Factors controlling microbial biomass in soils of Mt. Kilimanjaro

Dissertation

zur Erlangung des Grades Doktor der Naturwissenschaften (Dr. rer. nat.)
an der Fakultät Biologie / Chemie / Geowissenschaften
der Universität Bayreuth

vorgelegt von
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geb. am 04.07.1984 in Ulm

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Bayreuth, den 18. Juli 2014

Die vorliegende Arbeit wurde in der Zeit von 12.2010 bis 07.2014 in Bayreuth am Lehrstuhl für Agrarökosystemforschung sowie in Göttingen in der Abteilung Ökopedologie der gemäßigten Zonen unter der Betreuung von Herrn Professor Dr. Yakov Kuzyakov angefertigt.

Vollständiger Abdruck der von der Fakultät für Biologie, Chemie und Geowissenschaften der Universität Bayreuth genehmigten Dissertation zur Erlangung des akademischen Grades eines Doktors der Naturwissenschaften

Dissertation eingereicht am: 18.07.2014

Zugelassen durch die Prüfungskommission: 06.08.2014

Wissenschaftliches Kolloquium: 21.01.2015

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“Education is the most powerful weapon which you can use to change the world.”

Nelson Mandela

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General Summary

Abbreviations

The author is aware that in the three studies, different abbreviations were used for similar terms. It is pointed out that for the general chapters of this thesis (introduction, summary), the abbreviations C_{org}, C_{mic} and WOC are used.

Abbreviation	Meaning	Dimension/unit	Used in study
AIC_c	Aikaike Inormation Criterion		3
a.s.l.	above sea level		1, 2
C	Carbon		
C_{mic}, MBC	Microbial biomass carbon	mg g^{-1}	1, 2, 3
C_{org}	(Soil) organic carbon	g kg^{-1}	2
C_{sol}	Water extractable (organic) carbon	mg g^{-1}	
GWR	Geographically weighted regression		3
KINAPA	Kilimanjaro National Park		1, 2
LOOCV	Leave-one-out cross-validation		3
LR	Linear regression		3
MAP	Mean annual precipitation	mm	2
MAT	Mean annual temperature	°C	2
MB	Microbial biomass		3
N	Nitrogen		
N_{mic}	Microbial biomass nitrogen	mg g^{-1}	3
NPP	Net primary production	Mg ha^{-1}	1, 2
OK	Ordinary kringing		3
PLSR	Partial least squares regression		3
qCO_2	Metabolic quotient	$mg(C_{CO2})\ g^{-1}(C_{mic})\ h^{-1}$	2
q_sCO_2	Specific metabolic quotient	$mg(C_{CO2})\ g^{-1}(C_{mic})\ h^{-1}$	2
RI	Relative improvement	%	3
RK	Regression kriging		3
$RMSE$	Root mean squared error		3
$RMSE_r$	Root mean squared error of prediction	%	3
SFA	Soil fauna activity	%	3
SOC	Soil organic carbon	g kg^{-1}	1, 3
SOM	Soil organic matter		
Vis-NIR-DRS	Visible to near-infrared diffuse reflectance spectroscopy		3
WOC	Water extractable organic carbon	mg g^{-1}	1
θ	Soil water content	%	

Summary

The contents of organic matter and microorganisms in soils are sensitive parameters to evaluate soil quality. In general, high contents in organic and microbial carbon (C_{org}, C_{mic}) are related to high soil fertility. Especially in the tropics, climate and land use have strong direct effects on basic soil parameters and soil microbial biomass. Furthermore, alterations of the basic soil parameters (e.g. in contents, stocks or distribution) also entail changes of soil microorganisms. Although these major factors and their controlling effect on soil microbial biomass are known, detailed studies including soils of multiple major ecosystems of a region are scarce, especially in Africa. Various climates can be observed on the African continent and the projected climate change is assumed to have regionally diverging effects. Furthermore, at the expense of natural ecosystems, the high population growth in Africa leads to an increasing demand for agricultural land and high rates of land-use change. To evaluate the soils' environmental services and its vulnerability, it is crucial to understand these changes and their effects on soil microbial biomass. Africa's highest mountain, the Kilimanjaro, offers outstanding potential to investigate C_{org} and C_{mic} in soils of various climates, ecosystems and land-use types. Hence, the overall purpose of this investigation was to examine factors controlling microbial biomass in soils of Mt. Kilimanjaro.

The work was conducted on the southern slopes of Mt. Kilimanjaro and covered an climate/elevation gradient from 950 to 3880 m a.s.l.. Up to twelve ecosystems that developed in different climates were investigated, classified into natural (6 plots), semi-natural by men slightly affected habitats (3) and agriculturally managed sites (3). Basic soil parameters and soil microbial biomass were measured in multiple depths and different spatial scales. Sampling was conducted between January 2011 and October 2013. The effects of climate and land use on basic soil parameters and soil microbial biomass were statistically analyzed and compared.

Elevation distinctly influences temperature and precipitation along the slopes of Mt. Kilimanjaro and thus was used to investigate the climatic effect on soil microbial biomass. Along the investigated elevation gradient, C_{org} and C_{mic} contents in soils were found to follow a hump-shaped distribution with a maximum in the consistently warm and humid forest ecosystems at elevations between 2000 m and 3000 m a.s.l.. In addition, the forest belt exhibited also the strongest negative trends in C contents with depth. C_{mic} stocks did not show a direct correlation to climate. However, C_{org} stocks varied depending on water availability, temperature and net primary production (NPP) along the elevation gradient. In ecosystems with a dry character at low elevations, soil C_{org} stocks increased by 3 kg m^{-2} and in the consistently humid ecosystems at higher elevations by 1 kg m^{-2} per 1000 m in elevation, respectively. The variability in soil C_{mic} contents during the climatic transition phase from dry-to-wet season was more pronounced at low elevations / dry climate and lead to a decrease of C_{mic} when the rain season began. At similar elevations, the pronounced contrast between climatic seasons also resulted in a high increase in CO_2 efflux and the specific metabolic quotient (q_sCO_2) under increased precipitation.

Contents and stocks of C_{org} and C_{mic} were altered by human influences on the ecosystems, which was revealed by the investigation of two land use conversions typical for the region and on a similar elevation/climatic level. Compared with C_{org}, the contents and stocks of C_{mic} were stronger decreased by the negative effect of intensive land use. This effect was especially distinct in the upper soil horizons. Intensive agricultural management also resulted in an up to 3-fold decrease of the substrate available for microbial growth (C_{mic}:C_{org} ratio). In addition, soil CO_2 efflux and q_sCO_2 in soils of agricultural fields were up to four times higher than in the soils of less disturbed ecosystems.

A detailed heterogeneity study in the savannah ecosystem revealed small-scale patterns of basic soil parameters and soil microbial biomass. C_{org}, N, C_{mic} and N_{mic} contents varied several-fold between and within 15 × 15 m plots in the same area and climate. Basic soil parameters (e.g. C_{org}, N) are controlled by factors such as climate, vegetation and relief even on a small scale. Because of their correlation to soil microbial biomass, such basic soil parameters provide additional information for multivariate prediction techniques and are able to increase the calculation's accuracy.

Climate, land use and NPP were identified as the main drivers affecting the microbial biomass in soils of Mt. Kilimanjaro. Climate and land use are independent of each other but both distinctly influence the NPP and/or vegetation of an ecosystem. The

consistent humid climates in ecosystems above 2000 m a.s.l. supports high NPP, high contents and stocks of C_{org} and C_{mic} as well as increased substrate availability in soil. The soils of natural ecosystems in the National Park (> 2000 m a.s.l.) and of slightly disturbed ecosystems at low elevations are characterized by effective, closed nutrient and C cycles in a steady-state, but are nevertheless highly vulnerable to the negative consequences of land-use change. The agricultural land use in the densely populated areas of Mt. Kilimanjaro negatively alters important and sensitive parameters within the C cycle. The observed reduction in C_{org}, C_{mic}, available substrate and microbial efficiency leads to the assumption of an open C cycle entailing a further decline in the contents and stocks of C_{org} and C_{mic} with increased land use.

Zusammenfassung

Die Gehalte an organischer Bodensubstanz und die im Boden befindlichen Mirkoorganismen sind sensitive Parameter für die Bodenqualität. Im Allgemeinen werden hohe Gehalte an organischem und mikrobiellem Kohlenstoff (C_{org}, C_{mic}) mit hoher Bodenfruchtbarkeit in Verbindung gebracht. Vor allem in den Tropen haben das Klima und die Landnutzung starke direkte Effekte auf allgemeine Bodenparameter und die mikrobielle Biomasse in Böden. Weiterhin haben Änderungen der allgemeinen Bodenparameter (z.B. in deren Gehalte, Menge oder Verteilung) auch Veränderungen in der mikrobielle Biomasse zur Folge. Obwohl diese Faktoren und ihre Wirkung auf die mikrobielle Biomasse in Böden bekannt sind, befassen sich nur wenige Studien mit den Böden mehrerer wichtiger Ökosysteme einer Region. Der afrikanische Kontinent ist durch mehrere Klimazonen charakterisiert und die Auswirkungen des vorhergesagten Klimawandels werden vorraussichtlich regional unterschiedlich ausfallen. Weiterhin führt das hohe Bevölkerungswachstum Afrikas, auf Kosten natürlicher Ökosysteme, zu einem steigenden Bedarf an landwirtschaftlicher Nutzfläche und einer hohen Rate an Landnutzungsänderungen. Um die ökologischen Dienstleistungen sowie die Verwundbarkeit von Böden zu bewerten ist es nötig diese Änderungen und deren Effekt auf die mikrobielle Biomasse zu verstehen. Afrikas höchster Berg, der Kilimanjaro, bietet außergewöhnliche Möglichkeiten C_{org} und C_{mic} in Böden verschiedener Klimate, Ökosysteme und Landnutzungstypen zu untersuchen. Daher war das Hauptziel dieser Dissertation Faktoren, die die mikrobielle Biomasse in Böden des Kilimanjaro's beeinflussen wissenschaftlich zu untersuchen.

Die Arbeiten wurden am Südhang des Kilimanjaro zwischen 950 bis 3880 m ü. NN durchgeführt. Die Untersuchungen umfassten bis zu zwölf, in unterschiedlichen Klimaten entwickelte Ökosysteme, eingeteilt in natürliche (6 Flächen), halb-natürliche, durch den Menschen geringfügig beeinflusste Habitate (3) und landwirtschaftlich genutzte Flächen (3). Allgemeine Bodenparameter und die mikrobielle Biomasse in Böden wurden in mehreren Tiefen und auf unterschiedlichen räumlichen Skalen bestimmt. Die Beprobungen fielen in den Zeitraum von Januar

2011 bis Oktober 2013. Die Effekte von Klima und Landnutzung auf allgemeine Bodenparameter und die mikrobielle Biomasse wurden statistisch analysiert und verglichen.

Da am Berg die Temperatur und Niederschlagsverteilung entscheidend durch die Höhe beeinflusst wird, wurde diese genutzt um den Effekt des Klimas auf die mikrobielle Biomasse zu untersuchen. Entlang des untersuchten Höhengradienten verliefen die C_{org} und C_{mic} Gehalte der Böden glockenförmig, mit den höchsten Werten in den konstant warm-humiden Waldökosystemen auf einer Höhe zwischen 2000 m und 3000 m ü. NN. Zusätzlich zeigten die Kohlenstoff-Gehalte dieser Böden die stärkste Abnahme mit der Tiefe. Die Gesamtmengen an C_{mic} hatten keine direkte Korrelation zum Klima. Die Gesamtmengen an C_{org} variierten jedoch abhängig von der Wasserverfügbarkeit, Temperatur und Netto-Primär-Produktion (NPP) entlang des Höhengradienten. In den eher trockenen Ökosystemen am Fuße des Berges stiegen die Mengen an C_{org} um 3 kg m^{-2}, in den konstant humiden Habitaten in größerer Höhe um 1 kg m^{-2}, pro 1000 m in Höhe. Die Variabilität der C_{mic} Gehalte der Böden war während des klimatischen Übergangs von Trocken- zu Regenzeit in den niedriger gelegenen Ökosystemen bzw. trockeneren Klimaten stärker ausgeprägt und eine Abnahme an C_{mic} wurde zu Beginn der Regenzeit beobachtet. Auf der gleichen Höhenstufe und während erhöhtem simulierten Niederschlag resultierte der ausgeprägte Unterschied zwischen den klimatischen Jahreszeiten in einem starken Anstieg der CO_2 Ausgasung und des spezifischen metabolischen Quotienten (q_sCO_2).

Die Untersuchung von zwei, für die Region typischen, Landnutzungsänderungen auf gleicher Höhenstufe zeigte, dass die Gehalte und Gesamtmengen an C_{org} und C_{mic} durch die menschlichen Einflüsse auf die Ökosysteme verändert wurden. Im Vergleich mit C_{org}, wurden die Gehalte und Gesamtmengen an C_{mic} stärker durch den negativen Effekt der Landnutzung verringert. Dieser Effekt war besonders in den oberen Bodenhorizonten ausgeprägt. Intensive landwirtschaftliche Nutzung resultierte auch in einer bis zu dreifachen Verringerung des für die mikrobielle Biomasse verfügbaren Substrats (Verhältnis C_{mic}:C_{org}). Weiterhin war die CO_2 Ausgasung sowie q_sCO_2 in Böden landwirtschaftlicher Nutzflächen bis zu vierfach höher als in Böden von weniger beeinflussten bzw. gestörten Ökosystemen.

Eine detailierte Heterogenitätsstudie in der Savanne offenbarte kleinräumige Muster der allgemeinen Bodenparameter und der mikrobiellen Biomasse. Die Gehalte von C_{org}, N, C_{mic} und N_{mic} varriierten im gleichen Gebiet und Klima mehrfach zwischen sowie innerhalb von 15 x 15 m Untersuchungsflächen. Auch auf kleinräumiger Skala werden allgemeine Bodenparameter (z.B. C_{org}, N) durch das Klima, die Vegetation und das Relief beeinflusst. Aufgrund ihrer Korrelation zur mikrobiellen Biomasse in Böden, bieten diese allgemeinen Bodenparameter zusätzliche Information für Vorhersagen mit multivariaten Techniken und können dadurch die Genauigkeit der Kalkulationen erhöhen.

Klima, Landnutzung und NPP wurden als die wichtigsten, die mikrobielle Biomasse in Böden des Kilimanjaros, beeinflussenden Faktoren identifiziert. Klima und Landnutzung sind von einander unabhängig, jedoch beeinflussen beide die NPP und/oder die Vegetation eines Ökosystems. Die konstant humiden Klimate der Ökosysteme oberhalb von 2000 m ü. NN. begünstigen hohe NPP, hohe Gehalte und Gesamtmengen an C_{org} und C_{mic} sowie eine erhöhte Substratverfügbarkeit in Böden. Die Böden natürlicher Ökosysteme innerhalb des Nationalparks (> 2000 m ü. NN.) und der geringfügig beeinflussten Ökosysteme niedrigerer Höhen sind durch einen sich im Gleichgewicht befindenden, effektiven geschlossenen Kohlenstoff-Kreislauf gekennzeichnet. Jedoch sind sie auch deutlich anfällig für die negativen Konsequenzen aus Landnutzungsänderungen. Die agrarwirtschaftliche Nutzung der Böden in den bevölkerungsreichen Gebieten am Fuße des Berges wirkt sich negativ auf empfindliche Parameter innerhalb des Kohlenstoff-Kreislaufs aus. Die beobachtete Reduzierung der Gehalte und Mengen an C_{org} und C_{mic} sowie die Verringerung der Substratverfügbarkeit und der mikrobiellen Effektivität lässt offene Kohlenstoff-Kreisläufe und ein anhaltendes Sinken der Gehalte und Mengen an C_{org} und C_{mic} in den landwirtschaftlichen Flächen vermuten.

General Introduction

Soil organic matter and microbial biomass

The sum of all organic substances in soil derived from plant, microbial and animal detritus is referred to as soil organic matter (SOM) (Batjes & Sombroek, 1997). The "*importance of soil organic matter"* has been extensively described in the eponymous report by Bot & Benites (2005). Summarily, during decomposition, SOM is transformed to organic and inorganic molecules, i.e. plant-available nutrients (Juma, 1999). At steady state, the equilibrium between decomposition rate and the addition of new organic matter keeps the level of SOM constant. A shift in this equilibrium will result in accumulation or loss of SOM, depending whether the decomposition rate is lower or higher than the rate of addition of new material (Davidson & Janssens, 2006).

The benefits of SOM for soil fertility are widely known (Johnston et al., 2009; Reddy, 1995; Sollins et al., 1996; Tiessen et al., 1994; Zech et al., 1997). It stabilizes the soil structure and thus protects the soil against erosion, but also improves its water retention and other hydraulic properties (Batjes & Sombroek, 1997). SOM is estimated to contain on average 58% of organic C (C_{org}). In addition, it is a revolving source of nutrients (e.g. N, P, S, K) for plants and microorganisms and an important determinant of the cation exchange capacity – especially in tropical soils (Batjes & Sombroek, 1997).

Biological mechanisms responsible for SOM turnover are of major importance in global C model projections (Wieder et al., 2013). Consequently, soil has taken a central part in recent discussions on climate change (IPCC, 2014; Vose et al., 2004). Soil microbial biomass C (C_{mic}) is an important and sensitive parameter for C_{org} turnover and soil fertility (Powlson et al., 2001), adequately described by Bot &

Benites (2005): *"By breaking down carbon structures and rebuilding new ones or storing the C into their own biomass, soil biota plays the most important role in nutrient cycling processes and, thus, in the ability of a soil to provide the crop with sufficient nutrients to harvest a healthy product."*

To evaluate the importance of the soils' environmental services, as well as its vulnerability and sustainability, it is crucial to understand the factors controlling soil microbial biomass.

The influence of climate

Soil is the largest terrestrial C pool with approximately 1600 Pg of C_{org} (Batjes, 1996; Eswaran et al., 1993; Lal, 2004). Tropical ecosystems have a major effect on biogeochemical element cycles (Girardin et al., 2010; Melillo et al., 1993). Around 500 Pg, or one third of the soil C is stored in the tropics, with 30–80% found in the topsoil to a depth of 0.4 m (Batjes, 1996; Detwiler, 1986). The net primary productivity (NPP) and the mineralization rate of SOM are climate sensitive factors controlling the amount of C_{org} in natural soils (Craine et al., 2010; Kirschbaum, 1995). In general, the hot and humid climate conditions in the tropics support high NPP and high turnover rates of litter and SOM (Melillo et al., 1993; Nemani et al., 2003; Zech et al., 1997). The effect of climate on NPP and soil conditions was evident in several studies. For example, Bruijnzeel & Veneklaas (1998) discussed the role of tropical montane cloud forests. Compared to forests in tropical lowlands, these forests exhibit a low aboveground NPP which is attributed to limited evapotranspiration (Nullet & Juvik, 1994) and photosynthesis (Bruijnzeel & Veneklaas, 1998; Ishibashi & Terashima, 1995). Due to unfavorable soil conditions like persistently high water-saturation and/or low nutrient availability, high amounts of C are put in the formation of large root systems, further limiting the forests productivity (Bruijnzeel & Veneklaas, 1998). Similar to the NPP, the sensitivity of SOM to temperature has been studied extensively, but some uncertainty still remains (Fang et al., 2005; Giardina & Ryan, 2000; Knorr et al., 2005; Jobbágy & Jackson, 2000). Davidson & Janssens (2006) reviewed literature on the temperature sensitivity of soil C decomposition and its relation to the projected climate change. Gaseous efflux from soil is an important source of the greenhouse-gas carbon dioxide (CO_2) and is almost completely controlled by root respiration and the microbial mineralization of SOM (Bond-Lamberty & Thomson, 2010; Kuzyakov, 2006). The quotient of the amount of CO_2 released by microbial respiration and the total amount of microbial biomass is related to the energy demand and activity of soil microorganisms. It can be used as a parameter of the microbial efficiency as well as a parameter of the microbial potential for C utilization (Anderson & Domsch, 1978). It is strongly dependent on temperature and soil moisture. Whereas hot temperatures are known to increase the microbial activity and therefore the mineralization rate of SOM in soils, cold temperatures are negatively correlated with the metabolism of soil microorganisms but not with their amount (Blume et al., 2002; Zech et al., 1997). Tropical ecosystems are subjected to pronounced dry and wet seasons, which have distinct impacts on productivity and nutrient cycling. Many studies dealt with the positive correlation between soil moisture and CO_2 efflux from soil (amongst others Reichstein et al., 2003). However, there have been only few attempts to investigate soil properties during the transition from dry-to-wet or wet-to-dry season (e.g. Eaton, 2001). As a consequence, the seasonal variability of soil microbial biomass is not yet fully understood, since high amounts have been found in dry as well as in wet seasons (Devi & Yadava, 2006; Maithani et al., 1996; Montaño et al., 2007). Due to their importance for soil fertility, soil microorganisms are a major factor for the sustainability of tropical agricultural systems (Sanginga et al., 1992). However, changes in land use massively alter (amongst others) the CO_2 efflux and the C_{mic} content of soils (Calderón et al., 2000; Iqbal et al., 2010).

The influence of land use

Ecosystem goods and services are the basis for human life and its development on earth. Anthropogenic factors often influence these benefits negatively. The high relevance of land-use change has recently been shown, as the loss of ecosystem goods and services has been estimated to \$4.3–\$20.2 trillion per year (from 1997-2011, Costanza et al., 2014). This estimate also includes changes in soil properties and fertility. A conversion of natural ecosystems to croplands reduces productivity and mineralization of SOM (Ogle et al., 2005), leading to an average decrease in C_{org} stocks of 25-50% (Detwiler, 1986; Don et al., 2011; Lal, 2004), with most of the decrease in the highly organic topsoil layers (Guo & Gifford, 2002). This decrease in C_{org} contents is accompanied by a release of the greenhouse gas CO_2 from soil (Lal, 2004; Powlson et al., 2001). Because of their high NPP (Schuur, 2003), mineralization rates (Zech et al., 1997) and C stored in the vegetation, the negative effect of land-use changes is especially distinct in tropical ecosystems: compared to temperate regions on average twice as much C is lost from vegetation and soil (West et al., 2010). Consequently, several studies focused on anthropogenic disturbances and land-use changes in tropical regions (Don et al., 2011; Lambin et al., 2003; Walker, 2004). An important factor for the sustained productivity of agricultural systems is a constant level of SOM (Bot & Benites, 2005). However, during the last century, the removal of large amounts of nutrients together with insufficient input of fertilizers led to degradation and nutrient depletion of tropical soils (Buresh et al., 1997; Lal & Bruce, 1999; Sanchez, 2002). Therefore, depending on climate, soil type and management, mean crop yield in the tropics is approximately half that of temperate regions (West et al., 2010). Nonetheless, despite their low rate of C sequestration, tropical soils are supposed to have a high potential to act as C sink (Lal, 2004).

The relationship between spatial environmental heterogeneity and diversity is a basic but complex concept in ecology (Tamme et al., 2010; Wilson, 2000). Especially at a small-scale, biological parameters, e.g. plant growth and animal species diversity are spatially diverse and strongly affected by biogeochemical soil properties, soil moisture and temperature (Herbst & Diekkrüger, 2003; Reichstein et al., 2003). However, these biological parameters also contribute to the spatial distribution of physical and chemical characteristics of soil (Wiens, 2000). In natural savannahs, soils under tree canopies are known to contain distinctly higher amounts of C_{org} and C_{mic} (Isichei & Muoghalu, 1992). Disturbances of ecosystems often go hand in hand with a change in vegetation structure, which may result in a distinct change of the soils' spatial heterogeneity once the system or vegetation is disturbed (Krummel et al., 1987; Rossi et al., 2009). While the amounts of C and nutrients in soils may recover after abandonment of agriculture, land use may have had an enduring effect on their spatial distribution (Fraterrigo et al., 2005; Schulp & Verburg, 2009). Compared to natural reference sites, management practices like the mixing of soil horizons and the removal of plant debris reduce the spatial variability of C contents (Fraterrigo et al., 2005). However, the heterogeneity of C_{org}, C_{mic} and selected nutrients (e.g. P, K, Mg) on agricultural land is increased by deposition of animal manure (Augustine & Frank, 2001; Tessier et al., 1998). Both, the nutrient enriched as well as the infertile spots feed back on the productivity of the ecosystems and hence also on the soil microbial biomass (Day et al., 2003). Beside the spatial effects of land use, the projected climatic change results in spatially varying responses of crop yields, implicating the necessity of localized approaches to adapt to future changes in climate (Thornton et al., 2009).

Soil has always been a major aspect in human development and the increasing human population enhances the need for arable land and food production (McNeill & Winiwarter, 2004). Hereby Africa deserves a special focus: A fivefold increase in human population from 1950 to 2013 resulted in massive land cover changes on the African continent (United Nations, 2013a). On cost of natural vegetation, Africa's agriculturally managed and barren land area has increased by 57% and 15% (1975–2000), respectively (Brink & Eva, 2009). Especially in the Southern and Eastern part of the continent, forests diminish rapidly, resulting in the highest forest decrease rates worldwide (FAO, 2011). Today, 15.5% or 1.1 billion of the world's 7.2 billion people are living in Africa and this number is projected to rise to 25% in 2050 (United Nations, 2013b). The provision of food and a balanced diet for the growing population is included in the Millennium Development Goals adopted by the United Nations (United Nations, 2013b). But at present, low crop yields in Africa's agricultural systems result in high rates of malnourishment and hunger (FAO, 2013). Summed up, the projected climate change, the fast growing population, the increase in agricultural land area and the low food production demands that an increasing part of international and interdisciplinary research should be focused on the African continent.

Why Mt. Kilimanjaro?

The effect of land-use changes on soil properties has been studied extensively. Nonetheless, compared to other regions, little is known about African ecosystems and subtropical and tropical research is mostly focused on South America and Asia. A recent meta-analysis concentrated on land-use changes in the tropics and their effects on SOC stocks (Don et al., 2011). However, publications on the changes of soil microbial properties are scarce. Mt. Kilimanjaro offers exceptional opportunities to study East African habitats, depending on land-use and elevation/climate. Compared to other regions in Tanzania, huge amounts of C are stored in the vegetation and soils of Mt. Kilimanjaro (Miles et al., 2009). On average the annual human population growth rate in Mt. Kilimanjaro region is 1.8% and increasing (National Bureau of Statistics, 2013). Consequently, the increasing need for arable land and land-use conversions threaten the SOC pools. Owing to its topography as a high isolated mountain, various ecosystems similar to East Africa have developed (Mayaux et al., 2004), ranging from hot-dry savannah on its lower slopes to cold alpine deserts above 4500 m (Hemp, 2006a). The climate, rainfall patterns and the hydrology of Africa's highest mountain are well known and described in several studies (Chan et al., 2008; Coutts, 1969; Duane et al., 2008; McKenzie et al., 2010; Røhr, 2003). Also the mountain's vegetation and its distribution have been studied extensively and in detail (amongst others Axmacher, 2003; Hemp, 2002, 2006a, 2006b). Information on soils of Mt. Kilimanjaro, however, is mainly available on soil development and paleosols (Little & Lee, 2006; Zech, 2006; Zech et al., 2011, 2014), but only to a lesser extend on soil nutrients, land-use change and soil microbial

Figure A: Homegarden – a traditional agroforestry system of the Kilimanjaro native Chagga tribe; Photo by J. Röder, University of Marburg properties (Kaihura et al., 1999; Mganga & Kuzyakov, 2014; Misana et al., 2003; Schrumpf, 2004). Amongst all African habitats savannahs and native bushland have been the most extensively investigated ones. Several studies concentrated on C turnover, soil microorganisms and greenhouse gas exchange (Angassa, 2007; Hernández-Hernández & López-Hernández, 2002; Otieno et al., 2010). However, the spatial variability of these parameters was considered only in a few studies which were undertaken in South and West Africa (Hagos & Smit, 2005; Wang et al., 2009).

