LAND USE AND PRECIPITATION AFFECT ORGANIC AND MICROBIAL CARBON STOCKS AND THE SPECIFIC METABOLIC QUOTIENT IN SOILS OF ELEVEN ECOSYSTEMS OF MT. KILIMANJARO, TANZANIA

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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 3,880 m asl. 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 leads 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_sCO2 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. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS: 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 a very complex but central component of all ecosystems (Brevik *et al.*, 2015). A particular focus on tropical ecosystems is justified because they have a crucial effect on the global climate. In surplus, tropical ecosystems take a central part in global C turnover and sequestration (Melillo *et al.*, 1993; Dixon *et al.*, 1994). 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 (Zech *et al.*, 1997; Chambers *et al.*, 2004).

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 (Don *et al.*, 2011; Bruun *et al.*, 2013; de Souza Braz *et al.*, 2013). 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 lead to declines in C stocks, the loss of originally forest-derived C_{org}, changes in soil physical characteristics and advance 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; Don *et al.*, 2011; Bruun *et al.*, 2013). 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 (Cerdà *et al.*, 2009; Bravo-Espinosa *et al.*, 2014). 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

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rhizodeposits (Dinesh *et al.*, 2003). These are crucial declines that 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 ecophysiological 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 that is directly linked to mineralization and is massively altered by land-use change (Iqbal *et al.*, 2010; Don *et al.*, 2011). 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 (Insam & Haselwandter, 1989; Anderson & Domsch, 1993). 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 in the preceding text, 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 with that of 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 asl) to cold-wet alpine zone with *Helichrysum* cushion vegetation at approximately 4,000 m asl, and on elevations higher than 4,000 m asl, 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 11 natural and anthropogenically altered tropical ecosystems. Particularly, our objectives were the following: (1) to evaluate the effects of land-use changes on C_{org}, C_{mic} and qCO_2; (2) subsequently, to investigate the intensity of disturbances based on qCO_2; and (3) to determine the effects of increased precipitation on CO_2 efflux and qCO_2.

MATERIALS AND METHODS

Study Area

Mount 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 11 sites of natural and disturbed ecosystems were investigated, whereas the disturbances included anthropogenic (e.g. land-use change) as well as natural effects (e.g. fire) (Table I). These 11 ecosystems are the most common ecosystems on Mt. Kilimanjaro and representative for most of East Africa. Namely, the ecosystems were savannah, maize field, Chagga homegarden, coffee plantation, lower montane forest, *Ocotea* forest, disturbed *Ocotea* forest, *Podocarpus* forest, disturbed *Podocarpus* forest, *Erica* forest and alpine *Helichrysum*. The investigated ecosystems covered an elevation gradient from 950 to 3,880 m above sea level and the mean annual temperature (MAT) ranged from 6·8 to 22·5 °C (Table I). Mt. Kilimanjaro is characterized by a bimodal rainfall pattern and, the mean annual precipitation (MAP) varies between 536 and 2,998 mm y^{-1} (Table I). 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 I). Several studies described the vegetation in the respective ecosystems and the net primary production (NPP) in tropical ecosystems in general (e.g. Clark *et al.*, 2001; Hemp, 2006). Most soils are classified as andosols developed from volcanic ash (<75,000 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

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

Ecosystem	ID	Elevation (m asl)	MAP[a] (mm yr^{-1})	MAT[b] (°C)	de Martonne aridity index (A_{dM})	Land-use class	Current human-induced disturbances	Disturbance
Helichrysum	HEL	3,880	778	6·8	46·3	Natural	No	
Erica forest	FER	3,880	1,188	6·8	70·7	Natural	No	Fire; >20 years ago
Podocarpus forest disturbed	FPD	2,990	1,564	7·5	89·4	Natural	No	
Podocarpus forest	FPO	2,850	1,773	9·0	93·3	Natural	No	Cutting, timber; >20 years ago
Ocotea forest disturbed	FOD	2,470	1,526	13·6	64·7	Natural	No	
Ocotea forest	FOC	2,120	2,998	15·6	117·1	Natural	No	
Forest lower montane	FLM	1,920	2,378	17·9	85·2	Semi-natural	Yes	Timber, firewood
Coffee plantation	COF	1,300	1,485	20·3	49·0	Agricultural	Yes	Monoculture, pesticides, fertilizers, soil compaction
Homegarden	HOM	1,260	1,336	20·3	44·1	Agricultural	Yes	Crop rotation, hand hoe, organic fertilizer
Maize field	MAI	1,020	693	22·5	21·3	Agricultural	Yes	Monoculture, pesticides, fertilizers, soil erosion
Savannah	SAV	950	536	22·3	16·6	Semi-natural	Yes	Cutting, grazing, fire

