page 131 for details).

Plant functional traits were collected for the 153 most abundant and widespread species at the research plots in the different ecosystem types. Undisturbed plots at low elevations were dominated by annual grasses and scattered trees, shifting to weeds in cultivated areas and woody life forms in the rainforest. Alpine vegetation was mainly composed of shrubs and perennial herbs and grasses. We chose traits that describe vegetative growth, persistence and reproductive characteristics. We sampled 15 individuals per species for specific leaf area (SLA), leaf dry matter content (LDMC) stem specific density (SSD), leaf nitrogen content (leaf $\mathrm{N_{mass}}$), leaf phosphorus content (leaf $\mathrm{P_{mass}}$), seed crop frequency, fruit number, and fruit size. Additionally, the total plant biomass per plot was calculated with allometric equations using complete tree and undergrowth inventories (details in Ensslin et al., 2015). Sampling and processing of plant material followed Kleyer et al. (2008).

Percentage cover values from vegetation surveys were used to calculate community-weighed mean trait values (CWMs, Garnier et al., 2007). Correlated traits were aggregated to avoid multicollinearity. To this end, the first axis of a principal components analysis (PCA) using SLA, LDMC, SSD, leaf $\mathrm{N_{mass}}$ and leaf $\mathrm{P_{mass}}$ was extracted and termed "leaf economics" (for correlations of variables see Tab. 4.2). The traits used are related to the worldwide leaf economics spectrum (Shipley et al., 2006a), reflecting a gradient from fast resource use and nutrient turnover to slow and persistent growth. To quantify nectar and fruit availability on the plots we recorded pollination and dispersal syndromes from the Flora of Tropical East Africa (Turrill and Milne-Redhead, 1952). As no data on flower nectar contents was available, we used the abundance-weighed fraction of insect-pollinated plant species as a proxy for nectar availability to describe food resources for bees and moths per plot. To assess food resources for frugivorous birds, we used average fruit numbers (fn) per plant individual, average fruit size (fs), seed crop frequency (scf), and relative abundance (ra) to calculate the bird-dispersed fruit CWM (bdf) according to the following formula:

$$bdf = \sum_{species} ra * \overline{fn} * \overline{fs} * scf * \delta_{bdf}$$

δ_{bdf} equals 1 for species producing fruits consumed by birds and 0 otherwise. Birds were observed through point counts and mist-netting, both in dry and wet seasons to include temporal variation (see Ferger et al., 2014, for methodology). Bees and moths were sampled with pan traps at the forest floor and in the canopy of woody vegetation. Sampling was repeated several times to account for temporal variation (see Classen et al., 2014). Body masses of birds were derived from Dunning Jr (1992). For bees, body mass was approximated with highly correlated intertegular distance (ITD, $\mathrm{R}^2 = 0.96$, Cane, 1987). For moths, we used body length instead of body mass, as length was measured after collection, while body mass would likely be biased after the liquid preservation of animals. Within animal groups of similar

Table 4.2: **Pearson correlations between plant functional traits and leaf economics**

Leaf economics is the first axis of a PCA including specific leaf area (SLA), leaf dry matter content (LDMC), stem specific density (SSD), leaf nitrogen per unit mass (leaf N_{mass}), and leaf phosphorus per unit mass (leaf P_{mass}).

	LDMC	SSD	Leaf N_{mass}	Leaf P_{mass}	Leaf Economics
SLA	-0.72	-0.85	0.77	0.73	0.92
LDMC		0.82	-0.91	-0.62	-0.92
SSD			-0.76	-0.62	-0.92
Leaf N_{mass}				0.56	0.91
Leaf P_{mass}					0.78

body structure, body length and body mass are highly correlated (Honěk, 1993).

As with plant traits, body mass was weighed by species abundance, yielding a body mass CWM for each taxon or guild to avoid giving rare species the same weight as abundant ones (Huston and Wolverton, 2011). Total body masses of moths and bees as food resources for insectivorous birds were calculated as the sum of all individuals of the respective groups sampled. For means and ranges of plant functional traits, animal CWMs, total bee ITD, and total moth body length see Appendix S2 at page 132.

Data analysis We applied structural equation modeling with mixed effect models to explain mean body masses with environmental data and plant functional traits (Shipley et al., 2006b). Mixed effect models offer the possibility to include site-specific and plot type-specific random effects. For simplicity, we assumed linear relationships between all parameters. This may not always be the case. Nevertheless, we expected linearity within the limited ranges of the variables investigated. Variables were standardized prior to analysis. To obtain correct p values, we followed the recommendations of Barr et al. (2013) and included random slopes and random intercepts. All calculations were done in R (Team, 2014). For mixed effect models, we used the lmer function in R package lme4 (Bates et al., 2008) with Gaussian error structure obtaining maximum likelihood estimates (option REML=F). We ran one separate model for each animal group investigated to keep total variable numbers low with regard to the number of observations. For each group, we first ran the hypothesized model including all predicted inter-dependencies. We then ran an improved model omitting the non-significant terms at a p value of 0.05. We report coefficients, p values and R^2 values for both initial and “significant” models. Table 4.3 lists the detailed hypotheses defining the structural equation models.

Results

We found large differences in the individual relationships and effect sizes inferred from the structural equation models (Fig. 4.1). Table 4.4 shows partial regression coefficients and p values. Overall, expectations concerning the abiotic environment and plant functional traits were confirmed by our analyses, but relationships between plant functional traits and body mass CWMs were much weaker and not always according to the hypotheses. Between individual variables, explained marginal R^2, i.e. the proportion of variance explained by linear regressions, was between 0.16 and 0.58, while conditional R^2 values expressing the summed effect of linear regressions and accounting for ecosystem type-differences ranged from 0.16 to 0.89 (Tab. 4.4). Overall model R^2 values ranged from 0.32 to 0.76. Exclusion of non-significant terms from the initial hypotheses (dashed lines in Fig. 4.1), had a positive effect on model R^2 values, especially for birds.

The relationships between leaf economics and total plant biomass were the same for all models. Both were positively related to precipitation. Disturbance had a negative effect on total plant biomass, but a positive on leaf economics. Insect-pollinated plants were explained by total plant biomass and leaf economics, both with positive coefficients. Bird-dispersed fruits were negatively related to leaf economics and positively to total plant biomass. Moth and frugivorous bird body masses were explained by temperature alone, while those of bees and insectivorous birds were also related to total plant biomass. Both moth and frugivorous bird body mass decreased with temperature (Fig. 4.1A, C). As hypothesized, bee body mass increased with disturbance and decreased with temperature (Fig. 4.1B). Contrary to our expectation, insectivorous bird body mass was positively related to temperature (Fig. 4.1D). Total plant biomass affected bee body mass positively, but was negatively related to insectivorous bird body mass, contradicting our hypotheses. Food availability had no positive effect on insectivorous bird body mass as indicated by the lack of a relationship with total body mass of moths and bees. Total body mass of moths in turn was positively related to temperature, while total body mass of bees decreased with increasing total plant biomass.

Table 4.3: **Hypotheses defining the structural equation models**
The structural equation models relating plant traits to animal body mass CWMs were implemented according to expected relationships between abiotic environment, plant functional traits, animal body mass CWMs, and animal total biomass. Abbreviations: M: moths model, B: bee model, F: frugivorous birds model, I: insectivorous birds model. *moths and bees. References in the table: [1]Bergmann (1848), [2]Brown et al. (2004), [3]Kaspari and Vargo (1995), [4]Wright et al. (2004), [5]Churkina and Running (1998), [6]Kühner and Kleyer (2008), [7]Geist (1987), [8]Wolverton et al. (2009), [9]Iwasa et al. (1994), [10]Regal (1982), [11]Howe and Smallwood (1982), [12]Allen et al. (2006), [13]Raich et al. (2006), [14]McNaughton et al. (1989).

Model	Response	Predictor	Hypothesized Relationship	Explanation
M, B, F, I	Disturbance	Temperature	+	Anthropogenic activities are strongest at low elevations close to settlements
M, B, F, I	Body mass CWM	Temperature	−(+)	More effective energy use of larger animals in cold environments[1,2], but for bees, colony size is relevant, thus decreases expected[3]
I	Total body mass*	Temperature	−	More effective energy use of larger animals/ colonies in cold environments[1,2]
M, B, F, I	Leaf economics	Precipitation	+	Tougher leaves conserve water[4]
M, B, F, I	Total plant biomass	Precipitation	+	Water is a limiting factor for primary productivity[5]
M, B, F, I	Leaf economics	Disturbance	+	Fast growth and turnover necessary[6]
M, B, F, I	Total plant biomass	Disturbance	−	Biomass removal
B	Body mass CWM	Disturbance	+	Large productive species provisioned with hives, “more food hypothesis”[7,8]
M, B	Insect-pollinated plants CWM	Leaf economics	+	High-leaf economics plants in study area are mostly insect-pollinated weeds
F	Bird-dispersed fruits CWM	Leaf economics	−	High-leaf economics plants mostly produce small wind-dispersed seeds
M	Body mass CWM	Leaf economics	+	Lower C:N ratio, higher food quality[9]
M, B	Insect-pollinated plants CWM	Total plant biomass	+	Reduced wind speed through persistent foliage in forests makes wind-pollination less effective[10]
F	Bird-dispersed fruits CWM	Total plant biomass	+	Advantage of far transport of large seeds through animals in forests[11]
M, B, F, I	Body mass CWM	Total plant biomass	+	Structural complexity allows for more species and[12]
M, B	Total body mass*	Total plant biomass	+	Higher primary productivity resulting in larger animal biomass[13,14]
M, B	Body mass CWM	Insect-pollinated plants CWM	+	Increase in resources through more biomass, “more food hypothesis”[7,8]
F	Body mass CWM	Bird-dispersed fruits CWM	+	Increase in resources through more biomass, “more food hypothesis”[7,8]
I	Body mass CWM	Total body mass*	+	Increase in resources through more biomass, “more food hypothesis”[7,8]

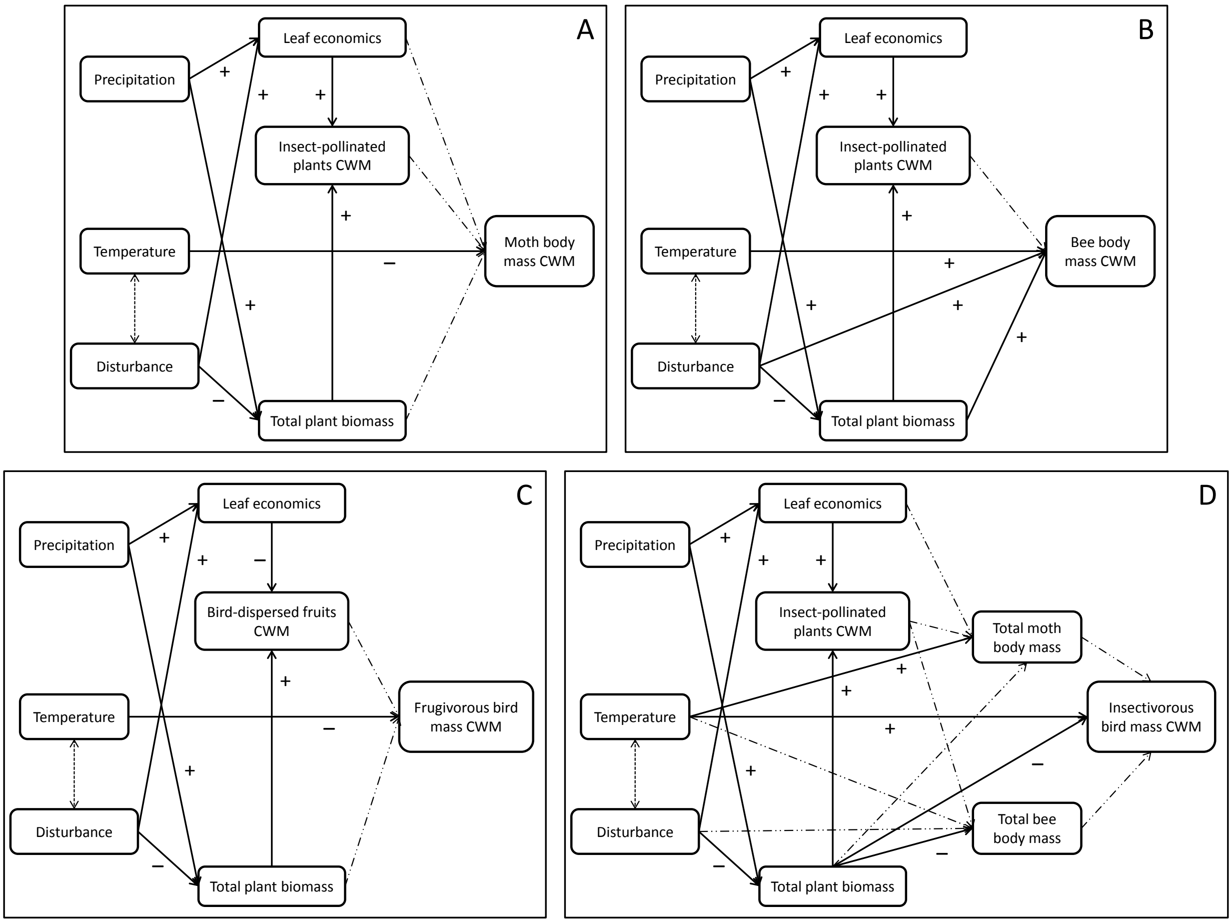

Figure 4.1: **Structural equation model showing the relationship between the abiotic environment, disturbance, plant functional traits, and community-weighed means of animal body masses for moths, bees, insectivorous birds, and frugivorous birds**

