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Research Article

# Ecometric modelling of limb proportions and vegetation index among non-human primates in South America

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## Abstract

Ecometric modelling assesses how the functional morphology of ecogeographic communities relates to environmental variables. This improves understanding of how the interaction between organism and environment can result in morphological adaptation. This technique has mainly been used to model paleoenvironments, but has the capacity to aid conservation by quantifying how communities are structured through space and time. Here we test the relationship between limb proportions and the habitat ecology of South American non-human primates. There is a significant but weak fit between limb proportions and habitat, consistent with the environment exerting weak selective pressure on limb proportions. In contrast, body size and phylogeny are strongly correlated with IMI. Together, these findings suggest that habitat was a selection pressure that shaped how New World monkeys' limb proportions evolved but this selection pressure was secondary to that of body size. Research into these functional relationships is important not only to improve scientific understanding of their evolutionary pathways but also in order to aid their protection by informing conservation practices. Ensuring these species have the capacity to move with their niche is an immediate concern, as they face mounting pressure due to deforestation of the Amazon basin.

## Introduction

Climate change, deforestation, and other human impacts on the biosphere have intensified rapidly over the last 50 years (Perino et al., 2019; Barnosky et al., 2017; Hughes et al., 2017; Oakleaf et al., 2015). With these changes set to escalate as the human population and its associated demands continue to increase, 'planning for the Anthropocene' has become imperative to conservation. The most successful conservation practices are dependent upon knowledgeable comparisons between current conditions and ancient environments (Barnosky et al., 2017). By adapting methods used in paleontology and paleobiology to investigate current conditions, direct comparisons can be made throughout geological time, situating contemporary research to be applied effectively in mitigating the effects of anthropogenic change on the biosphere.

Ecometric modelling is one technique which can be used both to reconstruct ancient environments and understand the synergy between extant species and their habitats. Ecometrics is the study of how variation in specific morphological traits can be used to predict environmental or climatic factors. Ecometric traits are those which are responsible for how the organism interfaces with their environment and as such have a functional role in the organism's ability to successfully inhabit their environment (Polly and Head, 2015). When morphological traits are correlated with characteristics of the abiotic environment it is possible to make predictions about the environment, through analysis of the local species morphology. These types of analyses are increasingly relevant within the context of ongoing and undeniable anthropogenic climate change. Modelling the link between communities and the environment will inform conservation choices in the present and future, ensuring the best use of the finite resources available to protect the biosphere. For conservation efforts to be truly effective they must anticipate change not merely react to it (Barnosky et al., 2017).

Ecometric modelling has established a link between morphology and environment in diverse clades including ungulates, carnivorans, and rodents (Vermillion et al., 2018; Tapaltsyan et al., 2015; Polly, 2010; Fortelius et al., 2002), and these models have been effective in predicting spatial niche occupation through time. However, this approach has never been applied to South American fauna, despite the critical conservation status of the region. Here we carry out ecometric analysis of South American non-human primates (New World monkeys/Platyrrhini). South American primates are ideally situated to study deforestation of the Amazon basin, a key conservation concern, due to their evolutionary history. When primates arrived in South America 26 million years ago (Perez et al., 2013; Cowlishaw and Dunbar, 2000), the terrestrial herbivore niche was filled by ground sloths (Fleagle et al., 1999). As such, primates were restricted to exploiting arboreal locomotory niches and today exhibit several morphological specializations for navigating arboreal habitats, including prehensile tails and forward-facing eyes. Although all species are arboreal specialists, they vary widely in their microhabitat use, inhabiting a range of ecological niches throughout the continent. We hypothesize that the mean and distribution of the locomotor traits of South American primate communities are highly correlated with features of the local abiotic environment.

We focus on variation in one key locomotor trait, intermembral index (IMI), which measures the ratio of forelimb length to highlimb length. This metric is thought to correlate with differences in locomotor behavior and has been used to assess primate locomotor adaptations, canopy level and diet (Granatosky, 2018; Jungers, 1985). We test whether IMI is a suitable ecometric variable for conservation biology by using continent-scale climatic data to quantify the relationship between environmental variables and this phenotypic trait. We further evaluate the effects of phylogeny and allometry to fully interrogate the forces driving variation in limb proportions in this clade.

