

# 1 Stable carbon and nitrogen isotopic composition of leaves, litter, and 2 soils of various ecosystems along an elevational and land-use 3 gradient at Mount Kilimanjaro, Tanzania

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## 11 **Abstract**

12 Variations in the stable isotopic composition of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) of fresh leaves, litter and topsoils were  
13 used to characterize soil organic matter dynamics of twelve tropical ecosystems in the Mount Kilimanjaro region, Tanzania.  
14 We studied a total of 60 sites distributed along five individual elevational transects (860 – 4,550 m a.s.l.), which define a  
15 strong climatic and land use gradient encompassing semi-natural and managed ecosystems. The combined effects of  
16 contrasting environmental conditions, vegetation, soil, and management practices had a strong impact on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
17 values observed in the different ecosystems. The relative abundance of  $\text{C}_3$  and  $\text{C}_4$  plants greatly determined the  $\delta^{13}\text{C}$  of a  
18 given ecosystem. In contrast,  $\delta^{15}\text{N}$  values were largely controlled by land-use intensification and climatic conditions. Both  
19  $\delta^{15}\text{N}$  values and calculated  $\delta^{15}\text{N}$ -based enrichment factors ( $\delta^{15}\text{N}_{\text{litter}} - \delta^{15}\text{N}_{\text{soil}}$ ) suggest tightest nitrogen cycling at high-  
20 elevation (>3,000 m a.s.l.) ecosystems, and more open nitrogen cycling both in grass-dominated and intensively managed  
21 cropping systems. However, claims about the nature of the N cycle (i.e. open/close) should not be made solely on the basis  
22 of soil  $\delta^{15}\text{N}$  as other processes that barely discriminate against  $^{15}\text{N}$  (i.e. soil nitrate leaching) have been shown to be quite  
23 significant in Mt Kilimanjaro's forest ecosystems. The negative correlation of  $\delta^{15}\text{N}$  values with soil nitrogen content and the  
24 positive correlation with mean annual temperature suggest reduced mineralisation rates, and thus limited nitrogen  
25 availability, at least in high-elevation ecosystems. By contrast, intensively managed systems are characterized by lower soil  
26 nitrogen contents and warmer conditions, leading together with nitrogen fertilizer inputs to lower nitrogen retention, and  
27 thus, significantly higher soil  $\delta^{15}\text{N}$  values. A simple function driven by soil nitrogen content and mean annual temperature

28 explained 68 % of the variability in soil  $\delta^{15}\text{N}$  values across all sites. Based on our results, we suggest that in addition to land  
29 use intensification, increasing temperatures in a changing climate may promote soil carbon and nitrogen losses, thus altering  
30 the otherwise stable soil organic matter dynamics of Mt. Kilimanjaro's forest ecosystems.

## 31 **1 Introduction**

32 Conversion of natural ecosystems to agriculture is a worldwide phenomenon, which is of particular significance in tropical  
33 regions where human population growth rates are currently the highest (FAO and JRC, 2012). Changes in climate and land-  
34 use significantly alter vegetation composition and biogeochemical cycles, causing a strong impact on carbon (C) and  
35 nitrogen (N) turnover and stocks (Smith et al., 2014). Tropical forest biomes are particularly relevant in this context, as they  
36 are significant C storages and N turnover hotspots (Bai et al., 2012; Hedin et al., 2009; Lewis et al., 2009; Pan et al., 2011;  
37 Vitousek, 1984). Considering the increasing pressure on natural land, it gets even more crucial to understand how  
38 anthropogenic interventions affect ecosystem C and N cycling, and gain better knowledge about the main drivers of nutrient  
39 cycling, and associated exchange processes with the atmosphere and hydrosphere in tropical environments.

40 Research exploiting the natural abundance of stable isotopes has proved quite suitable for investigating potential impacts of  
41 land-use and/or climate change on C and N cycling in terrestrial systems (Michener and Lajtha, 2007; Pannetieri et al., 2017;  
42 Saiz et al., 2015a). Variations in the stable isotopic composition of C ( $\delta^{13}\text{C}$ ) and N ( $\delta^{15}\text{N}$ ) in plants and soils are the result of  
43 fractionation processes occurring during ecosystem exchange of C and N. Thus,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  can serve as valuable  
44 indicators about ecosystem state and provide useful insights on how these systems respond to biotic and abiotic factors  
45 (Dawson et al., 2002; Högberg, 1997; Ma et al., 2012; Pardo and Nadelhoffer, 2010; Peterson and Fry, 1987; Robinson,  
46 2001).

47 Plants discriminate against  $^{13}\text{CO}_2$  (carbon dioxide) during photosynthetic  $\text{CO}_2$  fixation depending on plant metabolism (i.e.  
48  $\text{C}_3$  and  $\text{C}_4$  photosynthetic pathways). Most tropical grasses typically employ the  $\text{C}_4$  photosynthetic pathway ( $\delta^{13}\text{C}$  values  $>-$   
49  $15\text{‰}$ ), while trees and shrubs use the  $\text{C}_3$  photosynthetic pathway ( $\delta^{13}\text{C}$  values  $<-24\text{‰}$ ) (Bird et al., 1994; Bird and Pousai,  
50 1997; Cernusak et al., 2013; Farquhar et al., 1980). The distribution of  $\text{C}_3$  and  $\text{C}_4$  vegetation show clear patterns along  
51 elevational gradients, with increasing abundance of  $\text{C}_3$  species towards high elevations (Bird et al., 1994; Körner et al., 1991;  
52 Tieszen et al., 1979). Environmental conditions such as water availability also exert a significant influence on isotopic  
53 discrimination during atmospheric  $\text{CO}_2$  fixation. Accordingly, compared to optimal moisture conditions, water stress leads to  
54 enrichment of  $^{13}\text{C}$  in  $\text{C}_3$  plants (Farquhar and Sharkey, 1982), while this isotopic fractionation is less obvious or even absent  
55 in  $\text{C}_4$  plants (Ma et al., 2012; Swap et al., 2004).

56 The soil organic matter (SOM) pool integrates the isotopic signature of the precursor biomass over different spatiotemporal  
57 scales (Saiz et al., 2015a). Variation in soil  $\delta^{13}\text{C}$  values represents a valuable tool to better assess SOM dynamics,

58 mineralisation processes, or reconstruct past fire regimes (Saiz et al., 2015a; Wynn and Bird, 2007). The  $\delta^{13}\text{C}$  of SOM in a  
59 given ecosystem is greatly controlled by the relative abundance of  $\text{C}_3$  and  $\text{C}_4$  plants due to their contrasting C isotopic  
60 composition. Therefore, strong variations in soil  $\delta^{13}\text{C}$  can also be used to identify sources of particulate organic matter as  
61 well as vegetation shifts such as woody thickening. However, fractionation effects associated to differential stabilisation of  
62 SOM compounds, microbial re-processing of SOM, soil physico-chemical characteristics, and the terrestrial Seuss effect  
63 preclude a straightforward interpretation of soil  $\delta^{13}\text{C}$  values (Saiz et al., 2015a).

64 Plant and soil  $\delta^{15}\text{N}$  relate to environmental and management conditions controlling N turnover, availability, and losses.  $\delta^{15}\text{N}$   
65 values of soils are generally more positive than those of vegetation due to the relatively large isotopic fractionation occurring  
66 during soil N transformations (Dawson et al., 2002). The N-cycle of a given ecosystem may be characterized as closed, if  
67 both efficient microbial N retention and absence of external N-inputs (e.g. atmospheric deposition and fertilizer additions)  
68 prevent substantial gaseous and/or leaching N-losses. In contrast, open ecosystem N-cycling is characterized by significant  
69 inputs and losses of N. On the one hand, gaseous N losses from soils are strongly depleted in  $^{15}\text{N}$  due to the high  
70 fractionation factors associated to these processes (Denk et al., 2017). This results in high  $\delta^{15}\text{N}$  values of the residual  
71 substrate, which consequently leaves less importance to impacts of external N additions (Robinson, 2001; Zech et al., 2011).  
72 On the other hand, N leaching seems to only discriminate slightly against ecosystem  $^{15}\text{N}$ . According to Houlton and Bai  
73 (2009)  $\delta^{15}\text{N}$  values of drained water agree well with those of soils across various natural ecosystems worldwide. Moreover, it  
74 is also important to consider that soil  $\delta^{15}\text{N}$  may also be influenced by other factors including rooting depth, uptake of  
75 different N compounds, and symbiotic  $\text{N}_2$ -fixation (Nardoto et al., 2014). Variations in  $\delta^{15}\text{N}$  values of plants and soils have  
76 been successfully applied to characterize N cycling across a large variety of ecosystems worldwide (Amundson et al., 2003;  
77 Booth et al., 2005; Craine et al., 2015a, 2015b; Martinelli et al., 1999; Nardoto et al., 2014). This includes research work that  
78 has particularly focused on the study of N-losses derived from land-use changes or intensification (Eshetu and Högberg,  
79 2000; Piccolo et al., 1996; Zech et al., 2011).

80 Information on ecosystem C and N cycling is still scarce in many tropical ecosystems, particularly in remote regions of  
81 Africa (Abaker et al., 2016; 2018; Saiz et al., 2012; Townsend et al., 2011). Furthermore, feedbacks between C and N cycles  
82 such as limitations of N availability in ecosystem C sequestration and net primary productivity of tropical forest require  
83 urgent investigations (Gruber and Galloway, 2008; Zaehle, 2013). In such context, the Kilimanjaro region in Tanzania offers  
84 the rare possibility to study a broad range of tropical ecosystems across contrasting land-use management intensities and  
85 varying climatic conditions. This region hosts a large variety of semi-natural and managed ecosystems as a result of the  
86 strong elevational and land-use gradient.

87 We hypothesized that (i) vegetation composition ( $C_3/C_4$ ) is the main control for ecosystem  $\delta^{13}C$  values, whereas (ii)  $\delta^{15}N$   
88 values are rather controlled by land use management and climatic conditions. The main aim of this study is to evaluate the  
89 potential of  $\delta^{13}C$  and  $\delta^{15}N$  values in plant and soil material to assess C and N cycling across a broad variety of semi-natural  
90 and managed ecosystems under varying climatic conditions.

## 91 **2 Materials and Methods**

### 92 **2.1 Study Sites**

93 This study was conducted on the southern slopes of Mount (Mt.) Kilimanjaro (3.07° S, 37.35° E, 5,895 m a.s.l.) in North-  
94 East Tanzania. The climate is characterized by a bimodal precipitation pattern with a major rainy season between March and  
95 May, and the other peak between October and November. Recently, Appelhans et al. (2016) used a network of 52  
96 meteorological stations strategically deployed in the Kilimanjaro region to measure air temperature and precipitation. They  
97 then used geo-statistical and machine-learning techniques for the gap filling of the recorded meteorological time series and  
98 their regionalization, which provides the means to calculate the meteorological data used for the complete set of sites (60)  
99 used in our work. Please refer to Appelhans et al. (2016) for more details. Maximum mean annual precipitation (MAP) of  
100 2,552 mm occurs at an elevation of around 2,260 m a.s.l., decreasing towards lower as well as higher elevations, reaching  
101 657 and 1,208 mm  $y^{-1}$  at 871 and 4,550 m respectively (Table 1). Variations in air temperature are dominated by diurnal  
102 rather than seasonal patterns (Duane et al., 2008). Mean annual temperature (MAT) decreases with increasing elevation,  
103 ranging from 24.8 °C at 860 m to 3.5 °C at 4,550 m (Table 1).

104 Five altitudinal transects ranging from 860 to 4,550 m a.s.l. were established along the mountain slopes. At each transect,  
105 twelve ecosystems occurring over a strong land use gradient encompassing intensively managed cropping systems and semi-  
106 natural stands were investigated. Hence, the total number of plots studied was 60 (5 transects x 12 ecosystems; Table 1 and  
107 Fig. 1). The cropping systems comprised multi-layer and multi-crop agroforestry homegardens (Hom), monoculture coffee  
108 plantations (Cof) with dispersed shading trees, and maize fields (Mai) subject to regular albeit moderate fertilizer and  
109 pesticide applications. Plant litter is regularly removed from Cof and Mai sites. Homegardens are manually ploughed, while  
110 combustion engine machinery is used for ploughing coffee plantations and maize fields. Coffee plantations are irrigated with  
111 drip irrigation systems. Both Hom and Cof sites still host indigenous forest trees that include *Albizia schimperi*, a species  
112 that may potentially fix atmospheric N. This is one of the 5 most abundant species in 2 and 4 of the Hom and Cof sites  
113 respectively, making up less than 25% of the vegetation cover in all cases. Grasslands (Gra) and savannas (Sav) are  
114 extensively managed by means of domestic grazing and occasional grass cutting, thus having significantly lower  
115 anthropogenic disturbances than cropping systems. Semi-natural ecosystems include several montane forest stands. These  
116 include lower montane (Flm), *Ocotea* (Foc), *Podocarpus* (Fpo), *Erica* (Fer), and alpine shrub vegetation *Helichrysum* (Hel).