Positive and negative relationships are marked with "+" and "−". Double-headed arrows with dotted lines show correlations. Dashed lines indicate hypothesized relationships that were not supported by the data, i.e. which turned out to be non-significant in the regression models. See Table 4.1 for coefficients, individual p values and generalized R^2 values. (A) Moths, (B) Bees, (C) Frugivorous birds, (D) Insectivorous birds.

Table 4.4: **Standardized coefficients, p values, and generalized R^2 values of the structural equation models**

The relationships between the abiotic environment (precipitation, disturbance), total plant biomass, and leaf economics were the same for all models and coefficients and p values are given only once. For each taxonomic group or guild, data is presented for initial models ("hypothesis") and improved models dropping non-significant paths ("significant"). Stars indicate p values smaller than 0.05, 0.01 and 0.001, respectively.

Model	Response	Predictor	Estimate	P value		Marginal R^2	Conditional R^2	Model R^2
All	Precipitation		0			0	0.73	
	Temperature		0			0	0.96	
	Disturbance	(Intercept)	-0.15			0.38	0.91	
	Disturbance	Temperature	0.49	3.54E-04	***			
	Leaf economics	(Intercept)	-0.09			0.52	0.77	
	Leaf economics	Disturbance	0.43	0.01	**			
	Leaf economics	Precipitation	0.43	2.85E-06	***			
	Total plant biomass	(Intercept)	0			0.32	0.72	
	Total plant biomass	Disturbance	-0.30	0.04	*			
	Total plant biomass	Precipitation	0.37	1.00E-03	**			
Moths hypothesis	Insect-pollinated plants CWM	(Intercept)	0.05			0.47	0.71	0.55
	Insect-pollinated plants CWM	Leaf economics	0.62	9.16E-06	***			
	Insect-pollinated plants CWM	Total plant biomass	0.24	0.04	*			
	Moth CWM	(Intercept)	0.11			0.49	0.51	
	Moth CWM	Insect-pollinated plants CWM	-0.08	0.61				
	Moth CWM	Leaf economics	-0.15	0.35				
	Moth CWM	Temperature	-0.59	2.00E-04	***			
	Moth CWM	Total plant biomass	0.11	0.39				
Moths significant	Insect-pollinated plants CWM	(Intercept)	0.05			0.47	0.71	0.76
	Insect-pollinated plants CWM	Leaf economics	0.62	9.16E-06	***			
	Insect-pollinated plants CWM	Total plant biomass	0.24	0.04	*			
	Moth CWM	(Intercept)	0.14			0.49	0.51	
	Moth CWM	Temperature	-0.76	2.52E-06	***			
Bees hypothesis	Bee CWM	(Intercept)	0.02			0.53	0.53	0.27
	Bee CWM	Disturbance	0.40	0.03	*			
	Bee CWM	Insect-pollinated plants CWM	-0.11	0.37				
	Bee CWM	Temperature	0.38	0.02	*			
	Bee CWM	Total plant biomass	0.52	4.42E-04	***			
	Insect-pollinated plants CWM	(Intercept)	0.05			0.47	0.71	
	Insect-pollinated plants CWM	Leaf economics	0.62	9.16E-06	***			
	Insect-pollinated plants CWM	Total plant biomass	0.24	0.04	*			
Bees significant	Bee CWM	(Intercept)	0.01			0.58	0.66	0.41
	Bee CWM	Disturbance	0.32	0.04	*			
	Bee CWM	Temperature	0.49	1.10E-03	**			
	Bee CWM	Total plant biomass	0.50	0.01	*			
	Insect-pollinated plants CWM	(Intercept)	0.05			0.47	0.71	
	Insect-pollinated plants CWM	Leaf economics	0.62	9.16E-06	***			
	Insect-pollinated plants CWM	Total plant biomass	0.24	0.04	*			
Frugivorous birds hypothesis	Bird-dispersed fruit CWM	(Intercept)	0.01			0.17	0.89	0.36
	Bird-dispersed fruit CWM	Leaf economics	-0.26	0.34				
	Bird-dispersed fruit CWM	Total plant biomass	0.14	0.05	*			
	Frugivorous bird CWM	(Intercept)	0.03			0.35	0.41	
	Frugivorous bird CWM	Bird-dispersed fruit CWM	0.49	0.18				
	Frugivorous bird CWM	Temperature	-0.21	0.54				
	Frugivorous bird CWM	Total plant biomass	-0.05	0.82				
Frugivorous birds significant	Bird-dispersed fruit CWM	(Intercept)	0.01			0.17	0.89	0.7
	Bird-dispersed fruit CWM	Leaf economics	-0.26	0.34				
	Bird-dispersed fruit CWM	Total plant biomass	0.14	0.05	*			
	Frugivorous bird CWM	(Intercept)	0.12			0.16	0.16	
	Frugivorous bird CWM	Temperature	-0.44	0.05	*			

Table 4.4: **Continued**.

Model	Response	Predictor	Estimate	P-value	Marginal R^2	Conditional R^2	Model R^2
Insectivorous birds hypothesis	Insect-pollinated plants CWM	(Intercept)	0.05		0.47	0.71	0.25
	Insect-pollinated plants CWM	Leaf economics	0.62	9.16E-06 ***			
	Insect-pollinated plants CWM	Total plant biomass	0.24	0.04 *			
	Insectivorous bird CWM	(Intercept)	-0.01		0.33	0.33	
	Insectivorous bird CWM	Temperature	0.46	9.41E-04 ***			
	Insectivorous bird CWM	Total bee biomass	0.01	0.96			
	Insectivorous bird CWM	Total moth biomass	-0.02	0.85			
	Insectivorous bird CWM	Total plant biomass	-0.26	0.05 *			
	Total bee biomass	(Intercept)	0		0.31	0.31	
	Total bee biomass	disturbance	-0.17	0.39			
	Total bee biomass	Insect-pollinated plants CWM	0.06	0.61			
	Total bee biomass	Temperature	-0.14	0.41			
	Total bee biomass	Total plant biomass	-0.62	3.06E-05 ***			
	Total moth biomass	(Intercept)	0		0.27	0.27	
	Total moth biomass	Insect-pollinated plants CWM	0.22	0.16			
	Total moth biomass	Leaf economics	-0.37	0.04 *			
	Total moth biomass	Temperature	0.65	4.06E-05 ***			
	Total moth biomass	Total plant biomass	0.01	0.90			
Insectivorous birds significant	Insect-pollinated plants CWM	(Intercept)	0.05		0.47	0.71	0.81
	Insect-pollinated plants CWM	Leaf economics	0.62	9.16E-06 ***			
	Insect-pollinated plants CWM	Total plant biomass	0.24	0.04 *			
	Insectivorous bird CWM	(Intercept)	-0.01		0.33	0.33	
	Insectivorous bird CWM	Temperature	0.45	3.07E-04 ***			
	Insectivorous bird CWM	Total plant biomass	-0.26	0.02 *			
	Total bee biomass	(Intercept)	-0.05		0.23	0.3	
	Total bee biomass	Total plant biomass	-0.45	8.75E-04 ***			
	Total moth biomass	(Intercept)	-0.01		0.22	0.24	
	Total moth biomass	Temperature	0.44	2.49E-03 **			

Discussion

Assuming body mass distributions depend on multiple causal processes, we investigated the effects of plant functional traits and temperature on the body mass of moths, bees, insectivorous and frugivorous birds. Differences in body masses have been the subject of many studies, often yielding contentious results (Huston and Wolverton, 2011). To our knowledge, the potential of plant functional traits to explain animal mean body masses has not been addressed before. Plant traits strongly responded to precipitation and disturbance. We also found strong associations of body mass with temperature. In contrast, plant traits were only partly linked to body mass.

Environment – Plant functional traits

We found that precipitation and disturbance favored increases in correlated traits associated with nutrient acquisition and turnover ("leaf economics"), which has been widely documented on global and local scales (Wright et al., 2004; Minden et al., 2012; Reich et al., 1999). Díaz et al. (1999) described a strong separation of slow-growing persistent xeromorphic plants and fast growing high palatability-annuals along a water stress and elevation gradient in the Argentinean Andes. Differently to Mount Kilimanjaro, a linear decrease of water availability with elevation did not allow for a separation of the temperature and water effects in this study. Although the influence of temperature on plant functional traits is undisputed (Moles et al., 2014), our results show that at Mount Kilimanjaro the strongest driver of total plant biomass and leaf economics is precipitation. Some individual traits may be driven by changes in temperature, but most growth traits used to characterize "leaf economics" were invariant towards it. In contrast, the strong positive effect of disturbance (logging, grazing) on leaf economics is concordant with other studies worldwide (e.g. Díaz et al., 1999; Lienin and Kleyer, 2011).

The observed increases in insect-pollinated plants with increasing leaf economics were expected due to the taxonomic and functional differences between undisturbed savanna and forests on one hand and agricultural areas on the other. At Mount Kilimanjaro, strongly disturbed habitats mostly harbor dicotyledonous weeds, while corresponding natural systems are dominated by wind-pollinated grasses. Additionally, in our study system, species from undisturbed areas rely more on wind- and gravitational dispersal, expressed by the negative relationship of leaf economics and bird-dispersed fruits.

Large differences between marginal and conditional R^2 values were evident in total plant biomass, insect-pollinated plants, and bird-dispersed fruits. This indicates non-linear relationships of predictors and traits or factors not accounted for by the predictors (Zuur et al., 2009). In the case of pollination and dispersal, synchronized evolutionary changes of plants and animals may have influenced plant attributes (Schaefer et al., 2004). Total plant biomass may be affected by nutrient availability, and thus not be completely linearly related to precipitation along the whole gradient, as size limitations on tree growth and negative effects of nutrient leaching could cancel out positive effects of increasing water availability (Havlin et al., 1999).

Environment – Animal CWMs

Temperature was the only significant predictor of animal body mass community-weighed means (CWMs) in all models. Bergmann's rule and its recent formulations in the framework of the metabolic theory of ecology (Brown et al., 2004) predict decreases in body mass with temperature. Moths and frugivorous birds were in concordance with this expectation, in line with previous studies (e.g. Ashton, 2002; Atkinson, 1994; Meiri and Dayan, 2003).

