Land cover versus functional diversity based assessments of ecosystem properties in a heterogeneous landscape

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Summary

Sustainable measures to reduce negative impacts of global change processes on the provision of ecosystem services (ES) in sub-Saharan Africa have to be established urgently. This can only be achieved on the basis of a sound understanding of how different stressors influence those biodiversity components and ecosystem properties (EP) that control ES provision. So far, assessments of biodiversity and EP sensitivity to environmental influences have been focussing mainly on homogeneous ecosystems like grasslands. However, in heterogeneous landscapes, which are of particular importance due to their multifunctionality, this ecological background of ES vulnerability has not yet been extensively studied.

As a contribution to fill this research gap, this thesis tested different approaches to evaluate (1) biotic responses to environmental gradients and (2) combined effects of environmental factors and biodiversity on EP in a heterogeneous landscape in North-East Tanzania. The study area was located in the central Mkomazi Water Basin, which is characterized by a diverse inventory of natural and cultivated ecosystems.

In a first approach the sensitivity of biodiversity was described in terms of land cover tolerance to different environmental gradients. Multivariate logistic regression analysis and model averaging were applied to identify the major drivers of land cover distribution in the study area. Subsequently, these models were used to calculate tolerance ranges of 15 land cover types along gradients of the most important land cover determinants which were disturbance and climatic factors. Evergreen highland forests, riparian woodlands and homegardens were least tolerant to these factors and therefore highly vulnerable to expected environmental changes. This is particularly critical since these three land cover types were those with the highest annual net primary productivity (NPP) and litter thickness, as a subsequent analysis of the relation between EP and land cover types revealed.

In order to gain a more detailed and mechanistic understanding of the links between environmental stressors, biodiversity response and EP sensitivity, two approaches were applied that took a functional perspective on biodiversity. Firstly, stepwise modelling was used to assess EP response to environmental gradients and to measures of plant functional diversity, namely community weighted mean traits (CWM) and community trait distribution metrics (CDM). Combined effects of abiotic factors, CWM and CDM best explained the variability in all three modelled EP (NPP, litter thickness, erosion intensity). The second idea was to add the influences of biotic responses. Thereto, specific trait effects on NPP were hypothesized in conjunction with specific trait responses to environmental gradients. Path analysis with directional separation tests was applied to assess the significance of each hypothesized environment-trait-NPP link based on data from the entire study area as well as from each of the two major ecological zones (lowlands and highlands) individually. Across the entire study area, as well as in the lowlands, NPP was mainly determined by direct effects of aridity, whereas in the highlands trait-mediated effects of disturbance were most relevant.

Based on observations and regional predictions of climate change and population growth major environmental changes have to be expected in central Mkomazi Water Basin. These comprise increasing aridity, intensification of disturbance and reductions of flow water availability. The results of this thesis revealed that particularly NPP would be negatively affected by the projected environmental changes. While increasing aridity is expected to directly limit NPP, increasing disturbance takes its effect on NPP mainly through the loss of productive forests and their functional trait attributes.

Land cover based assessments of biodiversity and EP sensitivity have the great advantage that they allow for rapid assessments, since relevant data are readily accessible. However, they lack considerable detail since only EP responses to environmental changes that translate into land cover change can be detected. Furthermore, the biodiversity components that are responsible for the tolerance of land cover types to environmental gradients cannot be identified. These problems are avoided if EP sensitivity is assessed based on functional trait responses and effects. As the results of this thesis showed, this approach can be generally applied to heterogeneous landscapes, even though it is rather elaborate. A protocol is proposed that outlines how this could be realized.

The approaches to conduct EP assessments in heterogeneous landscapes proposed in this thesis still need to be thoroughly tested in other regions. Moreover, the relevance of trophic interactions, intraspecific functional variability and repercussion effects for EP sensitivity should be examined. Efforts should be made to answer these open questions in order to provide the knowledge base for sustainable land use management that strives to safeguard livelihoods in rural sub-Saharan Africa.

Zusammenfassung

Zur nachhaltigen Minderung der negativen Auswirkungen von global wirksamen Umweltveränderungen auf Ökosystemdienstleistungen (ÖSD) in Sub-Sahara Afrika, müssen dringend adäquate Maßnahmen ergriffen werden. Dies kann nur auf Grundlage eines umfassenden Verständnisses der spezifischen Effekte verschiedener Stressfaktoren auf Biodiversität und wesentliche Ökosystemeigenschaften (ÖSE) geschehen. Bisherige Untersuchungen zur Sensitivität von Biodiversität und ÖSE gegenüber Umwelteinflüssen haben sich vornehmlich auf relativ strukturarme Ökosysteme wie zum Beispiel Grünländer konzentriert. In heterogenen, multifunktionalen Landschaften hingegen, wurden diese ökologischen Hintergründe für die Gefährdung von ÖSD bisher nur wenig erforscht.

Diese Arbeit soll dazu beitragen diesen Forschungsbedarf zu stillen. Dazu wurden auf Basis verschiedener Ansätze folgende Fragestellungen untersucht; 1. wie Biota auf Umweltgradienten reagieren und 2. wie sich Umwelteinflüsse und Biodiversität auf ÖSE auswirken. Das Untersuchungsgebiet befand sich im zentralen Einzugsgebiet des Mkomazi Flusses im Nordosten Tansanias. Dieses zeichnet sich durch eine hohe Vielfalt an natürlichen und bewirtschafteten Ökosystemen aus.

Im ersten Ansatz wurde die Sensitivität von Biodiversität durch die Toleranz verschiedener Vegetations- und Landnutzungstypen (VLT) entlang mehrerer Umweltgradienten beschrieben. Unter Anwendung multivariater logistischer Regressionsanalysen wurden Störungen, wie Beweidung, Holzeinschlag und Bodenbearbeitung, sowie klimatische Faktoren als wichtigste Einflüsse für die Verbreitung von VLT im Untersuchungsgebiet identifiziert. Entlang dieser Gradienten wiesen immergrüne Bergwälder, Auwälder und Agroforstsysteme die geringste Toleranz auf. Gleichzeitig waren dies die VLT in denen zwei der untersuchten ÖSE, Nettoprimärproduktion (NPP) und Mächtigkeit der Streuauflage, die höchsten Werte erzielten.

Um ein detaillierteres Verständnis der Beziehungen zwischen Umweltveränderungen, den Reaktionen ökologischer Gemeinschaften und der Sensitivität von ÖSE zu erhalten, wurden zwei Ansätze verfolgt die auf dem Konzept der funktionellen Diversität basieren. Zunächst wurden die Reaktionen von ÖSE auf Umweltgradienten und funktionelle Pflanzenmerkmale durch stufenweise Modellierung analysiert. Die Variabilität von NPP, Streuauflage und Erosionsintensität wurden jeweils am besten

erklärt durch kombinierte Effekte abiotischer Faktoren und funktioneller Merkmale. Im zweiten Ansatz wurden zusätzlich die Reaktionen funktioneller Merkmale auf Umweltgradienten berücksichtigt. Ein hypothetisches Pfadmodell wurde entwickelt, welches die Reaktionen funktioneller Merkmale auf Umweltgradienten mit deren Effekten auf NPP synchronisierte. Dieses Pfadmodell wurde an den im Gelände erhobenen Daten getestet; zum einen für das gesamte Untersuchungsgebiet und zum anderen jeweils einzeln für die beiden wesentlichen Naturräume innerhalb des Untersuchungsgebietes: das Hochland und das Flusstal. Während im gesamten Untersuchungsgebiet und im Flusstal starke direkte Effekte von Aridität auf NPP hervortraten, dominierten im Hochland indirekte Effekte von Störungen auf NPP, welche über die Reaktionen funktioneller Merkmale zum Tragen kamen.

Erhöhte Aridität, Intensivierung von Störungen und verringerte Verfügbarkeit von Oberflächenwasser sind wesentliche Umweltveränderungen die im Untersuchungsgebiet zu erwarten sind. Die Ergebnisse dieser Arbeit zeigen, dass insbesondere NPP negativ von diesen Umweltveränderungen betroffen sein wird. Dies geschieht vor allem durch direkte negative Effekte von erhöhter Aridität, sowie durch erhöhte Störung welche sich unter anderem durch den Verlust produktiver Bergwälder und der darin vorherrschenden funktionellen Merkmale nachteilig auf NPP auswirkt.

Untersuchungen der Sensitivität ökologischer Gemeinschaften und ÖSE basierend auf VLT profitieren von der guten Verfügbarkeit geographischer Daten, auch für sub-Sahara Afrika. Allerdings können mit Hilfe dieses Ansatzes nur Auswirkungen von Umweltveränderungen auf ÖSE beschrieben werden, welche mit einer Veränderung der VLT einhergehen. Weiterhin sind keine detaillierten Rückschlüsse über die funktionellen Merkmale möglich welche die Toleranz der VLT gegenüber Umweltgradienten bedingen. Ansätze die sich auf die Analyse von Reaktionen und Effekten funktioneller Merkmale stützen vermeiden diese Probleme. Auch wenn dies einen wesentlich höheren Untersuchungsaufwand bedeutet, ist diese Methodik gut auf heterogene Landschaften anwendbar. Am Ende dieser Arbeit wird ein Leitfaden vorgeschlagen der aufzeigt wie dies umgesetzt werden kann.

Die in dieser Arbeit genutzten Ansätze zur Untersuchung von ÖSE in heterogenen Landschaften sollten noch umfassend in anderen Regionen getestet werden. Zudem bleiben offene Fragen zur Relevanz von trophischen Wechselbeziehungen, innerartlicher funktioneller Variabilität und Rückkopplungseffekten für die Sensitivität von ÖSE. Diese Forschungsaufgaben sollten angegangen werden um das nötige ökologische Verständnis zu erlangen welches für ein nachhaltiges Landnutzungsmanagement unabdingbar ist. Dies würde wesentlich zur Existenzsicherung ländlicher Gemeinden in sub-Sahara Afrika beitragen.

Chapter 1

Introduction and research objectives

1 Introduction and research objectives

1.1 Properties, functions and services of ecosystems under change

Human well-being is founded on a multitude of goods and services that are provided by ecosystems (Sekercioglu 2010). This dependency is particularly high among smallholder farmers and livestock keepers in rural sub-Saharan Africa and other tropical regions (Scholes & Biggs 2004; Kumar & Yashiro 2014). Due to their limited political and economic strength, these communities often lack the capacity to substitute the services which they obtain from ecosystems (Díaz *et al.* 2006). Essentially, these services comprise the provision of natural resources (e.g. crops, fodder, timber, firewood) and non-material values for the communities' benefit (e.g. ritual places), the regulation of biogeochemical processes (e.g. water and nutrient cycling) and the maintenance of ecosystem functioning in neighbouring agro-ecosystems. They have been described as provisioning, cultural, regulating and supporting 'ecosystem services' (ES) (MEA 2005).

Each ecosystem provides a specific set of ES. Consequently, in heterogeneous landscapes a lot of different ES are provided, which are however unevenly distributed (Willemen *et al.* 2008; Burkhard *et al.* 2009; Bolliger *et al.* 2011). Rural communities in sub-Saharan Africa commonly rely on a multitude of ES (see examples in: Scholes & Biggs 2004; Sileshi *et al.* 2007). In order to maintain their livelihoods, it is therefore important to sustain the multifunctionality of landscapes (Bolliger *et al.* 2011). This can only be accomplished if land use managers have access to information about how ES respond to different land use activities and environmental changes (Willemen *et al.* 2008; Yapp, Walker & Thackway 2010).

However, ES response is not directly controlled by anthropogenic and abiotic stressors. Instead, land use and environmental change influence ES through their effects on biodiversity and the properties and processes that characterize ecosystems (Hooper *et al.* 2005; Díaz *et al.* 2006). Changes in major ecosystem properties and processes modify ecosystem functioning, which in turn affects the type and quality of services provided by ecosystems (de Groot *et al.* 2010; Burkhard *et al.* 2012). In other words, the effects of land use and environmental changes on ES provision are conditioned by the responsiveness of biodiversity and ecosystem properties and processes to the changing environmental factors.

Sound understanding of this ecological background is a major requirement for robust assessments of the various threats to ES provision (Bennett *et al.* 2015). In this thesis, approaches to build this understanding in heterogeneous landscapes with a regional focus on sub-Saharan Africa were tested and discussed. In detail, possibilities were explored to assess (1) the size and direction of biotic responses to gradients of environmental conditions and disturbances and (2) the combined effects of environmental influences, disturbances and biodiversity on ecosystem properties. Ecosystem processes were not assessed, hence this thesis simply refers to ecosystem properties (EP) for the sake of convenience. Nevertheless, ecosystem processes are equally concerned by the issues covered in this thesis.

Several approaches exist to analyse the effects of environmental stressors on biodiversity and EP. Each of them examines biodiversity at a different scale. Probably the first idea would be to focus on species and populations. Their responses to environmental gradients can be determined at relatively high detail by the application of species distribution models (Elith & Leathwick 2009). However, investigating species' effects on EP is complicated, since this relies on information about the functional roles of each individual species (Díaz & Cabido 2001). Especially, in heterogeneous landscapes with high species richness that have not yet been extensively studied, this kind of information commonly is incomplete. Therefore, alternative options have to be used. One is the concept of 'landscape functions' that has already been adopted by several planning authorities (Burkhard *et al.* 2009). It simply relates multiple EP and ecosystem functions to different types of ecosystems or land cover units, which describe biodiversity at rather low resolution. EP response and threats to ecosystem functioning can then be explored directly from potential land cover changes. Another alternative is to examine biodiversity in terms of functional diversity. This idea acknowledges that it is not primarily the identity of species which controls their effects on EP, but rather their functional traits (Díaz & Cabido 2001; Díaz *et al.* 2006; Sekercioglu 2010). In addition, functional traits determine biodiversity response to environmental gradients (Lavorel & Garnier 2002; Laliberté & Tylianakis 2011) and, consequently, provide powerful links to evaluate potential effects of environmental change on EP (Díaz *et al.* 2013). Both, the land cover based approach as well as the functional trait approach have been applied and evaluated in this thesis.

Box 1

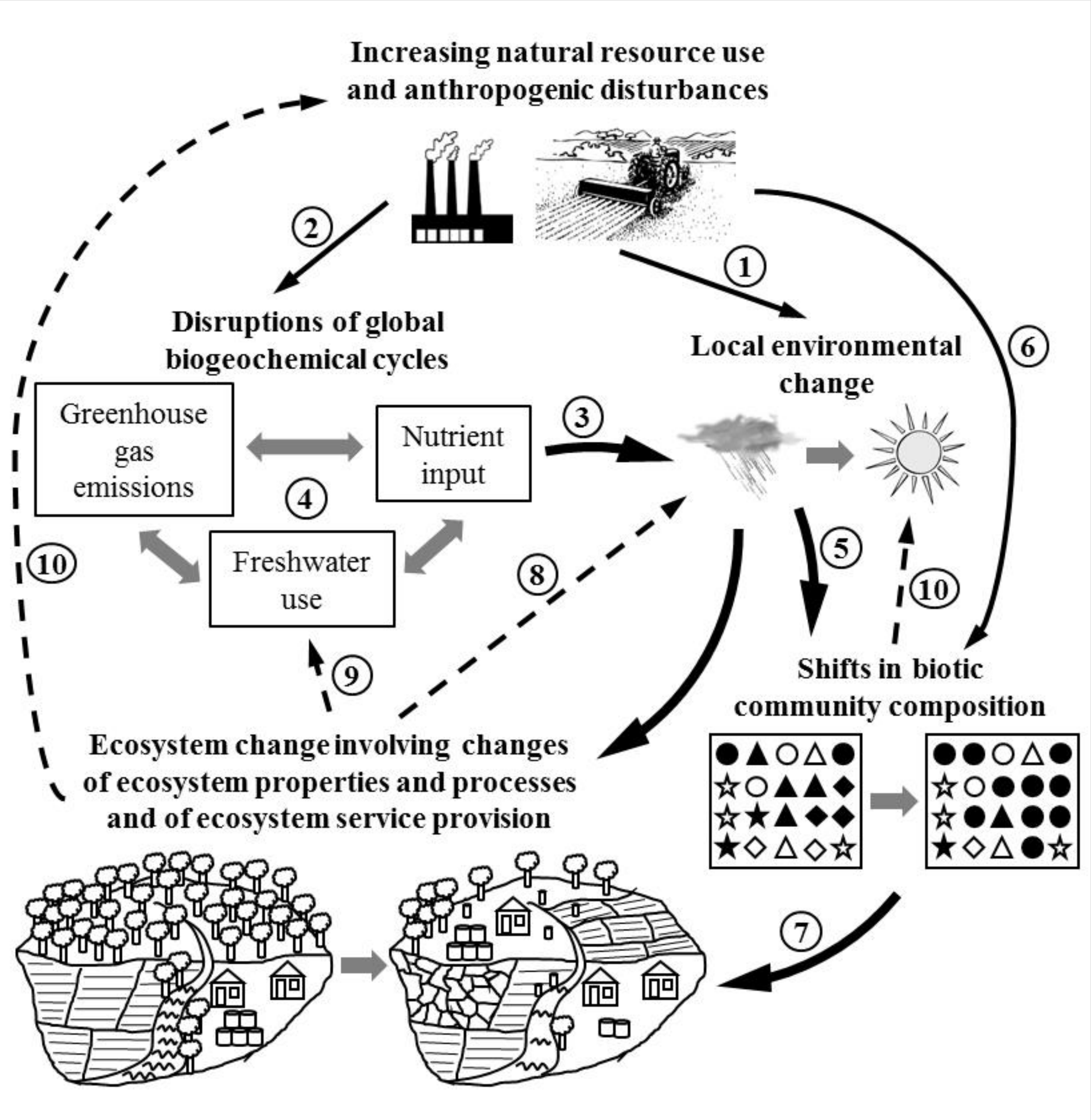


Figure Box 1. The cycle of global change. The numbers on the arrows mark explanations that follow in the text below

Accelerating resource exploitation and land use intensification have direct and indirect impacts on local environmental conditions. (1) Direct impacts comprise for instance habitat fragmentation or pollution. (2, 3) Indirectly, the increasing anthropogenic interferences in ecosystems affect local environmental conditions through disruptions of global biogeochemical cycling (Vitousek *et al.* 1997; Foley *et al.* 2005). For instance, the substantial increase of anthropogenic greenhouse gas emissions causes global temperature rise and shifts in global heat and moisture circulation (IPCC 2013). This leads to extensive changes of regional and local climate. Extraction and pollution of water resources, regulation and channelization of rivers, as well as surface sealing in catchment areas diminish freshwater reserves and change hydrological processes (Vörösmarty *et al.* 2010). Industrial production of reactive nitrogen and its excessive application in agriculture lead to the depletion of other soil nutrients and cause eutrophication of soils, freshwater ecosystems and coastal marine habitats (Fowler *et al.* 2013). (4) Carbon, water and nutrient cycles are interrelated, hence the disruption of one global biogeochemical cycle affects the others as well (Vitousek *et al.* 1997).

Box 1 (continued)

(5) Local environmental change involves modifications of biotic communities' habitats. This triggers invasion and extinction processes, which often cascade through several trophic levels and affect individuals, local populations, as well as entire species (Chapin *et al.* 2000; Sekercioglu 2010). (6) Additionally, biotic communities are directly influenced by human interferences like biomass removal in the wake of harvesting or weed control and the introduction of alien species (Brook, Sodhi & Bradshaw 2008; Peres 2010). (7) The shifts in biotic community composition as well as direct effects of local environmental change entail alterations of ecosystem properties, processes and functions (Chapin *et al.* 2000; Díaz *et al.* 2006; Hooper *et al.* 2012).

Eventually, the cycle of global change is closed by feedback effects of biodiversity loss and ecosystem change on local environmental conditions and global biogeochemical cycling. (8) Prevailing ecosystem properties and processes influence local abiotic conditions. For example, changes in albedo, transpiration and heat flux due to alterations of litter layer and canopy structure, affect local microclimate and soil water availability (Chapin 2003). (9) Furthermore, fundamental ecosystem processes like primary production, respiration and decomposition considerably contribute to global carbon, water and nutrient cycles (Loreau *et al.* 2001; Sekercioglu 2010; Settele *et al.* 2014). Consequently, ecosystem changes might further enhance the human-induced disruptions of biogeochemical cycles. For instance the loss of tropical forest ecosystems in response to global change, eliminates carbon sinks and increases the rate of carbon emissions (Phat, Knorr & Kim 2004). On the other hand, ecosystem change can contribute to reduce the disruptions of biogeochemical cycles (e.g. formation of additional carbon sinks by afforestation of farm land). (10) Lastly, biodiversity loss and changes in ecosystem functioning affect the availability of natural resources and the suitability of ecosystems for different land use activities (Chapin *et al.* 2000).

Sound knowledge about ecosystem response to different stressors and the effects on ES provision have become particularly important in the light of current threats by global change processes. Following population growth, economic development and technological advancement human demands for natural resources have been rising rapidly. In order to meet these demands, land use activities have been intensified in most parts of the world (Vitousek *et al.* 1997; Foley *et al.* 2005). This led to changes in local environmental conditions, global biogeochemical cycling, biodiversity and ecosystem functioning. Box 1 outlines the most important aspects of this vicious cycle of global change. Biodiversity loss and ecosystem degradation in the wake of global change impair the provision of crucial ES and therefore endanger the multifunctionality of landscapes (Díaz *et al.* 2006; Sekercioglu 2010). Particularly the poor, ES dependent rural communities of sub-Saharan Africa are threatened by this development. They already face impacts of global change processes, including the depletion of soil nutrients, the reduction of freshwater availability and in some regions fuel wood shortages (Smaling, Nandwa & Janssen 1997; Scholes & Biggs 2004; van Jaarsveld *et al.* 2005). In order to re-establish and maintain human well-being in sub-

Saharan Africa, biodiversity loss and ecosystem degradation have to be countered urgently.

Irreparable negative impacts of global change on ecosystem functioning and livelihoods in sub-Saharan Africa and elsewhere can still be avoided (Scholes & Biggs 2004). Strategies to achieve this aim should prioritize two aspects: (1) safeguard the provision of ES crucial for local communities' livelihoods (MEA 2005) and (2) address multiple processes that fuel global change simultaneously, persistently and across different scales (Brook, Sodhi & Bradshaw 2008; Heller & Zavaleta 2009). Meaningful concrete measures differ among the scales of action. At global scale, the major objective should be to attenuate the disruptions of biogeochemical cycles with a specific focus on carbon cycling and climate change. However, commensurable effects will delay by several decades due to enormous time lags between the emission of carbon and its effects on climate (IPCC 2013). Moreover, until today no international consensus exists upon a global action plan (Chapin *et al.* 2010). At regional and local scales it is therefore often necessary to adapt to changing climatic conditions (Heller & Zavaleta 2009). Many other threats to ecosystems and the related ES provision emerge from local land use activities and anthropogenic disturbances (MEA 2005; Chapin *et al.* 2010). Minimizing these negative land use effects on environmental conditions and biodiversity can help to sustain ecosystem functioning and at the same time increases resilience to climate change (Klausmeyer *et al.* 2011; Settele *et al.* 2014). Assessments of ES vulnerability and the underlying EP sensitivity are necessary to identify detrimental influences on ecosystems and to select appropriate counteractive measures.

Thesis outline

This thesis presents the results of a research which was conducted in North-East Tanzania between 2011 and 2015. This study investigated (1) biodiversity response to environmental gradients and (2) ecosystem properties response to environmental gradients and biodiversity. Apart from an evaluation of the specific EP sensitivity in the study area, the aim was to compare the applicability and performance of land cover based versus functional diversity based approaches in heterogeneous landscapes.

In spite of the high relevance of ES provision in rural sub-Saharan Africa, this part of the world is still insufficiently studied. Like in other developing regions, capacities to undertake research on global change threats to biodiversity and ecosystem functioning are still strongly limited (Barber *et al.* 2014). This calls for increased efforts to improve the availability of relevant data in sub-Saharan Africa. Therefore, a particular interest of this thesis was to put a regional focus on sub-Saharan Africa. It was based in North-East Tanzania, which is highly representative for rural sub-Saharan Africa.

In Chapter 2 the study area is introduced and methods are described that were applied to build the general data base. The assessment of land cover response to different potential environmental stressors as a tool for rapid assessments of biodiversity and EP sensitivity is addressed in Chapter 3. In order to gain additional detail, Chapter 4 explores the response of EP to environmental gradients and plant functional traits across the entire study area. In Chapter 5, more complexity is gained by an application of functional response-effect modelling to the heterogeneous landscape of the study area. Chapter 6 synthesizes the major results concerning the sensitivity of biodiversity and EP to different stressors in the research area. Advantages and disadvantages of land cover and functional diversity based approaches are discussed. Finally, the land cover and functional diversity approaches are combined into a protocol for the assessment of EP responsiveness to environmental factors mediated by biodiversity effects at the landscape scale.

1.2 Frameworks to describe global change threats to ecosystem functioning

As outlined above, a major precondition for the development of sustainable land use management strategies is to ascertain how global change affects ecosystem functioning and ES provision. The key to identify these ecological threats is sound understanding of biodiversity and EP responses to environmental stressors. In order to describe this context a framework had been devised which is discussed in the following sections.

1.2.1 The concepts of vulnerability and resilience

Global change processes impact not only ecosystems and their functions, but equally concern societies, economies and politics. Unsurprisingly, a wide range of research communities (e.g. ecologists, geographers, social scientists, economists) conceptualized the evaluation of global change threats in various frameworks (Miller *et al.* 2010). Most popular and widely recognized in this context are the concepts of vulnerability and resilience. The notion of vulnerability emerged from geography and gained considerable relevance in climate change research (Janssen 2007). It describes the susceptibility of a system to environmental change and its (in-)ability to adapt (Adger 2006). Resilience originates from ecology (Janssen 2007). It essentially describes the ability of a system to resist stresses, to maintain major functions in the event of disturbance and to recover (Carpenter *et al.* 2001). In spite of their opposing perspectives (vulnerability: negative; resilience: positive) both concepts have a lot of commonalities (Miller *et al.* 2010). Hence, they equally suit to explain global change threats to different systems. As a matter of fact, neither is resilience restricted to ecology nor is vulnerability restricted to geography and climate change research.

However, a major problem in the application of both concepts is that definitions of vulnerability and resilience determinants vary among different schools of thought (Gallopín 2006; Miller *et al.* 2010). Contradiction, overlap and confusion in the use of terms related to vulnerability and resilience hamper cross-sectoral evaluation of global change threats (Gallopín 2006). To minimize these problems, Miller *et al.* (2010) called for clear definitions in vulnerability and resilience research.

This thesis adhered to the vulnerability concept since major components of vulnerability suit well to depict the role of biodiversity and EP as modulators of global change threats to ecosystem functions.

1.2.2 Ecosystem functioning vulnerability framework

In the context of this thesis, ‘vulnerability’ refers to the susceptibility of ecosystem functions and related ES to negative effects of different environmental stressors. This is in accordance to other, more general definitions of vulnerability (e.g. Turner *et al.* 2003; Williams *et al.* 2008). As outlined by Turner *et al.* (2003), the vulnerability of a system is generally determined by external as well as system-intrinsic features. On account of this principle and based on the framework by Klausmeyer *et al.* (2011), here vulnerability determinants are described as illustrated in Figure 1.

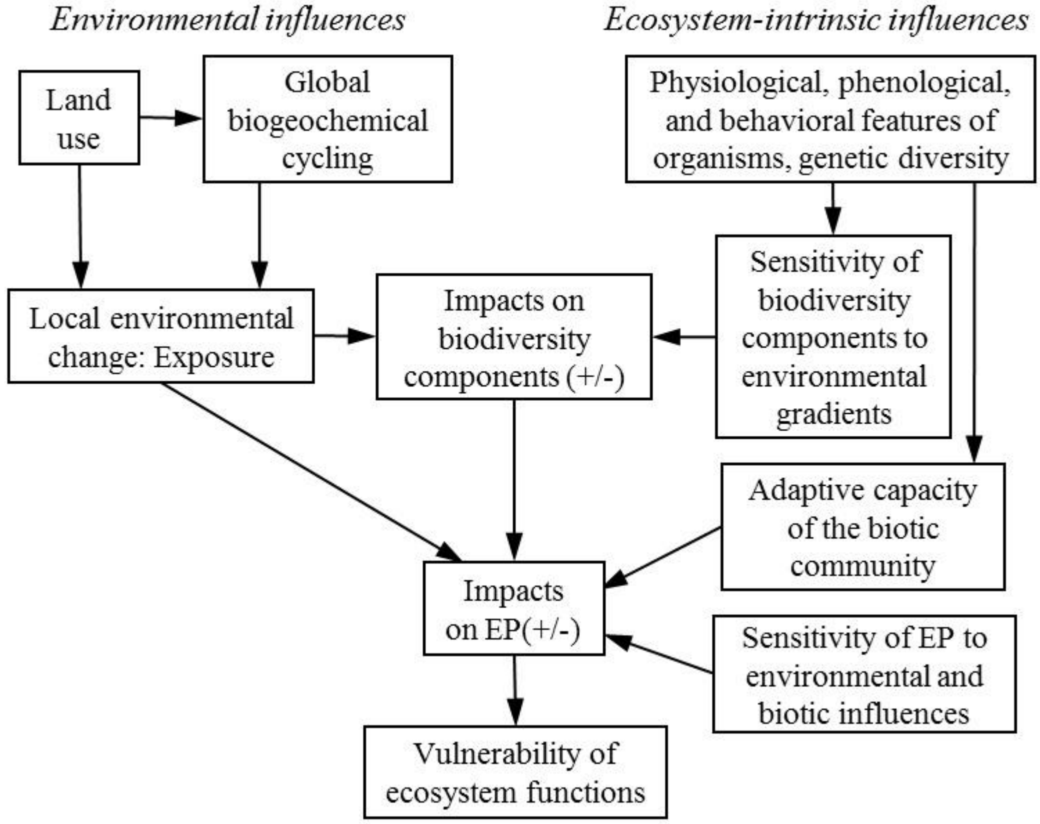


Figure 1. Framework for the assessment of ecosystem functions vulnerability

External vulnerability determinants include all those environmental changes and direct anthropogenic interferences that take affect at the place of question (Gallopín 2006). They are referred to as ‘exposure’ (corresponding to ‘local environmental change’ in Figure Box 1). Governed by physiological features, ecological behaviour and genetic diversity, ecosystem-intrinsic biodiversity components show differential responsiveness to different environmental gradients (sensitivity) (Williams *et al.* 2008). Consequently, the level of sensitivity is decisive about the ‘impact’ an exposure has on a biodiversity component (corresponding to ‘shifts in biotic community composition’ in Figure Box 1). Likewise, the impacts of environmental change on EP are controlled by EP sensitivity to the respective environmental gradients (Díaz *et al.* 2007b). In addition however, EP are affected by biodiversity shifts, depending on their sensitivity to biotic influences (Lavorel & Grigulis 2012). For this reason, impacts on EP might be buffered if the changes of multiple biodiversity components that contribute to the same EP compensate for each other. This effect, commonly known as 'biotic response diversity' (Mori, Furukawa & Sasaki 2013), constitutes 'adaptive capacity'. The impacts of environmental changes and biodiversity shifts on EP can either be positive (increased performance) or negative (decreased performance). If negative impacts prevail, ecosystem functions' vulnerability will be correspondingly high. On the other hand, ecosystem functioning might benefit if relevant EP respond positively to environmental change. Figure 2 illustrates how differences in the sensitivity of biodiversity components and EP control the impacts of different environmental changes on EP in three abstract examples.

In order to gauge vulnerability, all relevant vulnerability determinants have to be assessed (Turner *et al.* 2003). Thanks to extensive efforts by the scientific community and collaborations like the Intergovernmental Panel on Climate Change (IPCC), exposure generally can be ascertained at relatively high detail. Projections of future changes in global land use, climate, water availability, nutrient load and other factors yield increasingly robust outputs (e.g. IPCC 2013; Seager *et al.* 2013). And even though higher-resoluted, regional data are not yet available for all parts of the world, approaches to downscale global models are well advanced (e.g. Tadross & Wolski 2010). Furthermore, uncertainties in predictions of future environmental conditions can be compensated by the development of internally consistent scenarios (Peterson, Cumming & Carpenter 2003).

In contrast, the evaluation of ecosystem-intrinsic vulnerability determinants remains challenging (Williams *et al.* 2008). This accounts particularly to the sensitivity of biodiversity and EP to changing environmental factors. Probably to avoid these challenges, many studies of ecosystem vulnerability to climate change acknowledged only exposure, but disregarded ecosystem-intrinsic features (Watson, Iwamura & Butt 2013). However, as explained in Figure 1, this information is integral to reliably determine ecosystem functions' vulnerability.

In the light of these problems, this thesis intended to study and evaluate different approaches for the assessment of biodiversity and EP sensitivity. However, the aim was not to perform entire vulnerability assessments.

Sensitivity of biodiversity components to abiotic factors

		Abiotic factors		
		1 ▥	2 ▦	3 ▨
Biodiversity components	a ▲	++	0	++
	b ●	+	- -	0
	c ◆	0	0	- -

Sensitivity of EP to abiotic factors and biodiversity components

	Abiotic factors			Biodiversity components		
	1 ▥	2 ▦	3 ▨	a ▲	b ●	c ◆
✕ EP	+	0	0	++	+	++

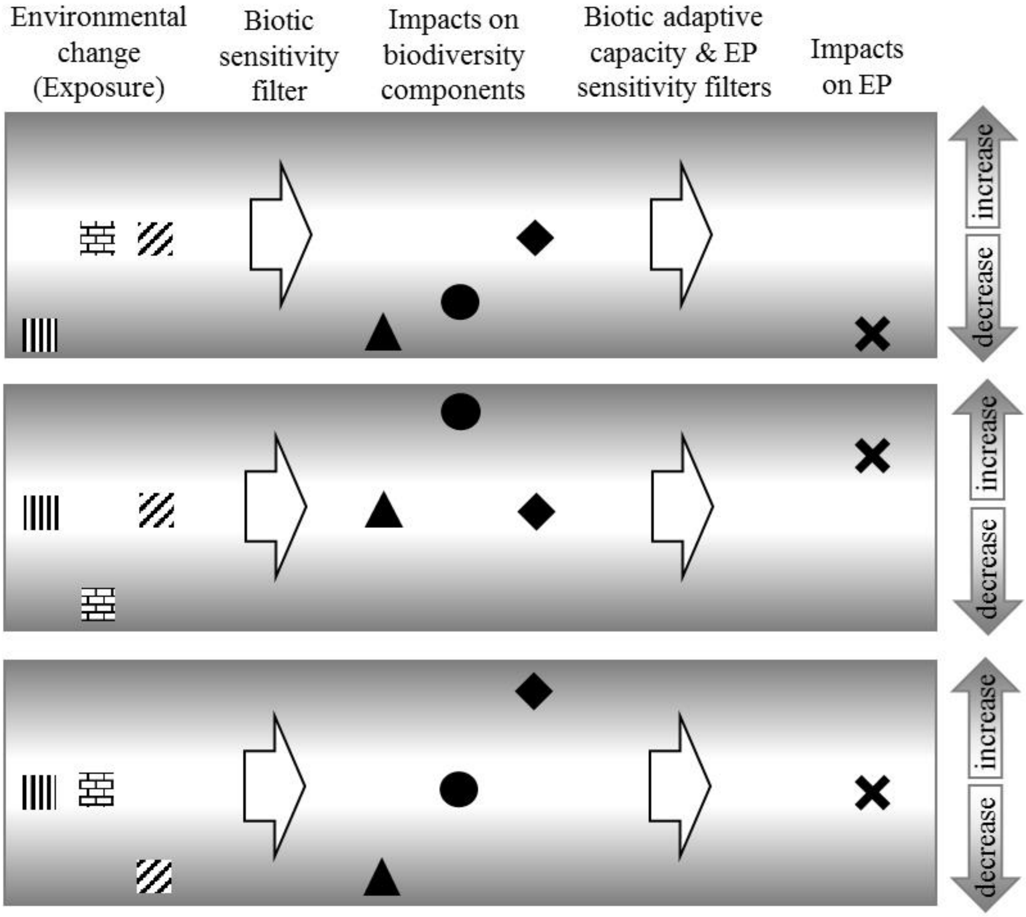


Figure 2. Theoretical impacts of different local environmental changes on biodiversity components and an ecosystem property (EP). Each biodiversity component shows different sensitivity to different abiotic factors (left table): ++ strongly positive relation, + positive relation, 0 no relation, - negative relation, - - strongly negative relation. Controlled by that, each environmental change has specific impacts on each biodiversity component (the three graphs). Likewise, the EP shows different sensitivity to different abiotic factors and biodiversity components (right table). EP response can be buffered by the diversity of impacts on biodiversity components that have similar effects on the EP (see lowermost graph). The white area in the middle of each graph indicates the conditions before changes occurred. The distance by which each environmental factor, biodiversity component and EP deviated from this white area indicates the size of change

1.3 Biodiversity and EP sensitivity: the land cover perspective

The most distinct manifestation of ecosystem response to global change processes certainly is the transition of one 'ecosystem type' into another (Lambin, Geist & Lepers 2003). Therefore, the susceptibility of an ecosystem to change into another type is a possible measure of ecosystem vulnerability, albeit of rather low detail. However, a clear description of different ecosystem types is problematic. The reason is that ecosystems lack distinct boundaries, cover multiple scales and are nested within each other (Settele *et al.* 2014). To bypass this challenge, some scholars delineated ecosystem types through land cover classes (e.g. Lung & Schaab 2010; Burkhard *et al.* 2012). Certainly, this is a radical simplification of ecosystems. Still, it is justified by the fact that land cover essentially represents vegetation, which is the most distinct component of biodiversity in ecosystems and performs crucial functions like primary production (Yapp, Walker & Thackway 2010).

