Biogeographic Variation in the Diet and Behaviour of *Cercopithecus mitis*

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Abstract

Primate species are characterised by variation in foraging behaviour and dietary composition across their geographic range. Here we examine how ecological conditions account for variation in the behavioural ecology of a widespread arboreal guenon, *Cercopithecus mitis*. Although substantial variation existed in time budgets, group size, home range and day journey length, clear biogeographic patterns were not apparent. In contrast, dietary variation was correlated with underlying climatic conditions. Temperature seasonality, which tends to increase with latitude, was significantly positively related to the proportion of fruit in the diet and negatively related to the proportion of animal matter. Both dietary components were 'preferred' foods, with the variability between populations reflecting the availability of different food types across their geographic range. Although we found no significant relationships between climate and the proportion of leaves in the diet, the ability for *C. mitis* to vary their diet to include a diversity of food types, and to incorporate a significant proportion of leaves when preferred sources are scarce, likely underpins their ability to survive across such a large distribution.

Introduction

Climatic conditions are known to have important effects on the availability of food for primates [Lehmann et al., 2007; Willems and Hill, 2009; Korstjens et al., 2010]. As a consequence, climate is an important driver of species' distributions through its impact on underlying resource distributions [Eeley and Foley, 1999; Eeley and Lawes, 1999; Chuine, 2010]. All primates must attribute their available time to a number of different activities, mainly foraging, socialising and resting [Dunbar, 1992]; for an individual to survive they must meet their minimum calorific intake within the time they are able to attribute to foraging. This likely accounts for why primates with large geographical distributions, such as baboons (*Papio spp*) and vervet monkeys (*Chlorocebus aethiops*) tend to be classed as diet generalists able to access a broader range of dietary options. With the potential for diet to be such an important constraint on primate distribution it is perhaps surprising that the topic still remains relatively understudied.

In one of the few studies to investigate macro-spatial variation in the diet of a primate species, Hill and Dunbar [2002] used data on 15 baboon populations to assess the relationship between dietary composition and environmental variables. They found that the proportion of time spent feeding on fruit by baboons increased with increasing average temperature, decreasing altitude and with increasing Primary Productivity Index, a measure of the number of productive months in a year. Their results also showed that time spent eating leaves and subterranean foods had a negative relationship with temperature, indicating their status as 'fall-back' foods eaten when fruit was limiting. In a study of gorillas (*Gorilla* spp.), Lehmann et al. [2008b] observed that in areas of low fruit availability gorillas spent more time resting, due to the increased digestive effort associated with elevated leaf consumption. These studies indicate that geographically variable climatic conditions can have significant effect on underlying ecological conditions, which in turn influences a genus' or species' diet and behavioural profiles. Comparative data sets allow investigations into how species adapt behaviourally to survive under different environmental conditions and the implications this has for species distributions [Altmann, 1974]; here we attempt such an investigation focussing on the arboreal monkey species, *Cercopithecus mitis*.

C. mitis (referred to as samango monkeys, blue monkeys or Syke's monkeys in different parts of their range) are medium sized (adult females ~4.4kg, adult males ~7.6kg: [Harvey et al., 1987]), arboreal, diurnal guenons, which form single-male multi-female groups with group sizes ranging from 4-65 [Butynski, 1990; Beeson et al., 1996; Smith et al., 2008; Houle et al., 2010; Lawes et al., 2013]. Home ranges have been reported as large as 253ha [Butynski, 1990], but most groups tend to have ranges of less than 80ha [Cords, 1986; Butynski, 1990; Lawes, 1991; Beeson et al., 1996; Kaplin et al., 1998; Fairgrieve and Muhumuza, 2003; Coleman, 2013; Tesfaye et al., 2013]. The distribution of *C. mitis* extends from central Ethiopia in the north to the Eastern Cape, South Africa, in the south (a range of approximately 5000km), and west-east from western Angola to Somalia (approximately 3200km) (Figure 1). Within this distribution they are present in a range of different forest types including riverine forest, bamboo forest and lowland and montane tropical moist forest [Lawes, 1990]. With such a large and diverse range *C. mitis* make an ideal study species for investigating how and why diet and behaviour may vary geographically.

Although most forest guenons have diets dominated by fruit [Gautier-Hion, 1988; Beeson et al., 1996; Chapman et al., 2002], *C. mitis* tend to have a broader diet than most other arboreal Cercopithecine species [Lawes, 1991; Chapman et al., 2002]. *C. mitis* supplement their diet from a variety of different sources such as leaves [Fairgrieve, 1995; Beeson et al., 1996], insects [Butynski, 1990; Kaplin, 2001] and flowers [Schlichte, 1978]. This dietary diversity and increased leaf consumption is reflected in the gut morphology of *C. mitis*, which have longer caecums, a larger numbers of cellulases and more cellulose digesting bacteria than other Cercopithecines [Bruorton et al., 1991].

The ability of *C. mitis* to consume a diverse diet may account for their geographic range extending to more southerly latitudes than other arboreal guenons [Wolfheim, 1982]. *C. m. erythrarchus* is one of the most southerly sub-species of *C. mitis*, with samango monkeys ranging throughout Mozambique, Zimbabwe and northern South Africa where it experiences a highly seasonal climate. Previous work has shown that *C. m. erythrarchus* in South Africa increase their leaf consumption during colder months to subsidise their normally highly frugivorous diet [Lawes, 1991; Coleman, 2013]. In some more equatorial populations, the total proportion of foliar material in the diet of *C. mitis* has been observed to drop below 10% [Moreno-Black and Maples, 1977; Cords, 1986; 1987], indicating that these populations do not supplement their diets with leaves to the same extent.

Here we investigate the environmental factors underlying variation in samango monkey behaviour and diet composition across different populations of this widely distributed arboreal primate species. In doing so we assess the degree to which dietary flexibility in samango monkeys accounts for their ability to extend their range into more southerly latitudes than other forest guenons.