History of land use on Mt. Kilimanjaro

Mt. Kilimanjaro ecosystems have always been utilized and are under severe pressure as a result of land-use changes. During the last 2000 years, settled agricultural people widely cleared the forests below 1700 m (Schmidt, 1989). Traditionally, the Kilimanjaro native *Chagga* tribe established grasslands and an agroforestry system in the fertile highlands, which nearly lead to the disappearance of the native vegetation of lower montane forests (Mwasaga, 1991). This traditional agroforestry system is referred to as homegarden. With its high crop diversity it provided food throughout the year and was seen as a form of traditional sustainable subsistence agroforestry (Clemm, 1964; Fernandes et al., 1985). In the late 19th century, large scale coffee plantations started to replace these traditional homegardens (Mbonile et al., 2003). However, homegardens and plantations reached their maximal distribution before 1960 and have not expanded since (Soini, 2005). In consequence of the continuously growing population, land scarcity and variations in prices of agricultural products (e.g. coffee), homegardens were more recently affected by fragmentation and changes in cultivated plant species (Mbonile et al., 2003; Soini, 2005). Based on analysis of aerial photographs from 1961, 1982 and 2000, the recent major land-use or land-cover change on the mountain's southern slopes can be described as a pronounced loss of natural bushland and savannah, accompanied by a simultaneous extensive increase in agriculturally cultivated land (Soini, 2005).

The protection of the mountain's forest above 1700 m began with the establishment of the Kilimanjaro Forest Reserve in 1904 (Newmark, 1991). After a strong increase in wood harvesting during the Second World War, Wood (as cited in Schrumpf, 2004) reported efforts to support natural afforestation. During the same time, a half-mile forest strip was established to lessen the pressure on the Forest Reserve and to provide the rapidly growing population with natural resources. Nevertheless, to the present day, this half-mile buffer zone is severely exploited and constantly changed by land-use (William, 2003). Authorized as well as illegal logging intensified again in the second half of the 20th century, leading to the mosaic fragmentation of the forest found today (Lamprey et al., 1991). On the southern slopes, illegal logging focused on the large scale exploitation of Camphor (*Ocotea usambarensis*), whereas on the north-eastern slopes it concentrated on Cedar (*Juniperus procera*) (Lambrechts et al., 2002; Lovett & Pócs, 1993). In 2005, the Kilimanjaro Forest Reserve was included into the Kilimanjaro National Park (KINAPA), further limiting unauthorized logging. Still, the past interferences and their consequences are still visible in forests at elevations below 2500 m a.s.l.. In addition, it is assumed that illegal logging and charcoal production persist to be major threats to Mt. Kilimanjaro's forests (Lambrechts et al., 2002; Soini, 2005). Also the function of the half-mile strip is carried on, as the National Park areas at lower elevations are used by the local population for collecting firewood and animal feeds.

General objective

Although the factors controlling soil microbial biomass in tropical soils are in general already known, detailed studies including multiple major ecosystems of a region are scarce. Despite the high rate of land-use change, the fast growing population and the projected climate change, Africa mostly was left out in studies concerning the quality and fertility of soils. The topography of Mt. Kilimanjaro, specifically its climate/elevation gradient, lead to the development of several ecosystems typical for East Africa. Because of the high human population density and growth, natural ecosystems in the region are threatened by land-use change to agricultural ecosystems. Therefore the aim of the present thesis was to investigate the effect of (already known) factors on soil microbial biomass in multiple ecosystems of Mt. Kilimanjaro. Specifically, these factors were addressed in three separate studies (Figure B):

1. The first study focused on two specific objectives (blue, Figure B):
    - The effect of increasing soil moisture on soil microbial biomass during the climatic transition phase from dry-to-wet season
    - The effect of land use on contents of C_{mic} and water-extractable C (WOC) and their distribution with depth
2. Study 2 (orange, Figure B) addressed two objectives associated with the topics of Study 1:
    - Land use and climate as the controlling factors for changes in C_{org} and C_{mic} stocks
    - The dependency of soil CO_2 efflux and the specific metabolic quotient to increased land management intensity and precipitation.
3. The third study (yellow, Figure B) dealt with small-scale variability of basic soil parameters and their usefulness to predict soil microbial biomass. Due to the high experimental effort, this study was conducted in only one ecosystem (savannah).

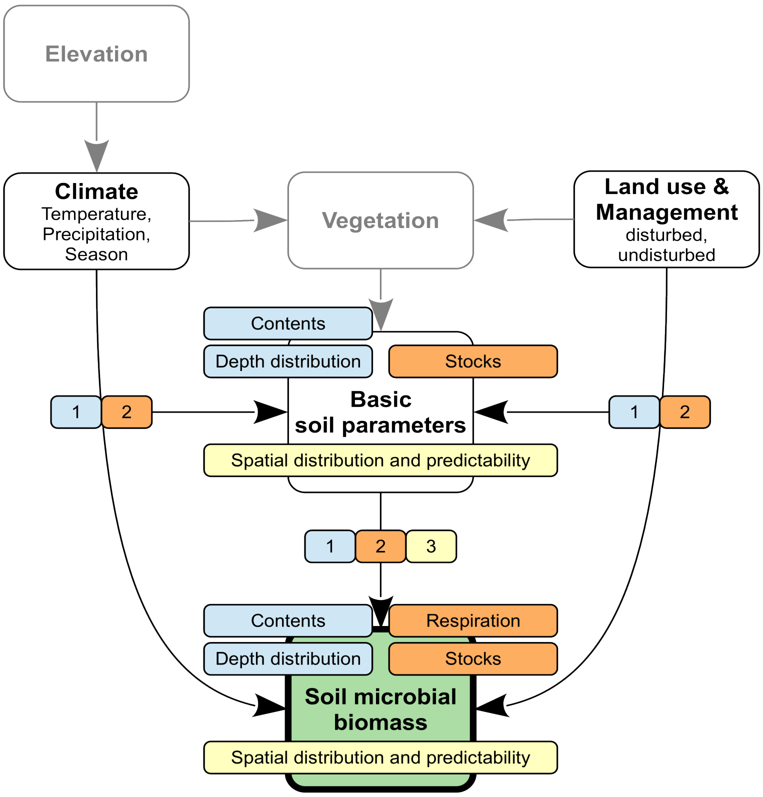

Figure B: Schematic view of the factors controlling microbial biomass in soils of Mt. Kilimanjaro. The objectives and relationships addressed in studies 1, 2 and 3 are displayed in blue, orange and yellow colors, respectively.

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Contribution to included manuscripts and publications

Study 1:

Effect of land-use and elevation on microbial biomass and water extractable carbon in soils of Mt. Kilimanjaro ecosystems

Authors	Contribution	
Holger Pabst	87%	Experimental design, field sampling, data preparation and analysis, preparation of manuscript
Anna Kühnel	3%	Provision of bulk density data, suggestions to improve manuscript
Yakov Kuzyakov	10%	Discussions on the results, suggestions to improve manuscript

Status at date of thesis submission:
published in Applied Soil Ecology
DOI: 10.1016/j.apsoil.2013.02.006 & 10.1016/j.apsoil.2014.03.002

Status at date of thesis printing:
published in Applied Soil Ecology
DOI: 10.1016/j.apsoil.2013.02.006 & 10.1016/j.apsoil.2014.03.002

Study 2:

Land use and precipitation affect organic and microbial carbon stocks and the specific metabolic quotient in soils of eleven ecosystems of Mt. Kilimanjaro, Tanzania

Authors	Contribution	
Holger Pabst	77.5%	Experimental design, field sampling, data preparation and analysis, preparation of manuscript
Friederike Gerschlauer	10%	Field sampling soil cores, provision of CO2 data, discussions on the results, suggestions to improve manuscript
Ralf Kiese	5%	Discussions on the results, suggestions to improve manuscript
Yakov Kuzyakov	7.5%	Discussions on the results, suggestions to improve manuscript

Status at date of thesis submission:
submitted to Land Degradation & Development, 13.07.2014
reference number LDD-14-0207

Status of date of thesis printing:
accepted for publication in Land Degradation & Development, 01.06.2014

Study 3:

Microbial biomass in savannah soils at Mt. Kilimanjaro – Vis-NIR DRS and spatial analysis		
Authors	Contribution	
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Holger Pabst	44.5%	Field sampling, microbial biomass, data preparation and analysis, preparation of manuscript
Christina Bogner	5%	Data evaluation, suggestions to improve manuscript
Yakov Kuzyakov	3%	Discussions on the results, suggestions to improve manuscript
Bernd Huwe	3%	Field sampling, Discussions on the results, suggestions to improve manuscript

Status at date of thesis submission:
submitted to European Journal of Soil Science

Status at date of thesis printing:
in preparation, to be submitted to an open-access journal with a fitting scope

Study 1

Effect of land-use and elevation on microbial biomass and water extractable carbon in soils of Mt. Kilimanjaro ecosystems

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published in Applied Soil Ecology (http://www.journals.elsevier.com/applied-soil-ecology/) as

Pabst, H., Kühnel, A., Kuzyakov, Y., 2013. Effect of land-use and elevation on microbial biomass and water extractable carbon in soils of Mt. Kilimanjaro ecosystems. Appl. Soil Ecol. 67, 10–19,
DOI: http://dx.doi.org/10.1016/j.apsoil.2013.02.006

and

Pabst, H., Kühnel, A., Kuzyakov, Y., 2014. Erratum. Appl. Soil Ecol. 77, 80-81,
DOI: http://dx.doi.org/10.1016/j.apsoil.2014.03.002

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Abstract

Microbial biomass carbon (MBC) and water-extractable organic carbon (WOC) – as sensitive and important parameters for soil fertility and C turnover – are strongly affected by land-use changes all over the world. These effects are particularly distinct upon conversion of natural to agricultural ecosystems due to very fast carbon (C) and nutrient cycles and high vulnerability, especially in the tropics. The objective of this study was to use the unique advantage of Mt. Kilimanjaro – altitudinal gradient leading to different tropical ecosystems but developed all on the same soil parent material – to investigate the effects of land-use change and elevation on MBC and WOC contents during a transition phase from dry to wet season. Down to a soil depth of 50 cm, we compared MBC and WOC contents of 2 natural (*Ocotea* and *Podocarpus* forest), 3 seminatural (lower montane forest, grassland, savannah), 1 sustainably used (homegarden) and 2 intensively used (maize field, coffee plantation) ecosystems on an elevation gradient from 950 to 2850 m a.s.l. Independent of land-use, both MBC and WOC strongly increased with elevation on Mt. Kilimanjaro corresponding to ecosystem productivity and biodiversity. Through the agricultural use of ecosystems MBC and WOC contents decreased – especially in surface layers – on average by 765 mg kg^{-1} for MBC and 916 mg kg^{-1} for WOC, compared to the respective natural ecosystems. The decrease with depth was highest for forests > grasslands > agroecosystems and also was positively correlated with elevation. We conclude that MBC and WOC contents in soils of Mt. Kilimanjaro ecosystems are highly sensitive to land-use changes, especially in topsoil. The MBC and WOC contents were considerably reduced even in sustainable agricultural systems. Since MBC and WOC are very fast reacting and sensitive C pools, we expect a decrease in other soil C pools accompanied by a strong decrease in fertility and productivity due to changes in land use from natural to agricultural ecosystems.

Keywords: Microbial carbon dynamics, elevation gradient, tropical ecosystems, water-extractable carbon, land-use changes, Andosol

Introduction

Land-use and climate change, habitat destruction as well as other human perturbations strongly alter natural ecosystems. Understanding these responses is crucial to forecast the sustainability of environmental services. Tropical ecosystems are known for high biodiversity and for important effects on global climate and biogeochemical cycles, especially on C turnover and sequestration (Detwiler and Hall, 1988; Gascon et al., 1999; Katovai et al., 2012; Malhi and Phillips, 2004). Due to faster transformation processes during litter decomposition, tropical soils have higher turnover rates than soils in colder climates (Zech et al., 1997). Therefore, tropical ecosystems are in special focus in recent studies concerning anthropogenic disturbances and C budgets (Don et al., 2011; Houghton and Goodale, 2004). Conversion from natural to agricultural ecosystems led to an average decrease in C stocks of 25-30% (Don et al., 2011; Houghton and Goodale, 2004). Organic carbon contents in both moist and dry soils in tropical ecosystems are especially altered by land-use change (Ogle et al., 2005).

Several studies have been conducted on soil microbial biomass in tropical ecosystems. For example, Sanginga et al. (1992) described the importance of soil microorganisms for sustainability of agricultural soils in tropical ecosystems. Management practices, such as tillage, also influence soil microbial activity (Calderón et al., 2000). Singh and Yadava (2006) investigated the dynamic of microbial biomass in soils in north-east India and found a decrease of 16% in microbial biomass within four years after the conversion from grassland into an agroecosystem.

The increasing demand for agricultural land directly accelerates deforestation and a decrease of up to 75% in both soil organic carbon C and microbial biomass was recorded for the conversion from forest to agricultural ecosystems (Lemenih et al., 2005; Houghton and Goodale, 2004; Waldrop et al., 2000). Although deforestation is a common practice for the conversion of natural to agricultural managed land-use systems, afforestation has become a much discussed topic in recent years. In a few years after abandoning agriculture, soil microbial biomass contents are nearly as high as in the natural forests (Maithani et al., 1996; Templer et al., 2005). Consequently, microbial biomass is a sensitive C (and N) pool responding to land-use changes much faster than total organic matter and the most other C pools in soils (Hu et al., 1997; Powlson et al., 1987; Trumbore et al., 1996).

Most studies on land-use change effects on tropical ecosystems were conducted on the Southern American or Asian continent. Processes, nutrient stocks and biological diversity during land-use change in the tropical part of Africa remain widely unknown. This is despite the fact that East Africa's forest area has an annual decrease rate of 1.01% (2000-2010) (FAO, 2011), which is amongst the highest in the world. Due to its unique topographical conditions as an isolated high mountain, Mt. Kilimanjaro offers outstanding potential to investigate land-use changes in African tropical habitats along an elevation gradient. This reflects with at least two facts. First, tropical ecosystems from dry savannah to montane rainforest are present at different elevations of Mt. Kilimanjaro (Hemp, 2006a). Second, most soils originated from similar parent material (volcanic ash) and have similar age (<400 ky) (Schrumpf, 2004). Consequently, according to the soil forming factors concept (Jenny, 1994), the main differences in soil properties are connected with climate and vegetation (which is a function of climate) as well as land-use. Dry and rainy seasons are two extrema in tropical ecosystems which have a major influence on productivity, nutrient cycling and microbial biomass. Several studies report seasonal variability of microbial biomass, but depending on ecosystem, the highest contents of soil microbial biomass were found in both, dry (Maithani et al., 1996; Montaño et al., 2007) and wet seasons (Devi and Yadava, 2006). This was mostly explained by the general effect of soil moisture on microbial biomass (Wardle and Parkinson, 1990). Nonetheless, the processes and dynamics during the transition seasons remain mostly unknown. Eaton (2001) detected a fast and significant effect of wet-to-dry and dry-to-wet transitions on microbial activity and nutrient cycling in Belize, Central America. Apparently, no attempt has been made to investigate the soil microbial properties during a climatic transition phase in Eastern Africa.

The occurrence of each, two pronounced dry and wet seasons, contributes to the high soil fertility in the Kilimanjaro region. Kaihura et al. (1999) found higher SOC contents and nutrient use efficiency in Kilimanjaro soils compared to other regions in Tanzania. Investigations of the montane rainforest of Mt. Kilimanjaro by Schrumpf et al. (2006; 2007) showed low inputs of nutrients through rainfall and due to the combination of low nutrient availability and high plant uptake, small to no losses of base cations by leaching were assumed. Despite the studies above, little is known about the biogeochemical – especially the microbial – properties of the soils of Africa's highest mountain.

Today, 1.4 Mio. people inhabit the Kilimanjaro region, with 79% of them living in rural areas (103 persons km^{-2}) (National Bureau of Statistics, 2006). This has a strong influence on the ecosystems, including land-use change due to a higher demand of agricultural land, anthropogenically induced fires, illegal logging and the introduction of new plant species through tourism (Hemp, 2008, 2009; Lambrechts et al., 2002; Soini, 2005; Torbick et al., 2009). The agricultural productivity in the East African region varies enormously during the year and is strongly affected by climatic change (Thornton et al., 2009). Due to the slow plant growth and nutrient uptake during dry seasons, the reported high amounts of microbial biomass retain nutrients (Singh et al., 1989). In the rainy seasons fast plant growth and root activity as well as drastic changes in soil moisture stimulate fast turnover of microbes (Fierer and Schimel, 2003). This leads to lower microbial biomass contents and increasing CO_2 efflux rates (Otieno et al., 2010; Singh et al., 1989; Sugihara et al., 2010). Hence, it is assumed that in tropical ecosystems with a bimodal climatic pattern soil microbes represent both a sink and source of nutrients (Srivastava, 1992).

We therefore used the advantages of Mt. Kilimanjaro to simultaneously observe several natural and anthropogenically affected ecosystems. In the present study we analyzed microbial biomass carbon (MBC) and water extractable organic carbon (WOC) in eight ecosystems at increasing altitudes on Mt. Kilimanjaro on a monthly basis during the transition phase from March to May (dry-to-wet). We assumed that the increasing precipitation during the transition from dry to wet season affects soil microbial biomass.

This study focused on three hypotheses: (1) land-use changes from natural to agricultural ecosystems strongly affect the contents of MBC and WOC. (2) Temporal changes of MBC and WOC contents during the transition phase from dry-to-wet season are affected by elevation as the temperature and precipitation patterns change with altitude. (3) Stronger changes in MBC and WOC during the transition from dry to wet seasons are expected in the topsoil as compared to deeper soil layers.

Our objectives within this study at Mt. Kilimanjaro were (1) to assess the dynamics of soil MBC and WOC during the transition from dry to wet season; (2) to assess the effect of land-use on soil microbial biomass and WOC; and (3) to obtain an overview of the effect of altitude and climate on soil microbial biomass and WOC.

Materials and methods

Study area

This study was conducted at the southern slopes of Mt. Kilimanjaro (3°4'33"S 37°21'12"E), located in the northeastern region of Tanzania. Soil sampling was performed in the Machame area of Kilimanjaro National Park, as well as in the southern areas Kibosho and Kilema and in the southeastern region of Lake Chala from March to May 2012. This time period of three months marked the transition period from dry to wet season. Eight sites in eight different natural and anthropogenically affected ecosystems were investigated, i.e., savannah, Chagga homegardens, coffee plantation, maize field, grassland, lower montane forest, *Ocotea* forest and *Podocarpus* forest. The elevation of the investigation sites varied between 950 m and 2850 m above sea level (Table 1). The respective vegetation was described in detail by Axmacher (2003) and Hemp (2006a,b,c) and approximations for net primary production (NPP) in tropical ecosystems were presented by Clark et al. (2001) and Schuur (2003). The investigated sites were classified in land-use classes, i.e. natural, seminatural, sustainably and intensively used (Table 1). Natural ecosystems did not show considerable disturbances, whereas seminatural plots were altered through collection of firewood and occasional mowing. Intensively used ecosystems were characterized by mechanical cultivation, the use of pesticides and relatively frequent fertilization. Fernandes et al. (1985), Fernandes and Nair (1986) and Hemp (2006b) described the sustainably used agroecosystem referred to as homegarden, which mostly developed through anthropogenic influence on the lower montane forests of Mt. Kilimanjaro. To satisfy the demand of building material, firewood and farmland, lower montane forests are often also converted to grasslands which subsequently could be used to establish coffee plantations. The rising demand for farmland leads also to the clear cutting of Acacia trees in the savannah and to ground suitable for maize cultivation. Soils from the Kilimanjaro area are described as Andosols and the pH of the investigated ecosystems was between 3.5 and 5.8 (Table 1). The bulk density and soil organic carbon contents in the surface layer were in the range of 0.26–1.21 g cm^{-3} and 14.54–214.57 mg g^{-1}, respectively (Table 1). Using the climate classification system of Köppen–Geiger, the Mt. Kilimanjaro region is characterized by a seasonal tropical wet and dry climate (Hess and McKnight, 2011; Peel et al., 2007) and an equatorial rainfall regime with rainy seasons from March to May and around November (Hemp, 2006a; Sarmiento, 1986). The annual precipitation in the research areas is strongly

Table 1: Land-use, abiotic and physico-chemical properties of the investigated ecosystems on the southern slope of Mt. Kilimanjaro at 0-10 cm depth*

Ecosystem	Elevation (m a.s.l.)	Precipitation[a] (mm yr^{-1})	Temperature[b] (°C)	Land-use type
Podocarpus forest	2850	1250	10.5	natural
Ocotea forest	2120	1850	14.0	natural
Forest lower montane	1920	1800	15.5	semi-natural
Grassland	1660	1650	16.5	semi-natural
Coffee plantation	1300	1250	19.0	agricultural
Homegarden	1260	1200	19.0	sustainably used
Maize field	1020	775	20.5	agricultural
Savannah	950	770	21.0	semi-natural

Ecosystem	pH (1:2.5 KCl)	Organic C (mg g^{-1})	Total N (mg g^{-1})	C/N	Bulk density (g cm^{-3})
Podocarpus forest	3.83	205.91	10.01	20.56	0.26 ± 0.03
Ocotea forest	3.49	214.57	12.37	17.35	0.26 ± 0.03
Forest lower montane	4.34	134.84	9.22	14.63	0.34 ± 0.09
Grassland	4.59	148.56	10.05	14.79	0.51 ± 0.01
Coffee plantation	4.28	18.89	1.85	10.24	1.02 ± 0.06
Homegarden	5.79	32.05	2.78	11.55	0.77 ± 0.04
Maize field	4.56	14.54	1.25	11.67	1.21 ± 0.03
Savannah	5.38	27.53	1.99	13.84	0.83 ± 0.05

[a] From Røhr and Killingtveit (2003)
[b] From Hemp (2006a)
* Table was adapted to fit page width

dependent on elevation (Basist et al., 1994) and differs between 700 and 2000 mm, with a maximum at an altitude of approximately 2100–2200 m (Hemp, 2006a; Røhr and Killingtveit, 2003). The mean annual temperature of the investigation sites varied between 10 and 21°C (Table 1).

Soil sampling

Soils of natural, semi-natural and anthropologically changed ecosystems were sampled on a monthly basis in March, April and May 2012 – during the transition phase from dry to wet season. Within the exploratory design of this study, one slope-parallel experimental plot of 50 m × 50 m was established in each of the ecosystems and to retrieve the exact position at a later sampling, ground nails (length: 0.5 m) were used to mark the corners. Using a soil auger (2 cm diameter × 60 cm depth), samples were taken in four corners and in the center of each plot, giving a total of five positions per sampling. For the May sampling of grassland and savannah soils, only four positions were used, since at that the same time vegetation was recorded (Hemp, unpublished) and the middle position could not be accessed. To obtain composite samples per depth and position, four augers were taken per position, subdivided into depths of 0–10, 10–20, 20–30 and 30–50 cm and mixed, respectively. At one sampling this lead to a total of 20 samples per ecosystem and to 472 samples overall. Since the O horizon in montane rainforests is often densely rooted (Schrumpf, 2004), only the litter layer was removed. After removing visible plant debris, replicates were sieved through a 2-mm mesh screen and stored under field moist conditions at 4–6°C until analysis.

Soil analysis

All samples were analyzed for microbial biomass carbon (MBC), water extractable organic carbon (WOC) and soil moisture. The concentration of inorganic carbon in the investigated soils is negligible and consequently no correction was conducted. MBC was analyzed by the fumgation–extraction method (Vance et al., 1987). Summarily, ethanol-free $CHCl_3$ was used to fumigate 7 - 8 g of each field-moist soil sample for 24 h in an exsiccator at room temperature. After fumigation, $CHCl_3$ was removed and soluble C from fumigated and non-fumigated samples was extracted with 60 ml of 0.5 M K_2SO_4 by shaking on an orbital shaker (60 min, 120 rotations min^{-1}). C content in K_2SO_4 extracts from respective soil samples without $CHCl_3$ fumigation was accepted as WOC (Beck et al., 1997; Blagodatskaya et al., 2009). Soluted organic C in fumigated and non-fumigated extracts was determined. Since not all of the soil carbon can be extracted by K_2SO_4, a k_{EC} factor of 0.45 (Joergensen, 1996) was used to convert microbial C flush (difference between extractable C from fumigated and non-fumigated samples) into MBC.

Statistical analysis

The investigated ecosystems are affected differently by the start of the wet season, which is due to the fact that the independent variable of sampling date in this study represents a change in climatic conditions, which on the other hand varies with topographic location. Therefore, temporal changes in MBC, WOC and soil water contents were detected using ANOVA for each ecosystem, respectively. Using data from all three samplings, a second ANOVA was calculated to detect the effects of ecosystems (vegetation) and soil depth on MBC and WOC. For the investigation of land-use changes, pairs of semi-natural and its respective anthropogenically used ecosystem were compared by using another, third, ANOVA. All ANOVAs were coupled with Bonferroni outlier and Tukey's post hoc tests. All statistical analyzes were performed with R v2.15.1. All results expressed in the text for MBC and WOC are on a dry-weight basis as the mean over sampling dates ± standard deviation.

Results

Microbial biomass carbon

Microbial biomass carbon (MBC) varied between sampling dates (Supplementary Table 1) and also between investigation sites and soil depth (Supplementary Table 2). It correlated positively with altitude and therefore was generally higher in the upper ecosystems (Fig. 1). The highest portion of MBC in the 0-10 cm layer were observed in Podocarpus forest, 2850 m a.s.l. (4440 ± 416 mg kg^{-1}), and the lowest values (179 ± 53 mg kg^{-1}) were under the maize field, 1009 m a.s.l. (Fig. 2).

The investigated ecosystems homegarden, lower montane forest, maize field and savannah showed significantly lower ($p < .05$) microbial C contents in the wet (May 2012) compared to dry season (March 2012). Contrary to the before mentioned ecosystems, the higher altitude ecosystems of *Ocotea* and *Podocarpus* forest showed significant ($p < .05$) differences between April and May, but not between March and May. This temporal effect was bigger on lower plots (e.g. savannah) than in ecosystems at high elevation (e.g. *Ocotea* forest), probably because of the lesser contrast between dry and wet season. For the grassland and coffee plantation the portion of microbial C in soil did not vary noticeably between sampling dates ($p > .05$).

The ANOVA, comparing all ecosystems during the whole three-month sampling campaign, showed significant differences ($p < .01$) in MBC contents (Supplementary Table 2). Based on pairwise comparisons of the Tukey HSD-test, *Podocarpus* forest, *Ocotea* forest and homegarden were different from any other investigated ecosystem. Based on the same ANOVA, the remaining ecosystems could be categorized into intrinsically indistinguishable groups, such as grassland and lower montane forest as well as coffee plantation, maize field and savannah.

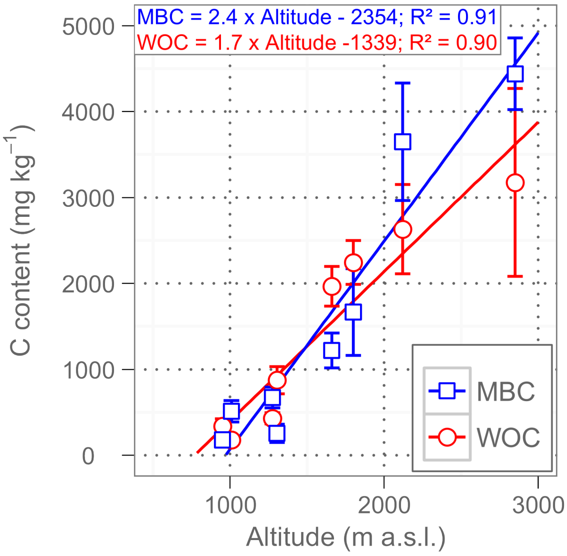

Fig. 1. Regression between altitude and MBC (squares, blue) or WOC (circles, red) in the 0–10 cm layer of soils at the southern slope of Mt. Kilimanjaro. Displayed values are means of the three-month sampling campaign. Standard errors are shown as vertical bars. (For interpretation of the references to color in this artwork, the reader is referred to the web version of the article.)