Since land cover represents vegetation, it can be expected that most of the stressors which affect primary producers in ecosystems also influence the spatial distribution of land cover units (Yapp, Walker & Thackway 2010). Hence, responses of primary producers to environmental change, sooner or later translate into land cover change. In sub-Saharan Africa for example, increasing disturbance induced by land use expansion led to extensive land cover changes (Box 2). Putting these aspects into vulnerability terms, land cover units, as representatives of biodiversity, are responsive to different environmental gradients. Consequently, the sensitivity of biodiversity can be assessed as the sensitivity of different land cover units.

Box 2

Since the colonial era, considerable land cover changes have been occurring in many parts of sub-Saharan Africa. Similar to developments in other world regions, the expansion of croplands at the expense of natural ecosystems has been the most prevalent transformation (Lambin, Geist & Lepers 2003). Brink and Eva (2009) found that between 1975 and 2000 agricultural land area in sub-Saharan Africa increased by 57% with regional hotspots in West and East Africa. Most of the newly established cultivated land replaced dry forests and non-forested savannas, whereas humid forests were less affected than in other tropical regions. In addition, locally relevant land cover changes include the transition of forests into pastures (open woodlands, grasslands) and the loss of croplands to expanding urban infrastructure (Lambin, Geist & Lepers 2003).

There are further aspects that support the suitability of land cover for ecosystem vulnerability assessments. Most land cover types can be characterized by specific predominant EP (Yapp, Walker & Thackway 2010). Several examples exist where this was implemented (e.g. Egoh *et al.* 2008; Davies *et al.* 2011). Therefore, it is possible to assess the impacts of environmental changes on EP through information about the sensitivity of land cover units. Additionally, ecosystem functions and related ES ('landscape functions') can be linked to different land cover units based on stakeholder interviews, expert knowledge or measurements (Burkhard *et al.* 2009; Burkhard *et al.* 2012). Hence, the land cover distribution in a landscape provides spatially explicit information about ES (de Groot *et al.* 2010; Bolliger *et al.* 2011). As land cover changes in the wake of environmental change, ecosystem functioning and the provision of ES are affected accordingly (Yapp, Walker & Thackway 2010; Burkhard *et al.* 2012).

The key to assess the vulnerability of ecosystem functioning based on land cover is the analysis of land cover sensitivity. Several efforts have been made to study land cover response to gradients of land use and environmental factors and to predict future land cover distributions. The application of Markovian transition probability models (TPM) (Usher 1981), presumably is the most common approach (e.g. Serneels & Lambin 2001; Rutherford *et al.* 2008). To build TPM, observed land cover changes are related to the environmental conditions under which they occurred. Alternatively, geographers for instance relate land cover changes to socio-economic conditions (e.g. Maeda *et al.* 2010). Each TPM evaluates the probability for a specific land cover transition along these gradients. The relevance of each stressor can be estimated from its relative importance for the different modelled land cover transitions (cf. Rutherford *et al.* 2008). Furthermore, TPM can predict land cover changes that are likely to occur under different scenarios of future climate, water availability, land use etc.

In spite of their popularity, land cover TPM have several shortcomings. One is their dependence on historical land cover data. In cases when these data are not available at adequate spatial and temporal resolution, modelling results will not be reliable. Another problem is that with increasing number of studied land cover units (k) and time steps (m), the number of transitions which have to be modelled rises exponentially (k^m) (Usher 1981). In most cases a relatively large number of theoretical land cover transitions will not be observed in the dataset. These transitions are automatically assigned zero probabilities in the modelling process. However, this is not necessarily true for each of them. The occurrence of environmental changes that had not been observed before might cause unpredicted trajectories of land cover change. Finally, TPM are not focussing explicitly on land cover units, but on their specific changes. As a result of this, conclusions on sensitivity and adaptive capacity of specific land cover units cannot be drawn directly from the modelling output. Instead it is necessary to analyse all TPM that include a certain land cover unit.

Analyses of land cover sensitivity to environmental gradients and land use do not necessarily have to be based on data that cover temporal variation. Alternatively, land cover response can be derived from variation along spatial gradients of environmental conditions and land use. This approach originates from species distribution modelling (Elith & Leathwick 2009). The basic idea is that the distribution of each land cover type in a landscape is limited by a specific range of environmental conditions and land use regimes (Di Gregorio & Jansen 2005). These limits can be determined for each land cover unit, based on its observed distribution. Moreover, it is assumed that land cover units shift as the limits are exceeded in the wake of environmental change (Lambin, Geist & Lepers 2003). The distance between the limits indicates how much environmental variation the respective land cover type can tolerate.

Box 3

For the distinction of different land cover units, numerous classification systems are available, normally tailored to specific scales, regions and purposes. For example in Europe, the CORINE land cover classification is widely applied (CEC 1995) and Thompson (1996) developed a classification for South Africa, whereas UNESCO (1973) proposed a classification for global land cover. However, most land cover classification systems are limited to the scale and region for which they were fitted. Furthermore, comparison and translation between different classification schemes is complicated. As Jansen and Di Gregorio (2002) pointed out, the reason for these problems is that the discrimination between land cover classes is often based on descriptions. Criteria to distinguish between classes are not clearly defined, are used inconsistently or have no relation to land cover (see Jansen and Di Gregorio (2002) for examples). Furthermore, many classifications fail to clearly discriminate between land cover and land use. This is probably due to the close relation between both. Land cover is defined as vegetation and man-made structures on the surface of the earth, whereas land use depicts all human activities that affect land cover (Di Gregorio & Jansen 2005). Some land cover types emerged from specific land use activities, which can therefore be depicted directly from observations (e.g. housing). However, in most cases land cover alone does not provide sufficient information to determine all existing land uses at a specific place (Verburg *et al.* 2009). Hence it should be avoided to mix them up.

In the light of these problems the Food and Agriculture Organization of the United Nations (FAO) and the United Nations Environment Programme (UNEP) developed the Land Cover Classification System (LCCS) (Di Gregorio & Jansen 2005). LCCS is applicable in every part of the world at any desired scale and is compatible with other existing land cover classifications.

Even though there are examples for 'land cover distribution modelling' (e.g. Peppler-Lisbach 2003; Bader & Ruijten 2008), methods to measure the tolerance ranges for land cover units have not yet been established. In Chapter 3 of this thesis an approach to measure tolerance ranges along multiple environmental gradients is described and discussed at length. This metric was denoted as *land cover tolerance* and can be interpreted as an inverse of land cover sensitivity. A narrow tolerance range, for instance, would imply that a land cover unit cannot tolerate much variability of the respective environmental factor.

A problem in land cover related research is that the most commonly applied land cover classification systems are affected by inconsistencies and poor reproducibility. The validity of ecosystem vulnerability assessments based on these classification systems therefore might be confined. However, an alternative classification scheme is available that overcomes these problems (Box 3). It was applied in this study to determine land cover units in the research area (Chapter 3).

1.4 Biodiversity and EP sensitivity: the functional diversity perspective

1.4.1 Functional diversity and biotic response-effect relations

A mechanistic understanding of the links between environmental stressors, biodiversity response and EP sensitivity can be built if biodiversity is viewed from a functional perspective (Díaz *et al.* 2007b; Díaz *et al.* 2013; Wood *et al.* 2015). This involves the description of biotic communities through ecologically relevant features of organisms. These morphological, physiological, phenological and behavioural features are referred to as 'functional traits' (Violle *et al.* 2007).

Each biotic community features a certain range of functional trait 'attributes' (*sensu* Violle *et al.* 2007) determined by the differences between individual organisms and species within the community. Identity and diversity of the trait attributes in a community are described as 'functional diversity' and play a central role in major ecological processes (Díaz & Cabido 2001; Petchey & Gaston 2006). Firstly, functional diversity determines how biotic communities affect EP (Hooper *et al.* 2005; Díaz *et al.* 2006; Díaz *et al.* 2007b). This influence is mediated by the attributes of all those functional traits that exert a direct impact on ecosystem operation, commonly called 'effect traits' (Suding *et al.* 2008). For example, leaf traits, like specific leaf area (SLA) or leaf dry matter content, were found to have considerable effects on primary production and litter decomposition (e.g. Laliberté & Tylianakis 2011; Lienin & Kleyer 2012). Moreover, functional diversity controls biodiversity response to environmental gradients and disturbance regimes, determined by specific attributes of functional 'response traits' (Lavorel & Garnier 2002; Suding *et al.* 2008). For instance, intensive grazing filters plants with defence structures or low canopy height against unprotected or high growing species (Skarpe & Hester 2008; Lienin & Kleyer 2011).

Functional diversity based assessments of EP response fit well into the ES vulnerability framework (Figure 1). Response traits control the impacts of environmental change on biodiversity, since they determine the sensitivity of biodiversity components to different environmental gradients. Likewise, impacts of environmental and biodiversity change on EP are governed by EP sensitivity to different environmental gradients and effect traits. Finally, functional diversity based approaches can depict the adaptive capacity of biotic communities which buffers impacts on EP. Adaptive capacity is determined by the response diversity of biodiversity components that share common effect traits (Mori, Furukawa & Sasaki 2013).

Several relationships between environmental conditions, functional diversity components and EP have been found to follow general trends (e.g. 'leaf economics spectrum' (Wright *et al.* 2004), 'fast-slow plants economic spectrum' (Reich 2014)). Furthermore, the focus on functional diversity allows comparisons between phylogenetically different biotic communities (cf. Cowling & Witkowski 1994), something that species-based approaches cannot render. Consequently, assessments of biodiversity and EP sensitivity based on functional diversity should be applicable across broad spatial scales and in heterogeneous landscapes with wide environmental gradients (Dray & Legendre 2008).

1.4.2 Options to measure functional diversity

Probably the most long-lived ideas to measure functional diversity in ecosystems are based on the description of 'functional types'. Each functional type is composed of species that share biological characteristics (Lavorel *et al.* 1997). Correspondingly, they either show analogous responses to environmental influences or they have similar effects on EP ('functional response and effect groups' (Lavorel & Garnier 2002)). Species are grouped into functional types either *a priori* (Hooper & Vitousek 1997) or based on ordination techniques (Duckworth, Kent & Ramsay 2000). Commonly applied are correspondence analysis or the more advanced RLQ and fourth-corner methods that have been developed by Dolédec *et al.* (1996) and Dray and Legendre (2008), respectively (e.g. Díaz & Cabido 1997; Lienin & Kleyer 2011; Minden *et al.* 2012). Functional diversity is measured either as the number of functional types that occur in an ecosystem ('functional type richness') or as the identity of the prominent functional types ('functional type composition') (Hooper & Vitousek 1997). Assessments of functional diversity based on functional types are well applicable in heterogeneous landscapes and along wide environmental gradients (e.g. Kleyer 1999).

The functional type approach has, however, several shortcomings. Often a bunch of species cannot be definitely grouped into one or another functional type so that different functional types tend to be nested within each other (Díaz & Cabido 2001). Moreover, there are no universal functional types, because each function or response in focus requires to group species differently (Lavorel *et al.* 1997). Following from that, functional types that indicate biotic responses often are composed of other sets of species than those that determine biotic effects (Lavorel & Garnier 2002; Lavorel *et al.* 2007). In addition, the functional types approach is limited in its ability to depict biotic response and effect in multivariate situations (when multiple environmental gradients and multiple EP are considered) (Lavorel & Garnier 2002). Finally, grouping species into functional types emphasizes the between-group differences but disregards within-group differences (Petchey & Gaston 2006). Hence, measuring functional diversity based on functional types involves a considerable loss of information.

An alternative option to measure functional diversity is to scale species-level averages of trait attributes to the community level (Lavorel & Garnier 2002). Thereby, functional diversity is described by community-specific attributes of individual traits. The focus on individual traits allows to precisely unravel biotic responses to multiple environmental factors and biotic effects on multiple EP at once (Díaz *et al.* 2007b; Suding *et al.* 2008). Consequently, functional diversity assessments based on continuous community level trait attributes are much more detailed and operational than the functional types approach (Lavorel & Garnier 2002). On account of these issues, in this thesis functional diversity was described by community-level trait attributes.

There are two general modes to calculate community-level trait attributes (Díaz *et al.* 2007b). One emphasizes the trait attributes of dominant species and builds community averages weighted by species abundance ('community weighted means': CWM). The other mode highlights the community distribution of trait attributes in trait space. Several metrics exist that focus on different aspects of distribution, including richness, evenness, divergence and dispersion (Laliberte & Legendre 2010). In this thesis these metrics were summarized under the label *community distribution metrics* (CDM). Further details about theories behind CWM and CDM as well as their significance in heterogeneous landscapes are provided in Chapters 4 and 5.

1.4.3 Assessment of EP response to community-level trait attributes

Two strategies have been developed to study how community-level trait attributes control EP. One is to analyse individual and combined effects of environmental factors and functional traits (CWM and CDM) on different EP in a stepwise sequence (Díaz *et al.* 2007b). This is a straightforward procedure, however it does not account for the role that functional diversity response to environmental factors might play for EP. The second strategy integrates this aspect by simultaneously modelling functional trait response to environmental gradients and functional trait effects on EP (Suding *et al.* 2008). This 'response-effect framework' can be used to disentangle the relevance of direct environmental effects on EP versus the relevance of indirect, trait mediated effects. Response-effect modelling requires additional data, hence it might be more elaborate than the stepwise modelling of EP response.

Both strategies to assess EP response to community-level trait attributes should be generally applicable at the landscape scale. Nevertheless, so far they have been mainly applied in homogenous ecosystems like grasslands (de Bello *et al.* 2010; Lavorel 2013), whereas experiences from heterogeneous landscapes are still rare (e.g. Lavorel *et al.* 2011; Paquette & Messier 2011; Conti & Díaz 2013). Moreover, agroecosystems and cultivated land have been largely excluded from functional diversity based assessments of EP response (Wood *et al.* 2015). These research gaps need to be filled in order to evaluate in how far stepwise EP response modelling and response-effect modelling can be utilized for EP sensitivity assessments at the landscape scale.

In order to address these issues, in this thesis the suitability of both strategies for the assessment of EP sensitivity in a heterogeneous landscape comprising natural and cultivated land was examined (Chapter 4 and 5). The question was in how far the additional efforts required for response-effect modelling compared to stepwise EP response modelling are justified by information gains. In both studies functional diversity was solely represented by plant functional traits, which is in accordance to the majority of functional diversity research (Lavorel *et al.* 2013). This is founded on the fact that plants, as primary producers, influence a wide range of EP and major ecosystem functions, like primary productivity and decomposition (Díaz & Cabido 2001).

1.5 Thesis objective and research questions

This thesis pursued two major objectives:

- (1) to explore the specific sensitivity of biodiversity and ecosystem properties in North-East Tanzania and to draw conclusions for the vulnerability of local ecosystem functioning and the provision of ES.
- (2) to compare the applicability and informative value of land cover and functional trait based approaches for the assessment of biodiversity and EP sensitivity in heterogeneous landscapes.

The investigation of biodiversity and EP sensitivity in the research area was guided by the following questions:

- How sensitive are different land cover types, plant functional diversity and ecosystem properties in the research area to changing environmental factors and disturbances?
- What does this imply for ecosystem functioning and future ecosystem services provision in the research area?
- What can be done to reduce negative effects on ES provision in the research area?

The comparison of different approaches to study biodiversity and EP sensitivity in heterogeneous landscapes was guided by the following questions:

- What are the advantages and disadvantages to assess ecosystem properties' sensitivity in heterogeneous landscapes based on discrete versus continuous measures of biodiversity?
- How relevant are biotic responses to environmental gradients for the sensitivity of EP in heterogeneous landscapes? Is crucial information lost if biotic responses are disregarded at the landscape scale?
- How can both approaches to study EP sensitivity in heterogeneous landscapes be combined into a general protocol

Chapter 2

Research area and general study design

2 Research area and general study design

2.1 Criteria for the selection of the research area

The selection of a study area where the major research questions of this thesis could be properly investigated was guided by the following criteria.

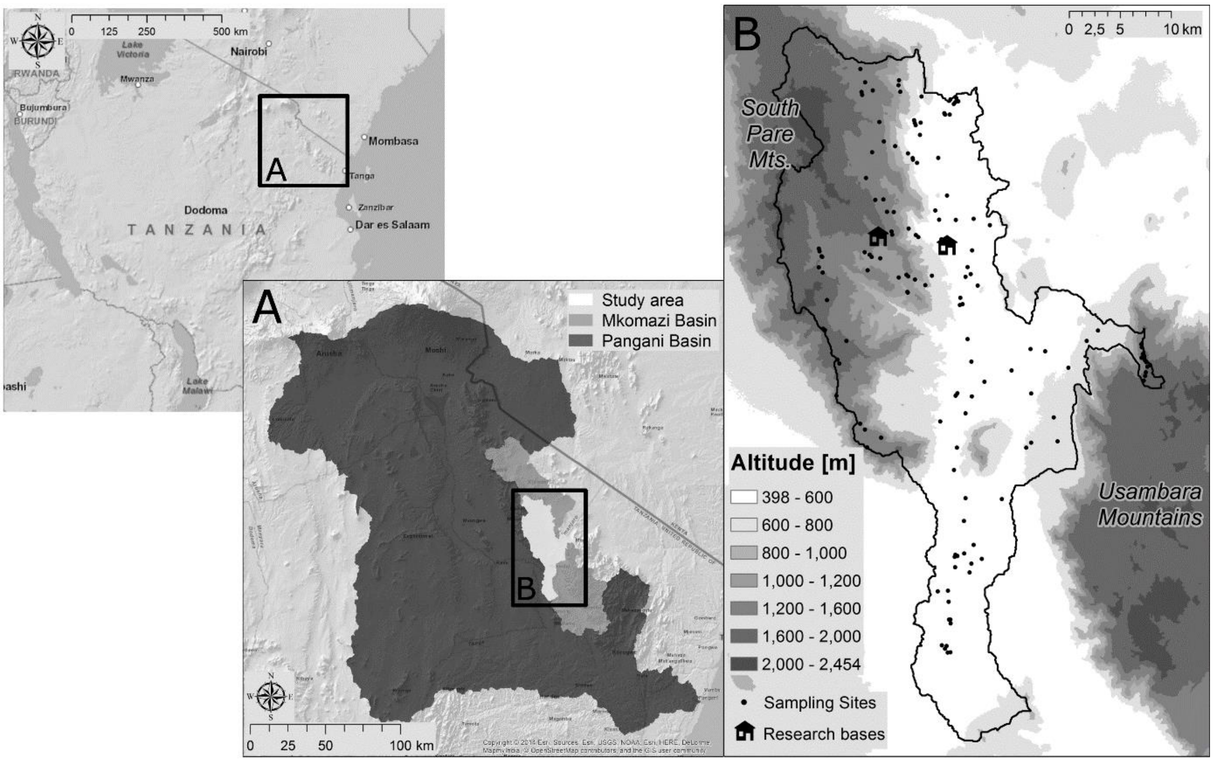
In order to facilitate an adequate representation of the target region North-East Tanzania, the research area had to comprise characteristic ecosystems like grass-, bush- and woodland savanna, forests and swamps (cf. Knapp 1973). Moreover, common land use activities of the region, including farming, pasturing, logging and charcoal production (cf. Lambin, Geist & Lepers 2003) had to be covered. The intended comparison of different approaches for the assessment of biodiversity and EP sensitivity in heterogeneous landscapes required to select a study area where wide ranges of environmental conditions and disturbances entail a high diversity of ecosystems. Finally, this research targeted areas where local economies highly depend on ecosystem services and where at the same time environmental changes and land use intensification are imminent.

In semi-arid regions like North-East Tanzania, the aforementioned required conditions can be found in perennial river basins that connect relatively dry areas with humid headwaters. Contrasting climatic conditions and differences in water and nutrient availability facilitate a high diversity of ecosystems and land use activities in these river basins. Land use activities in North-East Tanzania usually concentrate on water source areas and river floodplains due to the convenient availability of water resources and favourable soil conditions (PBWO & IUCN 2009; Notter 2010). Accordingly, these areas are particularly concerned by the intensification and expansion of land use activities in the region. In order to evaluate how these developments might affect ES provision across river basins in North-East Tanzania, data on biodiversity and EP sensitivity are needed urgently.

On account of this context, a perennial river basin in North-East Tanzania was proposed to be suitable as study area for this research. The central Mkomazi River Basin was selected since this area provided a reasonable compromise between feasible size and sufficient representation of all important ecological features of the region.

2.2 Central Mkomazi Water Basin

This research was carried out in the basin of Mkomazi River which is a major tributary of Pangani River, the largest stream in North-East Tanzania (PBWO & IUCN 2009). Mkomazi River drains wide endorheic swamps around the Tussa and Kisima Hills as well as the moist South Pare and West Usambara mountain ridges (Figure 3). In order to reduce the study area to a feasible size it was limited to the central part of the basin, which is hydrologically most relevant and 1100 km² large.

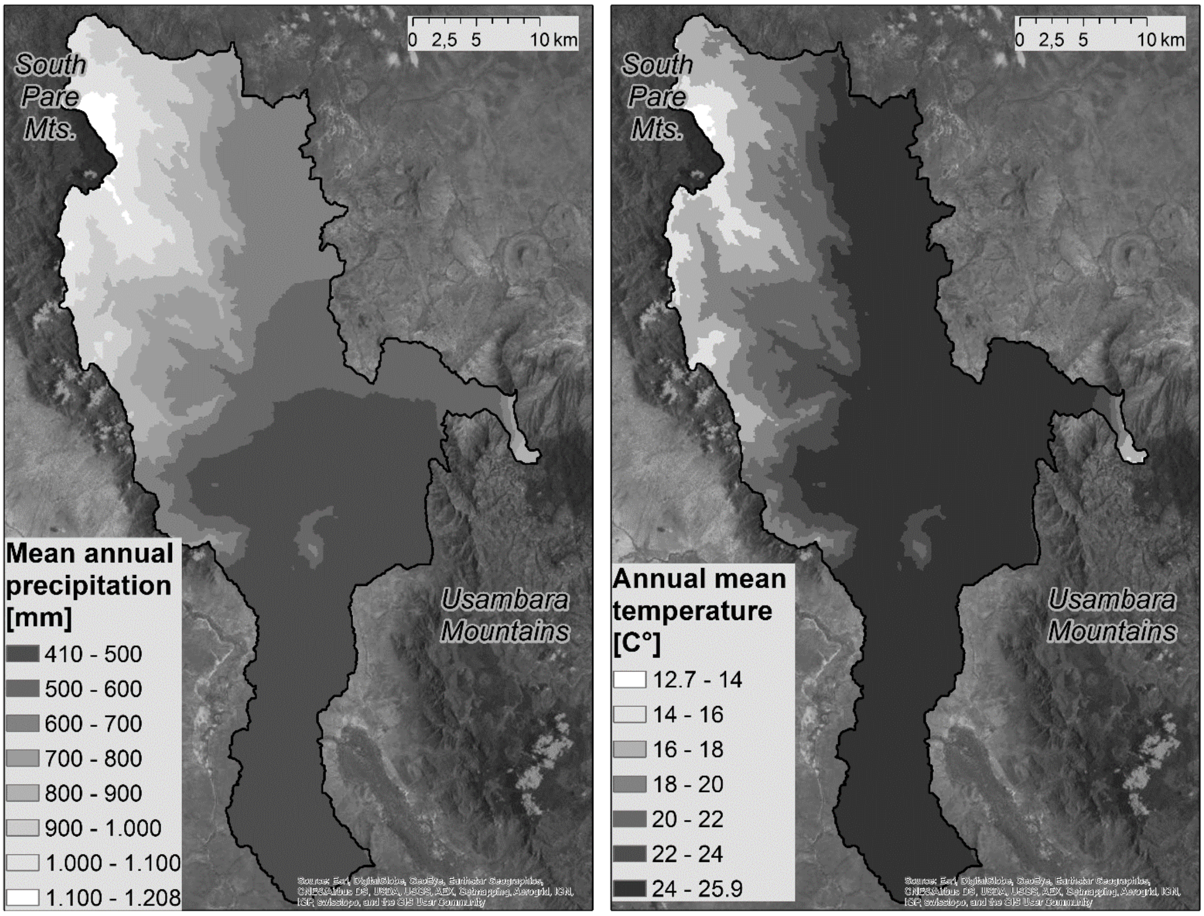


Source: Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Figure 3. Location of the research area. Left: location of Pangani Basin in Tanzania. Centre: location of Mkomazi Basin and the research area within Pangani Basin. Right: Map of the research area with sampling sites and research stations. Elevation data: SRTM (Jarvis et al. 2008)

The central Mkomazi Water Basin is characterized by contrasting climatic conditions and water availability. While the South Pare and Usambara Mountains enjoy sufficient rainfall and cool climate during most times of the year, the valley is rather dry and hot, particularly in the southern half. This area is insulated from easterly rainfall by the Usambara Mountains (Figure 4). Base flow from the highlands feeds Mkomazi River and connected floodplains, therefore in this riparian zone water availability is high despite the semi-arid valley climate.

Geological maps (GST 1965; GST 2005) and soil pit data from sampling sites revealed that the study area features a large spectrum of soil types. Built from Precambrian metamorphic rocks, a variety of acidic soils have developed on the mountain blocks. These include Leptosols and Cambisols on eroding slopes as well as deeply weathered Ferralsols and Umbrisols in more stable sites (e.g. under pristine forest). In the valley slightly acidic to extremely alkaline soils have developed from different sediments. On red and yellow sands Ferralsols and Acrisols are abundant; the extensive swamps in the northern part of the study area are characterized by Vertisols (black cotton soils); Fluvisols and Gleysols have developed on alluvial sediments; in areas with surface limestone Calcisols predominate.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community

Figure 4. Maps of mean annual precipitation (left) and annual mean temperature (right) in the research area. Both maps were based on climatic data provided by G. Mmbando & M. Kleyer (unpubl. data)

The long environmental gradients facilitate a high diversity of ecosystems. Remarkable evergreen cloud forests naturally cover the mountain areas. These are part of the 'Eastern Arc Biodiversity Hotspot', a chain of montane evergreen forests rich in endemic plant and animal species that inhabit mountain ridges in Kenya and Tanzania (Burgess *et al.* 2007). Along perennial streams, the evergreen forests reach into less humid slope sections further downhill. These intermediate slopes as well as the foothills are predominated by deciduous woodlands with *Combretum*, *Commiphora* and *Adansonia* species. On the plains of the northern part of the valley relatively moist conditions support deciduous *Acacia* woodlands, whereas in the south deciduous *Acacia-Commiphora* bushlands are most abundant. The floodplains and swamps along Mkomazi River are accompanied by a reservoir (Kalimawe) and two natural lakes (Karamba and Manka) with strongly fluctuating water levels. In these wetland areas reeds and grasslands predominate; locally halophytic communities occur. Groundwater and stream flow from Hingilili River, one of the larger streams emerging from the South Pare Mountains, support a unique evergreen lowland forest near Gonja town.

A lot of different land use activities are supported in central Mkomazi Water Basin. Economically most important is farming (Notter 2010). Hotspots are located in the cool highlands of South Pare and Usambara Mountains as well as the wetlands along Mkomazi River in the semi-arid valley. In the mountains pristine cloud forests partly have been transformed into irrigated terrace farms and rain-fed agroforestry systems, denoted elsewhere as homegardens (Hemp 2006). Along perennial streams, these farmlands (terraces) reach down to the foothills. In the floodplains and swamps along Mkomazi River extensive irrigation schemes have been set up for rice cultivation in paddy fields (JICA 1984). The deciduous woodlands on the mountain slopes and the bushland savannahs in the valley are less suitable for farming due to remoteness, slope and water scarcity. Accordingly, only scattered rain-fed farms have been established in these areas. Another important land use activity in the study area is livestock grazing, which concentrates on grasslands in wetland areas affected by salinization and the extensive bush- and woodland savannas in the lowlands. Occasionally flocks of livestock are grazing also on the foothills and slopes of South Pare and Usambara Mountains. In the highlands however, livestock husbandry commonly is stationary. In most parts of the study area, wood extraction for charcoal, firewood and timber production is a crucial alternative source of income (Notter 2010; Schaafsma *et al.* 2012). Virtually all ecosystems with woody plants are used, forests mainly for timber and savannas for fuelwood. In addition, traditional medicines and vegetables are collected from these ecosystems. Finally, Kalimawe Reservoir, Lake Karamba and Lake Manka are regionally relevant sources of fish.

In particular logging, fuel wood extraction and forest clearance for farms have been causing considerable land cover changes in Mkomazi Water Basin, similar to reports from all over the Eastern Arc Mountains (Burgess *et al.* 2007). Furthermore, expansion of paddy fields into reeds and grasslands as well as bushland degradation due to overgrazing in the vicinity of settlements are ongoing land cover changes observed during field visits.

2.3 General sampling design and GIS data processing

In order to determine the inventory of ecosystems across all environmental gradients in the study area, satellite imagery (Google Earth™) analysis and ground truthing were carried out. Based on the gathered data and Knapp's (1973) classification of African vegetation, 30 preliminary land cover units were designated. In each of them four to six sampling sites (total number: 150) were distributed randomly. However, strictly random stratified sampling could not be realized, since parts of the study area were not accessible. Regular sampling sites had dimensions of 10 x 10 m, but in linear structures such as riparian woodlands they measured 5 x 20 m to ensure homogeneity.

Field work was undertaken between October 2011 and December 2012. Survey dates were optimized to ensure full vegetative development of the majority of plants in each site. Moreover temporal inaccessibility of several sampling sites during rainy seasons had to be considered. Deciduous savanna, rain-fed farms, homegardens, plantation forests and fallow land were mainly surveyed during the rainy seasons (November and December, March to May); swamp areas and paddy rice fields mainly during the short dry season (January and February); and highland forests and riparian woodlands mainly during the long dry season (June to October). At each sampling site topographic features, soil conditions, disturbances, vegetation structure and plant functional traits were measured. Detailed methods of data collection and analysis relevant for the specific research questions in Chapters 3, 4 and 5 are described in the respective chapters. Here the focus lies on GIS analyses of remote sensing and map data to generate some of the base data used in Chapters 3, 4 and 5.

The following spatial data sources were used:

- A digital elevation model (DEM) based on SRTM data (Shuttle Radar Topography Mission) with a spatial resolution of 90 x 90 m and a measurement accuracy of ± 1 m (Jarvis *et al.* 2008)
- Topographic maps distributed by the Surveys and Mapping Division of the Tanzanian government in Dar es Salaam at a scale of 1:50,000 (SMD 1974; SMD 1988)
- Geological maps distributed by the Geological Survey Division of the Tanzanian government in Dodoma at a scale of 1:125,000 (GST 1965; GST 2005)
- A digital administrative map of ward boundaries (Notter 2010)
- Satellite images derived from Google Earth™
- Digital maps of yearly net primary productivity obtained from MODIS data (Moderate Resolution Imaging Spectroradiometer) for the years 2000 to 2010 with a resolution of about 1 km² (NTSG & UMT 2014)

Based on these spatial data sources, maps of inclination, compound topographic index (CTI), distance to next waterbody and population density were generated using the Spatial Analyst toolbox in ArcGIS 10.1. The inclination map was derived directly from the DEM. CTI, also known as topographic wetness index, was calculated at each raster cell according to (Beven & Kirkby 1979):

$$CTI = ln\left(\frac{A_s}{\tan\beta}\right)$$

where A_s is the area of flow generation above each raster cell ("specific catchment area") and β is the slope at each raster cell (Gessler *et al.* 1995).

Distance to next water body was introduced as another indirect estimate of groundwater availability. However, it was not calculated as simple geographical distance from each raster cell to the next stream or lake, since this would have neglected the expected differences in water availability between flat and sloping areas. Instead, inclination was used as a factor to increase distance to next water body in sloping areas. Additionally, it was assumed that in flat areas the relevance of one unit change in inclination for water availability is higher than on steep slopes. To account for this effect, inclination was logarithmized. Prior to that all raster cell values below 1.1 were set to 1.1 to avoid calculation errors for non-defined solutions (logarithm not defined for values < 1, cost-distance tool in Spatial Analyst does not allow values of 0). The raster map of water bodies for the distance calculation was derived from satellite pictures, topographic maps and a flow accumulation raster (Spatial Analyst calculation based on the DEM).

A population density map was generated from the map of ward boundaries, ward population data from NBS and OCGS (2013) and satellite imagery. Based on the satellite images, polygons of populated and unpopulated areas were delineated and each populated polygon was assigned a population number P_{poly} as follows:

$$P_{poly} = \frac{P_{ward} \times A_{poly}}{A_{pop}}$$

where P_{ward} is the population number of each ward, A_{poly} the size of the polygon and A_{pop} the size of all populated areas in the respective ward. The population density of each polygon was calculated as P_{poly} divided by A_{poly}. In a next step, all populated polygons were transformed into raster points (300 x 300 m). To all points that emerged from an individual polygon, the population density of this polygon was assigned. Based on the raster points, the final population density map was derived from kernel density calculations with a search radius of 3300 m.

Apart from the generation of secondary variables, the spatial source data was used to upscale soil features measured at plot level to the landscape scale. This was done by the determination of linear least squares regression models. Soil-pH was predicted from inclination and the geological units (R^2 = 0.58, p-value < 0.001), electric conductivity was predicted from soil-pH (R^2 = 0.72, p-value < 0.001) and carbonate content was predicted from soil-pH and electric conductivity (R^2 = 0.77, p-value < 0.001). These data were used for the analyses covered by Chapter 3.

Chapter 3

Assessing land cover tolerance to environmental gradients in North-East Tanzania

3 Assessing land cover tolerance to environmental gradients in North-East Tanzania

Maximilian Petzold

Pius Z. Yanda

Michael Kleyer

Abstract

Land cover distribution in Africa has been found to be largely governed by rainfall, however the relevance of disturbance might have been underestimated. This study aimed to investigate this issue and to determine land cover tolerance to environmental change in North-East Tanzania. Data on vegetation structure, abiotic factors and disturbance were sampled in 150 survey plots in the central Mkomazi Water Basin. Multivariate logistic regression analysis and model averaging based on information theory were applied to determine the relevance of environmental factors for land cover distribution and to calculate tolerance measures. Climatic factors were among the most important determinants for the distribution of 11 out of 15 modelled land cover units. Disturbance was of slightly higher relevance since it considerably influenced 14 land cover units. Highly tolerant land cover units occurred in intermediate ranges of environmental gradients; those of less tolerance were found near gradient extremes. Evaluation of land cover vulnerability based on tolerance measures should consider which environmental factors restrict tolerance and where optima are located along environmental gradients. Given their low tolerance to disturbance and climate and their limited ability to shift in space, evergreen highland forests and traditional homegardens were most vulnerable.

3.1 Introduction

The distribution of land cover, which describes natural and cultivated vegetation as well as man-made features, is determined by the spatio-temporal variability of abiotic factors, biotic interactions and human land-use (Jansen & Di Gregorio 2002; Di Gregorio & Jansen 2005). Some of these drivers are subject to severe changes, particularly on the African continent. For example, economic development and population growth entail rapid land-use changes in various African regions (Lambin, Geist & Lepers 2003). Furthermore, regional impacts of global climate change have started to emerge during the last few decades which included rising temperatures and higher variability in seasonal rainfall (Niang *et al.* 2014). Climate and land-use change cause shifts in land cover distribution, often at the expense of ecosystem services (Vitousek *et al.* 1997; Lambin, Geist & Lepers 2003) which are essential for African livelihoods (van Jaarsveld *et al.* 2005). Land management aiming to halt adverse land cover changes relies on the identification of all relevant determinants of land cover distribution as well as information about the tolerance of land cover types to environmental change.

Studies at continental and regional scales have consistently identified rainfall as the most important determinant of land cover distribution in Africa (Bucini & Hanan 2007; Sankaran, Ratnam & Hanan 2008; Greve *et al.* 2011). At smaller scales however, other factors, such as soil nutrient availability or disturbance, are relevant as well (Murphy & Bowman 2012). Despite these insights, further research is required to fully understand land cover distribution in specific African regions. Some studies focused solely on woody plant cover (Bucini & Hanan 2007; Sankaran, Ratnam & Hanan 2008) and it remains unclear if their results can be transferred to land cover units. Moreover, several studies excluded cultivated land from their analyses (but see: Bucini & Hanan 2007). Therefore, substantial disturbances related to farming were not represented in these studies (e.g. ploughing). Possibly, this led to an underestimation of the importance of disturbance for land cover distribution. Finally, knowledge about the potential of specific land cover types to tolerate changes in major drivers, like decreasing rainfall for instance, is still strongly limited. We addressed these issues by analysing responses of natural and cultivated land cover types to environmental factors in North-East Tanzania, a region which comprises typical land cover features of semi-arid, tropical Africa.

