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Factors influencing terrestriality in primates of the Americas and Madagascar

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Among mammals, the order Primates is exceptional in having a high taxonomic richness in which the taxa are arboreal, semiterrestrial, or terrestrial. Although habitual terrestriality is pervasive among the apes and African and Asian monkeys (catarrhines), it is largely absent among monkeys of the Americas (platyrrhines), as well as galagos, lemurs, and lorises (strepsirrhines), which are mostly arboreal. Numerous ecological drivers and species-specific factors are suggested to set the conditions for an evolutionary shift from arboreality to terrestriality, and current environmental conditions may provide analogous scenarios to those transitional periods. Therefore, we investigated predominantly arboreal, diurnal primate genera from the Americas and Madagascar that lack fully terrestrial taxa, to determine whether ecological drivers (habitat canopy cover, predation risk, maximum temperature, precipitation, primate species richness, human population density, and distance to roads) or species-specific traits (body mass, group size, and degree of frugivory) associate with increased terrestriality. We collated 150,961 observation hours across 2,227 months from 47 species at 20 sites in Madagascar and 48 sites in the Americas. Multiple factors were associated with ground use in these otherwise arboreal species, including increased temperature, a decrease in canopy cover, a dietary shift away from frugivory, and larger group size. These factors mostly explain intraspecific differences in terrestriality. As humanity modifies habitats and causes climate change, our results suggest that species already inhabiting hot, sparsely canopied sites, and exhibiting more generalized diets, are more likely to shift toward greater ground use.

primate communities | primate evolution | evolutionary transitions | niche shift | climate change

Eutherian mammal radiations are characterized by multiple evolutionary transitions between terrestrial, arboreal, fossorial, and aquatic lifestyles (1, 2). In primates, arboreality is hypothesized to be the ancestral condition (2–5). The evolutionary shift in some primate lineages to terrestrial niches is associated with various morphological/skeletal adaptations (6–10). Terrestriality is the prevalent strategy among some lineages of Catarrhini primates (i.e., African and Asian monkeys and great apes) (9, 11). Conversely, adaptations for predominantly terrestrial lifestyles are notably absent among living Platyrrhini of the Americas and Strepsirrhini of Africa (including Madagascar) and Asia (7, 12–14). However, some of these arboreal, diurnal primates periodically use the ground (15–21).

The evolutionary transition from arboreality to terrestriality is complex and carries debated costs and benefits (22, 23), of which three main areas are discussed. First,

Significance

Primates from the Americas and Madagascar are predominantly arboreal but occasionally descend to the ground. This increased ground use was associated with multiple ecological drivers, including increased temperature and a decrease in canopy cover, as well as species-specific traits, including a dietary shift away from fruits and larger group size. As anthropogenic impacts to habitats and climate worsen, our results suggest that diurnal species already inhabiting hot, sparsely canopied sites, and exhibiting more generalized diets, are more likely to shift toward greater ground use.

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descending to the ground may come at the cost of greater predation risk (24, 25). Yet, it is unclear whether arboreal or terrestrial lifestyles are characterized by greater predation risks (22, 23, 26–28). Regardless, ground use by arboreal primates exposes them to novel predators and predation patterns. Recent natural and anthropogenically driven ecological changes, however, negatively impact native carnivore occupancy (29, 30), and may reduce terrestrial predation risk, thus facilitating ground use in primates (17, 20, 31–33). It should be noted, however, that native carnivores are often supplanted by nonnative carnivores, including dogs, which can have a negative impact on primate populations (29, 34, 35). Second, species occurring in naturally open canopy habitats have been shown to use the ground frequently (36). To such a degree, environmental changes and increasing anthropogenic encroachment on tropical forests may act as catalysts for species to adopt terrestrial habits as canopy cover becomes patchy and forest fragments provide fewer or lower quality resources. As a result, species may descend to the ground to cross open areas more frequently to fulfill their energetic requirements, access reproductive opportunities, or to disperse (17, 32, 37, 38). Therefore, plasticity in use of additional ecological niches (e.g., terrestrial stratum) may enhance resilience to disturbance and persistence in some fragmented landscapes (39–41). Third, extreme temperatures limit species' biological functions (42, 43). As the understory and terrestrial environments are cooler than the upper canopy (43, 44), intense seasonal heat in previously dense tropical forest environments may drive arboreal species to seek thermoregulatory relief on the ground (45, 46). Arboreal primates during hot periods regularly descend to the ground to access terrestrial water sources for drinking or immersive cooling (18, 38, 47–51), and this behavior may become increasingly common given the cascading impacts of climate change (e.g., extreme heatwaves and droughts) (52, 53).