Methods

Behavioural and diet data

Data were extracted from the literature on the behavioural ecology and diet composition of 13 populations of *C. mitis* (Tables 1 and 2; Figure 1). Only studies with a duration of at least 6 months were included in our analysis. If the studies reported data from more than one group per population the mean of these groups was used. Where available, home range area, group size and mean day journey length were extracted. Time budget data were restricted to four categories: feeding, resting, moving and socialising (following Dunbar [1992]).

Published dietary data had been collected using a series of methods, including direction observation, faecal analysis and the analysis of stomach contents, with some studies reporting a combination of methods. Diet components were separated into fruits (including seeds), leaves, flowers, other plant (e.g. bark), animal matter (usually invertebrates, e.g. caterpillars, ants), fungi and unknown. The figures reported in Table 2 represent the proportion of the diet these components comprise in each population. For Budongo Forest, Uganda [Fairgrieve and Muhumuza, 2003], only unlogged forest data were used as this was more comparable to other study sites. Similarly for the population in Jibat Forest, Ethiopia [Tesfaye et al., 2013], only undisturbed forest data were used.

Climatic data

Climatic data for Africa were extracted from a 1950-2000 data set [Hijmans et al., 2005] at a resolution of 30s of a degree (equating to 0.86km^2 at the equator). Using ArcGIS 10.2 (Environmental Systems Research Institute, California), the following climatic variables were extracted for each site: mean annual temperature, diurnal temperature range (mean of monthly (max temperature – min temperature)), temperature seasonality (standard deviation of monthly values), maximum temperature of warmest month, minimum temperature of coldest month, annual temperature range (max temperature warmest month – min temperature coldest month), annual precipitation, precipitation seasonality (coefficient of variation) and altitude (Table 3). These variables were chosen after assessment of indices used by previous cross-populational primate studies [Williamson and Dunbar, 1999; Hill and Dunbar, 2002; Lehmann et al., 2008b; a; Willems and Hill, 2009]. Along with these bioclimatic variables the Primary Productivity Index (PPI) was calculated as the number of months in which total precipitation (in mm) exceeds twice the monthly average temperature (in ^{o}C). PPI has been show to equate to the length of the growing season, which itself yields a very strong correlation with primary productivity ([Le Houerou, 1984]. Williamson [1997] highlighted the value of PPI for describing rainfall seasonality and previous studies have illustrated its value in explaining biogeographic patterns of primate dietary variation and behavioural ecology [Hill and Dunbar, 2002; Lehmann et al., 2008a; 2010]. To complement this, information on primary productivity was obtained from the remotely-sensed Normalized Difference Vegetation Index (NDVI), a well-established and successful satellite-derived measure of photosynthetic activity [Kerr and Ostrovsky, 2003; Pettorelli et al., 2011] that has been successfully applied to studies of primate biogeography [Zinner et al., 2001; 2002; Willems and Hill, 2009]. NDVI data were derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument and extracted from the MODIS subsetted land products [Oak Ridge

National Laboratory Distributed Active Archive Center (ORNL DAAC), 2012]. The data were based on field site coordinates overlaid onto satellite imagery, and extracted for a 2.5km subset for the period 2001-2010. A small subset area was selected to ensure that estimates were centred on preferred forest habitats, even for those populations inhabiting relatively small forest fragments. From the 2.5km subsets, mean annual NDVI composites were computed from all pixels passing quality filtering criteria. Finally, day length variation (length of longest day – length of shortest day) was calculated for each population using data from the Astronomical Applications Department of the U.S. Naval Observatory (http://aa.usno.navy.mil/data/docs/Dur_OneYear.php), since this has also been shown to account for geographic variation in primate behaviour [Hill et al., 2003].

Exploratory analysis revealed highly significant correlations between some climate variables (Appendix1). As a consequence the original 11 variables were reduced to seven independent variables for analysis: altitude, mean annual temperature, temperature seasonality, mean annual precipitation, diurnal temperature range, PPI and NDVI. The remaining variables incorporated the three main dimensions of climatic variation identified through a large factor analysis of 80 sub-Saharan weather stations (annual rainfall, average temperature and seasonality: Williamson and Dunbar [1999]) and mirror those used in previous studies of this type [Hill and Dunbar, 2002; Lehmann et al., 2008a; 2010].

Statistical analysis

A parametric correlation analysis was conducted to investigate bivariate relationships between the six climatic variables and group size, home range and diet composition data. Time budget data were only available for five populations and so no statistical analyses were attempted. For the home range data, we excluded from statistical analyses the estimates from Kibale by Butynski [1990] since they represent the cumulative home ranges over a 6 year period, which for the Ngogo group in particular, results in an abnormally large estimate. The Kibale home range estimate from Rudran [1978] is retained. For the dietary data, Lawes et al. [1990] used two different methods of data collection, so each data set was given a weighting of 0.5 in the analyses to allow all available data to be incorporated without inflating the sample sizes for any one population. The two studies conducted at Kanyawara, Kibale Forest, Uganda, were both included since they were 12 years apart (Rudran 1978, Butynski 1990), but each was weighted 0.5 within the analysis (if only one of these studies was used for a particular analysis then the weighting was returned to 1). All climatic variables, home range, day journey length, group size and all diet components except fungi were normally distributed (Kolmogorov-Smirnoff: fungi: $p < 0.001$; all other variables: $p > 0.05$). Only two studies reported fungi being consumed and thus percentage fungi in the diet was not included as a response variable in the analyses.

Previous studies have highlighted potential problems with multiple tests [Hochberg, 1988; Rice, 1989; Bland and Altman, 1995], although others have questioned correcting for multiple testing due to the potential problems associated with the correction methods, such as increased Type II errors [Perneger, 1998; Moran, 2003; Nakagawa, 2004]. Although we do not apply corrections for multiple tests here, all significant relationships were evaluated on the basis of a requirement for substantial effect sizes (i.e. minimum r =0.5: [Nakagawa, 2004] and the biological merit of the correlations to minimise the potential for Type I errors.

Stepwise linear regression analyses were used to further investigate any statistically significant relationships between the climate variables and the diet and behavioural categories. From these analyses, regression equations were derived which were used in GIS, using the raster calculator function, to produce new layers displaying the category's variation over the species' distribution based on the underlying climatic parameters in the Hijmans et al. [2005] Africa data set.

