

# Area and environmental heterogeneity could shape the hump-shaped pattern of species richness along elevation gradient

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## Research article

**Keywords:** species richness, elevation, hump-shaped pattern, area, environmental heterogeneity. =

**Posted Date:** November 5th, 2019

**DOI:** <https://doi.org/10.21203/rs.2.16808/v1>

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# Abstract

Background Numerous studies have been conducted on species richness patterns along elevation gradients in temperate, tropical and sub-tropical mountains. However, few studies have been done to evaluate the combined effect of area and environmental heterogeneity (abiotic and biotic) on species richness. Numerous ecological studies have also failed to quantify environmental heterogeneity which we have done in this research. In this research, we studied the impact of area on environmental heterogeneity on species richness by considering the climate factors, annual mean temperature (AMT), annual mean precipitation (AMP), annual total solar radiation (ATSR), and Soil factors, soil organic carbon (SOC), Soil total nitrogen (STN), Soil extractable phosphorous (SEP), and Soil extractable potassium (SEK). Results Our analysis showed that species richness had a skewed hump-shaped pattern, with the highest species richness being at mid-elevation. The results also showed that climate factors had a strong positive correlation with species richness in relation to area as compared to soil factors. We also found that soil factors could be used to explain the species richness when combined rather than being interpreted individually. This study has showed that area could have profound effect on environmental heterogeneity therefore shaping species richness pattern along the elevation gradient in Mount Kenya. Conclusion The hump shaped species richness pattern can be due to the Ecophysiological constraints for example, low temperatures as elevation increases. The high species richness at the mid-elevation is because this zone has a large land area and also acts as transition zone between the extremes of the upper elevation range and lower elevation and species from either side can coexist since the environmental conditions are on the lower and higher limits for the existence of these plant species.

## Background

Understanding the spatial patterns of species richness is an important issue in ecology and conservation biology ever since 18<sup>th</sup> centuries [1–4]. The species richness was previously thought to decrease monotonically along elevational gradients, based on the elevational diversity pattern of birds in the tropics [5], and also had been confirmed in other studies [e.g., 6–9]. While an important review by Rahbek [10] completely reversed the understanding of researchers. There was another more common pattern of species richness along elevation gradients, namely hump-shaped pattern, i.e., species richness first increases, then decreases after the mid-altitude peak, and the maximum diversity occurs below the middle of the elevation gradients [e.g., 11–14].

Numerous hypotheses have been proposed to explain the monotonic or hump-shaped relationship between species richness and elevation, for instance the high productivity at mid-elevation and optimum humidity conditions at mid-elevation [10, 15]. There is also the temperature hypothesis which alludes that an increase in temperature leads to increase in species richness. However, it is also proposed that high elevation species are more sensitive to temperature changes and may become extinct in the event of temperature change [16]. Some researchers have proposed the resource diversity hypothesis where an increase in the diversity of available resources such as soils, leads to an increase in plant diversity [17, 18]. However, the resource diversity hypothesis cannot independently determine species diversity because

it is also dependent on rainfall and productivity. Precipitation hypothesis has also been championed by different studies, which reported a positive relationship between species richness and precipitation [19, 20], but it is worth noting that precipitation change is not consistent on different mountains because of the unique weather conditions found in each mountain [21].

There is also the hard boundary hypothesis proposed by Colwell and Hurt [22], which suggests that there is a higher species richness at mid elevation because of the overlapping ecotones and species range. The evolution time and species diversity rate hypothesis suggested that the species richness is higher in the regions with long evolutionary time, and the diversity rate of species in different groups can also lead to the difference of species richness in different regions [23]. In addition, the methods for estimating species diversity would also impact the hump-shaped relationship between species richness and elevation. In the analysis of the altitude gradient pattern of diversity, most studies assume that species are continuously distributed between the upper and lower limits of their distribution, so the number of species at different altitudes can be obtained through the distribution interval of species, thus underestimating the number of species near the upper and lower limits of the study area [24].