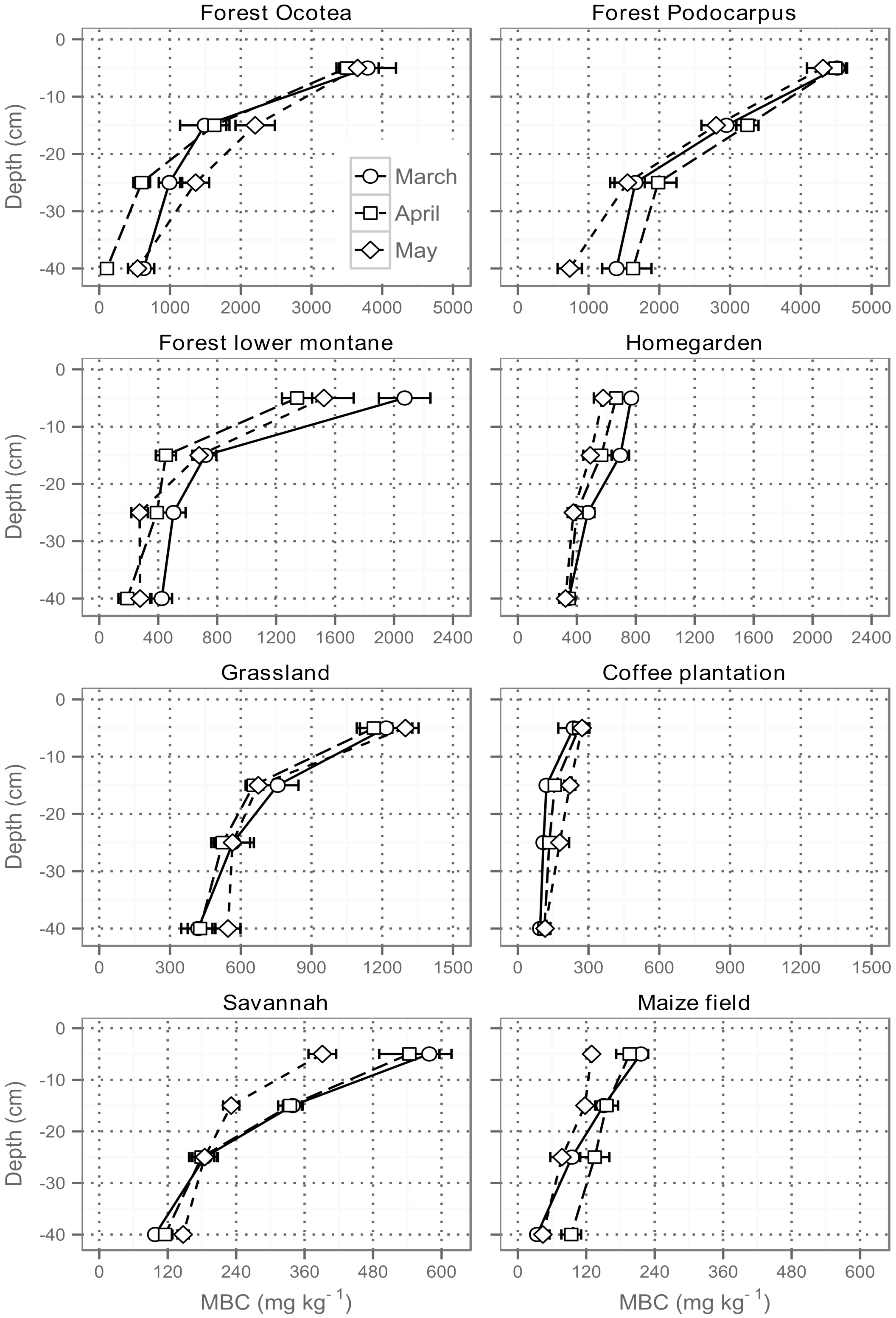

Fig. 2. MBC in Mt. Kilimanjaro ecosystems depending on soil depth and sampling date. *Ocotea* and *Podocarpus* forests represent natural ecosystems without a corresponding agroecosystem. Left-hand side semi-natural ecosystems (lower montane forest, grassland and savannah) are compared with the respective right-hand side agriculturally used ecosystems (homegarden, coffee plantation and maize field). Standard errors as black lines. Note different X scales for ecosystems at different elevation.

As expected, land-use had a strong effect on the MBC. This was revealed by analysis of factor-related variance (Supplementary Table 3). The MBC contents ($p < .01$) were much higher in all semi-natural compared to the respective anthropogenically used ecosystems, whereas the highest decrease was observed in the surface soil layer (Fig. 2). In the upper 10 cm, the semi-natural ecosystems lower montane forest and savannah (1668 ± 506 mg kg^{-1} and 512 ± 125 mg kg^{-1}) contained 2.5-fold higher portions of MBC than the agriculturally used ecosystems homegarden and maize field (672 ± 121 mg kg^{-1} and 179 ± 53 mg kg^{-1}). In contrast, MBC in grassland at 0–10 cm (1221 ± 203 mg kg^{-1}) is 5–fold higher than in the corresponding coffee plantation (256 ± 107 mg kg^{-1}). Except for the coffee plantation, a significant decrease in the microbial C content with increasing depth was observed and ratios of contents found in the 0–10 cm to 30–50 cm layer showed clear contrasts between the semi-natural and anthropogenically used ecosystems. The natural ecosystem *Ocotea* forest showed the strongest negative trend with depth from 3648 ± 684 mg kg^{-1} at 0–10 cm to 426 ± 360 mg kg^{-1} at 30–50 cm, whereas the smallest decrease of microbial C content with depth was found at the sustainably used homegarden site (672 ± 121 mg kg^{-1} at 0–10 cm to 339 ± 83 mg kg^{-1} at 30–50 cm).

Water extractable organic carbon (WOC)

Significant differences of WOC contents were discovered between investigation sites and soil depth (Supplementary Table 2) and also between sampling dates (Supplementary Table 1). In six of the eight investigated ecosystems the water extractable organic C was several-fold higher than the respective portion of MBC. Likewise to MBC, WOC followed a linear increase with altitude, although this trend with elevation was less distinct than for MCB (Fig. 1). WOC contents were the smallest at low altitudes receiving lowest precipitation, e.g. savannah (180 ± 29 mg kg^{-1}, 951 m a.s.l.), and highest (3175 ± 1094 mg kg^{-1}) in the *Podocarpus* forest (2850 m a.s.l.) (Fig. 3). In the ecosystems *Ocotea* forest, homegarden, coffee plantation and savannah, WOC levels were highest at the second sampling (April 2012), indicating dissolution of organic C and eventually redistribution within the soil profile with start of the wet season. For these ecosystems

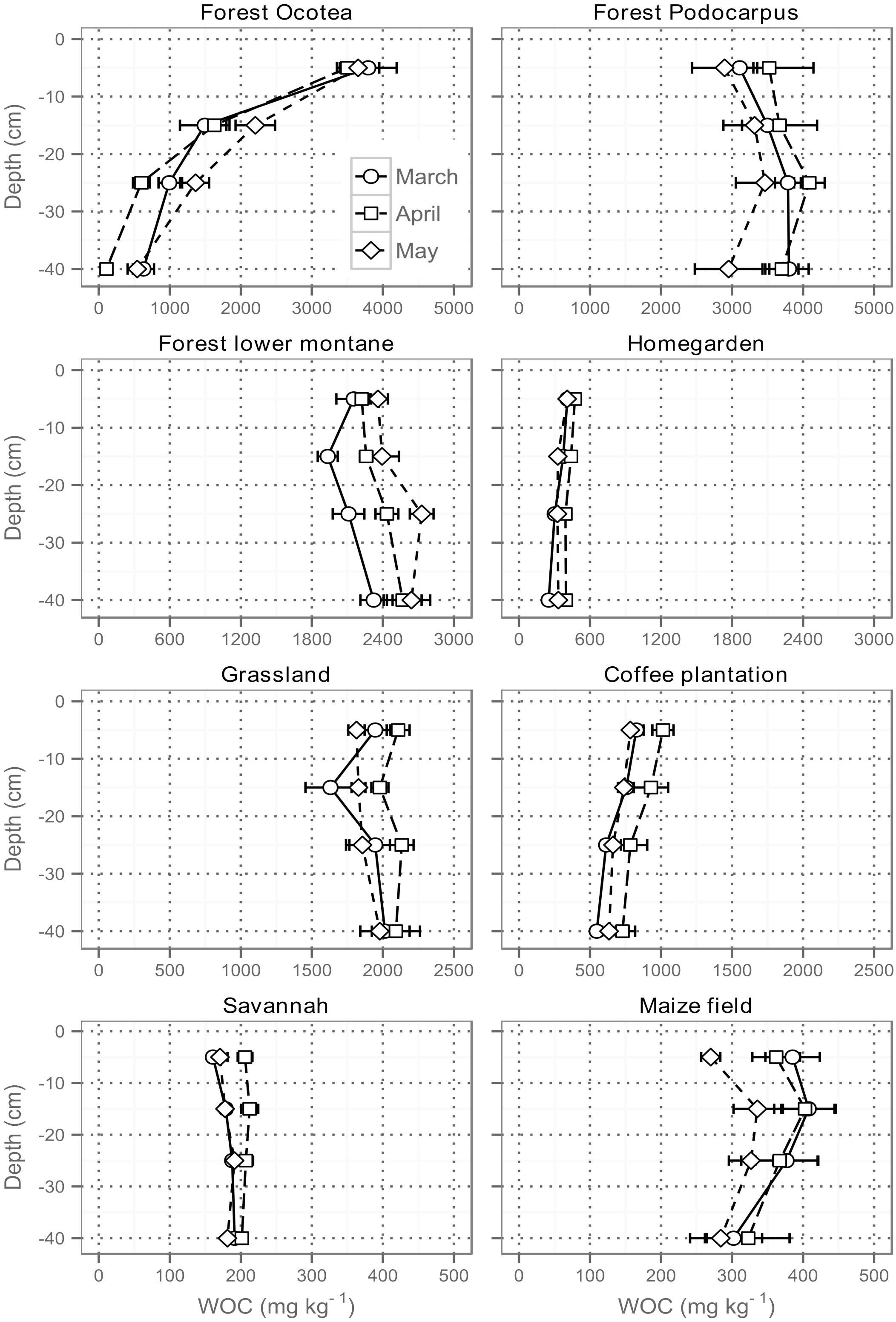

Fig. 3. WOC contents in Mt. Kilimanjaro ecosystems depending on soil depth and sampling date. *Ocotea* and *Podocarpus* forests represent natural ecosystems without a corresponding agroecosystem. Left-hand side semi-natural ecosystems (lower montane forest, grassland and savannah) are compared with the respective right-hand sideagriculturally used ecosystems (homegarden, coffee plantation and maize field). Standard errors as black lines. Note different X scales for ecosystems at different elevation.

a comparison with other sampling dates revealed a specific WOC dynamic (Fig. 3): from March to April 2012, WOC increased ($p < .05$), followed by a subsequent decrease ($p < .05$) with ongoing rains (May 2012). This pattern was more distinct in low-elevation ecosystems. Lower montane forest had its highest WOC level in May 2012 and its lowest in March 2012 – whereas significant differences ($p < .05$) could only be observed regarding March but not April and May. *Podocarpus* forest, grassland and maize field showed no significant temporal changes in WOC contents.

In contrast to MBC, for WOC the pairwise comparisons of ecosystems revealed only one intrinsically indistinguishable group ($p > .05$) – this group consisted of maize field, homegarden and savannah. All other ecosystems showed no similarities to any other investigated ecosystem.

Both, the variation of WOC with soil depth and total contents of water-extractable organic C in the semi-natural and agricultural ecosystems were influenced by land-use. Similar to MBC, significantly higher portions of WOC ($p < .05$) were found in semi-natural ecosystems of lower montane forest and grassland (2245 ± 257 mg kg^{-1} and 1966 ± 232 mg kg^{-1} in the 0-10 cm layer), whereas the corresponding

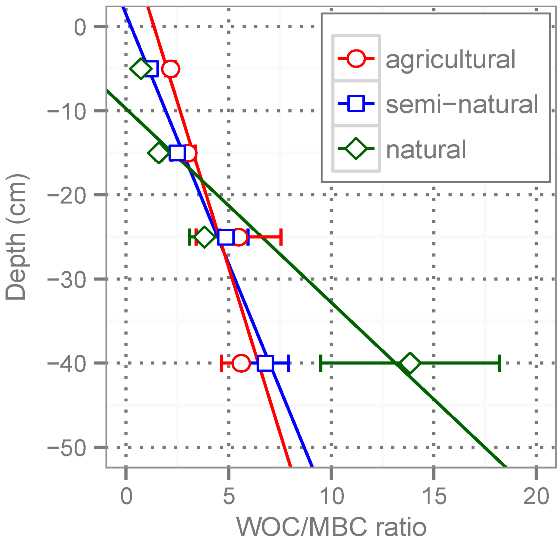

Fig. 4. WOC/MBC ratio in agriculturally used (circles, red, $R^2 = 0.77$), semi-natural (squares, blue, $R^2 = 0.98$) and natural (diamonds, green, $R^2 = 0.80$) ecosystems. Agricultural ecosystems represent homegarden, coffee plantation and maize field, whereas semi-natural stands for lower montane forest, grassland and savannah, *Podocarpus* and *Ocotea* forest are indicated as natural. Means over all three sampling dates, standard errors as horizontal bars. (For interpretation of the references to color in this artwork, the reader is referred to the web version of the article.)

agriculturally used homegarden and coffee plantation were strongly depleted in WOC (430 ± 66 mg kg^{-1} and 875 ± 160 mg kg^{-1} in the 0-10 cm layer). In contrast, the maize field exhibited higher WOC contents (339 ± 87 mg kg^{-1}) than its respective natural ecosystem of savannah (180 ± 29 mg kg^{-1}) (Fig. 3). The ratio of WOC contents in semi-natural and agroecosystems increased with elevation from ~ 0.5 at the savannah/maize field, over ~ 2 at the grassland/coffee plantation, to ~ 5 at the lower montane forest/homegarden. In contrast to the negative MBC trend with depth, no significant decrease could be observed for WOC contents – except for the coffee plantation and homegarden site (data not shown).

Soil water content

The effect of temporal change in precipitation and temperature on soil water content was investigated and varied in all of the investigated ecosystems during the three-month sampling campaign (Supplementary Table 1). Four ecosystems (savannah, maize field, coffee plantation, grassland) showed significantly increasing ($p < .05$) soil water contents between March and April as well as April and May 2012. Lower montane and *Podocarpus* forest showed increases, which were significant ($p < 0.05$) between April and May 2012 but not between March and April. For the above mentioned six ecosystems, soil water contents were positively correlated with elevation and ranged between 3.2–13.2%, 5.4–14.7% and 7.5–18.8%, for the three months respectively. Surprisingly, the homegarden and *Ocotea* forest sites exhibited different temporal regimes of soil water contents, whereas all changes were significantly different ($p < .05$). For the high-altitude *Ocotea* forest, soil water contents decreased from initially 15.9 ± 2.6% to 9.9 ± 1.9% and increased back to 18.7 ± 2.7%. Soil water contents in the homegarden on the other hand, strongly increased from 6.4 ± 0.9% to 17.1 ± 2.4% and decreased to 13.5 ± 2.7%. Some differences in soil water depth distributions were discovered, but not further investigated since this was not part of this study.

Discussion

Effect of elevation

Elevation was one of the two main factors affecting MBC and WOC. Both parameters and SOC (which is source of both, MBC and WOC) strongly increased with elevation in (semi-)natural and anthropogenically affected ecosystems. Schrumpf (2004) reported high contents of C in organic (O) horizons as well as densely rooted humus layers in the montane rainforests at Mt. Kilimanjaro, which correlates with this study (Table 1). Depending on changing altitudes from 100 to 2700 m in Costa Rica, an increasing litter layer is combined with a decreasing amount of annual litter fall (Heaney and Proctor, 1989). Moreover, the decrease in temperature with increasing altitude has a strong effect on soil microbial biomass. In a study by Blume et al. (2002), hot summer temperatures increased microbial activity by more than 80%. They also postulated that low temperature seasons negatively affect the metabolism of soil microorganisms but not the content of MBC. In addition, the productivity of tropical montane cloud forests, which is connected to the activity of soil microbial biomass, is known to be lower than in lowland tropical rainforests (Bruijnzeel and Veneklaas, 1998). Therefore, the very high contents of MBC and WOC we found in the surface layer of the high-altitude *Podocarpus* forest ecosystem (Figs. 2 and 3) are very likely due to the high availability of substrate coming with above- and below-ground litter input. Based on the vegetation records of Hemp (2006a) and the already mentioned effects of altitude on annual litter fall and productivity (Clark et al., 2001), we further assume a decrease of MBC and WOC in the higher sub-alpine heathland and lower alpine zone of Mt. Kilimanjaro. In the subnival zone of the Peruvian Andes at 5000 m a.s.l., portion of MBC decreased to 200–250 mg kg^{-1}, because of a strong decrease in productivity and partial absence of vegetation due to the extreme climatic and abiotic conditions (King et al., 2008).

Effect of land-use

Confirming our hypothesis that human-induced land-use change strongly decreases MBC and WOC, the investigated semi-natural ecosystems had on average 3-fold higher contents of MBC and WOC and 4-fold higher contents of SOC in the 0–10 cm layer than their respective agroecosystems. A decline in SOC after deforestation and cultivation also reduces MBC and DOC (Dinesh et al., 2003). Several land-use change types in the tropics and their SOC losses were reviewed by Don et al. (2011). They reported SOC losses from primary forest to cropland or perennial crops (–25% and –30%, respectively) and grassland to cropland (–10%). The same land-use changes occur at Mt. Kilimanjaro, e.g. lower montane forest to homegarden and grassland to coffee plantation. These losses of relative SOC reviewed by Don et al. (2011) are several-fold smaller than SOC losses in the investigated Mt. Kilimanjaro ecosystems (in the 0-10 cm layer; –76% and –87%, respectively). But in the southern highlands of Ethiopia at an elevation of 2100 m a.s.l., similar high decrease in SOC were observed after deforestation (Lemenih et al., 2005). The MBC and WOC contents on the other hand, decreased by 57% and 79%, which equals the values reported by Waldrop et al. (2000). Based on the assumptions of Clark et al. (2001) and Schuur (2003), at 2100 m a.s.l. at Mt. Kilimanjaro the ecosystems with the highest net primary production (NPP) occur (lower montane and *Ocotea* forest). Due to the effect of elevation on ecosystem productivity, decomposition and climate, the more elevated forest ecosystems at Mt. Kilimanjaro have more soluble organics in soil (Bruijnzeel and Veneklaas 1998; Heaney and Proctor 1989). This is reflected in the increasing difference in WOC contents between semi-natural and agriculturally used ecosystems with higher elevations at Mt. Kilimanjaro. Therefore we concluded that SOC, MBC and WOC contents in this mountains' ecosystems with high NPP are more affected by land-use change than ecosystems with comparably low NPP. Conclusively, elevation, topography and climate indirectly influence the magnitude of the land-use change effect.

In mineral soils of tropical and temperate regions, dissolved organic C leaching from O horizons is an important substrate source for microbial biomass (Fujii et al., 2009). The investigated agroecosystems have presumably much lower C input by litter and consequently much less WOC since in coffee plantations as well as maize fields the available litter is normally removed. Hence, less WOC in the investigated agricultural ecosystems are due to the absence of the litter layer and O horizons. The very strong decrease in MBC after the mid-altitudinal conversion from grassland to coffee plantation probably reflects the intensive use of pesticides and herbicides for coffee production. In coffee plantations at Mt. Kilimanjaro plant debris is removed after pruning of coffee bushes, which results in a decrease of SOC and low availability of substrate for microbial decomposition. MBC under grassland and savannah ecosystems is mostly attributed to the dense root system of the grass cover (Fall et al., 2012; Blume et al., 2002). In the maize field, however, this permanent dense root system is missing and the above ground litter input is strongly reduced since the whole plant is harvested. As a result of the before mentioned, MBC in the 0-10 cm layer (Fig. 2) is reduced. In contrast, the higher WOC content in soil under maize vs. savannah (Fig. 3) is very likely due to organic animal manure, which is applied by local farmers. Tessier et al. (1998) found several-fold higher DOC contents throughout the soil profile on manure-treated compared to unfertilized sites. Accordingly, MBC and WOC contents are influenced not only by the land-use change itself, but also by agricultural management practices (Emmerling et al., 2001; Friedel et al., 1996).

Effect of depth

The highest contents of MBC and WOC were found in the 0–10 cm layer. This is common in most ecosystems because much of the organic input is localized on and close to the soil surface. In Senegal, MBC in a savannah ecosystem was most abundant close to the surface and near Acacia trees (Fall et al., 2012). According to Blume et al. (2002) the upper 0–20 cm in semiarid forest soils of Spain show a much higher microbial population than lower layers. For the humid subtropical climate in southern Brazil, Babujia et al. (2010) reported more MBC in surface than in subsoil samples – independent of management practice. In homegardens, the substrate input by plant residues such as roots and exudates decreases with depth, which is directly reflected by MBC contents (Wichern et al., 2003). Forest ecosystems feature the strongest decrease in SOC with depth, followed by grass- and shrublands (Jobbágy and Jackson, 2000). This agrees with the correlation between depth and SOC, MBC or DOC found in our study. Jobbágy and Jackson (2000) also reported that SOC contents are influenced by temperature and precipitation (which corresponds to elevation in our study), whereas this effect is bigger in the surface soil layers. In their review, higher precipitation and lower temperatures lead to a stronger decline of SOC with depth, which is reflected in shallower SOC distribution – the same was observed in our study for SOC, MBC and water-extractable organic C contents. On the other hand, it should be noticed that this effect is eventually more due to changing vegetation along precipitation gradients than the precipitation itself (Jobbágy and Jackson, 2000).

Due to the advanced stage of weathering of Mt. Kilimanjaro soils (Schrumpf, 2004), the mountain's ecosystems are especially prone to nutrient and C losses through leaching. Strong rains – which also occur at Mt. Kilimanjaro – favor leaching and litter decomposition because more precipitation leads to higher DOC contents (Salamanca et al., 2003). Like MCB, DOC normally decreases with depth (Babujia et al., 2010; Fall et al., 2012; Goberna et al., 2006). In all of the investigated ecosystems, no organic fertilizer was manually mixed into the soil; in maize fields, manuring is done solely by surface application. Nevertheless, we observed more or less equal contents of WOC in all soil depths down to 50 cm. In contrast to the upper soil layers, sorption at minerals but not microbial decomposition controls DOC dynamics in deeper horizons of tropical ecosystems (Schwendenmann and Veldkamp, 2005). This supports the assumption that abundant WOC at greater depths originates from litter or surface layer. The excess of dissolved organic C at the surface, translocated into deeper horizons, will be partly adsorbed at minerals and hence is less available for the decreasing contents of microbial biomass – especially in dry seasons with low soil water contents (Schwendenmann and Veldkamp, 2005). As the WOC/MBC ratios increase with depth (Fig. 4), substrate shortage cannot be a limiting factor for microbial growth at greater depths. Therefore, we assume the possibility of C leaching in the investigated, especially in the natural, ecosystems.

Effect of season

Our results on the season-transitional pattern of MBC (decreasing contents with start of the rains) are supported by Maithani et al. (1996) and Montaño et al. (2007). They found a similar MBC pattern between the wet and dry season in a wet subtropical forest in north-east India and a tropical deciduous forest in Mexico. Ecosystem productivity and soil CO_2 fluxes – which also reflect microbial activity – are closely linked to precipitation and therefore to soil moisture contents as well. A decline in soil water content during the dry season in a Kenyan savannah reduced CO_2 fluxes from soil and lowered biomass productivity (Otieno et al., 2010). Following re-wetting of soils at the beginning of the wet season, tropical rain forests often show higher CO_2 effluxes, mainly due to briefly increased microbial activity. During the ongoing wet season, high soil moisture contents lead to oxygen limitation, which may decrease the microbial activity and the CO_2 efflux rates from soil (Schwendenmann et al., 2003).

For a deciduous forest in north-east India, Devi and Yadava (2006), in contrast, reported the highest contents of MBC during the rainy season and the lowest contents during the dry winter period. In subtropical soils of China as well, more MBC was present in the hot-humid than in the cold-dry season (Iqbal et al., 2010). Based on their successional stage, primary and secondary forests in a seasonally dry tropical region of Mexico are variously affected by the increased precipitation during the wet season (Saynes et al., 2005). The vast range of results found in these studies implies that seasonal variability of MBC in tropical ecosystems is strongly influenced not only by climate, but also by soil type, land-use, vegetation and indirectly by topography.

During the three-month sampling campaign, WOC levels were highest in April 2012, indicating dissolving of C in soil water and relocation within the soil profile with the onset of the rains rather than in the wet season itself. The partly mineralized litter layer formed during the past dry season represents a source of soluble C: during strong rains at the beginning of the wet season, high contents of WOC leached downward.

Ecosystems located at lower elevation were more strongly affected by the increased rainfalls during the wet season than the Ocotea and Podocarpus forests at higher locations. In tropical montane ecosystems, seasonal variability in temperature and precipitation is low due to cloud cover, high humidity, frequency of fog and a more or less constant level of solar radiance throughout the year (Buytaert et al., 2011). Sarmiento (1986) described precipitation patterns in tropical high mountains, including rain belts. These rain belts have only slight climatic variability, and rainfalls occur in varying frequencies during the whole year. Additionally, the closed canopy cover in forest ecosystems provides further protection against inter-annual climatic variations and microclimatic extremes at the soil surface (Martius et al., 2004). This, and the fact that *Ocotea* and *Podocarpus* forest sites are located in the rain belt of Mt. Kilimanjaro, reduce the influence of increasing rains on the portions of MBC and WOC in soils. The result is an insignificant effect of the transition from dry to wet season on C contents in the forest ecosystems of Mt. Kilimanjaro.

Conclusions

At Mt. Kilimanjaro the effect of climatic changes during transition periods on MBC and WOC is more distinct in lower elevated than higher elevated ecosystems. From 900 to 2900 m a.s.l. and through different ecosystems, MBC and WOC contents in soils of Mt. Kilimanjaro increase linearly. The mountains ecosystems are strongly affected by land-use: especially in the upper soil layers, soil microbial biomass and water-extractable C are decreased approximately three times compared to semi-natural ecosystems. Additionally, the magnitudes of the land-use change induced differences in the C balance are further influenced depending on net primary production and agricultural management practice, as well as elevation, climate and topography of the ecosystems.

Acknowledgments

This study was funded by the German Research Foundation (DFG) within the Research-Unit 1246 (KiLi) and supported by the Tanzanian Commission for Science and Technology (COSTECH), the Tanzania Wildlife Research Institute (TAWIRI) and the Mount Kilimanjaro National Park (KINAPA). Additionally the authors want to thank Dr. Andreas Hemp for selection and preparation of the research plots as well as the local helpers Samuel Augustino, Ayubu Mtaturu and George Philipo and the laboratory technicians Karin Schmidt and Martina Gebauer.

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Supplementary Material

Supplementary Table 1: ANOVA results of sampling date / change in climate effect on MBC, water-extractable organic C and soil moisture contents. Compared were the three sampling periods March, April and May 2012.

Ecosystem	Variable	Df	SumSq	MeanSq	F value	Pr(>F)	
Podocarpus forest	MBC	2	2,559,033	1,279,517	4.642	0.015	*
	WOC	2	3,589,635	1,794,818	1.982	0.149	
	soil moisture	2	344	172	27.037	0.000	***
Ocotea forest	MBC	2	1,852,053	926,027	2.950	0.062	
	WOC	2	2,814,049	1,407,024	4.672	0.014	*
	soil moisture	2	806	403	75.470	0.000	***
Lower montane forest	MBC	2	1,419,211	709,605	11.665	0.000	***
	WOC	2	1,513,047	756,524	8.872	0.001	***
	soil moisture	2	72	36	5.852	0.005	**
Grassland	MBC	2	8,729	4,365	0.090	0.914	
	WOC	2	516,537	258,268	2.529	0.091	
	soil moisture	2	180	90	27.219	0.000	***
Coffee plantation	MBC	2	28,573	14,286	2.467	0.096	
	WOC	2	383,411	191,706	6.624	0.003	**
	soil moisture	2	170	85	28.259	0.000	***
Homegarden	MBC	2	168,427	84,213	6.795	0.003	**
	WOC	2	96,885	48,442	11.653	0.000	***
	soil moisture	2	1,180	590	103.411	0.000	***
Maize field	MBC	2	25,309	12,654	8.174	0.001	***
	WOC	2	51,017	25,508	2.496	0.093	
	soil moisture	2	189	94	75.279	0.000	***
Savannah	MBC	2	39,061	19,530	4.725	0.014	*
	WOC	2	8,943	4,472	13.222	0.000	***
	soil moisture	2	137	68	134.683	0.000	***

* significant at the $p < 0.05$ level
** significant at the $p < 0.01$ level
*** significant at the $p < 0.001$ level

Supplementary Table 2: Statistical ANOVA results of the effect of ecosystems, depth and the interaction ecosystem x depth on MBC and soluble organic C contents. Compared were MBC and soluble organic C contents in eight ecosystems at four depths, respectively.