117 Even though lower montane forests are currently under protection they are still subject to sporadic illegal logging. In  
118 addition to sampling undisturbed forest ecosystems of *Ocotea* and *Podocarpus*, we purposely studied sites that had been  
119 affected by logging activities and fire events prior to the establishment of the Kilimanjaro National Park (Soini, 2005):  
120 *Ocotea* (Fod) and *Podocarpus* (Fpd) (Table 1). Erica forests represent Africa's highest forests in the subalpine zone. Higher  
121 above is the alpine zone, the realm of *Helichrysum* vegetation that is dominated by cushion plants and tussock grasses  
122 (Ensslin et al., 2015; Hemp, 2006). Potential ecosystem productivity and decomposition rates show a hump-shaped pattern  
123 resembling that of precipitation (Fig S1). It is interesting to see the close match between the two variables along the  
124 elevation range, albeit this trend weakens slightly towards higher elevation sites. Optimum growth and decomposition  
125 conditions are shown between 1,800 and 2,500 m.a.s.l.. These locations correspond to low altitude forest ecosystems (Flm  
126 and Foc) that do not experience severe seasonal limitations in moisture or temperature as it is otherwise the case in lower as  
127 well as higher elevation systems that are moisture and temperature limited respectively (Becker and Kuzyakov, 2018).

128 Detailed physico-chemical characteristics of the dominant soils are listed in Table 1. Soils in the Mt. Kilimanjaro region are  
129 mainly derived from volcanic rocks and ashes. The wide array of climatic conditions present along the elevational gradient  
130 influence soil genesis, which results in the occurrence of andosols at high elevations, and soils of more advanced genesis at  
131 lower elevations (e.g. nitosols) (Majule, 2003).

132 It is extremely difficult to provide reliable estimates of both fertilizers and pesticide rates used in small household farms in  
133 sub-Saharan Africa. This is because the actual use of these products is strongly dependent on both its availability in the  
134 local/regional market, the economic circumstances of each individual farmer, and individual perceptions about their use  
135 (Saiz and Albrecht, 2016). The only sites receiving fertilizer are the two monocultures: Maize (Mai) fields and Coffee (Cof)  
136 plantations, and to a lesser extent the homegardens (Hom) sites. In the latter sites Gütlein et al. (2018) report that weed  
137 control is mainly done by hand, and the use of mineral or organic N-fertilizers is low or non-existent. Extensively managed  
138 sites (i.e. Sav and Gra) receive varying amounts of organic inputs as a result of grazing activities, but again, their actual rates  
139 are unknown. A more detailed explanation on fertilizer and pesticides inputs used in the region is provided in the  
140 Supplementary Information.

## 141 **2.2 Sampling and Analyses**

142 Fieldwork took place in February and March in 2011 and 2012. Sampling was conducted on 50 x 50 m plots established at  
143 each of the 60 studied sites (12 ecosystems x 5 transects). Surface litter and mineral topsoil (0-5 cm) were sampled at five  
144 locations (four corners and the central point) at each plot. Additionally, fresh mature leaves of the five most abundant plant  
145 species covering 80% of total plant biomass per site were collected (Schellenberg Costa et al., 2017). All sampled materials  
146 (leaves, litter and soil) were air-dried until constant weight, and leaf material was subsequently oven-dried at 70 °C for 60

147 hours prior to grinding. Soil was sieved to 2 mm with visible root fragments being further removed prior to grinding with a  
148 mixer mill (MM200, Retsch, Haan Germany). Soil pH was determined with a pH meter (Multi Cal SenTix61, WTW,  
149 Weilheim, Germany) in a 0.01 M CaCl<sub>2</sub> solution, with a CaCl<sub>2</sub> to soil ratio of 2:1. Particle size distribution was determined  
150 gravimetrically using the pipette method (van Reeuwijk, 2002).

151 All soil, litter, and leaf samples were analysed with a dry combustion elemental analyzer (Costech International S.p.A.,  
152 Milano, Italy) fitted with a zero-blank autosampler coupled to a ThermoFinnigan DeltaPlus-XL using Continuous-Flow  
153 Isotope Ratio Mass Spectrometry (CF-IRMS) for determination of abundance of elemental C and N, and their stable isotopic  
154 composition ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ). Precisions (standard deviations) on internal standards for elemental C and N concentrations and  
155 stable isotopic compositions were better than 0.08 % and 0.2 ‰ respectively.

156 Natural  $^{13}\text{C}$  or  $^{15}\text{N}$  abundances are expressed in  $\delta$  units according to Eq. (1):

$$157 \quad \delta (\text{‰}) = (R_{\text{sample}} - R_{\text{standard}} / R_{\text{standard}}) \times 1000, \quad (1)$$

158 where  $R_{\text{sample}}$  denotes the ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  in the sample, and  $R_{\text{standard}}$  denotes the ratios in Pee Dee Belemnite or  
159 atmospheric N<sub>2</sub> (international standards for C and N, respectively). The average values for the plant samples were weighted  
160 considering their relative abundance at each site. Individual values for soil, litter, and leaves were averaged for each plot.

161 In addition,  $\delta^{15}\text{N}$ -based enrichment factors ( $\epsilon$ ) were calculated following Eq. (2):

$$162 \quad \epsilon = \delta^{15}\text{N}_{\text{litter}} - \delta^{15}\text{N}_{\text{soil}}, \quad (2)$$

163 These were used as indicators for ecosystem N status (Garten et al., 2008; Mariotti et al., 1981). Note that we use  $\delta^{15}\text{N}$   
164 values of litter material rather than fresh leaves from various species to calculate enrichment factors, since litter provides a  
165 more unbiased representation of the quality, quantity, and spatiotemporal dynamics of organic inputs entering the SOM pool  
166 (Saiz et al., 2015a).

### 167 **2.3 Statistical Analysis**

168 Normal distribution of the data was confirmed with the Shapiro-Wilk test. One-way ANOVA was performed to test for  
169 significant differences between ecosystems, while Tukey's HSD was used as post hoc procedure to test for significant  
170 differences across sites ( $P \leq 0.05$ ). Correlation analyses were performed to identify soil, foliar, and climatic variables  
171 influencing soil  $\delta^{15}\text{N}$  values. Subsequently, a principal component analysis (PCA) was conducted to reveal relationships  
172 between the main variables affecting soil  $\delta^{15}\text{N}$  values. The PCA was based on a correlation matrix including soil (C and N  
173 concentrations, C/N ratio,  $\delta^{13}\text{C}$ , pH values, sand and clay contents) as well as climatic parameters (MAT and MAP). A  
174 stepwise multiple regression was used to identify the main driving parameters determining soil  $\delta^{15}\text{N}$  across the elevational  
175 transect. All statistical analyses were conducted with R (version 3.2.2; R Core Team, 2015).

## 176 **3 Results**

### 177 **3.1 General soil characteristics**

178 Soil C and N contents were the highest in forest ecosystems and showed a decreasing trend towards managed sites (i.e.  
179 homegardens, grasslands, coffee and maize fields) (Table 1). Also, natural savannas and *Helichrysum* ecosystems had lower  
180 soil C and N values compared to forest ecosystems. The low temperatures and sandy nature of the *Helichrysum* sites play a  
181 strong role in their characteristically low productivity and moderate decomposition potentials (Table 1; Fig. S1), which  
182 unquestionably affects the comparatively low soil C and N contents of these alpine systems.

183 An opposite trend to that of soil C and N abundance was observed for soil C/N ratios, whereby managed sites showed  
184 significantly lower values compared to those of semi-natural ecosystems. Soil pH values revealed acidic conditions at all  
185 sites, with the lowest values observed in forest sites having comparatively higher MAP (Table 1).

### 186 **3.2 Variation of $\delta^{13}\text{C}$ values along the elevational and land-use gradient**

187 There were large variations in  $\delta^{13}\text{C}$  values along the elevational and land-use gradient, with distinct differences between  
188 managed and semi-natural ecosystems (Fig. 2). Compared to soils and litter, leaves invariably showed the lowest  $\delta^{13}\text{C}$  values  
189 in all the studied ecosystems, with the exception of grasslands and savannas that exhibited lower soil  $\delta^{13}\text{C}$  values than plant  
190 material.

191 The  $\delta^{13}\text{C}$  values of semi-natural ecosystems ranged between -32.8 and -24.1 ‰ (mean  $\pm$  SE: soil  $-26.0 \pm 0.2$  ‰; litter  $-27.2 \pm$   
192  $0.2$  ‰; leaves  $-29.3 \pm 0.3$  ‰), showing a progressive reduction with decreasing elevation (i.e. from 4,500 to 1,750 m a.s.l.;  
193 Fig. S2). The variation in  $\delta^{13}\text{C}$  values was much higher (-29.7 to -13.3 ‰) in managed ecosystems located at lower  
194 elevations (i.e. between 860 and 1,750 m a.s.l.; Fig. S2). The highest  $\delta^{13}\text{C}$  values were observed in  $\text{C}_4$ -dominated ecosystems  
195 (i.e. savannas, maize fields, and grasslands; soil  $-16.8 \pm 0.6$  ‰, litter  $-19.3 \pm 0.8$  ‰, leaves  $-18.8 \pm 1.1$  ‰); while lower  $\delta^{13}\text{C}$   
196 values were obtained for coffee plantations and homegardens (soil  $-24.8 \pm 0.5$  ‰, litter  $-27.2 \pm 0.4$  ‰, leaves  $-27.3 \pm 0.4$  ‰).  
197 Coffee plantations showed a slight influence of  $\text{C}_4$  vegetation in the soil data as a result of grasses growing between the rows  
198 of coffee plants. No significant variations were observed between  $\delta^{13}\text{C}$  values of soils and those of litter and leaves in the  
199 ecosystems with predominance of  $\text{C}_4$  vegetation (savannas, maize fields and grasslands). Exploratory data analyses revealed  
200 that in most cases, soil, litter, leaf, and climatic variables cross-correlated with each other (Table S1).

201 **Figure 3** shows relatively small variations in  $\delta^{13}\text{C}$  enrichment factors ( $> -1.25$  ‰) both in undisturbed semi-natural and  
202 extensively managed sites along the elevational gradient, while managed and disturbed sites show higher and more variable  
203  $\delta^{13}\text{C}$  enrichment factors.

### 204 **3.3 Variation of $\delta^{15}\text{N}$ values along the elevational and land-use gradient**

205 Significantly higher  $\delta^{15}\text{N}$  values were observed for all sampled materials in the intensively managed (cropping) systems  
206 compared to semi-natural and grass-dominated ecosystems (Fig. 4a). The  $\delta^{15}\text{N}$  values for managed systems ranged between -  
207 2.6 and 7.8 ‰ (mean  $\pm$  SE: soil  $5.6 \pm 0.3$  ‰, litter  $1.7 \pm 0.5$  ‰, leaves  $2.0 \pm 0.5$  ‰). By contrast, semi-natural ecosystems  
208 had considerably lower  $\delta^{15}\text{N}$  values, which ranged from -5.0 to 3.6 ‰ (soil  $1.5 \pm 0.2$  ‰, litter  $-2.1 \pm 0.2$  ‰, leaves  $-1.3 \pm 0.3$   
209 ‰). Soil  $\delta^{15}\text{N}$  values were significantly higher than those of leaves and litter across all the ecosystems studied, with the only  
210 exception of agroforestry homegardens (Fig. 4a).  $\delta^{15}\text{N}$  values of leaves and litter did not show significant differences within  
211 any given ecosystem.

212 Calculated  $\delta^{15}\text{N}$ -based enrichment factors showed high variability across all ecosystems with values ranging from -7.5 to -  
213 1.6 ‰ (Fig. 4b). A differentiation between managed and natural ecosystems was less clear than for  $\delta^{15}\text{N}$  values. The most  
214 negative enrichment factors ( $< -4.0$  ‰) were observed for *Helichrysum*, *Erica*, *Podocarpus* disturbed, and grass-dominated  
215 ecosystems (savannas and grasslands). These enrichment factors were significantly less negative for montane forests at lower  
216 elevations (*Podocarpus*, *Ocotea* and lower montane) and intensively managed (cropping) systems (i.e. homegarden, coffee,  
217 and maize; Fig. 4b).

### 218 3.4 Impacts of soil and climatic variables on soil $\delta^{15}\text{N}$ values

219 Two principal components (PC) explained 78.3 % of the total soil  $\delta^{15}\text{N}$  variation (Fig. 5). The first component explained  
220 55.8 % of the variability, and included soil chemistry and climatic variables (soil C and N concentrations, soil C/N ratio, soil  
221 pH, soil  $\delta^{13}\text{C}$ , MAP and MAT). Highly significant correlations ( $P < 0.001$ ) were obtained between PC 1 and the above  
222 factors ( $r = 0.93, 0.93, 0.61, -0.87, -0.76, 0.87, \text{ and } -0.63$ , respectively; Table S2). The second component explained an  
223 additional 22.5 % of soil  $\delta^{15}\text{N}$  variability and included soil texture (clay and sand contents) and MAT. These variables were  
224 highly correlated with PC 2 ( $r = -0.84, 0.82, \text{ and } -0.65$ ; Table S2). The principal component bi-plot showed a strong grouping  
225 between managed and semi-natural ecosystems (Fig. 5). Managed sites clustered around MAT, soil  $\delta^{13}\text{C}$ , and soil pH, while  
226  $\text{C}_4$ -dominated ecosystems (grassland, savannas, and maize fields) were preferentially influenced by the latter two variables.  
227 In contrast, semi-natural montane forest ecosystems, rather grouped around soil chemical properties such as C and N  
228 contents, C/N ratio, as well as MAP, while alpine *Helichrysum* ecosystems clustered around soil sand content.