Area can directly affect species richness or indirectly by influencing environmental factors which then determine the species richness [25, 26]. In general, the area decreases along elevations in most mountains and this means that species richness would decrease because of the reduced habitat sizes [27]. The species richness and floristic patterns are also impacted by environmental factors which include climatic factors such as precipitation, temperature and solar radiation [28] and soil factors (soil's chemical and physical properties). These environmental factors always put a physiological restriction to which plants can survive thus limiting the species richness and population sizes [19, 29]. In addition, environmental heterogeneity is recognized as a universal driver of species richness across different spatial scales, for it could increase the available niche space, provision of refuges and opportunities for isolation and divergent adaptation, thus could enhance species coexistence, persistence and diversification for communities [4, 30]. This is a cornerstone of ecology and has been confirmed in many studies, such as plants [31] and animals [32]. However, environmental heterogeneity along elevation gradient is difficult to quantify, and the relationship between species richness and environmental heterogeneity is not simple linear within the gradient range of the study [33]. Therefore, few studies have linked the hump-shaped species richness pattern with environmental heterogeneity along elevation gradient, including exploring the impact of area on environmental heterogeneity, thereby affecting species diversity.

In this paper, we studied the impact of area and environmental heterogeneity on species richness along the elevation gradient of Mount Kenya by considering the three climate factors, annual mean temperature (AMT), annual mean precipitation (AMP), annual total solar radiation (ATSR) and four soil factors, soil organic carbon (SOC), soil total nitrogen (STN), soil extractable phosphorous (SEP), and soil extractable potassium (SEK).

# Results

## 2.1 Relevance between environmental variables and Elevation

There was a positive correlation between elevation and climatic factor annual mean precipitation (AMP) (correlation = 0.795,  $P \leq 0.001$ ) and a negative correlation with annual mean temperature (AMT) and annual total solar radiation (ATSR) (correlation = -0.999, -0.870 respectively with  $P \leq 0.001$ ) (Table 1). An increase in elevation also led to an increase in all the soil factors soil organic carbon (SOC), soil total nitrogen (STN), soil extractable phosphorous (SEP), soil extractable potassium (SEK) (correlation = 0.830, 0.851, 0.930, and 0.619 respectively with  $P \leq 0.001$ ) (Table 1).

## 2.2 Area with the range size of environmental factors

Area has a positive significant relationship with the range sizes of the environmental factors annual mean precipitation range size (AMPr), annual total solar radiation range size (ATSRr), soil extractable phosphorous range size (SEPr), and soil extractable potassium range size (SEKr) (correlation = 0.934, 0.719, 0.764, 0.733,  $P \leq 0.001$ ) (Table 2). However, area has a negative relationship with the range size of annual mean temperature range size (AMTr) and soil organic carbon range size (SOCr) (correlation = -0.380, -0.125) (Table 2).

## 2.3 The relationship between species richness with environmental variables

Species richness descended along the elevation gradient ( $R^2 = 0.8827$ ,  $P < 0.001$ ), but showed a positively skewed (hump-shaped) pattern along the elevation gradient, with a pronounced mid-elevational peak at about 2000 m a.s.l. (Fig. 1a). The climate and soil variables negatively impacted on species richness along elevation gradient, except annual total solar radiation (ATSR) (Fig. 1b–g).

## 3.4 The relationship between species richness and environmental heterogeneity

Species richness was positively correlated with area along elevation gradient ( $R^2 = 0.8060$ ,  $P < 0.001$ ) (Fig. 2a), meanwhile, the range size of most climate and soil factors, i.e. environmental heterogeneity, could positively affect species richness, such as AMPr, ATSRr, STNr, SEPr, SEKr (Fig. 2c–h). The range size of annual mean temperature (AMTr) and soil organic carbon (SOCr) have no correlation with species richness (Fig. 2b & e).

# Discussion

Global data research showed that over 80% of species richness-elevation patterns occurring in the tropical mountains are hump-shaped pattern [38]. The species richness pattern along elevation gradient of Mount Kenya also show a strong support for the positively skewed pattern, showing a typical hump-shaped pattern with an increase from the foot to 2000 m a.s.l. and a steady decline from the mid-peak up to 4950 m a.s.l. and this is similar with other studies conducted in tropical rainforests (Fig. 1a) [38–41]. In Mount Kenya endemic species and different life forms i.e., trees, shrubs, lianas, climbers, shrubs,

lycophytes and ferns also show hump shaped pattern as shown by a study conducted by Zhou et al. [42]. The hump shaped pattern in Mount Kenya makes it possible to draw a conclusion that volcanic mountains in tropical East Africa for example, Mount Kilimanjaro have similar vegetation patterns [43].