The distribution of individual plant species along environmental gradients and their tolerance to environmental changes can be successfully determined by application of approaches derived from the niche concept (Hutchinson 1957). Based on presence/absence data, species' occurrences within a multi-dimensional space of environmental gradients are predicted (Elith & Leathwick 2009). Moreover, these predictions can be easily employed to calculate breadth and position of species' niches (Peppler-Lisbach 2008). As Broennimann *et al.* (2006) and Thuiller, Lavorel and Araujo (2005) showed, these are useful measures of species' tolerance to environmental change. Since most land cover types are characterized by one or more dominant plant species (Di Gregorio & Jansen 2005), their distribution is bound to the combined niches of these species. It is, however, questionable as to how far an application of the niche concept to land cover distribution patterns is feasible. For instance, expansion of cultivated land at the expense of natural ecosystems is controlled by socio-economic factors, which cannot be explained by the niche concept (Lambin, Geist & Lepers 2003). In spite of that, available statistical methods for the analysis of species distributions are also suitable to assess the distribution of plant communities and land cover types (Peppler-Lisbach 2003). Accordingly, we expected that measures analogical to niche breadth and position should be useful to evaluate land cover tolerance which we defined as follows:

(1) The volume occupied by a land cover type within the multi-dimensional environmental predictor space (MEPS), henceforth called 'volume of predicted occurrence' (VPO).
(2) The range length along a specific environmental gradient occupied by a land cover type, henceforth called 'range breadth'.

In this paper we applied multivariate regression analysis to determine the importance of environmental and anthropogenic factors for the distribution of land cover. Furthermore, we estimated VPOs and range breadths for different land cover types and used them as measures of land cover tolerance. Finally, we assessed potential effects of future climate and land use change on land cover.

We hypothesized that climatic factors are the major drivers of land cover distribution in North-East Tanzania (hypothesis H1a). Furthermore, we expected that disturbance is a crucial determinant as well since our study integrated natural and cultivated land (H1b). Studies of species' tolerance to environmental change have revealed that species occurring near the extremes of environmental gradients have smaller niche size than those occurring near the centroid (Thuiller, Lavorel & Araujo 2005; Broennimann *et al.* 2006). Accordingly, we hypothesized that land cover types occurring under the most extreme conditions are least tolerant to environmental change (Hypothesis H2).

3.2 Materials and Methods

3.2.1 Study area

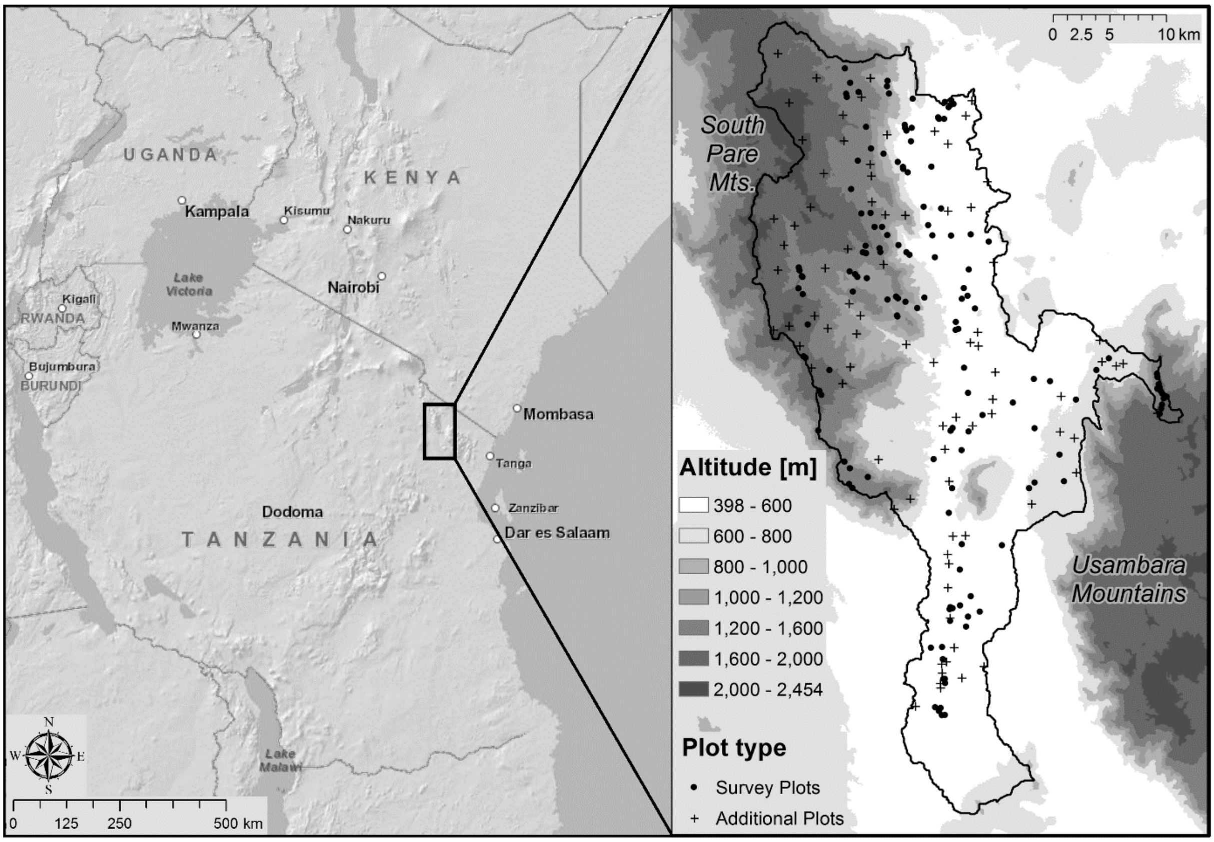


Figure 5. Location of the study area in Tanzania. Right: Extent of the study area and locations of field sampling sites and additional plots. Elevation data: SRTM (Jarvis *et al.* 2008)

Our study area was located in the central Mkomazi Water Basin, which adequately represented the high variation in environmental conditions of North-East Tanzania. It comprised the eastern flank of the South Pare Mountains, part of the western slope of the West Usambara Mountains and the large valley of Mkomazi River between these two mountain ridges (Figure 5). It has a North-South extension of 68 km (4°13'-4°50' S), a West-East extension of 37 km (37°54'-38°15' E) and a size of 1100 km^2. Features of climate, soils, land use as well as major land cover types of the study area have been described in Chapter 2.2.

3.2.2 Field surveys

In order to capture the variation in environmental conditions and the distribution of land cover types, 150 sampling plots were spread over the study area in a randomly stratified manner. Each plot had an area of 100 m^2 with dimensions of 10 × 10 m or 5 × 20 m in case of linear structures, such as riparian vegetation. In each plot, topography, disturbance, vegetation structure and dominant plant species were recorded. Disturbance data comprised information on intensity and frequency of logging, mowing, ploughing, fire, erosion and grazing. We estimated the yearly percentage loss of total plot plant biomass by these disturbances. The individual losses were summed up to yield a disturbance index. A disturbance index of value 1 represented a plant biomass removal of 100% a^{-1}, as in fields ploughed once a year. However, grazing could not be integrated into this index, as it was mostly nomadic and not restricted to fenced pastures. Therefore, an additional grazing index was calculated as the product of grazing frequency and dropping density weighted by the kind of grazing livestock (cows: 1, donkeys: 0.8, sheep and goats: 0.2). A value of 1 indicated one cow pat per plot at a grazing frequency of 365 $d \cdot a^{-1}$.

Furthermore, a soil pit of 1 m depth (on stony ground less) was dug in each site. Soil samples were collected from each soil horizon to a depth of 100 cm, air dried and sieved (2 mm). Carbonate content was determined on a seven-tier categorical scale (mass-% Carbonate 0 to > 10) based on audio-visual soil reaction to HCl (10%) (Ad-Hoc-AG Boden 2005). Soil pH was measured with indicator paper in soil-$CaCl_2$ dilutions. Electric conductivity of soil-water dilutions was quantified with a WTW TetraCon® 325 sensor.

3.2.3 Land cover classification

The classification of land cover in the study area was based on the Land Cover Classification System (LCCS), developed by Di Gregorio and Jansen (2005). LCCS is a hierarchical system where land cover classes are defined by different 'classifiers', which

Table 1. Classifiers applied for land cover classification in central Mkomazi Water Basin and resulting land cover units based on the Land Cover Classification System (Di Gregorio & Jansen 2005). At first, a general land cover unit (LCU) was assigned (NV – Natural and semi-natural vegetation, CT – Cultivated and managed terrestrial areas, NAV – Natural and semi-natural aquatic or regularly flooded vegetation, CA – Cultivated aquatic or regularly flooded areas). Secondly, different levels of classifiers were applied to specify final LCUs. Traits used for classifier levels I to III depended on the general LCU

General LCU	Level I classifiers	Level II classifiers	Level III classifiers	Final LCU and Abbreviations
NV	Closed to open shrubs, 1.5-3 m	evergreen	Suaeda monoica	Suaeda shrubland (Suaeda)
NV	Open shrubs, 3-5 m	deciduous	Acacia spp.	Acacia shrubland (Acacia)
NV	Closed to open shrubs, 3-5 m	mixed	-	Mixed thicket and shrubland (Thicket)
NV	Open trees, 3-7 m	deciduous	Commiphora spp.	Commiphora woodland (Comm)
NV	Closed to open shrubs 3-5 m / open trees 7-15 m	deciduous	Adansonia digitata, Combretum spp., Acalypha spp.	Deciduous shrub- and woodland on slopes** (WoSlope)
NV	Closed trees, 15-25 m	evergreen	Vepris spp.	Dry evergreen slope forest* (ForSlope)
NV	Closed trees, >25 m	evergreen	Milicia excelsa	Evergreen lowland forest* (ForLow)
NV	Closed trees, >25 m	evergreen	Parinari excelsa	Evergreen highland forest (ForHigh)
NV	Closed to open shrubs 1.5-3 m / closed forbs 0.3-3 m	mixed	Pteridium aquilinum	Mixed fallow grass- and shrubland** (Fallow)
NAV	Closed to open graminoids, 0.3-3m	temporary flooded	-	Temporary flooded reed and grassland (ReedGras)
NAV	Open trees, 7-15m	temporary flooded	Hyphaene thebaica, Acacia seyal	Temporary flooded woodland (WoFlood)
NAV	Closed to open trees, 15-25m	temporary flooded	-	Riparian woodland (WoRipar)
CA	Graminoids	irrigated	Rice	Paddy rice farms (FarmRice)
CT	Herbaceous and shrubby crops	rain-fed	Maize, beans, sisal	Rain-fed farms** (FarmRain)
CT	Herbaceous and shrubby crops	irrigated	Ginger, potatoes, cassava, maize	Irrigated terrace farms** (FarmTera)
CT	Tree crops	rain-fed	Bananas, cocoyam	Homegardens (FarmTree)
CT	Tree plantations	rain-fed	Eucalyptus spp., Acacia mearnsii	Plantation forest (ForPlant)

* Land Cover Unit not included in modelling due to limited geographical extent

** Combined Land Cover Unit

can be applied at different levels of detail. Hence, the classification for a specific site can be adapted to the desired resolution by addition or reduction of classifier levels. Based on LCCS classifiers, we identified 17 land cover units (Table 1). Two of them had negligible spatial extent in the study area and were excluded from the modelling.

3.2.4 Data preparation

Based on topographic maps from Surveys and Mapping Division Tanzania (scale 1:50,000), geological maps from Geological Survey Division Tanzania (scale 1:125,000), Google Earth™ satellite imagery and a Digital Elevation Model (DEM) derived from Shuttle Radar Topography Mission (SRTM) data (Jarvis *et al.* 2008), a GIS database was established. Records of soil conditions from the survey plots were upscaled to maps by linear regression with DEM and geology raster data. Based on a map of administrative borders, recent ward-specific population data (NBS & OCGS 2013) and satellite pictures to exclude unsettled areas, a population density map was created (see Chapter 2.3). By application of the ArcGIS Cost Distance Tool to log-transformed inclination data, a map illustrating the distance to the next waterbody was calculated. Finally, we obtained climatic data from a study by G. Mmbando & M. Kleyer (unpubl. data).

Due to poor accessibility of steep mountain slopes and swamps, it was not possible to consistently sample the entire environmental gradient range of the central Mkomazi Water Basin. In order to fill gaps and to facilitate robust distribution modelling, we introduced 83 additional plots, which were gained by stratified random selection (Figure 5). Land cover unit, climate, topography, soil and population data for these sites were obtained from our GIS database. Disturbance and grazing data were generated by logspline density estimation based on the observed variation in our field data. An overview of the data sources for model building in the field survey plots and the additional plots is given in Table 2.

3.2.5 Fitting and validation of logistic regression models

We assessed the land cover distribution in our study area and identified major drivers by application of Generalized Linear Models (GLM) with logit link (see Peppler-

Table 2. Predictors for land cover modelling. Data for 150 sampling plots (a) and 83 additional plots (b) originated from: Field – Field surveys, GIS – GIS database, LS – logspline density estimation

Environmental predictor	Abbreviation	Predictor set	Data source
Mean annual rainfall	RainAnn	Climate	GIS[a,b]
Mean dry season rainfall (May-October)	Rain5_10	Climate	GIS[a,b]
Mean wet season rainfall (November-April)	Rain11_4	Climate	GIS[a,b]
Annual mean temperature	TMean	Climate	GIS[a,b]
Mean annual maximum temp.	TMax	Climate	GIS[a,b]
Mean annual minimum temp.	TMin	Climate	GIS[a,b]
Mean annual potential evapotranspiration	ETpAnn	Climate	GIS[a,b]
Mean annual net rainfall*	netRainAnn	Climate	GIS[a,b]
Mean dry season net rainfall*	netRain5_10	Climate	GIS[a,b]
Mean wet season net rainfall*	netRain11_4	Climate	GIS[a,b]
Inclination	Incl	Topography	Field[a], GIS[b]
Distance to next water source	DToWat	Topography	GIS[a,b]
Compound topographic index	CTI	Topography	GIS[a,b]
Soil pH	pH	Soil	Field[a], GIS[b]
Carbonate content	Carb	Soil	Field[a], GIS[b]
Conductivity	Cond	Soil	Field[a], GIS[b]
Population density	PopDens	Population Density	GIS[a,b]
Disturbance index (fire, logging, mowing, ploughing)	Disturb	Disturbance	Field[a], LS[b]
Grazing index	Grazing	Disturbance	Field[a], LS[b]

* Net rainfall: rainfall subtracted by evapotranspiration

Lisbach (2003) for an example of GLM-based land cover distribution modelling). Multivariate logistic regression models predicting the distribution of each land cover unit were fitted using the R-function 'logistf' (Heinze *et al.* 2013). Robust candidate models with Δ-AIC (Akaike Information Criterion) of less than 10 were averaged based on AIC-weights as suggested by Burnham and Anderson (2002). This gave a final model for each land cover unit. The importance of each explanatory variable in these final models was calculated as the summed AIC-weights of all candidate models which contained the respective variable. Additionally the final model output provided performance measures, namely AUC (Area under the ROC curve) and Cohen's Kappa (Cohen 1960). The discrimination between predicted presence and absence necessary for their calculation was based on thresholds maximizing Kappa values as suggested by Peppler-Lisbach (2008). More details concerning the model building process can be obtained from Kattwinkel *et al.* (2009).

Tenfold cross-validation was carried out to validate the land cover models. We divided our dataset into 10 subsets of identical size. Stratified random selection ensured equal representation of all land cover units within each subset. Based on nine subsets, we performed fitting and averaging of models and subsequently tested model performance on the remaining 10th subset. This procedure was repeated, until each of the 10 subsets was excluded from model building and used for model validation once. Finally, Kappa and AUC statistics extracted from all 10 cross-validation runs were compared to those from the original models.

3.2.6 Calculation of land cover tolerance measures

In order to limit computational effort, we restricted the calculation of volumes of predicted occurrences (VPO) to the six most important land cover determinants. These had been identified in the primary land cover models based on all environmental variables listed in Table 2 (Regression Analysis 1). At first, model building and validation were repeated for the reduced dataset (Regression Analysis 2). Furthermore, we determined the approximate geometry of the multi-dimensional environmental predictor space (MEPS) for our study area. This was done using the R-package 'hypervolume' (Blonder *et al.* 2014), which performed a multivariate kernel density estimation of the MEPS.

In order to determine the MEPS region occupied by each individual land cover, we extracted 12^6 evenly distributed sample points from all areas of the MEPS. At each sample point the occurrence probability of each land cover unit was calculated by applying the averaged logistic regression models gained in Regression Analysis II. To distinguish between presence and absence we applied a Kappa-optimizing threshold. The number of presences obtained for each land cover unit in relation to the total number of sample points (12^6) represented the relative VPO of the respective land cover unit. We assigned low tolerance to land cover units with small VPO and high tolerance to land cover units with large VPO. Finally, we extracted predictor-specific range breadths for each land cover unit from the estimated VPO.

3.3 Results

Disturbance was the most important predictor group to describe land cover distribution in the study area as Regression Analysis I revealed (Table 3). Climatic and topographic factors were highly relevant as well. The most important single explanatory variables in Regression Analysis I were disturbance index – which was relevant for 11 land cover units – grazing index, wet season rainfall, mean annual minimum temperature, distance to next water source and compound topographic index (Table A 1). These variables were retained for Regression Analysis II to calculate volumes of predicted occurrences (VPO) and range breadths. Results concerning importance of land cover predictors outlined in this chapter derived from Regression Analysis I. For Regression Analysis II this information can be found in Table A 2.

Based on their altitudinal distribution, we grouped the 15 prevalent land cover units of the central Mkomazi Water Basin into three ecological zones: highlands (> 1200 m asl), slopes (> 600 m to 1200 m asl) and lowlands (up to 600 m asl). These zones were characterized by strong differences in mean annual minimum temperature and total wet-season rainfall (highlands: 11.4 °C, 689 mm; slopes: 17.2°C, 534 mm; lowlands: 20°C, 430 mm).

The predominant land cover unit in the highlands was species-rich, indigenous evergreen highland forest (ForHigh). However, considerable forest areas have been transformed into homegardens (FarmTree), *Eucalyptus* and *Acacia mearnsii* plantation forests (ForPlant) or secondary communities of grasses, *Pteridium aquilinum* and shrubs (mixed fallow grass- and shrublands: Fallow).

Climate and disturbance were the most important predictor sets for land cover distribution in the highlands (Table 3). While ForHigh and FarmTree were limited to low disturbance and ForPlant was confined to low annual minimum temperatures, Fallow tolerated a relatively wide range of annual minimum temperature (Figure 6, Table A 3). Accordingly, VPO of ForHigh, FarmTree and ForPlant were small, whereas Fallow had a relatively large VPO. According to the Kappa values, ForHigh, FarmTree

Table 3. Importance of predictor sets (see Table 2) in averaged multivariate land cover models. All groups with at least one predictor of relative importance >= 0.5 are marked with x. Land cover unit abbreviations: see Table 1

	Land Cover Unit	Climate	Topography	Soil	Disturbance	Population Density
Highlands	ForPlant	x	-	-	-	-
	Fallow	x	-	-	x	-
	ForHigh	x	-	-	x	-
	FarmTree	-	-	-	x	x
Slopes	FarmTera	-	-	x	x	x
	WoSlope	x	x	-	x	-
	FarmRain	x	-	-	x	-
	WoRipar	x	x	-	x	-
Lowlands	Comm	x	x	-	x	-
	Thicket	x	x	-	x	-
	WoFlood	x	x	-	x	-
	FarmRice	-	x	-	x	-
	ReedGras	-	x	-	x	-
	Acacia	x	x	-	x	-
	Suaeda	-	x	-	x	-
Sum		10	9	1	14	2

and ForPlant models showed good to excellent performance in Regression Analyses I and II, even under consideration of deviations in cross-validation (Table 4). In contrast Fallow model performance was poor, particularly in Regression Analysis II.

Mountain slopes were characterized by deciduous shrub- and woodlands (WoSlope) (communities distinguished by *Adansonia digitata*, *Sterculia appendiculata* and *Combretum molle*). Along streams and rivers WoSlope was intersected by riparian woodlands (WoRipar). Depending on the availability of irrigation water, irrigated terrace farms (FarmTera) (main crops: ginger, cassava, maize) or rain-fed farms (FarmRain) (main crops: maize, beans, sisal) were found in the vicinity of settlements.

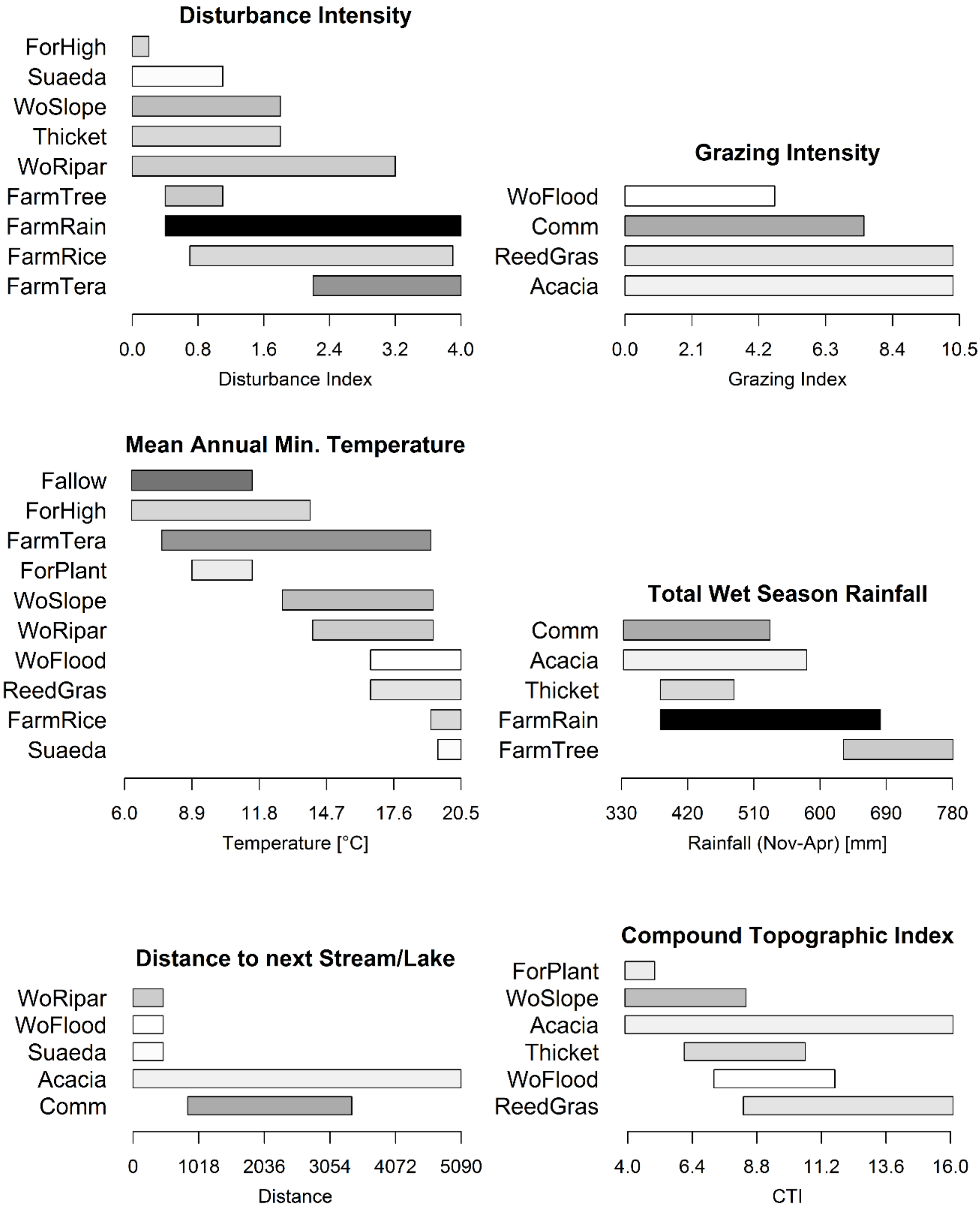


Figure 6. Importance of predictor sets (see Table 2) in averaged multivariate land cover models. All groups with at least one predictor of relative importance >= 0.5 are marked with x. Land cover unit abbreviations: see Table 1

Disturbance was the most relevant predictor set for these land cover units, followed by climate and topography (Table 3). Generally, range breadths of land cover units on the mountain slopes were moderate or large along most predictor variables (Figure 6, Table A 3). For example, along the disturbance index optimal ranges of WoSlope and FarmTera were moderately wide and those of WoRipar and FarmRain almost boundless. This explains the large VPO of FarmRain and the moderate VPO of FarmTera and WoSlope. Conversely, the VPO of WoRipar was relatively small as it only occurred close to water bodies. Model performance for WoRipar, WoSlope and FarmTera was good to excellent (Table 4) and even under consideration of bias in cross-validation satisfactorily. Nevertheless, WoSlope and FarmTera performed worse in Regression Analysis II due to elimination of important determinants (Inclination for WoSlope, Population Density and Carbonate Content for FarmTera, see Table A 1). The models for FarmRain were less reliable; they showed only fair performance and high deviation in cross-validation.

Table 4. Performance of Land cover models represented by AUC and Kappa scores. Mean absolute differences to scores from 10-fold cross-validation are provided in brackets. Two regression analyses were performed: analysis I based on the full predictor set and analysis II based on a reduced predictor set. Evaluation of Kappa values according to Monserud and Leemans (1992): < 0.05 (no agreement), 0.05 to < 0.4 (poor agreement), 0.4 to < 0.55 (fair agreement), 0.55 to < 0.85 (good agreement), 0.85 to < 1 (excellent to perfect agreement). Land cover unit abbreviations: see Table 1

	Land Cover Unit	AUC-I	AUC-II	Kappa-I	Kappa-II
Highlands	ForPlant	0.96 (0.05)	0.95 (0.07)	0.57 (0.2)	0.57 (0.27)
	Fallow	0.95 (0.04)	0.9 (0.05)	0.51 (0.19)	0.36 (0.2)
	ForHigh	1 (0.01)	1 (0)	0.97 (0.06)	0.97 (0.03)
	FarmTree	0.99 (0.08)	0.98 (0.05)	0.86 (0.28)	0.73 (0.24)
Slopes	FarmTera	0.98 (0.06)	0.97 (0.05)	0.79 (0.23)	0.64 (0.23)
	WoSlope	0.99 (0.02)	0.97 (0.03)	0.84 (0.15)	0.75 (0.2)
	FarmRain	0.94 (0.09)	0.94 (0.09)	0.45 (0.34)	0.45 (0.34)
	WoRipar	0.99 (0.02)	0.99 (0.02)	0.86 (0.21)	0.86 (0.21)
Lowlands	Comm	0.98 (0.04)	0.98 (0.04)	0.76 (0.23)	0.76 (0.25)
	Thicket	0.99 (0.02)	0.98 (0.03)	0.85 (0.15)	0.74 (0.2)
	WoFlood	0.96 (0.07)	0.95 (0.07)	0.56 (0.23)	0.5 (0.2)
	FarmRice	1 (0.01)	1 (0.02)	0.93 (0.11)	0.9 (0.11)
	ReedGras	0.98 (0.04)	0.98 (0.03)	0.76 (0.24)	0.74 (0.22)
	Acacia	0.97 (0.05)	0.97 (0.04)	0.73 (0.16)	0.71 (0.18)
	Suaeda	0.93 (0.06)	0.92 (0.07)	0.47 (0.11)	0.43 (0.2)

The lowlands were dominated by tree and bush savanna. Tree savanna comprised *Commiphora* woodlands (Comm) and temporary flooded woodlands (WoFlood) composed of communities with *Acacia seyal* on black cotton soils and *Hyphaene thebaica* on saline/sodic soils. Bush savanna comprised *Acacia* bushlands (Acacia) as well as mixed thicket and shrublands (Thicket) consisting of thicket-forming succulents, evergreen coriaceous shrubs and *Commiphora* species. In the floodplains of Mkomazi River major land cover units were paddy rice fields (FarmRice) and temporary flooded reeds and grasslands (ReedGras). Dense *Suaeda* bushlands (Suaeda) were observed along the edges of the floodplains and on sandy stream banks.

These land cover units were mainly determined by disturbance and topography (Table 3). Additionally, the savanna units (Comm, WoFlood, Thicket, Acacia) strongly depended on climatic factors. Range breadths along disturbance and grazing indices were moderate to wide for all lowland land cover units (Figure 6, Table A 3).

Nevertheless, each of them had only a small VPO, except for the moderately large VPO of Comm. The small VPO of Suaeda and WoFlood originated from their restriction to short distances to next waterbody. Acacia, Thicket, ReedGras and FarmRice were confined to low wet season rainfall and high minimum temperatures. Except for Suaeda and WoFlood in Regression Analysis II, lowland land cover models performed good to excellent and bias in cross-validation was at acceptable levels (Table 4).

To identify how tolerances of different land cover types were related to relevant drivers, we plotted size and median positions of VPO along disturbance index and annual minimum temperature gradients (Figure 7). Generally, land cover units with low tolerance occurred near climatic extremes and minimal disturbance intensities, while those characterized by moderate to high tolerance occurred under intermediate climatic conditions and disturbance.

3.4 Discussion

This study successfully identified major determinants of land cover distribution in North-East Tanzania and assessed the tolerance of land cover units to different environmental factors. Climatic factors were highly relevant determinants of land cover distribution in the central Mkomazi Water Basin, nevertheless they were not the primary drivers as we had expected under hypothesis H1a. Instead, disturbance was

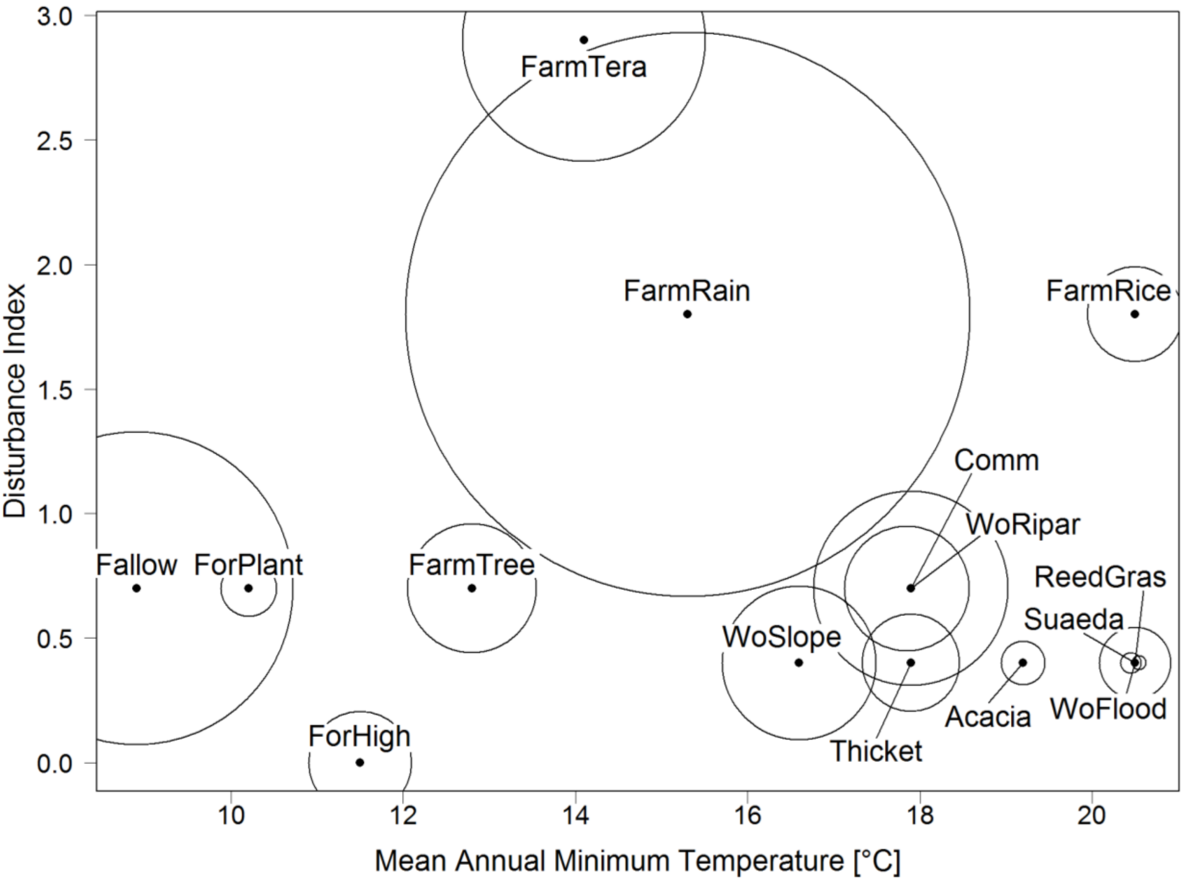


Figure 7. Median positions of land cover specific relative volumes of predicted occurrence (VPO) on the temperature and disturbance gradients, marked by black dots. The circles around the dots indicate the size of each VPO (cf. Table A 3) which was the integral over all six predictors used in Regression Analysis II

the most important determinant of land cover distribution (Table 1, Table A 1). Although we hypothesized that disturbance would be of considerable relevance (H1b), we did not expect that it would be the major predictor. Sankaran *et al.* (2005) revealed a discontinuous response of woody savanna vegetation to the rainfall gradient, which could explain why H1a and H1b were not fully supported by our results. According to their findings, herbivory and fire replace rainfall as the major driver above a threshold of 650 mm annual precipitation. However, a different pattern emerged from our results. Land cover units poorly explained by climatic factors did not show bias towards the semi-humid highlands but occurred in all parts of the study area (Table 3). This indicates that the relevance of disturbance can be underestimated when cultivated land is excluded from analyses. Given the fact that a considerable part of sub-Saharan Africa is now cultivated, this should be of concern.

Disturbance and climate are subject to ongoing regional changes. The growing population of North-East Tanzania (NBS & OCGS 2013) strongly depends on utilization of natural resources (Tanzania 2012). This poses a high potential for intensification of land-use activities and related disturbances. For instance in the South Pare Mountains combined effects of population growth and introduction of a highly water-consumptive crop (ginger) led to increased water abstraction (Komakech *et al.* 2012). During the past 50 years temperatures have risen and rainfall patterns changed significantly in North-East Tanzania (Enfors & Gordon 2007). Regional climate-change projections indicate a continuation of these trends, namely temperature increases of 1.5-2.3 °C as well as rainfall decrease in dry seasons and increase in wet seasons (Tadross & Wolski 2010).

The tolerance of land cover units occurring near the medians of the climate and disturbance gradients was relatively high (large VPO), whereas those occurring near the extremes were less tolerant (moderate to small VPO) (Figure 7). Only mixed fallow grass- and shrublands did not fit well into this pattern. Despite this inconsistency, we found adequate support for hypothesis H2. Just as species with small niche breadths, land cover units with small VPO agglomerate near the margins of the environmental gradients (Thuiller, Lavorel & Araujo 2005; Broennimann *et al.* 2006).

Only rain-fed farms and mixed fallow grass- and shrublands had relatively large VPO (Figure 7, Table A 3). At least the case of rain-fed farms is somewhat surprising, since it is often expected to be highly vulnerable to climate change (e.g. Mongi, Majule & Lyimo 2010). In central Mkomazi Water Basin, however, rain-fed farms occur in all three ecological zones (highlands, mountain slopes, lowlands). Therefore, rain-fed agriculture featuring specific production systems might be vulnerable at the local scale (e.g. under decreasing rainfall in the lowlands) but at the scale of the entire study area rain-fed farms appear relatively invulnerable.

All other land cover units in the study area had only moderate to low tolerance (Figure 7, Table A 3). At first sight this seemed to indicate that several land cover units were threatened by the projected changes in disturbance and climate. However, it would be misleading to judge land cover vulnerability from VPO size alone without considering the factors that limited VPO. This is important since VPO of several land cover units were controlled by a distinct bottleneck effect. Strong limitation by a single predictor resulted in small VPO even if restriction by other predictors was insignificant. For example, reeds and grasslands had a small VPO (Figure 7), although they were significantly restricted to only one predictor (minimum temperature). Range breadths along the other relevant predictors (CTI and grazing intensity) were moderate to wide.