Results

Although the time budget data did not permit statistical analysis, substantial variation existed between populations. For example, feeding time varies from 49% at Kakamega, Uganda, to just 28% at Lajuma, South Africa. Latitude differences may not account for this variation, however, with large differences in resting time reported for the two South African populations (Lajuma 42%, Cape Vidal, 22%). There were no significant correlations involving group size or day journey length (Table 4), but these also differ markedly between populations. Day journey lengths vary from 799m in Jibat Forest to 1906m in Lajuma. The smallest average group size was found in the Jibat Forest with 9 individuals and the largest found in Kakamega Forest, Kenya with 43. There was one significant relationship involving home range size which was a positive correlation with the proportion of animal matter in the diet.

The proportion of fruit in the diet of *C. mitis* had significant negative relationships with proportion of animal matter and leaves, indicating that populations consuming less fruit supplement their diet with animal matter and/or leaf material (Table 5). The amount of leaf material in the diet shared no other significant relationships with any of the other variables considered. Proportion of fruit in the diet had a significant positive relationship with temperature seasonality (Figure 2a), with animal matter showing the opposite trend with a significant negative relationship with temperature seasonality (Figure 2b). The amount of animal matter in the diet was also significantly positive correlated to PPI (Figure 2c). Other plant material in the diet was significantly negatively correlated with NDVI, with Figure 2d suggesting a non-linear relationship. Indeed a significant quadratic relationship exists between the variables (R^2 = 0.847, F = 27.721, p < 0.001). The category “flowers” was not significantly correlated with any of the variables investigated.

Using linear stepwise regression analyses equations were derived to describe how proportion of animal matter and fruit within the diet varied with climatic conditions. We exclude other plant material from this analysis since the category includes a diversity of material and accounts for only a small proportion of the diet across populations (mean 5.2%) :

$$\textbf{Animal \% = (−8.10 × Temperature seasonality) +22.71}$$

$R^2 = .561$, F = 16.343, t = -4.043

$$\textbf{Fruit \% = (8.22 × Temperature seasonality) +41.46}$$

$R^2 = .279$, F = 5.651, t = 2.377

The maps of the predicted dietary variation derived from these equations show that as temperature seasonality becomes more pronounced at southerly latitudes, the proportion of animal matter declines too, with a corresponding increase in the proportion of fruit in the diet (Figure 3). Nevertheless, fruit remains the primary dietary component, with the analysis indicating that it comprises a minimum of 40% of the diet across the species' range, with maximum values of 75% of a population's diet. Below a latitude of approximately 11°S, the proportion of animal matter in the diet is predicted to be very low in *C. mitis*.

Discussion

Previous studies have shown that time budgets and diet can vary considerably across primate species distributions [Lawes, 1991; Dunbar, 1992; Hill and Dunbar, 2002; Hill et al., 2003; Lehmann et al., 2008b; Willems and Hill, 2009; Korstjens et al., 2010]. Here we examined how *C. mitis* behaviour, and particularly diet composition, varied across the large geographic range of *C. mitis*. Although sample sizes for the activity budget variables were insufficient for statistical analysis, the data suggest substantial variation between populations. Small sample size may account for the lack of any significant relationships involving day journey length and group size and may also be the reason for the positive relationship between home range size and proportion of animal matter in the diet, as there appears no obvious behavioural reason for this correlation (but see below for one possibility). More data are required to investigate this potential relationship in more detail and assess whether there is a genuine correlation or if the result emerges as a

Type I error. Nevertheless, the current available data suggest substantial variation in the behaviour and ecology of *C. mitis* throughout their range [Lawes, 1991; Chapman et al., 2002].

Only a single relationship existed between NDVI and any of the behavioural variables, with the percentage of other plant material in the diet significantly negatively correlated with NDVI. The suggests that the consumption of other plant material declines as primary productivity increases, although the absence of relationships between NDVI and other dietary and behavioural parameters is perhaps surprising. Willems and Hill [2009] found NDVI, and thus primary productivity, to be the most significant environmental parameter explaining vervet monkey distribution, with NDVI a significant predictor of feeding time (and thereby resting time), as well as the proportion of leaves in the diet, which itself influenced moving time demands. Similarly, two previous studies on primate distribution reported that hypothetical circular home ranges of baboons and vervet monkeys in Eritrea had higher NDVI values than the broader study area [Zinner et al., 2001; 2002], while vervet monkeys prefer ranging areas with elevated productivity and reduced NDVI seasonality in South Africa [Willems et al., 2009]. Such small-scale selection for areas of high NDVI may account for the absence of relationships at a larger spatial scale for *C. mitis*. As an arboreal species, the range of C *mitis* is restricted to forest habitat in these areas [Lawes, 1990; Skinner and Chimimba, 2005; Kingdon et al., 2008]. While some of the populations sampled in this study inhabit large areas of continuous forest (e.g. Kibale: Butynski [1990]; Budongo: Fairgrieve and Muhumuza [2003]), others live in isolated or fragmented forest pockets (e.g. Diani Beach: Moreno-Black and Maples [1977]; Zomba Plateau: Beeson et al. [1996]; Lajuma: Coleman [2013]). As a consequence, despite using a small sampling area for NDVI estimation at each study site, the pixels selected may have incorporated non-forest habitat in the isolated or fragmented forest populations such that NDVI values may not precisely reflect primary productivity within their core ranging areas. It is certainly the case that NDVI values were considerably lower for C. mitis populations outside of large forested areas (Table 3), with the values overlapping those reported for more open-habitat vervet monkey populations [Willems, 2007; Willems and Hill, 2009]. Temporal factors may also be important, since the 10-year average used here may not precisely depict the conditions when the studies were conducted. Nevertheless, satellite-derived measure of photosynthetic activity offer enormous potential for future studies of primate ecology [Pettorelli et al., 2011]. Studies examining patterns of habitat selection by *C. mitis* in relation to NDVI at an appropriately fine temporal and spatial resolution within populations will be invaluable in determining whether remotely sensed data on primary productivity can be used to explore biogeographical patterns in this species in future.