Primate community structure may also play an important role leading to terrestriality. Typically, sympatric species maintain separate niches to reduce ecological competition (54, 55). Therefore, in sites with high primate species richness (i.e., number of species) and greater potential for interspecific competition, species that can expand into terrestrial niches may experience reduced competition. As sympatric competitors, including other primate species, are potentially crowded into smaller ranges due to habitat losses, interspecific competition may increase until a new state is reached (56).

Species-specific factors have also been suggested to facilitate niche transition. Limited resource availability in the canopy may lead to shifts in foraging strategies (57), including increased terrestriality (11, 16, 38). For example, arboreal species reliant on seasonal resources may be more inclined to expand their dietary niche to include ground-based resources during periods of food scarcity (33). Furthermore, fully or semiterrestrial primates tend to be larger than strictly arboreal primates and tend to live in larger groups (22, 58, 59). Both characteristics are likely adaptations to high predation pressure and resource availability (28, 59–62) and may have facilitated the shift to terrestriality. Additionally, quadrupedal locomotion along the forest canopy, which mainly includes largely horizontal substrates, may have selected for hind- and forelimbs of similar length (7). This is in contrast to species using vertical clinging and leaping (VCL) locomotion from vertical substrates, which is associated with much longer hindlimbs (7). Species in the former category are predicted from a biomechanical perspective to have more effective cursorial quadrupedalism in a terrestrial environment (8, 63). Such species-specific factors may have facilitated the evolutionary transition of some primates to terrestrial lifestyles (9, 11, 64).

We focus on diurnal primates of the Americas and Madagascar to explore anthropogenic and ecological factors, and species-specific traits that are associated with greater use of the ground in two independent radiations. We did not include monkeys and apes from Africa and Asia as many of these species regularly exhibit semiterrestrial and terrestrial lifestyles (9, 11), and thus they experienced their niche transition presumably millions of years ago. Specifically, we are not interested in testing adaptations to terrestriality, but rather in the ecological, anatomical, and behavioral traits that make terrestriality a possible option for an arboreal primate. Regarding ecological and anthropogenic factors, we predict that terrestriality will be greater in species at sites: 1) where fewer native terrestrial predators pose a risk; 2) with more open, degraded, or fragmented forest areas, (i.e., less canopy cover); 3) with higher maximum temperatures favoring behavioral thermoregulation; 4) with high primate species richness; and 5) in greater distance from both roads and areas of higher human population densities (Fig. 1). Considering species-specific traits that may promote ground use, we predict that terrestriality will be greater in species: 1) that rely less on a diet of fruit as folivores tend to have gut adaptations more suitable for terrestrial resources; 2) with larger bodies; 3) that form larger groups; and 4) that exhibit anatomical adaptations for arboreal quadrupedalism (Fig. 1).