229 In addition to PCA, multiple regression analyses were performed using a stepwise procedure that identified soil N content  
230 and MAT as the main driving variables explaining the variation in soil  $\delta^{15}\text{N}$ . A paraboloid model explained 68 % of this  
231 variability ( $P < 0.05$ ; Fig. 6). The combination of relatively high soil N contents (1 to 3 ‰), and low MAT (up to 14 °C),  
232 invariably corresponded to low soil  $\delta^{15}\text{N}$  values ( $< 2$  ‰) characteristic of semi-natural ecosystems. Conversely, the relatively  
233 high soil  $\delta^{15}\text{N}$  values ( $> 2$  ‰) observed in managed ecosystems corresponded to low soil N contents ( $< 1$  ‰) and  
234 comparatively high MAT (17 to 25 °C).



235 The relationship between soil  $\delta^{15}\text{N}$  values and climatic and edaphic variables provided valuable information about  
236 potentially different SOM dynamics in the various ecosystems studied, with data showing a clear differentiation between  
237 semi-natural and managed ecosystems (Fig. S4). The former is characterized by comparatively higher C/N ratios and lower  
238  $\delta^{15}\text{N}$  values (averaging 15.5 and 1.5 ‰ respectively), while the latter showed lower C/N ratios and higher soil  $\delta^{15}\text{N}$  values  
239 (averaging 11.9 and 3.5 ‰ respectively). Managed ecosystems further grouped into intensively cropped (homegardens,  
240 maize fields, and coffee plantations) and extensively managed grass-dominated ecosystems (savannas and grasslands).

## 241 **4 Discussion**

### 242 **4.1 Factors influencing the variation of $\delta^{13}\text{C}$ values along the elevational and land-use gradient**

243 The  $\delta^{13}\text{C}$  values of leaves in  $\text{C}_3$ -dominated (semi-natural) ecosystems in Mt. Kilimanjaro increased with elevation (Figs. 1  
244 and S2), which is in agreement with findings from other mountainous ecosystems in the tropics, Europe, and North America  
245 (Bird et al., 1994; Körner et al., 1991; Ortiz et al., 2016; Zhou et al., 2011; Zhu et al., 2009). The wider scatter of  $\delta^{13}\text{C}$  values  
246 observed in leaves relative to soils is most certainly due to the inherently large (inter- and intra- specific) variability of  $\delta^{13}\text{C}$   
247 in plants (Bird et al., 1994). Different tissues within the plant can present widely divergent  $\delta^{13}\text{C}$  values as a result of  
248 fractionation processes associated with the C compounds involved in their construction (Dawson et al., 2002). Moreover,  
249 other factors including light intensity, humidity, and the re-utilization of previously respired low  $^{13}\text{C}$ - $\text{CO}_2$  within the canopy  
250 may further contribute to the variability of  $\delta^{13}\text{C}$  in leaf tissues (Ometto et al., 2006; van der Merwe and Medina, 1989).

251 While fractionation effects preclude a straightforward interpretation of  $\delta^{13}\text{C}$  of SOM, this variable provides an integrated  
252 measure of the isotopic composition of the precursor biomass at the ecosystem level (Bird et al., 2004; Saiz et al., 2015a).  
253 Mass balance calculations that assume (i) 5% (w/w) average root mass (< 2 mm) in soil samples, and (ii) leaves having  
254 similar isotopic signals as roots, show that the removal of visible sieved roots might cause a very small effect on soil isotopic  
255 values. This would amount to values  $\sim 0.15\text{‰}$  higher than the original soil isotopic values, with such discrepancy being even  
256 smaller if root samples were considered having values 0.5-1‰ higher than leaves as is commonly reported in the literature  
257 (calculations not shown). Besides the natural variability of soil  $\delta^{13}\text{C}$  values observed in  $\text{C}_3$ -dominated semi-natural  
258 ecosystems, there were distinct patterns in  $\delta^{13}\text{C}$  values of soil samples collected in extensively managed, low-elevation  
259 ecosystems where woody and grass vegetation coexist (i.e. grasslands and savannas), which indicate the strong influence  
260 exerted by  $\text{C}_4$  vegetation on the C isotopic composition of all sampled materials (Fig. 2). The results obtained in semi-natural  
261 ecosystems at Mt. Kilimanjaro fit well within the interpretative framework for elevational soil  $\delta^{13}\text{C}$  data proposed by Bird et  
262 al. (1994). These authors suggest that besides temperature and atmospheric pressure, other primary factors influencing soil  
263  $\delta^{13}\text{C}$  values are the age and degree of decomposition of SOM, as well as variables related to the characteristics of the canopy,

264 including the proportion of respired CO<sub>2</sub> that is recycled during photosynthesis, the relative contribution of leaf and woody  
265 litter to SOM, and soil moisture.

266 Besides the factors explained above, soil δ<sup>13</sup>C values are strongly influenced by the balance between ecosystem C inputs and  
267 outputs. It seems reasonable to assume that in the case of natural ecosystems there may be a steady state between SOM  
268 inputs and decomposition rates. This should be in contrast with the typically altered nutrient dynamics of disturbed systems,  
269 particularly those under agricultural management (Wang et al., 2018). Low fractionation factors in δ<sup>13</sup>C are commonly  
270 reported between plant material and topsoils in natural systems mainly because of the relatively limited humification of  
271 recent organic matter prevalent in topsoils (Acton et al., 2013; Wang et al., 2018). Thus, we hypothesized that if carbon  
272 inputs and outputs were roughly in balance, then the difference in δ<sup>13</sup>C values between plant material and topsoil would be  
273 smaller in undisturbed sites compared to managed or disturbed sites. The results shown in Fig. 3 agree well with this notion.

274 Soil δ<sup>13</sup>C values decreased with increasing MAP and decreasing MAT, which also corresponded with higher SOC contents  
275 (Fig. S3). This suggests that the relatively cooler and wetter conditions of high elevation semi-natural forest ecosystems (i.e.  
276 Foc, Fpo) promote the accumulation of SOM, which is similar to previous findings of work conducted along elevational  
277 gradients (Bird et al., 1994; Kohn, 2010). Compared to high-elevation locations, the climatic conditions of mid-elevation  
278 ecosystems are more favourable for the activities of SOM decomposers, as these sites are consistently warmer and drier than  
279 the characteristically cool and occasionally waterlogged high-altitude ecosystems (Fig. S1; Becker and Kuzyakov, 2018;  
280 Borken and Matzner, 2009; Garten et al., 2009; Kirschbaum, 1995; Leirós et al., 1999). The comparatively high soil δ<sup>13</sup>C  
281 values observed in the disturbed *Podocarpus* (Fpd) and *Erica* forest (Fer) plots may have been partly caused by recurrent fire  
282 events (Hemp, 2005) leading to reduced SOC contents and higher C/N ratios (Saiz et al., 2015a). Further variations in soil  
283 δ<sup>13</sup>C values could also be related to the biochemical composition of the precursor biomass. For instance, herbaceous  
284 vegetation is pervasive at high elevations, and contains relatively low amounts of lignin – an organic compound  
285 characteristically depleted in <sup>13</sup>C (Benner et al., 1987). This may contribute to explain the higher δ<sup>13</sup>C values observed in  
286 plant and soil materials in alpine ecosystems dominated by *Helichrysum* vegetation, compared to forest ecosystems at lower  
287 elevations (Fig. 2).

288 Elevation also has a strong influence on the seasonal litterfall dynamics observed in Mt Kilimanjaro, and thus may have  
289 significant implications in the SOM cycling across the various ecosystems (Becker et al., 2015). These authors suggest that  
290 the large accumulation of particulate organic matter observed at the end of the dry season in low and mid altitude ecosystems  
291 may result in the increased mineralization of easily available substrates (Mganga and Kuzyakov, 2014) and nutrient leaching  
292 (Gütlein et al., 2018) during the following wet season. Agricultural practices such as the removal of biomass or ploughing  
293 deplete SOM, particularly in the intensively managed systems (i.e. maize, homegardens and coffee plantations), thus leading

294 to lower SOC contents and C/N ratios, and slightly higher soil  $\delta^{13}\text{C}$  values than those observed in semi-natural ecosystems at  
295 comparable elevations (e.g. lower montane forests; Fig. S3). Indeed, the relationship between  $\delta^{13}\text{C}$  enrichment factors and  
296 soil C/N ratios shown in Fig. 3 is quite informative regarding SOM dynamics. As previously mentioned, soil C/N ratios  
297 provide a good indication of SOM decomposition processes, typically showing comparatively low values in managed and  
298 disturbed systems. These correspond well with sites having large enrichment factors ( $< -1.25\text{‰}$ ; i.e. intensively managed  
299 and disturbed sites), which agree with the notion of altered SOM dynamics. Therefore, besides the systematic removal of  
300 plant biomass characteristic of agricultural systems, annual litterfall patterns may also explain the comparatively lower  
301 contents of C and N observed in the topsoils of intensively managed sites (Table 1; Figs. S3, S4). Moreover, low-elevation  
302 ecosystems contain a variable mixture of  $\text{C}_3$  and  $\text{C}_4$  vegetation, which have been shown to have differential mineralization  
303 dynamics as demonstrated by incubation experiments (Wynn and Bird, 2007), and field-based research (Saiz et al., 2015a).

304 Our data show strong relationships between temperature and variables directly related to SOM dynamics such as soil  $\delta^{13}\text{C}$ ,  
305 C, N and C/N ratios (Table S1). These results agree well with recent findings by Becker and Kuzyakov (2018) who studied  
306 SOM decomposition dynamics at these very sites. An important finding revealed by that study is that of seasonal variation in  
307 temperature is a major controlling factor in litter decomposition. Their study shows that small seasonal variations in  
308 temperature observed at high elevation sites exert a strong effect on litter decomposition rates. Therefore, the authors argue  
309 that the projected increase in surface temperature may result in potentially large soil C losses at these sites due to the  
310 comparatively strong temperature sensitivity to decomposition that is commonly observed at low temperatures and at high  
311 elevations sites (Blagodatskaya et al., 2016).

312 Savannas and grasslands are subject to recurrent fire events, and thus the soils of these ecosystems may potentially contain  
313 significant amounts of fire-derived (pyrogenic) C (Saiz et al., 2015b). This can be partly demonstrated by the higher soil C/N  
314 ratios observed in these ecosystems compared to  $\text{C}_4$ -dominated agricultural systems protected from fire (e.g. maize  
315 plantations; Fig. S3d). Moreover, the  $\delta^{13}\text{C}$  values of soils in grasslands and savannas were lower than those of leaves, which  
316 may be due to the savanna isotope disequilibrium effect (SIDE) (Bird and Pousai, 1997; Saiz et al., 2015b). The latter  
317 concept explains the difference in C isotopic composition between the precursor vegetation and pyrogenic C compounds  
318 produced during the combustion of biomass. Saiz et al. (2015b) have demonstrated that savanna fires produce pyrogenic C  
319 that is relatively  $^{13}\text{C}$  depleted with respect to the precursor biomass. Furthermore, the combustion of  $\text{C}_4$  vegetation produces  
320 finer pyrogenic C particles than woody biomass, resulting in the preferential export of grass-derived pyrogenic particles from  
321 the site of burning, which further enhances the depletion of  $^{13}\text{C}$  in these soils (Saiz et al., 2018).