Generally, the species richness of a mountain is greatly affected by the environmental variables because these elements change along the elevational gradients and plant species have different adaptations to these dynamic conditions [44]. In our study for instance, there is a positive relationship between species richness and annual mean temperature (AMT) along the elevation gradient (Fig. 1b), and this trend is attributed to the fact that as you go up Mount Kenya there is a decline in temperature thus making it difficult for plants to survive in this harsh environment. Soil factors such as high soil total Nitrogen (STN) and extractable Phosphorus (SEP) also reduce species richness along the elevation gradient while the impacts of potassium are not well distinguished (Fig. 1f & g). High nitrogen content decreases species richness by causing ammonium toxicity and soil acidification [45–48]. Nitrogen is also responsible for random loss of species that are not adapted to high soil nutrient content through competition by fast growing species [45, 46, 49–53] and low species richness has also been recorded in areas with high P levels [54–56]. The SEK fails to influence species richness positively past the mid elevation zone because plant species might not be able to utilize the available soil extractable potassium due to other biotic factors such as low temperature as shown by a research conducted by John et al. [57]. There is a positive link between annual total solar radiation with species richness along the elevation gradient and this is because ATSR controls productivity (Fig. 1d) [58].

What is surprising in Mount Kenya is that there is a decline in species richness with increase in precipitation contrary to the common trend of positive correlation between high rainfall with high species richness (Fig. 1c). In Mount Kenya rainfall increases with elevation and this is expected to favor high productivity. However, there is a decline in temperature with elevation and this negates the effect of high precipitation on species richness since most plants lack cold stress adaptation. The positive effect of precipitation on species richness can also be masked by other abiotic processes for example low acquisition of N, P, and amount of SOC which are limited by low temperatures as found by other studies [59].

In our study, the range size of annual mean precipitation (AMPr) had the most significant linear relationship with rainfall because Mount Kenya has a wet South Eastern side and a dry North Western side (Figure 2c) [60, 61]. Lack of a linear relationship between species richness with the range size of annual mean temperature (AMTr) is due to the fact that temperature change is affected by the elevation change [21] rather than spatial change and species richness is determined by the ability of plants to adapt to low temperatures (Figure 2b). There is a significant positive relationship between the range size of annual total solar radiation (ATSRr) with species richness (Fig. 2d) since high ATSR is associated with high productivity. ATSR varies because different zones of the mountain receive different total solar radiation since the amount received is determined by several things such as the sun's angle (due to time of day, season and latitude), scattering elements for instance clouds, and elevation above sea level [58]. The species range size along the altitudinal gradient could also shape the species richness pattern along

the elevation gradient in Mount Kenya due to the findings that species in low latitude topical mountains have a low range size as compared to those in high altitude mountains which have a very wide range [3]. Based on the environmental range size, species that have the same environmental conditions requirement will appear in similar vegetation belt along the elevation and this can be responsible for the skewed species richness pattern in Mount Kenya.

Area has a profound impact on environmental heterogeneity since the larger the distance between environmental patches the larger the environmental heterogeneity and this has a significant impact on species richness pattern in Mount Kenya (Table 2, Fig. 2). Large area affects environmental heterogeneity and significantly affects species richness due to the diverse environmental conditions, increased structural complexity, and diversity of resources which increase niche space thus promoting species coexistence [62]. Land area creates the aspect of spatial heterogeneity as shown by the correlations which affects species richness by creating variable climatic conditions and spatial configuration of habitats which determines the rates of ecological processes such as competition and dispersal. The range size of the environmental factors creates diverse microsites or habitats across the entire mountain and this provides a platform for high species richness in the different elevation bands. The range sizes of the different environmental factors were affected by land area (Table 2) and had different relationships with species richness (Figure 2). When the environmental factors have a high range size, they favor the presence of generalist species (species with a broad niche) across the mountain while short range size favors the establishment of specialists (species with a narrow niche) [63].

## Conclusions

The species richness of Mount Kenya along elevation gradient showed a typical hump-shaped pattern, i.e., increases firstly, then decreases after the mid-altitude peak, and the maximum diversity occurs below the middle of the elevation gradients, and this can be attributed to the decline in land area as elevation increases and this means that there are a few microsites for plants to occupy as also shown in other species richness elevation studies [64–66]. Ecophysiological constraints, for instance, low temperatures and ecosystem productivity, also play a major role in shaping the species richness pattern in Mount Kenya [67]. Most plants species lack adaptation to Mount Kenya alpine zone night frosts of -5 to -10 degrees and this leads to a decline in species richness as you go up the elevation (Fig 1b) [61]. The high species richness at the mid-elevation is because this zone acts as transition zone between the extremes of the upper elevation range and lower elevation and species from either side can coexist since the environmental conditions are on the lower and higher limits for the existence of these plant species, and the land area at mid-elevation is also relatively large meaning that it recruits more species as compared to the area near the peak of the mountain and this explains the high species richness at this point.