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## Methods

Intermembral index describes the ratio between the lengths of the forelimb and the hindlimb (Eqn. 1).

$$\mathrm{IMI} = \frac{\mathit{Humerus\ length} + \mathit{Radius\ Length}}{\mathit{Femur\ Length} + \mathit{Tibia\ Length}} \times 100 \tag{1}$$

We quantified IMI for 52 species of South American primates, representing approximately 43% of extant species, using a combination of published data (Granatosky, 2018; Wright et al., 2015; Fleagle et al., 2013) and direct measurements (Supplemental Data Table 1). We restricted our dataset to species for which mean body size and spatial occurrence data are known. We examined the relationship between IMI and three measures of spatial ecology: vegetation density, temperature, and precipitation. We used Normalized Difference Vegetation Index (NDVI) as a proxy for vegetation density. NDVI is a metric that uses satellite imagery to measure the density of vegetation. Because this data shows temporal heterogeneity related to seasonal changes in vegetation, we used time series averages over a period of one year. We downloaded 74 frames of NDVI data from USGS (2020) Earth Explorer USGS (USGS, eMODIS NDVI). We took the frames from January 2018–January 2019, to avoid the forest fire events which occured in mid-2019 as smoke and cloud cover disrupts the collection of satellite imagery (Carlson and Ripley, 1997). NDVI datasets contain metadata that indicates the “quality” of each datapoint; geographic points are scored on whether they were imaged clearly or if they were obscured by clouds or snow at the moment of imaging. Any low quality data points were removed and the remaining data was averaged using the R package `raster` (Hijmans, 2019), generating an annual mean vegetation score for each spatial point. Temperature and precipitation data were downloaded from the WorldClim database.

We divided South America with a hexagonal grid with centres 5000 m apart using the R package `dggridR` (Barnes, 2018). Using a discrete hexagonal grid gives equally spaced points on the globe, making it preferable to latitude/longitude based gridding. We extracted the NDVI, mean temperature, minimum temperature, annual precipitation, and maximum precipitation for each grid hexagon, sampling at the center point of the hexagon. We selected NDVI in order to test the relationship between IMI and vegetation which was the primary aim of the study. We selected the additional variables based upon which of the bioclim variables were the most ecologically limiting to the sample. Ecologically limiting factors are those which act to constrict species occurrence, and the most accurate reconstructions are created when they are used to model the species relationship with the environment (Oksanen et al., 2019). Although this study is not a reconstruction of paleoenvironment, the same methodologies are applied to model the relationships between trait and environment.

Minimum temperature and precipitation in the wettest month have been previously documented as commonly ecologically limiting factors, due to their relationship with net primary productivity (Oksanen et al., 2019; Žliobaitė et al., 2016). However, we conducted our own preliminary study to determine which factors had the greatest constricting affect on our sample species distribution. We constructed a MaxEnt model of the sample to enable us to select the variables with the most power to model the distribution of the sample species. This model was produced using occurrence records from GBif and ecological data from the Worldclim2 database (Fick and Hijmans, 2017). We ran three MaxEnt models with three combinations of variables. From these models we found that maximum temperature had a negligible contribution to the model, so we excluded it from the analyses. We further found the precipitation in the driest month had 0.0% contribution to the model so it was discarded. The final model we constructed included minimum temperature, mean annual temperature, precipitation in the wettest month and annual precipitation; and had the greatest predictive strength. Hence we selected these variables for our main analysis.

Species occurrence data were downloaded from the IUCN redlist (www.iucnredlist.org/). By overlaying species occurrences with the hexagonal spatial grid, we extracted the list of species present in each hexagon. Across the whole of continental South America, these grid spaces each contained a number of primate species ranging from zero to eleven. In order to retain sufficient data for building predictive models, we excluded regions with fewer than 5 species. We then calculated mean and standard deviation of IMI for the remaining cells. We used linear regressions to model the relationship between IMI and each of the environmental measures. We also assessed the strength of phylogenetic signal in IMI under a recent primate phylogenetic hypothesis (Sehner et al., 2018; Püschel et al., 2017; Aristide et al., 2015). Phylogenetic signal was estimated using Pagel’s lambda with the function `phylosig` in the R package `phytools` (Revell, 2012) and phylogenetic data data downloaded from VertLife (a maximum clade credibility tree derived from a random sample of 500 trees, Upham et al. (2019); http://vertlife.org/). We further interrogated the evolution of limb proportions in South American primates by calculating the relationship between IMI and body size using linear regression and phylogenetic linear regression.