Source	Variable	Df	SumSq	MeanSq	F value	Pr(>F)	
Ecosystem	MBC	7	294,853,170	42,121,881	530.48	0.000	***
	DOC	7	699,074,476	99,867,782	731.21	0.000	***
Depth	MBC	3	85,704,142	28,568,047	359.78	0.000	***
	DOC	3	3,363,901	1,121,300	8.21	0.000	***
Ecosystem x Depth	MBC	21	97,012,378	4,619,637	58.18	0.000	***
	DOC	21	14,370,011	684,286	5.01	0.000	***

*** significant at the $p < 0.001$ level

Supplementary Table 3: Statistical ANOVA results of the effect of land-use change on MBC and soluble organic C contents. Compared were MBC and soluble organic C contents in seminatural and the respective agroecosystem as well as the interaction of ecosystem and depth. The depth effect alone was not significant.

Source	Variable	Df	SumSq	MeanSq	F value	Pr(>F)	
Lower montane forest vs. homegarden							
Ecosystem	MBC	1	1,042,218	1,042,218	28.07	0.000	***
	DOC	1	115,190,822	115,190,822	2086.55	0.000	***
Ecosystem x Depth	MBC	3	4,523,330	1,507,777	40.61	0.000	***
	DOC	3	763,512	254,504	4.61	0.004	**
Grassland vs. coffee plantation							
Ecosystem	MBC	1	9,199,815	9,199,815	566.25	0.000	***
	DOC	1	41,558,090	41,558,090	639.84	0.000	***
Ecosystem x Depth	MBC	3	1,644,352	548,117	33.74	0.000	***
	DOC	3	711,418	237,139	3.65	0.015	*
Savannah vs. Maize field							
Ecosystem	MBC	1	713,935	713,935	171.02	0.000	***
	DOC	1	690,639	690,639	126.86	0.000	***
Ecosystem x Depth	MBC	3	304,727	101,576	24.33	0.000	***
	DOC	3	23,880	7,960	1.46	0.229	

* significant at the $p < 0.05$ level

** significant at the $p < 0.01$ level

*** significant at the $p < 0.001$ level

Study 2

Land use and precipitation affect organic and microbial carbon stocks and the specific metabolic quotient in soils of eleven ecosystems of Mt. Kilimanjaro, Tanzania

Short title: Land use and precipitation affect soil properties at Mt. Kilimanjaro

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accepted by Land Degradation and Development; 01.06.2015
(http://onlinelibrary.wiley.com/journal/10.1002/%28ISSN%291099-145X)

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Abstract

Tropical ecosystems are under increasing pressure of land-use changes, strongly affecting the carbon cycle. Conversion from natural to agricultural ecosystems is often accompanied by a decrease in the stocks of organic and microbial carbon (C_{org}, C_{mic}) as well as changes in microbial activity and litter decomposition. Eleven ecosystems along an elevation gradient on the slopes of Mt. Kilimanjaro were used to investigate impacts of land-use changes on C_{org} and C_{mic} stocks as well as the specific metabolic respiration quotient (q_sCO_2) in surface soils. Six natural, two semi-natural and three intensively used agricultural ecosystems were investigated on an elevation gradient from 950 to 3880 m a.s.l.. To estimate the effects of precipitation, rainfall regimes of 3.6 and 20.0 mm were simulated. C_{org} stocks were controlled by water availability, temperature and net primary production. Agricultural management resulted in decreases of C_{org} and C_{mic} stocks by 38% and 76%, respectively. In addition, agricultural systems were characterized by low C_{mic}:C_{org} ratios, indicating a decline in available substrate. Enhanced land-use intensity lead to increased q_sCO_2 (agricultural > semi-natural > natural). The traditional homegardens stood out as a sustainable land-use form with high substrate availability and microbial efficiency. Soil CO_2 efflux and q_sCO_2 generally increased with precipitation level. We conclude that soils of Mt. Kilimanjaro's ecosystems are highly sensitive to land-use changes and are vulnerable to changes in precipitation, especially at low elevations. Even though q_sCO_2 was measured under different water contents, it can be used as an indicator of ecosystem disturbances caused by land-use and management practices.

Keywords: land use; soil microbes; C_{mic}:C_{org}; soil respiration; elevation; precipitation

Introduction

Close relationships to and interactions with the atmosphere, biosphere, hydrosphere and lithosphere make soil is a very complex but central component of all ecosystems (Brevik et al., 2015). A particular focus on tropical ecosystems is justified since they have a crucial effect on the global climate. In surplus, tropical ecosystems take a central part in global C turnover and sequestration (Dixon et al., 1994; Melillo et al., 1993). Litter and soil organic matter are decomposed faster in tropical soils than in soils under colder climatic conditions and therefore higher C turnover rates and CO_2 efflux to the atmosphere are observed (Chambers et al., 2004; Zech et al., 1997).

Worldwide, the anthropogenic effect on soils and ecosystems is undeniable. Especially land-use change strongly affects composition and nexus in these complex systems and may – depending on the present type of land-use change and soil – lead to soil and land degradation (Bruun et al., 2013; de Souza Braz et al., 2013; Don et al., 2011). A frequently used conversion method is the burning of forests as nutrient rich ashes increase nutrient availability and soil pH during the first years after conversion (de Souza Braz et al., 2013). However, beside the evident change in plant diversity, extended time of land use, mismanagement and the repeated use of fire often leads to declines in C stocks, the loss of originally forest-derived C_{org}, changes in soil physical characteristics and increases the rate of land degradation (Bruun et al., 2013; de Souza Braz et al., 2013). In general, the conversion of natural habitats to agriculturally managed systems in the tropics and subtropics is accompanied by an average decrease in C_{org} stocks of 25-50% (Basu & Behera, 1993; Bruun et al., 2013; Don et al., 2011). Other studies showed that the conversion of natural forests to agriculturally used orchards may decrease water infiltration and aggregate stability, consequently enhancing the risk of soil erosion (Bravo-Espinosa et al., 2014; Cerdà et al., 2009). In combination with large doses of chemical fertilizers, the increased runoff may lead to a potential risk of eutrophication of water resources (Bravo-Espinosa et al., 2014).

Soil microbial biomass, being directly correlated with soil C_{org}, is a sensitive parameter for C_{org} turnover and soil fertility. After tropical forest conversion, Basu & Behera (1993) reported declines of 40-46% and 52-58% in C_{org} and C_{mic}, respectively.

Deforestation and cultivation decreases C_{mic}, mainly caused by a decline in the availability of organic substrates due to strongly reduced input of litter and rhizodeposits (Dinesh et al., 2003). These are crucial declines which have a major negative impact on soil fertility in tropical ecosystems (Sanginga et al., 1992). The ratio of C_{mic}:C_{org} in soils can be used as an eco-physiological parameter to evaluate these changes and indicates C_{org} available for microbial growth (Anderson, 2003).

Within the C cycle, soil CO_2 efflux is an important and major process which is directly linked to mineralization and is massively altered by land-use change (Don et al., 2011; Iqbal et al., 2010). Soil CO_2 efflux is strongly depending on precipitation as higher efflux rates are observed during the tropical wet season (Iqbal et al., 2010). Lower efflux during the dry season is often related to drought stress and associated to decrease of C mineralization (Abera, 2013).

As microbial parameters are sensitive to disturbance, the soil metabolic quotient (qCO_2, CO_2 efflux to microbial biomass ratio) was introduced as an indicator for ecosystem succession and microbial activity (Anderson & Domsch, 1993; Insam & Haselwandter, 1989). This ratio is related to the microbial energy demand. It therefore can be used as parameter of the efficiency of present microorganisms as well as their potential of C utilization (Anderson & Domsch, 1990; Wardle & Ghani, 1995). It is assumed that ongoing progressive succession of an ecosystem is accompanied with a decrease in qCO_2, as the microorganisms change to more efficient communities (Insam & Haselwandter, 1989), indicating an increased microbial stability of the system (Anderson & Domsch, 1993) and a shift from r- to K-strategists (Blagodatskaya et al., 2014). As described above, disturbances (e.g. land-use change) have negative impacts on soil microbial properties and therefore increase qCO_2. Crop fields in India exhibited approximately two times higher qCO_2 if compared with adjacent tropical forests (Basu & Behera, 1993), while Behera & Sahani (2003) reported three times higher qCO_2 in a *Eucalyptus* plantation compared to a dry tropical forest.

Considering that the United Nations predicted an enormous population growth in Africa until the year 2050 (United Nations, 2013), the demand for arable land will increase and Africa's natural ecosystems are consequently particularly threatened by land-use change to semi-natural as well as intensively used agricultural ecosystems.

The annual deforestation rate of the African forests is among the highest worldwide (FAO, 2011). However, most studies on the effects of land-use change in tropical ecosystems are conducted in Southern America and Asia, thus the affected soil processes, nutrient stocks and soil biology in tropical African ecosystems remain widely unknown.

The topography of Mt. Kilimanjaro as a high isolated mountain enabled development of various ecosystems depending on elevation and therefore climatic conditions. A bimodal rainfall pattern leads to dry and wet extremes – also affecting soil microbial processes. Mt. Kilimanjaro ecosystems range from hot-dry savannahs at the bottom of the mountain (~900 m a.s.l.) to the cold-wet alpine zone with *Helichrysum* cushion vegetation at approximately 4000 m a.s.l. and on elevations higher 4000 m a.s.l., no vegetation is present (Hemp, 2006). The area around Mt. Kilimanjaro is traditionally inhabited and cultivated by the Chagga tribe, but its ecosystems are threatened and altered by the increasing population. Thus, Mt. Kilimanjaro offers the possibility to investigate several tropical ecosystems under different climatic conditions as well as the alteration of these ecosystems by land-use change.

We hypothesized that: (1) intensive agriculture leads to decreased stocks of C_{org} and C_{mic} and reduces the efficiency of the microbial community (increases CO_2 efflux to C_{mic} ratio) and (2) the elevation and/or precipitation gradients affect C_{org}, C_{mic}, CO_2 efflux and their ratios.

We used the unique situation of Mt. Kilimanjaro to study surface soils of eleven natural and anthropogenically altered tropical ecosystems. Particularly our objectives were (1) to evaluate the effects of land-use changes on C_{org}, C_{mic} and qCO_2; and subsequently (2) to investigate the intensity of disturbances based on qCO_2 as well as (3) to determine the effects of increased precipitation on CO_2 efflux and qCO_2.

Materials and Methods

Study area

Mt. Kilimanjaro is situated in northeastern Tanzania (3°4'33''S; 37°21'12''E). This study was conducted on its southern slopes and the investigation sites were located between the Machame area in the West and the region of Lake Chala in the East. A total of eleven sites of natural and disturbed ecosystems were investigated, whereas

Table 1: Elevation, climatic conditions, land-use classes and disturbances of the ecosystems on the southern slope of Mt. Kilimanjaro

Ecosystem	ID	Elevation	MAP[a]	MAT[b]	de Martonne aridity index (A_{dM})
		(m a.s.l.)	(mm yr^{-1})	(°C)	
Helichrysum	HEL	3880	778	6.8	46.3
Erica forest	FER	3880	1188	6.8	70.7
Podocarpus forest disturbed	FPD	2990	1564	7.5	89.4
Podocarpus forest	FPO	2850	1773	9.0	93.3
Ocotea forest disturbed	FOD	2470	1526	13.6	64.7
Ocotea forest	FOC	2120	2998	15.6	117.1
Forest lower montane	FLM	1920	2378	17.9	85.2
Coffee plantation	COF	1300	1485	20.3	49.0
Homegarden	HOM	1260	1336	20.3	44.1
Maize field	MAI	1020	693	22.5	21.3
Savannah	SAV	950	536	22.3	16.6

Ecosystem	Land-use class	Current human-induced disturbances	Disturbance
Helichrysum	natural	no	
Erica forest	natural	no	
Podocarpus forest disturbed	natural	no	Fire; > 20 yr ago
Podocarpus forest	natural	no	
Ocotea forest disturbed	natural	no	Cutting, timber; > 20 yr ago
Ocotea forest	natural	no	
Forest lower montane	semi-natural	yes	Timber, firewood
Coffee plantation	agricultural	yes	Monoculture, pesticides, fertilizers, soil compaction
Homegarden	agricultural	yes	Crop rotation, hand hoe, organic fertilizer
Maize field	agricultural	yes	Monoculture, pesticides, fertilizers, soil erosion
Savannah	semi-natural	yes	Cutting, grazing, fire

[a] from Appelhans et al. (*Eco-climatic and land-cover characteristics across 12 land-cover types at Mt. Kilimanjaro*, under-review)

[b] from Duane et al. (2008)

* Table was adjusted to fit page width

the disturbances included anthropogenic (e.g. land-use change) as well as natural effects (e.g. fire) (Table 1). These eleven ecosystems are the most common ecosystems on Mt. Kilimanjaro and representative for most of East Africa. Namely, the ecosystems were savannah (SAV), maize field (MAI), Chagga homegarden (HOM), coffee plantation (COF), lower montane forest (FLM), *Ocotea* forest (FOC), disturbed *Ocotea* forest (FOD), *Podocarpus* forest (FPO), disturbed *Podocarpus* forest (FPD), *Erica* forest (FER) and alpine *Helichrysum* (HEL). The investigated ecosystems covered an elevation gradient from 950 to 3880 m above sea level and the mean annual temperature (MAT) ranged from 6.8 to 22.5°C (Table 1). Mt. Kilimanjaro is characterized by a bimodal rainfall pattern and the mean annual precipitation (MAP) varies between 536 and 2998 mm per year (Table 1). MAT and MAP are strongly dependent on elevation and topographic position. The de Martonne aridity index (A_{dM}) is commonly used to express the ratio of precipitation and evaporation (Botzan et al., 1998). It uses the temperature to estimate the local evaporation: A_{dM} = MAP [mm] · (MAT [°C]+10°C)$^{-1}$. Aridity increases with lower A_{dM} values (Table 1). Several studies described the vegetation in the respective ecosystems and the NPP in tropical ecosystems in general (e.g. Clark et al., 2001, Hemp, 2006). Most soils are classified as Andosols developed from volcanic ash (< 75000 years) which have a high potential for C sequestration (Zech et al., 2014). The mostly volcanic parent materials were described by Nonnotte et al. (2008). High nutrient use efficiencies and C_{org} contents result in high soil fertility (Kaihura et al., 1999). Despite the occurrence of high precipitation events, leaching of base cations as well as nutrient input via rainwater are negligible (Schrumpf, 2004). The C_{mic} contents in Mt. Kilimanjaro soils are strongly dependent on elevation and ecosystem (Pabst et al., 2013). However, Pabst et al. (2013) observed little to no changes in C_{mic} contents between the climatic wet and dry seasons.

The investigated ecosystems were assigned to three land-use classes, i.e. natural, semi-natural and agricultural (Table 1). Ecosystems were classified as natural if they did not show any disturbances or if the disturbances occurred more than 20 years ago. At elevations above 1750 m a.s.l., the logging of precious camphor trees was limited in 2005 when the Kilimanjaro Forest Reserve was included in the National Park. However, after years of regeneration, the consequences of the past interference are still visible in the disturbed *Ocotea* forest. At elevations between 2800 and 3500 m, lightning-caused fires promoted a vegetation change and today the former *Podocarpus* forest is dominated by *Erica* (hereafter disturbed *Podocarpus* forest, FPD). Under unaltered conditions, *Podocarpus* would still dominate these areas today. The two other land-use classes were characterized by current human-induced disturbances at different intensities (Table 1). Several types of disturbances of natural ecosystems result in altered semi-natural ecosystems. In the lower elevation areas at Mt. Kilimanjaro, low impact anthropogenic disturbances such as occasional mowing and collection of firewood are strengthened by population pressure and characterize savannah. Illegal logging and charcoal production are major threats to Mt. Kilimanjaro's lower montane forests (Lambrechts et al., 2002; Soini, 2005). In addition, these forests within the National Park are used by the local population for the collection of firewood and animal feeds. During the last centuries, the Kilimanjaro native tribe of the Chagga developed a widely used form of agroforestry system (hereafter referred as agricultural homegarden, HOM) described in detail by Fernandes & Nair (1986). Agriculturally-used ecosystems such as maize fields and coffee plantations are characterized by typical management practices, such as the use of pesticides and mineral fertilizers in combination with intensive mechanical cultivation. The high population pressure in the area causes the conversion of savannahs to maize fields and multinational companies convert traditional homegardens to coffee plantations.

Sampling methodology

Experimental plots (50 x 50 m, slope-parallel), representative of the respective ecosystem, were established in 2010. Litter layer and soil horizons were identified in soil pits of a depth of >0.75 m and soil bulk density was sampled once for each of the investigated ecosystems. Bulk density values for the litter layer/O horizon were estimated from literature to a value of 0.15 g cm^{-3} (Matthews, 2005), since no volume-based sampling was possible. Starting from the first horizon of the mineral soil, three undisturbed soil cores (100 cm^{-3}) per horizon were taken. Samples were dried at 105°C until constant weight, stones and bigger roots were excluded by sieving the samples through a 2 mm mesh sieve. Using the same soil pits, separate samples were taken per horizon (including O horizon) for determination of C_{org}.

With regard to C_{mic}, seven of the eleven ecosystems were sampled in March 2012 and results are published in Pabst et al. (2013). Based on the same methodology the remaining four ecosystems (*Helichrysum*, *Erica* forest, disturbed *Podocarpus* forest, disturbed *Ocotea* forest) were sampled during February 2013 under comparable conditions as in 2012. Briefly, samples were taken in four corners of the plots and depths of 0–10 and 10–20 cm. Hereby O horizons were included in the samples, since these horizons of montane rainforests are densely rooted (Schrumpf, 2004) and contain high amounts of C_{mic} (Pabst et al., 2013). Visible plant debris was removed and soil was sieved using a 2 mm mesh screen. All samples for determination of C_{mic} were stored under field-moist conditions at 4–6°C until analysis.

In all investigated ecosystems, five undisturbed soil cores (12.5 cm inner diameter, 20 – 25 cm depth) were extracted for analysis of CO_2 effluxes. Plots below 2000 m a.s.l. were sampled during dry season in February 2011, sites at higher elevations during March 2012. Cores were covered with a plastic lid on the bottom and on top with Parafilm M® (Bemis Company, Inc, Oshkosh, WI, USA) to allow air exchange but reduce moisture losses to a minimum. Soil cores were shipped to laboratory facilities of KIT, IMK-IFU, Germany. The core samples from February 2011 were kept at room temperature (~20°C), whereas samples from March 2012 were stored field-moist at 10°C until further analysis.

Soil analysis

Analysis of C_{mic} was done by the fumigation–extraction method (Vance et al., 1987). Briefly, 7–8 g of field-moist soil were incubated for 24 h at room temperature in a $CHCl_3$ (ethanol-free) atmosphere. Subsequently, $CHCl_3$ was removed and soluble C from all samples (fumigated and non-fumigated control samples) was extracted with 60 ml of 0.5 M K_2SO_4 by shaking on an orbital shaker (60 min, 120 rotations min^{-1}). Dissolved C in fumigated and non-fumigated extracts was determined (multi N/C 2100S, Analytikjena, Jena, Germany). Since not all of the soil C can be extracted by K_2SO_4, an extractability factor (k_{EC}) of 0.45 (Vance et al., 1987) was used to convert microbial C flush (difference between extractable C from fumigated and non-fumigated samples) to C_{mic}. Dried and grinded soil samples from soil pits were analyzed for C_{org} contents using dry combustion (vario max CN, Elementar, Hanau, Germany).

Undisturbed soil cores were incubated in three consecutive five-day stages (Lovibond incubator ET 651-8, Tintometer GmbH, Germany) with one measurement per day. The first stage implied the preincubation during which the temperature was set to site-specific MAT to allow stabilization of microbial activity. In the second stage, soil was moistened with standard rain mixture according to Breuer et al. (2002). The solution added was equivalent to 3.6 mm precipitation, corresponding to 44 ml per soil core. In the third incubation stage added water was equivalent to additional 20 mm of precipitation (= 245 ml). The achieved volumetric water contents ranged from 13.2 to 36.0% (Table 2). Moisture levels were kept stable during each incubation stage and temperature was continuously at MAT (±1°C). Measurements of CO_2 concentration development were conducted with a dual quantum cascade laser (Aerodyne Research Inc., Billerica, MA, USA, precision). From the 2 liter headspace of each soil core, 50 ml air were sucked per minute through Teflon tubes to the measurement cell of the laser and recirculated to the headspace for a measuring time of 20 minutes. The set up was similar to static chamber measurements. Observations of pressure conditions in the headspace controlled for constant conditions avoiding over- or low pressure. Subsequently, CO_2 effluxes were calculated from the linear increase of CO_2 in headspace concentration over time. Only effluxes with $r^2 \geq 0.8$ between time and CO_2 were accepted for further analysis. Per ecosystem, the medians across the single incubation stages were used for further calculations.

The CO_2 efflux for the calculation of qCO_2 is supposed to be measured at a soil water potential of -240 kPa (Anderson & Domsch, 1993). Since the moisture level of the soil cores was kept constant during the incubation stages but independent of the actual soil water potential, the specific metabolic quotient (q_sCO_2) was used instead of qCO_2. Hence, q_sCO_2 indicates qCO_2 under the volumetric water contents achieved by the simulated precipitations of 3.6 and 20 mm. However, the values of q_sCO_2 and qCO_2 remain comparable, since the achieved soil moisture levels were in the same range as in the study by Anderson & Domsch (1993).

Weighted arithmetic means were used to adjust C_{mic} contents to horizon depths. Then, C_{org} and C_{mic} stocks were calculated per horizon and square meter (as mentioned above, the bulk density of O horizons was estimated to 0.15 g cm^{-3}

(Matthews, 2005)). Subsequently, stocks and CO_2 effluxes were proportionally attributed to the minimum cylinder depth of 18 cm. Depending on number of horizons, number of CO_2 effluxes with $r^2 \geq 0.8$ and variable (C_{org}, C_{mic}, q_sCO_2), this resulted in different numbers of observations per ecosystem. The ratio of CO_2 efflux per hour to total C_{mic} stock in the soil package was calculated as q_sCO_2 (in mg C_{CO2} g^{-1} C_{mic} h^{-1}).

Statistical analysis

Since our data showed non-normally distributed characteristics (Shapiro-Wilk test, non-normally distributed if $p < 0.1$), Kruskal-Wallis tests with ensuing post-hoc tests were used to detect significant differences between the ecosystems and p-values were adjusted according to Benjamini & Hochberg (1995). Differences were accepted as significant if $p < 0.05$ and the presentation of individual p-values is omitted in the text. Comparisons between two factors (precipitation regimes, land-use conversion) were done by Mann-Whitney-U tests. The arithmetic mean was not appropriate, due to the skewed distributions of the data, hence the median was used in the following figures and text. All values are referring to the upper soil layer of 18 cm. Statistical analysis were done using R 3.0 (R Development Core Team, 2008).

Results

Soil bulk density

The soil bulk density of the upper 18 cm ranged from 0.19 ± 0.00 g cm^{-3} to 1.22 ± 0.03 g cm^{-3}. Natural and forest ecosystems showed the lowest bulk densities with a maximum of 0.38 ± 0.03 g cm^{-3} in the lower alpine *Helichrysum*. The cultivation of maize on savannah soil lead to an increase in bulk density from 0.86 ± 0.04 to 1.22 ± 0.03 g cm^{-3} and the conversion of homegarden to coffee plantation raised the soil bulk density from 0.77 ± 0.04 to 1.05 ± 0.04 g cm^{-3}. These soil bulk densities are in accordance with other observations at Mt. Kilimanjaro (Schrumpf, 2004).

C_{org} and C_{mic} stocks

C_{org} stocks in the surface layer differed between ecosystems and ranged between 2.1 and 9.3 kg C_{org} m^{-2}. C_{org} stocks were positively correlated with elevation (Figure 1). At

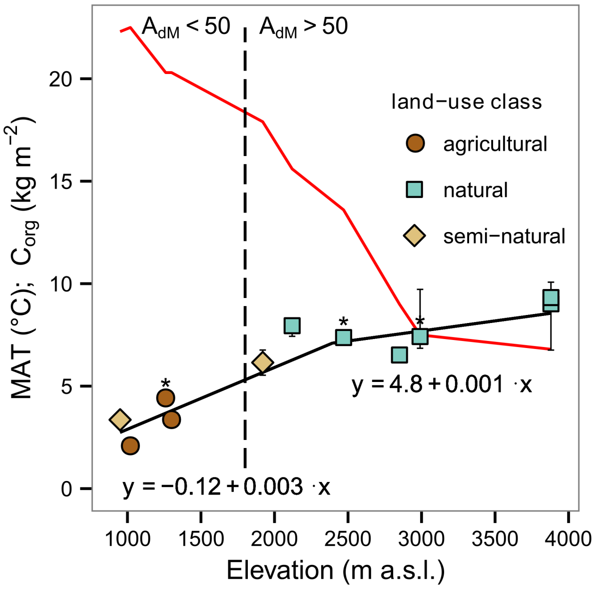

Figure 1: Temperature, elevation and organic carbon (C_{org}) stocks in surface soil (18 cm) of Mt. Kilimanjaro ecosystems. Displayed C_{org} values are medians ± 25% and 75% quantiles, temperature (MAT, red line); linear regressions of C_{org} vs. elevation depending on A_{dM} value (left side: A_{dM} < 50; right side: A_{dM} > 50); symbols and colors of ecosystems: agricultural (circles, dark brown); semi-natural (diamonds, light brown); natural (squares, green); stars denote the specific ecosystems of homegarden, disturbed *Ocotea* forest and disturbed *Podocarpus* forest; for description of the land-use classes, please refer to Table 1

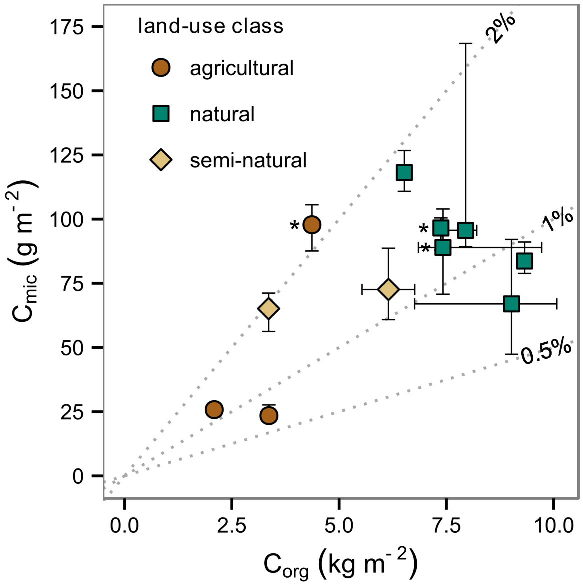

Figure 2: Stocks of C_{mic} and C_{org} in surface soils (18 cm) of Mt. Kilimanjaro ecosystems. Displayed values are medians ± 25% and 75% quantiles. Dotted lines refer to C_{mic}:C_{org} ratio of 0.5%, 1% and 2%, respectively. Symbols and colors of ecosystems: agricultural (circles, dark brown); semi-natural (diamonds, light brown); natural (squares, green); stars denote the specific ecosystems of homegarden, disturbed *Ocotea* forest and disturbed *Podocarpus* forest; for description of the land-use classes, please refer to Table 1

approximately 4000 m a.s.l., the natural *Helichrysum* ecosystem contained about 4.5 times more C_{org} than the agriculturally used maize field at 950 m a.s.l.. Based on A_{dM} values above and below 50 (Table 1), two linear regressions between C_{org} stocks and elevation were fitted. Although its A_{dM} was below 50, the *Helichrysum* ecosystem at an elevation of 3880 m a.s.l. was excluded from the regressions, since its cold climate is not comparable with hot savannahs or maize fields at elevations of around 1000 m a.s.l.. In ecosystems at low elevations with higher aridity, C_{org} stocks increased by 3 kg m^{-2} per 1000 m in elevation (Figure 1). This increase with elevation declined to one-third in the soils more humid ecosystems at higher elevations (Figure 1). C_{org} stocks were higher in natural compared to semi-natural and semi-natural compared to agriculturally used ecosystems (Table 3). At similar elevation levels, the C_{org} stock in soil of the maize field was 38% lower than in adjacent savannah and the soil of the coffee plantation was decreased by 23% if compared with the traditional homegarden.