Insectivorous bird mass decreased with temperature. Although the relationship between moth and bee total biomass as an indicator of food resource and insectivorous birds was not significant, we assume that small body size at high elevations was related to low food supply. Hence, even if temperature affects body mass distributions, resource availability may be a strong counteracting factor.

Bee size distribution was contrary to Bergmann's rule, with the smallest mean body masses occurring at the highest elevations in the alpine *Helichrysum* shrubland. As only a single bee species was found at highest elevations, there might be an adaptation unrelated to body mass enabling this species to survive in low-temperature habitats. Disturbance as an indicator for the conversion of grass-dominated landscapes to such with dicotyledonous weeds explained bee body mass relatively well, contrary to the resource-oriented CWM of insect-pollinated plants. Disturbance has a negative effect on bee diversity through application of pesticides and habitat destruction (Winfree et al., 2009). However, we assume that relative increases in large honey bees resulted in the positive relationship observed. The hypothesis that colony size, thus total hive biomass, follows Bergmann's rule instead of individual body size, could not be tested, as colony size data were not available.

A general issue with changes in CWMs is the dependence on both species body masses and abundance: While body masses of species may decrease, changes in abundances may result in increases of the CWMs calculated (Anderson-Teixeira et al., 2012). This is evidenced by the changes in total body mass of moths and bees, which were opposed to those of the corresponding CWMs with temperature and total plant biomass, respectively. Thus, increases or decreases in average animal size can be counterbalanced by changes in overall abundance. This could be a reason for the positive relationship of insectivorous bird body mass and temperature too, meaning that at higher elevations, small species might have more individuals than large ones compared to lower elevations.

Plant functional traits and total biomass – Animal CWMs and total body mass

The food availability hypothesis (Huston and Wolverton, 2011) and the textural discontinuity hypothesis (Allen et al., 2006) justified the expectation of a strong influence of plant functional traits and total plant biomass on animal body mass CWMs. However, we did not find any significant relationship between body mass and functional traits indicating food availability. Assuming the "more food hypothesis" was correct, a shortcoming of the approach presented here might be that the traits used were too crude estimates of the "true" food resources. We used leaf and stem traits indicating a gradient from carbon-rich, hard tissue to soft, nutrient-rich tissue as an indicator for moth food availability (Freschet et al., 2010), however this may not adequately reflect the amount of palatable tissue for moths, as Lepidoptera tend to be specialize to particular host plants (Thompson and Pellmyr, 1991). In moths, a correlation between body size distributions and size distributions of floral resources has been observed (Agosta and Janzen, 2005), indicating that nectar quantity may have predictive potential for body mass. Still, the CWM of insect-pollinated plants may be a too coarse estimate of the nectar actually available for bees and moths, as flower rewards, inflorescence sizes and nectar contents can vary strongly across plant species (Zimmerman, 1988).

Being a direct measure of food resources, we expected bird-dispersed fruits to have a strong influence on frugivorous bird body mass. Although fruit number counts entered in the calculation of bird-dispersed fruits CWM, considering the high mobility of birds, landscape heterogeneity may obscure patterns. Mean body mass of insectivorous birds did not respond to the total mass of bees and moths, which represent a potential food source. Possible reasons include temporal changes in insect abundance not captured in our surveys and other food sources not quantified. While temporal variability may be an issue in savanna and maize fields, the other ecosystem types are characterized by aseasonality, making a strong influence of this factor unlikely. Including other insect taxa, however, would likely change the food availability pattern observed. Thus, a precise estimation of total insect body mass should also include other relevant groups, e.g. Diptera and Coleoptera.

The textural discontinuity hypothesis formulated by Allen et al. (2006) states that structurally complex environments should harbor more species than environments that are structurally simple, owing to the fact that animals perceive their environment depending on their own body size. Compared to open habitats, forests offer a larger diversity of possible niches for birds and insects, which could result in an overall increase in CWMs. Still, in our study, results were ambiguous: While total plant biomass was related to increases in body mass in bees, no changes were observed for moths and frugivorous birds, and insectivorous bird size decreased. Thus, although structural complexity may affect available niches and body masses, other factors might be more relevant to understand changes in body mass CWMs.

Body mass distributions could depend on other factors not considered in our study. Large body size may be caused by sexual selection or elevated fecundity of large individuals (Blanckenhorn, 2000). The interplay of sexual selection for larger individuals and natural selections for smaller ones can complicate patterns (Wikelski and Trillmich, 1997). Blanckenhorn (2000) proposed selective forces favoring small body size: Larger individuals need more resources, may be preferred by parasites and predators, suffer from reduced agility in competition for mating partners and may have reduced fecundity if reproducing late. However, quantifying these parameters in a comparative empirical approach across multiple taxa or guilds along multiple environmental gradients is difficult.

Conclusion

Our multivariate multi-taxa approach allowed investigating different facets of the relationship of body mass community-weighed means with the abiotic environment, plant functional traits, and total plant biomass. Plant functional traits served as proxies for animal resource availability. Strong variation in abiotic conditions and plant functional composition along the slopes of Mount Kilimanjaro facilitated the analysis exemplifying how the environment affected plant composition, total biomass, and animal body mass, including the question whether plant functional traits can predict body mass. In our case, it was temperature, not food availability, which exhibited the strongest influence on animal body mass. Still, temperature - body mass relationships were not always in line with expectations. Plant functional traits associated with food quantity and quality did not significantly predict body mass, although we concede that the traits used did not quantify food sources to the desirable detail. Textural discontinuity represented by total plant biomass had no clear effect on body mass, being related both positively and negatively in different models. However, the causal chain of responses and effects in each structural equation model shows that animal body mass responds to multiple factors and processes, which differ among taxa or guilds.

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Appendices

Appendix S1: Disturbance index calculation
Disturbance is a broad term including many distinct and sometimes habitat-specific alterations in ecosystems (White and Jentsch, 2001). By recording a large range of possible perturbations in our plots, we derived a meaningful classification of the degree of disturbance. Our index was calculated as a composite metric including the effects of biomass removal, input of chemicals and overall landscape structure in the vicinity of the research plots (1500 m radius). Biomass removal has a strong impact on vegetation structure and biodiversity by impeding slow-growing species from reproducing (Lambers et al., 2008). Chemicals strongly alter soil nutrient availability in the case of fertilizers and kill weeds and natural enemies as fungi or insects. A strongly disturbed landscape matrix can influence plants and animals through edge effects (Murcia, 1995). See Kleyer, 1999 for similar composite indices in temperate landscapes. All terms in the summary formula and the sub-formulas were linearly standardized to [0,1].

Summary formula:

$$\text{disturbance} = \text{biomass removal} + \text{input of chemicals} + \text{disturbance of the surrounding landscape matrix}$$

Biomass removal:

$$\text{biomass removal} = \text{current timber harvest} + \text{historic timber harvest} + \text{mowing+grazing} + \text{ploughing} + \text{fire (last 30 yrs)}$$

Input of chemicals:

$$\text{input of chemicals} = \text{pesticide application} + \text{fungicide application} + \text{herbicide application} + \text{fertilizer} + \text{irrigation}$$

Disturbance of the surrounding landscape matrix:

$$\text{disturbance of the surrounding landscape matrix} = \text{overall NDVI difference of research plot vicinity to natural habitat}$$

Appendix S2: Means and ranges of plant functional traits, animal CWMs, bee total intertegular distance (ITD), and moth total body length

Means of variables are given for each ecosystem type with values in parentheses marking minima and maxima, respectively. Bee ITD and moth body length are highly correlated with body mass, and have been referred as such in the text. Variables were scaled prior to analysis. NAs in the bird-dispersed fruits and frugivorous bird body weight CWMs indicate no respective species were found in these ecosystem types.

Ecosystem Type	Fraction Of Insect-Pollinated Plants	Bird-Dispersed Fruits CWM	Leaf Economics Spectrum	Total Plant Biomass [t*ha^{-1}]	Moth Body Length CWM [mm]
Helichrysum shrubland	0.71 (0.52-0.8)	NA NA	-2.1 (-2.3–1.9)	6.34 (1.3-13.5)	17 (17-17)
Erica forest	0.37 (0.14-0.56)	NA NA	-2.2 (-2.4–2)	35.29 (22.2-44.12)	13.8 (8.8-16.5)
Podocarpus forest	0.48 (0.24-0.86)	1047 (402-1923)	-0.8 (-2.3-0.8)	372.33 (364.2-378.7)	15.6 (14.2-17.1)
Disturbed *Podocarpus* forest	0.33 (0.14-0.63)	83 (3-148)	-1.6 (-2.7-0)	166.1 (51.91-259.53)	16.2 (13.8-19)
Ocotea forest	0.66 (0.57-0.78)	403 (182-638)	0.1 (-0.4-0.5)	281.58 (140.6-390.2)	13.1 (11.3-15)
Disturbed *Ocotea* forest	0.77 (0.61-0.9)	228 (94-425)	0.3 (-0.6-0.9)	357.94 (284.7-423.9)	12.2 (8.6-14.2)
Lower montane forest	0.86 (0.56-0.99)	141 (85-275)	-0.1 (-0.3-0.5)	361.04 (162.5-664.3)	14.2 (11.6-15.9)
Homegardens	0.94 (0.88-1)	200 (130-337)	2.6 (0.8-3.9)	93.24 (46.4-134.3)	10.9 (9.6-13.1)
Grasslands	0.2 (0.09-0.27)	7 (0-16)	-0.5 (-1.6-0.4)	3.52 (1.7-7)	11.1 (7.5-14.1)
Coffee plantations	0.97 (0.94-1)	195 (138-289)	3.8 (3.1-4.7)	57.95 (30.25-145)	10.8 (8-13.5)
Savanna	0.37 (0.18-0.67)	29 (7-58)	-1.6 (-2.8–0.5)	10.42 (3.9-15)	10.8 (8.1-14.9)
Maize fields	0.66 (0.48-1)	36 (0-53)	2.1 (1.6-2.4)	16.62 (9.6-24.8)	8 (3.5-11.2)

Ecosystem Type	Bee ITD CWM [mm]	Frugivorous Bird Body Weight CWM [g]	Insectivorous Bird Body Weight CWM [g]	Moth Total Body Length [mm]	Bee Total ITD [cm]
Helichrysum shrubland	1.1 (1.1-1.1)	N/A N/A	20.1 (17.7-21)	3.4 (0-17)	39.8 (2.1-82.3)
Erica forest	1.1 (1.1-1.1)	N/A N/A	17.7 (9.8-32.7)	24.7 (0-82.7)	24.5 (5.1-60.6)
Podocarpus forest	2.4 (2-2.8)	130.2 (45-195)	13.6 (12.9-14.4)	154.5 (34.1-283.3)	2.7 (0-7.5)
Disturbed *Podocarpus* forest	2.1 (1.5-2.9)	253.7 (119.1-400)	13.7 (13-15)	140.5 (67.2-193)	4.9 (0-21.5)
Ocotea forest	1.9 (1.4-2.2)	171 (93.1-278.4)	13.7 (12.4-14.8)	115.1 (11.3-344.8)	1.6 (0-3.8)
Disturbed *Ocotea* forest	2.2 (2.1-2.4)	149.7 (100.2-224.2)	18.1 (15.7-19.6)	306.6 (99.3-701.5)	0.8 (0-1.9)
Lower montane forest	1.9 (1.3-2.3)	141 (93.8-203.2)	17.1 (13.4-22)	347.2 (92.5-616.8)	3.3 (0.8-10.5)
Homegardens	2 (1.3-2.7)	108.5 (21.5-302.1)	22.3 (10.1-52.5)	549.1 (176.9-1045.4)	6 (2.3-11.8)
Grasslands	2 (1.6-2.4)	40.2 (28.4-46)	25.2 (20.2-31.5)	320 (7.5-901.6)	17.8 (5.6-35.8)
Coffee plantations	2.2 (1.8-2.5)	188.7 (42.5-401.7)	22.5 (12.9-32.9)	297.8 (194.4-578.3)	14.2 (3.9-23.4)
Savanna	2 (1.6-2.2)	45.8 (31.5-84.3)	30 (22.2-43.9)	1052.3 (74.6-2951.1)	17 (13.3-23.1)
Maize fields	2.3 (2-2.5)	83.4 (26.8-214.1)	38.7 (15.8-59.4)	333.7 (169.6-677)	14.7 (9.6-23.9)

Chapter 5

Synthesis

5.1 Pieces of the effect-response jigsaw puzzle

Although differing in their objectives and using different methods, the three preceding chapters involved the effect-response framework. The relationship of the abiotic environment and plant traits was a common theme, but each study included additional data highlighting another facet of the interactions within plant communities or between plants and animals.