As temperature seasonality increases there is an increase in the proportion of fruit in the diet of *C. mitis*. This is surprising since it suggest fruit consumption is increasing in areas of lower overall productivity, a result contrary to a previous study of baboons [Hill and Dunbar, 2002]. The most likely explanation reflects the availability of animal matter in the environment. Cercopithecines often consume relatively high proportions of invertebrates in their diets [Chapman et al., 2002], with diets of red tail monkeys (*Cercopithecus ascanius*) rarely comprising less than 20% insects. This reflects the value of insects in offering a readily digestible source of protein [Redford and Dorea, 1984]. Both animal matter and fruit are thus "preferred" food sources, providing dietary protein and easily accessible carbohydrate respectively [Lawes, 1991], such that in areas where they are both abundant they are both likely to comprise a significant component of *C. mitis* diet. In contrast, the results here suggest that invertebrate availability is low for *C. mitis* populations inhabiting areas where temperature seasonality is high. In the absence of invertebrates, *C. mitis* increase the proportion of time foraging on fruit in these highly seasonal environments, incorporating additional protein from a more diverse array of food sources. In this respect it is interesting that we do not find a negative relationship between animal matter and the proportion of leaves or flowers in the diet, since both young leaves and flowers provide an alternative protein source, albeit in a less digestible form [Richard, 1985; Lawes, 1991]. An increase in the proportion of plant material in the diet would thus have been anticipated in response to a reduction in the availability of insects and it is possible that the coincidental seasonal availability of new leaves, flowers and invertebrates at higher latitudes may mask this expected correlation. The fact that the proportion of fruit increases is unlikely to indicate a direct trade-off between fruit and animal matter, however, given their selection for carbohydrate and protein respectively. Instead it could reflect the effects of increased competition from other primate species for populations at more equatorial latitudes ([Wolfheim, 1982; Cowlishaw and Hacker, 1997]; but see [Connell, 1980]). For example, Lawes [1991] attributed the high levels of fruit consumption in the seasonal Cape Vidal population, South Africa, to the absence of other Cercopithecine primates and the presence of few frugivorous bird species and bats, and similar suggestions have been made for Ngoye Forest [Lawes et al., 1990].

Species richness for many animals increases in areas of high primary productivity [Currie, 1991; Kay et al., 1997; Hawkins et al., 2003], with plant species richness generally positively correlated with precipitation [Obrien, 1993; Adler and Levine, 2007] and increased plant diversity leading to more diverse animal (including invertebrate) communities [Hawkins et al., 2003; Novotny et al., 2006]. The relationships between animal matter in the diet and temperature seasonality are consistent with a decline in insect species richness in non-equatorial populations. Furthermore, with insect species diversity decreasing significantly during the dry season [Janzen and Schoener, 1968; Wolda, 1978], the increased seasonality with increasing latitude further underpins the absence of animal material in the diet in more southerly populations [Lawes, 1991].

Although the preceding discussion on fruit and animal matter intake highlights the flexibility in *C. mitis* diets, it doesn't provide compelling support for dietary diversity accounting for the geographic range of the species since fruit consumption increases in populations outside of the tropics. Guenons are characteristically frugivorous, but *C. mitis* are better adapted than other guenons for leaf consumption [Bruorton and Perrin, 1988; Bruorton et al., 1991; Bruorton and Perrin, 1991]. The analyses conducted here showed no correlation between any climatic variables and proportion of leaves in the diet, although the proportion of leaves and fruit in *C. mitis* diet had a strong negative relationship. This indicates that leaves may be a 'fall-back' food in areas of lower fruit availability. In some studies, leaf consumption is as high as 50% and it is probably this capacity for leaf consumption that allows *C. mitis* to survive at lower latitudes than any other arboreal Cercopithecines [Wolfheim, 1982; Lawes, 1991]. Research on southerly samango populations has shown that leaves are an important dietary supplement during winter months, which supports this hypothesis [Lawes, 1991; Coleman, 2013]. Since previous studies have highlighted that leaves are a more important protein source where food is seasonally available [Beeson, 1989; Lawes, 1991] the absence of clear biogeographical relationships in the data is surprising. Nevertheless, a flexible diet that allows the incorporation of significant levels of non-preferred fallback foods may be the explanation for the large geographical distribution of the species, allowing them to survive at seasonal southerly latitudes [Lawes, 1991] and in many different forest types [Kingdon et al., 2008].

The ability for *C. mitis* to consume a more varied diet, often with a relatively high proportion of leaf material [Bruorton et al., 1991; Bruorton and Perrin, 1991; Chapman et al., 2002] is probably the main reason for their ability to occupy a more southerly range compared to other arboreal guenons [Wolfheim, 1982; Lawes, 1990]. When food availability is low *C. mitis* are able to supplement their diet with a greater variety of foods [Rudran, 1978a; Lawes, 1991] with leaf material the major contributor to an increase in overall food intake in the Soutpansberg Mountains, South Africa [Coleman, 2013]. Such trade-offs were difficult to detect in the biogeographic relationships presented here, and further behavioural and dietary data from longer-term studies of *C. mitis* inhabiting a broader range of ecological conditions may help to distinguish these relationships. Further studies investigating the value of NDVI and other remote sensing indices may be particularly valuable in this regard given its value as a measure of photoynthetic activity [Kerr and Ostrovsky, 2003; Pettorelli et al., 2011]. With the future of our climate currently uncertain, it is important to be able to predict how well certain species will be able to adapt to different conditions. However, we should be careful in the way we interpret the results from such studies. It is unlikely that climatic variables, and their associated impact on resource availability, are the only factors driving a species' behaviour and information elements such as biotic interactions is needed (Pearson & Dawson 2003). Nevertheless, the flexibility observed in *C. mitis* behaviour and diets should allow the species to tolerate greater degrees of change across its geographic range than other Cercopithecine primates.

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List of Figures

Figure 1: Map showing locations of the *C. mitis* sites used in this study (red circles) and the known distribution of the species in grey [Kingdon et al., 2008]. See Table 1 for details of numbered populations.