## Results

There is a significant relationship between mean IMI and each environmental variable (Fig. 2, $p$<0.001), supporting the hypothesis that locomotor morphology (IMI) can be used to predict niche occupation. However, the goodness of fit between IMI and each environmental variable is extremely low (Fig. 2, summarised below). There is a stronger relationship between body size and IMI: $R^2 = 0.870$, $p$<0.001. The fit of this model is improved further by performing separate regressions for each family (Fig. 3).

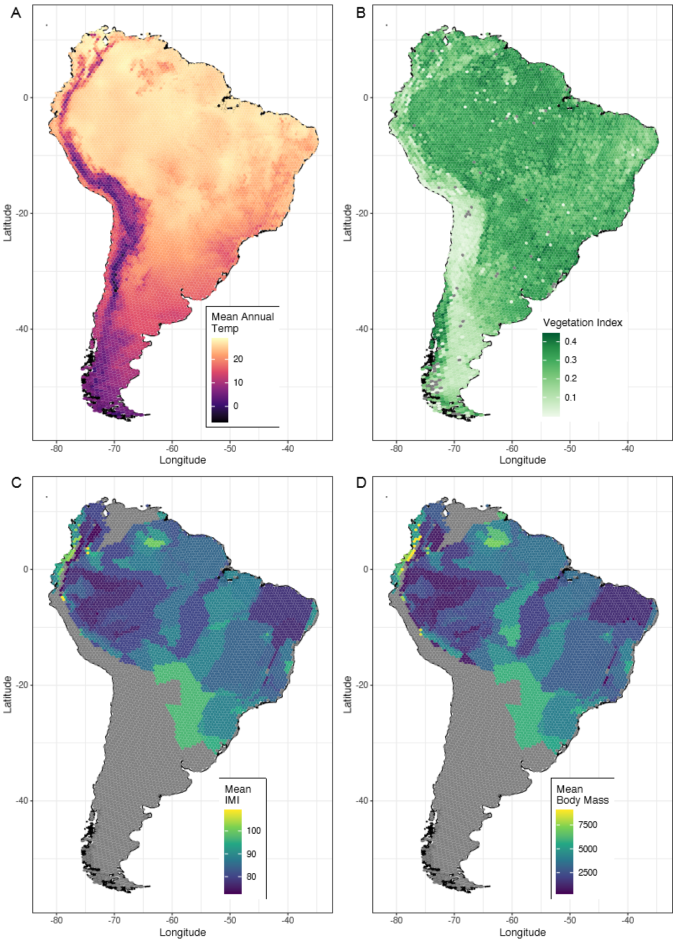

**Figure 1** – Maps of ecological and morphological variables partitioned on a 5000 m hexagonal grid. Mean annual temperature (A) was derived from the WorldClim database and mean vegetation index (B) was calculated from USGS eMODIS data. Mean intermembral index (C) was calculated from linear measurements of forelimb and hind limb measurements and mean body mass (D) was calculated from published species averages.