The second chapter only partly involved the effect-response framework, as the first analysis investigating niche breadths along environmental gradients had a descriptive character without establishing relationships with functional traits. The strong pattern of decreasing niche breadths with habitat age and temperature found provided a link between species optima and breadths. It was assumed that this link is mediated by competition, and α diversity was employed to prove this notion, although with moderate success. Finally, plant functional traits were related to niche optima, and implicitly to niche breadths because of the strong correlation of those niche parameters found before. Figure 5.1A displays the variables and relationships considered. Among the traits explaining species distributions, leaf area, specific leaf area, stem specific density, leaf δ^{13}C, plant life span, and dispersal syndrome were the "best" in that they were related to all environmental factors. Most of these have successfully been employed in previous studies to predict species distributions (Ackerly et al., 2002; Lebrija-Trejos et al., 2010).

The following chapter did not investigate individual species, but community-weighed means (CWMs) along environmental gradients (Figure 5.1B). In conjunction with Chapter 2, this gives the opportunity to compare the use of CWMs to

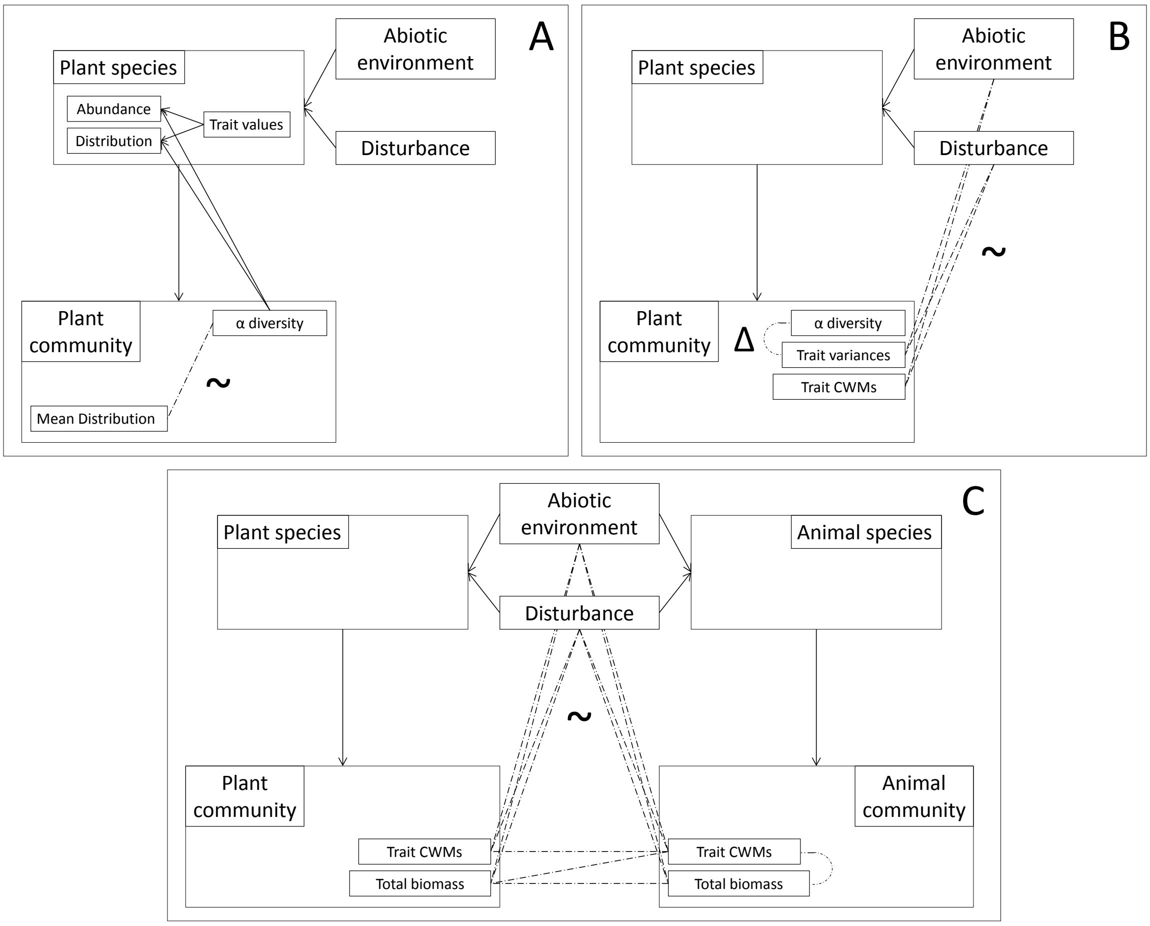

Figure 5.1: **Ecosystem components investigated in the different studies** The tilde represents hypothesized proportionality relationships between variables connected by dash-dotted lines. The Δ indicates that across-community differences in variables, not the variables themselves, were investigated. (A) Chapter 2, (B) Chapter 3, (C) Chapter 4.

trait values of dominant species to establish plant-environment relationships (Grime, 1998). As can be seen below, the results justified this approach. This study not only investigated the influence of the abiotic environment on CWMs, but also on trait variance, which turned out to large at benign conditions and small at harsh ones. The last analysis presented the relationship of differences in species and trait variance between communities to investigate evidence for neutral processes. However, it would also be interesting to explore the link of trait variance and α diversity. How differences in trait expressions among species relate to competition, is strongly debated (Scheffer and van Nes, 2006; Barabás et al., 2013; Laliberté et al., 2013; Kunstler et al., 2016). Given the strong relationship of environmental conditions and FDis and the ambiguous one between niche breadths and α diversity in Chapter 2, it should be explored whether α diversity is a driver of trait variance, or if rather environmental conditions both affect α diversity and trait variance simultaneously, and they are merely correlated.

The last study presented here focused on CWMs of animal species (Fig. 5.1C), and this is a novel approach to describe the complex food web interactions within ecosystems with functional traits. The main hypothesis was that shifts in CWMs of plants provoke shifts in CWMs of animals, a notion supported by the *mass ratio hypothesis* (Grime, 1998) and work specifically addressing animal body mass (Geist, 1987; Huston and Wolverton, 2011). Evidence for this hypothesis was rather low, and one shortcoming of this work is that contrary to Chapter 2, were the responses of individual plant species to the abiotic environment were investigated and can be compared with responses of the community, this was not done for animals. Interactions between species can be of reciprocal or unidirectional advantage or disadvantage, involve different number of interaction partners, the intensities of interactions may vary, and they can be obligatory to any degree for a certain species. Lotka-Volterra-models and their generalization to food webs give an idea of this complexity (Knebel et al., 2013; Schleuning et al., 2015). Especially for groups with many specialist species e.g. moths, it seems reasonable that identifying interaction partners for single species from the plant community would be more fruitful than exploring effects of changes in plant CWMs, as those do not necessarily affect the animals. Taking this into account, it is not surprising that explained variance was lowest in Chapter 4.

Stepping down a trophic level, for plants, evidence from this and previous work demonstrated CWMs to be appropriate measures to describe responses to the abiotic environment (Garnier et al., 2007). However, in some cases, idiosyncratic patterns

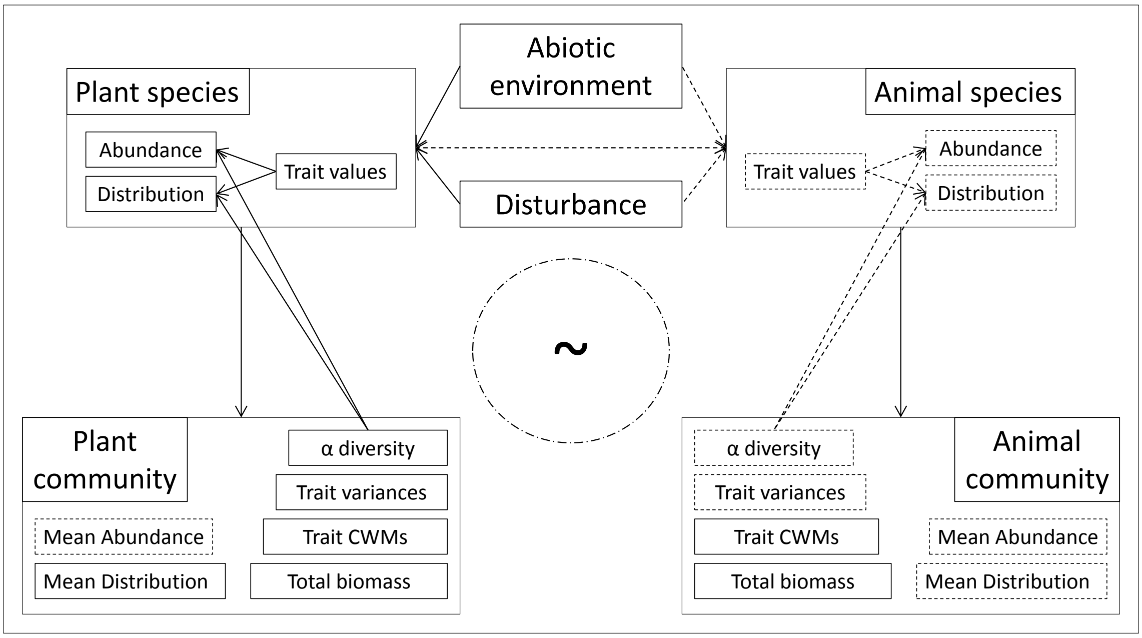

Figure 5.2: **An integrated framework of the ecosystem components investigated**

Solid lines and boxes represent measured relationships and variables, while dashed lines and boxes represent relationships and variables that were implicitly considered, but were not subject of this work. Competition between species is assumed to affect abundances and distributions, indicated by the arrows coming from α diversity. The circle with the tilde symbolizes assumed proportionality in functionally related variables throughout the system. This should allow for predictions concerning changes in one part of the system by knowing those within another. For clarity, within-community proportionality relationships are not drawn.

have been observed in plants, too (Navas, 1998; Chapin and Shaver, 1985), and they are a necessary feature of ecosystems to provide resilience against environmental change (Yachi and Loreau, 1999).

As has been shown, some relationships presented were more complex than initially thought, but other aspects of ecosystem functioning can be predicted by plant functional traits (Díaz et al., 2007). As an example, within the animal groups included in Chapter 4, the bee CWM was related to total plant biomass positively as expected. Thus, integrating the three main chapter into a common framework, this could be used to predict changes in most different components of ecosystems (Fig. 5.2). The knowledge of individual plant species' changes in abundance and distribution could be used to infer plant community changes and in turn predict bee body mass CWMs. Inversely, knowing the distribution of bee species at a particular site should allow for predictions of plant CWMs that narrow the possible number and kind of dominant plant species in nearby communities. This may ultimately work for the other animal groups, if all relevant variables and relationships are identified, allowing for inferences of changes in the whole ecosystem from the knowledge of some of the values of its components only.

5.2 Generality of plant responses to the abiotic environment

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As plant trait - environment relationships appeared in the three main chapters, the results can be compared to test their robustness against moderate changes in the data used and the statistical methods applied. Table 5.1 contrasts the different analyses. The selection of traits and environmental variables was indicated by the research questions, but also due to data availability, as not all data were readily available initially.