#### 322 4.2 Variation of $\delta^{15}\text{N}$ values along the elevational and land-use gradient

323 The  $\delta^{15}\text{N}$  values of leaves, litter, and topsoil presented here (Fig. 4a) agree well with the range of data reported from earlier  
324 investigations in the same study region (Amundson et al., 2003; Zech et al., 2011), but with our study involving more  
325 ecosystems, replicate sites and a far larger spatial sampling domain. Overall, the  $\delta^{15}\text{N}$  values for montane tropical forest  
326 ecosystems in Mt. Kilimanjaro are considerably lower than the mean values reported for a broad variety of tropical lowland  
327 forests worldwide (soil values ranging from 3 to 14 ‰; de Freitas et al., 2015; Martinelli et al., 1999; Nardoto et al., 2014;  
328 Piccolo et al., 1996; Sotta et al., 2008). Rather, the  $\delta^{15}\text{N}$  values observed in the montane forests investigated are in the same  
329 range of temperate forest ecosystems reported in a comprehensive literature review by Martinelli et al. (1999). These authors  
330 argue that, compared to tropical lowland forests, the lower  $\delta^{15}\text{N}$  values of temperate and montane tropical forests result from  
331 their lower N availability and thus lower ecosystem N losses. However, this hypothesis may not completely hold for the  
332 montane forest ecosystems of our study, since Gütlein et al. (2018) reported elevated soil  $\text{NO}_3^-$  and DON concentrations at  
333 deep soil solution (80 cm) and significant nitrogen leaching rates of 10 - 15 kg N ha<sup>-1</sup> y<sup>-1</sup>. The relatively low  $\delta^{15}\text{N}$ -based  
334 enrichment factors observed in the lower montane, *Ocotea* and undisturbed *Podocarpus* forest (Fig. 4b) were probably due  
335 to the prevalence of biological di-nitrogen fixation (BNF) at these ecosystems. The assumption of significant BNF is  
336 supported by leaf  $\delta^{15}\text{N}$  values close to 0 ‰ (Fig. 4a) and is in line with previous works (Craine et al., 2015a; Nardoto et al.,  
337 2014; Robinson, 2001). Furthermore, sporadic measurements of N-compounds in rainfall and throughfall conducted at our  
338 forest sites showed substantial input of N via atmospheric deposition, which may be in the order of N leaching losses  
339 (unpublished results). This agrees well with findings from Bauters et al. (2018) reporting 18 kg N ha<sup>-1</sup> y<sup>-1</sup> N inputs via wet  
340 deposition into tropical forests of the Congo Basin, which are predominantly derived from biomass burning and long-range  
341 atmospheric transport. High N inputs into these forest ecosystems are likely to be in a similar range as N outputs (prevalled  
342 by leaching losses particularly where MAP is highest; Gütlein et al., 2018), and therefore, they would not translate to strong  
343 effects on ecosystem  $\delta^{15}\text{N}$  values. The significantly more negative enrichment factors observed in the disturbed *Podocarpus*  
344 and *Erica* forests (Fig. 4b) may be related to past fire events (Hemp, 2005; Zech et al., 2011). Burning of vegetation may  
345 cause losses of <sup>15</sup>N-depleted  $\text{NO}_x$  gas and N leachate, resulting in higher soil  $\delta^{15}\text{N}$  values, thus producing variations in  $\delta^{15}\text{N}$ -  
346 based enrichment factors (Zech et al., 2011).

347 Previous studies have shown that  $\delta^{15}\text{N}$  values generally increase with land-use intensification (Martinelli et al., 1999;  
348 Stevenson et al., 2010), which corresponds well with the more positive  $\delta^{15}\text{N}$  values observed in the intensively managed  
349 agricultural systems occurring at the mountain's foot slope (Fig. 4a). Indeed, agronomic practices such as fertilization,  
350 removal of plant material after harvest, or ploughing, are factors known to affect N turnover processes that strongly affect  
351  $\delta^{15}\text{N}$  values (Bedard-Haughn et al., 2003; Saiz et al., 2016). However, our values are in the lower range of published data for  
352 other land-use gradients (Aranibar et al., 2008; Eshetu and Högberg, 2000; Traoré et al., 2015), and may partly be the result  
353 of comparably low to moderate organic and inorganic N fertilization rates currently applied in the region (anecdotal evidence

354 gathered by the authors and SI). Additionally, the nitrogen isotopic signal of mineral fertilizers commonly used in the region  
355 is  $\sim 0$  ‰ (Bateman and Kelly, 2007), and thus, it may not exert a significant additional bias on the interpretation of soil  $\delta^{15}\text{N}$   
356 values. However, the addition of manure ( $\delta^{15}\text{N} \sim 8$  ‰) in Hom systems, albeit used in low quantities (Gütlein et al., 2018),  
357 may have well contributed to the high  $\delta^{15}\text{N}$  values observed in this ecosystem (Fig. 4). Also, we suggest that the use of  
358 pesticides may not pose a strong bias in our isotopic results since their use is limited to intensively managed sites, and the  
359 actual isotopic values of pesticides work in the opposite direction to the observed data (Fig. 4; SI).

360 Compared to other low-elevation managed stands such as homegardens and coffee plantations, the higher  $\delta^{15}\text{N}$ -based  
361 enrichment factors observed in maize fields and in grass-dominated ecosystems (grasslands and savannas) (Fig. 4b) may be  
362 related to both the organic inputs resultant from grazing activities and the influence of  $\text{C}_4$  vegetation. Both Aranibar et al.  
363 (2008) and Wang et al. (2010) have suggested that variations in  $\delta^{15}\text{N}$  values within a given ecosystem could be due to  $\text{C}_3$  and  
364  $\text{C}_4$  plants preferentially absorbing chemical forms of N with differing  $^{15}\text{N}$  abundances. Moreover, recurrent fires  
365 characteristic of tropical grasslands and savannas may have also influenced their comparatively high soil  $\delta^{15}\text{N}$ , causing the  
366 relatively high  $\delta^{15}\text{N}$ -based enrichment factors.

#### 367 **4.3 Factors controlling soil $\delta^{15}\text{N}$ along the elevational and land-use gradient**

368 The strong controlling effects exerted by climatic and edaphic factors on soil  $\delta^{15}\text{N}$  values agree well with numerous previous  
369 works (Amundson et al., 2003; Conen et al., 2013; Eshetu and Högberg, 2000; Martinelli et al., 1999; Stevenson et al.,  
370 2010). The principal component analysis of factors controlling soil  $\delta^{15}\text{N}$  revealed a strong clustering between managed and  
371 semi-natural ecosystems (Fig. 5), which was also reflected in the multiple regression analysis and graphical representation  
372 depicting soil  $\delta^{15}\text{N}$  as a function of soil N concentration and MAT (Fig. 6). Semi-natural ecosystems were characterized by  
373 relatively low soil  $\delta^{15}\text{N}$  values, and occurred across a broad range of soil N contents in locations with low to medium MAT.  
374 By contrast, intensively managed ecosystems had higher soil  $\delta^{15}\text{N}$  values and corresponded to locations with low soil N  
375 contents and high MAT. The negative correlation of  $\delta^{15}\text{N}$  values with soil nitrogen content and the positive correlation with  
376 mean annual temperature suggest reduced mineralisation rates, and thus limited nitrogen availability, at least in high-  
377 elevation ecosystems.

378 The sharp contrast observed both in soil C/N ratios and  $\delta^{15}\text{N}$  values between managed and semi-natural ecosystems offers  
379 additional useful information about their potentially contrasting SOM dynamics (Fig. S4d). Intensively managed sites  
380 consistently showed low soil C/N ratios and high soil  $\delta^{15}\text{N}$  values, which may initially suggest a more open N cycle and  
381 potentially greater N losses as reported by Gerschlaier et al. (2016) for some of these ecosystems. This may due to C-  
382 limitation of heterotrophic microbial N retention under low C/N ratios (Butterbach-Bahl and Dannenmann, 2012). However,  
383 nitrate leaching is quite a relevant process that discriminates only slightly against  $^{15}\text{N}$  (Denk et al., 2017), which may

384 confound the interpretation of soil  $\delta^{15}\text{N}$  values. Indeed, Gütlein et al. (2018) have recently shown that nitrate leaching may  
385 be quite significant in Mt Kilimanjaro's semi-natural forests. Therefore, at least in these ecosystems, claims about the nature  
386 of the N cycle (i.e. open/close) should not be made solely on the basis of soil  $\delta^{15}\text{N}$ .

387 Grass-dominated ecosystems (grasslands and savannas) were noticeably different to the intensively managed croplands, as  
388 demonstrated by the higher soil C/N ratios and lower soil  $\delta^{15}\text{N}$  of the former, which suggest a lower degree of decomposition  
389 of organic matter and potentially lower N turnover rates (Saiz et al., 2016). Within the intensively managed sites, the stands  
390 under maize cultivation show an interesting case of enhanced SOM dynamics. These sites are under an intensive  
391 management regime that involves the removal of aboveground vegetation after harvest. This fact combined with the faster  
392 decomposition rates reported for  $\text{C}_4$ -derived SOM (Saiz et al., 2015a; 2016; Wynn and Bird, 2007) may invariably lead to  
393 their characteristically low SOC and N contents (Table 1; Figs. S3, S4). Furthermore, low soil C/N ratios have been reported  
394 to enhance gaseous losses in semi-arid systems, which leads to increased soil  $\delta^{15}\text{N}$  values (Aranibar et al., 2004) and may  
395 explain why maize stands showed the highest soil  $\delta^{15}\text{N}$  values of all the land uses studied.

396 Semi-natural ecosystems showed rather high soil C/N ratios and low soil  $\delta^{15}\text{N}$  values compared to managed sites (Fig. S4d).  
397 The more humid and cooler conditions prevalent in forest ecosystems may limit decomposition processes, thereby  
398 contributing significantly to their higher SOM abundance (Table 1). A small variation range in soil  $\delta^{15}\text{N}$  values was also  
399 reported by Zech et al (2011) for semi-natural ecosystems (Foc and Fpo) when working along the same land-use and  
400 elevation gradient. Like us, these authors also observed a strong significant correlation of soil  $\delta^{15}\text{N}$  with MAT, but not with  
401 MAP (Table S1). Additionally, site-specific soil characteristics, and the structural composition of vegetation have a strong  
402 influence on ecosystem nutrient dynamics (Saiz et al., 2012; 2015a). Ecosystem disturbances (e.g. fire, selective logging,  
403 etc.) cause changes in vegetation cover that affect SOM cycling and may translate into variations in soil C/N ratios (Saiz et  
404 al., 2016). Both *Ocotea* and *Podocarpus* forests contain disturbed (Fod, Fpd) and undisturbed stands (Foc, Fpo), though only  
405 the *Podocarpus* ecosystems allow for a general overview of disturbance impacts on SOM-related properties. While changes  
406 in the isotopic composition of C and N were not significant, soil C/N ratios were heavily influenced by disturbance (Fig. S4).  
407 Compared to non-disturbed sites, the lower C and N contents observed in the soil of disturbed ecosystems indicate reduced  
408 OM inputs to the soil and/or enhanced decomposition of SOM (Table 1). The higher soil C/N ratios observed in the  
409 *Podocarpus* disturbed and *Erica* forests may well be the result of fire, which may preferentially promote N losses while  
410 accruing relatively recalcitrant C forms (i.e. pyrogenic C). Woody biomass combustion produces pyrogenic C that  
411 accumulates preferentially close to the site of production (Saiz et al., 2018), thus likely contributing to the higher soil C/N  
412 ratios observed at these disturbed ecosystems. The lowest soil C/N ratios among all semi-natural ecosystems were observed  
413 at the alpine *Helichrysum* sites, which may relate to their characteristically sparse vegetation and extremely low MAT.

414 Under such circumstances soil development, biomass inputs, decomposition processes, and thus, soil N turnover may be  
415 strongly limited, as it was confirmed by a recent study conducted at one of these sites (Gütlein et al., 2017).

## 416 **5 Conclusions**

417 The variations in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values combined with interpretation of other indices such as  $\delta^{13}\text{C}$ - and  $\delta^{15}\text{N}$ -based  
418 enrichment factors and soil C/N ratios, enabled a qualitative characterisation of regional differences in C and N dynamics as  
419 affected by vegetation characteristics, environmental conditions, and management activities.

420 Our data show that SOM contents are higher in cold and wet high-elevation ecosystems than at low-elevation managed sites.  
421 Management practices such as tillage, harvest, and vegetation burning promote the loss of OM, with SOM decomposition  
422 being further enhanced by the warm and moderately wet conditions of the mountain's foot slope. Based on our results, we  
423 suggest that besides management, increasing temperatures in a changing climate may promote C and N losses, thus altering  
424 the otherwise stable SOM dynamics of Mt. Kilimanjaro's forest ecosystems. Moreover, the current situation of low N inputs  
425 in managed systems of sub-Saharan Africa is likely to change, since national efforts aim to increase fertilizer use are  
426 currently <10% of recommended rates (Hickman et al., 2014). Therefore, our data may also be valuable as a generic  
427 reference for low-elevation tropical agrosystems managed under low N inputs, while it may also allow the monitoring of  
428 expected changes in agricultural management, and associated impacts on ecosystem N cycle through the study of the  
429 variation in  $\delta^{15}\text{N}$  values.

430 In addition to climatic and edaphic factors,  $\delta^{15}\text{N}$  values of plant and soil material can largely depend on both the amount and  
431  $\delta^{15}\text{N}$  signal of atmospheric deposition and BNF, which highlights the importance of conducting additional measurements of  
432 site specific N cycling, when comparing ecosystem  $\delta^{15}\text{N}$  values across different biomes and regions. The combination of  
433 qualitative isotope natural abundance studies at a large number of sites (this study) with more elaborated quantitative process  
434 studies using enriched isotope labelling and N losses on a lower number of selected sites represent an ideal approach to  
435 characterize ecosystem C and N cycling of the larger Mt. Kilimanjaro region with its diverse ecosystems, climate, and  
436 management.

## 437 **Author contribution**

438 FG contributed to design, performed the study, and co-wrote the paper; GS contributed to analyses and co-wrote the paper;  
439 DSC and MK provided plant samples and contributed to writing; MD contributed to writing; and RK designed the study and  
440 contributed to analyses and writing.