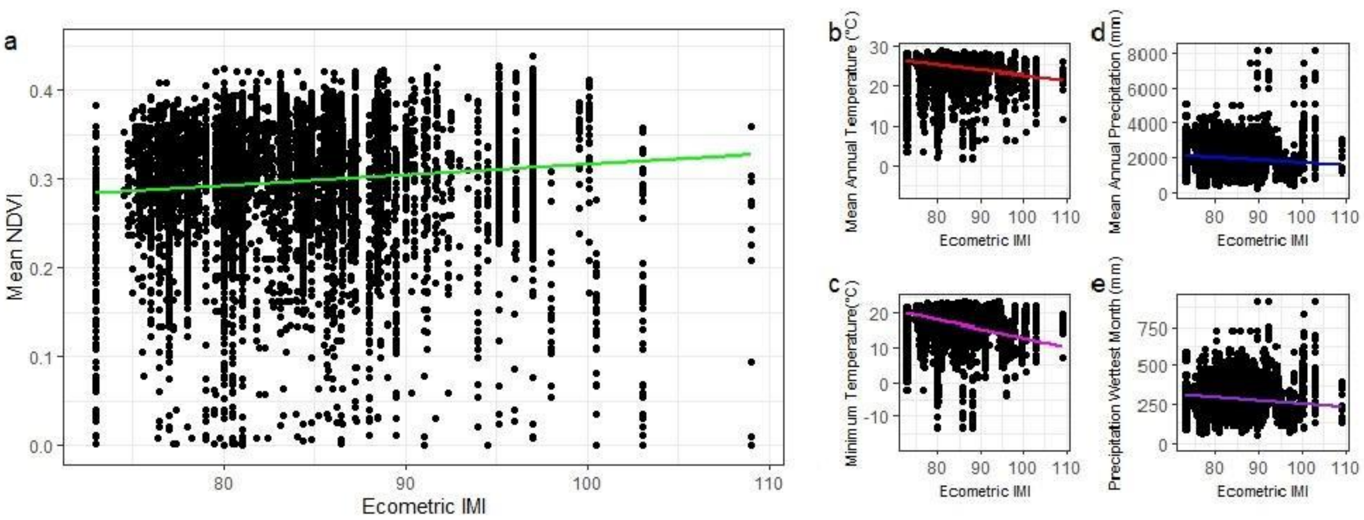

**Figure 2** – The relationship between ecometric intermembral index and each ecological variable: Mean vegetation index (A), mean annual temperature (B), minimum annual temperature (C), mean annual precipitation (D), and precipitation in the wettest month (E).

### NDVI

There is a significant relationship between NDVI and IMI (Figure 2a, $p$<2.2e-16). However, the goodness of fit is very low, with only 1.6% ($R^2$ = 0.016) of variance in NDVI explained by variation in IMI.

### Temperature

There is a significant relationship between IMI, and both mean annual temperature and minimum annual temperature (Figure 2b, $p$<2.2e-16). The goodness of fit remains very low for mean annual temperature, with $R^2$ = 0.018. However, IMI had a stronger fit with minimum annual temperature with $R^2$ = 0.11 (11% of variance explained)

### Precipitation

Again, the relationship between IMI and both precipitation variables (mean annual precipitation and precipitation in the wettest month) is statistically significant (Fig 2d, $p$<2.2e-16). As with temperature, the annual precipitation showed a weak correlation with IMI, $R^2$ = 0.006. Conversely, the precipitation in the wettest month showed the strongest correlation of any variable, with $R^2$ = 0.20. This means that in both scenarios, given that all of the sampled individuals tested negative in the ELISA and qPCR assay, the probability that the examined population is negative for exposure to SQPV is higher than 99.9%.

### Phylogeny and Allometry

Intermembral index exhibits high phylogenetic signal (l = 0.95), reinforcing the strong influence of shared ancestry on limb proportions. Allometry also has a significant effect on IMI as estimated by linear regression (adjusted $R^2$ = 0.69, $p$=1.2 x 10-5) and phylogenetically informed linear regression (adjusted $R^2$: 0.26, $p$=0.9 x 10-6).

## Discussion

In South American primate communities, intermembral index is not a good predictor of vegetation, temperature, or rainfall. Rather, IMI is strongly correlated with body size and phylogeny. This supports the hypothesis that the early diversification of New World monkey's into locomotory niches was determined by body size and has been followed by a period of evolutionary stasis (Aristide et al., 2015). The significant but weak relationship between IMI and all ecological variables measured is consistent with the environment exerting weak selective pressure on limb proportions. Species which inhabit sparse tree cover need to leap more often, resulting in longer hindlimbs than forelimbs (Martin, 1990; Jungers, 1985), which produces a low IMI value. Primates living in areas with dense tree cover will be able to walk on all fours between branches, reducing the risk of injury by falling (Martin, 1990; Jungers, 1985) . Having hindlimbs and forelimbs of similar length will make for efficient quadrupedal locomotion and gives an IMI value of close to 100. However, our analysis shows it is a species' body size, rather than their environment which exhibits the strongest relationship with IMI. This relationship is as a result of the biomechanical demands imposed by high body mass. The bodyweight of a species determines and limits how the animal can move (Schaffler et al., 1985). Therefore, the limbs must primarily be adapted to allow manipulation of the species mass through the environment. Secondarily adapting to maximise efficiency in moving through the habitat. As such, the structure of primates' forelimbs and hindlimbs reflect their relative use in propulsion and weight bearing (Schaffler et al., 1985).