Depending on the identity of VPO-limiting factors, small VPO had to be judged individually. In cases where VPO were mainly limited by topographic factors (e.g. riparian woodlands and temporary flooded woodlands: Figure 6), land cover vulnerability was supposed to be rather low, as topography is unlikely to be affected by climate change and land use intensification. Conversely, the small VPO of relevant forest and farming land cover units (ForHigh, ForPlant, FarmRice and FarmTree) were mainly governed by low tolerance to variation in disturbance and annual minimum temperature. However, levels of vulnerability to changes in disturbance and climate were not equal among these land cover units. Broennimann *et al.* (2006) and Thuiller, Lavorel and Araujo (2005) found that the vulnerability of plant species was not only affected by niche breadths but also by the position of species optima along environmental gradients and their proximity to barriers preventing range shifts. Accordingly, land cover units occurring in intermediate positions along a changing environmental gradient, could potentially relocate their spatial extent in accordance to the changes on the gradient. For instance, plantation forests could be shifted uphill to a location with lower temperatures (Figure 6). Vulnerability of land cover units restricted to the extreme ends of changing environmental gradients depended on the direction of the expected environmental change. Land cover units confined to high temperatures, like *Suaeda* bushlands (Figure 6), have the potential to adapt their extent when temperatures rise. Consequently, they were less vulnerable than land cover units confined to extremes that are likely to be 'cut off' by coming changes. This accounted for evergreen highland forests and homegardens, which were restricted to low temperatures and minimal disturbances (Figure 6). As temperatures rise and disturbances increase, areas with favourable conditions for both land cover units may diminish. Evergreen highland forests are already restricted to the uppermost mountain regions in central Mkomazi Water Basin. Upward shifts of the forests in adaption to rising temperatures consequently will result in decreases of their spatial extent. Likewise, homegardens can only be shifted in their extent by further decreasing the forest area.

Our assessment showed that evergreen highland forests and homegardens were the most vulnerable land cover units in central Mkomazi Water Basin. This confirmed findings from other areas in North-East Tanzania (Hemp 2006; Hemp 2009). Both land cover units play a crucial role in the provision of ecosystem services. Smallholder farms strongly benefit from the combination of agricultural and forest products provided by homegardens (Hemp 2006). Thanks to their biodiversity the forests hold a large variety of timber products, local medicines, vegetables and fruits (Burgess *et al.* 2007). Furthermore, the forests are of particular importance for the water balance of the entire basin as they replenish groundwater storages and maintain stream flow (cf. Hemp 2009). Considerable forest loss is likely to cause adverse changes of the hydrological regime, including reduced base flow and increased frequency and intensity of extreme flow events (Bradshaw *et al.* 2007). This might affect surface water-dependent land cover units such paddy fields, irrigated terrace farms or seasonally flooded grasslands and woodlands.

3.5 Conclusions

In this paper we showed that land cover distribution in North-East Tanzania is mainly governed by disturbance, whereas climatic factors are less relevant. In accordance to these results, impacts of climate change on land cover distribution might be less severe than those of land use change (Settele *et al.* 2014). Assessing land cover vulnerability to climate and land use requires considering factors restricting land cover distribution and the position of the predicted distribution on environmental gradients. The majority of land cover units in central Mkomazi Water Basin did not show considerable direct vulnerability, with the exception of evergreen highland forest and agroforestry areas. However, serious indirect threats might occur due to potential hydrological regime changes triggered by expected forest loss. In particular land cover units which are bound to permanent water sources (paddy fields, temporary flooded woodlands, riparian woodlands & reeds and grasslands) are likely to suffer from reductions in stream flow. In other words, the high vulnerability of evergreen highland forests raises the vulnerability of land cover units that depend on services provided by the forests.

However, adverse land cover changes in central Mkomazi Water Basin are not inevitable. Although not much can be done at local scale to prevent climate changes, changes in disturbance intensity are directly controlled by land use activities. An appropriate land use and resource management in North-East Tanzania could prevent increasing disturbance intensities even if population growth continues.

Chapter 4

Effects of abiotic factors and functional diversity on ecosystem properties

4 Effects of abiotic factors and functional diversity on ecosystem properties

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Michael Kleyer

Abstract

Abiotic factors, disturbance and effects of biodiversity are known to determine ecosystem properties (EP) and the related provision of ecosystem services (ES). So far, EP response research focused mainly on individual ecosystems like grasslands, whereas studies in landscapes of multiple ecosystems are still rare. In this study we assessed the effects of different explanatory factor sets on three EP in North-East Tanzania. Relevant data were collected in 147 sampling sites covering the central Mkomazi Water Basin, a highly diverse landscape ranging from dry savannas to montane evergreen forests. A stepwise modelling approach was applied. Firstly, generalized linear models were built to explain EP by either environmental factors, community weighted mean trait values (CWM) or community trait distribution metrics (CDM). Subsequently, it was tested if combined effects of different factor sets improved the prediction of EP response. In each step model averaging was applied to all candidate models with Δ-AIC ≤ 10 to gain a final model. Combined effects of abiotic and biotic factors best explained variability in all three EP. Biotic effects were equally represented by CWM and CDM in these models, hence our results favour neither the mass-ratio hypothesis nor the diversity hypothesis. These results shed light on the forces that drive EP and related ES in diverse landscapes, however they also raise new questions. Abiotic conditions and functional diversity which both considerably influence EP are closely linked to each other. Without further knowledge of how these links influence EP, predictions of future EP states and availability of related ES would not be very reliable.

4.1 Introduction

Ecosystems are characterized by specific bio-physical properties and processes which respond to local environmental conditions, land use and biodiversity (Hooper *et al.* 2005; Díaz *et al.* 2006; de Bello *et al.* 2010). A better understanding of these responses is crucial for the assessment of potential global change impacts on livelihoods. This is due to the fact that ecosystem properties (EP) link to the benefits humans gain from ecosystems, commonly referred to as ecosystem services (MEA 2005; Díaz *et al.* 2007a; de Groot *et al.* 2010). Consequently, considerable research has already been conducted to evaluate the importance of different EP determinants (e.g. Lavorel *et al.* 2011; Paquette & Messier 2011).

Despite extensive efforts to advance our understanding of EP, several challenges remain. EP research has often been restricted to individual ecosystems, mainly grasslands (Loreau *et al.* 2001; de Bello *et al.* 2010). Apart from that, there is a significant lack of studies from developing countries (Seppelt *et al.* 2011), notwithstanding the high relevance of healthy ecosystems for people's livelihoods in these regions.

One example is sub-Saharan Africa, where important economic sectors (e.g. agriculture and tourism) as well as livelihood activities of rural communities rely on the state of ecosystems (Scholes & Biggs 2004; Sileshi *et al.* 2007; Kumar & Yashiro 2014). Current regional climate change (Niang *et al.* 2014) and land use intensification (Lambin, Geist & Lepers 2003; Scholes & Biggs 2004) are expected to cause ecosystem degradation (e.g. Sileshi *et al.* 2007; Hemp 2009). In appreciation of these developments, research in sub-Saharan Africa commonly emphasized abiotic and land use effects on EP but disregarded biotic factors (e.g. Doherty *et al.* 2010; Swetnam *et al.* 2011). Only a few studies, geographically restricted to South Africa, investigated and emphasized the links between biodiversity and EP / ES (van Wilgen *et al.* 2008; Egoh *et al.* 2009). However, in these studies biodiversity was solely measured in terms of species richness, which is a relatively weak determinant of EP (Díaz & Cabido 2001; Cadotte, Carscadden & Mirotchnick 2011).

Alternatively, biodiversity can be described as functional diversity of biotic communities, which is a much more suitable link to EP (Díaz *et al.* 2006; de Bello *et al.* 2010; Lavorel 2013). Functional diversity can be characterized either by abundance-weighted trait averages, which reflect functional effects of the dominant species ("mass-ratio hypothesis") (Grime 1998) or by the distribution of trait attributes in a community. This measure may indicate complementary effects of functional dissimilarity within a community ("diversity hypothesis") (Tilman *et al.* 1997).

Here, we analysed the response of annual net primary productivity (NPP), litter thickness and erosion intensity to changes in abiotic conditions, disturbance and functional trait composition in a diverse landscape in North-East Tanzania. NPP is one of the most important ecosystem properties, as it is part of the global carbon cycle and provides the resource base for herbivores and decomposers (Scurlock, Johnson & Olson 2002). Litter thickness is a local carbon stock component which is relevant for energy and moisture exchange between soil and atmosphere (Ogée & Brunet 2002). Erosion intensity links to erosion control, which is an important ES in agricultural land (Pimentel *et al.* 1995).

Our two major objectives were to investigate how strongly EP are influenced (1) by abiotic versus biotic effects and (2) by community weighted mean plant functional traits (CWM) versus community distribution metrics (CDM) (cf. Díaz *et al.* 2007b; Lavorel *et al.* 2011; Conti & Díaz 2013).

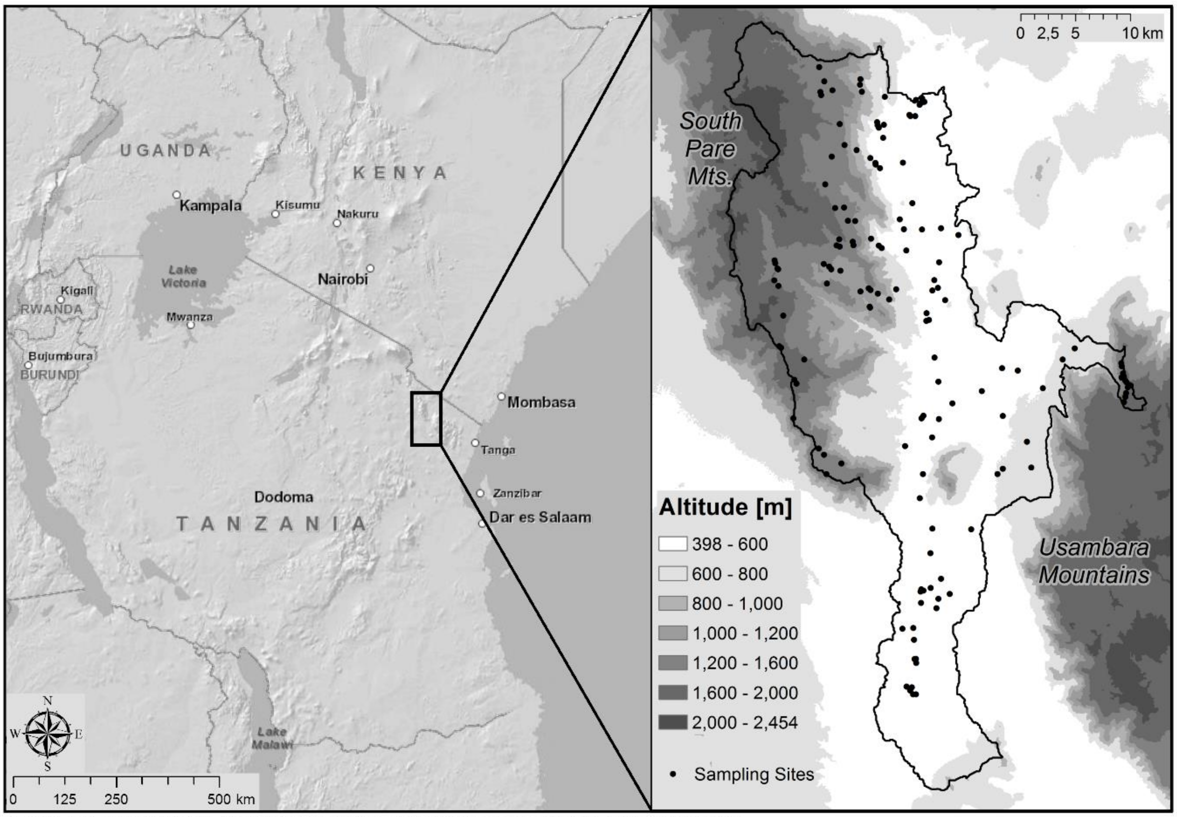
Research in grasslands often found that plant functional diversity is more relevant for EP than abiotic factors and disturbance (e.g. Chanteloup & Bonis 2013). However, strong biotic signals on EP in grasslands are often favoured by a lack of variation in abiotic factors or disturbances. Our study area however, is characterized by long environmental gradients. Therefore, we expected prominent response of EP to both, plant functional diversity and environmental factors (H1) (Loreau *et al.* 2001). In particular we hypothesized strong effects of climate (Paquette & Messier 2011; Chollet *et al.* 2014) and disturbance (Chambers *et al.* 2004; Klumpp & Soussana 2009) on NPP, but also significant effects of plant traits indicative of the resource acquisition-conservation trade-off like specific leaf area (SLA) (H1a) (Klumpp & Soussana 2009; Lienin & Kleyer 2012; Chanteloup & Bonis 2013). We expected that litter thickness strongly depends on climate due to differences in decomposition between hot-dry and cool-moist conditions (Chambers *et al.* 2004) as well as on plant height and leaf traits (Díaz *et al.* 2007b; Grigulis *et al.* 2013) (H1b). Erosion was expected to respond primarily to topography (Fox & Bryan 2000) and vegetation structure (Hartanto *et al.* 2003; Zheng 2006), indicated by variance in life and growth forms (H1c).

We hypothesized that EP respond more prominently to CWM compared to CDM (H2). Due to the extended environmental gradients, differences between communities should be more important than the variance within communities (Paquette & Messier 2011; Lienin & Kleyer 2012; Grigulis *et al.* 2013).

Finally, we assumed that the three EP influence each other: litter thickness was expected to increase with NPP (H3a), whereas erosion intensity should be reduced as litter thickness increases (Pimentel *et al.* 1995) (H3b).

4.2 Materials and Methods

4.2.1 Study area



Source: Esri, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors, and the GIS user community

Figure 8. Left: Location of the study area in Tanzania. Right: Extent of the study area and sampling site locations

This study focused on the central Mkomazi River Basin, a major tributary of Pangani River in North-East Tanzania. The research area comprised the eastern flank of the South Pare Mountains, part of the western slope of the West Usambara Mountains and the wide valley of Mkomazi River between these two mountain ridges (Figure 8). It had a North-South extension of 68 km (4°13’ S to 4°50’ S), a West-East extension of 37 km (37°54’ E to 38°15’ E) and a size of 1100 km^2. Features of climate, soils, land use as well as major land cover types of the study area have been described in Chapter 2.2.

4.2.2 Data sources

Data were collected at 147 plots and comprised abiotic factors, disturbance, plant functional traits and EP. The sample locations were evenly distributed over preliminarily defined land cover types within the study area (see Chapter 2.3). Data were either directly measured at the plot, derived from remote sensing or calculated from plot data (Table 5). Remote sensing data was derived from various sources (see below) and compiled in a GIS database. Standard plot size was 10 x 10 m, however a few plots were sized 5 x 20 m to maintain homogeneity (e.g. in riparian woodlands). Unfortunately, our study lacked the means to conduct laboratory analyses of soil and plant material, due to the remoteness of the field site.

Population density was calculated in ArcGIS based on an administrative map, ward specific population data and satellite pictures to exclude unsettled areas (see Chapter 2.3). Disturbance data was recorded in the field and included intensity and frequency of logging, mowing, ploughing, harvesting, fire and grazing. A disturbance index was estimated based on yearly biomass removal. Additionally, a grazing index indicated density and frequency of grazing (see Chapter 3.2.2).

Rainfall, temperature and evapotranspiration as well as inclination, distance to next water source and compound topographic index were partly correlated and therefore merged into aggregated climatic and topographic factors by principal component analysis (PCA). We applied the R function ‘pcomp’ (R Core Team 2014) and retained the first component of each PCA for EP modelling. These first axes accounted for 92% of total variance in climatic data and 75% of total variance in topographic data. Since the aggregated climatic factor ranged from humid-cool conditions at its minimum to dry-hot conditions at its maximum, it was called aridity. The aggregated topographic factor represented the gradient between flat sites with short distance to next water source and steep slopes.

In each of the 147 plots vascular plant species abundance was estimated as percentage cover. Dominant species were identified as those species which collectively

Table 5. Analysed ecosystem properties (EP) (response variables), environmental factors and plant traits (explanatory variables) and their data sources. In addition to the listed variables the following factors were measured but did not significantly contribute to explain EP: electrical conductivity of soil solution, clay and sand content, water holding capacity, abundance of growth forms* other than trees and palms, abundance of life forms* other than phanerophyts, latex in plant organs

Data	Abbreviation	Unit	Data source
Ecosystem properties (EP)			
Annual net primary productivity	NPP	$kg*m^{-2}*a^{-1}$	GIS database
Litter thickness	Litter	cm	Plot data
Erosion intensity	Erosion	-	Calculated from plot data
Environmental factors (Environ)			
1st axis of climate data PCA	Aridity	-	PCA
Rainfall	-	mm	GIS database
Temperature	-	°C	GIS database
Evapotranspiration	-	mm	GIS database
1st axis of topographic data PCA	Topo	-	PCA
Inclination	-	°	Plot data, GIS database
Compound topographic index	-	-	GIS database
Distance to next water source	-	-	GIS database
Soil pH	pH	-	Plot data
Bulk density	BulkD	$g*cm^{-3}$	Plot data
Plant available soil water capacity	Pore	Vol-%	Calculated from plot data
Soil hydraulic conductivity	HydCond	$mm*d^{-1}$	Calculated from plot data
Human population density	PopDens	$Persons*m^{-2}$	GIS database
Disturbance index (ploughing, logging, mowing, fire)	Disturb	-	Calculated from plot data
Grazing index	Graz	-	Calculated from plot data
Plant functional traits (CWM and CDM)			
Abundance of trees and palms*	Trees	%	Plot data
Abundance of phanerophyts*	Phanpht	%	Plot data
Plant height	PHeight	m	Plot data

Table 5. Continued

Data	Abbreviation	Unit	Data source
Stem diameter at breast height	DBH	cm	Plot data
Abundance of succulent leaves	LSucc	%	Plot data
Abundance of hairy leaves	LHair	%	Plot data
Whole leaf area	LArea	mm^2	Plot data
Specific leaf area	SLA	mm^2*g^{-1}	Plot data
Chemical defensive substances	DefChem	%	Plot data
Spinescence	Spine	-	Plot data

* Growth forms and life forms according to Cornelissen *et al.* (2003)

contributed to at least 80% of the vegetation cover in each sampling site. These comprised woody as well as herbaceous plants. In each site plant functional traits were measured from two healthy individuals of each dominant plant species. Five individuals per site were sampled from species which were dominant in just one or two sites. In total, we recorded traits of 237 vascular plant species. Plant height, stem diameter at breast height (DBH), life form, growth form, leaf structure and spinescence of each replicate were determined in situ. Leaf samples were collected to measure whole leaf area and whole leaf dry mass. At the remote field site in North-East Tanzania, no lab-standard oven was available to dry leaves at constant temperatures. Therefore, prior to mass weighing all leaves were air-dried for at least 72 hours. This period was extended as much as necessary for large and thick leaves. Data regarding chemical defences (e.g. alkaloids) was collected from literature and web-based plant species databases (Protabase: http://www.prota4u.info/, World Agroforestry Centre: http://www.worldagroforestry.org/resources/databases/agroforestree, JTOR global plants: http://plants.jstor.org/).

To represent the functional diversity of plant communities, we calculated community weighted mean trait values (CWM) and two community distribution metrics (CDM), namely Rao’s Quadratic Entropy (RaoQ) (Rao 1982) and Functional Dispersion (FDis) (Laliberte & Legendre 2010). For each site RaoQ and FDis were calculated from single traits which better link to EP than multi-trait indices (Paquette & Messier 2011; Butterfield & Suding 2013). For calculation of CWM, RaoQ and FDis the R-package “FD” was used (Laliberte & Legendre 2010).

Mean annual net primary productivity (NPP) for the years 2000 to 2010 was extracted from Moderate Resolution Imaging Spectroradiometer (MODIS) data (NTSG & UMT 2014) for each plot. An erosion intensity index was calculated as the product of plot area affected by erosion and a factor of erosion intensity. This was assessed on an arbitrary ordinal scale based on signs of sheet and rill erosion (Table 6). Litter thickness was measured in the vicinity of the soil pits (see above).

Table 6. Factors of erosion intensity and criteria for their assessment

Factor	Erosion intensity	Rill erosion	Sheet erosion	Vegetation damage
0	no erosion	no rill erosion	no sheet erosion	no damage
0.2	slight	rill width < 5 cm, width-depth ratio > 2:1	minor signs of sediment transport from bare soil	no damage
0.6	intermediate	rill width < 10 cm, width-depth ratio < 2:1	topsoil partly eroded	roots of herbs partly washed out
1	severe	rill or gully width > 10 cm, width depth ratio < 2:1	severe topsoil erosion leaving behind large pebbles and stones	uprooting of herbs, roots of woody plants washed out

4.2.3 Modelling EP responses

Extent and character of abiotic factors, disturbance and plant functional trait effects on EP were evaluated with Generalized Linear Models (GLM) following Díaz *et al.* (2007b). Erosion index and litter thickness data were strongly right-skewed and zero-inflated. We added a constant to both variables, which was calculated as half of the lowest value above zero and then applied GLM of the Gamma family (inverse link). NPP models were built as GLM of the Gaussian family (identity link).

First, EP response to each independent factor was fitted to different univariate response functions (linear, rational and quadratic). Selected independent variables were transformed by square-root, log or boxcox transformation to improve model fit. Model performance was assessed by Chi-squared (χ^2) test of likelihood ratios against null-models and internally validated by bootstrapping. Models were assumed to be sufficiently robust if in more than 95% of all bootstrap runs (n = 500) p-values (p_{null_boot}) remained below 0.1. For each independent factor the best performing univariate model option was retained. Independent factors which did not provide any robust prediction were omitted from further modelling of the respective EP. Additionally, among correlated independent factors only those with best performing univariate models were kept (Table A 4).

Subsequently, we applied all-subsets-regression to build multivariate models for each EP from different sets of independent factors. A maximum of four independent variables were allowed in each multivariate model to limit computation efforts. At first, multivariate models were fitted from all abiotic factors & disturbances, then from CWM values and next from CDM. Finally, multivariate models were built from combinations of these factor sets. In each model p-values were extracted for coefficient estimates (p_{coef}) and χ^2 - tests of likelihood ratios against null-models (p_{null}) and against a model reduced by one dimension (p_{red}). Models with any $p_{coef} > 0.05$, $p_{null} > 0.05$ and $p_{red} > 0.1$ were rejected. Univariate land cover models were rejected at this stage when none of their coefficients complied with the p_{coef} limit.

To avoid the drawbacks of selecting one 'best' model, we applied model averaging following Burnham and Anderson (2002). All significant multivariate and univariate models from each factor set were ranked by AICc and models with Δ-AICc > 10 were excluded. The remaining models were averaged based on AICc weights. Significance of 'conditional' and 'full' model-averaged coefficients was determined. While the former were averaged only over models where the respective parameter appears, the latter were averaged over non-occurrences as well (Barton 2015). R-squared and pseudo-R-squared values (Nagelkerke 1991) were averaged across all candidate models weighted by AICc weights.

Univariate and multivariate GLM were built using the glm() function in R Core Team (2014). Model averaging was realized by application of the R-package 'MuMIn' (Barton 2015).

4.3 Results

4.3.1 EP response to environmental factors

Most environmental factors were significant determinants of NPP and litter thickness, but only topography and soil hydraulic conductivity explained variation in erosion intensity (Table 7). Averaged models revealed that multivariate combinations of environmental factors had the highest explanatory power for all three EP (Table 8, Figure 9). For erosion intensity however, only topography passed the selection criteria in multivariate modelling and the resulting model performed weakly.

Table 7. Univariate response of ecosystem properties (EP) to explanatory variables from different factor sets. Schematic response shapes and p-values of χ^2-tests in bootstrapping (see Chapter 4.2.3). Only the most robust models are listed. For each EP - CDM relation only the most significant is listed (either Rao`s quadratic entropy (RaoQ) or Functional Dispersion (FDis)). Predictor abbreviations see Table 5

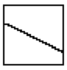
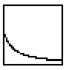
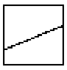
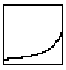
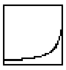
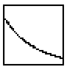
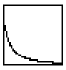
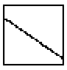
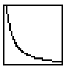
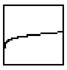
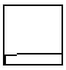
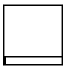
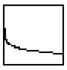
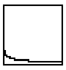
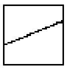
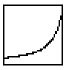
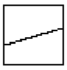
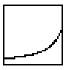
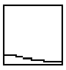
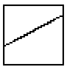
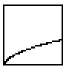
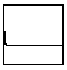
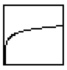
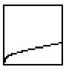
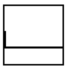
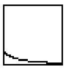
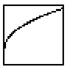
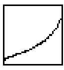
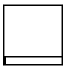
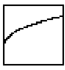
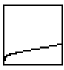
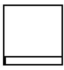
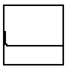
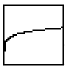
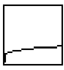
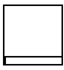
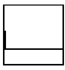
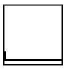
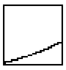
Predictors	Net Primary Productivity		Litter Thickness		Erosion Intensity	
	p_{null_boot}	*Response*	p_{null_boot}	*Response*	p_{null_boot}	*Response*
Environmental factors						
Aridity	<0.001		<0.001		>0.1	-
Topo	<0.001		0.003		0.012	
pH	<0.001		<0.001		>0.1	-
BulkD	<0.001		<0.001		>0.1	-
HydCond	0.072		0.004		0.05	
Graz	<0.001		<0.001		>0.1	-
Community weighted mean traits						
Trees	<0.001		<0.001		>0.1	-
Phanpht	0.012		0.002		0.083	
PHeight	<0.001		<0.001		>0.1	-
LSucc	<0.001		>0.1	-	>0.1	-
LArea	<0.001		0.031		>0.1	-
Spine	<0.001		<0.001		>0.1	-
Community distribution metrics						
PHeight	<0.001	 RaoQ	<0.001	 FDis	0.001	 RaoQ
DBH	<0.001	 RaoQ	0.071	 FDis	<0.001	 FDis
LSucc	<0.001	 RaoQ	>0.1	-	>0.1	-

Table 7. Continued

Predictors	Net Primary Productivity		Litter Thickness		Erosion Intensity	
	p_{null_boot}	*Response*	p_{null_boot}	*Response*	p_{null_boot}	*Response*
Community distribution metrics						
LArea	<0.001	 FDis	0.025	 RaoQ	0.001	 RaoQ
Spine	<0.001	 RaoQ	<0.001	 RaoQ	>0.1	-
Ecosystem properties						
NPP	-	-	<0.001		>0.1	-
Litter	-	-	-	-	>0.1	-

4.3.2 EP response to biotic effects

NPP and litter thickness significantly responded to several plant functional traits, comprising both, community weighted means (CWM) and community distribution metrics (CDM) (Table 7). Erosion intensity was explained by CDM of several traits, but did not significantly respond to most CWM values. Multivariate combinations of CWM and CDM, respectively, gave contrasting results for the different EP (Table 8, Figure 9). A considerable share of variation in NPP was explained by multiple functional traits, with a slightly better performance of CDM compared to CWM. Litter thickness response to CWM was moderately strong but explanatory power of CDM was relatively weak. Multivariate models of erosion intensity built from CWM values included only abundance of phanerophyts and this model was of poor performance. None of the erosion models built exclusively from CDM passed the multivariate modelling criteria (coefficient estimates were insignificant ($p_{coef} > 0.05$)).

4.3.3 Relationships between EP

Litter thickness showed significant positive univariate response to NPP (Table 7). Nevertheless, in comparison to environmental factors and biotic effects, NPP had rather poor explanatory power for litter thickness (Table 8, Figure 9). Neither NPP nor litter thickness had significant effects on erosion intensity.

Table 8. Averaged multivariate models of ecosystem properties (EP) response to environmental factors, CWM and CDM. In the litter thickness and erosion intensity models, additionally the integration of other EP was tested. Multivariate models were built from each factor set as well as their combination ('All'), averaging was based on AICc weights (Burnham & Anderson 2002). Explanatory variables (EV) with importance < 5 are not listed. Cells were left empty where no satisfactory model was found. For all listed EV p-values of 'conditional' model-averaged coefficients remained below 0.05. Only underlined EV had significant (p-value < 0.05) 'full' model-averaged coefficients. Further EV labels: superscript numbers - model averaged relative variable importance (0-100); (+)/(-) - EV has positive/negative effect on EP. Abbreviations of EP, factor sets and EV see Table 5

EP	Factor Set	R^2	Explanatory variables
NPP	Environ	0.74	$\underline{\text{Aridity}}^{100}$ (-), $\underline{\text{PopDens}}^{100}$ (+), $\underline{\text{Graz}}^{97}$ (-), $\underline{\text{BulkD}}^{93}$ (-), HydCond^{6} (+)
	CWM	0.6	$\underline{\text{Spine}}^{100}$ (-), $\underline{\text{PHeight}}^{100}$ (+), $\underline{\text{LArea}}^{100}$ (+), $\underline{\text{LHair}}^{98}$ (+)
	CDM	0.62	$\underline{\text{PHeight}}_{\text{RaoQ}}^{100}$ (+), $\underline{\text{Spine}}_{\text{RaoQ}}^{100}$ (-), $\underline{\text{LArea}}_{\text{FDis}}^{100}$ (+), LSucc$_{\text{RaoQ}}^{82}$ (+)
	All	0.78	$\underline{\text{Aridity}}^{100}$ (-), $\underline{\text{PopDens}}^{100}$ (+), $\underline{\text{PHeight}}_{\text{RaoQ}}^{100}$ (+), Spine$_{\text{RaoQ}}^{66}$ (-), LSucc^{20} (-), BulkD^{13} (-)
Litter Thickness	Environ	0.54*	$\underline{\text{Disturb}}^{100}$ (-), $\underline{\text{Graz}}^{89}$ (-), $\underline{\text{BulkD}}^{84}$ (-), Aridity^{24} (-), Pore^{14} (+)
	CWM	0.42*	$\underline{\text{Spine}}^{100}$ (-), $\underline{\text{PHeight}}^{99}$ (+), $\underline{\text{DefChem}}^{98}$ (+)
	CDM	0.31*	$\underline{\text{Spine}}_{\text{RaoQ}}^{100}$ (-), $\underline{\text{PHeight}}_{\text{Fdis}}^{99}$ (+)
	EP	0.22*	$\underline{\text{NPP}}^{100}$ (+)
	All	0.58*	$\underline{\text{Disturb}}^{100}$ (-), $\underline{\text{Spine}}_{\text{RaoQ}}^{100}$ (-), $\underline{\text{BulkD}}^{91}$ (-), Graz^{91} (-), Aridity^{6} (-)
Erosion intensity	Environ	0.1*	$\underline{\text{Topo}}^{100}$ (+)
	CWM	0.06*	$\underline{\text{Phanpht}}^{100}$ (-)
	CDM	-	-
	EP	-	-
	All	0.29*	$\underline{\text{Topo}}^{100}$ (+), $\underline{\text{Phanpht}}^{100}$ (-), $\underline{\text{DBH}}_{\text{FDis}}^{100}$ (+)

* Pseudo-R^2 values (Nagelkerke 1991). Note that they are not directly comparable to the standard R^2 values

4.3.4 Joint effects of environmental factors and functional traits

For all three EP best modelling results were achieved by multivariate combinations of environmental factors and functional traits (CWM and CDM) (Table 8, Figure 9). NPP was best explained by negative effects of aridity, variation in spinescence (RaoQ), leaf succulence and bulk density as well as by positive effects of population density and variation in plant height (RaoQ). Litter thickness was characterized by negative effects of disturbance, grazing, bulk density and variation in spinescence (RaoQ). Only one multivariate model with Δ-AICc ≤ 10 was found to explain erosion intensity. It comprised positive effects of topography and variation in stem diameter at breast height (FDis) as well as a negative effect of phanerophyt abundance.

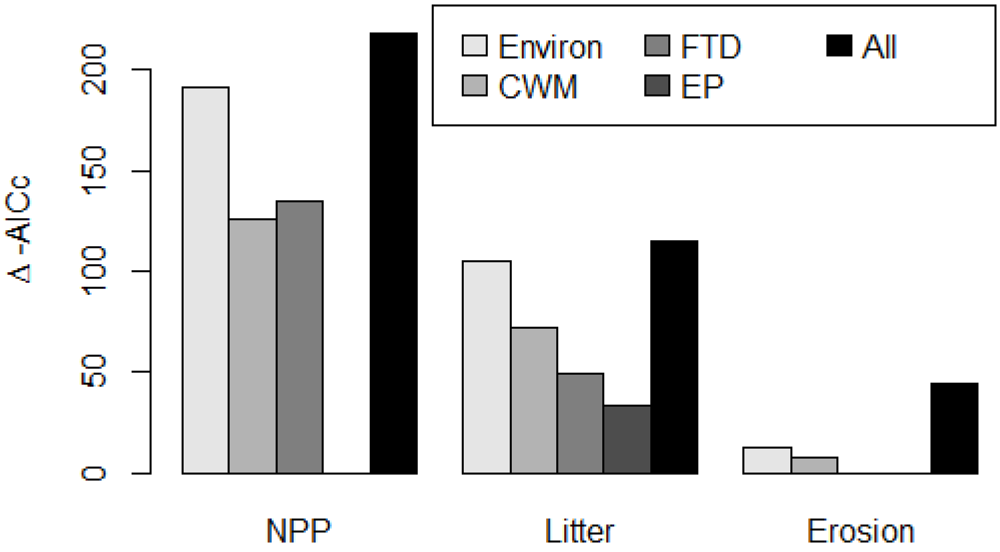


Figure 9. AICc improvement in ecosystem properties (EP) response models for different sets of explanatory variables (environmental factors, CWM, CDM, EP and all factors combined). Improvements were calculated as the absolute difference between the AICc of each EP's Null-model and the AICc of the model with the lowest AICc (=baseline for model averaging) from each factor set. EP abbreviations see Table 5

4.4 Discussion

In this study we identified determinants of NPP, litter thickness and erosion intensity across a wide range of cultivated and natural ecosystems in North-East Tanzania. To the best of our knowledge, it is the first attempt to identify relevant drivers of NPP, litter thickness or erosion intensity on the African continent by using both environmental and plant trait data.

4.4.1 Differences in EP model performance

While the response models of NPP performed very well and those of litter thickness were on a moderate level, erosion intensity model performance was rather poor (Table 8, Figure 9). We assume that these differences can be attributed to statistical features of litter thickness and erosion intensity, as well as to missing explanatory variables. Litter thickness is a function of leaf turnover and litter decomposition (Díaz *et al.* 2007b). Our analysis did not disentangle these two processes since neither was directly measured. Soil erosion is driven by stochastic heavy rainfall events which vary in space and time (Edwards & Owens 1991). Our assessment was based on visual proof of past events, such as the presence of rills or gullies (see Table 6). However, these erosion marks could have been cleared by farmers or covered by ground vegetation, which might have resulted in false absences in the data set. Moreover, alternative factors determining erosion intensity, like soil erodibility (Laflen *et al.* 1991), were not integrated into our models.

4.4.2 Relevance of abiotic versus biotic effects

In spite of differences in model performance, all three EPs were best explained by the combined effects of environmental factors and plant functional traits (Table 8). These results were well in line with hypothesis H1 ('EP respond to environmental factors and traits'). Similar outcomes had been found in grasslands (Díaz *et al.* 2007b; Lavorel *et al.* 2011) and rangelands with scattered shrubs (Chollet *et al.* 2014). However, environmental factors were the most relevant single factor set for all three EP and therefore of greater weight than biotic predictors (Loreau *et al.* 2001; Paquette & Messier 2011).

Hypothesis H1a was supported by negative effects of aridity and grazing on NPP, (cf. Oesterheld *et al.* 1999; Peñuelas *et al.* 2007). However, the influence of traits indicating resource use, such as the observed negative effects of succulence and variation in spinescence (Vendramini *et al.* 2002; Fine *et al.* 2006), were less significant than expected. Moreover, specific leaf area was insignificant and therefore not selected as predictor variable. Commonly traits representing resource use ('leaf/plant economics spectrum') have been recognized as relevant biotic determinants of ecosystem functioning across different ecosystems (Reich 2014). Instead, in our study NPP was strongly affected by variation in plant height. The relevance of the plant size axis has been acknowledged before (cf. Chapin 2003; Díaz *et al.* 2004).

The expected effects of aridity, plant height and leaf traits on litter thickness were insignificant, hence our results did not support hypothesis H1b. Instead disturbance, grazing and spinescence negatively affected litter thickness. Disturbances either directly reduce the amount of accumulated litter (e.g. fire, farming) (Wardle *et al.* 2003; Snyman 2005) or indirectly reduce litter accumulation by the removal of living biomass (e.g. herbivory) (Facelli & Pickett 1991). The importance of spinescence for litter thickness could be explained by the negative effect of investment in structural defences on leaf production, which results in reduced litter accumulation (Coley 1988; Facelli & Pickett 1991).

As we had hypothesized, erosion intensity increased with topography but decreased as phanerophyt abundance increased (Hypothesis H1c). However, this finding was opposed by the positive response of erosion intensity to variation in DBH. We assume that this inconsistency was caused by the problematic statistical properties of erosion intensity discussed before.