## 441 **Competing Interests**

442 The authors declare no competing interests.

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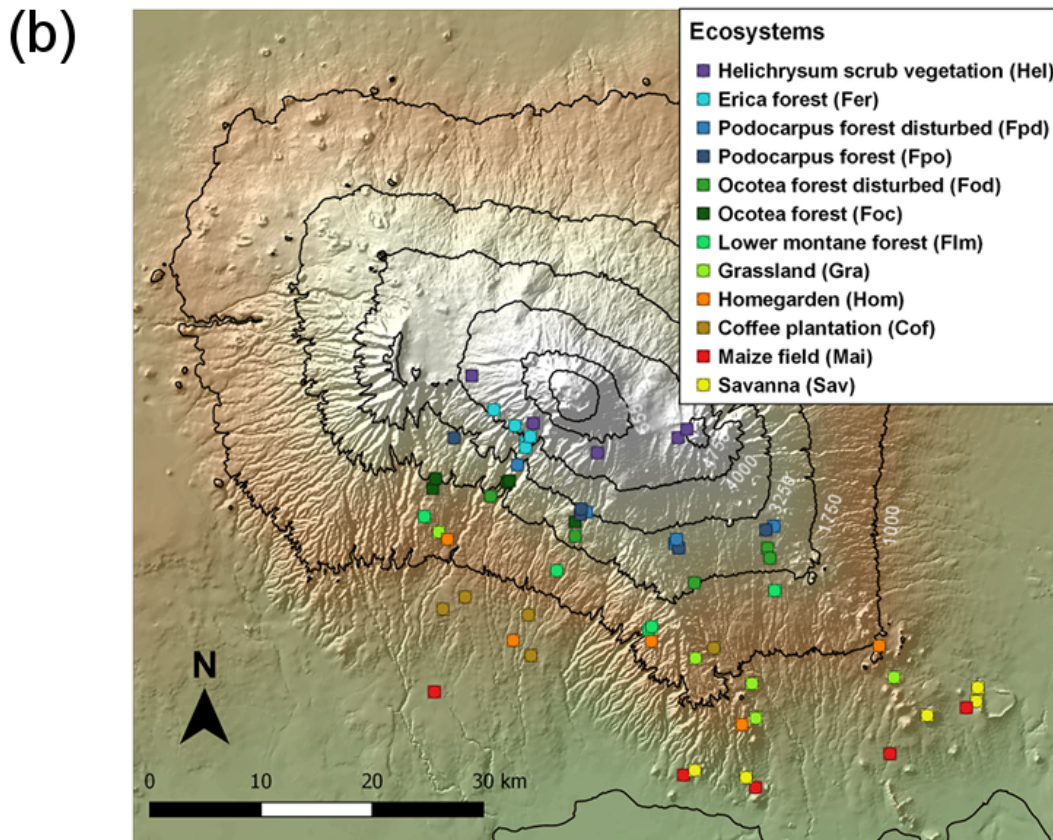
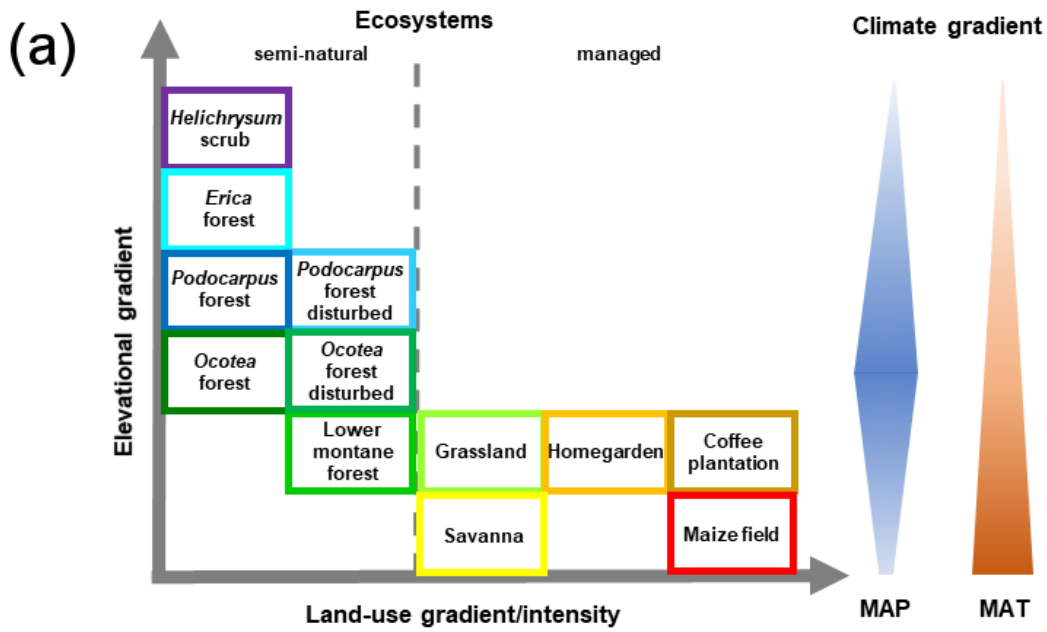
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**Table 1** General characteristics of ecosystems investigated at Mt. Kilimanjaro, Tanzania.

Ecosystem	Land-use type	Elevation (m a.s.l.)	MAP (mm)	MAT (°C)	Soil properties						
					Soil type	pH (CaCl <sub>2</sub> )	Clay (%)	Sand (%)	Organic carbon (%)	Total nitrogen (%)	C/N ratio
Savanna (Sav)	(M) extensive grazing, grass cutting	971 (40)	764 (50)	23.7 (0.3)	Leptosol	6.6 (0.3)	27.3 (4.0)	39.3 (8.7)	3.5 (0.4)	0.2 (0.0)	13.5 (0.2)
Maize field (Mai)	(M) cropped agriculture	938 (25)	674 (34)	23.6 (0.4)	Nitisol	5.6 (0.3)	37.4 (4.5)	20.3 (7.7)	1.6 (0.2)	0.1 (0.0)	11.8 (0.1)
Coffee plantation (Cof)	(M) cropped agriculture	1,349 (78)	1,393 (96)	19.8 (0.7)	Vertisol	4.5 (0.3)	45.2 (8.0)	17.8 (4.5)	4.2 (0.4)	0.4 (0.0)	10.5 (0.2)
Homegarden (Hom)	(M) cropped agroforestry	1,478 (112)	1,656 (177)	18.7 (0.8)	Andosol	5.4 (0.4)	45.4 (8.0)	16.5 (5.8)	6.7 (1.3)	0.6 (0.1)	11.5 (0.4)
Grassland (Gra)	(M) extensive grazing, grass cutting	1,506 (84)	1,610 (135)	18.9 (0.7)	Umbrisol	5.1 (0.4)	48.1 (8.1)	16.0 (5.1)	5.3 (2.1)	0.4 (0.2)	12.6 (0.2)
Lower montane forest (Flm)	(S-N) montane forest	1,806 (71)	2,201 (33)	15.5 (0.3)	Andosol	4.7 (0.3)	47.3 (5.2)	14.5 (2.2)	22.7 (4.9)	1.6 (0.2)	13.3 (1.5)
<i>Ocotea</i> forest (Foc)	(S-N) montane forest	2,464 (106)	2,388 (73)	11.5 (0.4)	Andosol	3.5 (0.2)	52.3 (4.5)	10.4 (2.3)	40.2 (1.5)	2.7 (0.1)	14.9 (0.7)
<i>Ocotea</i> forest disturbed (Fod)	(S-N) montane forest	2,378 (56)	2,334 (35)	11.9 (0.4)	Andosol	3.6 (0.2)	53.9 (3.4)	10.1 (2.5)	32.0 (1.8)	2.2 (0.2)	15.1 (1.3)
<i>Podocarpus</i> forest (Fpo)	(S-N) montane forest	2,856 (41)	2,036 (27)	9.6 (0.2)	Andosol	3.8 (0.1)	48.7 (1.1)	9.4 (1.3)	37.0 (1.0)	2.4 (0.1)	15.5 (0.8)
<i>Podocarpus</i> forest disturbed (Fpd)	(S-N) montane forest	2,904 (48)	2,056 (29)	9.7 (0.3)	Andosol	4.0 (0.2)	45.8 (3.4)	12.6 (3.3)	33.8 (2.3)	1.7 (0.0)	19.9 (1.4)
<i>Erica</i> forest (Fer)	(S-N) montane forest	3,716 (77)	1,517 (54)	6.2 (0.6)	Andosol	3.9 (0.2)	29.5 (5.1)	24.1 (6.2)	28.1 (2.4)	1.5 (0.1)	18.9 (0.7)
<i>Helichrysum</i> vegetation (Hel)	(S-N) alpine scrub vegetation	4,250 (100)	1,293 (31)	4.2 (0.4)	Andosol	5.7 (0.3)	7.9 (1.4)	69.9 (9.5)	6.1 (3.3)	0.3 (0.2)	12.0 (1.1)

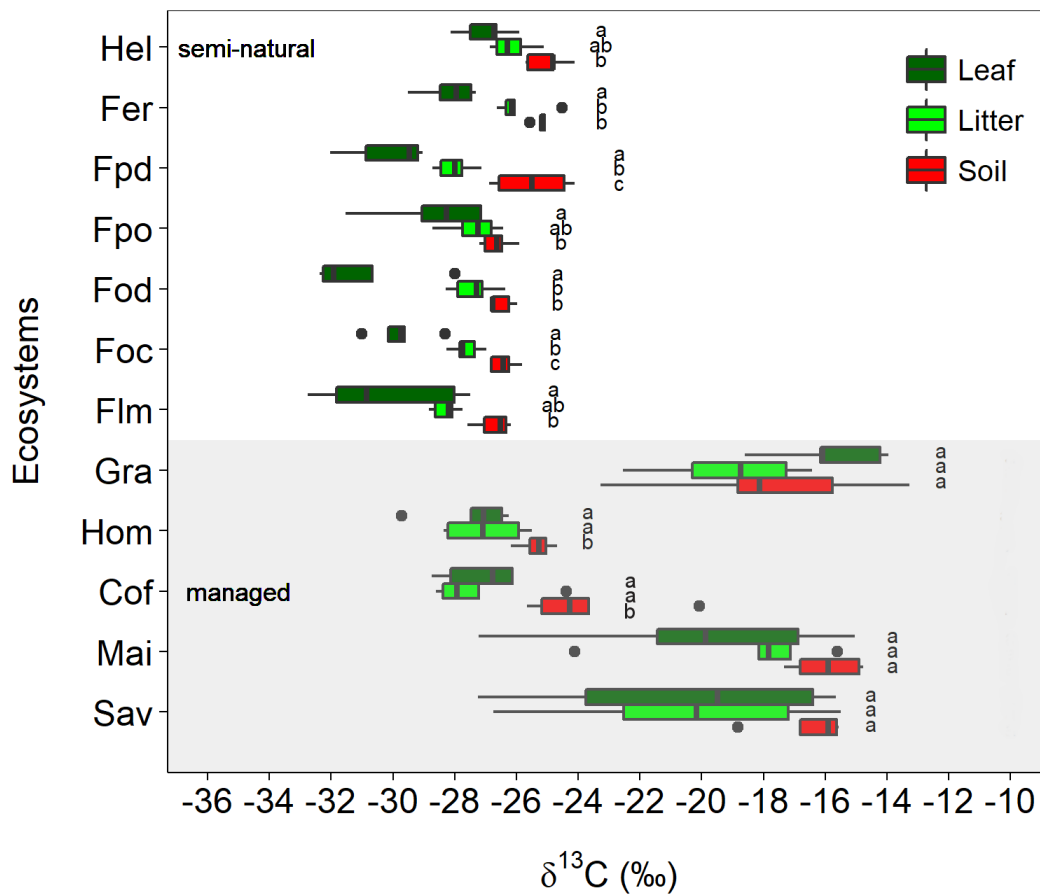
681 Land uses are generically classified as managed (M) and semi-natural ecosystems (S-N). MAP and MAT stand for mean annual precipitation and temperature respectively.  
682 Climatic values are according to Appelhans et al. (2016). Data represent mean values ( $n = 5 \pm SE$ ) for different ecosystems. The most representative soil type is shown for each  
683 ecosystem. Soil properties are given for topsoil (0 – 10 cm for pH and soil texture, 0 – 5 cm for soil organic carbon and total nitrogen).