C_{mic} differed between the investigation sites, but was independent of elevation. High amounts of C_{mic} were found in natural and semi-natural ecosystems, while highest C_{mic} stocks were observed in natural forests (for *Ocotea* forest and *Podocarpus*

Table 2: Volumetric water contents before and after the additions of standard rain mixture. The content before addition refers to the water contents during estimated from the chloroform-fumigation method

Ecosystem	ID	Volumetric water contents [%]		
		before addition	after 44ml of solution	after 245ml of solution
Helichrysum	HEL	12.3	14.3	25.4
Erica forest	FER	12.3	14.3	25.4
Podocarpus forest disturbed	FPD	16.8	18.8	29.9
Podocarpus forest	FPO	19.3	21.3	32.4
Ocotea forest disturbed	FOD	13.1	15.1	26.2
Ocotea forest	FOC	22.9	24.9	36.0
Forest lower montane	FLM	11.2	13.2	24.3
Coffee plantation	COF	16.8	18.8	29.9
Homegarden	HOM	16.4	18.4	29.5
Maize field	MAI	11.8	13.8	24.9
Savannah	SAV	12.9	14.9	26.0

forest: 96 and 118 g C_{mic} m^{-2}, respectively). A decrease in C_{mic} stocks by intensive agriculture could be observed in regard of the typical land-use changes of savannah to maize field and homegarden to coffee plantation with -60% and -76%, respectively. The influence of temperature on C_{org} and C_{mic} was especially distinct in the natural land-use class. In the humid-warm forests, C_{mic} contributed between 1 and 2% to total C_{org}, whereas the cold ecosystems at an elevation of 3880 m a.s.l. exhibited ratios below 1% (Figure 2). A similar distribution of the proportion of readily metabolized C_{org} was also observed on a topical volcano in Mexico (Campos et al., 2014). Major differences were observed in the agricultural land-use class, where the conversion of homegarden to coffee plantation decreased the C_{mic}:C_{org} ratio from 2.2 to 0.7% (Figure 2).

CO_2 efflux

Under simulated rainfall of 3.6 mm, CO_2 efflux from soil differed between the ecosystems and ranged from 4.6 mg C_{CO2} m^{-2} h^{-1} (maize field) to 27.4 mg C_{CO2} m^{-2} h^{-1} (disturbed *Ocotea* forest) (Figure 3). No differences could be observed between the

Table 3: Results of Kruskal-Wallis and post-hoc tests per land-use class for C_{org} stocks, C_{mic} stocks, soil CO_2 efflux and the specific metabolic quotient (q_sCO_2) under two different moisture regimes. Values are medians of surface soils (18 cm) of Mt. Kilimanjaro ecosystems. Letters “a”, “b” and “c” indicate statistical differences ($p < 0.05$)*.

Land-use class	C_{org}		C_{mic}		CO_2 (3.6 mm precipitation)	
	N	kg m^{-2}	N	g m^{-2}	N	mg C_{CO2} h^{-1}
natural	150	7.82 (a)	576	96.27 (a)	172	17.98 (a)
semi-natural	36	5.44 (b)	144	72.51 (a)	54	14.83 (b)
agricultural	39	3.16 (c)	156	31.52 (b)	71	13.44 (b)

Land-use class	CO_2 (20 mm precipitation)		q_sCO_2 (3.6 mm precipitation)		q_sCO_2 (20 mm precipitation)	
	N	mg C_{CO2} h^{-1}	N	mg C_{CO2} g^{-1} C_{mic} h^{-1}	N	mg C_{CO2} g^{-1} C_{mic} h^{-1}
natural	163	20.26 (c)	576	0.21 (b)	576	0.22 (c)
semi-natural	70	31.85 (b)	144	0.12 (c)	144	0.39 (b)
agricultural	89	40.79 (a)	156	0.34 (a)	156	1.50 (a)

* Table was adjusted to fit page width

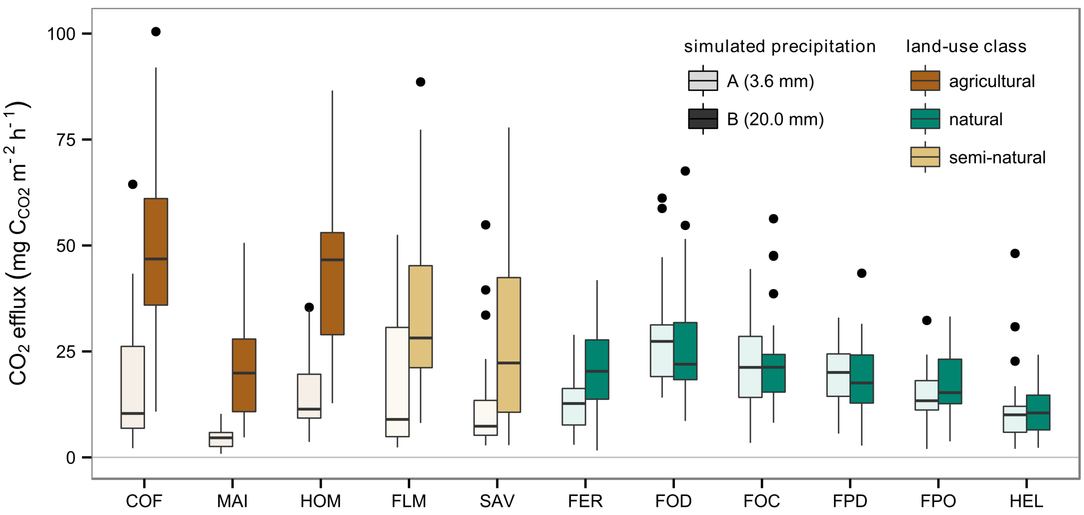

Figure 3: Soil CO_2 efflux (mg C_{CO2} m^{-2} h^{-1}, surface soil (18 cm)) under different simulated precipitations of agricultural (dark brown), semi-natural (light brown) and natural ecosystems (green) at Mt. Kilimanjaro; simulated precipitations are shown as two bars per ecosystem: 3.6 mm (left, light color), 20.0 mm (right, dark color); medians are displayed as horizontal lines within the colored bars; bars are limited by 25% and 75% quantiles and whiskers extend to maximum/minimum values within 1.5 times the interquartile range; data beyond whiskers are displayed as points; displayed medians were used for further calculations; for abbreviations of ecosystems please refer to Table 1

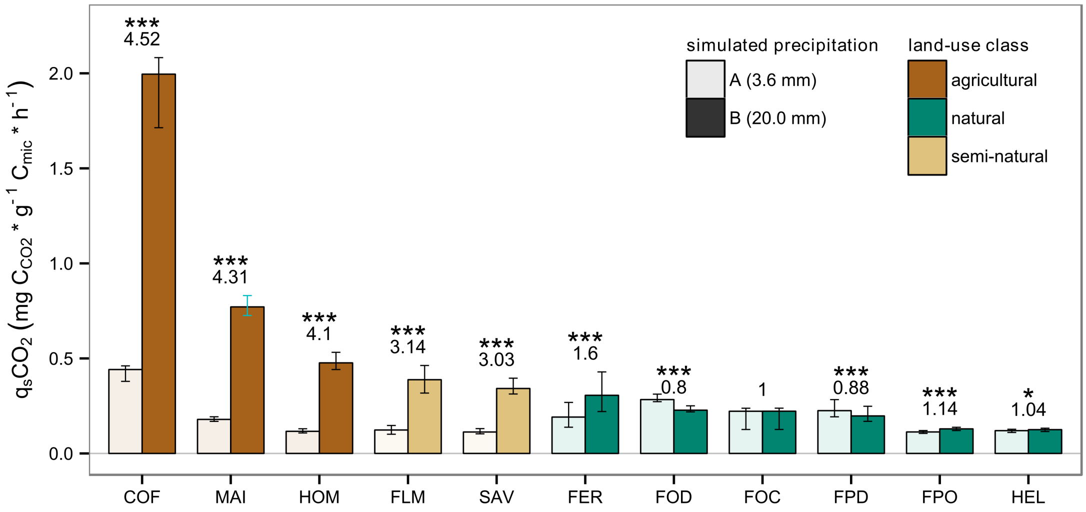

Figure 4: Specific metabolic quotients (q_sCO_2, surface soil (18 cm)) under simulated precipitations of agricultural (dark brown), semi-natural (light brown) and natural ecosystems (green) at Mt. Kilimanjaro. Simulated precipitations are shown as two bars per ecosystem: 3.6 mm (left, light color), 20.0 mm (right, dark color); numbers indicate factorial changes to 3.6 mm precipitation; significant differences between simulated precipitations are indicated as p(<0.05) = * and p(<0.001) = ***; displayed values are medians ± 25% and 75% quantiles; for abbreviations of ecosystems please refer to Table 1

agricultural and semi-natural land use classes, whereas the natural ecosystems had distinctly higher CO_2 efflux rates (Table 3).

Similar to lower precipitation, soil CO_2 efflux under additional 20 mm of precipitation revealed differences between the ecosystems and varied between 10.5 mg C_{CO2} m^{-2} h^{-1} (*Helichrysum*) and 46.8 mg C_{CO2} m^{-2} h^{-1} (coffee plantation) (Figure 3). A comparison of land-use classes at the higher precipitation but comparable volumetric water contents (Table 2) revealed significantly higher CO_2 effluxes in agricultural ecosystems compared to semi-natural and natural systems (Table 3). Elevation had no significant effect on CO_2 efflux under both precipitation regimes.

Higher precipitation resulted in higher CO_2 efflux rates in six of the ecosystems (coffee plantation, maize field, homegarden, savannah, lower montane forest, *Erica* forest). All other ecosystems showed no significant changes in CO_2 efflux with increased water additions.

Specific metabolic quotient

Under low precipitation regime (3.6 mm), q_sCO2 differed fourfold between the ecosystems (0.11 (savannah) vs. 0.44 mg C_{CO2} g^{-1} C_{mic} h^{-1} (coffee plantation); Figure 4). Soils under agriculture exhibited the highest q_sCO_2, followed by natural ecosystems (Table 3). q_sCO_2 in intensive agriculturally used coffee plantation was 3.8-fold as high as in traditional homegarden and q_sCO_2 in agricultural maize-field was increased 1.6-fold after the conversion from adjacent semi-natural savannah.

Additional 20 mm of precipitation revealed differences in q_sCO_2 between the ecosystems which varied up to 15-fold (0.13 (*Helichrysum*) vs. 2.00 mg C_{CO2} g^{-1} C_{mic} h^{-1} (coffee plantation)) (Figure 4). As expected, q_sCO_2 increased distinctly with increasing land-use intensity, shown in q_sCO_2(agricultural) > q_sCO_2(semi-natural) > q_sCO_2(natural) (Table 3). Again, the effect of intensive agriculture was revealed by comparison of savannah with maize-field and homegarden with coffee plantation, respectively. At more or less similar volumetric water contents (Table 2), q_sCO_2 of intensively used agricultural soils were 2.25 to more than 4 times higher as in less disturbed soils. The traditional cultivation used in the homegarden is an intermediate system between agricultural and semi-natural ecosystems (Figure 4).

The ecosystem-specific changes in CO_2 efflux caused by increased precipitation were evident in q_sCO_2 as higher precipitation lead to increases in q_sCO_2 (up to 4.5 times) in eight and slight decreases in two of the eleven ecosystems (Figure 4). The variation in precipitation did not affect q_sCO_2 in natural *Ocotea* forest, which is the ecosystem existing at elevations where natural precipitation levels are highest. Hence, this sample showed the highest volumetric water content before the addition of the rain mixture. Elevation had no relevant effect on q_sCO_2 under both simulated precipitation regimes (3.6 and 20 mm).

Discussion

C_{org} and C_{mic}

C_{org} stocks found in soils of the investigated ecosystems were generally in the same range as previously reported for soils of Mt. Kilimanjaro (Schrumpf, 2004). Elevation was used as a parameter controlling temperature and precipitation, presumably the major factors influencing C_{org} stocks along the investigated elevation gradient. The two fitted linear regressions for ecosystems with low and high aridity are reminiscent of the dry and saturated adiabatic lapse rates of air packages. The dry ecosystems at lower elevations ($A_{dM} < 50$) are characterized by a pronounced climatic seasonality (dry and wet). Soil moisture is presumably a limiting factor for some time of the year, indicated by the marked increase in q_sCO_2 at the simulated precipitation of 20 mm. This temporal limiting effect of soil moisture decreases with increasing precipitation. At higher elevations, air packages steadily have a higher degree of water saturation, resulting in a lesser seasonal variability and more or less consistent rainfall throughout the year (Buytaert et al., 2011). This consistent rainfall leads to vegetation growth and a continuous supply of litter, supporting the ecosystems with the highest NPP between 2000 and 3000 m a.s.l. (Clark et al., 2001; Ensslin et al., 2015). The lower temperatures and higher water contents also result in lowered turnover rates and thick, densely rooted organic soil horizons (Zech et al., 1997). The high C_{mic}:C_{org} ratios indicate high substrate availability, which is supported by high amounts of soluble organics (Pabst et al., 2013). Our data show that C_{org} stocks in soils along the slopes of Mt. Kilimanjaro are distinctly influenced by elevation dependent changes in water availability, temperature and NPP.

At low elevations of Mt. Kilimanjaro, the main land-use changes are conversions of semi-natural savannahs to agricultural maize fields and traditional homegardens to intensively used coffee plantations (Soini, 2005). Referred to these land-use changes, we observed strong decreases of C_{org} as well as C_{mic} stocks. These findings are similar to the reviewed land-use changes from natural to agricultural ecosystems, all resulting in lower C_{org} stocks (Don et al., 2011; Bruun et al., 2013). Also the C_{mic}:C_{org} ratio decreased which indicates a higher litter diversity and more available substrate in the soils of savannah and homegarden (Anderson & Domsch, 1989). A decline in C_{mic} caused by land-use change or land-use intensification has been reported for several other tropical soils (Basu & Behera, 1993; Nsabimana et al., 2004; Barua & Haque, 2013) and is often linked to a decline or change in amount and quality of organic matter input and the mechanical cultivation (Dinesh et al., 2003). In our study, maize plants are completely (except roots) harvested and mineral fertilizers are added, if at all, at small amounts. Nonetheless, farmyard manure is often used by small-scale farmers in the rural parts (e.g. homegardens) of Mt. Kilimanjaro area – but still, its application is selective and negligible. This is e.g. shown by forest-to-savannah or forest-to-cropland conversion in India, where, despite the regular input of organic fertilizers, lowest C_{mic} content was observed in cropland (Basu & Behera, 1993). Also erosion may contribute to lower C_{org} and C_{mic} stocks in agriculturally used ecosystems (Kaihura et al., 1999; Debasish-Saha et al., 2014), notably in surface soils. The surface soils of maize fields are especially prone to wind and water erosion, since soil is often left bare after harvesting, potential seedlings of grasses are browsed by communal livestock and soil aggregates are destroyed by mechanical cultivation. In contrast, permanent vegetation cover of natural savannah limits wind and water erosion (Mchunu & Chaplot, 2012) and consequently results in the higher amounts of C_{mic} and C_{org} in this ecosystem. The litterfall in shaded coffee plantations is estimated to a maximum of 1-2 g m^{-2} day^{-1} (Glover & Beer, 1986), mainly originating from shading trees. However, in the present coffee plantation, only some few scattered shading trees were present, hence, litter input is assumed to be lower. Homegarden showed distinctly higher stocks of C_{org} and C_{mic} as well as higher C_{mic}:C_{org} ratio compared to coffee plantation. Cultivation in the traditional agroforestry system is done by hand where plant material (banana, beans, maize, etc.) and surface soil is mixed thoroughly leading to lower bulk densities and better aeration, high substrate availability and quality. In contrast, mechanical cultivation of coffee plantations is very limited and the massive use of pesticides further decreases the litter input of grasses and herbs and may have negative effects on soil microbial functions (Mganga & Kuzyakov, 2014). As a consequence, low amounts of C_{mic} and C_{org} were found in this intensive agriculturally used ecosystem.

CO_2 efflux

CO_2 efflux from soil is mainly derived from respiration of autotrophic and heterotrophic organisms, whereas heterotrophs are strongly influenced by substrate availability and climatic variables such as temperature and soil moisture (Chambers et al., 2004; Kuzyakov, 2006). Respiration of autotrophs was absent in the soil cores, as no living roots were present at the time of the laboratory incubations. However, under field conditions in tropical forest ecosystems 45-50% of total soil CO_2 efflux originates from root respiration (Chambers et al., 2004). Consequently, soil CO_2 efflux measured in the present study represents only decomposition of soil organic matter and remaining root litter.

Air-drying may have affected the microbial activity within the cylinders as well. In soils of semi-arid and arid ecosystems ($A_{dM} < 50$, Table 1), microorganisms are adapted to re-occurring seasonal dryness and consequently air-drying has little to no effect on C_{mic} (Zornoza et al., 2007). In humid areas ($A_{dM} > 50$, Table 1), however, drying poses a stress situation to soil microbes, which may not be adapted to low moisture contents and consequently may die during drying and re-wetting (Zornoza et al., 2007). Nonetheless, the simulated precipitation resulted in significantly different CO_2 effluxes which are similar to trends observed in field measurements (Abera, 2013; Iqbal et al., 2010) and our CO_2 efflux values are in general comparable with other studies (Nouvellon et al., 2008; Sugihara et al., 2012).

Specific microbial respiration quotient

The metabolic quotient of soil microbial biomass has been used as an indicator for ecosystem succession and disturbance. Still, a comparison of its values and analysis of individual influencing factors is difficult since its calculation is based on several ecophysiological properties (Blagodatskaya & Anderson, 1998). This is also true for q_sCO_2 used in this study.

The ecosystems of coffee plantation and maize field are classical monocultures. After harvesting, the maize field is left bare during the dry season until next planting and therefore can be considered as monoculture. On the other hand, the traditional agricultural form of homegardens is characterized by higher diversity and continuous crop changes (more or less similar to crop rotation in classical sense and agroforestry) (Fernandes & Nair, 1986). Consequently, the higher q_sCO_2 in coffee plantation and maize field are attributed to management and the associated decreases in C_{mic} stocks and C_{mic}:C_{org} ratios. In early studies, agricultural monocultures exhibited higher qCO_2 but lower C_{mic}:C_{org} ratios than comparable areas under continuous crop rotation (Anderson & Domsch, 1989, 1990; Anderson, 2003). Also the conversion of savannah to cultivated land in India resulted in an 1.4-fold increase in qCO_2 (Basu & Behera, 1993). Still, in the present study, we found more than 4-fold increases in q_sCO_2 due to intensification in management practices, indicating that the effect of land use may be underestimated in the studies above.

Also at Mt. Kilimanjaro, Mganga & Kuzyakov (2014) found that decomposition rates of easily available substrates are up to three times higher in soils of intensively managed than in soils from semi-natural ecosystems. In contrast to intensive agriculture, agroforestry systems and forests showed potential for C sequestration and were therefore assumed to be more sustainable (Mganga & Kuzyakov, 2014). These findings confirm the lower q_sCO_2 but higher C_{mic}:C_{org} ratio in homegarden and forests compared to intensive agriculturally used maize fields and coffee plantations (Figure 2, Figure 4).

The ratio of CO_2 efflux to C_{mic} is also a sensitive indicator of stress (Killham, 1985; Zornoza et al., 2007). A change in land use often accompanies a change in the stress level which soil microorganisms are exposed to. Such stress-inducing factors are e.g. pesticides in coffee plantations and maize fields, mechanical disturbance (tillage) in maize fields and homegardens or fires in savannahs and forests. Also the watering of dry soil may increase the stress level of microorganisms and lead to increased q_sCO_2 (e.g. savannah and maize field, Figure 4). Yet, a clear separation of the effects of disturbance and stress is not possible (Wardle & Ghani, 1995).

In general, intensive agriculture poses unfavorable conditions for soil microorganisms, such as low substrate availability or increased disturbance through management practices (Nsabimana et al., 2004). As the amount of available substrate (C_{mic}:C_{org} ratio) decreases, so does the microbial substrate use efficiency, resulting in higher q_sCO_2. The high q_sCO_2 in agricultural managed ecosystems indicates a microbial community with a high nutrient demand but small nutrient use efficiency. Mt. Kilimanjaro ecosystems with a more natural or semi-natural character showed higher C_{mic}:C_{org} ratio and lower q_sCO_2 and therefore should be dominated by a more efficient soil microbial community with considerably better use of available substrate. Consequently, natural and semi-natural ecosystems have higher potential of C sequestration. The adjustment of the management practices to the local plant diversity and conditions enabled the development of a sustainable agroforestry system with high substrate availability and medium substrate use efficiency: the homegardens.

Metabolic quotients in a similar range were reported for dry tropical agroecosystems in Morogoro, Tanzania (Sugihara et al., 2010). Furthermore, Sugihara et al. (2010) found a strong correlation of soil moisture and qCO_2 with significantly higher values in the rainy season. The obtained correlation between soil moisture and q_sCO_2 represents a combinatorial effect of soil moisture and substrate limitation (Figure 2, Figure 4). Low substrate availability results in a large part of soil microorganisms being in the physiological state of “potentially active”, whereas this state cannot be observed under higher substrate availabilities (Blagodatskaya & Kuzyakov, 2013). Compared to soils of the forests, the available substrate in coffee plantation, maize field and savannah is low (Pabst et al., 2013), likely due to the shortage of water. Through additional precipitation of 20.0 mm this limitation is suspended as substrate becomes more available. Hence, the “potentially active” microorganisms become active within a few hours (Blagodatskaya & Kuzyakov, 2013) and increase CO_2 efflux significantly (Figure 3). Substrate availability as a factor limiting CO_2 efflux can be excluded in the other ecosystems since they exhibit high water-extractable C contents throughout the climatic seasons (Pabst et al., 2013) and high C_{mic}:C_{org} ratios. Therefore, the boost in CO_2 efflux at additional precipitation of 20.0 mm is assumed to be negligible. The effect of additional precipitation (20.0 mm) for ecosystems

>2000 m a.s.l. is also limited due to their adaption to high MAP and soil moisture contents (e.g. in the natural *Ocotea* forest). Also, in case of *Helichrysum* and *Erica* forest, the low MAT is limiting microbial mineralization (Zech et al., 1997). Higher precipitation showed strongest increase of CO_2 efflux for soils from agriculturally used ecosystems, clearly showing that decomposition of soil organic matter in these soils is limited by water availability.

Conclusions

C_{org} and C_{mic} stocks in soils of Mt. Kilimanjaro ecosystems decreased significantly with increasing management intensity. Beside the effect of land use, C_{org} stocks were correlated to the water availability, temperature and NPP in the respective ecosystem. The specific metabolic quotient (q_sCO_2) of soils was not dependent on elevation but was affected by land management and precipitation. We observed pronounced differences of q_sCO_2 between land-use classes. Summarily, in agricultural systems of coffee plantation and maize field, soil microorganisms have a high energy demand but low efficiency. The soil microorganisms in traditional homegardens and natural ecosystems are characterized by a lower energy demand and more efficient use of available substrate. Based on q_sCO_2, natural, semi-natural ecosystems and the traditional homegardens on Mt. Kilimanjaro have a higher potential of C sequestration than agriculturally used ecosystems. The specific metabolic quotient in surface soils of Mt. Kilimanjaro ecosystems is strongly depending on soil moisture content and therefore vulnerable to changes in rainfall patterns. Still, it was not possible to assign the change in q_sCO_2 to a single factor. Hence future studies including e.g. the in-situ determination of CO_2 efflux, socio-economic properties as well as the rates of land-use change will be necessary for a more precise view on C dynamics and the effect of climate and land-use change on C decomposition in soils of Africa's highest mountain.

Acknowledgments

This study was funded by the German Research Foundation (DFG) within the Research-Unit 1246 (KiLi) and supported by the Tanzanian Commission for Science and Technology (COSTECH), the Tanzania Wildlife Research Institute (TAWIRI) and the Mount Kilimanjaro National Park (KINAPA). Special thanks goes to Anna Kühnel (University of Bayreuth, Germany). Additionally the authors want to thank Dr. Andreas Hemp for selection of the research plots as well as the local helpers.

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Study 3

Microbial biomass in savannah soils at Mt. Kilimanjaro – Vis-NIR DRS and spatial analysis

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in preparation, to be submitted to an open-access journal with a fitting scope

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Abstract

Knowledge of spatial distribution of soil microbial biomass is important to understand the functioning of ecosystems. For East African savannah ecosystems such spatial knowledge is missing. In addition, these soil biological properties are not yet included in monitoring and evaluation plans of sustainable land management projects. This study compares the precision of the spatial prediction techniques ordinary kriging, regression kriging and geographically weighted regression. These techniques were used to predict microbial biomass carbon (C_{mic}) and microbial biomass nitrogen (N_{mic}) on two savannah sites. Predictor variables were soil attributes which are a) easy to measure (for example with reflectance spectroscopy), and b) are correlated to the target variables – such as C_{org}, nitrogen and pH. Regression kriging and geographically weighted regression performed better than ordinary kriging with R^2 for the prediction of C_{mic} and N_{mic} up to 0.71 and 0.76, respectively. C_{mic} and N_{mic} showed diverse spatial relations to the predictors and contrasting degrees of heterogeneity on the two plots. The use of visible to near infrared diffuse reflectance spectroscopy to predict soil properties in combination with multivariate prediction methods is a cost-efficient approach for monitoring changes in soil quality.

Introduction

Tropical ecosystems with their high biodiversity play an important role in global climate and biogeochemical cycles, especially in carbon (C) turnover and sequestration (Detwiler & Hall, 1988; Malhi et al., 2004). This is also true for savannah ecosystems which cover nearly 20% of the earth’s land surface and are affected by global change (Sankaran & Ratnam, 2013; D’Odorico et al., 2013). Therefore, savannahs have been the subject of several studies focusing on soil microbial biomass, C turnover, fire effects and greenhouse-gas exchange (Jones, 1973; Singh et al., 1989; Hagos & Smit, 2005).

Dead plant material is not only a major source of soil organic C but also delivers the energy needed for soil microbial growth. Consequently, plant patches and/or grass tussocks in savannah ecosystems are often hotspots of high soil quality (Garner & Steinberger, 1989). These hotspots are negatively influenced by grazing, cultivation and land degradation in general (Northup et al., 1999). Especially land degradation is projected to be a major ecological as well as economical concern in the near future and restoration of degraded land via the implementation of sustainable land management practices is becoming more relevant (IPCC, 2014; Bojö, 1996). A promising approach to continuously monitor and evaluate these practices is the combination of large-scale measures at the landscape level and fine-scaled monitoring at the plant-microbe-soil-interface (Northup et al., 1999).

A basic concept in biology is that there is a positive relationship between environmental heterogeneity and species diversity (Tamme et al., 2010). However, the concept of environmental heterogeneity is not clearly defined and the relations are scale dependent (Wilson, 2000). The animal species diversity in savannah ecosystem for example, is closely linked to the occurrence of large trees, as they function as food resource, shelter or nesting site (Tews et al., 2004). Canopy structure of savannah trees on the other hand influences throughfall, which affects soil moisture, soil fertility (Vetaas, 1992) and tree growth (Plath et al., 2011). Therefore, detailed knowledge of the spatial distribution of different parameters and the dependencies between them are of great concern.

Spatial interpolation techniques are a common tool for the estimation of C and nutrient pools (Kumar et al., 2012; Kuzyakova et al., 2001; Mishra et al., 2012). Spatial analyses focus on the variability of a given parameter over space and thus the heterogeneity of this parameter at the studied scale. However, spatial analysis of savannah soils was used in only few studies, mostly in South and West Africa (Hagos & Smit, 2005; Wang et al., 2009). In addition and since each physical and chemical analysis implies further costs, soil sample collection is often sparsely distributed over space. As measuring biological soil parameters like microbial C and N (C_{mic}, N_{mic}) are very laborious in the field as well as in the lab, the application of prediction techniques might make better use of the data and might lead to precise estimations based on only few data points.