MAP, mean annual precipitation; MAT, mean annual temperature.
[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).

(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, that is, natural, semi-natural and agricultural (Table I). 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 1,750 m asl, 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 2,800 and 3,500 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 I). 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 × 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), because 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 11 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 and 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, because 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 2,000 m asl 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 performed by the fumigation–extraction method (Vance *et al.*, 1987). Briefly, 7–8 g of field-moist soil was 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). Because 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 analysed for C_{org} contents using dry combustion (vario max CN, Elementar, Hanau, Germany).

Undisturbed soil cores were incubated in three consecutive 5-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

Table II. Volumetric water contents before and after the additions of standard rain mixture

| Ecosystem | ID | Volumetric water contents (%) | | |
		Before addition*	After 44 ml of solution	After 245 ml 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

*The content before addition refers to the water contents estimated from the chloroform-fumigation method.

ranged from 13·2% to 36·0% (Table II). 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 21 headspace of each soil core, 50 ml air was sucked per minute through Teflon tubes to the measurement cell of the laser and recirculated to the headspace for a measuring time of 20 min. The set up was similar to static chamber measurements. Observations of pressure conditions in the headspace controlled for constant conditions avoiding overpressure 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). Because 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, because 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 metre (as mentioned previously, 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} and 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 milligrams C_{CO2} g^{-1} C_{mic} h^{-1}).

Statistical Analysis

Because 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 and land-use conversion) were performed by Mann–Whitney U tests. The arithmetic mean was not appropriate, because of 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 was performed 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 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 leads 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 approximately 4,000 m asl, the natural *Helichrysum* ecosystem contained about 4.5 times more C_{org} than the agriculturally used maize field at 950 m asl. Based on A_{dM} values above and below 50 (Table I), 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 3,880 m asl was excluded from the regressions, because its cold climate is not comparable with hot savannahs or maize fields at elevations of around 1,000 m asl. In ecosystems at low elevations with higher aridity, C_{org} stocks increased by 3 kg m^{-2} per 1,000 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 with semi-natural and
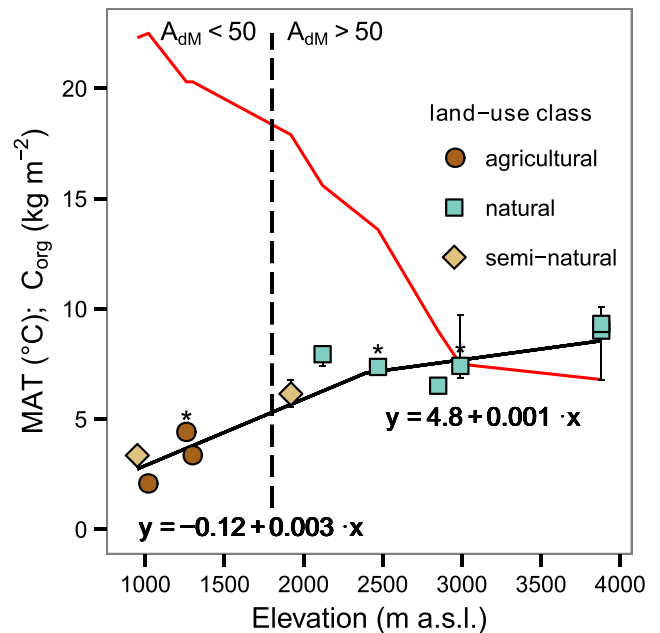