## Methods

### 5.1 Study area

Mount Kenya (0°10' S, 37°20' E) straddles the equator and is located in the central part of Kenya, about 193 km north-east of Nairobi and 480 km from the Kenyan coast. Firstly, the whole elevation range from 1250 to 4950 a.s.l was divided into 39, 100-m vertical elevation bands. Then we used 1 km × 1 km grid cells to rasterize our study area in ArcGis 10.2 [34], for easy access to data pertaining to area, climate and soil factors of each elevation band.

## 5.2 Species richness

The plant distribution data of Mount Kenya come from a comprehensive checklist of seed plants based on data from various scientific expeditions to Mount Kenya since the 1900s [14, 42]. The species richness was defined as the total number of species present in each elevation band referred to as  $\gamma$ -diversity [1, 35] and this was achieved by interpolation method by defining a species as being present in every 100-m elevation band between its lower and upper elevation limits [12, 15, 35].

## 5.3 Climate and soil variables

We extracted the climatic data of each grid cell using ArcGIS 10.2 [34], based on the Worldclim database (<https://www.worldclim.org>), including annual mean temperature (AMT), annual mean precipitation (AMP), and annual total solar radiation (ATSR). To acquire the mean values of temperature, precipitation and solar radiation in each of the 38, 100-m bands, an average of all the grid cells in each band based on the elevational value of each grid cell was done, meanwhile, we used the difference between maximum and minimum values of all grid cells in each band to measure the range size of temperature, precipitation and solar radiation. Soil data extracted from ISRIC-World Soil Information (<https://www.isric.org>), including soil organic carbon (SOC), soil total nitrogen (STN), soil extractable phosphorous (SEP), and soil extractable potassium (SEK). We used the same method in ArcGIS 10.2 [34] to get the mean and range size of the four soil variables in each band.

## 5.4 Statistical analysis

Pearson correlation analysis was used to determine the relationship among the elevation and mean value of environmental variables in each elevation band, as well as area and range size of environmental variables. Linear model was used to analysis the relationship between species richness with mean value and range size of environmental variables in each elevation band. These analyses were performed in R 3.3.3 software [36].

# Abbreviations

Annual mean temperature (AMT)

Annual mean precipitation (AMP)

Annual total solar radiation (ATSR)

Soil organic carbon (SOC)

Soil total nitrogen (STN)

Soil extractable phosphorous (SEP)

Soil extractable potassium (SEK)

Range size of annual mean temperature (AMTr)

Range size of annual mean precipitation (AMPr),

Range size of annual total solar radiation (ATSRr)

Range size of soil organic carbon (SOCr)

Range size of soil total nitrogen (STNr)

Range size of soil extractable phosphorous (SEPr)

Range size of soil extractable potassium (SEKr)

## **Declarations**

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and materials

Data and materials could be available from corresponding author up on request.

Competing interests

The authors declare that they have no competing interests.

Funding

This study was supported by National Science Foundation of China (31800176) and Sino-Africa Joint Research Center, CAS, China (Y323771W07 and SAJC201322).

Authors' contributions

WAN developed the study methods and compiled the dataset with valuable contribution from YZ and SW. WAN wrote the manuscript with contributions and modifications from YZ. WQ and WRG coordinated and led the work and commented on the manuscript. ACO edited the English grammar. All the authors contributed in reading, editing, commenting and approving the final manuscript.

#### Acknowledgments.

We wish to acknowledge Dr. Paul Musili and Geoffrey Mwachala of National Museums of Kenya, for helping us to get the specimens of Mount Kenya in East Africa Herbarium (EA).

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## Tables

Table 1. Pearson correlation between the elevation and mean value of environmental variables along elevation gradient. AMT, annual mean temperature, AMP, annual mean precipitation, ATSR, annual total solar radiation, SOC, soil organic carbon, STN, soil total nitrogen, SEP, soil extractable phosphorous, SEK, Soil extractable Potassium.