Results

The 47 arboreal diurnal primate species we studied spent little time on the ground ($2.5 \pm 0.1\%$ of the activity budget, monthly mean \pm SE; $n = 2,227$ mo), and for over half of the species (61.7%) terrestrial behavior comprised less than 1% of their total monthly activity. Lemurs spent $4.8 \pm 0.3\%$ (monthly mean \pm SE; $n = 1,002$ mo) of their time on the ground, whereas platyrrhine monkeys spent $2.4 \pm 0.2\%$ (monthly mean \pm SE; $n = 1,225$ mo) of their time on the ground. Lemurs were on average more terrestrial than platyrrhine monkeys (Table 1 and *SI Appendix, Table S2*).

In the complete model, which accounts for both intra- and interspecific variability, the most important ecological pressure positively associated with terrestriality was maximum temperature, while habitat canopy cover was negatively associated with time spent on the ground (*SI Appendix, Fig. S8 and Table S2*). Considering anthropogenic factors, distance to roads was positively associated with ground use (*SI Appendix, Fig. S8 and Table S2*). For species-specific factors, a species' degree of frugivory was negatively associated with terrestriality, whereas larger group size was positively associated with terrestriality (*SI Appendix, Fig. S8 and Table S2*). Furthermore, posthabitation time was negatively associated with ground use, meaning that species studied across a greater number of months were less likely to exhibit terrestriality (*SI Appendix, Fig. S8 and Table S2*).

For the within-species model, which evaluates the variability among conspecific populations (Table 1 and *SI Appendix, Fig. S9*), multiple ecological pressures influenced primate ground use. Similar to the complete model, maximum temperature and distance to roads were positively associated with terrestriality, while habitat canopy cover was negatively associated with terrestriality. Unlike the complete model, however, terrestriality decreased with increasing terrestrial predation risk, and increased with primate species richness. We also found a positive interaction between primate-rich habitats and habitat canopy cover, indicating an amplified effect of canopy cover on terrestriality in areas with higher primate species richness. Like the complete model, the three species-specific factors related