In Chapter 4, temperature was not included as predictor of plant traits albeit being correlated to individual traits from local to global scales (Felde et al., 2012; Moles et al., 2014). Plant traits are known to vary with temperature, but there is no common response and summarizing traits with a PCA, which was necessary to reduce variable numbers, canceled out the effects of temperature.

The choice of individual species instead of CWMs in Chapter 2 was a consequence of the species-centered approach used in this study. Another difficulty related to

Table 5.1: **Comparison of the plant trait-environment analyses performed in this work**

Abbreviations: Temp temperature, Prec precipitation, Nut soil nutrients, CWM community-weighed mean, PC first component of principal components analysis

Chapter	Abiotic Environment			Disturbance	Sample Unit		Traits		Method
	Temp	Prec	Nut		Species	CWM	Individual	PC	
2	x	x		x	x		x		Principal components regression
3	x	x	x	x		x	x		Partial least squares regression
4		x		x		x		x	Mixed effect models

Chapter 2 is the switch of response and predictor variables: Traits were used to predict environmental optima. As traits were more in number than environmental variables, relative effects of traits on environmental variables were smaller than the other way round, despite the standardization performed in all studies. Still, the kind of relationships, i.e. coefficient signs, should not be affected.

Table 5.2 presents coefficients of the different analyses for the traits used in the three studies. As expected, the magnitude of coefficients was generally larger when traits where response variables as when they predicted environmental conditions. Still, the majority of the traits with significant coefficients responded equally in the three studies, no matter if single species traits were compared to environmental optima or environmental conditions at sites, or if traits were calculated as CWMs or aggregated into a PCA axis.

The only exception to this pattern was leaf δ^{13}C, which decreased with disturbance analyzing single species in Chapter 2, but increased in CWMs. A reason may be that in Chapter 3, heavily disturbed maize fields with mostly dicotyledonous weeds were contrasted to natural savannas harboring C_4 grasses. In the larger dataset of Chapter 2, other less disturbed habitats were included, and C_4 metabolism may not show a linear response along this detailed gradient. This reminds that although the reliance on analyses detecting linear relationships throughout this study is a good starting point, contradictory or weak results should be tested for non-linear patterns in the future.

In summary, although there was quantitative variation in coefficients, this was expected given the different datasets and methods (Kleyer et al., 2012). The concordance between the studies underlines the strong relationship of the abiotic environment and functional traits.

Table 5.2: **Coefficients of trait-environment relationships from the different analyses of this work**

In Chapter 4, traits were summarized in a PCA, thus only the signs of relationships for the traits that contributed are given. Conforming significant coefficients from all studies are printed in bold. Except for leaf δ^{13}C, which showed a contradictory response, relationships for other traits lacked statistical power in one of the studies. Abbreviations: Temp temperature, Prec precipitation, Dist disturbance, Nut soil nutrients, PC first component of principal components analysis.

Predictor	Temperature		Precipitation			Disturbance		
	Individual Optima (Chap. 2)	CWM (Chap. 3)	Individual Optima (Chap. 2)	CWM (Chap. 3)	CWM (Chap. 4)	Individual Optima (Chap. 2)	CWM (Chap. 3)	CWM (Chap. 4)
Leaf area	**0.12** (±0.09)	**0.92** (±0.11)	**0.14** (±0.04)	**0.78** (±0.09)		**-0.05** (±0.03)	**-0.27** (±0.12)	
Canopy height	0.01 (±0.06)	0.39 (±0.14)	**0.07** (±0.04)	**0.67** (±0.09)		**-0.11** (±0.02)	**-0.57** (±0.12)	
SLA	**0.06** (±0.05)	**0.15** (±0.12)	**0.05** (±0.04)	**0.27** (±0.09)	**+**	**0.08** (±0.03)	**0.8** (±0.16)	**+**
LDMC	-0.01 (±0.06)	0.06 (±0.15)	**-0.14** (±0.05)	**-0.68** (±0.11)	**−**	-0.02 (±0.03)	-0.61 (±0.17)	−
SSD	-0.06 (±0.04)	-0.07 (±0.12)	**-0.07** (±0.04)	**-0.48** (±0.09)	**−**	**-0.08** (±0.04)	**-0.87** (±0.16)	**−**
Leaf C_{mass}	**-0.15** (±0.05)	**-0.58** (±0.16)	0.02 (±0.03)	0.1 (±0.11)		**-0.09** (±0.04)	**-0.22** (±0.11)	
Leaf N_{mass}	0.01 (±0.03)	-0.11 (±0.14)	**0.17** (±0.05)	**0.74** (±0.1)	**+**	0.02 (±0.03)	0.71 (±0.17)	+
Leaf P_{mass}	0.11 (±0.05)	0.02 (±0.15)	0.04 (±0.04)	0.11 (±0.1)	+	**0.08** (±0.04)	**0.51** (±0.17)	**+**
Relative seed number	-0.12 (±0.13)	-1.19 (±0.17)	0.04 (±0.06)	-0.19 (±0.12)		0.05 (±0.06)	0.82 (±0.11)	
Seed crop frequency	0.04 (±0.18)	-0.07 (±0.12)	**0.08** (±0.05)	**0.39** (±0.12)		0.07 (±0.07)	0.84 (±0.16)	
Leaf pubescence	**-0.23** (±0.15)	**-0.99** (±0.16)	-0.01 (±0.07)	-0.75 (±0.09)		-0.01 (±0.03)	0.18 (±0.1)	
Spinescence	0.1 (±0.14)	0.4 (±0.27)	0.01 (±0.05)	-0.1 (±0.18)		0.01 (±0.09)	-0.64 (±0.23)	
Leaf δ^{13}C	**0.18** (±0.09)	**0.68** (±0.2)	**-0.14** (±0.06)	**-0.55** (±0.14)		0.08 (±0.05)	-0.25 (±0.22)	

5.3 The metabolic theory of ecology

In the present work metabolic theory of ecology (MTE) was used as a baseline hypothesis to explain patterns of species distributions and aspects of ecosystem functioning. Predictions of MTE are built on the assumption of the universal scaling of metabolic rate (B), body mass (M), and temperature (T), expressed in the equation $B = b_0 M^{3/4} e^{-E/kT}$, where b_0, E, and k are constants. It has implications for individual animals up to whole ecosystems (Sibly et al., 2012). This work highlighted two of them: The hypothesis of faster speciation at higher temperatures mediated by faster chemical reactions, and the re-formulation of Bergmann's rule on the efficiency of body temperature regulation.

A corollary of the faster-speciation hypothesis is the equivalence of temperature and time for evolutionary processes: Higher temperatures speed the evolutionary clock, but waiting for long in a cold ecosystem will have the same effect in terms of species richness assuming extinction rates are low compared to speciation rates. Figure 5.3 shows increases in diversity for five ecosystems with equal initial species richness but different mean temperatures, assuming no extinction and density-dependent extinction rates, respectively.

MTE was supported by the niche breadth distributions along the environmental gradients seen in Chapter 2. This conclusion was challenged by the pattern of community species richness and niche breadth, the second analysis of this study. Some possible explanations to reconcile these patterns were already given. A point related to the combination of ideas from MTE and the effect-response framework, recently called the *trait driver theory* (Enquist et al., 2015), was discussed in two recent articles by Harmon and Harrison (2015) and Rabosky and Hurlbert (2015). They question whether ecosystems ever reach a dynamic equilibrium, or if speciation and extinction events always lag behind changes in abiotic conditions. If the latter was true, this would imply that species richness in ecosystems constantly increases as assumed by MTE, but before reaching carrying capacity, changes in abiotic conditions result in local mass extinctions, as species no longer pass the environmental filter. Then, species richness increases again due to colonizing species or speciation events. While competition increases with species richness, niche breadth shrinkage may lag behind colonization events and ecosystems would have an extinction depth (Tilman et al., 1994). Although this seems plausible, testing this hypothesis requires detailed data on historic environmental conditions and assumptions on extinction depth, which seems difficult to achieve.

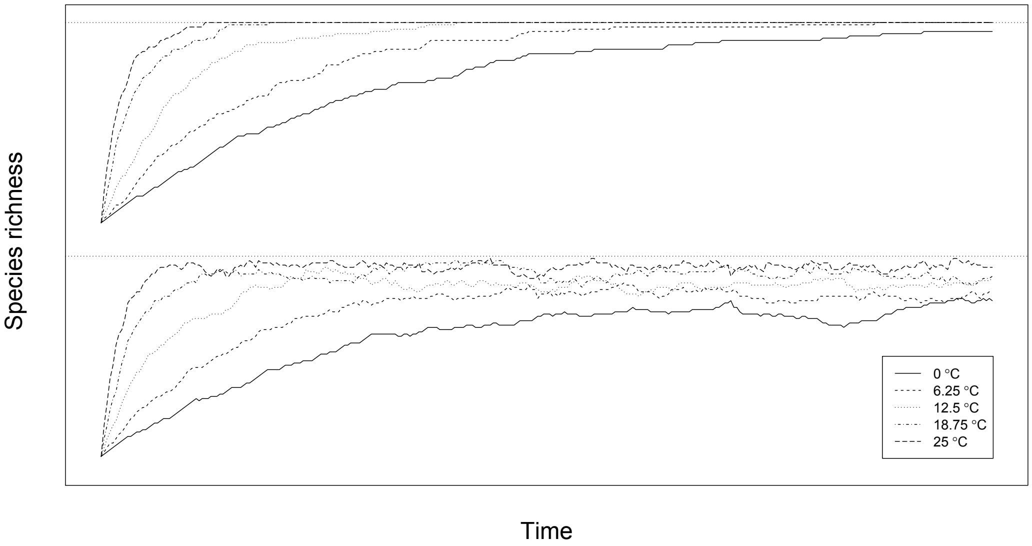

Figure 5.3: **Increases in species richness with time at different temperatures following the metabolic theory of ecology (MTE)**
The upper panel shows species richness over time for five communities with equal initial species richness but differing in mean temperature assuming no extinction takes place. After sufficient time, all communities reach carrying capacity with warmer ecosystems arriving first. The lower panel shows the same five communities, but extinction occurs and its probability increases with total species richness according to $P(extinction) = 0.01^{\frac{carrying\ capacity}{species\ richness}}$. Extinction probability is assumed to depend on the average area occupied per species. A *minimum area* is defined as the area occupied on average by each species at carrying capacity. Each minimum area becomes deserted with a probability of 0.01. At carrying capacity, each species thus has an extinction probability of 0.01. At species richness equaling half the carrying capacity, each species would occupy two minimum areas on average and extinction probability would be 0.01^2. As speciation rate increases with temperature, at colder temperatures, extinction rate levels out speciation rate at lower species numbers resulting in permanently lower species richness in cold ecosystems.

The second application of MTE focused on animal body mass. Interestingly, both the prediction of large body mass at low temperatures and of large body mass at high resource availability have their foundation in MTE. Large animals require more resources to maintain metabolism than small ones. Dividing metabolic rate by body mass, specific metabolic rate (B_S) is obtained: $B_S = B/M = b_0 M^{-1/4} e^{-E/kT}$. The proportionality $B_S \sim M^{-1/4}$ shows that on a mass basis, the pattern turns, larger animals needing less resources, thus being more efficient than smaller ones. This efficiency may allow survival at cold conditions, because proportionally, more energy is available for heat dissipation (Bergmann, 1848). It may also be advantageous where resource supply is high, because surplus energy compared to smaller, less efficient animals could be used for reproduction (Huston and Wolverton, 2011). Still, Chapter 4 did not investigate intraspecific differences in body mass or those of closely related species, but the community-weighed means (CWMs) of whole taxonomic groups or feeding guilds. As these were expected to shift according to food supply, not only canonical changes in individual body masses of many animal taxa were expected, but also constancy of abundance relationships, which may not hold (Anderson-Teixeira et al., 2012). Figure 5.4 illustrates possible relationships between body mass CWMs and resources, depending on whether increases in body mass with increasing resources are followed by changes or constancy in abundance relationships between species. Only if constancy occurs, the expected linear increase of body mass CWMs with resources may be observed. The same is valid for the other two predictors of body mass tested: temperature and structural complexity.