Figure 1. Temperature, elevation and organic carbon (C_{org}) stocks in surface soil (18 cm) of Mt. Kilimanjaro ecosystems. Displayed C_{org} values are medians ± 25% and 75% quantiles, temperature [mean annual temperature (MAT), red line]; linear regressions of C_{org} versus elevation depending on A_{dM} value (left side: $A_{dM} < 50$; right side: $A_{dM} > 50$); symbols and colours of ecosystems: agricultural (circles, dark brown), semi-natural (diamonds, light brown) and natural (squares, dark 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 I. This figure is available in colour online at http://wileyonlinelibrary.com/journal/ldr.

semi-natural compared with agriculturally used ecosystems (Table III). 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* 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 3,880 m asl 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

Table III. 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

Land-use class	C_{org}		C_{mic}		CO_2 (3·6 mm precipitation)		CO_2 (20 mm precipitation)		qCO_2 (3·6 mm precipitation)		qCO_2 (20 mm precipitation)	
	N	kg m^{-2}	N	g m^{-2}	N	mg C$_{CO2}$ h^{-1}	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	150	7·82 (a)	576	96·27 (a)	172	17·98 (a)	163	20·26 (c)	576	0·21 (b)	576	0·22 (c)
Semi-natural	36	5·44 (b)	144	72·51 (a)	54	14·83 (b)	70	31·85 (b)	144	0·12 (c)	144	0·39 (b)
Agricultural	39	3·16 (c)	156	31·52 (b)	71	13·44 (b)	89	40·79 (a)	156	0·34 (a)	156	1·50 (a)

Values are medians of surface soils (18 cm) of Mt. Kilimanjaro ecosystems. Letters 'a', 'b' and 'c' indicate statistical differences ($p < 0.05$); N refers to number of data values.

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

Similar to lower precipitation, soil CO_2 efflux under additional 20 mm of precipitation revealed differences between the ecosystems and varied between 10·5 (*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 II) revealed significantly higher CO_2 effluxes in agricultural ecosystems compared with semi-natural and natural systems

(Table III). 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 and *Erica* forest). All other ecosystems showed no significant changes in CO_2 efflux with increased water additions.

Specific Microbial Respiration Quotient (q_sCO_2)