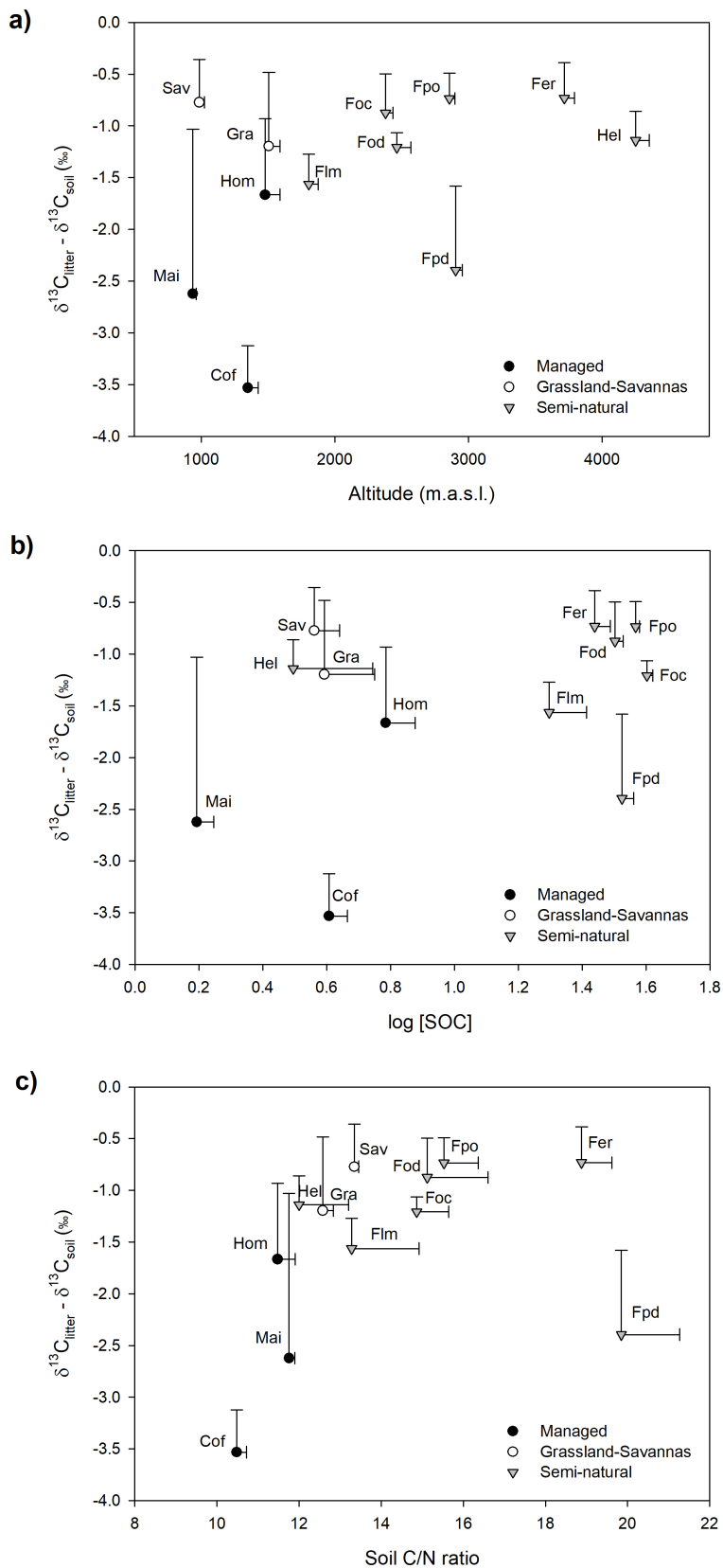
684

685 **Figure 1:** Geographical distribution of investigated ecosystems: a) along the elevational and land-use gradient. MAP denotes  
 686 mean annual precipitation and MAT mean annual temperature. Colours of boxes framing ecosystems' names match colours  
 687 of symbols in the GeoTIFF panel below; b) along the southern slope of Mt. Kilimanjaro. Symbols represent individual  
 688 ecosystems (12) replicated 5 times (60 study sites in total).



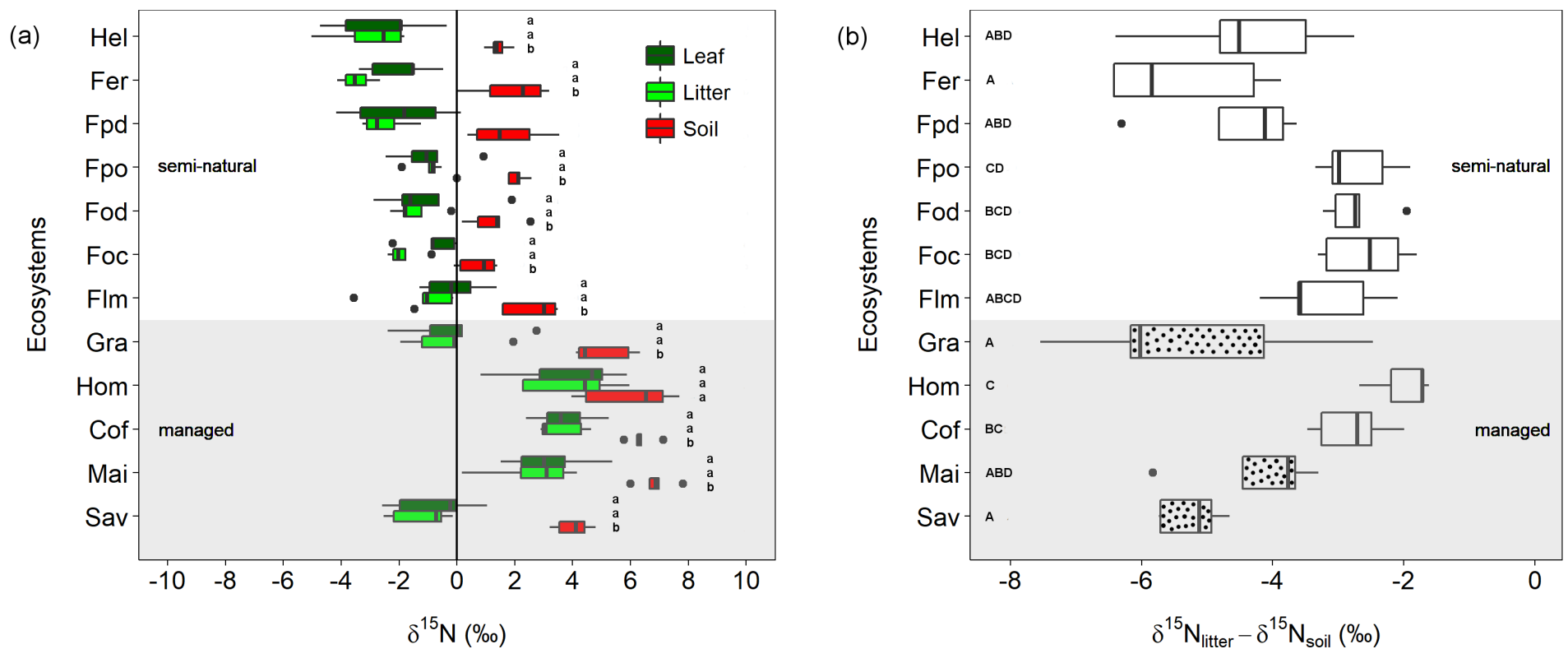
689 **Figure 2:** Variation in  $\delta^{13}\text{C}$  values for leaves, litter, and soil along the Kilimanjaro elevational and land-use gradient.  
 690 Ecosystem data represent the average values of five sites (one per each transect), with each site being composed of five  
 691 samples ( $n = 5$ ). Boxplots show median values per ecosystem with whiskers representing 1<sup>st</sup> and 3<sup>rd</sup> quartiles. Dots represent  
 692 outliers. The shaded region represents managed ecosystems (both intensively and extensively), while those un-shaded  
 693 indicate semi-natural ecosystems. Lower case letters show significant differences between sampled materials within each  
 694 ecosystem (one-way ANOVA followed by Tukey's HSD test as a post hoc procedure,  $P \leq 0.05$ ). The ecosystem acronyms  
 695 used are as per Table 1. Mai, Cof, and Hom are managed cropping sites, Gra and Sav are extensively managed grasslands and  
 696 savannas, while the rest represent semi-natural ecosystems. Sites are ordered by increasing altitude.

698



699

700 **Figure 3:** a) Variation in  $\delta^{13}\text{C}$ -based enrichment factors ( $\delta^{13}\text{C}_{\text{litter-soil}}$ ) with elevation; b) Relationship between  $\delta^{13}\text{C}$ -based  
 701 enrichment factors ( $\delta^{13}\text{C}_{\text{litter-soil}}$ ) and SOC concentration ( $\log \text{SOC}$ ); and c) Relationship between  $\delta^{13}\text{C}$ -based enrichment  
 702 factors ( $\delta^{13}\text{C}_{\text{litter-soil}}$ ) and soil C/N ratios. Note: A savanna site with large  $\text{C}_3$  influence was removed from the figure for clarity.



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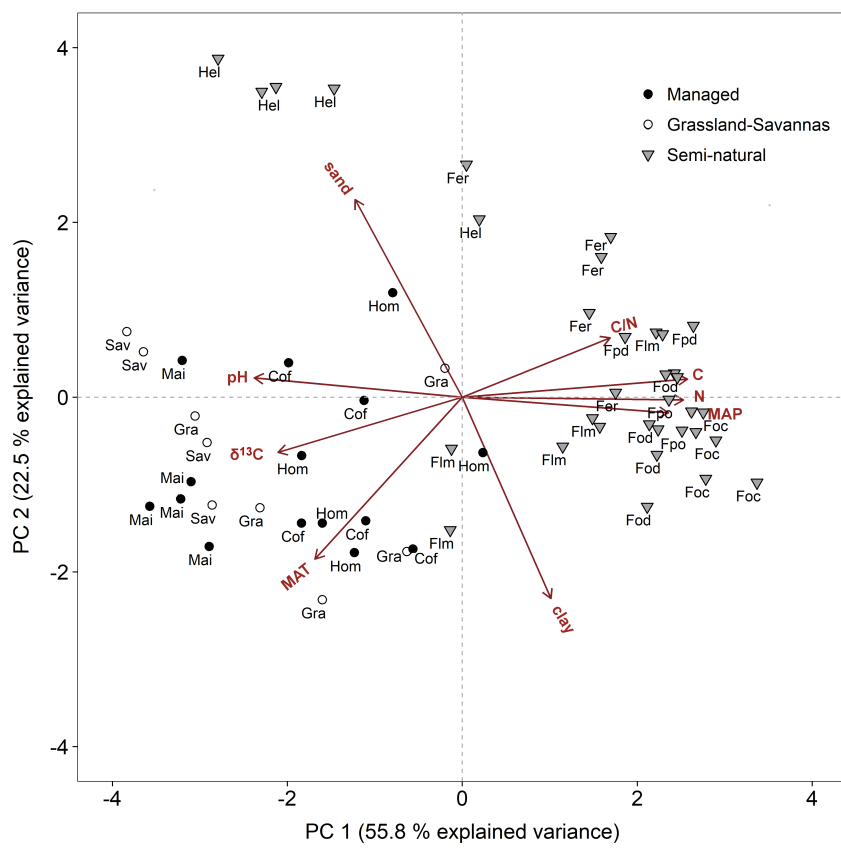
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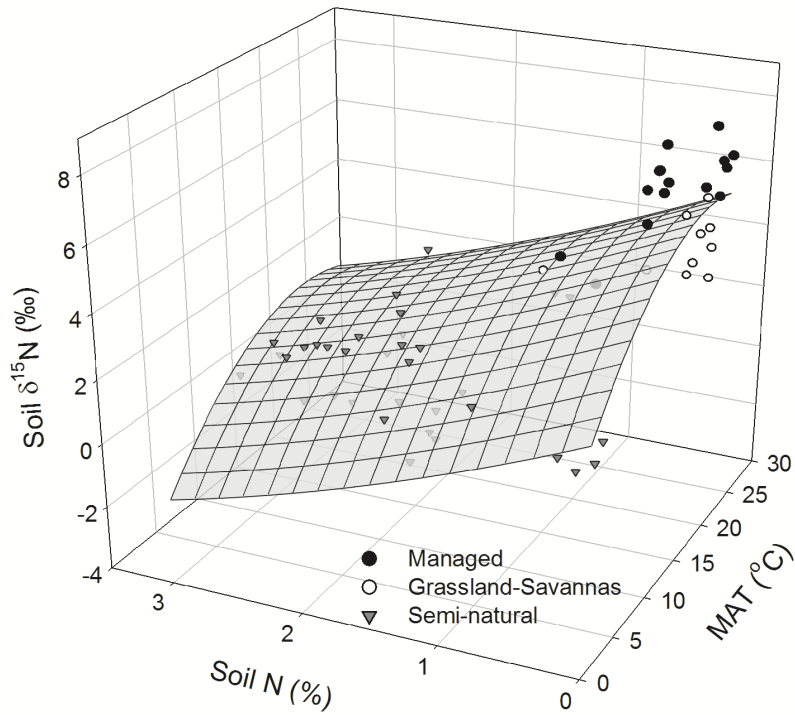
**Figure 4:** Variation in  $\delta^{15}\text{N}$  values and  $\delta^{15}\text{N}$ -based enrichment factors along the Kilimanjaro elevational and land-use gradient. a) Variation in  $\delta^{15}\text{N}$  values for leaves, litter, and soil material sampled along the Kilimanjaro elevational and land-use gradient. Boxplots show median values per ecosystem with whiskers representing 1<sup>st</sup> and 3<sup>rd</sup> quartiles. Dots represent outliers. Ecosystem data represent the average values of five sites (one per each transect), with each site being composed of five samples. Lower case letters show significant differences between sampled materials within each ecosystem (one-way ANOVA followed by Tukey's HSD test as a post hoc procedure,  $P \leq 0.05$ ); b) Variation in  $\delta^{15}\text{N}$ -based enrichment factors ( $\delta^{15}\text{N}_{\text{litter-soil}}$ ) calculated for the different



710

711 **Figure 5:** Principal component analysis bi-plot for soil and climate variables potentially controlling soil  $\delta^{15}\text{N}$ . Symbols are as  
 712 per all previous figures. Acronyms are as per Table 1. C/N = soil C/N ratio, C = soil carbon content, N = soil nitrogen  
 713 content, MAP = mean annual precipitation, clay = soil clay content, MAT = mean annual temperature,  $\delta^{13}\text{C}$  = soil  $\delta^{13}\text{C}$ , and  
 714 pH = soil pH.