4.4.3 Relevance of CWM versus CDM

We compared community weighted mean traits (CWM) with two community trait distribution metrics (CDM). In contradiction to what we had expected (H2: ‘CWM are better determinants of EP than CDM’), CWM and CDM were of equal relevance. As single factor sets CWMs were more important than CDM in litter thickness and erosion intensity models but CDM performed better in NPP models (Figure 9). Furthermore, the NPP and erosion intensity response models with combined effects comprised CWM and CDM factors (Table 8). Consequently, based on our findings, neither Grime’s (1998) mass-ratio hypothesis nor Tilman’s *et al.* (1997) diversity hypothesis could be rejected. This conclusion was supported by evidence provided in studies where CWM and CDM were found to be similarly relevant for biomass production (Chanteloup & Bonis 2013) or carbon storage (Conti & Díaz 2013). However, the equal importance of CWM and CDM in our models most likely accounted to strong positive correlations between both measures for most traits (Table A 4). While in grasslands similar effects were found only for a minority of traits (Chanteloup & Bonis 2013), strong relations between dominant trait values and trait variation are probably common across multiple contrasting ecosystems.

4.4.4 Relationships between EP

The expected positive response of litter thickness to NPP (H3a) was confirmed by our results (Table 7). Nevertheless, the influence of NPP on litter thickness was negligible in comparison to other effects (Figure 9). The response of erosion intensity to litter thickness was not significant, hence H3b was rejected. Based on these findings, we assume that relationships between NPP, litter thickness and erosion intensity are less relevant than their responses to environmental factors and biotic effects.

4.4.5 EP relationships with ES

Each of the three EP in the focus of this study is related to different ES. NPP connects to three provisioning ES; namely fodder, fibre and primary production (de Bello *et al.* 2010). Litter thickness is linked to water regulation through reduced soil water evaporation and maintenance of soil humidity (Facelli & Pickett 1991). Finally, erosion intensity is negatively related to the regulating ES erosion control. Aridity and disturbances in North-East Tanzania are expected to increase due to projected regional climate change (Tadross & Wolski 2010), economic development and population growth (NBS & OCGS 2013). These changes will have impacts on EP and related ES in the region. In accordance to our findings, increasing disturbance could reduce fibre and fodder production and negatively affect the maintenance of soil humidity. Increasing aridity could additionally impair crop production. Fodder and primary production provide the basis for agriculture, on which about 70% of the people in the region depend (Tanzania 2012; NBS & OCGS 2013). Farming yields are directly controlled by soil stability and water regulation. Finally, livelihoods in the region are additionally supported by fibre products (timber and fuel wood) (Enfors & Gordon 2008; Notter 2010; Schaafsma *et al.* 2012).

4.5 Conclusions

Three major conclusions concerning the determination of EP in diverse landscapes could be drawn from our study. First, different EP across multiple ecosystems are determined by mixed effects of abiotic and biotic factors with slightly higher importance of the former. Second, among biotic effects dominant functions and functional variation are equally important for EP. However, this was largely attributed to strong correlations between both measures. Hence our results favour neither the mass-ratio hypothesis (Grime 1998) nor the diversity hypothesis (Tilman *et al.* 1997). Third, the biotic effects on EP largely represent the leaf economics spectrum as well as the plant size axis. Although similar findings have been reported from studies of individual ecosystems, they had not yet been confirmed before in patterned landscapes with multiple ecosystems.

In a world of changing climate and intensification of land use it becomes more and more important to understand how EP and related ES provision respond to changes. Knowledge of the major EP determinants is a first requirement. However, the finding that abiotic and biotic factors influence EP likewise raises new questions. On the one hand climate change and land use intensification act directly on EP as alterations of abiotic conditions and disturbance regimes. On the other hand however, they lead to shifts in the functional composition of biotic communities, which in turn affect EP (Garnier *et al.* 2007; Laliberté & Tylianakis 2011; Hooper *et al.* 2012). To understand these indirect impacts, the focus has to be set on the relation between functions responding to environmental changes and those affecting EP.

Chapter 5

Consistency of direct environmental and functional trait mediated effects on primary productivity in North-East Tanzania

5 Consistency of direct environmental and functional trait mediated effects on primary productivity in North-East Tanzania

Maximilian Petzold

Michael Kleyer

Abstract

According to response-effect theory, functional traits mediate the impacts of environmental conditions on ecosystem properties (EP). However, the consistency of specific environment - trait - EP relations across different ecosystems has rarely been tested and the relative importance of direct environmental effects on EP versus trait-mediated effects is hardly known. Plant functional trait responses to environmental variables and effects on net primary productivity (NPP) were hypothesized for a diverse landscape in North-East Tanzania. Path analysis with directional separations tests was applied to verify this initial model on three data sets: ‘Basin’ (entire study area), ‘Lowlands’ and ‘Highlands’. In the Basin and Lowlands models the majority of expected paths were confirmed; in both models direct effects of climatic factors dominated NPP response. A lot of the hypothesized paths in the Highlands model were insignificant; in this model NPP response was mainly controlled by effects of disturbance mediated by plant height. Two major conclusions were drawn from these results. First, the relevance of direct versus trait-mediated effects on EP was strongly controlled by the degree of resource limitation represented by environmental gradients and much less by their length. Second, environment - trait - EP relations were not consistently significant across different ecological zones. This implied that response-effect assessments in complex landscapes have to focus on individual ecosystems.

5.1 Introduction

The properties and prevailing processes of ecosystems are governed by their abiotic environment, natural and anthropogenic disturbances as well as by the established biotic communities (Chapin 2003; Hooper *et al.* 2005). Current climate change, land use intensification and biodiversity loss consequently lead to alterations of ecosystem properties (EP). This is of great concern since EP are coupled with ecosystem services (ES), which are of substantial importance for human societies (MEA 2005; Díaz *et al.* 2006; Díaz *et al.* 2007b). Accurate predictions of EP responses to global change and impacts on related ES remain challenging tasks, however. Uncertainties in the projection of plant and animal community behaviour following environmental change hamper the estimation of future biotic effects on EP (Díaz *et al.* 2006; Lavorel *et al.* 2007).

Direction, timing and range of biota's responses to the environment and their effects on EP are controlled by functional traits (Díaz & Cabido 2001; Díaz *et al.* 2007b; Garnier *et al.* 2007). This context was described by Lavorel and Garnier (2002) in a conceptual framework which suggests that EP responses to abiotic factors are mediated by functional response and effect traits ('response-effect framework'). Even though the response-effect framework applies to all trophic levels and accordingly has been adjusted for multi-trophic analyses recently (Lavorel *et al.* 2013), our study was restricted to plants. Applications and advancements of the response-effect framework ascertained that the links between response and effect traits take a pivotal role in determining how environmental change translates into changes in EP (Suding *et al.* 2008; Pakeman 2011; Díaz *et al.* 2013). Strong positive or negative relations between plants' response and effects tend to amplify or reverse impacts on EP, respectively, whereas weak links attenuate EP response (Lavorel & Garnier 2002; Suding *et al.* 2008; Laliberté & Tylianakis 2011). Unfortunately, the determination of response-effect relations is complicated. Even though some general trait-trait links have been revealed – mostly corresponding to trade-offs in resource acquisition (Díaz *et al.* 2004; Wright *et al.* 2004; Reich 2014) – several links are inconsistent across species and communities (Reich, Walters & Ellsworth 1997; Lienin & Kleyer 2012). Furthermore, significance and direction of trait responses and effects are probably not uniform across different scales (Lavorel & Garnier 2002; Klumpp & Soussana 2009; Laliberté & Tylianakis 2011). Consequently, response-effect relations might become unstable in the event of environmental change. These uncertainties hinder accurate prediction of biotic response to environmental change and its impacts on EP.

Inconsistency in response-effect relations across different environmental regimes has not yet been extensively investigated (but see Lienin & Kleyer 2012). So far most applications of the response-effect framework focused on grasslands, where variation along environmental gradients was rather limited (e.g. Laliberté & Tylianakis 2011; Minden & Kleyer 2011; Chollet *et al.* 2014). Moreover, functional response-effect research has been conducted mainly in temperate and Mediterranean regions, examples from the tropics are rare. Particularly in sub-Saharan Africa, assessments of EP and related ES through functional ecology approaches are lacking, as outlined in Chapter 4.

As a contribution to fill these gaps we investigated environment - plant functional trait - EP relationships across contrasting savanna and forest ecosystems in North-East Tanzania. At first we devised an *a priori* model for our study area (see Chapter 5.2.8) to describe expected trait response to climate, soil and disturbance simultaneously with trait effects on annual net primary productivity (NPP). We selected NPP for this study since it is a major indicator of ecosystem functioning (Scurlock, Johnson & Olson 2002) and had been integrated in most applications of the response-effect framework. In addition, among the three EP assessed in Chapter 4, NPP showed the most robust response. To test our hypothesized models on field data, we applied path analysis as described in Shipley (2002) and Shipley (2009). Particularly, we were interested in:

(1) the relevance of direct environmental effects on NPP versus plant functional trait-mediated effects and
(2) how functional response-effect relations and trait-trait linkages vary between different ecological zones within the study area.

In their meta-analysis Hooper *et al.* (2012) showed that biodiversity effects on EP were larger at local scales than at global scales. Accordingly, we hypothesized that in areas with longer environmental gradients the strength of direct environmental effects on NPP is enhanced, whereas in areas with shorter environmental gradients the strength of trait-mediated effects is enhanced (H1). Lienin and Kleyer (2012) applied the response-effect framework to different grassland ecosystems and management regimes. According to the results of their study, we expected to detect ecological zone specific environment-trait and trait-EP relationships but rather general trait-trait linkages (H2).

5.2 Materials and Methods

5.2.1 Study area

This research focused on the central Mkomazi Water Basin in North-East Tanzania (1100 km^2, 4°13’ to 4°50’ S, 37°54’ to 38°15’ E) (Figure 3, Figure 8). The study area covered a large altitudinal gradient ranging from the valley of Mkomazi River (430 m a.s.l.) to the summits of West Usambara and South Pare Mountains (2450 m a.s.l.). Accordingly, climate and soil conditions showed considerable variation (Table 9). These features facilitated diverse land cover comprising evergreen forests, deciduous woodlands and bushlands, seasonally flooded grasslands and woodlands as well as Homegardens, rain-fed farms and paddy fields (see Chapter 3). About 130,000 people inhabit the central Mkomazi Water Basin (NBS & OCGS 2013), their livelihoods are mainly based on subsistence farming and livestock keeping.

5.2.2 Field surveys and GIS data

The data used in this study derived from two sources: field measurements in 147 sample plots and a GIS database (Table 9). Sample plots were distributed equally over preliminarily defined land cover classes in the entire study area (Figure 8). Each plot had a size of 10 x 10 m or exceptionally 5 x 20 m in places where linear structures like riparian woodlands were sampled. We conducted field work from October 2011 to January 2013, surveying plots with deciduous vegetation during the rainy seasons (Nov-Dec, Mar-May) and those with evergreen vegetation during the dry seasons (Jan-Feb, Jun-Oct). GIS data were processed in ArcGIS 10 and extracted at each sample plot location.

5.2.3 Environmental factors

At each plot location a soil pit of 1 m depth (on stony ground < 1 m) was dug. In each soil horizon we determined physical soil features according to Ad-Hoc-AG Boden (2005) and collected soil samples. Air-dried samples were sieved (2 mm) and diluted in 1 mol $CaCl_2$-solution for pH measurement with indicator paper. Electric conductivity

Table 9. Recorded variables, abbreviations and data ranges. Data derived either from field surveys (a) or the GIS database (b). Furthermore, related variables were aggregated by principal component analyses (PCA) (c)

			Data Range			
			Lowlands		Highlands	
Variable	Abbreviation	Unit	Min	Max	Min	Max
Environmental factors						
1st axis of climate data PCA (c)	Aridity	-	-0.36	3.62	-5.23	-0.55
Rainfall (b)	-	$\mathrm{mm \cdot a^{-1}}$	410	757	642	957
Temperature (b)	-	°C	23.2	26	16.7	23.3
Evapotranspiration (b)	-	$\mathrm{mm \cdot a^{-1}}$	1574	1727	1052	1557
1st axis of soil data PCA (c)	SoilChem	-	-4.37	1.38	-1.09	1.73
Soil pH (a)	-	-	4	9	3.6	6.7
Electrical conductivity (a)	-	$\mathrm{\mu S \cdot cm^{-1}}$	197	6887	153	458
Disturbance index (ploughing, logging, mowing, fire, erosion) (a)	Disturb	-	0	3.96	0	3.23
Grazing index (a)	Graz	-	0	10.3	0	2.4
Plant functional traits						
Plant height (a)	PHeight	M	0.1	28.9	0.7	20.7
Leaf size (a)	LSize	$\mathrm{mm^2}$	12	36631	116	52386
Abundance of woody plants (a)	Woody	%	0	100	0	100
Spinescence (a)	Spine	-	0	42.4	0	24.5
1st axis of leaf trait data PCA (c)	LeafInv	-	-4.4	3.31	-1.23	2.05
Abundance of succulent leaves (a)	-	%	0	100	0	22
Abundance of hairy leaves (a)	-	%	0	96	0	100
Specific leaf area (a)	SLA	$\mathrm{mm^2 \cdot g^{-1}}$	3	28	5.2	21.8
Ecosystem properties (EP)						
Annual net primary productivity (b)	NPP	$\mathrm{kg \cdot m^{-2} \cdot a^{-1}}$	0.28	1.33	0.81	1.7

of soil-water dilutions was quantified with a WTW TetraCon® 325 sensor. The mean of both soil variables weighted by horizon thickness was used as plot mean. Data on frequency and intensity of fires, logging, mowing, ploughing and grazing were collected at each plot. Based on estimates of biomass removal caused by all recorded disturbances except for grazing, a disturbance index was calculated (see Chapter 3.2.2).

Furthermore, an independent grazing index was built based on grazing frequency and herbivore abundance. Finally, we obtained climatic data from GIS maps provided by G. Mmbando & M. Kleyer (unpublished data).

5.2.4 Plant functional traits

Functional traits of the most abundant vascular plant species which collectively contributed to at least 80% of total vegetation cover at each plot location were measured. Two healthy individuals of frequently dominant species (highly abundant in three or more plots) and five individuals of rarely dominant species were sampled per site. In total, we recorded traits of 237 vascular plant species. In Chapter 4 plant height, leaf pubescence, leaf succulence, leaf size and spinescence were found to be relevant determinants of NPP. We selected these traits for our analysis and added specific leaf area (SLA) and woodiness which we expected to be important in the response-effect context (cf. Pakeman 2011). All traits were measured in situ, except for leaf size and SLA. To determine these, we collected leaf samples which were measured (height, width and area), air-dried for at least 72 hours (this period was extended as necessary) and finally weighed.

Two general measures exist to explain the functional diversity of biotic communities: the ‘community weighted mean’ (CWM) and indices of community variation in functional traits, hereafter ‘community distribution metrics’ (CDM) (Díaz *et al.* 2007b). These measures accord to competing views on how biodiversity affects ecosystem functioning, namely the mass-ratio (Grime 1998) and the diversity hypotheses (Tilman *et al.* 1997). Both, CWM and CDM values satisfactorily explained EP in North-East Tanzania but the high performance of CDM might be attributed to significant correlations between both trait measures (Chapter 4). In order to avoid these correlation effects, we calculated CWM for single traits and determined trait variation from multiple traits. As CDM measure we used ‘Functional Dispersion’ as proposed by Laliberte and Legendre (2010). CWM and functional dispersion were calculated from plant species abundance and species-trait data with the R-package ‘FD’ (Laliberte & Legendre 2010).

5.2.5 Net primary productivity

Data on annual net primary productivity (NPP) originated from Moderate Resolution Imaging Spectroradiometer (MODIS) resources (NTSG & UMT 2014). Values for the years 2000 to 2010 were extracted at each plot location with ArcGIS; for modelling we used the mean over all sampled years.

5.2.6 Factor aggregation by principal component analysis

Climatic data (temperature, rainfall and evapotranspiration), soil data (pH and electric conductivity) and leaf traits (SLA, succulence and pubescence) were merged into aggregated variables by principal component analysis (PCA). For that purpose we used the R function 'pcomp' (R Core Team 2014). 92% of total variance in climatic data was explained by the first PCA axis, hereafter called 'Aridity' since it ranged from humid-cool to arid-hot conditions. For soil data the first PCA axis ('SoilChem') accounted for 92% of total variance, it ranged from low to high pH and electric conductivity. The first PCA axis of leaf traits explained 58% of total variance and ranged from high to low SLA and leaf pubescence as well as low to high abundance of succulent leaves. It therefore represented the trade-off between low and high investment in leaf structure (Wright *et al.* 2004), with pubescence being part of a low investment strategy to cope with hot-dry conditions (Ehleringer & Mooney 1978). Accordingly, we called this axis 'Leaf Structure Investment' (LeafInv).

5.2.7 Model building

We applied path analysis as described by Shipley (2002) and Shipley (2009) to simultaneously analyse plant functional trait response and effect. Based on graph theory this approach evaluates the significance of a 'multivariate causal hypothesis' that is formulated in a path model. Probabilities of 'independence claims' made for all pairs of variables which are not directly connected by hypothesized paths are assessed in a directional separation (d-sep) test. Fisher's C is calculated over all determined probabilities and compared to a Chi-squared distribution. The resulting p-value (hereafter 'p_{model}') indicates strong support of non-hypothesized paths if it falls below the chosen significance level (here 0.05). In that case the hypothesized model has to be rejected.

Our *a priori* theoretical model is outlined in the next section. All data were standardized prior to modelling to gain standardized path coefficients. Hypothesized paths were tested for significance represented by coefficients' p-values (hereafter 'p_{coef}') obtained from general linear models. Insignificant paths were removed ($p_{coef} > 0.05$). D-sep tests were applied to identify relevant non-hypothesized links between variables. As far as they were justified by ecological reasoning, these links were added to the models aiming to achieve sufficient model significance ($p_{model} > 0.05$). Path coefficients of the final models were used to calculate direct, indirect and total effects on plant functional traits and NPP. We applied the R-package 'ggm' (Marchetti, Drton & Sadeghi 2014) to build directed acyclic graphs and to identify the basis set of independent claims (Shipley 2009). General linear models were fitted with the R-function 'lm()' (R Core Team 2014).

In order to investigate the consistency of response-effect relations across different ecological zones, we tested the hypothesized model not only on the entire dataset ('Basin': n=147) but also on two subsets ('Highlands': n=63, 'Lowlands': n=84). These were gained from k-means clustering based on Aridity using the R-function 'kmeans()' (R Core Team 2014).

5.2.8 *A priori model*

This paragraph briefly explains the initial hypothetical path model which was built according to response-effect theory and evidence from published research. Detailed characteristics of all hypothesized paths are listed in Table 10 alongside with relevant scientific references. Additionally, Figure A 1 gives a schematic overview of the hypothesized model.

Vulnerability to soil salinity and corresponding alkalic conditions increases with decreasing precipitation (Jordán *et al.* 2004), whereas soil pH is low under high rainfall regimes (Mizota, Kawasaki & Wakatsuki 1988). We therefore expected a positive effect of Aridity on SoilChem. Aridity and soil salinity limit plant metabolism, force plant economics into conservative allocation strategies (Minden & Kleyer 2011; Reich 2014) and restrict the diversity of physiological parameters (Currie *et al.* 2004).

Table 10. Hypothesized relations between environmental variables, plant functional traits and net primary productivity (NPP), relevant references and evaluated significance based on three datasets: Basin (entire study area) - B; Highlands - H; Lowlands - L. Label legend: ✓ - significant link; (✓) - link significant but effect size < 0.3; 0 - insignificant link; ! - link significant but opposite to expected direction. Abbreviations of variables see Table 9

Linkage	Hypotheses	Literature	B	H	L
Interrelations among environmental factors					
Aridity → SoilChem (+)	Salinization and pH increase as response to aridity	(Mizota, Kawasaki & Wakatsuki 1988; Jordán *et al.* 2004)	✓	0	✓
Disturb → Graz (-)	Grazing is excluded from sites with highest disturbance (= farms)	-	(✓)	0	(✓)
SoilChem → Graz (+)	Not hypothesized	-	✓	0	✓
Trait response to environmental factors					
Aridity → PHeight (-)	Plant growth is limited in dry environments	(Moles *et al.* 2009)	0	0	(✓)
Aridity → LeafSize (-)	Leaf size is minimized in dry environments to optimize convective heat loss	(Lavorel *et al.* 2007)	(✓)	0	✓
Aridity → LeafInv (+)	Carbon allocation to leaves is enhanced in dry environments	(Chapin 2003)	0	0	0
Aridity → Spines (+)	Spinescence increases with aridity	(Milton 1991)	✓	0	✓
Aridity → FunDis (-)	Increasing aridity supports less functional trait variance	(Currie *et al.* 2004)	0	0	0
Disturb → Woody (-)	Logging, ploughing and fire strongly select against woody plants	(Hoffmann, Schroeder & Jackson 2002; Lienin & Kleyer 2012)	✓	✓	✓
Disturb → PHeight (-)	Plant height is reduced in high disturbance regimes	(Garnier *et al.* 2007; Lienin & Kleyer 2012)	✓	✓	✓
Disturb → LeafSize (+)	Not hypothesized	-	0	0	✓
Disturb → LeafInv (-)	Rapid regrowth as response to disturbance reduces carbon allocation to leaves	(Garnier *et al.* 2007)	0	0	0
Graz → PHeight (-)	Herbivory avoidance by reduced plant height	(Díaz *et al.* 2007c)	✓	✓	✓

Table 10. Continued

Linkage	Hypotheses	Literature	B	H	L
Trait response to environmental factors					
Graz → LeafSize (-)	Herbivory avoidance by reduced leaf size	(Díaz, Noy-Meir & Cabido 2001)	(✓)	(✓)	o
Graz → LeafInv (-)	Rapid regrowth as response to grazing reduces carbon allocation to leaves	(Lienin & Kleyer 2012)	o	o	o
Graz → Spines (+)	Investment in structural defence as response to grazing	(Skarpe & Hester 2008)	✓	o	✓
Graz → FunDis (+)	Not hypothesized	-	(✓)	o	(✓)
SoilChem → LeafInv (+)	Carbon allocation to leaves is enhanced under high salinity	(Minden & Kleyer 2011)	✓	o	✓
SoilChem → FunDis (-)	High salinity and pH limits diversity of physiological features	(Currie *et al.* 2004)	(✓)	o	✓
Trait-trait linkages					
Woody → PHeight (+)	Increased stability of woody plants facilitates larger height	(Niklas 1993)	✓	✓	(✓)
Woody → LeafSize (-)	Not hypothesized	-	✓	✓	o
Woody → LeafInv (+)	Positive scaling between investment in different plant organs	(Reich 2014)	✓	✓	(✓)
Woody → Spines (+)	Spines are mainly associated with woody plants	(Milton 1991)	✓	o	✓
Woody → FunDis (+)	Not hypothesized	-	✓	o	✓
LeafInv → PHeight (+)	Greater plant height requires higher carbon allocation to leaves	(Cingolani, Posse & Collantes 2005)	(✓)!	o	(✓)!
LeafInv → FunDis (-)	Higher investment in leaf structures supports less trait diversity	(Lienin & Kleyer 2012)	(✓)	o	(✓)
Spine → PHeight (-)	Not hypothesized	-	(✓)	o	o
Effects on NPP					
Aridity → NPP (-)	In dry environments productivity is reduced	(Zhao & Running 2010)	✓	✓	✓

Table 10. Continued

Linkage	Hypotheses	Literature	B	H	L
Effects on NPP					
Disturb → NPP (+)	Not hypothesized	-	(✓)	o	(✓)
Woody → NPP (-)	Not hypothesized	-	o	o	(✓)
PHeight → NPP (+)	Higher plants carry more leaf area which facilitates higher NPP	(Chapin 2003)	✓	✓	✓
LeafSize → NPP (+)	Larger leaves improve whole-plant productivity due to reduced self-shading	(Falster & Westoby 2003)	o	o	o
LeafInv → NPP (-)	Productivity is increased where investment in leaf tissue is limited	(Reich, Walters & Ellsworth 1997)	(✓)	✓	o
Spines → NPP (-)	Investment in structural defence reduces productivity	(Fine *et al.* 2006)	(✓)	o	o
FunDis → NPP (+)	High functional trait diversity improves productivity	(Díaz *et al.* 2007a)	o	o	o

Hence we assumed a positive response of LeafInv and a negative response of functional dispersion to both factors. Hypothesized functional trait responses to disturbance and grazing represent different coping strategies: increased investment in structural defences (spinescence), avoidance by reduced plant height and leaf size or rapid regrowth expressed by low LeafInv (Díaz *et al.* 2007c; Skarpe & Hester 2008). Anticipated trait-trait relations included positive effects of woodiness on plant height (Niklas 1993), spinescence (Milton 1991) and LeafInv based on whole-plant economics convergence theory (Reich 2014). Furthermore, we hypothesized negative scaling of LeafInv on functional dispersion as described by Lienin and Kleyer (2012). We expected only one direct environmental effect on NPP, a negative impact of Aridity (Chapin 2003; Zhao & Running 2010). Other environmental influences were expected to be mediated by positive effects of plant height (Chapin 2003; Lienin & Kleyer 2012) and CDM (Díaz *et al.* 2007a) and negative effects of LeafInv and spinescence (Reich, Walters & Ellsworth 1997; Fine *et al.* 2006; Laliberté & Tylianakis 2011).

5.3 Results

None of the three datasets sufficiently supported the hypothesized path model which made several modifications necessary. In the Basin and Lowlands models 74% and 67% of the hypothesized paths, respectively, were confirmed; six non-expected links had to be added in each to gain significant models (Table 10). Highland data approved only 33% of the expected paths, however only one non-expected relation had to be added. All three final models were sufficiently robust with p_{model} well above 0.05 (Figure 10).

5.3.1 Interrelations among environmental variables

No significant links between environmental variables were found in the Highlands model. By contrast, both hypothesized relations between environmental variables were confirmed in the Basin and Lowlands models (Table 10). Particularly the strong positive effect of Aridity on SoilChem stood out. Additionally, a strong positive effect of SoilChem on Grazing was revealed (Figure 10), but most likely this was not a causal effect. High soil-pH and salinity were strongly restricted to the lowland floodplains, which were favoured by herbivores against the surrounding savanna due to prolonged water availability.

5.3.2 Trait response to environmental factors

Several hypothesized effects of environmental variables on traits could not be confirmed in the Basin and Lowlands models. In the Highlands model even the majority of paths was rejected due to the absence of any Aridity and SoilChem effects on traits (Table 10). In all three models most of the expected effects on LeafInv were insignificant. Strong negative effects of disturbance on woodiness and plant height were the most remarkable trait responses, consistently over all three models (Figure 10). Moreover, we found considerable positive effects of SoilChem on LeafInv as well as positive effects of Aridity and grazing on spinescence in the Basin and Lowlands models.

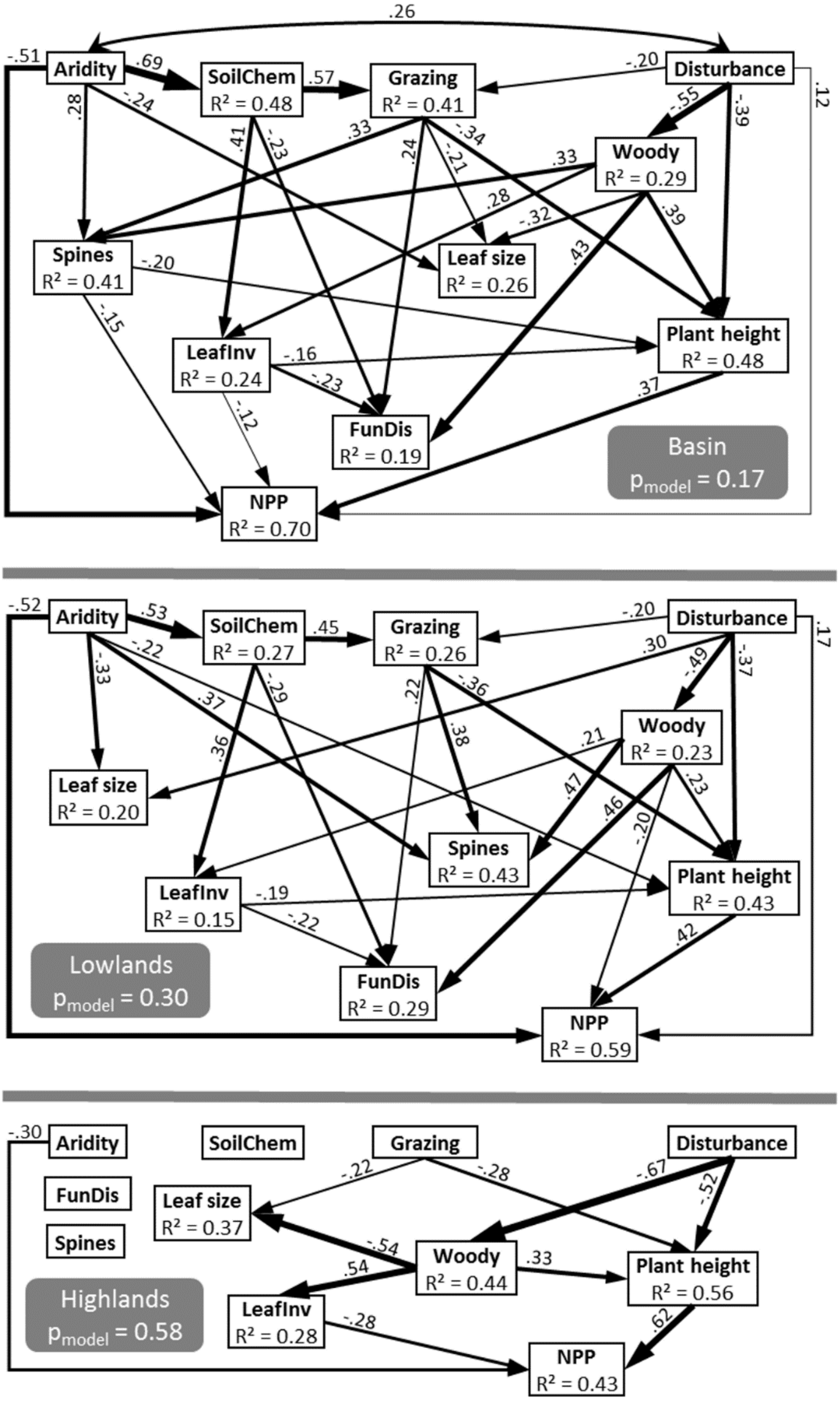


Figure 10. Final path models derived from the hypothesized model in Figure A 1 for data from the entire study area ('Basin') (n=147), the lowlands (n=84) and the highlands (n=63). Overall model significance (p¬model) was derived from Fisher's C of d-sep tests. Only significant paths are shown (pcoef > 0.05). Single-headed arrows represent direct effects (standardized partial regression coefficients). Double-headed arrows represent correlations. Relative effect sizes are given above each arrow and are additionally illustrated by arrow-width. R^2-values beneath each endogenous variable indicate their total explained variance. Abbreviations see Table 9

5.3.3 *Trait-trait linkages*

All hypothesized trait-trait linkages were confirmed in the Basin and Lowlands models, however the expected positive effect of LeafInv on plant height was found to be weakly negative (Table 10, Figure 10). In the Highlands model only two of five expected paths were significant, which was due to the irrelevance of spinescence and functional dispersion. Woodiness was found to have considerable effects on other traits in all three models. However, their individual strength was inconsistent across the three models. While in the Basin model woodiness had strongest effects on functional dispersion (+) and plant height (+), it mostly affected functional dispersion (+) and spinescence (+) in the Lowlands model. In the Highlands model considerable response of LeafInv (-) and leaf size (+) was observed.

5.3.4 *Direct environmental versus trait effects on NPP*

In the previous sections we solely considered direct links between model variables. Since our primary focus lied on the investigation of effects on NPP, we extended our analysis at this point and integrated indirect effects as well.

The most relevant direct effects on NPP in all three models were a negative effect of Aridity and a positive effect of plant height (Figure 10). However, while the Aridity effect was larger in the Basin and Lowlands models, plant height dominated NPP response in the Highlands model. Expected direct effects of other traits (spinescence, LeafInv) were weak and only confirmed in one or two models (Table 10). Furthermore, neither FunDis nor LeafSize had significant effects on NPP in any of the three final models.

In the Basin and Lowlands models the consideration of joint direct and indirect effects confirmed high relevance of Aridity and plant height as well as the low importance of other factors for the determination of NPP (Figure 11). Contrastingly, in the Highlands model total effects indicated that apart from plant height and Aridity, disturbance and LeafInv were crucial factors as well.

While in the Basin and Lowlands models NPP was mainly controlled by direct effects of Aridity, NPP response in the Highlands model was dominated by effects of disturbance mediated by woodiness, plant height and LeafInv.

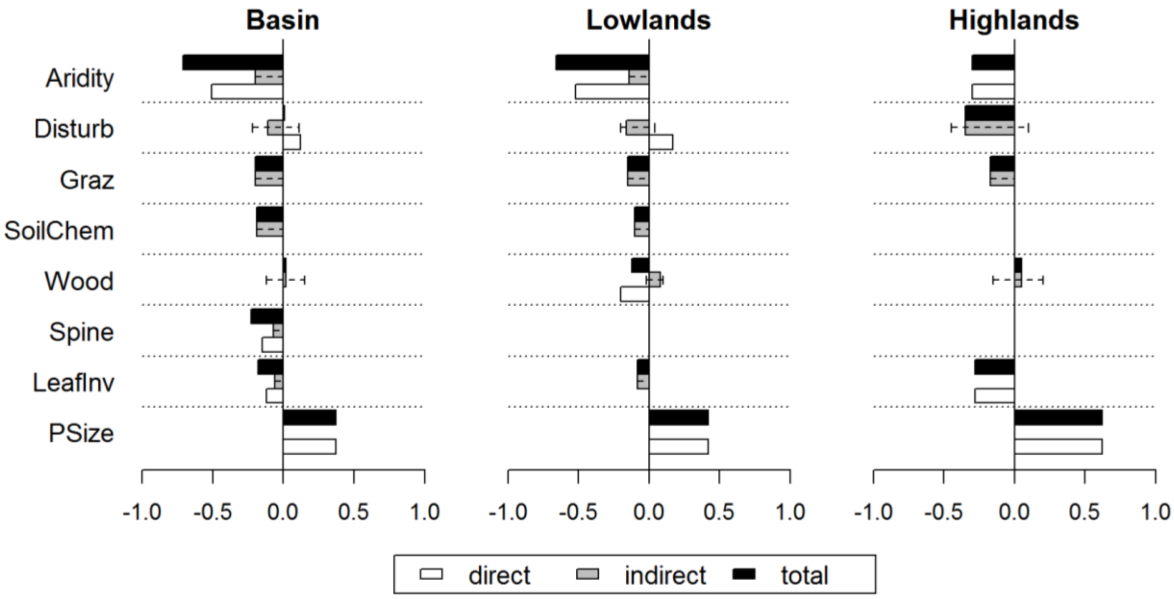


Figure 11. Direct, indirect and total effects of environmental factors and plant functional traits on NPP in the three final models. For indirect effects dashed lines show absolute indirect effect sizes (negative and positive). Abbreviations see Table 9

5.4 Discussion

In this study we analysed links between environmental factors, plant functional traits and net primary productivity in a diverse landscape by application of the response-effect framework (Lavorel & Garnier 2002). We explored inconsistencies in these links across two different ecological zones. Similar assessments of the response-effect framework along wide environmental gradients had rarely been conducted before and to our knowledge never focused on any part of the African continent.

5.4.1 Direct environmental versus trait-mediated effects in different ecological zones

In all three models (Basin, Lowlands, Highlands) direct environmental as well as trait-mediated effects on net primary productivity (NPP) were highly significant. As we had expected the strength of these two effect types differed across the three models. In the Basin model (long environmental gradients) direct effects of environmental factors on NPP were considerably stronger than trait-mediated effects (Figure 10), which was in favour of H1. Similarly strong direct effects on NPP had been detected in a grassland experiment over a long soil nutrient gradient (Laliberté & Tylianakis 2011). However, in the Lowlands and Highlands models (shorter environmental gradients) we found inconsistent patterns. While trait-mediated effects were dominant in the Highlands model (H1 confirmed), in the Lowlands model direct effects of Aridity were similarly strong as in the Basin model (H1 rejected). Paradoxically, temperature and evapotranspiration ranges in the highlands were more than twice as large as in the lowlands (Table 9). According to H1, we therefore would have expected that trait-mediated effects were of larger relevance in the lowlands than in the highlands. This discrepancy indicates that the transition between dominance of trait-mediated effects on NPP and dominance of direct environmental effects was not primarily controlled by the length of environmental gradients.