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 III). 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
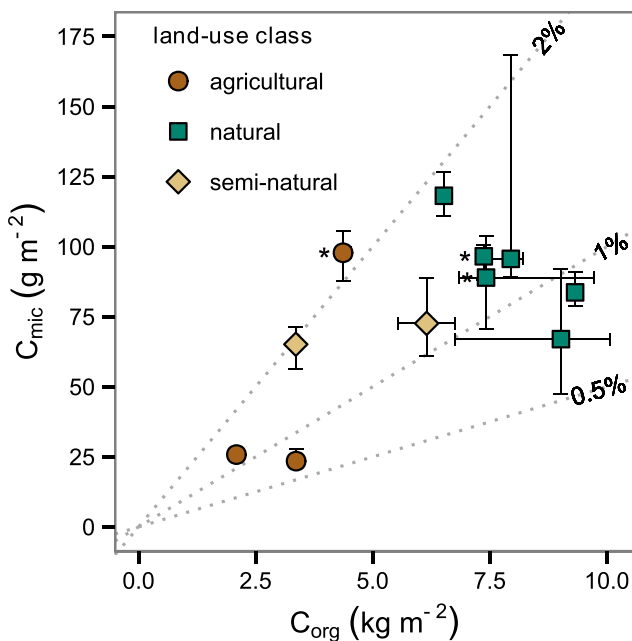
Figure 2. Stocks of C_{mic} and C_{org} in surface soils (18 cm) of Mt. Kilimanjaro ecosystems. Displayed values are medians ± 25% and 75% quantiles. Dotted lines refer to C_{mic}:C_{org} ratio of 0·5%, 1% and 2%, respectively. Symbols and colours of ecosystems: agricultural (circles, dark brown), semi-natural (diamonds, light brown) and natural (squares, dark 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 I. This figure is available in colour online at http://wileyonlinelibrary.com/journal/ldr.
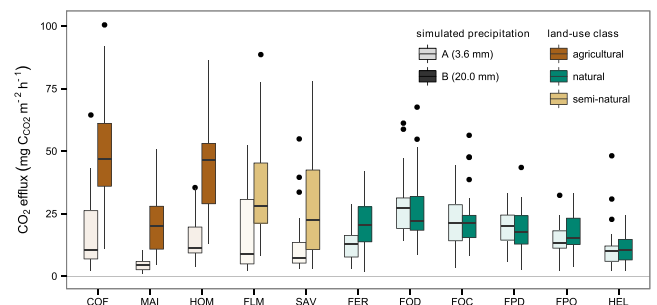
Figure 3. Soil CO_2 efflux [mg C_{CO2} m^{-2} h^{-1}, surface soil (18 cm)] under different simulated precipitations of agricultural (dark brown), semi-natural (light brown) and natural ecosystems (dark green) at Mt. Kilimanjaro; simulated precipitations are shown as two bars per ecosystem: 3·6 mm (left, light colour), 20·0 mm (right, dark colour); medians are displayed as horizontal lines within the coloured 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 I. This figure is available in colour online at http://wileyonlinelibrary.com/journal/ldr.
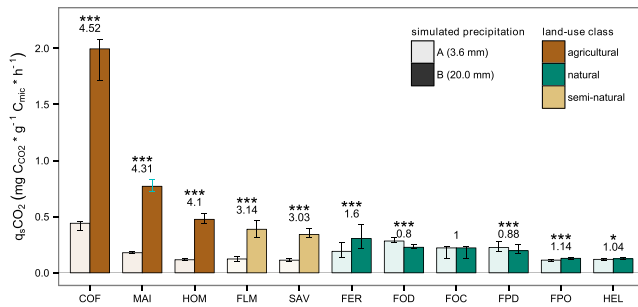
Figure 4. Specific metabolic quotients [q_sCO_2, surface soil (18 cm)] under simulated precipitations of agricultural (dark brown), semi-natural (light brown) and natural ecosystems (dark green) at Mt. Kilimanjaro. Simulated precipitations are shown as two bars per ecosystem: 3·6 mm (left, light colour), 20·0 mm (right, dark colour); 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 I. This figure is available in colour online at http://wileyonlinelibrary.com/journal/ldr.

q_sCO_2(agricultural) > q_sCO_2(semi-natural) > q_sCO_2(natural) (Table III). 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 II), q_sCO_2 of intensively used agricultural soils was 2·25 to more than four 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 leads to increases in q_sCO_2 (up to 4·5 times) in eight and slight decreases in two of the 11 ecosystems (Figure 4). The variation in precipitation did not affect q_sCO_2 in the 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 2,000 and 3,000 m asl (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 the Mt. Kilimanjaro area – but still, its application is selective and negligible. This is, for example, 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, because 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 with that of coffee plantation. Cultivation in the traditional agroforestry system is performed by hand where plant material (banana, beans, maize, etc.) and surface soil are 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.

CO₂ Efflux

CO₂ 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 I), 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 I), 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 (Iqbal *et al.*, 2010; Abera, 2013), 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

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 because 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 a 1·4-fold increase in qCO_2 (Basu & Behera, 1993). Still, in the present study, we found more than fourfold increases in q_sCO_2 due to intensification in management practices, indicating that the effect of land use may be underestimated in the studies in the previous text.

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 ecosystems 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 with that of intensive agriculturally used maize fields and coffee plantations (Figures 2 and 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 that soil microorganisms are exposed to. Such stress-inducing factors are, for example, 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 unfavourable 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 (Figures 2 and 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 with 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 $20 \cdot 0$ 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 because 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 $20 \cdot 0$ mm is assumed to be negligible. The effect of additional precipitation ($20 \cdot 0$ mm) for ecosystems >2,000 m asl 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 and 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, for example, the in-situ determination of CO_2 efflux, socio-economic properties and 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.

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