715



716

717 **Figure 6:** Measured and modelled soil  $\delta^{15}\text{N}$  values predicted as a function of soil N abundance and mean annual temperature  
 718 (MAT). Data points are classified by generic land uses (i.e. intensively managed cropping sites, extensively managed  
 719 grassland and savannas, and semi-natural ecosystems) observed along the elevational and land use gradient. The regression  
 720 takes the following form:  $\text{soil } \delta^{15}\text{N} = 1.10 + 0.49 (\text{MAT}) - 1.86 (\text{soil N}) - 0.01 (\text{MAT})^2 + 0.14 (\text{soil N})^2$ ; ( $r^2 \text{ adj} = 0.68$ ,  $P <$   
 721  $0.05$ ,  $n = 60$ ).

## 1 Appendix – Fertilizer and pesticide isotopic composition

### 2 *Fertilizers*

3 A general indication of fertilizer used in the region is provided here.

4 Giller et al. (1998) reported an estimate of ca. 40 kg N ha<sup>-1</sup> inorganic fertilizer use in the  
5 Kilimanjaro region. A more recent report by Senkoro et al. (2017) indicate a generic fertilizer  
6 use of 17 kg ha<sup>-1</sup> y<sup>-1</sup> on a country basis, with about 12% of the national fertilizer share being used  
7 in the Kilimanjaro and Arusha regions. Urea (48% N) and diammonium phosphate (18% N)  
8 accounted for about half the total volume of fertilizer used in 2010. The nitrogen isotopic values  
9 of both fertilizers is ~0 ‰ (Bateman and Kelly, 2007), and as such does not pose a significant  
10 additional bias on the interpretation of soil  $\delta^{15}\text{N}$  values. However, the addition of manure ( $\delta^{15}\text{N}$   
11 ~8 ‰) in Hom systems, albeit used in low quantities (Gütlein et al., 2018), may have well  
12 contributed to the high  $\delta^{15}\text{N}$  values observed in this ecosystem (Fig. 4).

13 Bateman, A. S., and Kelly, S. D. (2007). Fertilizer nitrogen isotope signatures. *Isotopes in environmental*  
14 *and health studies*, 43(3), 237-247.

15 Giller et al. (1998). Environmental constraints to nodulation and nitrogen fixation of *Phaseolus vulgaris* L  
16 in Tanzania II. Response to N and P fertilizers and inoculation with *Rhizobium*. *African Crop Science*  
17 *Journal*, 6(2), 171-178.

18 Gütlein et al (2018). Impacts of climate and land use on N<sub>2</sub>O and CH<sub>4</sub> fluxes from tropical ecosystems in  
19 the Mt. Kilimanjaro region, Tanzania. *Glob. Change Biol.* 24, 1239–1255.

20 Senkoro et al (2017). Optimizing fertilizer use within the context of integrated soil fertility management  
21 in Tanzania. *Fertilizer use optimization in Sub-Saharan Africa*. CAB International, Nairobi, Kenya,  
22 176-192.

23

### 24 *Pesticides*

25 The isotopic values of the two most commonly used pesticides are shown below. The actual  
26 product values may strongly depend on the manufacturer, which as in the case of  $\delta^{13}\text{C}$  can be  
27 quite different for glyphosate.

	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Glyphosate	-24.0 ; -34.0 <sup>1</sup>	-3.6 <sup>2</sup>
Atrazine	-28.9 ; -27.9 <sup>3</sup>	-0.2 ; -1.5 <sup>3</sup>

28 <sup>1</sup> Kujawinski, D. M., Wolbert, J. B., Zhang, L., Jochmann, M. A., Widory, D., Baran, N., & Schmidt, T. C. (2013).  
29 Carbon isotope ratio measurements of glyphosate and AMPA by liquid chromatography coupled to isotope ratio  
30 mass spectrometry. *Analytical and bioanalytical chemistry*, 405(9), 2869-2878.

31 <sup>2</sup> Tavares, C. R. D. O., Bendassolli, J. A., Ribeiro, D. N., & Rossete, A. L. R. M. (2010). <sup>15</sup>N-labeled glyphosate  
32 synthesis and its practical effectiveness. *Scientia Agricola*, 67(1), 96-101

33 <sup>3</sup> Meyer, A. H., Penning, H., Lowag, H., & Elsner, M. (2008). Precise and accurate compound specific carbon and  
34 nitrogen isotope analysis of atrazine: critical role of combustion oven conditions. *Environmental science &*  
35 *technology*, 42(21), 7757-7763.

36

37 **Appendix – Tables and Figures**

38 **Table S1** Pearson’s correlations coefficients (r) between soil, litter, leaf, and climatic parameters. Correlation analysis was conducted with all five  
 39 replicates of each of the twelve ecosystems (n = 60)

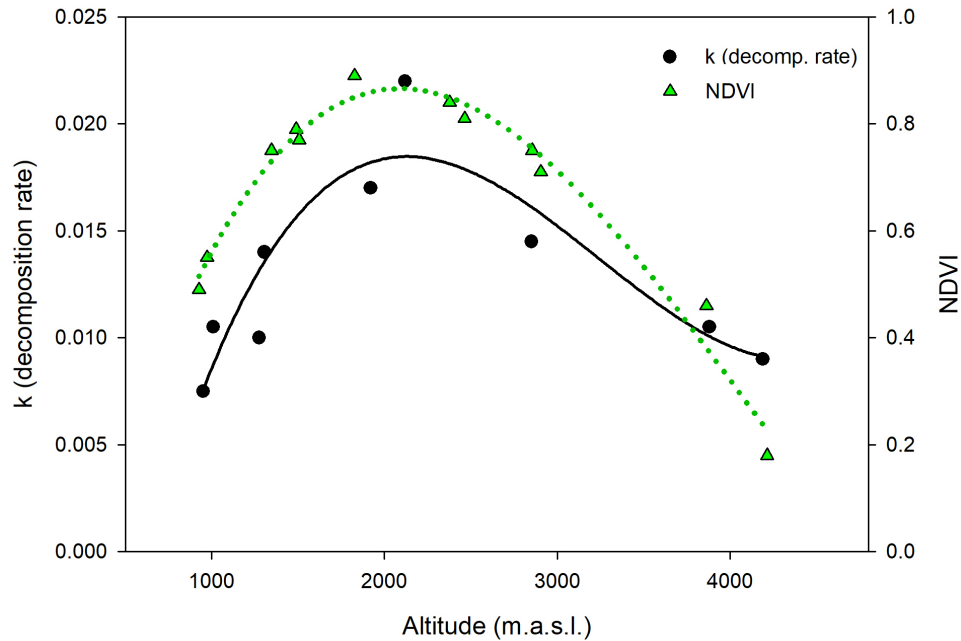
Variable	Soil					Litter					Leaf					
	$\delta^{15}\text{N}$	N content	$\delta^{13}\text{C}$	C content	C/N ratio	$\delta^{15}\text{N}$	N content	$\delta^{13}\text{C}$	C content	C/N ratio	$\delta^{15}\text{N}$	N content	$\delta^{13}\text{C}$	C content	C/N ratio	
<b>Soil</b>	$\delta^{15}\text{N}$	<b>-0.70***</b>	<b>0.52***</b>	<b>-0.76***</b>	<b>-0.54***</b>	<b>0.82***</b>	-0.13	<b>0.44***</b>	<b>-0.72***</b>	-0.06	<b>0.75***</b>	0.21	<b>0.47***</b>	<b>-0.38**</b>	<b>-0.27*</b>	
	N content		<b>-0.63***</b>	<b>0.96***</b>	<b>0.38**</b>	<b>-0.44***</b>	<b>0.49***</b>	<b>-0.56***</b>	<b>0.72***</b>	<b>-0.26*</b>	<b>-0.38**</b>	0.21	<b>-0.61***</b>	<b>0.34**</b>	-0.15	
	$\delta^{13}\text{C}$			<b>-0.61***</b>	0.01	0.18	<b>-0.60***</b>	<b>0.79***</b>	<b>-0.43***</b>	<b>0.51***</b>	0.15	<b>-0.31*</b>	<b>0.76***</b>	<b>-0.49***</b>	<b>0.28*</b>	
	C content				<b>0.56***</b>	<b>-0.53***</b>	<b>0.38**</b>	<b>-0.54***</b>	<b>0.76***</b>	-0.17	<b>-0.45***</b>	0.07	<b>-0.59***</b>	<b>0.42***</b>	-0.04	
	C/N ratio					<b>-0.59***</b>	-0.19	-0.15	<b>0.51***</b>	<b>0.303*</b>	<b>-0.54***</b>	<b>-0.40**</b>	-0.14	<b>0.39**</b>	<b>0.40**</b>	
<b>Litter</b>	$\delta^{15}\text{N}$						<b>0.26*</b>	0.13	<b>-0.68***</b>	<b>-0.48***</b>	<b>0.92***</b>	<b>0.53***</b>	0.20	-0.25	<b>-0.57***</b>	
	N content							<b>-0.66***</b>	<b>0.26*</b>	<b>-0.87***</b>	<b>0.26*</b>	<b>0.73***</b>	<b>-0.61***</b>	0.21	<b>-0.64***</b>	
	$\delta^{13}\text{C}$								<b>-0.42***</b>	<b>0.54***</b>	0.14	<b>-0.36**</b>	<b>0.88***</b>	<b>-0.54***</b>	0.22	
	C content									0.11	<b>-0.57***</b>	-0.05	<b>-0.49***</b>	<b>0.39**</b>	0.08	
	C/N ratio										<b>-0.42***</b>	<b>-0.69***</b>	<b>0.47***</b>	-0.12	<b>0.63***</b>	
<b>Leaf</b>	$\delta^{15}\text{N}$											<b>0.53***</b>	0.17	-0.17	<b>-0.61***</b>	
	N content												<b>-0.44***</b>	-0.13	<b>-0.92***</b>	
	$\delta^{13}\text{C}$													<b>-0.44***</b>	<b>0.30*</b>	
	C content														0.19	
	C/N ratio															
<b>Soil</b>	pH	<b>0.51***</b>	<b>-0.76***</b>	<b>0.65***</b>	<b>-0.78***</b>	<b>-0.28*</b>	<b>0.26*</b>	<b>-0.51***</b>	<b>0.44***</b>	<b>-0.55***</b>	<b>0.34**</b>	0.20	-0.24	<b>0.45***</b>	<b>-0.40**</b>	<b>0.26*</b>
	clay content	0.14	<b>0.33**</b>	-0.23	<b>0.27*</b>	-0.10	<b>0.32*</b>	<b>0.37**</b>	-0.12	0.02	<b>-0.34**</b>	<b>0.31*</b>	<b>0.44***</b>	-0.16	-0.06	<b>-0.46***</b>
	silt content	0.01	<b>0.27*</b>	-0.04	<b>0.30*</b>	0.20	0.08	0.22	0.02	0.14	-0.23	0.09	0.15	-0.01	0.05	-0.24
	sand content	-0.12	<b>-0.43***</b>	0.22	<b>-0.39**</b>	-0.04	<b>-0.31*</b>	<b>-0.43***</b>	0.09	-0.10	<b>0.41**</b>	<b>-0.31*</b>	<b>-0.45***</b>	0.14	0.02	<b>0.52***</b>
<b>MAP</b>	<b>-0.60***</b>	<b>0.81***</b>	<b>-0.72***</b>	<b>0.76***</b>	0.19	<b>-0.32*</b>	<b>0.58***</b>	<b>-0.65***</b>	<b>0.50***</b>	<b>-0.44***</b>	<b>-0.27*</b>	<b>0.33**</b>	<b>-0.60***</b>	<b>0.34**</b>	<b>-0.26*</b>	
<b>MAT</b>	<b>0.73***</b>	<b>-0.54***</b>	<b>0.66***</b>	<b>-0.60***</b>	<b>-0.33**</b>	<b>0.67***</b>	-0.16	<b>0.55***</b>	<b>-0.62***</b>	0.05	<b>0.61***</b>	0.25	<b>0.55***</b>	<b>-0.48***</b>	<b>-0.33*</b>	

40 Levels of significance: \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001



**Table S2** Correlation coefficients (r) and P values of selected variables included in the principal component analysis used to identify the main factors driving soil  $\delta^{15}\text{N}$ . Only variables showing  $r > 0.5$  were considered