Instead the strength of direct environmental effects on NPP was prominently controlled by the severity of water resource limitation represented by the Aridity gradient. Under strong resource limitation (as in the lowlands), a decrease in Aridity had a much more positive effect on NPP than the same decrease in Aridity had under higher resource availability (highlands) (Figure 12). In accordance to this pattern we suspect that under strong resource limitation, effects of variation along the resource gradient on NPP outperform effects of plant functional trait differences. The latter govern rather survival than productivity in stressful environments (Goldberg & Novoplansky 1997). By contrast, under higher resource availability environmental effects on NPP are outperformed by trait effects. Although our results were indicative of the water resource gradient only, we expect that our conclusion can be extended to the other two major plant resources as well (nutrients and light). For instance, data in Laliberté and Tylianakis (2011) uncovered a similar behaviour of above- and below-ground net primary productivity to a soil fertility gradient.

5.4.2 *Consistency of functional response-effect relations across ecological zones*

We found several consistent trait response and effect relations across the Basin, Lowlands and Highlands models. Nevertheless, most relations were confirmed in only one or two models and therefore inconsistent (Figure 10, Table 10). This is in line with the idea that in different ecosystems, different biodiversity effects on ecosystem functioning might prevail (Loreau *et al.* 2001). In contrast to our expectation under

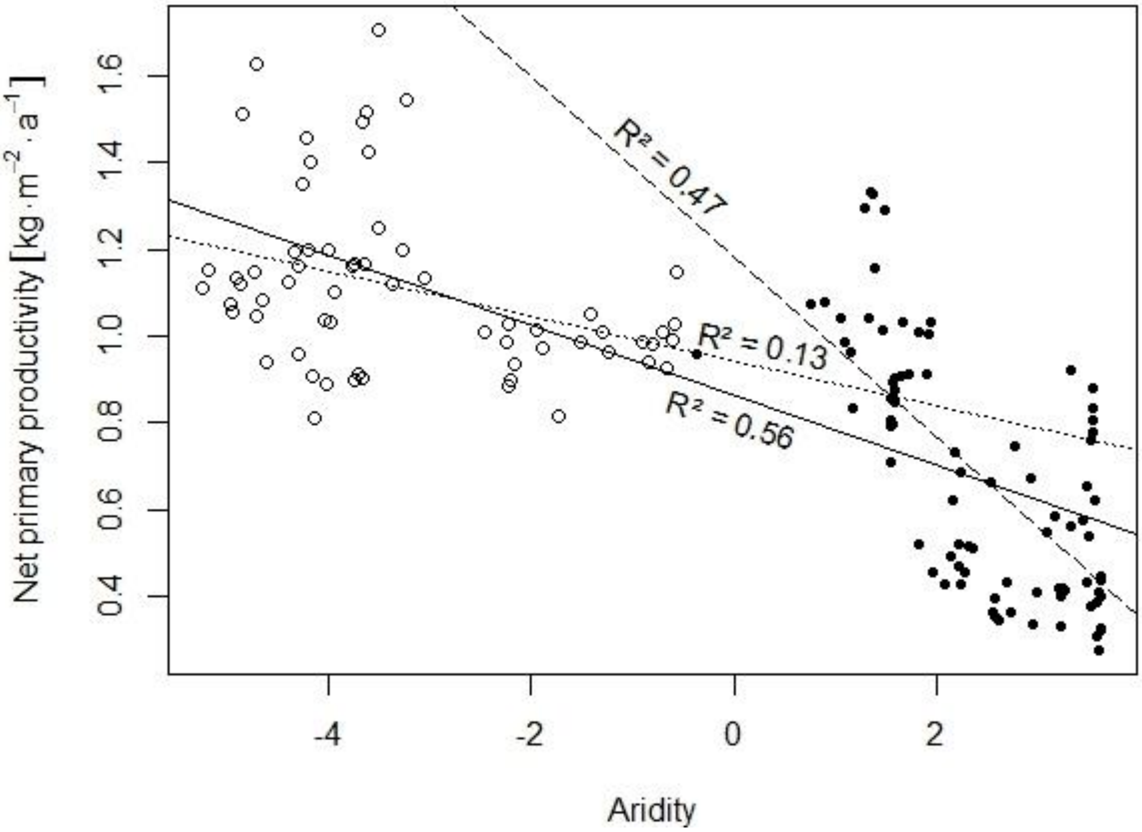


Figure 12. Relation between Aridity and net primary productivity for Lowland (filled dots) and Highland data (open dots). Regression lines and R^2 values were derived from simple linear regression from the entire dataset (solid line), the Lowlands data (dashed line) and the Highlands data (dotted line)

hypothesis H2, consistency in trait-trait relations did not significantly exceed that of environment-trait, trait-NPP and environment-NPP relations. Yet, our results revealed another distinct pattern: all relations involving plant height were consistent across the three models (Figure 10). Consistency of plant height response and effect across different ecosystems and regions had been hypothesized and found before (Díaz *et al.* 2004). Responses of LeafInv and woodiness were relatively consistent too, however their effects on NPP could not be confirmed in all three models. At least for LeafInv this outcome is surprising because in previous studies SLA had been strongly related to productivity over a wide range of ecosystems (e.g. Reich, Walters & Ellsworth 1997). None of the responses and effects of leaf size, spinescence and functional dispersion was consistent across the Lowlands, Highlands and Basin models. Therefore, these response-effect relations seemed to be ecosystem- or site-specific; in one system they were highly relevant, while they were insignificant in another system (e.g. response of spinescence to grazing and climate in lowlands versus highlands, Figure 10). Moreover, even in cases where we found consistent links in all three models, their importance differed considerably. For example, the effect of plant height on NPP was large in the highlands, whereas it was only of moderate size in the Basin and Lowlands models. Similar observations of inconsistencies in the significance or strength of response-effect relations across nutrient and climatic gradients were made elsewhere (Laliberté & Tylianakis 2011).

5.4.3 Highlights on specific response-effect relations

In all three models (Lowlands, Highlands and Basin) NPP responded most prominently to Aridity and effects of disturbance mediated by plant height (Figure 10, Figure 11). Strong negative effects of Aridity on NPP as revealed in this study had been reported before (Zhao & Running 2010). Nevertheless, climatic factors had not yet been integrated in response-effect models. Our study clearly indicated that climatic influences on EPP and trait response-effect relations should be considered at scales exceeding individual ecosystems. Negative responses of plant height to disturbance (Chollet *et al.* 2014) and positive plant height effects on productivity (Lavorel *et al.* 2011; Conti & Díaz 2013; Grigulis *et al.* 2013) were in line with published research. However, the weak but significant direct positive effect of disturbance on productivity (Augustine & McNaughton 1998; Wardle *et al.* 2003) neutralized this indirect negative effect in the Basin and Lowlands models. Similarly, indifferent effects of disturbance on productivity had been identified by Oesterheld *et al.* (1999). We assumed that the influence of disturbance on productivity depends on resource availability (Augustine & McNaughton 1998; Laliberté & Tylianakis 2011). In systems which comprise strongly resource-limited situations (e.g. high Aridity), disturbance effects are surpassed by effects of the resource gradient (as in the lowlands). In systems which comprise only moderately resource-limited conditions, (trait-mediated) disturbance effects on productivity prevail (as in the highlands).

Numerous studies stressed the high relevance of traits related to the plants economics spectrum (PES) for productivity (e.g. Chapin 2003; Laliberté & Tylianakis 2011; Lavorel & Grigulis 2012; Reich 2014). Still, LeafInv had only marginal effects on NPP in our models (Figure 11). As Reich (2014) pointed out, under different environmental regimes, a similar variety of successful growth strategies, represented by the PES, has been established. Therefore, we concluded that NPP generally shows no distinct response to the PES over moderate and long environmental gradients.

Several other expected relations were not confirmed by our models. These included the effects of functional dispersion, leaf size and spinescence on NPP (Table 10). According to the diversity hypothesis (Tilman *et al.* 1997) high functional dispersion has a positive effect on NPP. While empirical support for Tilman's hypothesis is sparse (e.g. Fry *et al.* 2013), it had been rejected in several studies (e.g. Laliberté & Tylianakis 2011; Chanteloup & Bonis 2013), particularly where a higher variation of plant communities was covered e.g. (Lienin & Kleyer 2012; Moretti *et al.* 2013). Our results fitted well into this pattern. We assumed that under highly variable environmental conditions, functional dispersion has no considerable effect on productivity. The expected positive effect of reduced self-shading by larger leaves on NPP (Falster & Westoby 2003) was insignificant in all three models. Consequently, we concluded that leaf size is generally not suitable to explain NPP response. Finally, we found a strongly localized importance of spinescence. While in the highlands, spinescence was not a typical grazing response strategy, in the lowlands it was much more common. This was most probably due to the stronger resource-limitation in the lowlands, which restricted quick regrowth as grazing response and required permanent defence structures (Fine *et al.* 2006; Skarpe & Hester 2008).

5.4.4 Critical aspects

The assessment of our results should consider the following shortcomings. Some environmental factors and functional traits, which proved to be highly relevant in response-effect relations, were not integrated into our models due to lack of data. These included root traits as important components of the plant economics spectrum (PES) (Kleyer & Minden 2015) and soil nutrients as relevant PES-determinants (Lavorel *et al.* 2007; Reich 2014). Furthermore, our models did not consider interactions between variables, although their relevance had been shown before (Laliberté & Tylianakis 2011). Finally, our analysis was limited to a single EP, whereas an integration of several inter-related EP might have revealed much more ecological insights (cf. Pakeman 2011).

5.5 Conclusions

This study uncovered crucial aspects of functional response-effect relations that had not yet been assessed before.

Firstly, we found that the importance of direct environmental versus trait-mediated effects on NPP (and most likely on other EPP as well) was not primarily controlled by the length of environmental gradients. The degree to which strongly resource-limited conditions are covered by environmental gradients seemed to be much more relevant. However, this hypothesis needs to be thoroughly tested in future research.

Secondly, it was evident that several environment – functional traits – productivity links as well as trait-trait relations are not consistent along environmental gradients. Indeed, our models supported previous research which found that a number of functional traits shows equal responses to certain environmental factors and equal effects on specific EP across different ecosystems (e.g. Reich, Walters & Ellsworth 1997; Díaz *et al.* 2004). However, the relative weight of these relations for EP response might differ greatly from ecosystem to ecosystem. Corresponding to these findings, we concluded that in different ecological zones, different prominent trait responses to different environmental factors filter different effect traits which influence EP in different ways. This implies that in heterogeneous landscapes response-effect analyses have to consider different ecological zones.

Chapter 6

Synthesis

6 Synthesis

In this chapter the answers that Chapters 3 to 5 could provide to the major research questions (Chapter 1.5) are synthesized and discussed. In the first part the particular sensitivity of biodiversity and EP in Mkomazi Water Basin is amplified. Moreover, implications for the vulnerability of ES provision in the area are evaluated. The second part compares the land cover and functional diversity based approaches to study biodiversity and EP sensitivity in heterogeneous landscapes. Advantages and disadvantages of both approaches are outlined and recommendations are given for their appropriate use. In the final part of this chapter, a protocol is developed that integrates both approaches. It might be used as a guideline to assess biodiversity and EP sensitivity in heterogeneous landscapes at different levels of detail.

6.1 Ecosystem sensitivity and vulnerability in central Mkomazi Water Basin

6.1.1 Regional environmental change

Environmental conditions in central Mkomazi Water Basin are expected to change considerably in the near future. The two most important sources for this development are global climate change and the intensification of local land use activities. Regional climate change models project a rise of monthly minimum and maximum temperatures by 1.5-2.3 °C for the period 2046-2065 compared to the period 1960-2000 (Tadross & Wolski 2010). Rainfall is projected to increase by 5-10% during rainy seasons, but to decrease by 20-40% during dry seasons. Human population in Mkomazi Water Basin is growing at an average rate of approximately 2% per annum (Kilimanjaro Region 1.8% and Tanga Region 2.2%: NBS & OCGS 2013). In response to the increased resource demands that accompany population growth, land use activities presumably will be expanded and intensified. This will particularly affect the highlands as well as the floodplains along Mkomazi River. Due to better resource availability, population growth rates in these areas are much higher than in the rest of the basin (cf. Notter 2010). The most obvious land use change that can be expected is the expansion of farmland. However, most of the areas in the central Mkomazi Water Basin where adequate crop yields can be gained are already utilized. Therefore, intensification of farming activities might become more relevant in the future. For instance, during the first years of the new millennium ginger was introduced in the South Pare Mountains, a crop with high economic returns but extensive irrigation requirements (Komakech *et al.* 2012). Nevertheless, intensification of farming requires investments (e.g. in irrigation infrastructure), which might not be feasible for the local communities. Consequently, alternative livelihood sources are expected to be tapped more extensively, as this already is practised in the region during droughts (Enfors & Gordon 2008). Most likely, livestock keeping, timber and fuelwood extraction as well as charcoal production will increase, particularly in the vicinity of growing settlements (Schaafsma *et al.* 2012). All these land use intensifications will lead to an increase of disturbances like ploughing, fire, grazing and logging. Furthermore, combined effects of expanding water abstraction for farming and increased aridity are likely to entail reductions of run-off in Mkomazi River and its tributaries, particularly during dry seasons (Tadross & Wolski 2010). This will impair drainage from the floodplains and increase the risk for soil salinization and sodification (Misana & Makoi 2001), especially in the paddy fields north of Lake Manga.

In summary, the following major environmental changes have to be expected in the foreseeable future:

- Increasing aridity over the entire Mkomazi Water Basin
- Increasing disturbance particularly in the floodplains along Mkomazi River, in the vicinity of growing settlements and in the highlands along the forest boundaries
- Reduced flow water availability in Mkomazi River and reduced flooding frequency in the adjacent floodplains
- Soil salinization and sodification in the floodplains along Mkomazi River

6.1.2 Land cover tolerance and consequences for EP

Based on the results of this thesis, it was possible to evaluate how the expected environmental changes might affect properties of ecosystems in the central Mkomazi Water Basin. A first overview could be gained from the collected information about the tolerance of different land cover types to the changing environmental factors (Chapter 3).

The most important determinants of land cover distribution in central Mkomazi Water Basin were climatic factors and disturbance. Moreover, several land cover types significantly responded to distance to next water body, which can be interpreted as an inverse proxy for flooding frequency. Against the background of these outcomes, the expected environmental changes in the study area, including increases of aridity and disturbances and reductions of river flow, most likely will entail considerable land cover shifts.

Responses to the projected environmental changes will vary significantly among the studied land cover units, due to their differential tolerance ranges as discussed in Chapter 3. Land cover changes that can be expected in central Mkomazi Water Basin are summarized in Table 11. Potential effects of rainfall change were not included since they could not be clearly determined. While land cover responses to dry and wet season rainfall were strongly correlated, the projected changes of dry and wet season rainfall were opposing (decrease vs. increase).

The land cover units that are likely to suffer most from the environmental changes in Mkomazi Water Basin are evergreen highland forests, deciduous shrub- and woodlands on slopes and riparian woodlands (Table 11). Due to their low tolerance to disturbance, evergreen highland forests will be negatively affected by land use intensification, particularly at their lower boundaries. This is in accordance to findings of forest change studies that were conducted across the Eastern Arc Mountains (Green *et al.* 2013) and on Mount Kilimanjaro (Hemp 2009). Moreover, rising temperatures will require an upward shift of the forest margins and hence a reduction of their occurrence range (Foster 2001). Slope woodlands will show negative responses to increased fuelwood extraction and the expansion of farms. For the Eastern Arc Mountains, high rates of predicted and observed woodland conversion have been stressed before (Green *et al.* 2013). Riparian woodlands will be extensively affected by reductions of flow water availability and flooding frequency, indicated by their high sensitivity to distance to next water body (cf. PBWO & IUCN 2009). Extensive effects of increasing disturbance and rising temperatures can also be expected for homegardens and plantation forests, respectively. Both might shift into areas currently covered by evergreen highland forests. This depends however on the degree to which

Table 11. Expected responses of land cover units to projected environmental changes: rising average minimum temperature (TMin); locally increasing disturbance, grazing and distance to next water body (DToWat). These changes can have strong (+), moderate (~) or weak (-) effects that diminish (⬂), relocate (⬄) or extend (⬀) the ranges of land cover units. These effects are controlled by relative range breadths (rRB) and the position of each land cover unit's occurrence range along the changing environmental gradients (pos.) (Figure 6). Occurrence ranges can cover the minimum (min), the maximum (max) or none of both extremes of a gradient (centre). Only effects of changing environmental factors that are important determinants of land cover distribution are listed (importance > 0.5, see Table A 2). Final land cover responses prepended by "!" are controversial. Land cover units abbreviations see Table 1

Land cover unit	TMin			Disturbance Index			Grazing Index			DToWat			Expected land cover response
	rRB	pos.	effect	rRB	pos.	effect	rRB	pos.	effect	rRB	pos.	effect	
ForPlant	0.2	centre	⬄(+)	-	-	-	-	-	-	-	-	-	Extensive range shifts
Fallow	0.4	min	⬂(~)	-	-	-	-	-	-	-	-	-	Moderate losses
ForHigh	0.5	min	⬂(~)	0.1	min	⬂(+)	-	-	-	-	-	-	Moderate losses, locally extensive losses
FarmTree	-	-	-	0.2	centre	⬄(+)	-	-	-	-	-	-	Extensive range shifts
FarmTera	0.8	centre	⬄(-)	0.5	max	⬀(~)	-	-	-	-	-	-	Moderate expansions
WoSlope	0.5	centre	⬄(~)	0.5	min	⬂(~)	-	-	-	-	-	-	Moderate range shifts, locally moderate losses
FarmRain	-	-	-	0.9	centre	⬄(-)	-	-	-	-	-	-	Locally minor range shifts
WoRipar	0.4	centre	⬄(~)	0.8	min	⬂(-)	-	-	-	0.1	min	⬂(+)	Extensive losses
Comm	-	-	-	-	-	-	0.7	min	⬂(-)	0.3	centre	⬄(~)	Locally moderate range shifts and minor losses
Thicket	-	-	-	0.5	min	⬂(~)	-	-	-	-	-	-	Locally moderate losses
WoFlood	0.3	max	⬀(~)	-	-	-	0.5	min	⬂(~)	0.1	min	⬂(+)	Ambiguous
FarmRice	0.1	max	⬀(+)	0.8	centre	⬄(-)	-	-	-	-	-	-	! Extensive expansion
ReedGras	0.3	max	⬀(~)	-	-	-	1	n.a.	n.a.	-	-	-	! Moderate expansion
Acacia	-	-	-	-	-	-	1	n.a.	n.a.	0.5	min	⬂(~)	! Locally moderate losses
Suaeda	0.1	max	⬀(+)	0.3	min	⬂(~)	-	-	-	0.1	min	⬂(+)	Ambiguous

these cultivated land cover types will be favoured by local land users. Particularly homegardens might be diminished in favour of more intensive farms (cf. Hemp 2006). In line with this, intensive farmland (terraced farms in the highlands and paddy fields in the lowlands) is likely to benefit most from the expected environmental changes in the study area. However, this might be challenged by reduced surface water availability in the lowlands which most likely will have negative effects on paddy fields (cf. Notter 2010). Finally, *Acacia* and *Commiphora* bushlands might benefit from rising temperatures and increasing disturbance, due to their high tolerance to these factors.

In order to evaluate the consequences of the expected land cover changes on different EP, their responses to land cover were analysed. In accordance to Chapter 4, the EP in focus were annual net primary productivity (NPP), litter thickness and erosion intensity. General linear models (GLMs) of the Gaussian family (identity link) were applied to assess NPP. For litter thickness and erosion intensity GLMs of the Gamma family (inverse link) were used (see Chapter 4.2.3). For the sake of model performance, the 17 originally studied land cover units (Table 1) were generalized into seven land cover classes (Table 12).

NPP response was well depicted by the seven land cover classes ($R^2 = 0.65$). The highest levels of NPP in Mkomazi Water Basin were reached within indigenous forests (Figure 13). Plantation forests and fallows as well as agroforestry and terraced farms, which might replace indigenous forests, had significantly lower NPP. A similar situation was found on the mountain slopes and in the lowlands where woodlands with

Table 12. Land cover classes used as EP determinants. Each land cover class derived from one or more land cover units described for Mkomazi Water Basin (see Chapter 3, Table 1)

Land cover classes	Land cover units
Agroforestry & terraced farms	Agroforestry, irrigated terrace farms
Rain-fed farms	Rain-fed farms
Indigenous forest	Evergreen highland forest, dry evergreen slope forest, evergreen lowland forest
Plantation forest & fallows	Plantation forest, mixed fallow grass- and shrubland
Grasslands, reeds & rice farms	Temporary flooded reed and grassland, paddy fields
Shrubland	*Suaeda* shrubland, *Acacia* shrubland, *Commiphora* shrubland, mixed thicket and shrubland
Woodland	Deciduous shrub- and woodland on slopes, temporary flooded woodland, riparian woodland

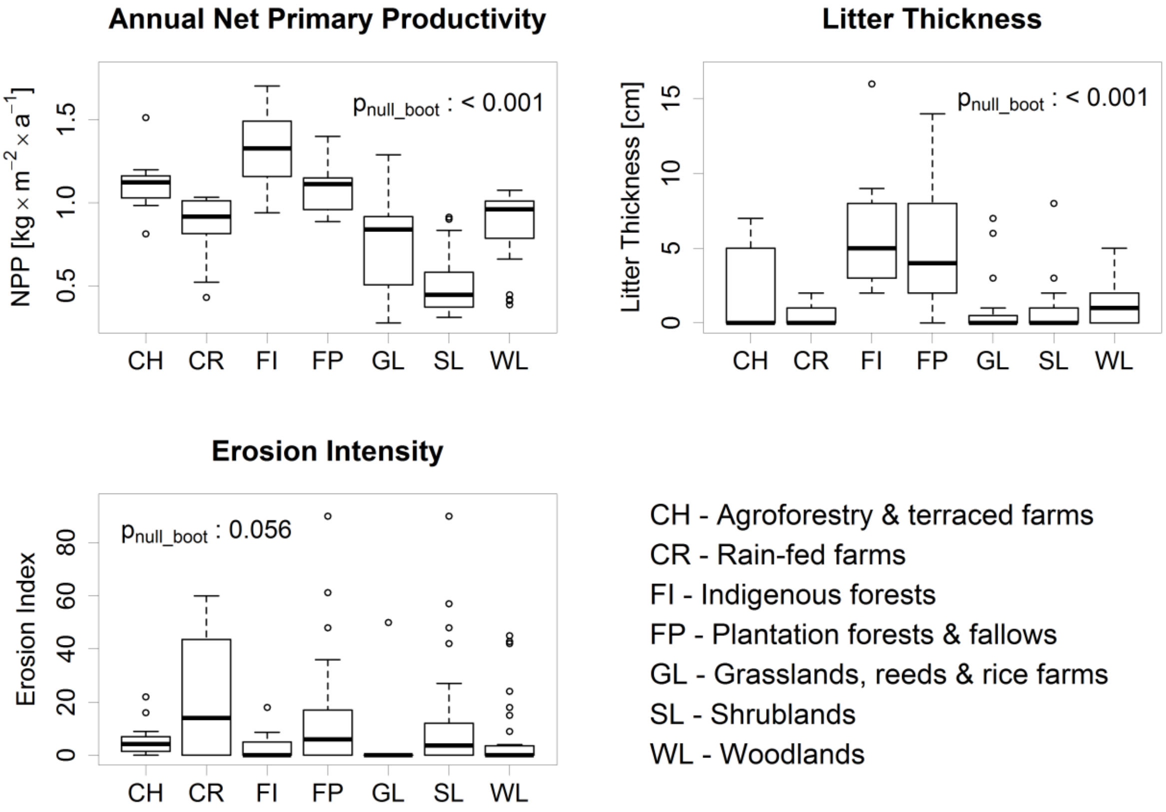


Figure 13. Ecosystem properties' (EP) variation across seven land cover classes in central Mkomazi Water Basin. The significance values (p_{null_boot}) were derived from Chi-squared ($\chi 2$) tests in bootstrapping runs (see Chapter 4.2.3)

moderate NPP might in parts be ousted by bushlands with low productivity. Based on these results, considerable decreases of NPP have to be expected in central Mkomazi Water Basin.

The model to describe the response of litter thickness to land cover classes performed moderately well (Pseudo-R^2 (Nagelkerke 1991) = 0.43). Highest litter thickness occurred in indigenous forests as well as in plantation forests and fallows (Figure 13). In all other land cover classes litter thickness was considerably lower. Hence, relevant changes of litter thickness can only be expected in areas where forests are replaced by farms. The response of erosion intensity to land cover classes was not significant. Therefore, a robust evaluation of the effects of land cover changes on erosion intensity in the study area was not possible.

The outcomes of this land cover based assessment provided a first overview about impacts of expected environmental changes on biodiversity and EP in central Mkomazi Water Basin. However, environmental changes that do not lead to obvious land cover changes can still have considerable effects on biodiversity and EP (Eigenbrod *et al.*

2010; Lavorel *et al.* 2011). In order to reveal these details, analyses of EP response along continuous environmental and biotic gradients were conducted in a next step.

6.1.3 Effects of abiotic factors and functional traits on EP

The assessment of the response of three EP (NPP, litter thickness and erosion intensity) along continuous environmental and biotic gradients in Mkomazi Water Basin firstly aimed to disentangle the role of abiotic effects versus biodiversity effects (see Chapter 4). Results revealed that the most important determinants for the responses of all three EP were environmental factors. NPP showed a distinct negative response to aridity. As temperatures in the study area are expected to rise and dry season rainfall to decrease (increasing aridity), NPP most likely will be reduced (Zhao & Running 2010). Disturbance, grazing and distance to next water body (as part of the topography factor) had no relevant direct effects on NPP. Consequently the expected intensification of land use activities and the reduction of flow water availability does not seem to directly impact NPP. In contrast to NPP, litter thickness showed only a weak negative response to aridity, but strongly decreased with increasing disturbance and grazing. Hence, considerable effects of increasing aridity on litter thickness cannot be expected in the study area, whereas intensifying land use will cause a noticeable reduction of litter thickness. This can be best explained by the litter removal in cultivated land and the reduction of leaf biomass available for litter production in grazed areas (Facelli & Pickett 1991). None of the environmental factors expected to change, significantly affected erosion intensity. Only topography had a significant positive effect on erosion intensity which could be mainly attributed to inclination (Fox & Bryan 2000). Therefore, environmental changes in central Mkomazi Water Basin are unlikely to directly influence erosion intensity.

Apart from the extensive abiotic effects, each of the three studied EP showed considerable sensitivity to functional diversity components. Since functional diversity also responds to environmental gradients, it can significantly modulate the effects of environmental changes on EP (Suding *et al.* 2008). To evaluate the role of functional diversity for EP in central Mkomazi Water Basin, plant functional trait effects on EP and responses to environmental gradients were analysed simultaneously. This analysis was restricted to NPP, however (Chapter 5). A major outcome was that many abiotic factor - trait, trait - trait and trait - NPP relations could not be generalized over the entire study area. Instead relevant response-effect relations differed between the lowlands and the highlands.

In the lowlands NPP was mainly determined by the aforementioned direct negative effect of aridity, which was reinforced by a negative trait-mediated effect. Furthermore, grazing had a minor negative trait-mediated effect, whereas the effect of disturbance on NPP was negligible. On account of these findings, the expected increase of aridity in the lowlands of Mkomazi Water Basin will reduce NPP, probably because it limits water availability for vegetation growth (Zhao & Running 2010). Moreover, the anticipated intensification of grazing might reduce average plant height and related NPP (Díaz *et al.* 2007c; Lienin & Kleyer 2012). In contrast, due to the low sensitivity of NPP to disturbance, the expected increases of logging, farming and fires are unlikely to have considerable impacts on productivity.

A different situation was found in the highlands of the study area. The direct negative effect of aridity on NPP was still distinct, but it was surpassed by a strongly negative trait-mediated effect of disturbance on NPP. Based on these results, similarly to the lowlands increasing aridity will cause a reduction of NPP. At the same time, increasing disturbance will reduce average plant height and woody plants abundance, which both mediate the reduction of NPP (Lavorel *et al.* 2011; Conti & Díaz 2013). This relationship more or less represents the transformation of forests into farms as discussed above.

Even though the functional response-effect relations that concern litter thickness and erosion intensity have not been modelled, some assumptions could be made. These were derived from the results about both EP's sensitivity to functional traits and the responses of these traits to environmental gradients. Litter thickness was negatively affected by spinescence, most probably because the investment in defence structures reduces leaf production (Coley 1988; Facelli & Pickett 1991). In the lowlands, spinescence in turn was positively affected by aridity and grazing. Therefore, in the lowlands the expected negative direct impacts of increasing aridity and grazing on litter thickness (see above) can be enhanced by indirect effects mediated by increasing spinescence. Due to their positive influence on erosion control, the abundance of phanerophyts had a negative effect on erosion intensity (Zheng 2006). In all parts of the basin the abundance of woody plants, which mostly involve phanerophyts, was negatively related to disturbance. Consequently, at least on steep slopes erosion intensity is likely to increase following land use intensification that triggers a reduction of woody plants abundance (Hartanto *et al.* 2003).

6.1.4 ES vulnerability and strategies to sustain livelihoods

In summary, the expected environmental changes in central Mkomazi Water Basin most likely will have the following impacts on NPP, litter thickness and erosion intensity:

- It is very likely that NPP will decrease in most parts of the study area. In the lowlands this results mainly from direct impacts of increasing aridity. In addition, intensification of grazing and reduction of flow water availability negatively affect lowland NPP, by decreasing average plant height and replacing woodlands with bushlands, respectively. In the highlands the major influence is increasing disturbance. It reduces NPP indirectly through biodiversity responses like reductions of woody plant abundance and average plant height as well as the conversion of forests into farms.
- Litter thickness most likely will be reduced by direct impacts of increasing aridity and grazing. In the lowlands this reduction might be enhanced by increasing spinescence following both environmental changes. In the highlands additional negative impacts on litter thickness evolve from the replacement of forests by farms.
- Erosion intensity is likely to increase on slopes where woody plants abundance is reduced in response to increasing disturbance.

In this section potential effects of the changes in NPP, litter thickness and erosion intensity on the provision of ES in Mkomazi Water Basin are evaluated. Moreover, options to tackle the environmental problems in the study area are discussed.

A reduction of NPP in the study area would be coupled to a decrease of carbon sequestration (Zhao & Running 2010) and thereby contribute to the disruptions of global carbon cycling (cf. Figure Box 1). Yet, this would not have immediate consequences for the local communities. From their perspective the fact that decreasing NPP equals to reduced phytomass production is of much greater concern. The reduction of NPP induced by aridity would seriously hit fibre, fodder and crop production (de Bello *et al.* 2010). All three are the basis for the majority of livelihood activities in the region, including timber extraction, charcoal production, livestock keeping and farming (PBWO & IUCN 2009; Notter 2010). However, crop production commonly is favoured over fibre and fodder production (e.g. transformation of forests into farmland). If this strategy is continued in the future, for example to compensate for crop productivity decline due to increasing aridity, multifunctionality in the study area will be at risk (Foley *et al.* 2005).

The potential reductions of litter thickness most importantly would accelerate the energy and moisture exchange between soil and atmosphere (Ogée & Brunet 2002). This would reduce the capacity for soil water retention and balancing heat fluxes. In other words it would increase the evaporation of soil moisture, which most likely would contribute to the decrease of primary production. Soils on slopes will be additionally affected by increasing erosion intensity (Hartanto *et al.* 2003). Effects of erosion, like the loss of humic topsoil, nutrient bleaching and soil structure deterioration, negatively influence soil fertility, nutrient cycling and water retention (Pimentel *et al.* 1995).

At this point, a further aspect has to be outlined that was not covered by the studied EP. The major biodiversity change, that has to be expected in Mkomazi Water Basin under a 'business as usual' scenario, is the degradation and loss of the indigenous evergreen highland forests (Chapter 3). Apart from the anticipated reduction of NPP and the related decrease of phytomass production and carbon sequestration, forest loss would entail serious disruptions of regional climate and water regulation. Tropical forests are renowned for their ability to 'generate' local rainfall due to their tremendous transpiration capacity (Boyce *et al.* 2010). Furthermore, forests proved to balance groundwater replenishment and run-off (Bradshaw *et al.* 2007). Consequently, the loss of considerable forest area would accelerate the process of increasing aridity and impair the perennial availability of surface water flow.

The decrease of ES provision can already be observed in Mkomazi Water Basin and has caused conflicts among different resource users (Notter 2010; Ndaki 2014). Farmers in the highlands partly overuse water resources for irrigation which causes problems for farmers and fishermen in the lowlands (Komakech *et al.* 2012). Moreover, particularly in the lowlands farmers and pastoralists compete for arable land and water resources.

In order to maintain local livelihoods, the negative effects of environmental change on biodiversity, EP and ES provision have to be addressed. The most promising strategy is to eliminate the root causes as far as possible (Chapin *et al.* 2010). Most importantly this comprises sustainable management of land use activities to confine the intensification of disturbances. Options to realize that despite rising resource demands are discussed below. In order to sustain flow water availability, fair water sharing among highland and lowland stakeholders should be implemented. This could follow the example of water governance systems that had been established by local chiefs in pre-colonial times (Komakech *et al.* 2012). Increasing aridity however, cannot be stopped by local measures since this is driven by global climate change (Tadross & Wolski 2010). Nevertheless, local management to sustain the integrity of indigenous forests can at least eliminate deforestation as an additional source for regional climate change. Beyond that, it will be necessary to take adaptive measures against increasing aridity. Increasing water use efficiency could be one component (PBWO & IUCN 2009). Further possibilities are the introduction of drought resistant crops and the improvement of farm practices to maintain soil moisture.

In addition to address the sources of decreasing crop, fodder and fibre production as well as of disruptions in climate and water regulation, it is advisable to specifically support sensitive biodiversity components. All those land cover types or plant functional traits should be focused that considerably influence the threatened ES and at the same time are highly sensitive to expected environmental changes (MEA 2005). In central Mkomazi Water Basin this accounts for evergreen highland forests and the different woodlands or to speak in functional terms, woody plants.

Measures to restrict disturbance intensification could be well combined with efforts to promote crucial biodiversity components. As far as possible, farmland should mainly be expanded into fallow shrublands, whereas forests and woodlands should be spared. This would limit negative effects on NPP and related ES. Furthermore, agroforestry systems should be preferred over other cropping systems, since they can substitute some of the ES provided by indigenous forests (Koh & Gardner 2010; Notter 2010). Logging and charcoal production should be banned from evergreen highland forests and woodlands. Instead these activities should be restricted to plantation forests ('land sparing' strategy: Koh & Gardner 2010). However, as long as illegal logging and charcoal burning in the region are not appropriately tackled by the responsible authorities, this approach will not be practicable. Alternatively, the implementation of ‘reduced impact logging’ (Koh & Gardner 2010) as well as the development of alternative sources of income (e.g. eco-tourism) might contribute to reduce land use pressures on forests and woodlands. In the woodland and bushland savannas of central Mkomazi Water Basin pasturing should be managed more effectively. Grazing pressure should be distributed more evenly, to relieve currently overgrazed bushlands in the vicinity of lowland settlements. Furthermore, to avoid future conflicts between farmers and livestock keepers, they should agree upon farmland and rangeland 'reserves'. Compensation mechanisms could be installed to handle cases of farmland expansion and cattle invasion into farms.

A final strategy to maintain the provision of crucial ES in central Mkomazi Water Basin is to support succession and re-establishment of (near-)natural vegetation in degraded forest or rangeland sites (Koh & Gardner 2010).

Even though projected environmental changes pose serious threats to biodiversity, ecosystem service provision and livelihoods in central Mkomazi Water Basin, a number of options exist to avoid extensive impacts. This is accounted to the finding that local land use activities are the major drivers of ecosystem change (Chapin *et al.* 2010). Nevertheless, the majority of the measures described above will only be successful if they are implemented before irreversible ecosystem changes have occurred. In consideration of the rapid degradation the evergreen highland forest and the potential loss of endemic species, this point might be reached soon (Swetnam *et al.* 2011).

6.2 Land cover versus functional diversity based assessment of ecosystem properties sensitivity

6.2.1 Land cover based ecosystem properties sensitivity assessment: data availability versus lack of detail

The strongest argument to base EP sensitivity assessments on land cover tolerance to environmental gradients, is the substantial availability of data. Current land cover data in form of unclassified satellite imagery (e.g. Google Earth™) nowadays can be obtained freely for most parts of the world at relatively high resolution. Moreover, spatially-explicit environmental and biogeographical data are accessible, for instance through the database of the U.S. Geological Survey (http://earthexplorer.usgs.gov). Examples are elevation (Jarvis *et al.* 2008) and NPP (NTSG & UMT 2014) that have been used in this thesis. Depending on the availability of other relevant data (e.g. climate, land use), it might therefore be possible to carry out rapid assessments of EP sensitivity based on land cover. Apart from ground truthing, extensive field work would not be necessary under these circumstances.

As explained in Chapter 1, land cover response and tolerance commonly has been modelled based on temporal variation (transition probability models). Historical data to determine temporal variation can be derived from worldwide Landsat imagery which is part of the USGS database. Unfortunately, Landsat data is much less detailed than the up-to-date satellite imagery. Hence, it is limited to studies where only a few land cover types are of interest (e.g. forest vs. non-forested areas) or to applications at transregional and global scales. Planners and land use managers commonly operate at regional scales, however. In sub-Saharan Africa, alternative sources for historical land cover data at the necessary detail often are lacking.