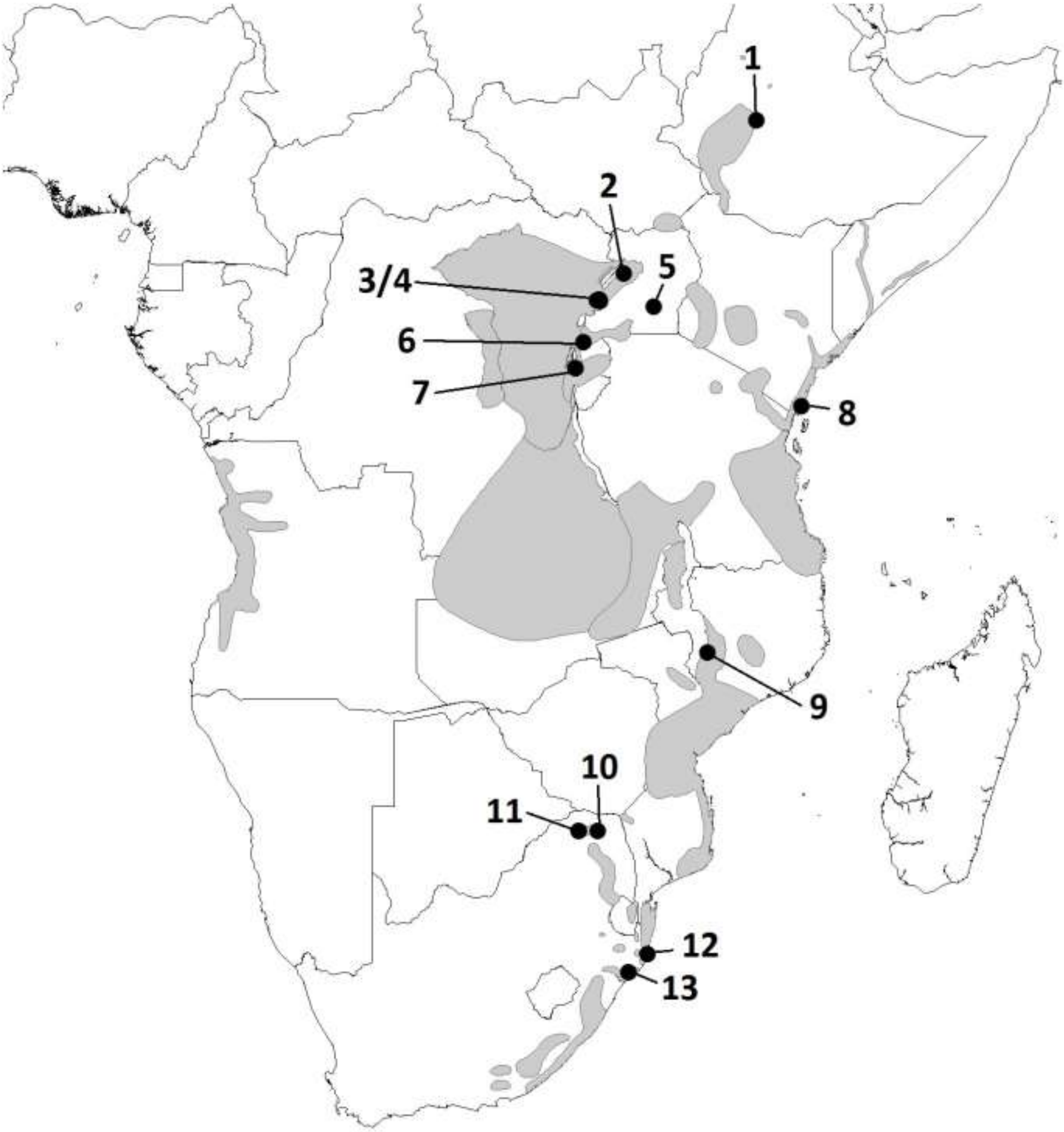

Figure 2: Relationships between diet and climatic variables across *C. mitis* populations. (a) percentage fruit in the diet and temperature seasonality (b) percentage of animal matter in the diet and temperature seasonality, (b) percentage of animal matter in the diet and PPI and (d) percentage of other plant material in the diet and NDVI.