Consequently, the lack of significance found in some relationships of body mass and its predictors and some counter-intuitive results as the decrease of body mass with elevation for insectivorous birds could be due to variability in abundance relationships. Fortunately, this can be tested in the future, as animal abundances were recorded and used to calculate CWMs.

Still, even controlling for abundance, it remains questionable if the spatial and temporal sampling scales of this work were appropriate to address the animal groups considered. Birds and insects are highly motile, and the plots at which they were observed may be poor samples of their actual feeding grounds, thus actual food resources may differ considerably from the observed ones, especially in heterogeneous habitats with human land use. Additionally, even if temperature and food resources are the strongest drivers of body mass, dispersal and evolution may not be “fast” enough to guarantee all ecosystems harbor animal communities optimally adapted to environmental conditions, similarly to the difficulty encountered in the

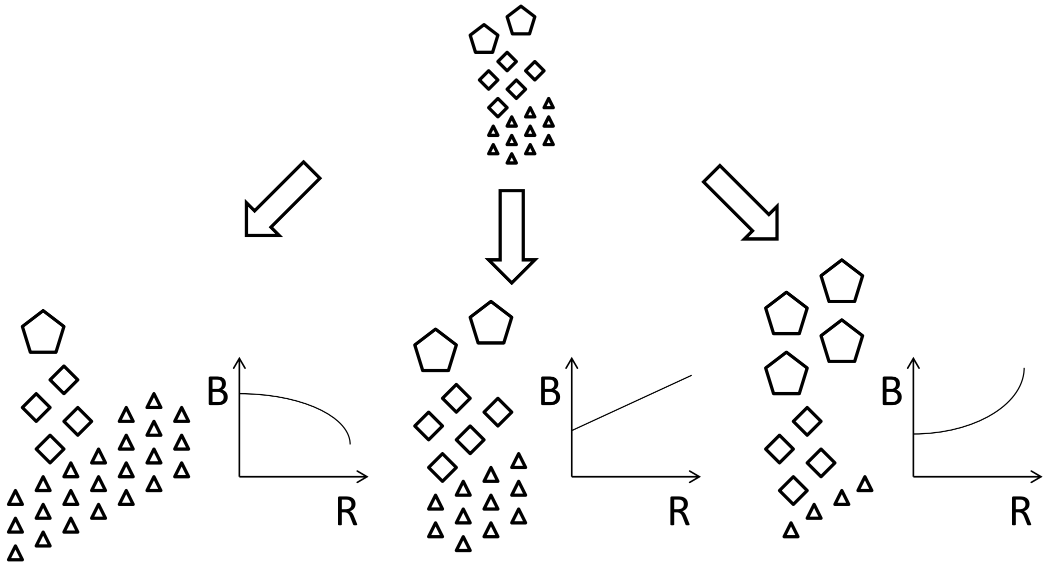

Figure 5.4: **Hypothetical changes in body mass community-weighed means (B) with increases in resource availability (R)**
The figure shows three scenarios of increases of individual species' body masses with resources, but different changes in abundances. Left: Large species decrease in abundance, while small species increase. Thus, B decreases nonlinearly with R. Middle: Abundances remain constant. B increases linearly with R as expected. Right: Large species become more abundant, while smaller species decrease in numbers. The relationship of B and R is positive, but increases are stronger than linear.

niche breadth-diversity relationship of Chapter 2. Body mass distributions could lag behind environmental changes because of lost habitat connectivity blocking dispersal corridors or the lack of adapted species in regional species pools. Nevertheless, data available from similar studies in other regions, and intensified sampling from phase 2 of the KiLi project may shed light on some of these uncertainties, supporting MTE and further advancing its concepts.

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Chapter 6

Outlook

This last chapter presents some ideas and ongoing research started at the time of writing this work. It addresses some of the issues raised in the synthesis chapter, but the traits gathered and the data collected within the whole KiLi project certainly offer more possibilities.

6.1 Hard traits, soft traits, and growth performance

Plant functional traits are often proxies of the actual traits linked both to responses to the environment and effects on ecosystem functioning and services. This is because the actual traits determining those responses or effects are often hard to measure. Examples include the use of SLA or leaf N_{mass} to describe carbon assimilation (Reich et al., 1997), or the deployment of the fractions of insect-pollinated or fruit-producing plants in Chapter 5. Traits used as proxies for other traits have been called *soft traits*, while those related directly to plant performance were termed *hard traits* (Díaz et al., 2004). Some soft traits are tightly linked to hard traits, but for others, the relationship is rather weak (Wright et al., 2005). Special consideration has been given to traits describing plant growth. Plant growth is linked to carbon fixation, which is an important variable to quantify climate change-driven alterations of the carbon cycle (Enquist et al., 2007). It has been shown that soft traits as SLA and leaf N_{mass} perform considerably well in approximating leaf photosynthesis and primary production (Reich et al., 1997). Nevertheless, changes in atmospheric CO_2 levels, temperature, and precipitation may interfere in the functioning of carbon assimilation. As not all species will be able to migrate following their climatic niche under changing environmental conditions (Thomas et al., 2004), this may affect the carbon fixation of entire landscapes. While the influence of CO_2 on the latter have been intensively studied (Poorter and Navas, 2003), less is known about the effects of changes in temperature and precipitation. Soft traits, especially their intraspecific variability, may relate to changes in growth performance with increasing temperatures and decreasing precipitation as expected in many climate change scenarios for African ecosystems (Sides et al., 2014). Net primary production of herbaceous species *in situ* and under elevated temperatures have been measured in the KiLi project, and the respective soft traits of those species collected. Herbaceous species were selected from a wide range of ecosystem types. The results obtained will translate to other regions and allow for better predictions of changes in plant growth and changes in the carbon cycle with climate change.

6.2 Epiphyte distribution and trait space

Epiphytes are a conspicuous characteristic of tropical forest ecosystems. They occur outside the tropics, but in lower species numbers, and their contribution to total biomass is less in general, although exceptions occur (Zotz, 2005). The reasons for this pattern are not completely understood, but temperature and humidity play key roles in limiting distributions of many taxa. Mount Kilimanjaro is an excellent model system for the study of these factors in controlling epiphyte distributions because at high elevations, cold temperature limits plant life in general, while towards the lowlands, precipitation decreases and becomes highly seasonal. The distribution of terrestrial and epiphytic plants can be compared to the trait expressions occurring within these groups. Epiphytes have no access to soil nutrients and water, which makes them physiologically more dependent on rainfall (Benzing, 2008). Owing to the different life strategies, differences in trait space involving traits related to water conservation, nutrient retention, or nutrient use efficiency should be observed. Trait space is understood as the hypervolume defined by the most extreme trait values of epiphytic and terrestrial taxa as a whole. Traits and abundance data on all vascular epiphyte species were collected along the elevation gradient at Mount Kilimanjaro, selecting individuals from the widest spectrum of plot elevations and tree heights to account not only for intraspecific variability along the elevation, precipitation, and disturbance gradients, but also for microhabitat differences within single host trees (Petter et al., 2015). The data will be compared to the abiotic environment and traits of co-occurring terrestrial plants to investigate the life strategy-dependency of environmental filtering.

6.3 Functional food webs

Functional data of plants and other life forms allows for inferences on competitive interactions, prey spectra, and predators, among others (McGill et al., 2006). Thus, a mechanistic understanding of ecosystem properties and processes across trophic levels could be achieved combining data on functional traits (Schmitz et al., 2004). These functional data are available for several animal groups, e.g. birds, bees, and ants, and are still collected in the KiLi project. Still, traits determining the interactions related to fluxes of energy and matter across trophic levels, i.e. growth traits, palatability traits, feeding traits, and decomposition traits were already gathered to a large extent and promise fostering our understanding of food web functioning and its implications for ecosystem services.

6.4 Predicting ecosystem functioning and services

Plant functional trait research has been confident in explaining ecosystems mechanistically with the use of traits (Lavorel and Garnier, 2002; McGill et al., 2006). Nevertheless, the complexity of species interactions across trophic levels and the choice of the "right" traits to predict ecosystem functioning and services has proven this work to be more tedious than initially expected (Lavorel et al., 2007; Lavorel, 2013). Following the deterministic concept forming the basis for the investigation of trait-environment relationships, it should be possible to explain ecosystem functioning and services considering sufficient traits and feedback mechanisms. The continuing large number of publications (1130 on Google Scholar including "ecosystem services" in their titles in 2015, queried 26/12/2015) and the introduction of a journal dedicated entirely to ecosystem services in 2012 (Braat, 2012) shows major efforts are undertaken to fill gaps of scientific knowledge in this field.

Not all approaches dealing with ecosystem services involve plant functional traits, and only a part of ecosystem functioning belongs to ecosystem services (Díaz et al., 2005; Naeem et al., 1999). Díaz et al. (2005) classified ecosystem services into four groups: Provisioning services, cultural services, supporting services, and regulating services. Provisioning services describe the capacity of ecosystem to provide resources in a sustainable way. Cultural services provide spiritual and recreational opportunities. Supporting services comprise primary production, habitat provision for animals, and element cycling. This includes the production of oxygen as well as the provision of fresh water collected in streams and lakes. Finally, regulating services relate to the capacity of ecosystems to provide pollinators, clean polluted water, suppress erosion, resist invasions of alien species, regulate climate, and control diseases.

Provisioning services related to plant functional traits have intensively been investigated in recent years (Lavorel, 2013; Laliberté and Tylianakis, 2011; Cadotte et al., 2011). Still, many evaluations are based on indirect measurements, or do not prove links between ecosystem components used as predictors and services (Seppelt et al., 2011). Additionally, the interdisciplinary approach needed to transfer knowledge into socio-economic contexts is often missing (Carpenter et al., 2009).

At Mount Kilimanjaro, first steps to quantify ecosystem services have been made. These include the collection of more exact data on fruit production and herbivory. Additionally, the benefits of forest products for the local population have been assessed. This could be extended to natural savanna ecosystems in the lowlands. In parallel, quantitative information on stakeholders' harvests in agricultural areas should be gathered. National park authorities could provide information on the financial benefits drawn from recreational tourism.

This data will allow for linking ecosystem processes to financial benefits, which is an issue of high importance considering the economic situation of rural populations in many tropical countries (Ingram et al., 2014).

6.5 Carbon fixation and storage

In the classification of Díaz et al. (2005), carbon stocks and balances belong to the provisioning services of ecosystems. Much attention has been given to biomass estimates recently, because in the light of global change carbon fixation and biomass estimation of forest ecosystems are urgently needed (Houghton, 2005). The KiLi project has already started adapting existing forest models for lower montane forest at Mount Kilimanjaro (Fischer et al., 2015). Recently, vegetation surveys for all major forest types at the mountain have been concluded, allowing for the parametrization of respective models with the help of plant functional traits. Those have been collected for all tree species at the mountain. Carbon storage can be estimated using data from vegetation surveys combined with wood densities, while carbon fixation will be estimated using correlations of growth rate and specific leaf area or leaf N_{mass}. Using satellite imagery to identify current ranges of forest types, this will allow for the quantification of carbon stocks at Mount Kilimanjaro.