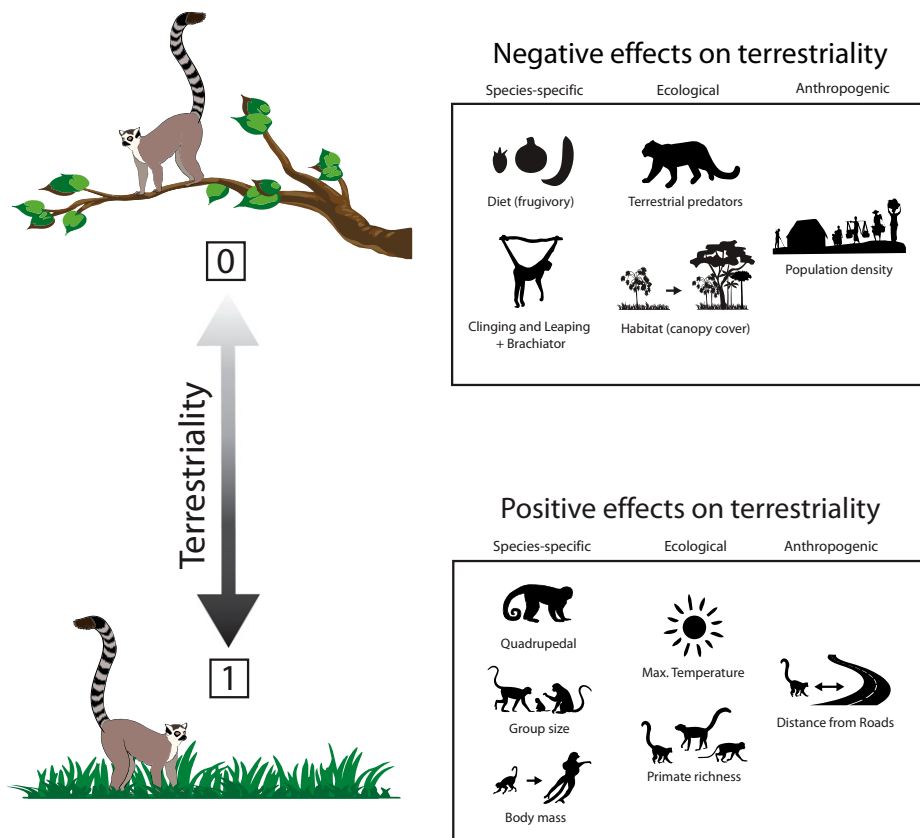


Fig. 1. Hypothesized relationships between species-specific traits, and ecological and anthropogenic factors and ground use by monkeys in the Americas and lemurs in Madagascar, and not any specific transition in one species or another. For species-specific traits, taxa exhibiting quadrupedal locomotion (inferred from their intermembral index (IMI)), have a larger group size, and have greater body mass are hypothesized to use the ground more. Taxa with diets consisting of more fruit, and exhibiting vertical clinging and leaping (VCL) and brachiator locomotion (inferred from their IMI) are hypothesized to spend less time on the ground. Regarding ecological factors, taxa inhabiting sites with higher maximum temperatures and greater primate species richness are hypothesized to use the ground more. Taxa inhabiting sites with a greater number of terrestrial predators and greater continuous canopy coverage are hypothesized to spend less time on the ground. Regarding anthropogenic factors, taxa inhabiting sites that are greater distances from roads are hypothesized to use the ground more, whereas taxa inhabiting sites that are closer to denser human populations are hypothesized to spend less time on the ground.

to terrestriality were degree of frugivory (negative), group size (positive), and posthabitation (negative).

In the between-species model, which measures variability across species (Table 1 and *SI Appendix, Fig. S10*), none of the factors were strongly related to terrestriality. The only ecological factor that exhibited a clear association was primate species richness (negative). Species in habitats with denser canopy cover and with fewer sympatric primate species spent a greater proportion of time on the ground. Terrestriality was positively related with body mass and negatively with group size, indicating smaller species and larger groups, respectively, spending more time on the ground.

Discussion

We found more terrestrial activity in hotter environments with more mammalian predators, larger groups, and taxa with less frugivorous diets. However, the degree of terrestriality varies both within and between species, and when this variation is analyzed separately it reveals a more complex picture. Our within-species comparison shows that groups living in more open habitats, with more potential predators, and richer primate communities exhibit greater degrees of terrestriality. Species at more remote sites (i.e., greater distances from roads) also spent more time on the ground. By comparison, our between-species analysis reveals that species that descend more often to the ground tend to be smaller and live in larger groups. Contrary to previous single-species studies that showed an observer

effect (15, 39, 65; but see ref. 33), shorter study duration (the number of posthabitation months) was strongly associated with ground use.

Ecological Correlates to Terrestriality. Maximum temperature showed a positive relationship with the time spent on the ground in both the complete and intraspecific models, while our proxy for seasonality (i.e., monthly precipitation) was not influential within any of the models. Gradual and rapid temperature increases correlate with behavioral shifts (compare refs. 66 and 67). A possible explanation is that lemurs and platyrrhine monkeys increase their use of the ground as an adaptive thermoregulation strategy (68, 69). For example, we found that primate species like *Eulemur fulvus* and *Eulemur rufifrons* spent considerably more time on the ground in relatively hotter tropical deciduous forest habitats of Madagascar compared to their conspecifics inhabiting the cooler humid forest habitats, likely to access terrestrial water sources (50). This finding supports the idea that shifting between arboreality and terrestriality is an effective thermoregulatory response, with important implications considering current global warming trends (52, 70, 71).