To address this problem, a different approach was used in this thesis: Instead of building models based on temporal variation, land cover response was assessed based on spatial variation (Chapter 3). Cross-validation tests confirmed that the procedure is sufficiently robust. However, the global measure of land cover tolerance that was introduced (volume of predicted occurrence: VPO) proofed to be of relatively low informative value. The reason was that each land cover unit’s tolerance to specific environmental factors strongly determined VPOs. Therefore, it was much more useful to derive EP sensitivity from the factor-specific land cover tolerance ranges (Chapter 6.1.2). Considerable information about EP sensitivity could be gained from this assessment, particularly for NPP.

On account of these results, it can be concluded that assessments of land cover tolerance in heterogeneous landscapes with long environmental gradients can reveal major trends of EP sensitivity. Nevertheless, there are several shortcomings that impair the information acquired by this procedure.

Major disadvantages of land cover based approaches to assess EP sensitivity are connected to the relation between land cover types and EP. Firstly, the assignment of specific EP values to land cover units disregards EP variability within each land cover unit (Eigenbrod *et al.* 2010; Lavorel *et al.* 2011). Accordingly, it is not possible to determine EP response to environmental changes which cause only subtle land cover alterations without shifts of land cover types. Figure 14 illustrates this issue. The disregard of EP variability within land cover units additionally precludes the application of land cover based approaches in homogenous study areas. Where the diversity of land cover types is too low, substantial variation in EP cannot be detected.

A second shortcoming of land cover based approaches, is that EP sensitivity is derived indirectly from the sensitivity of land cover types (Chapter 6.1.2). Hence, the root sources for EP sensitivity are not uncovered. The question in how far EP sensitivity is controlled by responses to abiotic gradients or biodiversity is not answered. Lastly, features of the established biotic community which might be responsible for the tolerance of a land cover type and the related EP sensitivity cannot be identified (Díaz *et al.* 2006). A third downside of land cover based approaches is that not all EP show significant variation among land cover types (e.g. litter thickness and erosion intensity in this thesis, Figure 13). This occurs when the root sources for EP sensitivity correspond neither to the environmental factors that control land cover distribution nor to those functional biotic features that characterize land cover types. A last problem of land cover based assessments is the inconsistency of land cover classification systems that has already been discussed in the introduction (Chapter 1, Box 3). The application of different land cover classifications could induce differential conclusions about EP sensitivity for the same area (Jansen & Di Gregorio 2002).

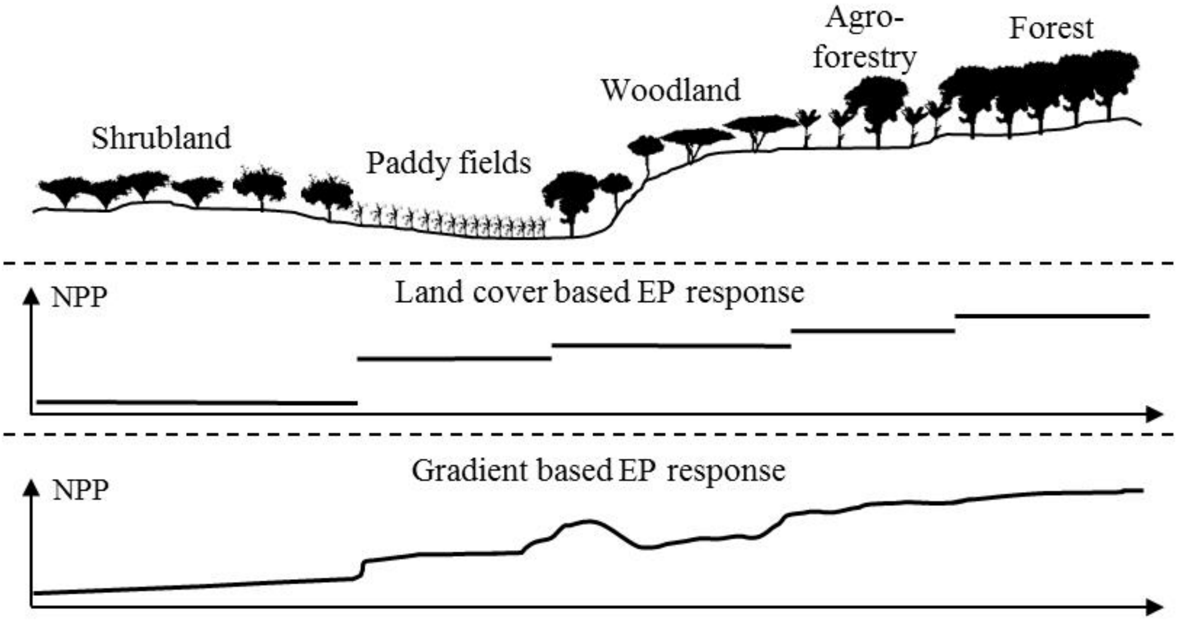


Figure 14. Detection of ecosystem properties‘ (EP) response to environmental and biotic influences by land cover versus gradient based approaches. The schematic landscape transect represents different situations of local climate, water availability and land use supporting various communities with differential productivity (NPP), similar to what was found in the research area. While land cover based assessments of EP depict only average values for each land cover unit, gradient based approaches facilitate a much better representation of natural variability

In conclusion, the evaluation of EP sensitivity based on land cover tolerance allows an unsophisticated identification of priority areas for sustainable land use management. However, apart from the environmental factors that are most influential on land cover tolerance, the procedure does not provide ecological explanations for EP sensitivity.

6.2.2 Functional diversity based assessment of EP sensitivity: Ecological explanations versus extensive efforts

The downsides of evaluating EP sensitivity indirectly through land cover tolerance are avoided if EP response is assessed directly along gradients of environmental conditions and functional diversity. This procedure allows to identify the individual contribution of each abiotic and biotic gradient to EP response (Díaz *et al.* 2007b). In other words, the root sources for EP sensitivity can be uncovered. Based on this knowledge, it is possible to predict how EP would respond to changes of specific environmental factors and functional diversity components (Díaz *et al.* 2006) (Figure 14). Another point that supports the assessment of EP response along abiotic and biotic gradients, is the possibility to determine significant influences for any EP of interest. The only precondition is that all relevant abiotic factors and functional diversity components are included in the analysis. Hence, careful selection of variables guided by ecologically sound hypothesis development is of large relevance for this approach (Pérez-Harguindeguy *et al.* 2013).

However, in heterogeneous landscapes the experience with assessments of EP response to environmental factors and functional diversity so far had been strongly limited. This thesis contributes to fill this research gap. The intention was to evaluate if stepwise EP response modelling (Díaz *et al.* 2007b) that disregards biotic response to environmental factors sufficiently depicts EP sensitivity in heterogeneous landscapes; or if it is more advisable to study EP response based on the functional response-effect framework (Suding *et al.* 2008), which is more elaborate.

The results of this thesis strongly indicate that even in heterogeneous landscapes, biotic response and effect are crucial influences for EP response and therefore should be integrated in EP sensitivity assessments. The models of EP response in central Mkomazi Water Basin that disregarded biotic response to environmental gradients detected the following effects on NPP: negative effects of aridity, spinescence and leaf succulence as well as a positive effect of plant height (Chapter 4). However, the NPP response model that integrated functional diversity response and effect revealed further highly relevant relationships (Chapter 5). Firstly, the negative direct effect of aridity on NPP, was enhanced by indirect effects mediated by spinescence, investment in leaf structure and plant height. Secondly and more importantly, the analysis of response-effect relations exposed disturbance as an additional, highly relevant negative effect on NPP. However, since this effect was entirely mediated by negative responses of plant height to disturbance, it could not be detected by the model that disregarded biotic response. Therefore, it can be concluded that the validity of response-effect theory is not restricted to the ecosystem level but equally applies at the landscape scale. Instead, disregarding biotic response to environmental factors is not advisable, since crucial effects on EP might not be detected (Suding *et al.* 2008).

The application of response-effect modelling for the assessment of EP sensitivity in heterogeneous landscapes is not straightforward, however. As the study in Mkomazi Water Basin ascertained, size and significance of specific environment-trait, trait-trait and trait-EP relations can vary along environmental gradients (Chapter 5) (cf. Laliberté & Tylianakis 2011; Lienin & Kleyer 2012). This variation seemed to be grounded on distinct clusters of environment-EP relations: the lowlands where biotic response and effect was mainly determined by aridity and the highlands that were governed much more by disturbance. On account of these findings, it seems advisable to investigate the occurrence of environment-EP clusters prior to response-effect modelling in heterogeneous landscapes. If distinct clusters can be identified, individual response-effect models should be built within each cluster.

At this point, the major disadvantage of the approach to assess EP sensitivity based on abiotic and biotic effects becomes apparent. In order to build robust response-effect models, extensive functional trait data is required that represents the diversity of ecosystems in heterogeneous landscapes. Based on floristic surveys, plant functional trait data could be obtained from one of several databases (e.g. LEDA: Kleyer *et al.* 2008, GLOPNET: Wright *et al.* 2004). However, even in the globally most comprehensive database (TRY: Kattge *et al.* 2011), entries from several world regions, among them sub-Saharan Africa, are still rare. For the time being, relevant functional trait data from most parts of sub-Saharan Africa can therefore only be acquired by elaborate field and laboratory measurements.

In spite of the efforts required to conduct the described EP sensitivity assessments, they provide valuable information for sustainable land use management. Especially, response-effect analyses can uncover biotic root sources for EP sensitivity besides the better known environmental drivers (Suding *et al.* 2008; Díaz *et al.* 2013). This knowledge can highlight alternative options to sustain crucial ecosystem functions in landscapes affected by environmental change.

6.3 A protocol for spatially-explicit assessments of ecosystem vulnerability

In the previous sections, it was outlined that knowledge about EP sensitivity can considerably contribute to identify sustainable land use management options. The determination of the underlying priorities for land use management though, relies on spatially-explicit information about ecosystem functioning and ES vulnerability (Bolliger *et al.* 2011). Several attempts have been made to assess ES provision at the landscape scale e.g. (e.g. Willemen *et al.* 2008; Swetnam *et al.* 2011; Burkhard *et al.* 2012). In most of these studies this was done by linking ES provision directly to land cover types based on interviews with experts and stakeholders. However, this is not an optimal method since it disregards the ecological basis for ES provision (Lavorel 2013).

This ecological basis is determined by ecosystem functioning, which in turn is governed by EP (de Groot *et al.* 2010). Consequently, knowledge about ecosystem functioning and ES vulnerability can be derived from information about EP sensitivity to changing environmental conditions and biodiversity (Bennett *et al.* 2015) (Figure 1). The link between EP and ES provision can again be examined by expert and stakeholder interviews (Quétier *et al.* 2007; Lavorel *et al.* 2011). On account of these issues, it becomes obvious that in order to gain sound spatially-explicit information about ES vulnerability, information about EP sensitivity has to be spatially-explicit as well.

In this final section a general protocol for spatially-explicit assessments of EP sensitivity is proposed, that combines land cover tolerance analysis and functional response-effect modelling. The major intention was to channel ideas how the findings of this thesis could be used for ecological landscape analyses that can guide land use planning and management. The proposed protocol should contribute to the ongoing debate about how spatially-explicit and ecologically sound assessments of EP and ES can be realized (de Groot *et al.* 2010; Swetnam *et al.* 2011). For this purpose, it should be capable to determine how multiple EP at each point in a landscape would respond to different scenarios of land use, environmental and biodiversity change.

The protocol comprises nine hierarchical steps that range from study area delineation and hypothesis development over data collection to spatially-explicit modelling based on land cover tolerance and plant functional trait response-effect relations. For rapid assessments of EP sensitivity, which would rely only on land cover tolerance analysis, only the first six steps apply.

1) Selection of the study area and the EP in focus

Prior to any assessment of EP the area that should be studied has to be selected and delineated. ES with particular importance for the local communities (or other ES of interest for the researchers) should be identified (cf. Quétier *et al.* 2007). The assessment can then be restricted to those EP that control the ES in focus.

2) Preliminary land cover classification and field visit

Existing land cover maps should be acquired to identify the inventory of land cover types in the study area. Alternatively available satellite imagery (e.g. GoogleEarth™) can be used to prepare a preliminary land cover map. A first field visit can help to ascertain a first impression of relevant environmental gradients and ecosystems.

3) Hypothesize land cover response and functional response-effect relations

On the basis of preliminary field observations, literature and expert knowledge land cover response to abiotic factors has to be hypothesized. If an extensive assessment is planned, additionally hypotheses have to be developed for functional response-effect relations between abiotic factors, functional traits and EP (Suding *et al.* 2008). This allows to determine the environmental factors and biodiversity components that have to be sampled.

4) Database compilation and selection of sampling sites

A GIS database is compiled that should contain relevant data on historical and current land cover, socio-economic features (e.g. population density), environmental conditions (e.g. topography, climatic data, soil data) and EP. All available data sources should be used, such as remote-sensing products and maps. A sufficient number of survey sites is selected to represent the major land cover types and environmental gradients in the study area. This should be done by random-stratified selection.

5) Field data sampling

If a rapid, land cover based assessment is conducted, field work might not be necessary depending on the quality of remotely sensed land cover and environmental data. In case the data quality is not satisfactory, sampling should cover vegetation structure, predominant land use and all relevant environmental data. These could include for instance topographic features, climatic factors, hydrological parameters, soil conditions and disturbance. For extensive assessments that integrate functional response-effect relations, additionally floristic surveys and trait measurements have to be conducted. The latter can be based on comprehensive manuals by Pérez-Harguindeguy *et al.* (2013) or Cornelissen *et al.* (2003).

6) Modelling land cover distribution and related EP

In accordance to the land cover classification system (LCCS) (Di Gregorio & Jansen 2005) the collected data on vegetation structure and land use are used to refine the preliminary land cover classification. Land cover distribution models are built as described in Chapter 3. If historical land cover data is available, alternatively transition probability models can be built. EP are related to land cover types by simple regression techniques (see Chapter 6.1.2). Finally, the models can be applied to calculate land cover and related EP response to spatially-explicit scenarios of future environmental change and land use management. In extensive assessments this step is optional.

7) Data partitioning based on environment-EP clusters

Cluster analysis is conducted to identify regions within the study area that show considerably differential environment-EP relationships. These could be for instance lowlands and highlands as in Mkomazi Water Basin, wetlands and dry plains, or dunes and salt marshes. Data are grouped into the identified clusters and for each of them the original hypotheses on functional response-effect relations (Step 3) are refined and translated into *a priori* path models as described in Chapter 5. Examples from elsewhere show that these models do not have to be restricted to one EP, however (Laliberté & Tylianakis 2011; Lienin & Kleyer 2012). Instead, relationships between EP can be integrated easily.

8) Testing path models on collected data

In accordance to the procedure applied in Chapter 5, the validity of the hypothesized path models is assessed by directional separation tests applied to the collected data (Shipley 2009). Data standardization prior to the model testing is only necessary if the surveyors are interested in each path's effect size. Relevant relations that had not been hypothesized are added and insignificant hypothesized paths are removed from the models.

9) Spatially-explicit calculation of functional diversity and EP

The final, validated path models for each cluster (Step 7) fitted to the original, non-standardized data are applied to the GIS database in a cascading manner. At first maps of functional traits are calculated from spatially-explicit environmental data by application of environment-trait path models. Secondly, based on trait-trait path models, maps are calculated for all those functional traits which are affected by other traits. Finally, environment-EP, trait-EP and EP-EP path models are used to build maps of each EP. After the EP maps have been built for each cluster, they are combined to cover the entire research area. In order to assess the effects of projected land use activities, environmental changes and biodiversity losses on EP, the cascading map calculation simply is repeated.

Although, major steps of the above protocol have been applied to study EP response in central Mkomazi Water Basin, it should not be taken as a fully operational tool until its applicability has been validated in other landscapes. Especially, the development of clustered functional response-effect models and their spatially-explicit application to calculate EP response have to be tested thoroughly. Within the protocol as well as throughout this thesis three major issues remained unattended which might considerably influence the outcomes of landscape-scale EP sensitivity assessments. These comprise the role of trophic interactions for biotic response and effect, the relevance of intra-specific trait variability (ITV) and the importance of repercussion effects of functional diversity components and EP on environmental factors, land use and disturbance. Future research should explore in how far each of the three issues should be integrated into assessments of EP in heterogeneous landscapes.

The functional diversity based studies of EP sensitivity in central Mkomazi Water Basin (Chapter 4 and 5) solely focused on plant functional traits. Without doubt, plants are the major biotic modulators of EP on account of their role as primary producers (Díaz & Cabido 2001). Nevertheless, other trophic levels can be highly relevant for EP as well, either by direct effects or through trophic interactions and cascades (Chapin *et al.* 2000; Sekercioglu 2010). The integration of multiple trophic levels can improve assessments of EP sensitivity and might contribute to avoid 'ecological surprises' (Díaz *et al.* 2006). Lavorel *et al.* (2013) proposed a framework to integrate multiple trophic levels into functional response-effect analyses that has already been successfully applied by Moretti *et al.* (2013). However, a major problem of extending ES assessments to multiple trophic levels is that it relies on enormous amounts of additional biological data. Land use planners who normally operate at the landscape scale commonly lack the capacity to undertake the required extensive analyses (Klausmeyer *et al.* 2011), particularly in sub-Saharan Africa.

For the sake of convenience, common approaches to measure functional diversity in ecosystems are founded on species level averages of trait attributes. However, 'phenotypic plasticity' along environmental gradients and genetic variation cause intra-specific functional trait variability (ITV) (Violle *et al.* 2007; Albert *et al.* 2012; Mori, Furukawa & Sasaki 2013). For some traits, ITV explains up to 40% of the entire variation (Kattge *et al.* 2011). Therefore, ITV can considerably influence functional diversity and conclusions about EP sensitivity drawn from analyses that disregarded ITV might not conform to reality (Albert *et al.* 2012). Even at relatively large spatial scales, ITV might be relevant. Albert *et al.* (2011) proposed a set of rules to decide when ITV should be considered and they provided methods to integrate ITV into assessments of functional diversity. These ideas could enhance the protocol to study EP sensitivity in heterogeneous landscapes. Poor availability of trait data for sub-Saharan African ecosystems requires trait measurements, anyway, hence the integration of ITV would only marginally increase efforts.

Finally, the aspect of repercussion effects shall be highlighted which is a relevant component of the cycle of global change (Box 1). As biotic communities and EP change in response to environmental stresses, they affect not only ecosystem functioning but additionally feed back on environmental conditions, land uses and disturbances (Chapin *et al.* 2000; Lambin, Geist & Lepers 2003; Díaz *et al.* 2007a). These repercussion effects potentially enhance ongoing environmental changes, or induce additional changes that had not been observed originally (Díaz *et al.* 2007a). Consequently, ecosystem functioning vulnerability can be considerably increased. EP sensitivity assessment that neglect biodiversity and EP feedbacks risk to underestimate the vulnerability of ES, at least in the medium term. However, the integration of feedbacks into the clustered response-effect modelling of the proposed protocol is not trivial. It would require temporally-explicit data and the development of circular process models.

6.4 Concluding remarks

Assessments of EP response to various abiotic and biotic stressors can uncover root sources for the vulnerability of ecosystem functions and related ES. Therefore, the results of these assessments highlight relevant starting points for land use management that aims to sustain the provision of multiple ES. This is of particular importance for rural communities in sub-Saharan Africa, since ES fulfil many of their societal and economic needs.

This thesis makes an important contribution to advance EP and ES assessments in heterogeneous landscapes. Due to good data availability for sub-Saharan Africa, land cover based approaches facilitate rapid determination of environmental effects on EP. However, they lack detail and fail to unravel the biodiversity components that govern how land cover types respond to environmental gradients. Functional diversity based approaches provide more information since they reveal in how far EP respond directly to environmental factors or indirectly via responses and effects of traits. The combination of land cover and functional diversity based EP assessments in a general protocol allows researchers to benefit from the advantages of both approaches. While the former can be used to identify the most critical ecosystems in a landscape, the latter can depict the abiotic and biotic root sources for EP sensitivity in these ecosystems.

There is still considerable research needed to understand how specific land use activities and environmental changes affect EP in heterogeneous landscapes and how biodiversity mediates these effects. These efforts definitely should be made, since a sound understanding EP sensitivity and related ES vulnerability at landscape scales is required for sustainable land use planning. The aim should be to develop general guidelines that can be readily applied by environmental consultants to identify the most appropriate measures to sustain the provision of important ES.

References

Ad-Hoc-AG Boden (2005) *Bodenkundliche Kartieranleitung,* 5th edn. Schweizerbart, Hannover.

Adger, W.N. (2006) Vulnerability. *Global Environmental Change,* **16,** 268-281.

Albert, C.H., de Bello, F., Boulangeat, I., Pellet, G., Lavorel, S. & Thuiller, W. (2012) On the importance of intraspecific variability for the quantification of functional diversity. *Oikos,* **121,** 116-126.

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

Augustine, D.J. & McNaughton, S.J. (1998) Ungulate Effects on the Functional Species Composition of Plant Communities: Herbivore Selectivity and Plant Tolerance. *The Journal of Wildlife Management,* **62,** 1165-1183.

Bader, M.Y. & Ruijten, J.J.A. (2008) A topography-based model of forest cover at the alpine tree line in the tropical Andes. *Journal of Biogeography,* **35,** 711-723.

Barber, P.H., Ablan-Lagman, M.C.A., Ambariyanto, Berlinck, R.G.S., Cahyani, D., Crandall, E.D., Ravago-Gotanco, R., Juinio-Meñez, M.A., Mahardika, I.G.N., Shanker, K., Starger, C.J., Toha, A.H.A., Anggoro, A.W. & Willette, D.A. (2014) Advancing biodiversity research in developing countries: the need for changing paradigms. *Bulletin of Marine Science,* **90,** 187-210.

Barton, K. (2015) MuMIn: Multi-Model Inference. *R Package.*

Bennett, E.M., Cramer, W., Begossi, A., Cundill, G., Díaz, S., Egoh, B.N., Geijzendorffer, I.R., Krug, C.B., Lavorel, S., Lazos, E., Lebel, L., Martín-López, B., Meyfroidt, P., Mooney, H.A., Nel, J.L., Pascual, U., Payet, K., Harguindeguy, N.P., Peterson, G.D., Prieur-Richard, A.-H., Reyers, B., Roebeling, P., Seppelt, R., Solan, M., Tschakert, P., Tscharntke, T., Turner Ii, B.L., Verburg, P.H., Viglizzo, E.F., White, P.C.L. & Woodward, G. (2015) Linking biodiversity, ecosystem services, and human well-being: three challenges for designing research for sustainability. *Current Opinion in Environmental Sustainability,* **14,** 76-85.

Beven, K.J. & Kirkby, M.J. (1979) A physically based, variable contributing area model of basin hydrology / Un modèle à base physique de zone d'appel variable de l'hydrologie du bassin versant. *Hydrological Sciences Bulletin,* **24,** 43-69.

Blonder, B., Lamanna, C., Violle, C. & Enquist, B.J. (2014) The n-dimensional hypervolume. *Global Ecology and Biogeography,* **23,** 595-609.

Bolliger, J., Bättig, M., Gallati, J., Kläy, A., Stauffacher, M. & Kienast, F. (2011) Landscape multifunctionality: a powerful concept to identify effects of environmental change. *Regional Environmental Change,* **11,** 203-206.

Boyce, C.K., Lee, J.-E., Feild, T.S., Brodribb, T.J. & Zwieniecki, M.A. (2010) Angiosperms Helped Put the Rain in the Rainforests: The Impact of Plant Physiological Evolution on Tropical Biodiversity. *Annals of the Missouri Botanical Garden,* **97,** 527-540.

Bradshaw, C.J.A., Sodhi, N.S., Peh, K.S.H. & Brook, B.W. (2007) Global evidence that deforestation amplifies flood risk and severity in the developing world. *Global Change Biology,* **13,** 2379-2395.

Brink, A.B. & Eva, H.D. (2009) Monitoring 25 years of land cover change dynamics in Africa: A sample based remote sensing approach. *Applied Geography,* **29,** 501-512.

Broennimann, O., Thuiller, W., Hughes, G., Midgley, G.F., Alkemade, J.M.R. & Guisan, A. (2006) Do geographic distribution, niche property and life form explain plants' vulnerability to global change? *Global Change Biology,* **12,** 1079-1093.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution,* **23,** 453-460.

Bucini, G. & Hanan, N.P. (2007) A continental-scale analysis of tree cover in African savannas. *Global Ecology and Biogeography,* **16,** 593-605.

Burgess, N.D., Butynski, T.M., Cordeiro, N.J., Doggart, N.H., Fjeldså, J., Howell, K.M., Kilahama, F.B., Loader, S.P., Lovett, J.C., Mbilinyi, B., Menegon, M., Moyer, D.C., Nashanda, E., Perkin, A., Rovero, F., Stanley, W.T. & Stuart, S.N. (2007) The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation,* **134,** 209-231.

Burkhard, B., Kroll, F., Müller, F. & Windhorst, W. (2009) Landscapes' capacities to provide ecosystem services–a concept for land cover based assessments. *Landscape online,* **15,** 22.

Burkhard, B., Kroll, F., Nedkov, S. & Müller, F. (2012) Mapping ecosystem service supply, demand and budgets. *Ecological Indicators,* **21,** 17-29.

Burnham, K. & Anderson, D. (2002) *Model selection and multimodel inference: A practical information-theoretic approach.* Springer, New York.

Butterfield, B.J. & Suding, K.N. (2013) Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology,* **101,** 9-17.

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

Carpenter, S., Walker, B., Anderies, J.M. & Abel, N. (2001) From Metaphor to Measurement: Resilience of What to What? *Ecosystems,* **4,** 765-781.

CEC (1995) *CORINE land cover*. Commission of the European Communities, Brussels.

Chambers, J., Higuchi, N., Teixeira, L., dos Santos, J., Laurance, S. & Trumbore, S. (2004) Response of tree biomass and wood litter to disturbance in a Central Amazon forest. *Oecologia,* **141,** 596-611.

Chanteloup, P. & Bonis, A. (2013) Functional diversity in root and above-ground traits in a fertile grassland shows a detrimental effect on productivity. *Basic and Applied Ecology,* **14,** 208-216.

Chapin, F.S. (2003) Effects of Plant Traits on Ecosystem and Regional Processes: a Conceptual Framework for Predicting the Consequences of Global Change. *Annals of Botany,* **91,** 455-463.

Chapin, F.S., Carpenter, S.R., Kofinas, G.P., Folke, C., Abel, N., Clark, W.C., Olsson, P., Smith, D.M.S., Walker, B., Young, O.R., Berkes, F., Biggs, R., Grove, J.M., Naylor, R.L., Pinkerton, E., Steffen, W. & Swanson, F.J. (2010) Ecosystem stewardship: sustainability strategies for a rapidly changing planet. *Trends in Ecology & Evolution,* **25,** 241-249.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S. (2000) Consequences of changing biodiversity. *Nature,* **405,** 234-242.

Chollet, S., Rambal, S., Fayolle, A., Hubert, D., Foulquié, D. & Garnier, E. (2014) Combined effects of climate, resource availability, and plant traits on biomass produced in a Mediterranean rangeland. *Ecology,* **95,** 737-748.

Cingolani, A.M., Posse, G. & Collantes, M.B. (2005) Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *Journal of Applied Ecology,* **42,** 50-59.

Cohen, J. (1960) A Coefficient of Agreement for Nominal Scales. *Educational and Psychological Measurement,* **20,** 37-46.

Coley, P.D. (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia,* **74,** 531-536.

Conti, G. & Díaz, S. (2013) Plant functional diversity and carbon storage – an empirical test in semi-arid forest ecosystems. *Journal of Ecology,* **101,** 18-28.

Cornelissen, J., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D., Reich, P., Ter Steege, H., Morgan, H. & Van Der Heijden, M. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany,* **51,** 335-380.

Cowling, R.M. & Witkowski, E.T.F. (1994) Convergence and non-convergence of plant traits in climatically and edaphically matched sites in Mediterranean Australia and South Africa. *Australian Journal of Ecology,* **19,** 220-232.

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

Davies, Z.G., Edmondson, J.L., Heinemeyer, A., Leake, J.R. & Gaston, K.J. (2011) Mapping an urban ecosystem service: quantifying above-ground carbon storage at a city-wide scale. *Journal of Applied Ecology,* **48,** 1125-1134.

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

de Groot, R.S., Alkemade, R., Braat, L., Hein, L. & Willemen, L. (2010) Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecological Complexity,* **7,** 260-272.

Di Gregorio, A. & Jansen, L.J.M. (2005) *Land Cover Classification System. Classification concepts and user manual. Software Version 2,* 2nd edn. Food and Agriculture Organization of the United Nations, Rome.

Díaz, S. & Cabido, M. (1997) Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science,* **8,** 463-474.

Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution,* **16,** 646-655.

Díaz, S., Fargione, J., Chapin, F.S., III & Tilman, D. (2006) Biodiversity Loss Threatens Human Well-Being. *PLoS Biol,* **4,** e277.

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P. & Zak, M.R. (2004) The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science,* **15,** 295-304.

Díaz, S., Lavorel, S., Chapin III, F.S., Tecco, P.A., Gurvich, D.E. & Grigulis, K. (2007a) Functional diversity—at the crossroads between ecosystem functioning and environmental filters. *Terrestrial ecosystems in a changing world*, pp. 81-91. Springer.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. (2007b) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences,* **104,** 20684-20689.

Díaz, S., Lavorel, S., McIntyre, S.U.E., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W.E.I., Clark, H. & Campbell, B.D. (2007c) Plant trait responses to grazing – a global synthesis. *Global Change Biology,* **13,** 313-341.

Díaz, S., Noy-Meir, I. & Cabido, M. (2001) Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology,* **38,** 497-508.

Díaz, S., Purvis, A., Cornelissen, J.H.C., Mace, G.M., Donoghue, M.J., Ewers, R.M., Jordano, P. & Pearse, W.D. (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution,* **3,** 2958-2975.

Doherty, R.M., Sitch, S., Smith, B., Lewis, S.L. & Thornton, P.K. (2010) Implications of future climate and atmospheric CO2 content for regional biogeochemistry, biogeography and ecosystem services across East Africa. *Global Change Biology,* **16,** 617-640.

Dolédec, S., Chessel, D., Braak, C.J.F. & Champely, S. (1996) Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics,* **3,** 143-166.

Dray, S. & Legendre, P. (2008) Testing the species traits-environment relationships: The fourth-corner problem revisited. *Ecology,* **89,** 3400-3412.

Duckworth, J.C., Kent, M. & Ramsay, P.M. (2000) Plant functional types: an alternative to taxonomic plant community description in biogeography? *Progress in Physical Geography,* **24,** 515-542.

Edwards, W.M. & Owens, L.B. (1991) Large storm effects on total soil erosion. *Journal of Soil and Water Conservation,* **46,** 75-78.

Egoh, B., Reyers, B., Rouget, M., Bode, M. & Richardson, D.M. (2009) Spatial congruence between biodiversity and ecosystem services in South Africa. *Biological Conservation,* **142,** 553-562.

Egoh, B., Reyers, B., Rouget, M., Richardson, D.M., Le Maitre, D.C. & van Jaarsveld, A.S. (2008) Mapping ecosystem services for planning and management. *Agriculture, Ecosystems & Environment,* **127,** 135-140.

Ehleringer, J.R. & Mooney, H.A. (1978) Leaf Hairs: Effects on Physiological Activity and Adaptive Value to a Desert Shrub. *Oecologia,* **37,** 183-200.

Eigenbrod, F., Armsworth, P.R., Anderson, B.J., Heinemeyer, A., Gillings, S., Roy, D.B., Thomas, C.D. & Gaston, K.J. (2010) The impact of proxy-based methods on mapping the distribution of ecosystem services. *Journal of Applied Ecology,* **47,** 377-385.

Elith, J. & Leathwick, J.R. (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics,* **40,** 677-697.

Enfors, E. & Gordon, L.J. (2007) Analysing resilience in dryland agro-ecosystems: a case study of the Makanya catchment in Tanzania over the past 50 years. *Land Degradation and Development,* **18,** 680-696.

Enfors, E.I. & Gordon, L.J. (2008) Dealing with drought: The challenge of using water system technologies to break dryland poverty traps. *Global Environmental Change,* **18,** 607-616.

Facelli, J. & Pickett, S.A. (1991) Plant litter: Its dynamics and effects on plant community structure. *The Botanical Review,* **57,** 1-32.

Falster, D.S. & Westoby, M. (2003) Leaf size and angle vary widely across species: what consequences for light interception? *New Phytologist,* **158,** 509-525.

Fine, P.V.A., Miller, Z.J., Mesones, I., Irazuzta, S., Appel, H.M., Stevens, M.H.H., Sääksjärvi, I., Schultz, J.C. & Coley, P.D. (2006) The Growth-Defense Trade-off and Habitat Specialization by Plants in Amazonian Forests. *Ecology,* **87,** S150-S162.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global Consequences of Land Use. *Science,* **309,** 570-574.

Foster, P. (2001) The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews,* **55,** 73-106.

Fowler, D., Coyle, M., Skiba, U., Sutton, M.A., Cape, J.N., Reis, S., Sheppard, L.J., Jenkins, A., Grizzetti, B., Galloway, J.N., Vitousek, P., Leach, A., Bouwman, A.F., Butterbach-Bahl, K., Dentener, F., Stevenson, D., Amann, M. & Voss, M. (2013) The global nitrogen cycle in the twenty-first century. *Philosophical Transactions of the Royal Society B,* **368**.

Fox, D.M. & Bryan, R.B. (2000) The relationship of soil loss by interrill erosion to slope gradient. *CATENA,* **38,** 211-222.

Fry, E.L., Manning, P., Allen, D.G.P., Hurst, A., Everwand, G., Rimmler, M. & Power, S.A. (2013) Plant Functional Group Composition Modifies the Effects of Precipitation Change on Grassland Ecosystem Function. *Plos One,* **8,** e57027.

Gallopín, G.C. (2006) Linkages between vulnerability, resilience, and adaptive capacity. *Global Environmental Change,* **16,** 293-303.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Lepš, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quested, H., Quétier, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.-P., Thébault, A., Vile, D. & Zarovali, M.P. (2007) Assessing the Effects of Land-use Change on Plant Traits, Communities and Ecosystem Functioning in Grasslands: A Standardized Methodology and Lessons from an Application to 11 European Sites. *Annals of Botany,* **99,** 967-985.

Gessler, P.E., Moore, I.D., McKenzie, N.J. & Ryan, P.J. (1995) Soil-landscape modelling and spatial prediction of soil attributes. *International Journal of Geographical Information Systems,* **9,** 421-432.

Goldberg, D. & Novoplansky, A. (1997) On the Relative Importance of Competition in Unproductive Environments. *Journal of Ecology,* **85,** 409-418.

Green, J.M.H., Larrosa, C., Burgess, N.D., Balmford, A., Johnston, A., Mbilinyi, B.P., Platts, P.J. & Coad, L. (2013) Deforestation in an African biodiversity hotspot: Extent, variation and the effectiveness of protected areas. *Biological Conservation,* **164,** 62-72.

Greve, M., Lykke, A.M., Blach-Overgaard, A. & Svenning, J.C. (2011) Environmental and anthropogenic determinants of vegetation distribution across Africa. *Global Ecology and Biogeography,* **20,** 661-674.

Grigulis, K., Lavorel, S., Krainer, U., Legay, N., Baxendale, C., Dumont, M., Kastl, E., Arnoldi, C., Bardgett, R.D., Poly, F., Pommier, T., Schloter, M., Tappeiner, U., Bahn, M. & Clément, J.-C. (2013) Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. *Journal of Ecology,* **101,** 47-57.

Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology,* **86,** 902-910.

GST (Geological Survey of Tanganyika) (1965) Mnazi (Kalimawe). Quarter Degree Sheet 90 - Same. Quarter Degree Sheet 89 - Hedaru. Quarter Degree Sheet 108.

1:125.000. Ministry of Commerce and Industry, Geological Survey Division, Dodoma.

GST (Geological Survey of Tanzania) (2005) Lushoto. Quarter Degree Sheet 109. Ministry of Energy and Minerals - Geological Survey of Tanzania, Dodoma.

Hartanto, H., Prabhu, R., Widayat, A.S.E. & Asdak, C. (2003) Factors affecting runoff and soil erosion: plot-level soil loss monitoring for assessing sustainability of forest management. *Forest ecology and management,* **180,** 361-374.

Heinze, G., Ploner, M., Dunkler, D. & Southworth, H. (2013) logistf: Firth's bias reduced logistic regression. *R package.*

Heller, N.E. & Zavaleta, E.S. (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation,* **142,** 14-32.

Hemp, A. (2006) The banana forests of Kilimanjaro: biodiversity and conservation of the Chagga homegardens. *Biodiversity and Conservation,* **15,** 1193-1217.