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Appendix A Ecosystem types

Helichrysum shrubland (HEL)

Erica forest (FER)

Disturbed *Podocarpus* forest (FPD)

Podocarpus forest (FPO)

Ocotea forest (FOC)

Disturbed *Ocotea* forest (FOD)

Lower montane forest (FLM)

Grassland (GRA)

Homegarden (HOM)

Coffee plantation (COF)

Savanna (SAV)

Maize field (MAI)

Appendix B Plant species list

Species are ordered by their occurrences within ecosystem types from high to low elevation. Species with underscores in their names have not been identified to genus or species level, respectively. Author names refer to family or genus authors in these cases. Scientific names are according to Tropicos.org (2015). Missouri Botanical Garden

Species	Family	Author	HEL	FER	FPD	FPO	FOC	FOD	FLM	GRA	HOM	COF	SAV	MAI
Erica rossii	Ericaceae	Dorr	x	x	x	x								
Helichrysum forskahlii	Asteraceae	(J.F. Gmel.) Hilliard & B.L. Burtt	x	x	x					x				
Agrostis kilimandscharica	Poaceae	Mez	x	x	x									
Alchemilla argyrophylla	Rosaceae	Oliv.	x	x										
Alchemilla johnstonii	Rosaceae	Oliv.	x	x										
Dendrosenecio kilimanjari	Asteraceae	(Mildbr.) E.B. Knox	x	x										
Euryops dacrydioides	Asteraceae	Oliv.	x	x										
Festuca abyssinica	Poaceae	Hochst. ex A. Rich.	x	x										
HEL1_Sporobolus1	Poaceae	R. Br.	x	x										
Helichrysum citrispinum	Asteraceae	Delile	x	x										
Helichrysum newii	Asteraceae	Oliv. & Hiern	x	x										
Pentaschistis borussica	Poaceae	(K. Schum.) Pilg.	x	x										
Geranium kilimandscharicum	Geraniaceae	Engl.	x		x									
Poa leptoclada	Poaceae	Hochst. ex A. Rich.	x											
Deschampsia cespitosa	Poaceae	(L.) P. Beauv.		x										
Poa schimperiana	Poaceae	Hochst. ex A. Rich.		x										
Asplenium friesiorum	Aspleniaceae	C. Chr.			x	x	x	x	x					
Cyperus derreilema	Cyperaceae	Steud.			x	x	x	x	x					
Embelia schimperi	Primulaceae	Vatke			x	x	x	x	x					
Peperomia fernandopoiana	Piperaceae	C. DC.			x	x	x	x	x					
Rubus steudneri	Rosaceae	Schweinf.			x	x	x	x	x					
Schefflera volkensii	Araliaceae	(Harms) Harms			x	x	x	x	x					
Mimulopsis kilimandscharica	Acanthaceae	Lindau			x	x	x	x						
Plectranthus sylvestris	Lamiaceae	Grke			x	x	x	x						
Podocarpus latifolius	Podocarpaceae	(Thunb.) R. Br. ex Mirb.			x	x	x	x						
Alchemilla volkensii	Rosaceae	Engl.			x	x								
Parochetus communis	Fabaceae	Buch.-Ham. ex D. Don			x	x								
Pycnostachys meyeri	Lamiaceae	Grke			x	x								
Myrica salicifolia	Myricaceae	Hochst. ex A. Rich.			x				x	x				
Agauria salicifolia	Ericaceae	(Comm. ex Lam.) Hook. f. ex Oliv.			x				x					
Helichrysum odoratissimum	Asteraceae	(L.) Sweet			x					x				
Festuca obturbans	Poaceae	St.-Yves			x									
FPD5_Helichrysum1	Asteraceae	Mill.			x									
Hypericum revolutum	Hypericaceae	Vahl			x									
Lycopodium clavatum	Lycopodiaceae	L.			x									
Myrsine africana	Primulaceae	L.			x									
Senecio maranguensis	Asteraceae	O. Hoffm.			x									
Ilex mitis	Aquifoliaceae	(L.) Radlk.				x	x	x	x					
Pilea usambarensis	Urticaceae	Engl.				x	x	x	x					
Xymalos monospora	Monimiaceae	(Harv.) Baill. ex Warb.				x	x	x	x					
Maytenus acuminata	Celastraceae	(L. f.) Loes.				x	x	x						
Psychotria cyathicalyx	Rubiaceae	E.M.A. Petit				x	x	x						
Selaginella kraussiana	Selaginellaceae	(Kunze) A. Braun				x		x	x		x			

Species	Family	Author	HEL	FER	FPD	FPO	FOC	FOD	FLM	GRA	HOM	COF	SAV	MAI
Oreosyce africana	Cucurbitaceae	Hook. f.				x		x			x	x		
Clausena anisata	Rutaceae	(Willd.) Hook. f. ex Benth.				x		x						
Begonia meyeri-johannis	Begoniaceae	Engl.					x	x	x					
Dracaena afromontana	Asparagaceae	Mildbr.					x	x	x					
Galiniera saxifraga	Rubiaceae	(Hochst.) Bridson					x	x	x					
Isachne mauritiana	Poaceae	Kunth					x	x	x					
Lasianthus kilimandscharicus	Rubiaceae	K. Schum.					x	x	x					
Macaranga kilimandscharica	Euphorbiaceae	Pax					x	x	x					
Ocotea usambarensis	Lauraceae	Engl.					x	x	x					
Piper capense	Piperaceae	L. f.					x	x	x					
Schefflera myriantha	Araliaceae	(Baker) Drake					x	x	x					
Cyathea manniana	Cyatheaceae	Hook.					x	x						
Isoglossa laxa	Acanthaceae	Oliv.					x	x						
Psychotria fractinervata	Rubiaceae	E.M.A. Petit					x	x						
Psychotria petiginosa	Rubiaceae	Brenan					x	x						
Pauridiantha paucinervis	Rubiaceae	(Hiern) Bremek.					x		x					
Allophylus ferrugineus	Sapindaceae	Taub.						x	x					
Plectranthus alboviolaceus	Lamiaceae	Grke						x	x					
Tabernaemontana stapfiana	Apocynaceae	Britten						x	x					
Dracaena fragrans	Asparagaceae	(L.) Ker Gawl.							x		x			
Culcasia falcifolia	Araceae	Engl.							x					
Entandrophragma excelsum	Meliaceae	Sprague							x					
Ficus sur	Moraceae	Forssk.							x					
Garcinia tanzaniensis	Clusiaceae	Verdc.							x					
Heinsenia diervilleoides	Rubiaceae	K. Schum.							x					
Leptonychia usambarensis	Malvaceae	K. Schum.							x					
Olinia rochetiana	Penaeaceae	A. Juss.							x					
Plectranthus autranii	Lamiaceae	(Briq.) A.J. Paton							x					
Strombosia scheffleri	Olacaceae	Engl.							x					
Syzygium guineense	Myrtaceae	(Willd.) DC.							x					
Ageratum conyzoides	Asteraceae	L.								x	x	x		x
Conyza bonariensis	Asteraceae	(L.) Cronquist								x	x	x		
Grevillea robusta	Proteaceae	A. Cunn. ex R. Br.								x	x	x		
Croton megalocarpus	Euphorbiaceae	Hutch.								x	x			
Justicia flava	Acanthaceae	Kurz								x	x			
Emilia discifolia	Asteraceae	(Oliv.) C. Jeffrey								x		x	x	x
Euphorbia hirta	Euphorbiaceae	L.								x		x	x	x
Tridax procumbens	Asteraceae	L.								x		x	x	x
Richardia scabra	Rubiaceae	L.								x		x		x
Centella asiatica	Apiaceae	(L.) Urb.								x		x		
Aristida adoensis	Poaceae	Hochst.								x			x	x
Rhynchelytrum repens	Poaceae	(Willd.) C.E. Hubb.								x			x	x
Acacia hockii	Fabaceae	De Wild.								x			x	
Annona senegalensis	Annonaceae	Pers.								x			x	
Dodonaea viscosa	Sapindaceae	Jacq.								x			x	
Heteropogon contortus	Poaceae	(L.) P. Beauv. ex Roem. & Schult.								x			x	
Hyparrhenia hirta	Poaceae	(L.) Stapf								x			x	
Maytenus senegalensis	Celastraceae	(Lam.) Exell								x			x	
Microglossa pyrrhopappa	Asteraceae	(Sch. Bip. ex A. Rich.) Agnew								x			x	
Sehima nervosum	Poaceae	(Rottler ex Roem. & Schult.) Stapf								x			x	
Trichodesma zeylanicum	Boraginaceae	(Burm. f.) R. Br.								x				x
Bulbostylis densa	Cyperaceae	(Wall.) Hand.-Mazz.								x				
Conyza subscaposa	Asteraceae	O. Hoffm.								x				
Dichrostachys cinerea	Fabaceae	(L.) Wight & Arn.								x				
Elionurus muticus	Poaceae	(Spreng.) Kuntze								x				
Eragrostis racemosa	Poaceae	(Thunb.) Steud.								x				
GRA1_Poaceae1	Poaceae	Barnhart								x				
GRA1_Poaceae4	Poaceae	Barnhart								x				
GRA2_Poaceae2	Poaceae	Barnhart								x				
GRA3_Hyparrhenia1	Poaceae	Andersson ex E. Fourn.								x				
GRA4_Poaceae2	Poaceae	Barnhart								x				
GRA5_Poaceae3	Poaceae	Barnhart								x				
Hyparrhenia rufa	Poaceae	(Nees) Stapf								x				

Species	Family	Author	HEL	FER	FPD	FPO	FOC	FOD	FLM	GRA	HOM	COF	SAV	MAI
Oldenlandia herbacea	Rubiaceae	(L.) Roxb.								x				
Rhamnus prinoides	Rhamnaceae	L'Hér.								x				
Rourea thomsonii	Connaraceae	(Baker) Jongkind								x				
Satureja abyssinica	Lamiaceae	(Benth.) Briq.								x				
Setaria sphacelata	Poaceae	(Schumach.) Stapf & C.E. Hubb. ex M.B. Moss								x				
Eragrostis tenuifolia	Poaceae	(A. Rich.) Hochst. ex Steud.								x				
Bidens pilosa	Asteraceae	L.									x	x		x
Galinsoga parviflora	Asteraceae	Cav.									x	x		x
Albizia schimperiana	Fabaceae	Oliv.									x	x		
Coffea arabica	Rubiaceae	L.									x	x		
Colocasia esculenta	Araceae	(L.) Schott									x	x		
Crassula alsinoides	Crassulaceae	(Hook. f.) Engl.									x	x		
Drymaria cordata	Caryophyllaceae	(L.) Willd. ex Schult.									x	x		
Galinsoga quadriradiata	Asteraceae	Ruiz & Pav.									x	x		
HOM1_Poaceae2	Poaceae	Barnhart									x	x		
Musa sp.	Musaceae	L.									x	x		
Oxalis corniculata	Oxalidaceae	L.									x	x		
Cordia africana	Boraginaceae	Lam.									x			
HOM3_Cucurbitaceae1	Cucurbitaceae	Juss.									x			
Milicia excelsa	Moraceae	(Welw.) C.C. Berg									x			
Persea americana	Lauraceae	Mill.									x			
Pseudechinolaena polystachya	Poaceae	(Kunth) Stapf									x			
Trichilia emetica	Meliaceae	Vahl									x			
Argemone mexicana	Papaveraceae	L.										x		x
Boerhavia erecta	Nyctaginaceae	L.										x		x
Euphorbia heterophylla	Euphorbiaceae	L.										x		x
Malvastrum coromandelianum	Malvaceae	(L.) Garcke										x		x
Albizia chinensis	Fabaceae	(Osbeck) Merr.										x		
COF2_Cyperaceae1	Cyperaceae	Juss.										x		
COF4_Poaceae1	Poaceae	Barnhart										x		
COF5_Poaceae2	Poaceae	Barnhart										x		
Galium aparinoides	Rubiaceae	Forssk.										x		
Stellaria media	Caryophyllaceae	(L.) Vill.										x		
Melhania velutina	Malvaceae	Forssk.											x	x
Ocimum americanum	Lamiaceae	L.											x	x
Sida acuta	Malvaceae	Burm. f.											x	x
Acacia nilotica	Fabaceae	(L.) Willd. ex Delile											x	
Balanites aegyptiacus	Zygophyllaceae	(L.) Delile											x	
Bothriochloa insculpta	Poaceae	(Hochst. ex A. Rich.) A. Camus											x	
Bridelia cathartica	Phyllanthaceae	G. Bertol.											x	
Cenchrus ciliaris	Poaceae	L.											x	
Combretum molle	Combretaceae	R. Br. ex G. Don											x	
Combretum mossambicense	Combretaceae	Engl.											x	
Dombeya rotundifolia	Malvaceae	(Hochst.) Planch.											x	
Eragrostis superba	Poaceae	Peyr.											x	
Kohautia caespitosa	Rubiaceae	Schnizl.											x	
Lantana camara	Verbenaceae	L.											x	
Oldenlandia wiedemannii	Rubiaceae	K. Schum.											x	
Ozoroa insignis	Anacardiaceae	Delile											x	
Rhus natalensis	Anacardiaceae	Bernh.											x	
SAV1_Combretum1	Combretaceae	Loefl.											x	
SAV2_Commiphora1	Burseraceae	Jacq.											x	
SAV5_Poaceae5	Poaceae	Barnhart											x	
Terminalia kilimandscharica	Combretaceae	Engl.											x	
Ximenia caffra	Ximeniaceae	Sond.											x	
Brachiaria deflexa	Poaceae	(Schumach.) C.E. Hubb. ex Robyns												x
Cassia siamea	Fabaceae	Lam.												x
Hyptis suaveolens	Lamiaceae	(L.) Poit.												x
MAI1_Commelina1	Commelinaceae	L.												x
MAI3_Leucas1	Lamiaceae	R. Br.												x
Momordica foetida	Cucurbitaceae	Schumach.												x
Moringa oleifera	Moringaceae	Lam.												x
Zea mays	Poaceae	L.												x