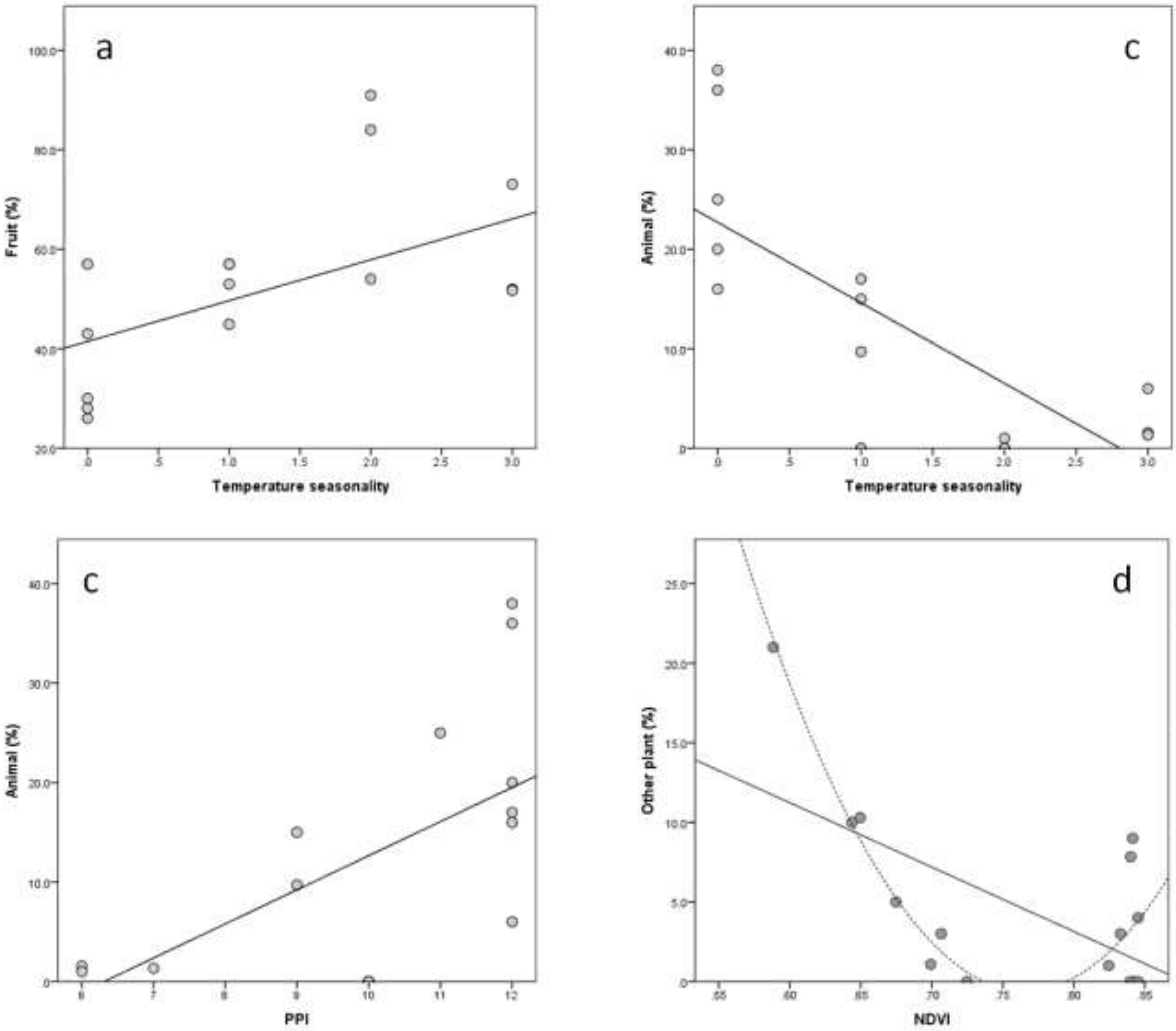

Figure 3: Predicted proportion of (a) animal matter and (b) fruit in the diet of *C. mitis* throughout the species range.

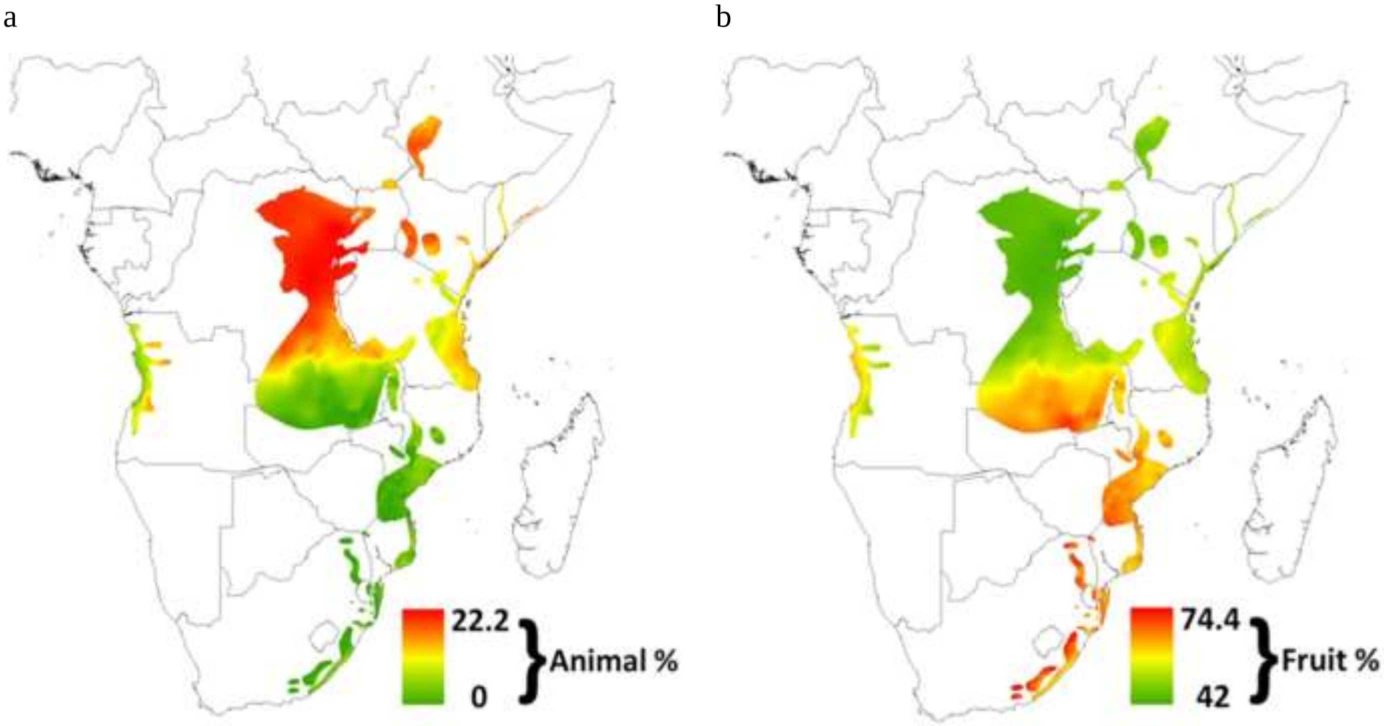

Table 1 Details of the study populations used in the analyses. Abbreviations: Pop – Population (see Figure 1); Dur – Study Duration (months); HR – home range size (ha); DJL – day journey length (m)