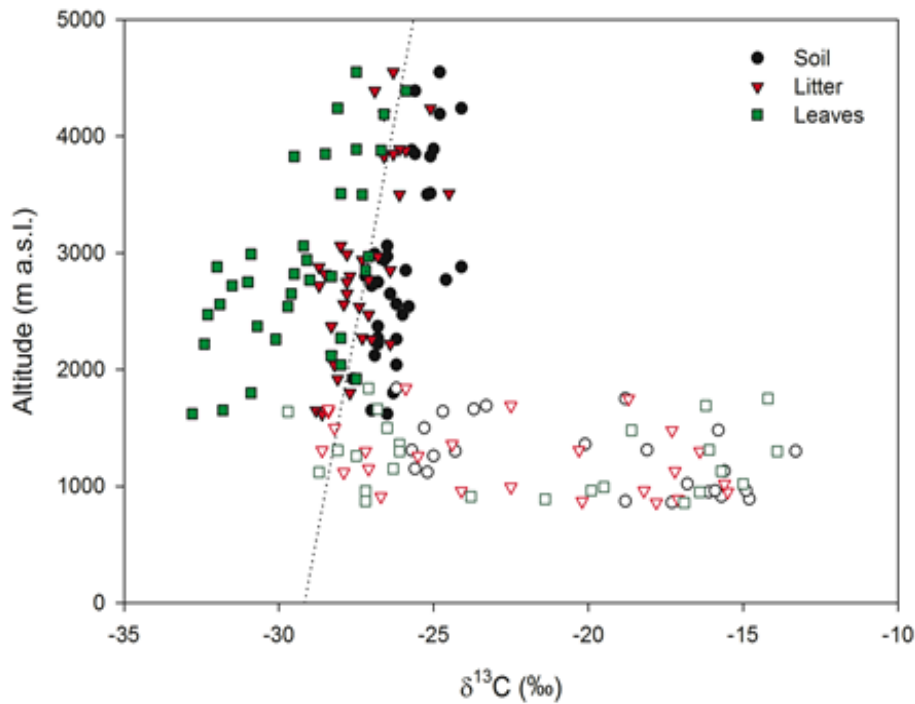
<b>Principal component</b>	<b>Variable</b>	<b>r</b>	<b>P value</b>
PC 1	Soil C content	0.93	<0.001
	Soil N content	0.93	<0.001
	Soil C/N ratio	0.61	<0.001
	Soil pH	-0.87	<0.001
	Soil $\delta^{13}\text{C}$	-0.76	<0.001
	MAP	0.87	<0.001
	MAT	-0.63	<0.001
PC 2	Soil clay content	-0.84	<0.001
	Soil sand content	0.82	<0.001
	MAT	-0.65	<0.001



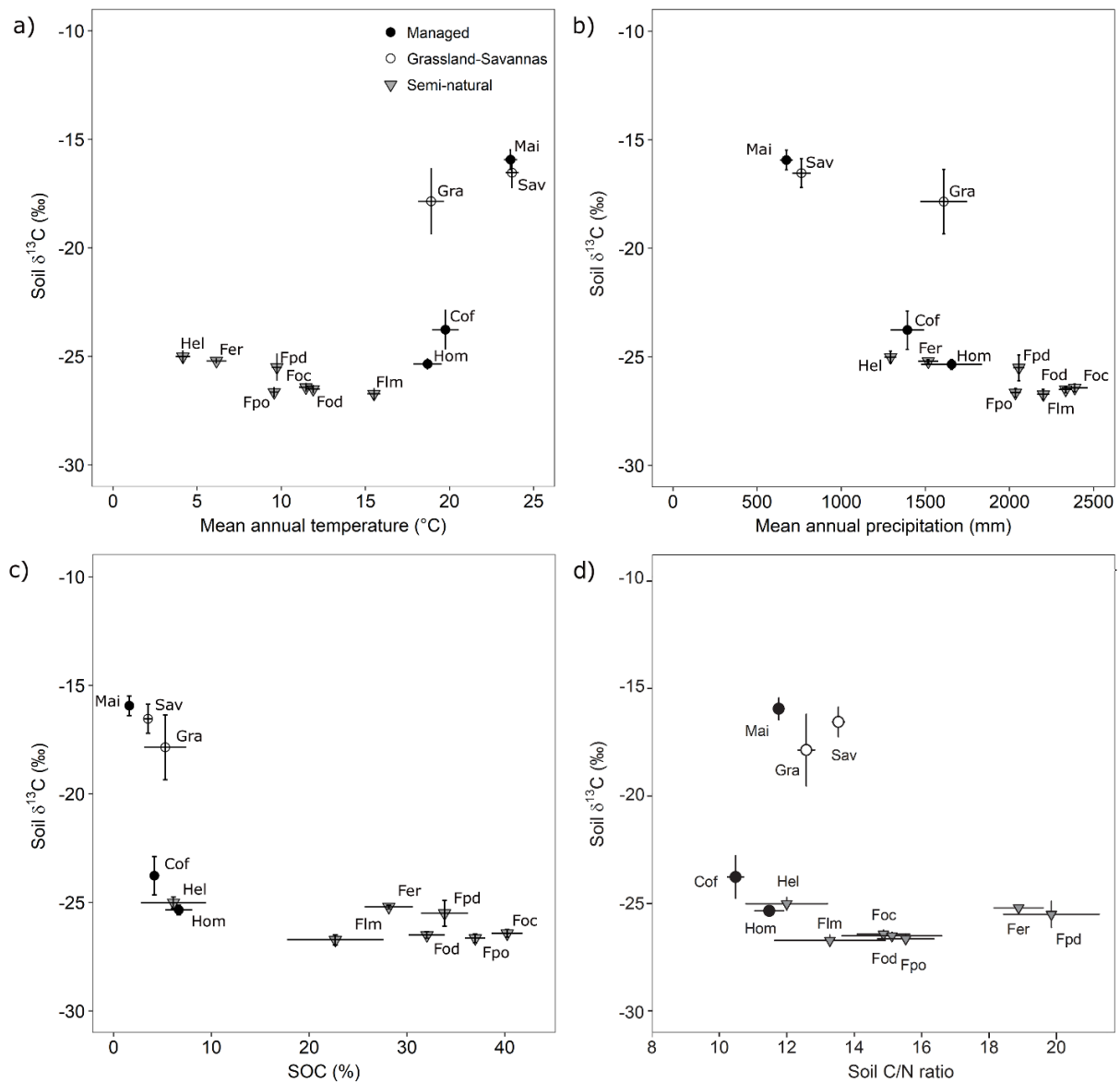
**Fig. S1** Annual means of Tea Bag Index decomposition rate constant ( $k$ ) reported by Becker and Kuzyakov (2018), and Normalized Difference Vegetation Index (NDVI) calculated by Röder et al. (2017) as a proxy for primary productivity (Kerr and Ostrovsky, 2003) for the same ecosystems studied in the Kilimanjaro land-use and elevational gradient. Solid and dotted line corresponds to  $k$  and NDVI 3rd degree polynomial regressions;  $r^2$  0.82 and 0.78 respectively.

*References:*

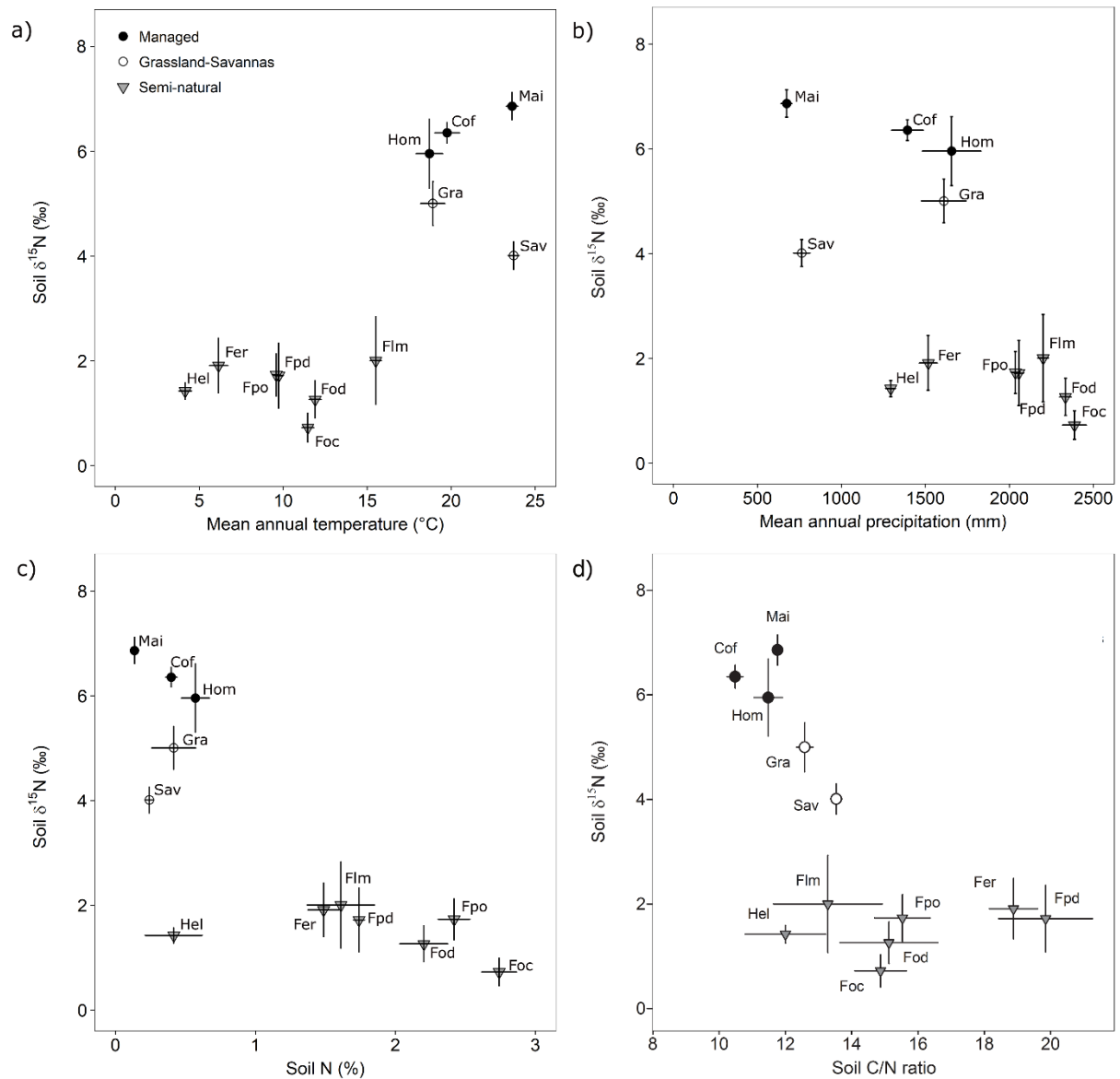
- Becker, J. N., and Kuzyakov, Y. (2018). Teatime on Mount Kilimanjaro: Assessing climate and land-use effects on litter decomposition and stabilization using the Tea Bag Index. *Land Degradation & Development*, 29(8), 2321-2329.
- Kerr, J. T., and Ostrovsky, M. (2003). From space to species: ecological applications for remote sensing. *Trends in ecology & evolution*, 18(6), 299-305.
- Röder, J., Detsch, F., Otte, I., Appelhans, T., Nauss, T., Peters, M. K., & Brandl, R. (2017). Heterogeneous patterns of abundance of epigeic arthropod taxa along a major elevation gradient. *Biotropica*, 49(2), 217-228.



**Fig. S2** Variation in  $\delta^{13}\text{C}$  values along the Kilimanjaro land-use and elevational gradient for leaves, litter, and soil. Solid symbols denote semi-natural ecosystems, while open symbols correspond to managed ecosystems. The dotted line represents the theoretical global relationship between altitude and  $\delta^{13}\text{C}$  of plant leaves ( $\text{C}_3$  vegetation only) developed by Körner et al. (1988) and is shown here for reference. The ecosystem acronyms used are as per Table 1. Mai, Cof, and Hom are managed cropping sites, Gra and Sav are extensively managed grasslands and savannas, while the rest represent semi-natural ecosystems. *Reference:* Körner, C., Farquhar, G.D., Roksandic, Z., 1988. A global survey of carbon isotope discrimination in plants from high altitude. *Oecologia* 74, 623–632. <https://doi.org/10.1007/BF00380063>.



**Fig. S3** Relationship between soil  $\delta^{13}\text{C}$  values and mean annual temperature (a), mean annual precipitation (b), soil organic carbon (c), and soil C/N ratios (d) for all ecosystems. Each data point represents the average of five sites, and bars denote standard error of the means. Symbols are as per all previous figures. The ecosystem acronyms used are as per Table 1.



**Fig. S4** Relationship between soil  $\delta^{15}\text{N}$  values and mean annual temperature (a), mean annual precipitation (b), soil nitrogen (c), and soil C/N ratios (d) for all ecosystems. Each data point represents the average of five sites, and bars denote standard error of the means. Symbols are as per all previous figures. The ecosystem acronyms used are as per Table 1.