Appendix C Plant functional traits list

Traits are ordered by sample unit and the parts of the plant they were sampled from. Stars indicate traits for which measurements were taken with and without petioles, respectively.

Trait	Unit	Sample Unit	Description
Corolla color		Species	Color of flower petals, if existent
Calyx color		Species	Color of flower sepals, if existent
Color of additional attracting plant parts		Species	E.g. showy bracts
Diaspore color		Species	Color of fleshy or dry fruit or spore
Diaspore type		Species	Type of dispersal unit
Hooked structures		Species	Presence of hooks on dispersal unit
Dispersal syndrome		Species	Type of transport of dispersal unit
Seed structure category		Species	Type of seed wall
Seed crop frequency		Species	Number of seed production events per year
Leaf pubescence		Species	Density of leaf hairs
Growth form		Species	Annual herb, perennial herb, liana, shrub, or tree
Perennial		Species	Plant lifespan, annual or perennial
Leaf distribution along stem		Species	Regularly or concentrated on upper or lower shoot ends
Branching		Species	Presence of branches
Shoot growth form		Species	Horizontal, ascending, or vertical
Liana		Species	Liana or self-supporting
Woodiness		Species	Presence of woody tissue
Spinescence		Species	Length and density of spines
Clonal growth organs		Species	Presence of clonal growth organs

Trait	Unit	Sample Unit	Description
Leaf area*	cm^2	Individual	One-sided leaf area
Specific leaf area*	mm^2*mg^{-1}	Individual	Leaf area per g leaf dry weight
Dry leaf mass*	mg	Individual	Leaf mass after drying 60 h at 72 °C
Fresh leaf mass*	mg	Individual	Leaf mass on vital plant
Leaf dry matter content*		Individual	Dry leaf mass/fresh leaf mass
Leaf C_{mass}	$mg*g^{-1}$	Individual	Leaf carbon content per g dry tissue
Leaf N_{mass}	$mg*g^{-1}$	Individual	Leaf nitrogen content per g dry tissue
Leaf P_{mass}	$mg*g^{-1}$	Individual	Leaf phosphorus content per g dry tissue
Leaf $\delta^{13}C$		Individual	Ratio of carbon isotopes relative to a standard
Leaf $\delta^{15}N$		Individual	Ratio of nitrogen isotopes relative to a standard
Stem dry matter content		Individual	Fresh stem mass/dry stem mass
Stem specific density	$g*cm^{-3}$	Individual	Dry stem mass/fresh stem volume
Canopy height	cm	Individual	Height of highest leaves
Seed releasing height	cm	Individual	Height of highest fruits or flowers
Seed number		Individual	Total plant seed number
Seed mass	mg	Individual	
Total dry green leaf mass	mg	Individual	Green leaves after drying 60 h at 72 °C
Total dry dead leaf mass	mg	Individual	Dead leaves still at plant after drying 60 h at 72 °C
Total dry stem mass	mg	Individual	All above-ground plant organs that are no leaves or belong to reproductive mass
Total dry reproductive mass	mg	Individual	Fruits with fructescences after drying 60 h at 72 °C
Total dry below-ground mass	mg	Individual	Roots and storage organs after drying 60 h at 72 °C

Appendix D *Curriculum vitae*

Personal information

Name	David Schellenberger Costa
Date and place of birth	07/11/1982 in Leipzig, Germany

Education and Employment

07/2010 - ongoing	PhD student at the University of Oldenburg Employment in the DFG-funded research group 1246 “KiLi - Kilimanjaro ecosystems under global change: Linking biodiversity, biotic interactions and biogeochemical ecosystem processes”
04/2008 - 09/2009	“Magister” course in mathematics at the University of Leipzig 09/2009 Final exams, overall grade 2.0 (good)
10/2002 - 03/2008	“Diplom” course in biology at the University of Leipzig 06/2007 - 03/2008 Diplom thesis on “The influence of altitude, water availability and succession on the abundance and distribution of the Bromeliaceae in the Mata Atlântica in the Brazilian state of Santa Catarina”, supervised by Prof. Dr. Ademir Reis, University of Florianópolis, Brazil, and PD Dr. Martin Freiberg, University of Leipzig, grade 1.3 (very good) 04/2007 Final exams, overall grade 1.2 (very good) 04/2004 Intermediate exams (“Vordiplom”), overall grade 1.5 (very good)
09/2001 - 07/2002	Civilian service in the Bavarian Society for Bird Conservation (“Landesbund für Vogelschutz in Bayern”)
08/1993 - 06/2001	Leibnizschule-Gymnasium, Leipzig Qualification for university entrance (“Abitur”)

Fieldwork

08/2010 - 09/2015	Collection of plant functional traits at Mount Kilimanjaro, Tanzania (University of Oldenburg, Prof Dr Michael Kleyer)
10/2009 - 01/2010	Guinea Baboon habituation, Senegal (German Primate Center, Prof Dr Julia Fischer)
06/2007 - 03/2008	Documentation of epiphytic bromeliad abundances and distributions, Atlantic rain forest, Brazil (University of Florianópolis, Prof Ademir Reis)
10/2006 - 12/2006	Construction of a botanical garden and plant specimen collection, Mexico (Universidad Autónoma Nacional de México, Prof Dr Elena Álvarez-Buylla Roces)
02/2006 - 04/2006	Plant inventories, phenology, and Bonobo habituation, Democratic Republic of the Congo (Max-Planck-Instititute for Evolutionary Anthropology, Dr Barbara Fruth, Dr Gottfried Hohmann)
09/2004 - 03/2005	Gibbon long-time monitoring with emphasis on behavioral changes following predation, Thailand (Max-Planck-Instititute for Evolutionary Anthropology, Dr Ulrich Reichard)

Teaching and professional work

10/2005 - 03/2006	Assistant in the “General Zoology practical”
04/2008 - 09/2008	Assistant in the “Botanical identification practical”
10/2008 - 09/2009	Research assistant in the research group General Zoology and Neurobiology, programming in MatLab

Publications

Fischer, R., A. Ensslin, G. Rutten, M. Fischer, **D. S. Costa**, M. Kleyer, A. Hemp, S. Paulick, and A. Huth, 2015. Simulating Carbon Stocks and Fluxes of an African Tropical Montane Forest with an Individual-Based Forest Model. *PLoS ONE* **10**.

Conference contributions

09/2014	Oral presentation on “Environmental filtering and trait-neutral species turnover” at the Annual Conference of the Society for Ecology (gfö)
07/2014	Oral presentation on “Environmental filtering and trait-neutral species turnover” at the Annual Meeting of the Association for Tropical Biology and Conservation (ATBC)
02/2014	Oral presentation on “Species’ niches, abundances and specialization” at the Annual Conference of the Society for Tropical Ecology (gtö)
08/2013	Oral presentation on “Testing the trait effect-response framework: Environment - plant trait - body mass relationships at Mt Kilimanjaro, Tanzania” at the Annual Conference of the Society for Ecology (gfö)
06/2013	Oral presentation on “Species niches and diversity along environmental gradients in a tropical mountain ecosystem” at the Annual Meeting of the Association for Tropical Biology and Conservation (ATBC)
04/2013	Oral presentation on “Species niches and diversity along environmental gradients at Mt Kilimanjaro, Tanzania” at the Annual Conference of the Society for Tropical Ecology (gtö)
06/2011	Poster contribution at the International Joint Meeting of the Association for Tropical Biology and Conservation (ATBC) & the Africa Section of the Society for Conservation Biology (SCB)

Appendix E Authors' contributions

Chapter 2: Plant niche breadth along environmental gradients and its relationship to plant functional traits

Authors David Schellenberger Costa, Michael Kleyer, Friederike Gerschlauer, Ralf Kiese, Markus Fischer, Andreas Hemp

MK conceived the study; AH performed vegetation surveys; AH measured elevation, precipitation, and disturbance; **DSC** collected plant trait samples; **DSC** processed samples in Tanzania and supervised sample processing in Oldenburg; RK performed leaf δ^{13}C measurements, **DSC** analyzed the data, **DSC** wrote the initial draft of the manuscript; all authors contributed to the final version of the manuscript.

Chapter 3: Convergence and divergence of plant functional traits along environmental gradients

Authors David Schellenberger Costa, Friederike Gerschlauer, Bernd Huwe, Ralf Kiese, Anna Kühnel, Yakov Kuzyakov, Holger Papst, Michael Kleyer

MK conceived the study; HP collected soil samples; **DSC** collected plant trait samples; **DSC** processed samples in Tanzania and supervised sample processing in Oldenburg; RK performed leaf δ^{13}C measurements; YK performed soil nutrient analyses; **DSC** analyzed the data; **DSC** wrote the initial draft of the manuscript; **DSC** and MK contributed to the current version of the manuscript.

Chapter 4: Do plant functional traits predict animal body mass?

Authors David Schellenberger Costa, Alice Classen, Stefan Ferger, Marcell Peters, Katrin Böhning-Gaese, Ingolf Steffan-Dewenter, Michael Kleyer

MK conceived the study; AC collected data on bee species and abundance; SF collected data on bird species richness and abundance; MP collected data on moth species richness and abundance; **DSC** collected plant trait samples; **DSC** processed samples in Tanzania and supervised sample processing in Oldenburg; **DSC** analyzed the data; **DSC** wrote the initial draft of the manuscript; **DSC** and MK contributed to the current version of the manuscript.

Appendix F Erklärungen gemäß der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften der Carl von Ossietzky Universität Oldenburg vom 21.03.2013

Hiermit erkläre ich, dass

- die vorliegende Dissertation von mir selbständig verfasst wurde und ich die benutzten Hilfsmittel vollständig angegeben habe.
- die vorliegende Dissertation weder in ihrer Gesamtheit noch in Teilen einer anderen wissenschaftlichen Hochschule zur Begutachtung in einem Promotionsverfahren vorliegt oder vorgelegen hat.
- der Grad eines Doktors verliehen werden soll.
- ich die Leitlinien guter wissenschaftlicher Praxis an der Carl von Ossietzky Universität Oldenburg befolgt habe.
- ich im Zusammenhang mit dem Promotionsvorhaben keine kommerziellen Vermittlungs- oder Beratungsdienste (Promotionsberatung) in Anspruch genommen habe.

Leipzig, den 21. Januar 2016

David Schellenberger Costa