Over the last century, soil-landscape modeling has shifted from qualitative methods, e.g. soil classification and soil survey maps, towards quantitative methods like fuzzy sets and multivariate geospatial models (Grunwald, 2006). Geospatial models can be used to estimate a soil property at an unknown location and modeling is considered more detailed and less error-prone than for example soil survey maps (Thompson & Kolka, 2005). One to several predictor variables which are available in a high resolution within the study area are used to estimate the variability of the sparsely sampled target variable (Thompson & Kolka, 2005; Mishra et al., 2010). However, there is no universal single best prediction method for all targeted parameters and therefore caution is advised when selecting the most suitable method for a certain variable (Li & Heap, 2011). The traditional technique of ordinary kriging (OK) uses data of the target variable, available at the observation points, to predict its value at new locations (Cressie, 1988). OK is widely used and its computation is easy compared to the more advanced multivariate methods, like regression kriging (RK). RK uses the available data of the dependent variable and, in addition, information from auxiliary or co-variables (e.g. topography, data that can be derived from satellite images, variables that are more easy to measure than the dependent variable, etc.) (Hengl, 2009). In addition to the commonly used geostatistical methods, (Brunsdon et al., 1996)) introduced the multivariate approach of the geographically weighted regression (GWR). Compared to OK and RK, GWR has the advantage, that it considers the possibility of varying relationships between the model variables over space (Brunsdon et al., 1996).

In order to gain information on soil parameters correlated to soil microbial biomass (e.g. C_{org}, N, pH), visible to near-infrared diffuse reflectance spectroscopy (Vis-NIR-DRS) can be used (Awiti et al., 2008; Viscarra Rossel & Behrens, 2010; Chang et al., 2001). It is an established method to predict several soil physical and chemical properties. Spectral measurements are mostly non-destructive, faster and less expensive compared to classical physical and chemical soil analysis. One of the main reasons for the speed and cost efficiency of Vis-NIR-DRS is that several different soil properties can be derived from a single spectroscopic measurement (Viscarra Rossel et al., 2006).

The objectives of this study were therefore a) to use Vis-NIR-DRS for the prediction of soil attributes (C_{org}, N), which then can be used to derive soil biological properties (C_{mic}, N_{mic}) and b) to use the derived soil attributes in spatial analysis and test if RK and GWR can increase prediction quality compared to OK. Our goal is to develop an easy and cost-efficient approach to monitor soil microbial parameters as well as their heterogeneity – properties which are commonly not included in monitoring plans of land restoration projects.

Materials and Methods

Study site

The study was conducted in a semi-arid savannah near Lake Chala, East of Mt. Kilimanjaro, Tanzania (3°18’39” S, 37°41’8” E, Figure 1). Mean annual rainfall is 536 mm, with a long rainy season from March to May and a short rainy season between October and December (Moernaut et al., 2010). Soils developed on superficial deposits from Kibo and Mawenzi peaks of Mt. Kilimanjaro and from the various small and steep craters in the east of the mountain complex (Nonnotte et al., 2008). On the slopes of these small volcanoes the main soil type is Leptosol, whereas Vertisols are dominant in the plains.

We worked on two different study sites. One site (P_{slope}) is situated on the outer foot slope of the crater rim of the Lake Chala caldera at an elevation of 960 m (Figure 1).

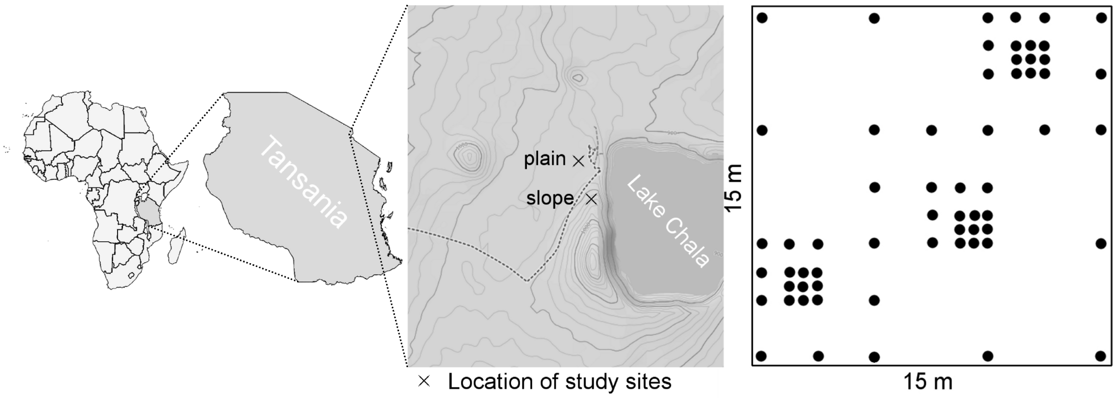

Figure 1: Study area with the location of the study plots (x) and study design. Source: commons.wikimedia and OpenStreetMap

It is north exposed with an inclination of about 10°. The soil is very shallow with a maximum depth of 25 cm, bedrock appearing directly at the surface in some parts of the area. It was classified as Rendzic Leptosol (Calcaric, Tephric, Sodic, Eutric, Skeletic) according to WRB (FAO, 2008). Dominating tree species at this site is *Combretum molle*, with some Acacias in between. Dominant grass species are the tussock grasses *Heteropogon contortus* and *Sehima nervosum*. The second study site (P_{plain}) is situated 400 m to the north-west, in the plains surrounding Lake Chala at 950 m a.s.l. with no inclination. The soil was classified as Sodic Vertisol (Hypereutric, Chromic). At this site, the dominating tree species are *Balanitis aegyptiaca* and different Acacias (*Acacia tortilis*, *Acacia senegal*, *Acacia nilotica*) with an undergrowth of *Heteropogon contortus*, *Erogrostis superba* and *Botriochloa insculpta*.

At both sites, the pressure by land use was classified as low to medium since the understorey vegetation is cut by hand and used as fodder for livestock in the nearby villages. A future increase in land-use pressure is assumed due to massive population growth and the increased demand for arable land.

Study design and field sampling

A detailed sampling campaign was carried out in October 2012. The sampling was conducted in a hierarchically nested grid design on two 15 m x 15 m plots, consisting of 61 grid points each (Figure 1). A mixed soil sample of the upper 5 cm was collected at each grid point. The samples were sieved through a 2 mm mesh screen and about 10-15 g of each of the thoroughly mixed samples was oven-dried at 45°C for spectral analysis. The remaining parts of the soil samples were stored under field moist conditions at 4-6°C until analysis for microbial biomass and pH. On most of the 61 observation points per plot a soil sample could be taken. However, some positions are missing because of surface adjacent bedrock.

Laboratory measurements

Soil microbial biomass

C_{mic} and N_{mic} were analyzed by the fumigation-extraction method (Vance et al., 1987). Summarily, 7-8 g of field moist soil were fumigated in an exsiccator with ethanol-free $CHCl_3$. Afterwards, soluble C and N from fumigated and non-fumigated samples was extracted with 60 ml of 0.5 M K_2SO_4. C and N in the solution were measured with a C-N-analyser (multi N/C 2100S, analytikjena, Jena, Germany). Since not all of the C and N can be extracted, a k_{EC} factor of 0.45 (Joergensen, 1996) and a k_{EN} factor of 0.54 (Joergensen & Mueller, 1996) was used to convert microbial C and N flush into C_{mic} and N_{mic}, respectively.

Soil attributes

All samples were manually analyzed for pH. Therefore, 10 g of soil per sample was mixed with 25 ml of 1 M KCl. After 10 min, pH was measured in the solution using a pH-probe.

For the determination of C_{org} and N, sixteen equally distributed samples per plot (Figure 1) were measured with a C-N-analyzer (multi N/C 2100S, analytikjena, Jena, Germany).

Visible to near infrared diffuse reflectance spectroscopy

Each soil sample was scanned with an AgriSpec portable spectrophotometer equipped with a contact probe (PANanalytical, Boulder, Colorado) in the range of 350–2500 nm. Predictions of C_{org} and N content from the spectra were made using an existing spectral database of soils from a larger area in the East of Mt. Kilimanjaro. Partial least square regression (PLSR) was used to develop models for each parameter and plot, as it is a common method to predict soil properties from spectral data (Wold et al., 2001; Viscarra Rossel, 2007). The specific modeling scheme is based on an approach of Bogner et al. (2015). The models were validated on the sixteen soil samples with known C_{org} and N content.

Spatial modeling

Ordinary Kriging

OK uses the differences of values, depending on the distance to each other, to estimate the spatial autocorrelation structure (Krige, 1951; Matheron, 1963; Hengl, 2009). The semivariances *Y(h)* of these differences are calculated by:

$$Y(h) = \frac{1}{2} E\left[\left(O(s_i) - O(s_i + h)\right)^2\right] \qquad \text{Eq. 1}$$

where $O(s_i)$ is the target variable at the location s_i and $O(s_i+h)$ is the value at a distance h from the location s_i. Subsequently, the semivariances are summarized by their separation distance h (called lag) and a variogram model is fitted.

Variograms are interpreted via three main values: the range, the sill and the nugget. The range is the distance at which the variances between points are more or less equal to the variance of all observed values of the data-set and the sill is the total variance at the range distance. The nugget is the semivariance at zero distance or in other words is the variance of sampling points within distances smaller than the smallest sampling interval, including unknown measurement errors.

Finally, predictions are made with the formula

$$P(s_o) = \sum_{i=1}^{N} \left(\Omega_i(s_0) \cdot O(s_i)\right) \qquad \text{Eq. 2}$$

where $P(s_0)$ stands for the predicted value at location s_0, Ω is the spatial weighting function based on the variogram, $O(s_i)$ is the observation at location s_i and N is the number of observations. In other words, in OK the value at a location is calculated as a weighted linear combination of measured values at locations s_i (i = 1, 2, …, N).

Regression Kriging

RK combines linear regression (LR) with a variogram analysis of the model residuals (Hengl et al., 2004). First, a LR between the dependent and independent variables is calculated. Then the residuals *r* of this model are predicted at all locations of interest using their respective variogram parameters. The RK model resembles an LR model, but instead of using one constant error term, the residual variance is calculated as the sum of the predicted residuals, weighted by distance:

$$P(s_0)=\sum_{k=0}^{l} \alpha_k \cdot V_k(s_0)+\sum_{i=1}^{N} \omega_i(s_0) \cdot r(s_0) \qquad \text{Eq. 3}$$
$$with \;\; V_0(s_0)=1$$

where α_k are the estimated linear model coefficients, V_k is the k-th predictor variable and w_i are weights based on the variogram analysis of the residuals.

Geographically weighted regression

GWR also uses a LR model. However, instead of estimating only one set of regression parameters for all sampling positions combined, this approach allows local variations in relationships between response and explanatory variables (Brunsdon et al., 1996; Fotheringham et al., 2002):

$$P(s_0)=\alpha_0(s_0)+\sum_{i=1}^{l} \alpha_i(s_0) \cdot V_i(s_0)+\epsilon(s_0) \qquad \text{Eq. 4}$$

where s_o stands for the location of the i-th point. Based on the proximity of an observation to a point i, the correlation of this observation to point i is estimated by weighted least squares regression.

Spatial predictions and mapping

C_{org}, N and pH were chosen as possible co-variables, because they can either be easily acquired with Vis-NIR-DRS (C_{org} and N) or are easy and cheap to measure (pH) and are related to the target variables C_{mic} and N_{mic}. The approach of this study consist of several consecutive steps:

Step 1 We used OK to predict C_{org}, N, pH, C_{mic} and N_{mic} at every point in a regular grid (15 m x 15 m, spacing 0.625 m), resulting in a grid with a total of 625 grid points. We tested three different variogram model types, namely exponential, linear and spherical. The variogram model type for the respective variable was then selected based on the highest R^2.

Step 2 The auxiliary information of C_{org}, N and pH were used in RK and GWR to predict C_{mic} and N_{mic} on the same 625 locations as in Step 1.

Step 3 This step consists of the validation and comparison of the used spatial methods and is implemented within step 1 and 2. We used LOOCV to evaluate the different prediction techniques OK, RK and GWR. Having a small data-set, we chose to include all points in the modeling process an not to set aside an independent validation data-set. LOOCV has furthermore far less bias compared to the validation on an independent data-set (Davis, 1987). Therefore, each grid point with known microbiological values was left out once and predicted on the data-basis of the remaining observation points. This was repeated N times, where N is the number of available observations. In order to assess model accuracies of the different geostatistical methods we used R^2 and the $RMSE$. Furthermore, to compare prediction accuracies directly, the $RMSE$ was divided by the known standard deviation of the observed values $sd(o_i)$. The resulting relative root mean squared error of prediction $RMSE_r$ is scale independent. R^2, $RMSE$ and $RMSE_r$ are directly calculated from the LOOCV of the respective variable. Any errors in the estimation of the co-variables are thus not relevant at this point.

$$R^2 = 1 - \frac{\sum_{i=1}^{N} \left(p_i - o_i\right)^2}{\sum_{i=1}^{N} \left(o_i - \bar{o}\right)^2} \qquad \text{Eq. 5}$$

$$RMSE = \sqrt{\frac{1}{N} \sum_{i=1}^{N} \left(p_i - o_i\right)^2} \qquad \text{Eq. 6}$$

$$RMSE_r(\%) = \frac{RMSE}{sd\left(o_i\right)} \cdot 100 = \frac{\sqrt{\frac{1}{N} \sum_{i=1}^{N} \left(p_i - o_i\right)^2}}{sd\left(o_i\right)} \cdot 100 \qquad \text{Eq. 7}$$

p_i are the predicted values, o_i the observed values and $\bar{o}$ is the mean of the observed values, N is the number of observations.

All statistical analysis were done using R 3.0 (R Development Core Team, 2008) and the packages gstat (Pebesma, 2004), spgwr (Bivand & Yu, 2013) and automap (Hiemstra et al., 2009).

Results and Discussion

Spectroscopy

The PLSR models, that were developed based on the spectroscopic measurements, successfully predicted C_{org} and N content in our soil samples (Table 1). The calibration for both plots was satisfactory, however, the validation revealed better results for P_{slope} than for P_{plain}.

Descriptive Statistics

Basic descriptive statistics of all variables are summarized in Table 2. The median is more robust than the mean and was used to interpret the data. The within-plot variation of most of the variables is up to 1.8 times higher on P_{slope} than on P_{plain}, most probably due to shallow-to-no soil areas on the P_{slope}. C_{org}, N, C_{mic} and N_{mic} values on P_{slope} were generally higher than on P_{plain}. These results are in general agreement with previous studies of savannah ecosystems (Jones, 1973; Wang et al., 2009; Michelsen et al., 2004). However, the maximum C_{org} content of P_{slope} is unusually high with 73.6 g kg^{-1}. C/N ratios varied between 10.4 and 13.4 on P_{slope} and 10.7 and 13.3 on P_{plain} – with median values of 12.2 for both plots – which is similar to the findings of other studies (Jones, 1973; Hernández-Hernández & López-Hernández, 2002).

C_{mic} and N_{mic} showed overall similarities, with much higher and more variable values for P_{slope}. For Eastern Kilimanjaro, Pabst et al. (Pabst et al., 2013; Pabst et al., 2014) found C_{org} and N contents as well as C_{mic} in the same range as measured on P_{plain} in this study. Other studies reported C_{mic} values up to 0.8 g kg^{-1} for the topsoil of a

Table 1: Accuracy and error parameters for the calibration and validation of PLSR models for the prediction of C_{org} and N

Plot	Parameter	Calibration			Validation		
		N	RMSE	R^2	N	RMSE	R^2
		-	mg g^{-1}	-	-	mg g^{-1}	-
P_{slope}	N	91	0.49	0.75	16	0.40	0.85
	C_{org}	91	6.17	0.70	16	4.79	0.83
P_{plain}	N	91	0.31	0.76	16	0.23	0.63
	C_{org}	91	4.48	0.72	16	2.61	0.70

Table 2: Descriptive statistics for predictor and target variables

Plot	Parameter	Predictor variables			Target variables	
		C_{org}	N	pH	C_{mic}	N_{mic}
		g kg^{-1}	g kg^{-1}	-	g kg^{-1}	g kg^{-1}
P_{slope}	min	29.0	2.30	7.80	0.53	0.063
	max	73.6	5.87	8.65	3.01	0.348
	mean	42.0	3.46	8.29	1.40	0.157
	sd	9.4	0.68	0.19	0.70	0.079
	median	38.7	3.32	8.32	1.15	0.121
	mad	9.8	0.60	0.21	0.63	0.061
P_{plain}	min	18.8	1.63	6.28	0.20	0.027
	max	35.7	3.05	6.96	1.00	0.103
	mean	27.1	2.23	6.60	0.59	0.059
	sd	3.4	0.28	0.16	0.17	0.017
	median	27.0	2.22	6.58	0.58	0.058
	mad	3.2	0.21	0.16	0.15	0.018

wooded grassland, but were in general lower than our findings (Singh et al., 1989; Michelsen et al., 2004; Hernández-Hernández & López-Hernández, 2002). C_{mic} on the investigated plots is known to decrease significantly with the start of the wet season, hence would be in the same range as in the aforementioned publications (Pabst et al., 2013; Pabst et al., 2014). A study of savannah in the Serengeti, East Africa, reported C_{mic} content of up to 3.1 g kg^{-1} (Ruess & McNaughton, 1987) which corresponds to the very high C_{mic} contents found on P_{slope}.

The typical soil pH in savannah ecosystems is assumed to vary around values between 4 and 6 (Hagos & Smit, 2005; Hernández-Hernández & López-Hernández, 2002). In contrast, pH values found in this study are much higher, with values on P_{slope} exceeding pH 7, probably due to the parent material.

Spatial data analysis

Predictor variables – C_{org} , N and pH

The best predictive quality for C_{org} on P_{slope} was obtained with a linear variogram model (Figure 2). A spherical model for N content and an exponential model for pH

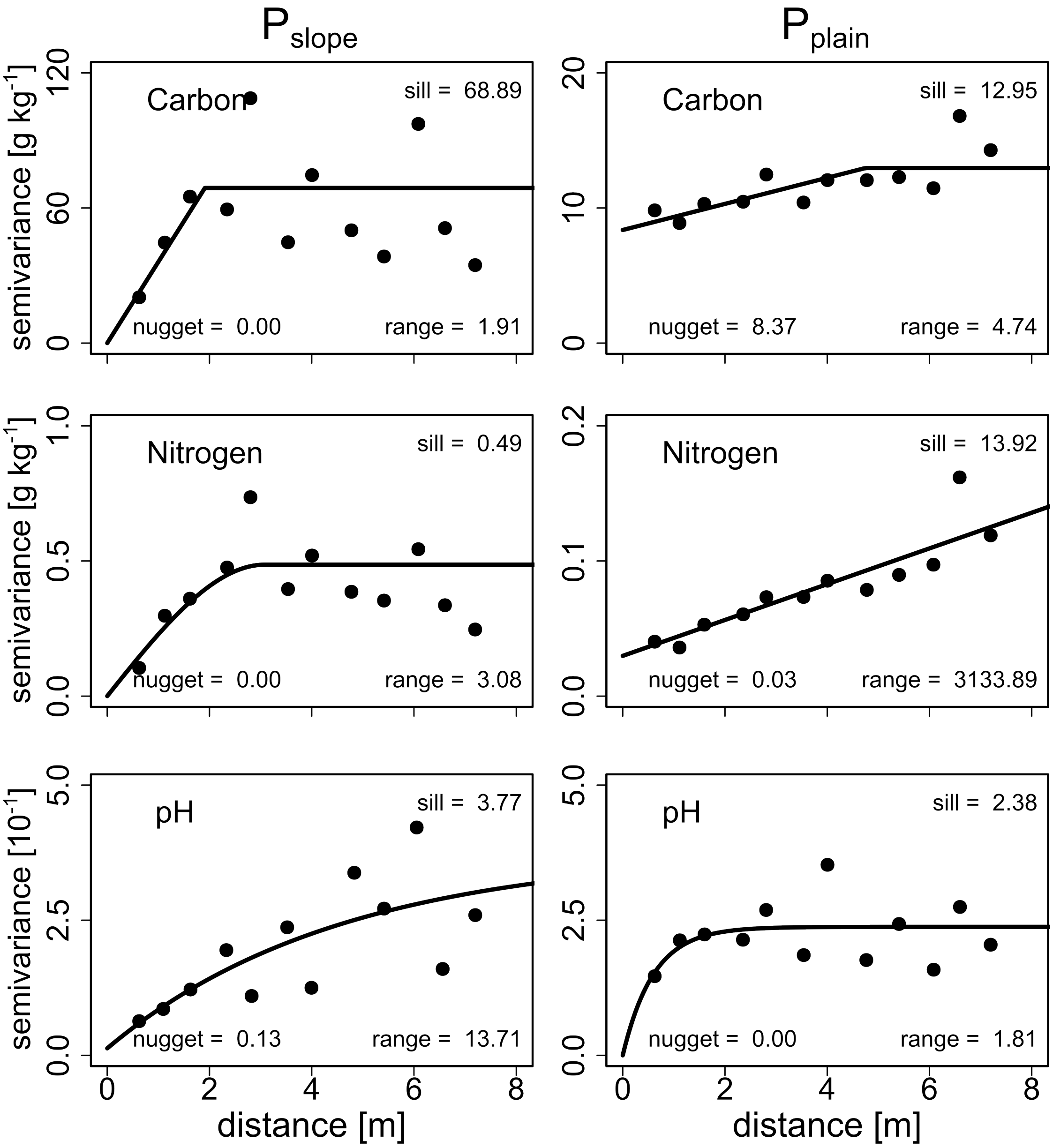

Figure 2: Variogram models of the predictor variables for P_{slope} and P_{plain}.

on P_{slope} were selected, respectively. For C_{org} on P_{plain} we chose a linear model and for N and pH an exponential model.

Both, C_{org} and N contents showed higher spatial ranges on P_{plain} (Figure 2), which were similar to ranges found in southern Africa savannahs (Wang et al., 2009). This indicates lower heterogeneity on P_{plain} since points are still correlated to each other, even at large distances. We predicted a very high range value for N on P_{plain} (3.13 km). Typically a variogram is computed up to one third of the maximal distance between points – in our case around 7 m. In greater distances, the number of point pairs and the quality of the experimental variogram decrease rapidly. We chose the variogram models based on the predictive quality and an exponential model was selected. In contrast, the best global fit to the data would likely be a linear variogram model with a range of 6.09 m and a sill of 0.01 m (data not shown). Both, the exponential as well as linear model follow a seemingly linear shape within the distance of 7 m and consequently the differences in predictions between these models are expected to be negligible. Wang et al. (Wang et al., 2009) assumed that a loss of woody vegetation and regional drying results in more heterogeneous soil pools. This acts as a possible explanation for the rather small ranges found for C_{org} and N on P_{slope}, since it was characterized by sparse woody vegetation, shallow soil depth and adjacent bedrock.

With the exception of pH, all parameters showed a low range on P_{slope}, indicating that values are not dependent on each other already at small distances. This is probably because of the patchy vegetation and the high heterogeneity of soil thickness. A consequence of the clustered sampling design was that the distance classes of the variogram models of P_{slope} often contained points clustered together at locations with either low or high vegetation cover, respectively. This resulted in high variation in the semivariances at higher distances and the high range (Figure 2). Including more points in the sampling design would probably strengthen the variogram and also lead to a lower range for pH on P_{slope}.

Due to the small sample size it was not possible to account for anisotropy of the data set and some of the variogram models showed a clear trend in the data, partly explaining the high ranges. The ratio of nugget/sill is an estimate of the spatial dependence within the investigated area. Both, low and high spatial dependencies were observed within the smallest sampling interval, whereas it stands out that for C_{org} on P_{plain} 65% of the total variance is explained by the nugget effect. For C_{org} on P_{slope} and N on both plots, the nugget effect was negligible (Figure 2). Yet, we can assume that some variability occurs within the smallest sampling interval of 0.625 m and/or measurement errors occurred in the analysis.

The observed spatial structures vary depending on sampling density across the study area (Mishra et al., 2010). Since we used the same sampling density/design in our study on both plots and for all variables, this indicates that the spatial structures of the investigated variables vary not only depending on sampling density but also because of local characteristics of the study sites.

Target variables – C_{mic}, N_{mic}

An exponential variogram model type was selected for C_{mic} on P_{plain} and N_{mic} on P_{slope} (Figure 3). For C_{mic} on P_{slope} a linear model and for N_{mic} on P_{plain} a spherical model was used, respectively. Similar to C_{org} and N contents, the sparse vegetation and patchy soil cover on P_{slope} resulted in lower ranges for C_{mic} and N_{mic} compared to P_{plain}. On both plots, N_{mic} showed ranges similar to the findings for savannah soil by (Wang et al., 2009). The nugget effects were zero on P_{slope}, and on P_{plain} they did not exceed 20% of the total variance. Consequently at least 80% of the spatial variation was explained by the chosen variogram model.

The linear regression models selected for RK and GWR are shown in Table 3. Since C_{org} is the main substrate for soil microbes, there are numerous studies linking C_{mic} to C_{org} (Singh et al., 1989; Michelsen et al., 2004). Similar, N_{mic} showed a good correlation with N as a predictor variable (Hernández-Hernández & López-Hernández, 2002).

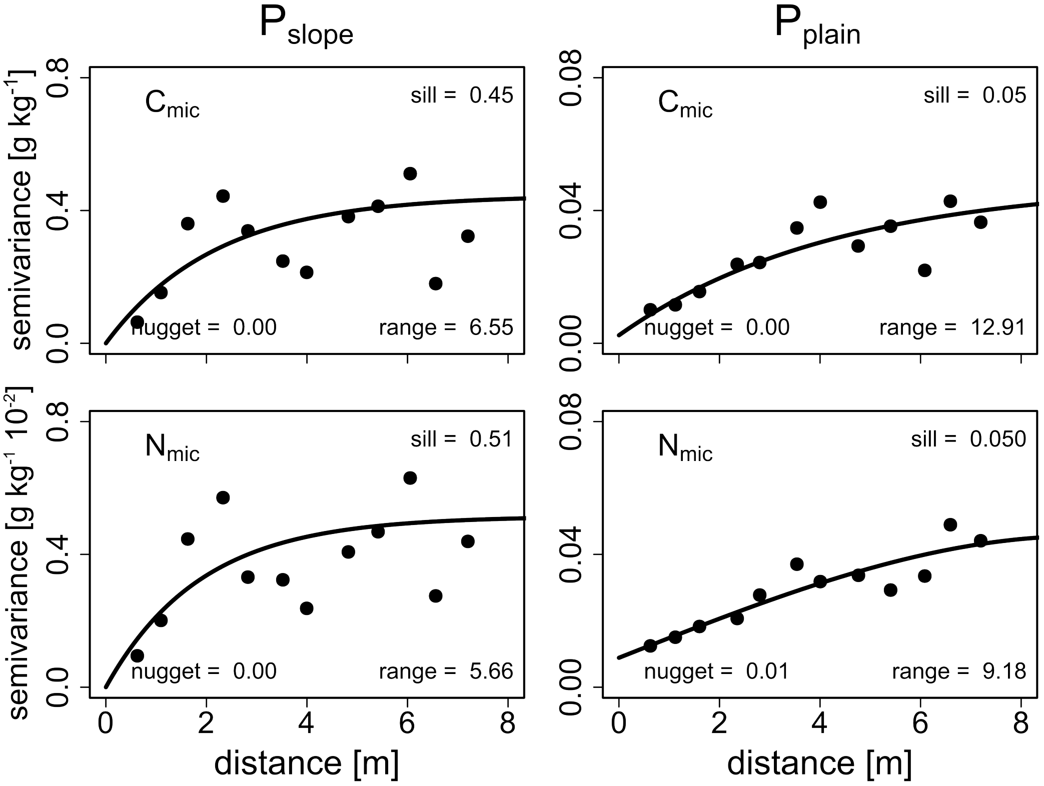

Figure 3: Variogram models for the target variables (C_{mic}, N_{mic}) for P_{slope} and P_{plain}.