Hemp, A. (2009) Climate change and its impact on the forests of Kilimanjaro. *African Journal of Ecology,* **47,** 3-10.

Hoffmann, W.A., Schroeder, W. & Jackson, R.B. (2002) Positive feedbacks of fire, climate, and vegetation and the conversion of tropical savanna. *Geophysical Research Letters,* **29,** 2052.

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

Hooper, D.U., Chapin, F.S., III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005) Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. *Ecological Monographs,* **75,** 3-35.

Hooper, D.U. & Vitousek, P.M. (1997) The Effects of Plant Composition and Diversity on Ecosystem Processes. *Science,* **277,** 1302-1305.

Hutchinson, G.E. (1957) Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology,* **22,** 415-427.

IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jansen, L.J.M. & Di Gregorio, A. (2002) Parametric land cover and land-use classifications as tools for environmental change detection. *Agriculture, Ecosystems & Environment,* **91,** 89-100.

Janssen, M.A. (2007) An Update on the Scholarly Networks on Resilience, Vulnerability, and Adaptation within the Human Dimensions of Global Environmental Change. *Ecology and Society,* **12**.

Jarvis, A., Reuter, H.I., Nelson, A. & Guevara, E. (2008) Hole-filled seamless SRTM data V4. International Centre for Tropical Agriculture (CIAT).

JICA (1984) Feasibility study on the Mkomazi valley area irrigation development project. Japan International Cooperation Agency, Tokio.

Jordán, M.M., Navarro-Pedreño, J., García-Sánchez, E., Mateu, J. & Juan, P. (2004) Spatial dynamics of soil salinity under arid and semi-arid conditions: geological and environmental implications. *Environmental Geology,* **45,** 448-456.

Kattge, J., DÍAz, S., Lavorel, S., Prentice, I.C., Leadley, P., BÖNisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin Iii, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., FernÁNdez-MÉNdez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., KÜHn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., LlusiÀ, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., MÜLler, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., NÖLlert, S., NÜSke, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., OrdoÑEz, J., Overbeck, G., Ozinga, W.A., PatiÑO, S., Paula, S., Pausas, J.G., PeÑUelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E. & Wirth, C. (2011) TRY – a global database of plant traits. *Global Change Biology,* **17,** 2905-2935.

Kattwinkel, M., Strauss, B., Biedermann, R. & Kleyer, M. (2009) Modelling multi-species response to landscape dynamics: Mosaic cycles support urban biodiversity. *Landscape Ecology,* **24,** 929-941.

Klausmeyer, K.R., Shaw, M.R., MacKenzie, J.B. & Cameron, D.R. (2011) Landscape-scale indicators of biodiversity's vulnerability to climate change. *Ecosphere,* **2,** art88.

Kleyer, M. (1999) Distribution of Plant Functional Types along Gradients of Disturbance Intensity and Resource Supply in an Agricultural Landscape. *Journal of Vegetation Science,* **10,** 697-708.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E. & Peco, B. (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology,* **96,** 1266-1274.

Kleyer, M. & Minden, V. (2015) Why functional ecology should consider all plant organs: An allocation-based perspective. *Basic and Applied Ecology,* **16,** 1-9.

Klumpp, K. & Soussana, J.-F. (2009) Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect trait approach. *Global Change Biology,* **15,** 2921-2934.

Knapp, R. (1973) *The vegetation of Africa.* Gustav Fischer, Stuttgart.

Koh, L.P. & Gardner, T.A. (2010) Conservation in human-modified landscapes. *Conservation biology for all* (eds N.S. Sodhi & P.R. Ehrlich), pp. 236-261. Oxford University Press, New York.

Komakech, H.C., Van der Zaag, P., Mul, M.L., Mwakalukwa, T.A. & Kemerink, J.S. (2012) Formalization of water allocation systems and impacts on local practices in the Hingilili sub-catchment, Tanzania. *International Journal of River Basin Management,* **10,** 213-227.

Kumar, P. & Yashiro, M. (2014) The Marginal Poor and Their Dependence on Ecosystem Services: Evidence from South Asia and Sub-Saharan Africa. *Marginality*, pp. 169-180. Springer.

Laflen, J.M., Elliot, W.J., Simanton, J.R., Holzhey, C.S. & Kohl, K.D. (1991) WEPP: Soil erodibility experiments for rangeland and cropland soils. *Journal of Soil and Water Conservation,* **46,** 39-44.

Laliberte, E. & Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology,* **91,** 299-305.

Laliberté, E. & Tylianakis, J.M. (2011) Cascading effects of long-term land-use changes on plant traits and ecosystem functioning. *Ecology,* **93,** 145-155.

Lambin, E.F., Geist, H.J. & Lepers, E. (2003) Dynamics of land-use and land cover change in tropical regions. *Annual Review of Environment and Resources,* **28,** 205-241.

Lavorel, S. (2013) Plant functional effects on ecosystem services. *Journal of Ecology,* **101,** 4-8.

Lavorel, S., Díaz, S., Cornelissen, J.H., Garnier, E., Harrison, S., McIntyre, S., Pausas, J., Pérez-Harguindeguy, N., Roumet, C. & Urcelay, C. (2007) Plant Functional Types: Are We Getting Any Closer to the Holy Grail? *Terrestrial Ecosystems in a Changing World* (eds J. Canadell, D. Pataki & L. Pitelka), pp. 149-164. Springer Berlin Heidelberg.

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

Lavorel, S. & Grigulis, K. (2012) How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology,* **100,** 128-140.

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Pellet, G. & Douzet, R. (2011) Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology,* **99,** 135-147.

Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology & Evolution,* **12,** 474-478.

Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R.J., Díaz, S. & Harrington, R. (2013) A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science,* **24,** 942-948.

Lienin, P. & Kleyer, M. (2011) Plant leaf economics and reproductive investment are responsive to gradients of land use intensity. *Agriculture, Ecosystems & Environment,* **145,** 67-76.

Lienin, P. & Kleyer, M. (2012) Plant trait responses to the environment and effects on ecosystem properties. *Basic and Applied Ecology,* **13,** 301-311.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science,* **294,** 804-808.

Lung, T. & Schaab, G. (2010) A comparative assessment of land cover dynamics of three protected forest areas in tropical eastern Africa. *Environmental Monitoring and Assessment,* **161,** 531-548.

Maeda, E.E., Clark, B.J.F., Pellikka, P. & Siljander, M. (2010) Modelling agricultural expansion in Kenya's Eastern Arc Mountains biodiversity hotspot. *Agricultural Systems,* **103,** 609-620.

Marchetti, G.M., Drton, M. & Sadeghi, K. (2014) ggm: Functions and Datasets for Graphical Markov Models. *R Package.*

MEA (Millennium Ecosystem Assessment) (2005) *Ecosystems and Human Well-being: Synthesis.* Island Press, Washington, DC.

Miller, F., Osbahr, H., Boyd, E., Thomalla, F., Bharwani, S., Ziervogel, G., Walker, B., Birkmann, J., van der Leeuw, S., Rockström, J., Hinkel, J., Downing, T., Folke, C. & Nelson, D. (2010) Resilience and Vulnerability: Complementary or Conflicting Concepts? *Ecology and Society,* **15**.

Milton, S.J. (1991) Plant Spinescence in Arid Southern Africa: Does Moisture Mediate Selection by Mammals? *Oecologia,* **87,** 279-287.

Minden, V., Andratschke, S., Spalke, J., Timmermann, H. & Kleyer, M. (2012) Plant trait–environment relationships in salt marshes: Deviations from predictions by ecological concepts. *Perspectives in Plant Ecology, Evolution and Systematics,* **14,** 183-192.

Minden, V. & Kleyer, M. (2011) Testing the effect–response framework: key response and effect traits determining above-ground biomass of salt marshes. *Journal of Vegetation Science,* **22,** 387-401.

Misana, S. & Makoi, J. (2001) The impact of irrigation on soil fertility and salinity/sodicity in the Pangani River Basin. *Water resources management in the Pangani River Basin. Challenges and Opportunities* (ed. J.O. Ngana), pp. 83-103. Dar es Salaam University Press, Dar es Salaam.

Mizota, C., Kawasaki, I. & Wakatsuki, T. (1988) Clay mineralogy and chemistry of seven pedons formed in volcanic ash, Tanzania. *Geoderma,* **43,** 131-141.

Moles, A.T., Warton, D.I., Warman, L., Swenson, N.G., Laffan, S.W., Zanne, A.E., Pitman, A., Hemmings, F.A. & Leishman, M.R. (2009) Global patterns in plant height. *Journal of Ecology,* **97,** 923-932.

Mongi, H., Majule, A.E. & Lyimo, J.G. (2010) Vulnerability and adaptation of rain fed agriculture to climate change and variability in semi-arid Tanzania. *African Journal of Environmental Science and Technology,* **4,** 371-381.

Monserud, R.A. & Leemans, R. (1992) Comparing global vegetation maps with Kappa statistic. *Ecological Modelling,* **62,** 275-293.

Moretti, M., de Bello, F., Ibanez, S., Fontana, S., Pezzatti, G.B., Dziock, F., Rixen, C. & Lavorel, S. (2013) Linking traits between plants and invertebrate herbivores to track functional effects of land-use changes. *Journal of Vegetation Science,* **24,** 949-962.

Mori, A.S., Furukawa, T. & Sasaki, T. (2013) Response diversity determines the resilience of ecosystems to environmental change. *Biological Reviews,* **88,** 349-364.

Murphy, B.P. & Bowman, D.M.J.S. (2012) What controls the distribution of tropical forest and savanna? *Ecology Letters,* **15,** 748-758.

Nagelkerke, N.J. (1991) A note on a general definition of the coefficient of determination. *Biometrika,* **78,** 691-692.

NBS & OCGS (National Bureau of Statistics, Tanzania & Office of Chief Government Statistician, Zanzibar) (2013) 2012 Population and Housing Census - Population distribution by administrative areas. pp. 244. Ministry of Finance, Tanzania and President's Office, Finance, Economy and Development Planning, Zanzibar, Dar es Salaam and Zanzibar.

Ndaki, P.M. (2014) Climate Change Adaptation for Smallholder Farmers in Rural Communities: the Case of Mkomazi Sub-Catchment, Tanzania. PhD Thesis, Carl von Ossietzky Universität Oldenburg.

Niang, I., Ruppel, O.C., Abdrabo, M.A., Essel, A., Lennard, C., Padgham, J. & Urquhart, P. (2014) Africa. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel of Climate Change* (eds V.R. Barros, C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea & L.L. White), pp. 1199-1265. Cambridge University Press, Cambridge and New York.

Niklas, K.J. (1993) Influence of Tissue Density-specific Mechanical Properties on the Scaling of Plant Height. *Annals of Botany,* **72,** 173-179.

Notter, B. (2010) Water-related ecosystem services and options for their sustainable use in the Pangani Basin, East Africa. PhD Thesis, University of Bern.

NTSG & UMT (Numerical Terradynamic Simulation Group & University of Montana) (2014) MOD17A3. Terra/MODIS Net Primary Production Yearly L4 Global 1km. NASA Land Processes Distributed Active Archive Center (LP DAAC).

Oesterheld, M., Loreti, J., Semmartin, M., Paruelo, J. & Walker, L. (1999) Grazing, fire, and climate effects on primary productivity of grasslands and savannas. *Ecosystems of Disturbed Ground* (ed. L.R. Walker), pp. 287-306. Elsevier.

Ogée, J. & Brunet, Y. (2002) A forest floor model for heat and moisture including a litter layer. *Journal of Hydrology,* **255,** 212-233.

Pakeman, R.J. (2011) Multivariate identification of plant functional response and effect traits in an agricultural landscape. *Ecology,* **92,** 1353-1365.

Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography,* **20,** 170-180.

PBWO & IUCN (Pangani Basin Water Office & International Union for Conservation of Nature) (2009) Final Project Report. *Pangani River Basin Flow Assessment,* pp. 89. Pangani Basin Water Board and IUCN Eastern & Southern Africa Regional Program, Moshi.

Peñuelas, J., Prieto, P., Beier, C., Cesaraccio, C., De Angelis, P., De Dato, G., Emmett, B.A., Estiarte, M., Garadnai, J., Gorissen, A., LÁNg, E.K., KrÖEl-Dulay, G., Llorens, L., Pellizzaro, G., Riis-Nielsen, T., Schmidt, I.K., Sirca, C., Sowerby, A., Spano, D. & Tietema, A. (2007) Response of plant species richness and primary productivity in shrublands along a north–south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. *Global Change Biology,* **13,** 2563-2581.

Peppler-Lisbach, C. (2003) Predictive modelling of recent and historical land-use patterns. *Phytocoenologia,* **33,** 565-590.

Peppler-Lisbach, C. (2008) Using species-environmental amplitudes to predict pH values from vegetation. *Journal of Vegetation Science,* **19,** 437-444.

Peres, C.A. (2010) Overexploitation. *Conservation biology for all* (eds N.S. Sodhi & P.R. Ehrlich), pp. 107-130. Oxford University Press, New York.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., ReichI, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S. & Cornelissen, J.H.C. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany,* **61,** 167-234.

Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters,* **9,** 741-758.

Peterson, G.D., Cumming, G.S. & Carpenter, S.R. (2003) Scenario Planning: a Tool for Conservation in an Uncertain World. *Conservation Biology,* **17,** 358-366.

Phat, N.K., Knorr, W. & Kim, S. (2004) Appropriate measures for conservation of terrestrial carbon stocks—Analysis of trends of forest management in Southeast Asia. *Forest ecology and management,* **191,** 283-299.

Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., Crist, S., Shpritz, L., Fitton, L., Saffouri, R. & Blair, R. (1995) Environmental and Economic Costs of Soil Erosion and Conservation Benefits. *Science,* **267,** 1117-1123.

Quétier, F., Lavorel, S., Thuiller, W. & Davies, I. (2007) Plant-Trait-Based Modeling Assessment of Ecosystem-Service Sensitivity to Land-Use Change. *Ecological Applications,* **17,** 2377-2386.

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rao, C.R. (1982) Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology,* **21,** 24-43.

Reich, P.B. (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. *Journal of Ecology,* **102,** 275-301.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences,* **94,** 13730-13734.

Rutherford, G.N., Bebi, P., Edwards, P.J. & Zimmermann, N.E. (2008) Assessing land-use statistics to model land cover change in a mountainous landscape in the European Alps. *Ecological Modelling,* **212,** 460-471.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. (2005) Determinants of woody cover in African savannas. *Nature,* **438,** 846-849.

Sankaran, M., Ratnam, J. & Hanan, N. (2008) Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography,* **17,** 236-245.

Saxton, K.E. & Rawls, W.J. (2006) Soil Water Characteristic Estimates by Texture and Organic Matter for Hydrologic Solutions. *Soil Science Society of America Journal,* **70,** 1569–1578.

Schaafsma, M., Morse-Jones, S., Posen, P., Swetnam, R.D., Balmford, A., Bateman, I.J., Burgess, N.D., Chamshama, S.A.O., Fisher, B., Green, R.E., Hepelwa, A.S., Hernández-Sirvent, A., Kajembe, G.C., Kulindwa, K., Lund, J.F., Mbwambo, L., Meilby, H., Ngaga, Y.M., Theilade, I., Treue, T., Vyamana, V.G. & Turner, R.K.

(2012) Towards transferable functions for extraction of Non-timber Forest Products: A case study on charcoal production in Tanzania. *Ecological Economics,* **80,** 48-62.

Scholes, R.J. & Biggs, R. (2004) *Ecosystem Services in Southern Africa: A regional assessment.* Council for Scientific and Industrial Research, Pretoria, South Africa.

Scurlock, J.M.O., Johnson, K. & Olson, R.J. (2002) Estimating net primary productivity from grassland biomass dynamics measurements. *Global Change Biology,* **8,** 736-753.

Seager, R., Ting, M., Li, C., Naik, N., Cook, B., Nakamura, J. & Liu, H. (2013) Projections of declining surface-water availability for the southwestern United States. *Nature Clim. Change,* **3,** 482-486.

Sekercioglu, C.H. (2010) Ecosystem functions and services. *Conservation biology for all* (eds N.S. Sodhi & P.R. Ehrlich), pp. 45-72. Oxford University Press, New York.

Seppelt, R., Dormann, C.F., Eppink, F.V., Lautenbach, S. & Schmidt, S. (2011) A quantitative review of ecosystem service studies: approaches, shortcomings and the road ahead. *Journal of Applied Ecology,* **48,** 630-636.

Serneels, S. & Lambin, E.F. (2001) Proximate causes of land-use change in Narok District, Kenya: a spatial statistical model. *Agriculture, Ecosystems & Environment,* **85,** 65-81.

Settele, J., Scholes, R., Betts, R., Bunn, S., Leadley, P., Nepstad, D., Overpeck, J.T. & Taboada, M.A. (2014) Terrestrial and inland water systems. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds C.B. Field, V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea & L.L. White), pp. 271-359. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Shipley, B. (2002) *Cause and correlation in biology: A user's guide to path analysis, structural equations and causal inference.* Cambridge University press.

Shipley, B. (2009) Confirmatory Path Analysis in a Generalized Multilevel Context. *Ecology,* **90,** 363-368.

Sileshi, G., Akinnifesi, F.K., Ajayi, O.C., Chakeredza, S., Kaonga, M. & Matakala, P. (2007) Contributions of agroforestry to ecosystem services in the Miombo eco-region of eastern and southern Africa. *African Journal of Environmental Science and Technology,* **1,** 68-80.

Skarpe, C. & Hester, A.J. (2008) Plant Traits, Browsing and Gazing Herbivores, and Vegetation Dynamics. *The Ecology of Browsing and Grazing* (eds I.J. Gordon & H.H.T. Prins), pp. 217-261. Springer, Berlin and Heidelberg.

Smaling, E.M.A., Nandwa, S.M. & Janssen, B.H. (1997) Soil Fertility in Africa Is at Stake. *Replenishing Soil Fertility in Africa* (eds R.J. Buresh, P.A. Sanchez & F. Calhoun), pp. 47-62. Soil Science Society of America, Madison, Wisconsin.

SMD (Surveys and Mapping Division) (1974) Mkomazi. Sheet 109/1. *East Africa 1:50.000 (Tanzania) - Y742*. United Republic of Tanzania - Ministry of Lands, Housing and Urban Development, Dar es Salaam.

SMD (Surveys and Mapping Division) (1988) Kisiwani. Sheet 89/2 - Makanya. Sheet 89/4 - Tussa Mountains. Sheet 90/1 - Kihurio. Sheet 90/3. *East Africa 1:50.000 (United Republic of Tanzania) - Y742 (D.O.S. 422)*. United Republic of Tanzania - Ministry of Lands, Housing and Urban Development, Dar es Salaam.

Snyman, H. (2005) Influence of fire on litter production and root and litter turnover in a semiarid grassland of South Africa. *South African Journal of Botany,* **71,** 145-153.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T. & Navas, M.-L. (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology,* **14,** 1125-1140.

Swetnam, R.D., Fisher, B., Mbilinyi, B.P., Munishi, P.K.T., Willcock, S., Ricketts, T., Mwakalila, S., Balmford, A., Burgess, N.D., Marshall, A.R. & Lewis, S.L. (2011) Mapping socio-economic scenarios of land cover change: A GIS method to enable ecosystem service modelling. *Journal of Environmental Management,* **92,** 563-574.

Tadross, M. & Wolski, P. (2010) Climate change modelling for the Pangani Basin to support the IWRM planning process. *Pangani River Basin Flow Assessment*, pp. 44. Moshi.

Tanzania (United Republic of Tanzania) (2012) National Sample Census of Agriculture - 2007/2008 Smallholder Agriculture. Regional Report - Kilimanjaro Region (Volume Vc). pp. 363. Ministry of Agriculture - Food Security and Cooperatives, Ministry of Livestock Development and Fisheries, Ministry of Water and Irrigation, Ministry of Agriculture, Livestock and Environment - Zanzibar, Prime Minister's Office, Regional Administration and Local Governments, Ministry of Industries, Trade and Marketing, National Bureau of Statistics, Office of the Chief Government Statistician - Zanzibar.

Thompson, M. (1996) A standard land cover classification scheme for remote-sensing applications in South Africa. *South African Journal of Science,* **92,** 34-42.

Thuiller, W., Lavorel, S. & Araujo, M.B. (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography,* **14,** 347-357.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The Influence of Functional Diversity and Composition on Ecosystem Processes. *Science,* **277,** 1300-1302.

Turner, B.L., Kasperson, R.E., Matson, P.A., McCarthy, J.J., Corell, R.W., Christensen, L., Eckley, N., Kasperson, J.X., Luers, A., Martello, M.L., Polsky, C., Pulsipher, A. & Schiller, A. (2003) A framework for vulnerability analysis in sustainability science. *Proceedings of the National Academy of Sciences,* **100,** 8074-8079.

UNESCO (1973) International classification and mapping of vegetation. *Ecology and Conservation,* **6,** 13-37.

Usher, M.B. (1981) Modelling ecological succession, with particular reference to Markovian models. *Vegetation dynamics in grasslans, healthlands and mediterranean ligneous formations* (eds P. Poissonet, F. Romane, M.A. Austin, E. van der Maarel & W. Schmidt), pp. 11-18. Springer Netherlands.

van Jaarsveld, A.S., Biggs, R., Scholes, R.J., Bohensky, E., Reyers, B., Lynam, T., Musvoto, C. & Fabricius, C. (2005) Measuring conditions and trends in ecosystem services at multiple scales: the Southern African Millennium Ecosystem Assessment (SAfMA) experience. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **360,** 425-441.

van Wilgen, B.W., Reyers, B., Le Maitre, D.C., Richardson, D.M. & Schonegevel, L. (2008) A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. *Journal of Environmental Management,* **89,** 336-349.

Vendramini, F., Díaz, S., Gurvich, D.E., Wilson, P.J., Thompson, K. & Hodgson, J.G. (2002) Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytologist,* **154,** 147-157.

Verburg, P.H., van de Steeg, J., Veldkamp, A. & Willemen, L. (2009) From land cover change to land function dynamics: A major challenge to improve land characterization. *Journal of Environmental Management,* **90,** 1327-1335.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos,* **116,** 882-892.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human Domination of Earth's Ecosystems. *Science,* **277,** 494-499.

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. & Davies, P.M. (2010)

Global threats to human water security and river biodiversity. *Nature,* **467,** 555-561.

Wardle, D.A., Hörnberg, G., Zackrisson, O., Kalela-Brundin, M. & Coomes, D.A. (2003) Long-Term Effects of Wildfire on Ecosystem Properties Across an Island Area Gradient. *Science,* **300,** 972-975.

Watson, J.E.M., Iwamura, T. & Butt, N. (2013) Mapping vulnerability and conservation adaptation strategies under climate change. *Nature Clim. Change,* **3,** 989-994.

Willemen, L., Verburg, P.H., Hein, L. & van Mensvoort, M.E.F. (2008) Spatial characterization of landscape functions. *Landscape and Urban Planning,* **88,** 34-43.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A. & Langham, G. (2008) Towards an Integrated Framework for Assessing the Vulnerability of Species to Climate Change. *PLoS Biol,* **6,** e325.

Wood, S.A., Karp, D.S., DeClerck, F., Kremen, C., Naeem, S. & Palm, C.A. (2015) Functional traits in agriculture: agrobiodiversity and ecosystem services. *Trends in Ecology & Evolution,* **30,** 531-539.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature,* **428,** 821-827.

Yapp, G., Walker, J. & Thackway, R. (2010) Linking vegetation type and condition to ecosystem goods and services. *Ecological Complexity,* **7,** 292-301.

Zhao, M. & Running, S.W. (2010) Drought-Induced Reduction in Global Terrestrial Net Primary Production from 2000 Through 2009. *Science,* **329,** 940-943.

Zheng, F.-L. (2006) Effect of Vegetation Changes on Soil Erosion on the Loess Plateau1. *Pedosphere,* **16,** 420-427.

Appendix

Appendix 1 List of figures

Appendix 2 List of tables

Appendix 3 Supplementary figures, tables and data

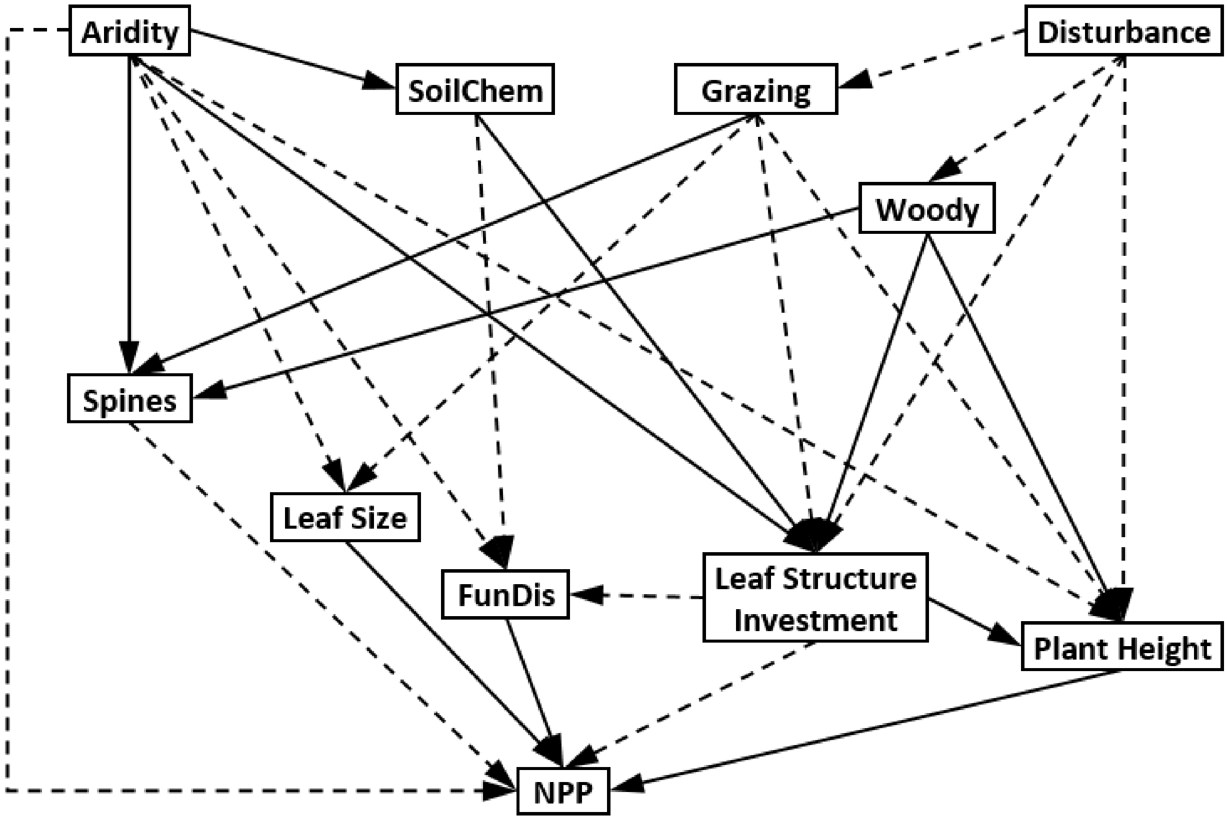


Figure A 1. Hypothesized path model. Solid lines indicate expected positive effects, dashed lines indicate negative effects. Abbreviations of variables see Table 9

Table A 1. Importance of environmental predictors of land cover distribution in % obtained from Regression Analysis I (complete dataset). Grey shaded values highlight factors of high importance. Abbreviations see Table 1 (land cover units) and Table 2 (predictors)

Predictor	ForPlant	Fallow	ForHigh	FarmTree	FarmTera	WoSlope	FarmRain	WoRipar	Comm	Thicket	WoFlood	FarmRice	ReedGras	Acacia	Suaeda
RainAnn	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rain5_10	0	0	50	0	0	0	0	62.5	0	0	5.1	0	0	0	48
Rain11_4	0	0	0	40.7	0	98	99.2	0	98	0	0	0	0	94.3	0
TMean	0	0	48.7	0	0	0	0	0	0	0	12.6	0	0	2.9	0
TMax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	31.5
TMin	1.9	4.7	0	9.9	0	2	0	37.5	0	0	0	13.4	36.3	0	0
ETpAnn	0	95.3	1.3	19.7	12	0	0	0	0	0	71.2	5.3	0	0	0
netRAnn	91.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
netR5_10	0	0	0	0	0	0	0	0	0	0	0	3.7	41.4	0	0
netR4_11	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0
Incl	0	0	0	23.9	7.1	98	0	0	0	0	3.3	77.5	0	28.7	0
DToWat	6.9	0	0	0	0	0	0	100	100	0	90.9	0.8	10.7	61.5	94.1
CTI	6.5	2.9	0	0	0	2	0	0	0	96.2	81.7	0	100	64.5	0
pH	6.9	0	0	0	0	0	0	0	0	0	0	0	21.2	2	2
Carb	0	18.9	16.8	0	79.1	0	0	0	0	0	0	0	0	0.8	17.8
Cond	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.7
PopDens	0	0	0	88.6	76.9	0	0	0	2	0	0	0	0	7.9	0
Disturb	0	98.6	100	100	100	100	100	92.9	0	96.3	79.8	100	0	0	91.6
Grazing	0	0	0	5.9	8.6	0	0	0	100	2.6	12.8	0	100	100	0

Table A 2. Importance of environmental predictors of land cover distribution in % obtained from Regression Analysis II (reduced dataset). The most important predictors of each land cover unit are highlighted by bold letters. Abbreviations see Table 1 (land cover units) and Table 2 (predictors)

	Land Cover Unit	Rain11_4	TMin	DToWat	CTI	Disturb	Grazing
Highlands	ForPlant	5.6	**94.4**	5.6	**64.5**	0	0
	Fallow	5.6	**94.4**	5.6	4	0	0
	ForHigh	0	**100**	0	0	**100**	0
	FarmTree	**72.3**	24.7	0	0	**100**	3
Slopes	FarmTera	0	**100**	0	0	**100**	0
	WoSlope	0	**100**	0	**100**	**98.9**	0
	FarmRain	**99.2**	0	0	0	**100**	0
	WoRipar	0	**100**	**100**	0	**93.6**	0
Lowlands	Comm	**100**	0	**100**	0	0	**100**
	Thicket	**100**	0	0	**88.5**	**96.9**	2.4
	WoFlood	0	61.5	**81.8**	**83.3**	48.8	50
	FarmRice	0	**99**	6.8	1	**100**	0
	ReedGras	0	**97.1**	9.5	**100**	0	**100**
	Acacia	**95.7**	4.3	**87.7**	**92**	0	**100**
	Suaeda	27.3	**72.7**	**95.7**	0	**93.1**	0

Table A 3. Volumes of predicted occurrence (VPO), predictor-specific range breadths (RB) and median predictor values (Med) for each land cover model. Abbreviations see Table 1 (land cover units) and Table 2 (predictors)

	Land cover unit	VPO	Rain11_4		TMin		DToWat		CTI		Disturb		Grazing	
			RB	Med	RB	Med	RB	Med	RB	Med	RB	Med	RB	Med
Highlands	ForPlant	0.043	448	682	2.58	10.2	9328	3392	1.11	3.85	3.96	0.72	4.67	0.93
	Fallow	0.24	498	682	5.17	8.89	9328	3392	7.79	6.08	3.96	0.72	4.67	0.93
	ForHigh	0.079	548	682	7.75	11.5	9328	3392	12.2	6.08	0.2	0	4.67	0.93
	FarmTree	0.099	149	682	14.2	12.8	9328	2544	12.2	7.2	0.72	0.72	9.34	0.93
Slopes	FarmTera	0.186	548	632	11.6	14.1	6784	1696	12.2	6.08	1.8	2.88	2.8	0.93
	WoSlope	0.118	548	532	6.46	16.6	9328	2544	4.45	4.96	1.8	0.36	10.3	1.87
	FarmRain	0.432	299	532	14.2	15.3	9328	1696	12.2	7.19	3.6	1.8	10.3	0.93
	WoRipar	0.096	548	532	5.17	17.9	467	0	12.2	9.41	3.24	0.72	10.3	1.87
Lowlands	Comm	0.149	199	433	14.2	17.9	2544	1696	12.2	7.19	3.96	0.72	7.47	1.87
	Thicket	0.075	100	433	14.2	17.9	6784	1696	4.45	8.3	1.8	0.36	10.3	1.87
	WoFlood	0.011	448	532	3.87	20.5	467	0	4.45	9.41	2.52	0.36	4.67	1.87
	FarmRice	0.073	448	483	1.29	20.5	6784	848	12.2	9.41	3.24	1.8	10.3	0.93
	ReedGras	0.055	448	483	3.87	20.5	6784	848	7.79	11.6	3.96	0.36	10.3	5.6
	Acacia	0.034	249	383	10.3	19.2	5088	848	12.2	4.96	3.96	0.36	10.3	4.67
	Suaeda	0.016	398	483	1	20.5	467	0	12.2	9.41	1.08	0.36	10.3	3.74

Table A 4. Groups of correlated explanatory factors ($r_{Spearman} \geq 0.7$). From each correlation group only one factor was selected for multivariate response models of NPP (*), litter thickness (†) and erosion intensity (#).

Correlation group
Aridity*†, pH, electrical conductivity
Aridity*†, Topography#
Trees, PHeight†, DBH, $PHeight_{FDis}$, DBH_{FDis}#, $PHeight_{RaoQ}$*, DBH_{RaoQ}
Trees†, Phanerophyts*#, PHeight, DBH
LSucc*†, $LSucc_{FDis}$#, $LSucc_{RaoQ}$
LArea*†, $LArea_{FDis}$, $LArea_{RaoQ}$#
DefChem†, $DefChem_{FDis}$#, $DefChem_{RaoQ}$
Spine, $Spine_{FDis}$, $Spine_{RaoQ}$*†
$LHair_{FDis}$#, $LHair_{RaoQ}$
SLA_{FDis}#, SLA_{RaoQ}

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Petzold, M. & Kleyer, M. (in prep.) Combined effects of abiotic factors and functional diversity govern ecosystem properties in a diverse landscape.

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Authors' contributions

Chapter 3

Petzold, M., Yanda, P.Z. & Kleyer, M. Assessing land cover tolerance to environmental gradients in North-East Tanzania. *Submitted to Journal of Tropical Ecology but declined due to insufficient compliance with JTO's contents. New submission planned to another journal.*

MK conceived the study and proposed the modelling approach; **MP** and MK designed the methodology for data collection; **MP** collected and analysed the data, conducted the modelling, prepared the graphs and tables and wrote the initial manuscript; MK, PY and **MP** contributed to revisions of the manuscript.

Chapter 4

Petzold, M. & Kleyer, M. Combined effects of abiotic factors and functional diversity govern ecosystem properties in a diverse landscape. *Submission in preparation.*

MK conceived the study; **MP** and MK designed the methodology for data collection; **MP** collected and analysed the data, conducted the modelling, prepared the graphs and tables and wrote the initial manuscript; MK and **MP** contributed to revisions of the manuscript.

Chapter 5

Petzold, M. & Kleyer, M. Consistency of direct environmental and functional trait mediated effects on primary productivity in North-East Tanzania. *Submission in preparation.*

MK conceived the study; **MP** and MK designed the methodology for data collection; **MP** collected and analysed the data, conducted the modelling, prepared the graphs and tables and wrote the initial manuscript; MK and **MP** contributed to revisions of the manuscript.

Als Betreuer der Arbeit bestätige ich die Richtigkeit der Darstellung der Beiträge der Autoren zu den Manuskripten.

……………………………………

Prof. Dr. Michael Kleyer

Erklärung

gemäß § 12 Abs. 2b der gemeinsamen Promotionsordnung der Fakultät II - Informatik, Wirtschafts- und Rechtswissenschaften (für ihr Department für Informatik), der Fakultät V – Mathematik und Naturwissenschaften und der Fakultät VI – Medizin und Gesundheitswissenschaften der Carl von Ossietzky Universität Oldenburg vom 05.09.2014.

Hiermit erkläre ich, dass ich die vorliegende Dissertation in allen Teilen selbstständig und nur mit den angegebenen Quellen und Hilfsmitteln angefertigt habe. Chapter 3, Chapter 4 und Chapter 5 sollen in Fachzeitschriften veröffentlicht werden. Weiterhin erkläre ich, dass diese Dissertation weder in ihrer Gesamtheit noch in Teilen einer anderen Hochschule zur Begutachtung in einem Promotionsverfahren vorliegt, und dies auch in der Vergangenheit nicht tat. Zudem erkläre ich, dass ich die Leitlinien guter wissenschaftlicher Praxis der Carl von Ossietzky Universität Oldenburg befolgt habe und dass ich im Zusammenhang mit dem Promotionsvorhaben keine kommerziellen Vermittlungs- oder Beratungsdienste in Anspruch genommen habe. Mit der Vorlage dieser Dissertation strebe ich eine Promotion zum Dr. rer. nat. an, es soll der Grad eines Doktors verliehen werden.

Oldenburg, 2. Februar 2016

(Maximilian Petzold)