	AMT	AMP	ATSR	SOC	STN	SEP	SEK
Elevation	-0.999 <sup>***</sup>	0.795 <sup>***</sup>	-0.870 <sup>***</sup>	0.830 <sup>***</sup>	0.851 <sup>***</sup>	0.930 <sup>***</sup>	0.619 <sup>***</sup>
AMT		-0.795 <sup>***</sup>	0.884 <sup>***</sup>	-0.837 <sup>***</sup>	-0.864 <sup>***</sup>	-0.936 <sup>***</sup>	-0.598 <sup>***</sup>
AMP			-0.660 <sup>***</sup>	0.708 <sup>***</sup>	0.682 <sup>***</sup>	0.841 <sup>***</sup>	0.427 <sup>**</sup>
ATSR				-0.845 <sup>***</sup>	-0.972 <sup>***</sup>	-0.859 <sup>***</sup>	-0.252 <sup>*</sup>
SOC					0.832 <sup>***</sup>	0.776 <sup>***</sup>	0.190 <sup>*</sup>
STN						0.826 <sup>***</sup>	0.198 <sup>*</sup>
SEP							0.506 <sup>**</sup>

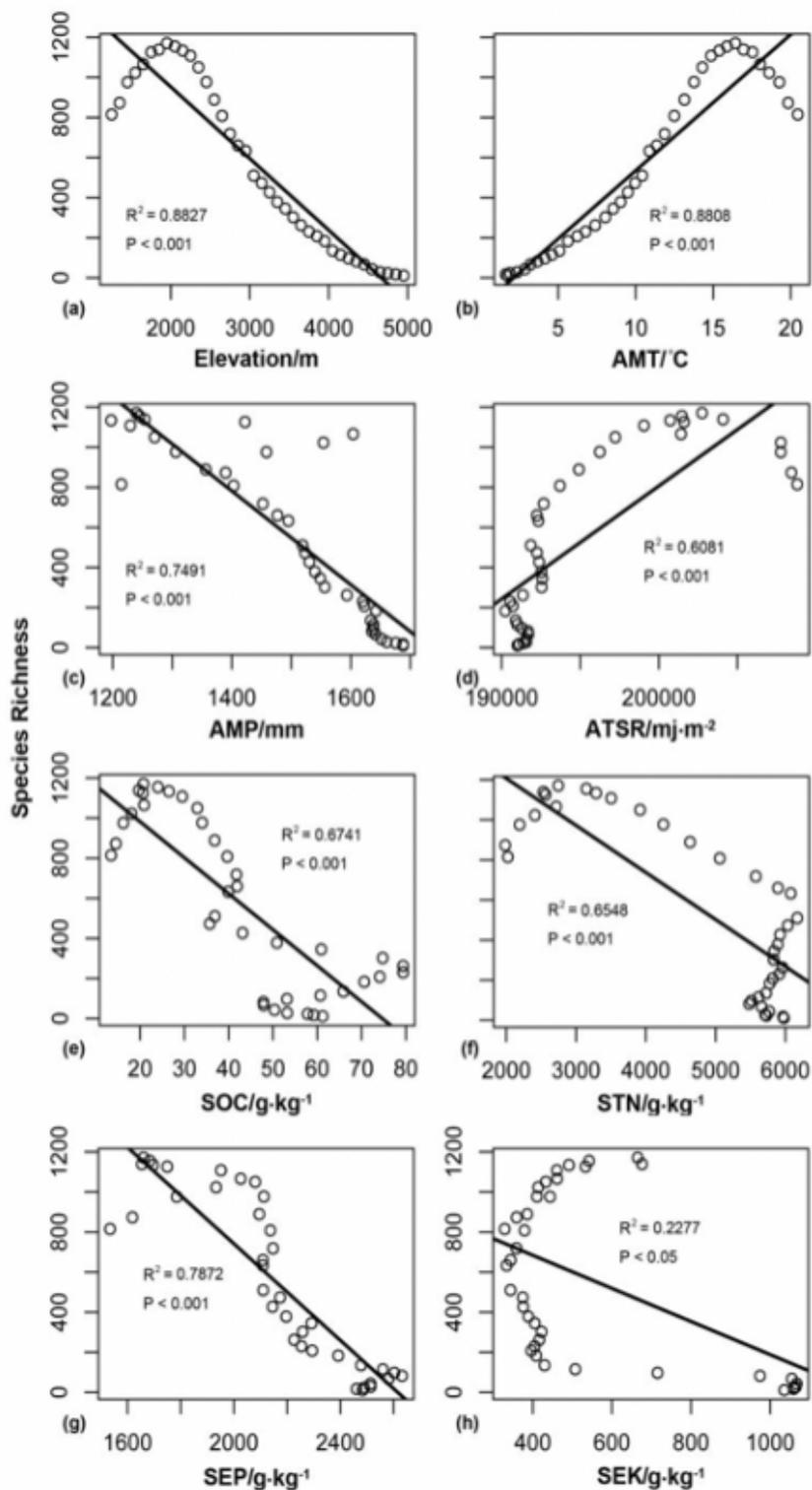
P-values, <sup>\*\*\*</sup> ≤ 0.001, <sup>\*\*</sup> ≤ 0.05, <sup>\*</sup> ≤ 0.5, <sup>#</sup> > 0.5