Table 3: Selected regression models for RK and GWR prediction methods

Plot	Target variable	Predictor variables	*AIC$_c$*	*F* value		*p* value	R^2
P$_{slope}$	C$_{mic}$	C$_{org}$, pH	76.1	F(2,40)	50.1	< 0.001	0.71
	N$_{mic}$	N, pH	68.4	F(2,40)	63.8	< 0.001	0.76
P$_{plain}$	C$_{mic}$	clay, N	136.7	F(2,56)	25.8	< 0.001	0.43
	N$_{mic}$	N	148.6	F(2,58)	33.1	< 0.001	0.36

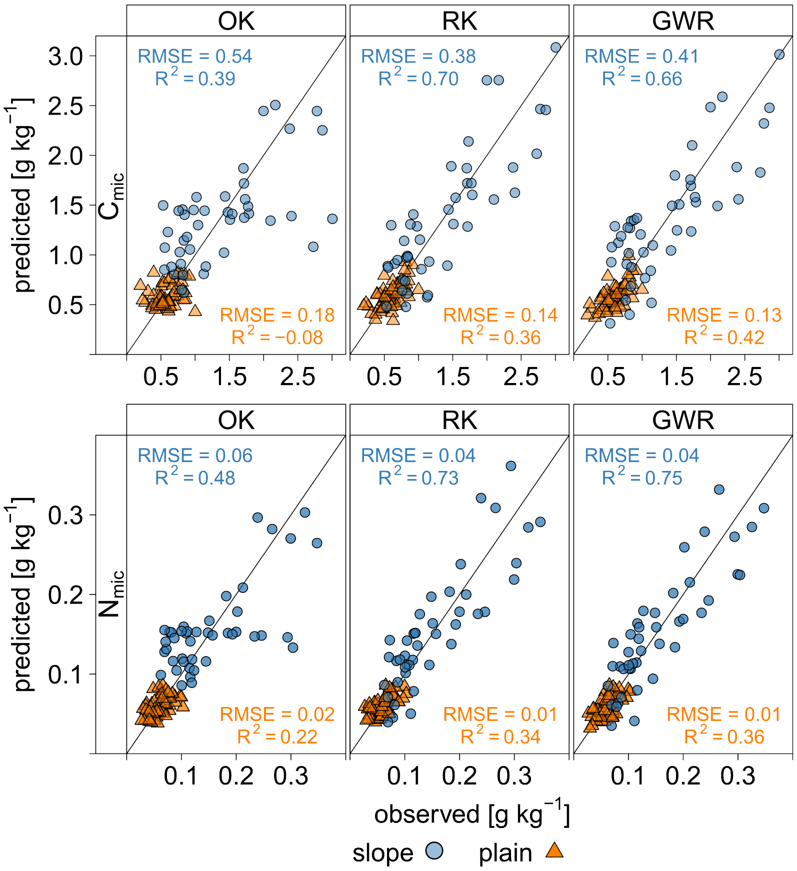

Figure 4: Observed versus predicted data of different geostatistical methods on P$_{plain}$ (orange) and P$_{slope}$ (blue)

Comparison of geostatistical methods

OK showed high *RMSE* and low *R^2* for both plots and variables, for C$_{mic}$ on P$_{plain}$ even <0. *R^2* was generally higher on P$_{slope}$ (Figure 4). The estimates improved when additional information in form of explanatory variables was used. *RMSE* values of RK and GWR were in a similar range and consistently lower than those of OK (Figure 4). Accordingly, *R^2* was increased by the use of RK and GWR (Figure 4). The improvement of prediction accuracy by using multivariate approaches – which is also the fact in this study – has been reported in several studies (Mishra et al., 2010; Li &

Heap, 2011; Mishra et al., 2012). For the calculation of C_{org} pools in the Midwestern United States, RK and GWR were seen as the best suited methods (Mishra et al., 2010). However, on P_{plain}, R^2 remained rather low even with the use of the multivariate prediction techniques since the variability within the observed data of P_{plain} was low. The ability of the presented two methods to improve the predictions, clearly showed the usefulness of including explanatory variables.

The $RMSE_r$ indicates the variation of prediction errors within the observed range of the sampled data. Is the variation in the observed data low, methods have to be more accurate to obtain low $RMSE_r$ values. Similarly, high variations in the observed data lead more easily to low $RMSE_r$ values. Compared to OK, the multivariate methods clearly improved the $RMSE_r$ on both plots (Table 4). However, the on-plot variation of the observed data was low on P_{plain} and consequently the $RMSE_r$ was still up to 86% for RK and GWR. For all target variables and both study plots, compared to OK the addition of explanatory variables in the models reduced the global estimation error (RI) by 8-31% (Table 4, $RI = (RMSE_{OK} - RMSE_N)/RMSE_{OK} \times 100$, where N is the respective new method). Nevertheless only very small to no differences could be observed in the accuracy of prediction between the different multivariate interpolation methods (Table 4). Since the prediction accuracy of RK and GWR clearly depend on available auxiliary information and their correlation to the response variables, a possible reason is that the deterministic component (LR) of RK was useful, but no spatial variation of the residuals was found to model in the geostatistical part of RK and to improve the prediction accuracy. In GWR it is possible to only use only a

Table 4: Error parameters for the prediction of C_{mic} and N_{mic} with methods OK, RK, GWR and the relative improvement (RI) by the use of RK, GWR for P_{slope} and P_{plain}.

Target variable	Method	P_{slope}		P_{plain}	
		$RMSE_r$ %	RI %	$RMSE_r$ %	RI %
C_{mic}	OK	77.12	-	103.28	-
	RK	53.99	29.99	79.62	22.90
	GWR	57.97	24.38	75.52	26.88
N_{mic}	OK	71.11	-	87.60	-
	RK	51.43	27.68	80.74	7.83
	GWR	49.24	30.76	79.39	9.37

subset of the available observations in the LR model. However, in our case, most or all of the observation points were included for both plots and variables. Hence the LR models of GWR are similar to the deterministic component in RK which results in similar accuracies of the two methods.

Maps

High levels of C_{mic} were observed at the upper-left corner of P_{slope} (Figure 5). A possible explanation is the presence of a mature individual of *Sclerocarya birrea*. Trees and shrubs in savannah ecosystems are known to have a great influence on nutrients and microorganisms (Vetaas, 1992; Wang et al., 2009). In dry savannah ecosystems, the C input through tree litter is restricted to the under canopy areas and trees, shrubs and grasses have a strong influence on the distribution and storage of C in soil (Wang et al., 2009; Northup et al., 1999). Compared to the remaining area of P_{slope}, different grass species occur within the tree's shading radius and a humus

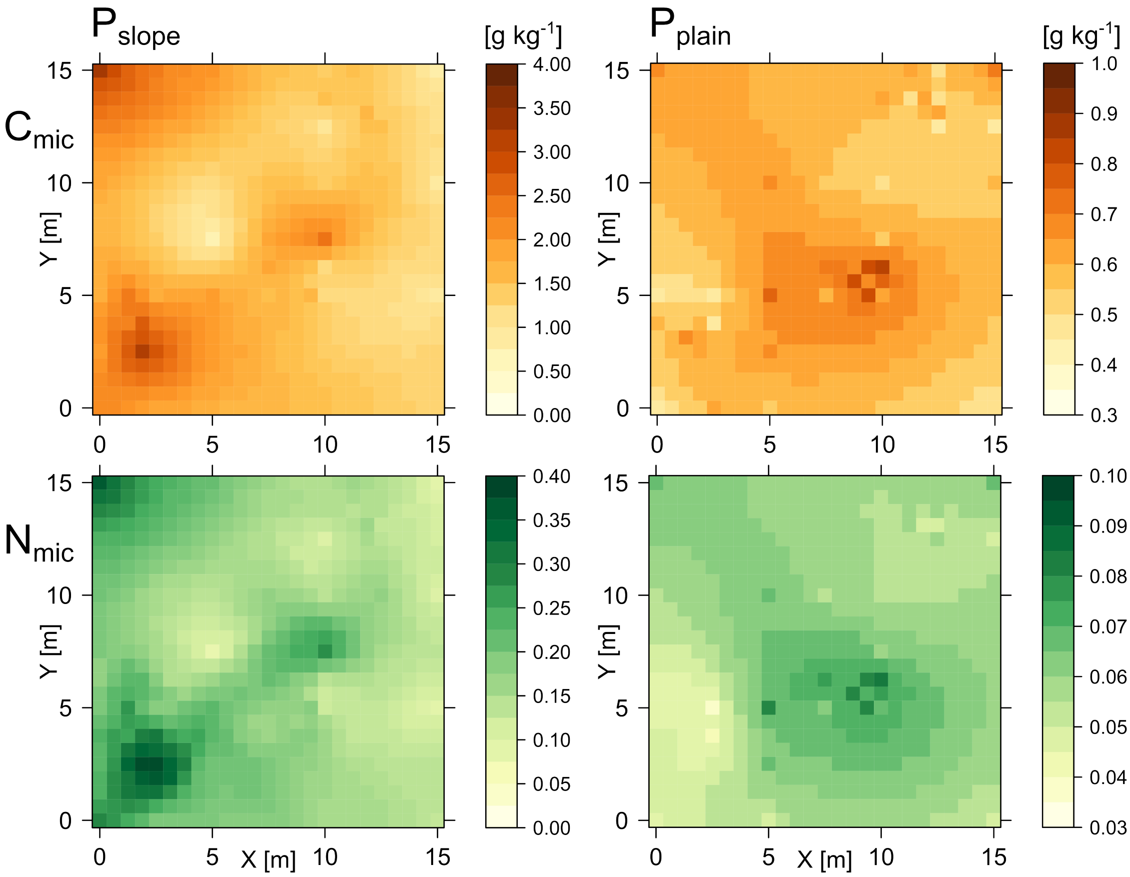

Figure 5: Maps of C_{mic} (top) and N_{mic} (bottom) for P_{slope} (left) and P_{plain} (right) produced by the method with the highest R^2 (here: GWR)

layer developed. Due to the high availability of substrate (C_{org}), higher amounts of C_{mic} could be observed. Also the heterogeneous terrain/soil structure of P_{slope} is replicated in the spatial distribution of C_{mic}. On this plot, rocks, shrubs and clusters of grasses act as a protection of erosion. In addition, dead plant material and plant exudates increase microbial growth, leading to higher microbiological activity and hotspots of soil quality in the vicinity of grass clusters. Low C_{mic} values were observed close to the areas with adjacent bedrock (Figure 5).

C_{mic} values of P_{plain} were generally lower than on P_{slope}, the pattern with higher values under trees and bushes however remained the same. In the middle of the plot a cluster of Acacia trees was observed, whereas the area in the upper right was only scarcely covered with grasses. Spatial distribution of N_{mic} showed very similar patterns as C_{mic} on both plots.

Conclusions

We have demonstrated that including additional variables (C_{org}, N, pH) improves the spatial prediction of soil microbial parameters such as C_{mic} and N_{mic}. The methods RK and GWR use the specific information provided by the parameters C_{org}, N and soil pH for higher accuracy of local prediction and/or less prediction errors. This study suggests multivariate methods for a satisfying estimation of soil microbial parameters and ecological interpretation of the local relationships. C_{org}, N and soil pH are seen as suitable variables to predict spatial relations of soil microbial parameters in savannah ecosystems of East Africa. The integration of soil parameters predicted with Vis-NIR-DRS proved useful. In combination with geostatistical methods, C_{mic} and N_{mic} can be predicted easily and with a minimum amount of laboratory analyses.

Until now, C_{mic} and N_{mic} are seldom included in the balance of land regeneration or sustainable land management projects. Since our approach is fast and applicable to the small scale as well as to the landscape level, it may increase the validity of these projects with an marginal increase of the costs and in surplus enable the detailed monitoring of temporal changes in parameters as well as in the heterogeneity.

Acknowledgments

This study was funded by the German Research Foundation (DFG) within the Research-Unit 1246 (KiLi) and supported by the Tanzanian Commission for Science and Technology (COSTECH) and the Tanzania Wildlife Research Institute (TAWIRI). For permission to conduct this study in its surrounding area, thanks goes to the Lake Chala Safari Camp. Additionally the authors want to thank T. Leipold, I. Otte, T. Appelhans, A. Ensslin and K. Schmidt for support in the field and in the laboratory.

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General Summary

Methodology

To obtain information on soil microbial properties, detailed studies were conducted on the southern slopes of Mt. Kilimanjaro. The study region extended from 950 to 3880 m a.s.l. and ranged from the Machame area in the West to Lake Chala in the East. A total of twelve ecosystems, representative for East Africa (Mayaux et al., 2004), were selected. The ecosystems were classified as natural, semi-natural and agricultural (for more detailed information, the reader is referred to Study 1 and 2). The basic soil properties (C, N, pH and bulk density) were determined per horizon on all plots. C_{mic} and N_{mic} was sampled in depths of 0-10, 10-20, 20-30, 30-50 cm and analyzed with the chloroform fumigation method (Vance et al., 1987). Soil cores were incubated at site-specific mean annual temperature (MAT) and different moisture levels for CO_2 efflux measurements. A detailed heterogeneity study on the spatial patterns of C_{mic} and N_{mic} was conducted in a savannah ecosystem. Factors controlling soil microbial biomass at Mt. Kilimanjaro were identified (Figure B) and their effects on soil microorganisms were statistically evaluated.

Results

Elevation distinctly influences temperature and precipitation along the slopes of Mt. Kilimanjaro and thus, in a way, represents climate. Elevation therefore was used to investigate the climatic effect on soil microbial biomass. The C_{mic} and C_{org} contents in surface soils of the investigated ecosystems along the elevation gradient varied widely. Study 1 detected a positive linear dependency of C_{mic} and WOC contents versus elevation on Mt. Kilimanjaro. Furthermore, a decline in colder climates (synonymous to higher elevation) was assumed and later confirmed in the context of

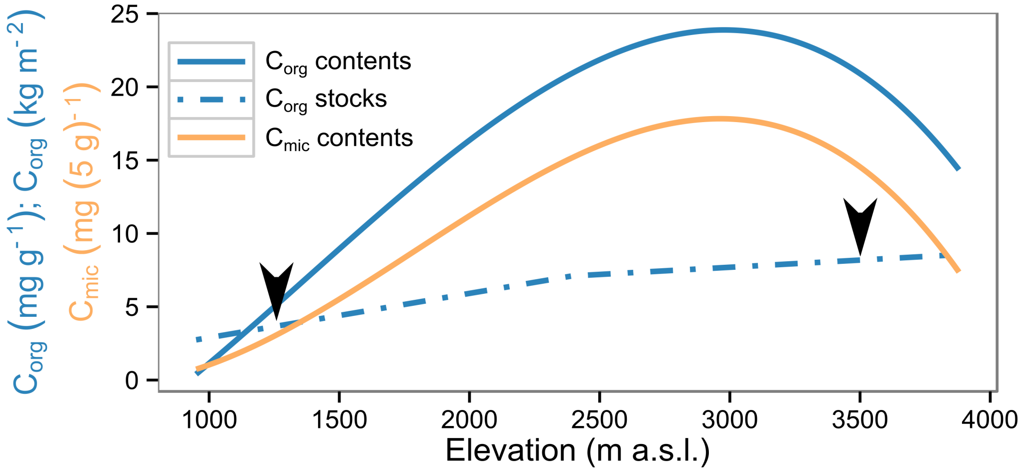

Figure C: Regressions fitted to the contents / stocks of C_{org} (blue, solid / blue, dashed) and the contents of C_{mic} (orange, solid) along the elevation/climate gradient of Mt. Kilimanjaro. Black arrows indicate possible overestimation of C_{org} stocks, based on the assumptions by Ellert & Bettany (1995).

Study 2. Hence, the investigated C contents follow a hump-shaped distribution along the climate/elevation gradient. Besides total maxima in C_{org} and C_{mic} contents, the warm-humid forest belt between 2000 and 3000 m a.s.l. exhibited also the strongest negative trends in C contents with depth, both attributed to the organic rich soil horizons of the forests. Cold ecosystems at highest elevations (~4000 m a.s.l.) showed contents in the medium range, whereas the minima were observed in the hot and dry ecosystem at low elevations (Figure C). The mathematical product of C contents and bulk densities are the stocks. The stocks of C_{org} in the upper soil layer (18 cm) increased depending on water availability, temperature and NPP (Study 2). In the elevation range of ecosystems with a more arid character, stocks increased by 3 kg m^{-2} per 1000 m in elevation. In soils of humid ecosystems at higher elevations, this increase in C_{org} stocks was reduced to 1 kg m^{-2} per 1000 m (Figure C). The variability in C_{mic} and WOC contents during the climatic transition phase from dry-to-wet season was addressed in Study 1. The beginning of the wet season resulted in a decrease of C_{mic} and an increase in WOC. With ongoing precipitation, WOC contents declined to levels of the dry season. This temporal variability was independent of land use, but was stronger in soils at lower elevations. This was attributed to the pronounced contrast between climatic dry and wet seasons and their associated vegetation periods. A similar pattern was observed for the soil CO_2 efflux and q_sCO_2

under increased precipitation in Study 2. Compared to soils in the warm-humid climates of the forests, the increase of both parameters was markedly more pronounced in soils of the dry ecosystems at low elevations. However, this difference is likely biased due to the high human population and land use intensity at elevations below the boarder of the National Park.

The intensity of land-use practices decreased with increasing elevation: from maize-fields at low elevations, via the traditional sustainable use of homegardens, to the ecosystems protected by the National Park at elevations >2000 m. Contents and stocks of C_{org} and C_{mic} were altered by human influences on the ecosystems. Throughout the studies, they were lower in soils of managed ecosystems than in soils of presumably undisturbed habitats in the National Park. The pure effect of land use was illustrated by two land use conversions typical for the region and on a similar elevation/climatic level: savannahs are used for maize cultivation and homegardens which were formerly forested land are transformed to coffee plantations. The more intensive land use lead to a decline in the contents and stocks of C_{org} and C_{mic} and to an increase in WOC. In relation to C_{org}, the more sensitive parameters of C_{mic} and WOC were more strongly influenced by the negative effect of land use, which has also been observed for other tropical soils (e.g. Waldrop et al., 2000). Since land management (e.g. tillage, harvest) concentrates on the soil surface, these losses were especially pronounced in the upper soil layers which resulted in a narrow depth distribution. Compared to the soils of less disturbed ecosystems, the amount of available substrate (C_{mic}:C_{org} ratio) was reduced up to three times by the intensive agricultural management. In addition and independent of two simulated precipitations, soil CO_2 efflux and q_sCO_2 in soils of agricultural fields were up to four times higher than in the soils of less disturbed ecosystems.

The detailed heterogeneity study in the savannah ecosystem revealed small-scale patterns of basic soil parameters and soil microbial biomass. Despite of being only 400 m apart, contents varied several-fold between and within 15 × 15 m plots. The relief had an effect on the spatial variation of C_{org}, N, clay content, soil pH as well as C_{mic} and N_{mic} contents. Most of this variation occurred within a perimeter of less than 13 m in the plain and 4 m on the slope, respectively. This variation was predicted using several geostatistical methods and visible to near-infrared diffuse reflectance spectroscopy enabled easy measurements of basic soil parameters (C_{org}, N, clay content and pH). The correlations of these soil parameters to soil microbial biomass enhanced the prediction accuracy of the geostatistical models for C_{mic} and N_{mic}.

Discussion and conclusions

The effects of land use and elevation on the investigated soil properties cannot be fully distinguished. This is due to an overlapping of land use and elevation gradients. The single effect of elevation could only be observed starting from the National Park upwards (>2000 m a.s.l.). At lower elevations, land use was likely the predominant factor for changes in soil properties.

The strong climate dependent net primary productivity (NPP) on the southern slopes of Mt. Kilimanjaro was found to follow a hump-shaped distribution with elevation – indicated by the biomass and structure of the vegetation (Ensslin et al., 2015; Rutten et al., 2015). A similar distribution was observed for the contents of C_{org} and C_{mic}, which are clearly influenced by the NPP (Figure C). In the forest belt between 2000 m and 3000 m a.s.l., climate conditions promote the highest NPP found at Mt. Kilimanjaro. Soils of highly productive ecosystems contain high amounts of soluble organics and microbial biomass (Bruijnzeel & Veneklaas, 1998; Heaney & Proctor, 1989) and the accumulation of litter on the forest floor leads to formation of organic horizons (Zech et al., 1997). Schrumpf (2004) reported high C_{org} contents in soils of montane forests at Mt. Kilimanjaro, which is in accordance with the maximum of the hump-shaped distribution along the elevation gradient (Figure C). Climate and the associated NPP are decisive factors for the vegetation's composition on Mt. Kilimanjaro (Hemp, 2006a). Lower temperatures and rainfall at higher elevations lead to a decline in plant and microbial productivity (Blume et al., 2002; Zech et al., 1997). This is shown in the decline of C_{org} and C_{mic} contents from *Podocarpus* forest (~3000 m a.s.l.) to *Erica* forest and *Helichrysum* (~4000 m a.s.l.). The extreme climatic conditions and very low productivity at an elevation of 5000 m a.s.l. in the Peruvian Andes, lead to low C_{mic} contents (King et al., 2008) and support the C_{mic} values found in the *Helichrysum* ecosystem at Mt. Kilimanjaro.

Due to its isolated position, Mt. Kilimanjaro decisively influences the climate in its region. Tropical montane forests normally have a low seasonal variability of temperature and precipitation (Buytaert et al., 2011). This is also true for forests on Mt. Kilimanjaro which are situated in an elevation range with more or less consistent precipitation throughout the year (Sarmiento, 1986). These near constant climatic conditions also have an effect on the soil microbial properties, explaining the negligible effect of the climatic transition phase and the smaller increase in C_{org} stocks with elevation. However, ecosystems at lower elevations (e.g. maize field and savannah), are characterized by a semi-arid climate with strongly seasonal precipitation. In these highly seasonal ecosystems, changes in water-availability may result in rapid changes in C_{mic} and WOC (Austin et al., 2004). The overall magnitude of climatic variability during the year, which is strongly depending on elevation, is therefore assumed to be the major aspect controlling the reaction of C_{mic} and WOC during climatic transition phases.

As described above, differences in climate and NPP result in low organic contents in soils above and below the forest belt of Mt. Kilimanjaro. Similarly, the same factors also strongly influence the soil C stocks as the fitted linear regressions were reminiscent of the adiabatic lapse rates along the elevation gradient (Figure C). Due to the distinct dry and wet seasons at low elevations, soil moisture presumably is a limiting factor for some time during the year (Otieno et al., 2010). In addition, limitation in water availability was indicated as higher simulated precipitation resulted in markedly higher q_sCO_2 in soils of dry ecosystems. An increase in elevation leads to lower temperatures and higher water saturation of the air packages, resulting in more or less consistent rainfall throughout the year (Buytaert et al., 2011; Sarmiento, 1986). Such constant humid climate leads to high NPP, vegetation growth and the formation of organic soil horizons (Zech et al., 1997). High C_{mic}:C_{org} ratios and WOC contents indicate a high substrate availability in these organic horizons. However, the observed changes in C_{org} stocks at Mt. Kilimanjaro are likely to be biased, since no correction to an equivalent soil mass was conducted (Ellert & Bettany, 1995). With no correction done, the C_{org} stocks might have been overestimated in soils of ecosystems above and below the forest belt (Figure C).

Besides the response on increased rainfall in dry ecosystems, q_sCO_2 showed no direct correlation to elevation/climate. In general, the protected ecosystems of the National Park showed smaller q_sCO_2 than ecosystems at lower elevations.

Supporting these results, Mganga & Kuzyakov (2014) discovered that microorganisms in forest soils of Mt. Kilimanjaro have comparably slow decomposition rates of easily available substrates. This indicates microorganisms of high efficiency with a low energy demand, compared to the ecosystems at lower elevations. The combination of high C contents and stocks, high substrate availability (C_{mic}:C_{org} ratio) and soil microbial efficiency further points to a closed nutrient and C cycle and consequently a steady-state of these ecosystems.

Investigations of land-use effects were concentrated on the highly populated areas below 2000 m a.s.l., since the National Park protects the ecosystems located at higher elevations from most anthropogenic influences. Human-induced disturbances of ecosystems around Mt. Kilimanjaro mainly consist in conversions of savannah to maize fields (~1000 m a.s.l.) and homegardens to coffee plantations (~1300 m a.s.l.) (Soini, 2005). The results show that both conversions negatively altered basic and microbial soil properties (C_{org}, C_{mic}), with up to 4-fold decreases in contents and stocks, respectively. This is in accordance with the general knowledge that cultivation of natural ecosystems leads to a decline of C_{org} contents. Losses in a similar range have been reported in several other studies (Dinesh et al., 2003; Don et al., 2011; Waldrop et al., 2000). The major factor for the C_{org} and C_{mic} decreases in soils of Mt. Kilimanjaro were changes in substrate input and quality. The decline in C_{mic}:C_{org} ratio indicates a decrease in litter diversity and substrate availability in both intensively used ecosystems (maize field, coffee plantation). Similar to the results of this thesis, other studies on land-use change reported lower C_{org} and C_{mic} contents, due to a change in amount and quality of organic matter input (Burton et al., 2010; Dinesh et al., 2003). Attention should be paid to the conversion of *Chagga* homegardens. This is a secondary change in land use, since the original natural habitat was lower montane forest (Mbonile et al., 2003; Mwasaga, 1991). Currently, no natural ecosystems are remaining on the elevation level of coffee plantations and as a consequence no direct comparisons are possible. However, it is assumed that soil C contents and stocks of the natural ecosystem originally were higher as they are in homegardens today.

q_sCO_2 has been widely applied in the assessment of cultivation practices (Yan et al., 2003). Higher land use intensity resulted in an increase of q_sCO_2 which was attributed to the change in management, substrate availability and the associated decrease in C_{mic}. Beside these factors, q_sCO_2 is determined by the decomposition rate of available substrate. The process of decomposition of easily available substrate in soils of intensively managed ecosystems is fast (Mganga & Kuzyakov, 2014). Compared to ecosystems with a more natural character, the high q_sCO_2 and the fast decomposition in intensively managed ecosystems suggests a higher nutrient demand but lower nutrient use efficiency in soils under agricultural land use. The low contents and stocks of C_{org} and C_{mic}, the low substrate availability (C_{mic}:C_{org} ratio) and low soil microbial efficiency, indicate open nutrient and C cycles in the agricultural used soils. Consequently, the contents and stocks of C_{org} and C_{mic}, as well as the soil quality and fertility, are assumed to decline further in the future until eventually a new lower equilibrium and a steady-state in soils is reached. The effects of land use on soil C_{org} and soil microbial parameters were more pronounced for the conversion of homegarden to coffee plantation (~1300 m a.s.l.) than for savannah to maize field (~1000 m a.s.l.). Based on the change in climate, NPP and C cycling with increasing elevation, it can be concluded that C_{org} and C_{mic} in soils at higher elevations are especially prone to (possible) changes in land use.

The small-scale variation and heterogeneity in soils of savannah ecosystems East of Mt. Kilimanjaro could partly be traced back to dry conditions and minor woody vegetation prevalent (Wang et al., 2009). The presence of trees was reported to have a positive effect on C_{org} and C_{mic} contents of soil within the trees' shading radius (Isichei & Muoghalu, 1992). A similar relationship was observed in the detailed heterogeneity study (Study 3), where distinctly higher C_{org} and C_{mic} contents were found in soils under the canopy of trees. The relief, or more specifically the slope and soil depth, were identified as additional important factors influencing the spatial distribution of basic soil parameters and soil microbial biomass. Also, on the small-scale, basic soil parameters (C_{org}, N clay content, pH) are controlled by factors such as climate, NPP (vegetation) and relief. Furthermore, the spatial heterogeneity of soil microbial biomass is decisively influenced by these basic soil parameters.

Consequently, these variables provide additional information for the multivariate spatial prediction of soil microbial parameters in savannah soils and improve the calculations' accuracy.

Climate, NPP and agricultural management were the main drivers affecting the soil microbial biomass in soils of Mt. Kilimanjaro. Climate and conversions of land use are independent of each other but both distinctly influence the NPP and/or vegetation of an ecosystem.

Adjusted to the distribution of the NPP, the contents of C_{org} and C_{mic} follow a hump-shaped form along the mountain's elevation gradient. C_{org} stocks are closely linked to the water availability or aridity of the ecosystem and are assumed to follow a sigmoid distribution. The national park protects ecosystems above 2000 m a.s.l. from human influences and the warm and humid climate supports high NPP, contents and stocks of C_{org} and C_{mic} as well as increased substrate availability. Because of consistent humid conditions, soil moisture is not a limiting factor for microbial growth and activity at higher elevations. This is in contrast to the hot and dry ecosystems at lower elevations, where a distinct seasonality in precipitation affects NPP and consequently also C_{org} and C_{mic} in soils.

The intensive land use on the mountain's lower slopes negatively alters important and sensitive parameters within the C cycle. The lack of available substrate in intensively managed surface soils increases the energy demand of soil microorganisms while decreasing their substrate use efficiency. This further diminishes the already declined contents and stocks of C_{org} and C_{mic} and indicates an open nutrient and C cycle. In contrast, soils of natural and less disturbed ecosystems are characterized by effective, closed nutrient and C cycles in a steady-state, but are nevertheless highly vulnerable to the negative consequences of land-use change.