Two ecological variables exhibit a moderately good fit with IMI: minimum annual temperature and precipitation in the wettest month. This pattern is of interest as these variables are most limiting to net primary productivity (NPP) (Oksanen et al., 2019). The strongest measured correlation was with precipitation in the wettest month. This may

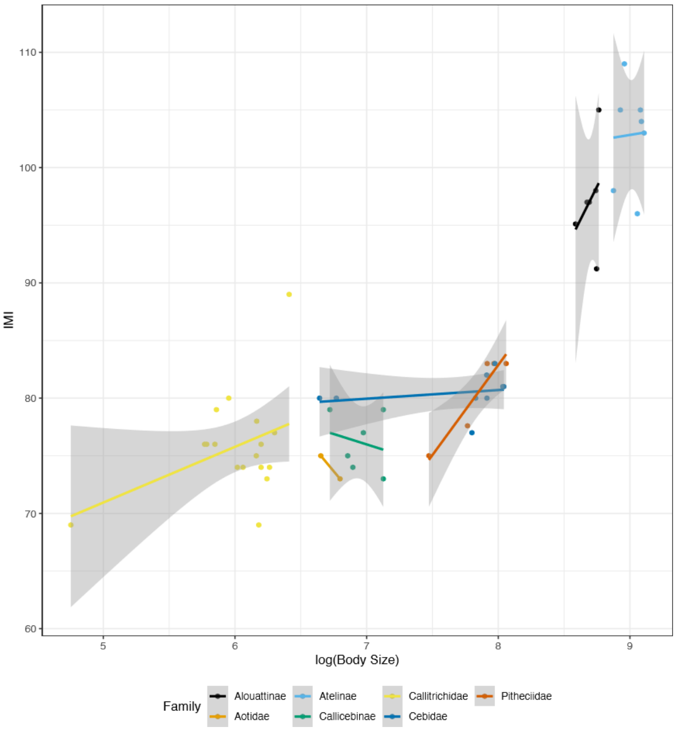

**Figure 3** – Relationship between Intermembral index (IMI) and body size. The linear regression by family is given as the line of best fit.

be due to the strong relationship between NPP in the tropics and precipitation (Oksanen et al., 2019; Liu et al., 2012). The stronger relationship of IMI with minimum temperature and precipitation in the wettest month, over the mean variables, suggest that limb ratios could represent a 'fallback adaptation' for low productivity seasons. Fallback adaptations are traits that are selected for performance at the limits of the species' climatic tolerance, the ecological 'worst case scenario', instead of their ideal to enable survival of harsh times (Ungar et al., 2018). Primate teeth have similarly been described as possessing fallback adaptations as they have been shown to be adapted for non-preferred foods (Ungar et al., 2018; Robinson and Wilson, 1998). This has implications for both primate conservation specifically and conservation planning as a wider field. While the evidence in this study is too little to conclude on the absence or presence of a 'fallback adaptation' beyond the documented dental examples; it identifies an exciting avenue for further research. The observation of greater model strength at climate extremes supports previous paleontological studies which found models could better predict climatic limits than mean values (Oksanen et al., 2019; Žliobaitė et al., 2016). If this greater correlation at climatic limits, than at means, is replicated in other species samples, this could impact greatly on models to predict species response to climate change. In addition to changing understanding of how species adapt to survive in non-ideal environments, and the potential role this has in speciation events.

It is crucial to understand the evolutionary history of New World monkeys in order to contextualise the risk anthropogenic change to their environment poses. Species will need to shift their ranges at a rate of 0.42 kmyr$^{-1}$ (global mean, Loarie et al. (2009) to remain in their ideal landscape. Ideally, all species would be able to shift with their climate range, while humans work to limit future change. In practice many species do not have the capacity to migrate as their suitable habitat shifts. New World monkeys are one such species, with 80% of Amazonian primates identified as not having the ability to disperse with their shifting habitat. Due either to fragmentation of migratory routes by human action or poor dispersal capacity due to canopy dependence (Sales et al., 2019).

As such it is unlikely that many New World monkey species will be able to migrate with their habitat under climate change. Raising immediate concern as to whether these species will be able to adapt to survive the pressures created by human actions. To assess this it is necessary to understand the rate of change in the habitat, the degree of plasticity inter- and intra- generational (Ezard et al., 2014) and the 'evolutionary space' available to the species. This research identified that New World monkeys still have 'evolutionary space' to adapt their locomotor strategy under climate change. Whether the rate of environmental change and plasticity are suited to facilitate this remains to be assessed.