Table 2. Pearson correlation between the area and range size of environmental variables along elevation gradient. AMTr, annual mean temperature range size, AMPr, annual mean precipitation range size, ATSRr, annual total solar radiation range size, SOCr, soil organic Carbon range size, STNr, soil total Nitrogen range size, SEPr, soil extractable Phosphorous range size, SEKr, soil extractable Potassium range size.

	AMTr	AMPr	ATSRr	SOCr	STNr	SEPr	SEKr
Area	-0.380 <sup>*</sup>	0.934 <sup>***</sup>	0.719 <sup>***</sup>	-0.125 <sup>#</sup>	0.234 <sup>#</sup>	0.764 <sup>***</sup>	0.733 <sup>***</sup>
AMTr		-0.161 <sup>#</sup>	0.262 <sup>#</sup>	0.720 <sup>***</sup>	0.431 <sup>*</sup>	-0.080 <sup>#</sup>	-0.186 <sup>#</sup>
AMPr			0.877 <sup>***</sup>	0.154 <sup>#</sup>	0.514 <sup>*</sup>	0.883 <sup>***</sup>	0.716 <sup>***</sup>
ATSRr				0.527 <sup>**</sup>	0.652 <sup>***</sup>	0.757 <sup>***</sup>	0.593 <sup>***</sup>
SOCr					0.546 <sup>**</sup>	0.259 <sup>#</sup>	0.044 <sup>#</sup>
STNr						0.541 <sup>**</sup>	0.310 <sup>#</sup>
SEPr							0.725 <sup>***</sup>

P-values, <sup>\*\*\*</sup> ≤ 0.001, <sup>\*\*</sup> ≤ 0.05, <sup>\*</sup> ≤ 0.5, <sup>#</sup> > 0.5