On a small-scale, vegetation and relief are the major factors influencing the spatial heterogeneity of basic soil parameters as well as soil microbial

biomass. Because of their correlation to soil microbial biomass, basic soil parameters (e.g. C_{org}, N) provide additional information in multivariate prediction techniques and are able to increase the calculation's accuracy.

Future perspectives for Mt. Kilimanjaro

Based on recent projections of the expected climate change, a warmer and wetter climate will develop in East Africa (IPCC, 2014). In this context, two major schemes can be distinguished: (1) an increase in extreme rainfall events during the wet seasons and (2) less severe drought events during the dry seasons (Shongwe et al., 2010).

High elevations amplify the increase in temperature, meaning that locations at higher elevations will experience a stronger warming compared to locations at low elevations (Gutzler, 1992; Schneider et al., 1999). In today's climate, the medium temperatures and high water contents in Mt. Kilimanjaro's forests lead to lowered microbial activity (Zech et al., 1997), but do not affect the content of soil microorganisms (Blume et al., 2002). The projected increase in temperature will influence the microbial activity in these systems and will lead to an enhanced mineralization and release of CO_2 from soil. In addition, future higher CO_2 concentrations might enhance NPP, leading to an additional supply of new substrate. Enhanced mineralization and substrate availability will change the extent and rate of the C cycle and possibly affect the steady state in soils of ecosystems within the National Park. This is of major concern, since these ecosystems are essential for the local climate and water balance in the region (Schrumpf, 2004).

An increase in the annual mean soil moisture levels and a generally wetter climate might be seen by the people of the Mt. Kilimanjaro area as a blessing, since the contrast between dry and wet seasons will be reduced in the densely populated ecosystems at lower elevations. More favorable conditions for soil microorganisms increase microbial activity and may lead to higher CO_2 efflux rates and a loss of SOM. Erosion-prone agricultural land will be further degraded by the increase of extreme rainfall events (Våje et al., 2005). Eventually a new equilibrium will be reached in soils under agricultural management. Until then, the contents and stocks of C_{org} and C_{mic} are assumed to decline further. To satisfy the growing population with enough food, the demand for mineral fertilizers is assumed to multiply. Pressure on the boarders of the National Park will increase, but land-use conversions will mainly concentrate on lower elevations when the habitats of bushland and savannah are lost and used for agricultural production.

Future studies on the C as well as nutrient cycle and turnover in ecosystems of Mt. Kilimanjaro are necessary to assess the full magnitude of these projected changes. It is of topmost importance that, based on these studies, sustainable land management practices are developed and adopted in the region of Mt. Kilimanjaro.

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Acknowledgments

First of all, I want to express my gratitude to my supervisor, Prof. Dr. Yakov Kuzyakov, for the opportunity of conducting the studies at Kilimanjaro, for many discussions, ideas and comments as well as for the help provided throughout the duration of this thesis.

I also would like to thank Prof. Dr. Ingolf Steffan-Dewenter for providing the possibility to manage the research station in Nkweseko. It enabled another view on how research is, or should be, conducted and showed a possible future field of work.

Thanks goes to the German Research Foundation (DFG) for financing the KiLi-Project (DFG Research-Unit 1246). Furthermore I want to thank the authorities for their support during the studies, specifically the Tanzanian Commision for Science and Technology (COSTECH), the Tanzanian Wildlife Research Institute (TAWIRI), the Kilimanjaro National Park (KINAPA) and the Lake Chala Safari Camp.

My heartfelt gratitude also goes to all of the Kweba family in Morogoro! Not only for making my first long-time stay in Africa unforgettable, but also to be there as my “Tanzanian family” and dear friends where I am always welcome. I am proud to call the house with the green roof my home!

A special friendship developed to the Mtaturu/Filemony family. We worked together, laughed together, discussed together and much more. Thank you, Ayubu, Rafiki, Eliza, Eva and especially Fortu, for making my “second” Tanzanian home.

Honestly, I don't know how to start mentioning all the friends and colleagues of the numerous wonderful stays in Tanzania. Anyway I try: Augusti, Wilbard, Ringo, Massam, Samuel, the Mushi family, George, J4, Chaky, Mama Tuma, Baba Msanya, Maromboso, Ramson, Jimmy, Alexi, Amini. But also Alice, Andi, Gemma, James, Stefan, Maria, Juliane, Julia, William, Toni, David, Anna, Friederike, Marcel, Tim, Ephraim, Thomas and all the others. We were a wonderful team and had a lot of fun!

I also want to thank my colleagues and friends from Bayreuth and Göttingen. Especially Anna, Kevin, Carolin, Marleen, Michl, Alexandra, Max, Joscha and Silke for valuable comments on manuscripts and this thesis. Anna and Linda for sharing the office and nice times and Karin for helping with the work in the lab. I won't mention all the others, but be aware that I didn't forget you...

And obviously last but **never** least: my family! They always supported me and were convinced that I will find my way. Thanks goes to my Dad as we had numerous interesting and funny discussions about statistics and general research topics.

Appendices

Additional manuscripts and publications, not included in the dissertation

- Kühnel, A., Bogner, C., Pabst, H., Huwe, B., 2013. Visualizing small scale variability of clay content on soils at Mt. Kilimanjaro by VIS-NIR spectroscopy. In: Gebbers, R., Lück, E., Rühlmann, J. (Eds.): 3rd Global Workshop on Proxmial Soil Sensing 2013. (Bornimer Agrartechnische Berichte, 82), Potsdam-Bornim, Germany, pp. 123–128.

- Becker, J., Pabst, H., Mnyonga, J., Kuzyakov, Y. (under review) Litterfall dynamics and nutrient deposition depending on elevation and land use at Mt. Kilimanjaro, Biogeosciences

Site specific data

In the following Appendix, specific data of the different investigation sites are provided. This thesis was prepared in a research group, containing several subgroups and professional disciplines. Several data used in this thesis was provided by members of other subprojects, as listed below.

Data	Provided by	Affiliation
Mean annual precipitation (MAP)	Dr. Tim Appelhans[1]	Environmental Informatics, University of Marburg, Germany
Characteristics of soil profiles, soil texture and soil water contents at different matrix potentials	Anna Kühnel	Soil Physics Group, University of Bayreuth, Germany
Soil CO_2 efflux	Friederike Gerschlauer	Institute of Meteorology and Climate Research, Atmospheric Environmental Research, Karlsruhe Institute of Technology, Germany
Vegetation details	Dr. Gemma Rutten[2]	Institute of Plant Sciences, University of Bern, Switzerland
Vegetation details, aboveground biomass	Dr. Andreas Ensslin[3]	Institute of Plant Sciences, University of Bern, Switzerland

Mean annual temperature was obtained from the publication below.

- <u>Mean annual temperature (MAT)</u>

  Duane, W.J., Pepin, N.C., Losleben, M.L., Hardy, D.R., 2008. General characteristics of temperature and humidity variability on Kilimanjaro, Tanzania. Arct. Antarct. Alp. Res. 40 (2), 323–334.

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[1] Appelhans, T., Detsch, F., Otte, I., Mwangomo, E., Nauss, T., Hemp, A. (in preparation). Eco-climatic and land-cover characteristics across 12 land-cover types at Mt. Kilimanjaro. To be submitted to Erdkunde.

[2] Rutten G, Ensslin A, Hemp A, Fischer M. 2015. Forest structure and composition of previously selectively logged and non-logged montane forests at Mt. Kilimanjaro. *Forest Ecology and Management* **337**: 61–66. DOI 10.1016/j.foreco.2014.10.036.

[3] Ensslin A, Rutten G, Pommer U, Zimmermann R, Hemp A, Fischer M. 2015. Effects of elevation and land use on the biomass of trees, shrubs and herbs at Mount Kilimanjaro. Ecosphere **6**: 45. DOI 10.1890/ES14-00492.1.

Coffee plantation (COF)

Ecosystem:	Coffee plantation
Land-use class:	Agricultural (intensive)
Disturbance:	Monoculture, pesticides, fertilization, soil compaction

Coordinates (UTM):	313226 / 9641160
Elevation:	1300 m a.s.l.
Vegetation:	*Coffea arabica*
MAT:	20.3°C
MAP:	1485 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-4	22.7	2.1	10.5	4.24	0.99 ± 0.03
4-20	16.6	1.7	10.0	4.31	1.07 ± 0.08
20-40	15.5	1.6	9.6	4.38	1.13 ± 0.03
40-60	11.4	1.3	8.6	4.68	0.96 ± 0.06
60-80	9.9	1.2	8.2	4.86	0.92 ± 0.02
80-100	8.0	1.0	7.9	4.94	0.90 ± 0.02

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	256.41 ± 106.51	874.63 ± 159.58
10-20	166.51 ± 64.72	807.79 ± 202.42
20-30	140.31 ± 70.82	686.74 ± 194.92
30-50	108.78 ± 45.07	636.93 ± 157.54

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	$Quantile_{25\%}$	$Quantile_{75\%}$	Median	$Quantile_{25\%}$	$Quantile_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	46.82	35.93	61.07	2.00	1.71	2.08

Aboveground biomass type	[Mg ha^{-1}]
Herbs	0.8
Shrubs	2.5
Trees	27.6
Total standing biomass	30.9

Depth	clay	silt	sand	water content (θ) at different matrix potentials				
[cm]	[%]	[%]	[%]	$\theta_{1.0}$ [%]	$\theta_{1.5}$ [%]	$\theta_{1.8}$ [%]	$\theta_{2.0}$ [%]	$\theta_{4.2}$ [%]
0-4	61	33	6	50.7	43.9	39.4	36.7	24.4
4-20	62	31	7	51.0	47.0	42.8	40.1	29.5
20-40	62	33	5	52.2	49.8	45.5	42.7	31.5
40-60	63	31	6	52.0	46.3	38.7	34.8	29.7
60-80	63	32	5	53.3	48.3	42.7	39.2	23.1
80-100	60	36	4	52.5	50.3	43.5	39.2	23.8

Erica forest (FER)

Ecosystem:	*Erica* forest
Land-use class:	Natural
Disturbance:	-
Coordinates (UTM):	310164 / 9659637
Elevation:	3880 m a.s.l.
Vegetation:	*Erica trimera*
MAT:	6.8°C
MAP:	1188 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-10	150.4	8.7	17.2	4.54	0.38 ± 0.14
10-22	118.1	6.8	17.4	4.54	0.33 ± 0.05
22-33	101.0	5.8	17.4	4.64	0.59 ± 0.09
33-45	49.2	3.1	15.9	4.81	0.71 ± 0.10

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	1571.29 ± 522.25	1390.48 ± 259.73
10-20	393.80 ± 102.51	1388.71 ± 142.90
20-30	394.73 ± 278.06	1790.78 ± 263.25
30-50	346.06 ± 45.38	2027.65 ± 74.50

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	$Quantile_{25\%}$	$Quantile_{75\%}$	Median	$Quantile_{25\%}$	$Quantile_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	20.31	13.72	27.72	0.31	0.22	0.43

Aboveground biomass type	[Mg ha^{-1}]
Herbs	9.5
Shrubs	NA
Trees	NA
Total standing biomass	NA

No soil texture and no soil water contents at different matrix potentials available.

Grassland (GRA)

Ecosystem:	Grassland
Land-use class:	Semi-natural
Disturbance:	Cutting, mowing, grazing

Coordinates (UTM):	305222 / 9648626
Elevation:	1660 m a.s.l.
Vegetation:	no information available
MAT:	18.3°C
MAP:	1878 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-17	148.6	10.0	14.8	4.59	0.44 ± 0.01
17-26	96.9	7.3	13.3	4.70	0.56 ± 0.06
26-44	88.1	6.1	14.4	4.70	0.46 ± 0.02
44-59	84.5	5.9	14.4	4.77	0.45 ± 0.03
59-79	68.6	5.0	13.7	4.99	0.41 ± 0.02
79-100	70.4	4.9	14.3	5.02	0.41 ± 0.03

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	1221.40 ± 202.97	1966.24 ± 231.66
10-20	696.82 ± 141.17	1811.87 ± 304.76
20-30	551.09 ± 160.10	1987.30 ± 332.77
30-50	461.00 ± 152.80	2031.91 ± 378.30

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	Quantile$_{25\%}$	Quantile$_{75\%}$	Median	Quantile$_{25\%}$	Quantile$_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	54.64	34.59	67.49	0.60	0.58	1.05

Aboveground biomass type	[Mg ha^{-1}]
Herbs	7.0
Shrubs	0
Trees	0
Total standing biomass	7.0

No soil texture and no soil water contents at different matrix potentials available.

Helichrysum (HEL)

Ecosystem:	*Helichrysum*
Land-use class:	Natural
Disturbance:	-
Coordinates (UTM):	308188 / 9662706
Elevation:	3880 m a.s.l.
Vegetation:	*Helichrysum* cushion plants and tussock grasses
MAT:	6.8°C
MAP:	778 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-21	141.2	9.4	15.0	NA	0.42 ± 0.03
21-46	89.0	6.2	14.2	NA	0.46 ± 0.07
46-55	77.2*	5.5*	13.9*	NA	0.50 ± 0.02
55-74	NA	NA	NA	NA	0.52 ± 0.03
74-100	NA	NA	NA	NA	0.62 ± 0.07

* Related to depth of 46-50 cm

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	2326.44 ± 426.19	1278.57 ± 158.38
10-20	725.07 ± 51.61	2008.07 ± 400.14
20-30	514.23 ± 100.78	2224.10 ± 261.98
30-50	423.84 ± 138.76	2423.49 ± 1029.03

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	$Quantile_{25\%}$	$Quantile_{75\%}$	Median	$Quantile_{25\%}$	$Quantile_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	10.48	6.48	14.68	0.13	0.12	0.13

Aboveground biomass type	[Mg ha^{-1}]
Herbs	13.5
Shrubs	0
Trees	0
Total standing biomass	13.5

No soil texture and no soil water contents at different matrix potentials available.

Homegarden (HOM)

Ecosystem:	Homegarden
Land-use class:	Sustainable / traditional
Disturbance:	Crop rotation, hand hoe, organic fertilization

Coordinates (UTM):	332480 / 9631278
Elevation:	1260 m a.s.l.
Vegetation:	the reader is referred to Fernandes et al. (1985)
MAT:	20.3°C
MAP:	1336 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-23	32.1	2.8	11.5	5.79	0.77 ± 0.04
23-40	16.8	1.7	9.8	5.29	0.83 ± 0.04
40-60	9.8	1.0	9.3	5.18	1.00 ± 0.04
60-80	7.4	0.9	8.5	5.16	0.94 ± 0.02
80-100	6.4	0.7	9.2	5.22	0.96 ± 0.02

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	672.07 ± 120.94	429.59 ± 65.53
10-20	584.61 ± 164.77	380.67 ± 68.52
20-30	417.24 ± 99.83	339.98 ± 74.78
30-50	338.89 ± 83.16	326.82 ± 91.13

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	$Quantile_{25\%}$	$Quantile_{75\%}$	Median	$Quantile_{25\%}$	$Quantile_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	46.61	28.95	53.03	0.48	0.44	0.53

Aboveground biomass type	[Mg ha^{-1}]
Herbs	0.6
Shrubs	18.8
Trees	61.1
Total standing biomass	80.4

Depth	clay	silt	sand	water content (θ) at different matrix potentials				
[cm]	[%]	[%]	[%]	$\theta_{1.0}$ [%]	$\theta_{1.5}$ [%]	$\theta_{1.8}$ [%]	$\theta_{2.0}$ [%]	$\theta_{4.2}$ [%]
0-23	73	21	6	45.7	36.9	34.3	34.2	19.5
23-40	85	10	5	47.2	40.5	37.3	37.3	21.4
40-60	72	22	6	49.7	45.6	42.3	40.8	25.8
60-80	76	17	7	52.9	47.5	41.6	38.0	24.7
80-100	81	13	6	53.2	47.6	41.5	37.6	24.1

Lower montane forest (FLM)

Ecosystem:	Lower montane forest
Land-use class:	Semi-natural
Disturbance:	Timber, firewood
Coordinates (UTM):	303912 / 9650029
Elevation:	1920 m a.s.l.
Vegetation:	*Newtonia, Strombosia, Entandrophragma, Macaranga*
MAT:	17.9°C
MAP:	2378 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-6	171.1	10.8	15.9	4.15	0.23 ± 0.12
6-20	80.5	6.9	11.7	4.63	0.51 ± 0.05
20-33	75.4	5.3	14.1	4.63	0.43 ± 0.01
33-65	55.2	3.9	14.3	4.93	0.58 ± 0.34
65-100	41.0	2.2	19.0	5.14	0.59 ± 0.04

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	1667.90 ± 505.54	2244.67 ± 256.95
10-20	616.90 ± 191.84	2195.46 ± 305.44
20-30	389.63 ± 165.15	2402.40 ± 364.52
30-50	297.10 ± 181.92	2510.08 ± 363.49

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	$Quantile_{25\%}$	$Quantile_{75\%}$	Median	$Quantile_{25\%}$	$Quantile_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	28.17	21.16	45.24	0.39	0.32	0.46

Aboveground biomass type	[Mg ha^{-1}]
Herbs	1.6
Shrubs	3.8
Trees	157.1
Total standing biomass	162.5

No soil texture and no soil water contents at different matrix potentials available.

Maize field (MAI)

Ecosystem:	Maize field
Land-use class:	Agricultural
Disturbance:	Monoculture, pesticides, fertilization, soil erosion
Coordinates (UTM):	304818 / 9634213
Elevation:	1020 m a.s.l.
Vegetation:	*Zea mays*, no additional information available
MAT:	22.5°C
MAP:	693 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-15	14.5	1.2	11.7	4.56	0.87 ± 0.04
15-35	11.0	1.0	11.2	4.38	0.57 ± 0.09*
35-65	7.5	0.7	10.2	4.32	NA

* Volume fraction of stones >50%

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	179.33 ± 53.09	339.14 ± 86.97
10-20	141.35 ± 37.50	382.14 ± 93.91
20-30	102.44 ± 51.51	356.88 ± 103.98
30-50	57.17 ± 40.28	303.02 ± 111.49

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	$Quantile_{25\%}$	$Quantile_{75\%}$	Median	$Quantile_{25\%}$	$Quantile_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	19.89	10.79	27.93	0.77	0.73	0.83

Aboveground biomass type	[Mg ha^{-1}]
Herbs	14.8
Shrubs	0
Trees	0.1
Total standing biomass	14.9

Depth	clay	silt	sand	water content (θ) at different matrix potentials				
[cm]	[%]	[%]	[%]	$\theta_{1.0}$ [%]	$\theta_{1.5}$ [%]	$\theta_{1.8}$ [%]	$\theta_{2.0}$ [%]	$\theta_{4.2}$ [%]
0-15	31	36	33	45.2	37.5	32.0	28.6	15.4
15-35	32	28	40	45.4	36.7	32.4	30.1	16.5

Ocotea forest (FOC)

Ecosystem:	*Ocotea* forest
Land-use class:	Natural
Disturbance:	-
Coordinates (UTM):	304929 / 9653424
Elevation:	2120 m a.s.l.
Vegetation:	*Ocotea usambarensis*
MAT:	15.6°C
MAP:	2998 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-9	224.5	13.1	17.1	3.46	0.25 ± 0.03
9-20	125.0	5.6	22.4	3.77	0.31 ± 0.01
20-40	97.5	4.1	23.6	4.20	0.37 ± 0.03
40-70	80.8	3.3	24.4	4.67	0.60 ± 0.01
70-100	38.4	1.7	23.2	4.97	0.52 ± 0.04
100-110	25.1	1.2	20.2	5.04	0.71 ± 0.01

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	3648.25 ± 684.25	2631.66 ± 520.33
10-20	1774.32 ± 710.59	3032.02 ± 546.88
20-30	1012.92 ± 483.54	3701.79 ± 671.62
30-50	426.46 ± 359.88	3156.65 ± 543.84

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	$Quantile_{25\%}$	$Quantile_{75\%}$	Median	$Quantile_{25\%}$	$Quantile_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	21.26	15.40	24.29	0.22	0.13	0.24

Aboveground biomass type	[Mg ha^{-1}]
Herbs	1.3
Shrubs	7.7
Trees	376.0
Total standing biomass	385.0

No soil texture and no soil water contents at different matrix potentials available.

Ocotea forest disturbed (FOD)

Ecosystem:	Disturbed *Ocotea* forest
Land-use class:	Natural
Disturbance:	Cutting, timber; > 20 yr ago

Coordinates (UTM):	317484 / 9648259
Elevation:	2470 m a.s.l.
Vegetation:	*Podocarpus latifolius,* (*Ocotea usambarensis*), *Erica excelsa*
MAT:	13.6°C
MAP:	1526 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-10	246.2	12.4	19.7	NA	0.22 ± 0.01
10-20	198.7	9.2	21.5	NA	0.39 ± 0.01
20-30	175.9	8.2	21.4	NA	0.35 ± 0.01
30-50	140.7	6.3	22.3	NA	0.36 ± 0.03

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	3880.15 ± 446.47	3074.36 ± 499.55
10-20	1943.32 ± 733.50	3168.86 ± 253.64
20-30	1027.61 ± 158.98	3297.33 ± 100.52
30-50	770.26 ± 616.39	3231.06 ± 596.89

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	$Quantile_{25\%}$	$Quantile_{75\%}$	Median	$Quantile_{25\%}$	$Quantile_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	21.98	18.24	31.81	0.23	0.22	0.25

Aboveground biomass type	[Mg ha^{-1}]
Herbs	1.8
Shrubs	2.3
Trees	280.6
Total standing biomass	284.7

No soil texture and no soil water contents at different matrix potentials available.

Podocarpus forest (FPO)

Ecosystem:	*Podocarpus* forest
Land-use class:	natural
Disturbance:	-
Coordinates (UTM):	306582 / 9657105
Elevation:	2850 m a.s.l.
Vegetation:	*Podocarpus latifolius*
MAT:	9.0°C
MAP:	1773 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-4	249.5	12.7	19.6	3.61	0.30 ± 0.04
4-26	176.8	8.2	21.5	3.97	0.16 ± 0.01
26-35	97.4	3.5	27.5	4.54	0.23 ± 0.03
35-60	47.5	1.6	30.4	4.81	0.72 ± 0.06
60-80	51.3	1.7	31.0	4.88	0.67 ± 0.09
80-86	42.7	1.4	30.2	4.95	0.80 ± 0.06
86-91	64.1	2.1	29.9	4.85	0.75 ± 0.05
91-98	58.1	1.9	30.3	4.90	0.88 ± 0.07
98-105	35.5	1.5	23.6	4.97	0.79 ± 0.06

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	4439.81 ± 415.87	3175.78 ± 1094.37
10-20	3013.97 ± 429.23	3507.20 ± 963.72
20-30	1732.52 ± 643.90	3779.70 ± 713.24
30-50	1253.25 ± 631.12	3485.25 ± 887.24

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	$Quantile_{25\%}$	$Quantile_{75\%}$	Median	$Quantile_{25\%}$	$Quantile_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	15.27	12.67	23.16	0.13	0.12	0.14

No soil texture and no soil water contents at different matrix potentials available.

Aboveground biomass type	[Mg ha^{-1}]
Herbs	3.1
Shrubs	3.6
Trees	372.0
Total standing biomass	378.7

Podocarpus forest disturbed (FPD)

Ecosystem:	Disturbed *Podocarpus* forest
Land-use class:	Natural
Disturbance:	Fire; > 20 yr ago
Coordinates (UTM):	318502 / 9650434
Elevation:	2990 m a.s.l.
Vegetation:	*Erica excelsa, Podocarpus latifolius*
MAT:	7.5°C
MAP:	1564 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-10	276.1	14.7	18.7	3.74	0.24 ± 0.09
10-20	152.2	7.3	20.9	4.36	0.34 ± 0.03
20-30	149.0	6.9	21.6	4.46	0.36 ± 0.10
30-50	144.2	7.1	20.7	4.46	0.48 ± 0.04

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	2970.62 ± 677.79	2097.23 ± 561.32
10-20	2059.42 ± 616.54	2046.33 ± 463.38
20-30	1453.40 ± 450.91	2709.33 ± 915.36
30-50	1026.67 ± 563.34	2957.82 ± 1050.16

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	$Quantile_{25\%}$	$Quantile_{75\%}$	Median	$Quantile_{25\%}$	$Quantile_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	17.56	12.81	24.16	0.20	0.17	0.25

Aboveground biomass type	[Mg ha^{-1}]
Herbs	3.5
Shrubs	17.2
Trees	254.5
Total standing biomass	275.3

No soil texture and no soil water contents at different matrix potentials available.

Savannah (SAV)

Ecosystem:	Savannah
Land-use class:	Semi-natural
Disturbance:	Cutting, grazing, fire
Coordinates (UTM):	353702 / 9634606
Elevation:	950 m a.s.l.
Vegetation:	Acacia, *Terminalia, Grewia, Combretum*
MAT:	22.3°C
MAP:	536 mm yr^{-1}

Depth [cm]	C [mg C g^{-1}]	N [mg N g^{-1}]	C/N [-]	pH [-]	Bulk density [g cm^{-3}]
0-6	34.6	2.4	14.3	5.62	0.76 ± 0.08
6-24	17.0	1.4	12.6	5.02	0.86 ± 0.04
24-41	10.8	1.1	10.1	4.96	1.18 ± 0.08
41-54	8.7	0.9	9.3	5.09	1.07 ± 0.12
54-83	8.2	0.8	10.2	5.14	1.14 ± 0.07
83-101	7.2	0.8	8.5	5.47	1.22 ± 0.08

Depth [cm]	C_{mic} [mg kg^{-1}]	C_{sol} [mg kg^{-1}]
0-10	512.45 ± 125.17	179.75 ± 28.58
10-20	306.60 ± 64.47	190.50 ± 25.73
20-30	182.92 ± 51.30	194.81 ± 17.67
30-50	118.25 ± 31.44	192.04 ± 14.38

Depth	Soil CO_2 efflux			Specific metabolic quotient (q_sCO_2)		
	Median	Quantile$_{25\%}$	Quantile$_{75\%}$	Median	Quantile$_{25\%}$	Quantile$_{75\%}$
[cm]	[mg C_{CO2} m^{-2} h^{-1}]			[mg C_{CO2} g^{-1} C_{mic} h^{-1}]		
0-18	22.27	10.65	42.43	0.34	0.31	0.40

Aboveground biomass type	[Mg ha^{-1}]
Herbs	5.0
Shrubs	6.4
Trees	3.6
Total standing biomass	15.0

Depth	clay	silt	sand	water content (θ) at different matrix potentials				
[cm]	[%]	[%]	[%]	$\theta_{1.0}$ [%]	$\theta_{1.5}$ [%]	$\theta_{1.8}$ [%]	$\theta_{2.0}$ [%]	$\theta_{4.2}$ [%]
0-6	66	32	2	55.4	44.9	36.4	31.5	17.9
6-24	74	23	2	53.7	47.9	39.1	34.0	21.3
24-41	79	19	2	54.3	49.7	40.8	35.4	22.8
41-54	81	17	2	52.1	49.6	43.3	38.6	23.9
54-83	79	19	2	57.1	52.5	43.9	38.6	24.7
83-101	80	18	2	50.9	48.6	43.5	40.3	25.0

Affidavit

Eidesstattliche Versicherung und Erklärungen

§5 Nr. 4 Promotionsordnung

Hiermit erkläre ich, dass keine Tatsachen vorliegen, die mich nach den gesetzlichen Bestimmungen über die Führung akademischer Grade zur Führung eines Doktorgrades unwürdig erscheinen lassen.

§8 S. 2 Nr. 5 Promotionsordnung

Hiermit erkläre ich mich damit einverstanden, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung hinsichtlich der eigenständigen Anfertigung der Dissertation unterzogen werden kann.

§8 S. 2 Nr. 7 Promotionsordnung

Hiermit erkläre ich eidesstattlich, dass ich die Dissertation selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.

§8 S. 2 Nr. 8 Promotionsordnung

Ich habe die Dissertation nicht bereits zur Erlangung eines akademischen Grades anderweitig eingereicht und habe auch nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden.

§8 S. 2 Nr. 9 Promotionsordnung

Hiermit erkläre ich, dass ich keine Hilfe von gewerblichen Promotionsberatern bzw. -vermittlern in Anspruch genommen habe und auch künftig nicht nehmen werde.

Bayreuth, den 2. Juni 2015