Location	Pop	Latitude	Longitude	Dur	Group size	HR	DJL	Feeding (%)	Resting (%)	Moving (%)	Socialising (%)	Other (%)	Reference
Jibat Forest, Ethiopia	1	8°43'N	37°33'E	10	9	72	799	-	-	-	-	-	Tesfaye et al. [2013]
Budongo Forest, Uganda	2	1°35'-1°55'N	31°18'-31°42'E	13	-	10	-	-	-	-	-	-	Fairgrieve and Muhumuza [2003]
Kanyawara, Kibale Forest, Uganda	3	0°34'N	30°21'E	24	20.8	72.5	-	-	-	-	-	-	Rudran [1978b]
Kanyawara, Kibale Forest, Uganda	3	0°34'N	30°21'E	63	18.4	32.4	1216	36.2	32.7	19.7	8.3	0	Butynski [1990]
Ngogo, Kibale Forest Uganda	4	0°13'-0°41'N	30°19'-30°32'E	63	15	252.75	1406	31.7	36.2	24.7	7	0	Butynski [1990]
Kakamega Forest, Kenya	5	0°14'N	34°52'E	11	43	38	1136	49.4	31.7	15.8	1.2	1.9	Cords [1986]; 1987]
Mgahinga Gorilla National Park, Uganda	6	1°23'17''S	29°38'31''E	6	-	-	-	-	-	-	-	-	Twinomugisha et al. [2006]
Nyungwe Forest, Rwanda	7	2°17'-2°50'S	29°07'-29°26'E	8	29	112.2	1306.7	-	-	-	-	-	Kaplin et al. [1998]; Kaplin [2001]
Diani Beach Forest, Kenya	8	4°17'S	39°35'E	6	-	-	-	-	-	-	-	-	Moreno-Black and Maples [1977]
Zomba Plateau, Malawi	9	15°20'S	35°19'E	12	15	16.5	-	-	-	-	-	-	Beeson et al. [1996]
Entabeni Forest, South Africa	10	23°02'S	30°17'E	9	-	-	-	-	-	-	-	-	Breytenbach [1988]
Lajuma, South Africa	11	23º02'23"S	29º26'05"E	12	40	54.7	1906	28.1	41.5	23.2	7.1	0.1	Coleman [2013]; Coleman and Hill [2014]
Cape Vidal Forest, South Africa	12	28°05'35"S	32°33'40"E	13	32.5	15	-	35.8	22.6	29.4	12	0	Lawes [1990]
Ngoye Forest, S.A.	13	28°50'S	31°42'E	12	16	-	-	-	-	-	-	-	Lawes et al. [1990]

Table 2: Diet composition data from all available *C. mitis* studies with a minimum study period of 6 months. Abbreviations: Obs – feeding observations; Fae – faecal analysis; Sto – Stomach content analysis; No. Spp. – number of food species.

Location	Method	No. Spp.	Fruit (%)	Leaves (%)	Flowers (%)	Other (%)	Animal (%)	Fungi (%)	Unknown (%)
Jibat Forest, Ethiopia	Obs	24	53.1	14.2	7.3	10.4	14.7	0	0.4
Budongo Forest, Uganda	Obs	40	44.9	29.0	6.2	10.3	9.7	0	0
Kanyawara, Kibale Forest, Uganda (Rudran)	Obs	59	42.7	21.3	11.8	4.4	19.8	0	0
Kanyawara, Kibale Forest, Uganda (Butynski)	Obs	40	27.7	33.0	6.9	0	37.7	0	0.6
Ngogo, Kibale Forest Uganda	Obs	52	30.1	22.8	9.8	0	35.9	0	1.3
Kakamega Forest, Kenya	Obs	104	54.6	18.9	3.7	5.5	16.8	0	0.5
Mgahinga Gorilla National Park	Fae	33	26.3	51.6	0	4.6	16.3	0	1.2
Nyungwe Forest, Rwanda	Obs	59	47.4	6.2	6.2	0	24.9	0	6.2
Diani Beach Forest, Kenya	Obs/Fae	27	57.1	7.1	14.3	21.4	0	0	0
Zomba Plateau, Malawi	Obs	33	53.5	32.6	10.2	2.9	0.8	0	0
Entabeni Forest, South Africa	Sto	-	73.1	13	4.51	7.8	1.5	0	0
Lajuma, South Africa	Obs	35	51.7	43.9	0.4	1.1	1.3	1.6	0
Cape Vidal Forest, South Africa	Obs	57	51.7	25.8	13.4	0.9	5.8	0	2.3
Ngoye Forest, South Africa	Obs	30	91.1	3.0	2.1	0	0	0	3.8
Ngoye Forest, South Africa	Fae	30	84.4	1.6	0.6	8.9	0.4	0.5	0

Table 3: Climatic data for *C. mitis* study sites used in the analyses. Abbreviations: DLV – Day length variation (mins); Alt – altitude (m); T - mean annual temperature (^{o}C); DTR - diurnal temperature range (^{o}C); TS - temperature seasonality; HT – highest temperature of warmest month (°C); LT - lowest temperature of coldest month (°C); ATR - Annual temperature range (°C); R - mean annual rainfall (mm); RS - rainfall seasonality (mm); PPI – Primary Productivity Index; NDVI - Normalised Difference Vegetation Index.

Location	DLV	Alt	T	DTR	TS	HT	LT	ATR	R	RS	PPI	NDVI
Jibat Forest, Ethiopia	61	2519	15.8	14.3	0.83	25.1	7.1	18.0	1359	81	9	0.644
Budongo Forest, Uganda	12	1079	23.0	11.8	0.80	31.1	16.5	14.6	1330	43	9	0.650
Kanyawara, Kibale Forest, Uganda	3	1503	19.5	12.0	0.42	26.9	12.7	14.2	1446	44	12	0.845
Ngogo, Kibale Forest Uganda	3	1450	20.7	12.2	0.40	27.6	13.9	13.7	1267	38	12	0.840
Kakamega Forest, Kenya	2	1144	21.5	10.8	0.54	28.3	15.3	13.0	1455	33	12	0.833
Mgahinga Gorilla National Park	9	2989	11.5	9.8	0.25	17.0	6.4	10.6	1823	42	12	0.675
Nyungwe Forest, Rwanda	18	2298	15.5	9.6	0.35	21.5	9.9	11.6	1663	51	11	0.725
Diani Beach Forest, Kenya	30	14	26.6	8.2	1.44	33.1	20.4	12.7	1277	79	10	0.588
Zomba Plateau, Malawi	131	1737	17.2	9.4	1.88	25.0	9.2	15.8	1416	96	6	0.707
Entabeni Forest, S.A.	170	740	20.6	11.6	2.70	29.0	9.4	19.6	899	84	6	0.840
Lajuma, South Africa	170	1372	17.0	12.9	3.35	26.1	3.8	22.3	799	83	7	0.699
Cape Vidal Forest, S.A.	215	72	21.3	9.3	2.72	29.4	11.6	17.8	1063	37	12	0.825
Ngoye Forest, S.A.	221	417	19.6	9.9	2.40	27.3	10.5	16.8	1140	44	10	0.842