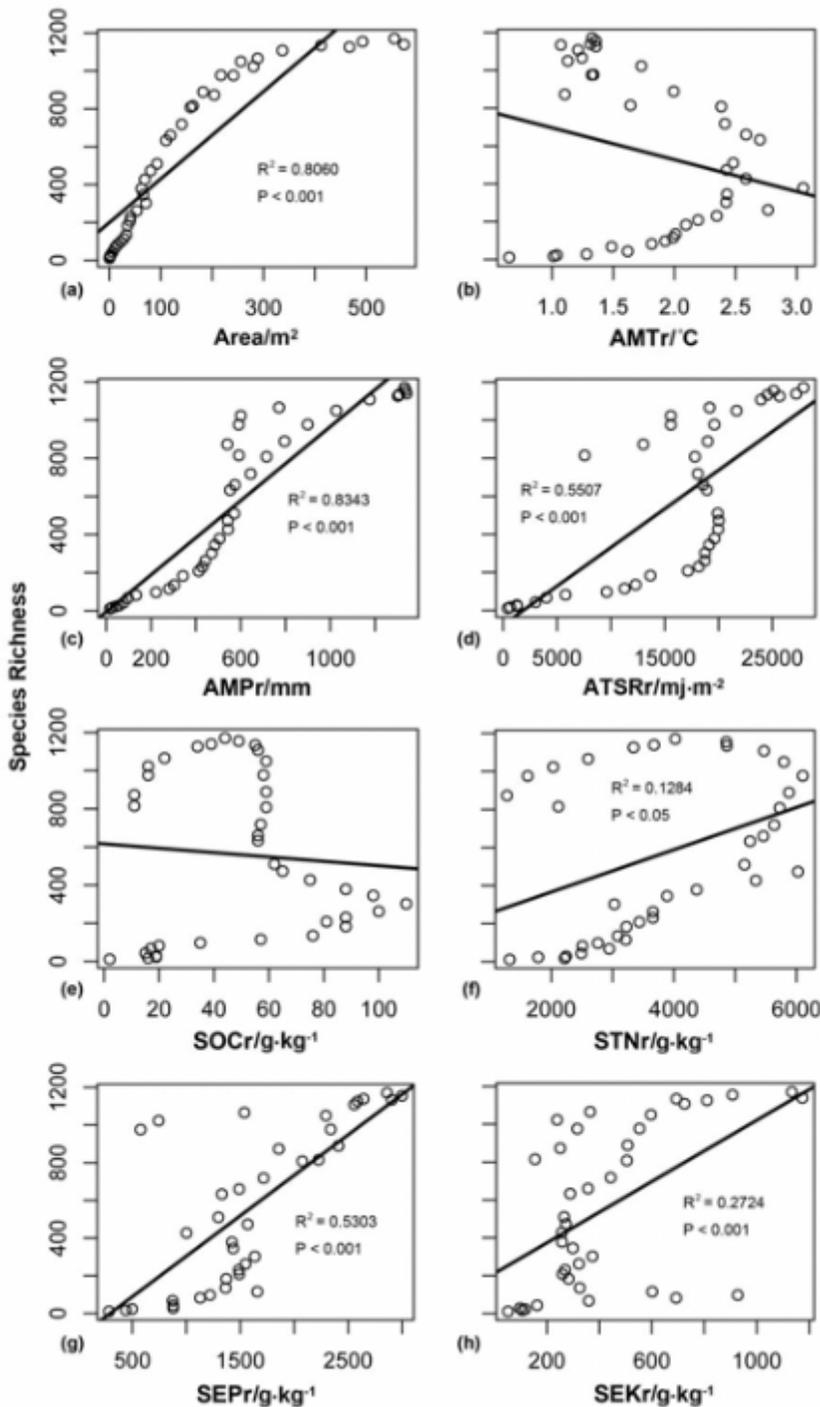
## Figures



**Figure 1**

The linear regression between Species richness against Elevation gradient and mean values of AMT/°C, AMP/mm, ATSR/mj-m, SOC/g-kg<sup>-2</sup>, STN/g-kg<sup>-2</sup>, SEP/g-kg<sup>-2</sup>, and SEK/g-kg<sup>-2</sup>. (a) Species richness and Elevation ( $R^2 = 0.8827$ ,  $P < 0.001$ ); (b) Species richness and AMT ( $R^2 = 0.8808$ ,  $P < 0.001$ ); (c) Species richness and AMP ( $R^2 = 0.7491$ ,  $P < 0.001$ ); (d) Species richness and ATSR ( $R^2 = 0.6081$ ,  $P < 0.001$ ); (e) Species richness and SOC ( $R^2 = 0.6741$ ,  $P < 0.001$ ); (f) Species richness and STN/g.Kg-1 ( $R^2 = 0.6548$ ,  $P$

< 0.001); (g) Species richness and SEP/g.Kg-1 ( $R^2 = 0.7872$ ,  $P < 0.001$ ); (h) Species richness and SEK/g.Kg-1 ( $R^2 = 0.2277$ ,  $P < 0.001$ ).



**Figure 2**

Linear regression of species richness with the range size of the environmental factors/environmental heterogeneity AMTr, AMPr, ATSRr, SOCr, STNr, SEPr, and SEKr. (a) Relationship between land area and species richness ( $R^2 = 0.8060$ ,  $P < 0.001$ ). (b) Relationship between AMTr/°C and species richness ( $R^2 = 0.0339$ ,  $P = 0.0339$ ). (c) Relationship between AMPr/mm and species richness ( $R^2 = 0.8343$ ,  $P < 0.001$ ).

(d) Relationship between ATSRr/mj.m-2 and species richness ( $R^2 = 0.5507$ ,  $P < 0.001$ ). (e) relationship between Species richness and SOCr ( $R^2 = 0.0062$ ,  $P = 0.6372$ ); (f) relationship between species richness and STNr/g.Kg-1 ( $R^2 = 0.1264$ ,  $P < 0.05$ ); (g) relationship between species richness and SEPr/g.Kg-1 ( $R^2 = 0.5303$ ,  $P < 0.001$ ); (h) relationship between species richness and SEKr/g.Kg-1 ( $R^2 = 0.2724$ ,  $P < 0.001$ ).

## Supplementary Files

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