A strong fit between NDVI and IMI would have indicated that New World monkeys are ecological specialists, exploiting particular arboreal substrates. It is known that ecological specialists are at greater risk of extinction under anthropogenic change (Sagot and Chaverii, 2015). Ecological specialists are particularly vulnerable due to their inability to exploit alternative resources when their ideal is lost. The weak fit identified in this research shows that New World monkeys remain generalised in their locomotion strategy, decreasing their extinction risk. However, their survival is still contingent on migration corridors and the introduction of protection in these areas (Sales et al., 2019).

These findings add to a growing body of evidence that the high locomotor variation in primates has not resulted in corresponding diversity in the postcranial skeleton. Intermembral index is an established proxy for primate locomotor strategy used by primatologists to study both extinct and extant specimens (Martin, 1990; Fleagle et al., 2013; Granatosky, 2018). However, more recent phylogenetic comparative analyses of the clade-level relationship between ecology and IMI (rather than community level as in this study) found no relationship between IMI and locomotor diversity within primates (Granatosky, 2018). This indicates that IMI does not accurately represent all the locomotor strategies a particular primate may adopt. Primate locomotor repertoires thus seem to reflect the principle of 'many-to-one mapping' in which a single phenotype can produce a wide range of behaviour, performance, and fitness due to differences in neuromuscular control (Wainwright et al., 2005). This is a possible limiting factor to this study, as IMI not representing all the locomotor strategies of the sample species may have reduced the model fit.

### Avenues for Further Research

One avenue for further research is to use comparative data from Malagasy lemurs to test if the relatively generalised locomotor strategies in New World monkeys are due to limited selection on their locomotion. The lemuriform clade offers interesting paleoecological and evolutionary parallels to the New World monkeys having also evolved in geographic isolation from other primates. Unlike the neotropical primates which have an estimated predation rate of 6.7% (Hart, 2002); Malagasy primates experience the highest predation risk of any of the four major ecogeographical primate groups. The locomotion of prey species is often the most important aspect of their predator evasion strategies (Whitford et al., 2019; Domenici et al., 2007). Malagasy primates will have had to evolve far more effective predator evasion tactics than primates inhabiting the neotropics in order to survive. Repeating this study using a comparative sample of Malagasy primates, could support or discredit our proposed explanation of the weak fit between New World monkey IMI and habitat as being due to limited selective pressure. Depending on whether a better fit was found between Malagasy primate IMI and ecology.

## Conclusion

This study represents a preliminary ecometric analysis of South American non-human primates. Analysing the functional relationship between New World monkey's locomotor strategies and their environment. For the species sampled, intermembral index (a locomotion proxy) and the ecology of the habitat were in a significant but weak relationship. Rather, limb proportions are strongly influenced by body size and shared ancestry. This result reveals several avenues for further research into this group of primates.

New World monkeys are a charismatic group of species under significant pressure from anthropogenic climate change and habitat loss. This research into their functional relationships is important not only to improve scientific understanding of their evolutionary pathways but to aid their protection. Comparative research could enrich understanding of the pressures which shape the divergence of a lineage into different locomotor strategies. Meanwhile, knowledge of the weak relationship between New World monkeys' intermembral indices and their habitat, can aid in ensuring suitable migration pathways are available to species as they face habitat loss. This would be greatly supported by analysis of New World monkey's fitness landscape and distance from their selective optima, which would improve modelling of these species' adaptive capacities under various projected scenarios of anthropogenic change.

Prevention of further habitat fragmentation and protection of New World monkey's migratory pathways is of concern. Locomotion is at the core of this issue, as a determinant of whether species have the physical and evolutionary space to move with their niche, as their range shifts. As the pressure of human actions continue to increase all conservation disciplines must act collectively to mitigate impacts on non-human life. Research, such as this study, which models the link between communities and the environment will inform conservation choices presently and into the future.

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## Supplemental information

Additional Supplemental Information may be found in the online version of this article:

**Table S1** Intermembral index (IMI) and body size for all species included in the study is listed. Body size is listed as the mean of all values of body size found for that species. Where more than one specimen was available for measurement, IMI is taken as the average of values.

**Table S2** The long bone measurements of all species collected from the Natural History Museum (London) are shown, with the Intermembral Index (IMI) calculated from them. Species are listed under the name being used in this study, with the specimen number and name used in the collection listed alongside. Bone lengths listed are the mean of values obtained from measurements of the specimen.

### Online data accessibility

All R code used for these analyses is archived at https://github.com/rnfelice/Primate_Ecometrics