Table 4 Correlations between selected climatic variables and group size, home range and day journey length. Significant correlations (p=<.05) are presented in bold. Abbreviations: Alt – altitude (m); T - mean annual temperature (°C); DTR - diurnal temperature range (°C); TS - temperature seasonality; R - mean annual rainfall (mm); PPI – Primary Productivity Index; NDVI - Normalised Difference Vegetation Index; HR – home range size (ha); DJL – day journey length (m).

Variable	Statistic	Alt	T	DTR	TS	R	PPI	NDVI	Other (%)	Flowers (%)	Animal (%)	Leaves (%)	Fruit (%)	HR	DJL
Group Size	r	-.317	.307	-.127	.325	-.274	.154	.156	-.415	-.325	-.166	.299	.050	-.113	.539
	p	.406	.421	.774	.393	.476	.692	.689	.267	.393	.670	.434	.898	.809	.306
	n	9	9	9	9	9	9	9	9	9	9	9	9	7	6
Day Journey Length	r	-.531	-.034	-.096	.553	-.683	-.414	.094	-.698	-.544	-.315	.722	-.124		
	p	.314	.953	.867	.291	.165	.449	.869	.153	.301	.572	.133	.828		
	n	6	6	6	6	6	6	6	6	6	6	6	6		
Home Range	r	.701	-.619	.298	-.586	.388	.250	-.013	-.232	-.215	**.730**	-.619	.221		
	p	.053	.102	.474	.127	.342	.551	.976	.581	.610	**.040**	.102	.599		
	n	8	8	8	8	8	8	8	8	8	**8**	8	8		

Table 5: Correlations between selected climatic variables and diet composition (n=13). Significant correlations (p=<.05) are presented in bold. Abbreviations: Alt – altitude (m); T - mean annual temperature (°C); DTR - diurnal temperature range (°C); TS - temperature seasonality; R - mean annual rainfall (mm); PPI – Primary Productivity Index; NDVI - Normalised Difference Vegetation Index.

Variable	Statistic	Alt	T	DTR	TS	R	PPI	NDVI	Other %	Flowers %	Animal %	Leaves %
Fruit %	r	-.508	.296	-.158	.583	-.501	-.432	.192	.173	-.134	-.645	-.682
	p	.076	.325	.607	**.037**	.081	.141	.530	.572	.663	**.017**	**.010**
Leaves %	r	.419	-.491	.144	.012	.124	-.033	-.170	-.310	-.305	.067	
	p	.154	.088	.638	.970	.686	.916	.578	.303	.310	.827	
Animal %	r	.473	-.226	.311	-.773	.548	.638	.285	-.434	.070		
	p	.139	.458	.301	**.002**	.052	**.019**	.345	.139	.819		
Flowers %	r	-.406	.534	-.381	-.072	-.001	.156	-.064	.276			
	p	.169	.060	.199	.815	.997	.610	.836	.362			
Other %	r	-.291	.518	-.180	-.009	-.054	-.205	-.623				
	p	.362	.070	.556	.976	.862	.501	**.023**				

Appendix 1: Results of correlation analysis between all climatic variables, altitude and day length. Significant correlations (p=<.05) are presented in bold. r = Pearson correlation coefficient, N = 13. Abbreviations: NDVI - Normalised Difference Vegetation Index; PPI – Primary Productivity Index; RS - rainfall seasonality (mm); R - mean annual rainfall (mm); ATR - annual temperature range (°C); LT - lowest temperature of coldest month (°C); HT – highest temperature of warmest month (°C); DTR - diurnal temperature range (^{o}C); TS - temperature seasonality; T - mean annual temperature (^{o}C); DLV – day length variation (mins).

Variable	Statistic	NDVI	PPI	RS	R	ATR	LT	HT	TS	DTR	T	DLV
Altitude	r	-.272	.066	.046	.654	-.314	-.576	-.856	-.547	.368	-.855	-.476
	p	.369	.830	.882	**.015**	.296	**.039**	**<.001**	.053	.216	**<.001**	.100
Day length variation	r	.281	-.475	.299	-.736	.775	-.400	.159	.895	-.130	-.003	
	p	.352	.101	.332	**.004**	**.002**	.176	.604	**<.001**	.672	.992	
Mean annual temperature	r	.067	.026	-.063	-.391	.020	.863	.951	.176	-.245		
	p	.828	.932	.838	.187	.949	**<.001**	**<.001**	.566	.419		
Diurnal temperature range	r	.093	-.189	.091	-.237	.432	-.400	-.064	-.028			
	p	.761	.537	.767	.436	.140	.176	.836	.928			
Temperature seasonality	r	.154	-.624	.423	-.854	.857	-.278	.361				
	p	.616	**.023**	.150	**<.001**	**<.001**	.358	.226				
Highest temperature warmest month	r	.057	-.169	.095	-.586	.288	.712					
	p	.854	.580	.757	**.035**	.340	**.006**					
Lowest temperature coldest month	r	-.037	.356	-.306	.115	-.465						
	p	.905	.233	.309	.708	.110						
Temperature range	r	.141	-.664	.506	-.900							
	p	**.646**	**.013**	.078	**<.001**							
Mean annual rainfall	r	-.225	.535	-.377								
	p	.461	.059	.204								
Rainfall seasonality	r	-.444	-.857									
	p	**.128**	**<.001**									
PPI	r	.262										
	p	**.387**										