Canopy cover has long been considered a factor in many evolutionary shifts (72). However, the degree to which this may result in a more terrestrial primate lifestyle is unclear (11). Denser canopy cover was associated with spending less time on the ground within species, but was not associated with ground use in the between-species model. The former is in line with our expectation that terrestrial activity tends to be higher in

Table 1. Summary results of the within-species model (variability within species) and the between-species model (variability between species) testing the influence of potential ecological drivers and species-specific factors on monthly terrestrial activity by arboreal primates from the Americas and Madagascar

Model	Estimate	Error	CI	PD
Within-species model				
Intercept	-4.33	1.35	-6.94 to -1.46	100%
Predation risk	0.29	0.14	0.01 to 0.57	98%
Habitat (canopy cover)	-0.35	0.12	-0.57 to -0.11	100%
Temperature maximum	0.16	0.04	0.08 to 0.24	100%
Precipitation	0.01	0.03	-0.06 to 0.07	58%
Primate species richness	0.28	0.15	-0.01 to 0.56	97%
Habitat × Primate species richness	0.17	0.08	0.01 to 0.33	98%
Diet (frugivory)	-0.17	0.04	-0.25 to -0.10	100%
Group size	0.10	0.05	0.00 to 0.19	98%
Posthabitation	-0.07	0.04	-0.15 to 0.00	97%
Human population density	-0.04	0.15	-0.33 to 0.25	60%
Distance to road	0.23	0.12	0.00 to 0.46	97%
Between-species model				
Intercept	-3.84	2.39	-8.74 to 0.79	95%
Region (Americas)	-1.29	2.74	-6.73 to 4.25	70%
Predation risk	-0.02	0.46	-0.94 to 0.84	52%
Habitat (canopy cover)	0.26	0.38	-0.48 to 1.00	76%
Temperature maximum	0.17	0.35	-0.55 to 0.82	69%
Precipitation	0.45	0.40	-0.34 to 1.22	87%
Primate species richness	-0.25	0.18	-0.60 to 0.11	92%
Habitat × Primate species richness	-0.04	0.10	-0.24 to 0.15	67%
Diet (frugivory)	-0.22	0.25	-0.71 to 0.28	82%
Body mass	-0.43	0.34	-1.08 to 0.25	90%
Group size	0.41	0.27	-0.10 to 0.94	94%
IMI (quadrupedal)	0.24	1.30	-2.43 to 2.70	58%
IMI (VCL)	1.58	1.77	-1.99 to 5.02	82%
Human population density	-0.12	0.37	-0.84 to 0.61	62%
Distance to road	0.33	0.41	-0.48 to 1.12	79%

Estimate, mean of the posterior distribution; Error, SD of the posterior distribution; CI, 95% credible intervals; PD, probability of direction indicating the probability of a coefficient being different from zero. Coefficients with PD > 90% are considered strong evidence of directional effects and are highlighted in bold. IMI intercept is a categorical variable and corresponds to brachiator, whereas VCL and quadrupedalism are the estimated differences from the intercept.

habitats with sparser canopies, such as those disturbed by anthropogenic activities (19, 38). Arboreal species in more open habitats (i.e., sparser canopies) may need to descend to the ground to forage and drink (19, 34, 38, 73, 74), although their ability to do so may be guided by species-specific characteristics acting as a predisposition (i.e., behavioral and anatomical exaptations) (75, 76).

Primate species richness had contrasting results, with a negative effect on terrestriality in the interspecific model and positive effect in the intraspecific model. As all primates within the communities examined are arboreal, greater numbers of species at a site may lead to higher competition for canopy resources, including both food and space. Under specific circumstances, descending to a rarely exploited niche (the forest floor) may be critical for coping with periods of limited resources (77). The positive interaction effect between canopy cover and primate species richness in the intraspecific model supports our hypothesis. Essentially, the negative effect of canopy cover on terrestriality was weaker as sympatric taxa richness increased. In other words, when canopy cover increases, the decrease in terrestriality is less pronounced in habitats with high primate diversity where we would expect higher competition. However, it is possible that at sites where a species may have recently become locally extirpated, this loss may result in competitive release, allowing one or more of the remaining species to partially, or fully, exploit newly available resources (78–80). Compared to many mammal taxa, primates tend to

exhibit a high degree of behavioral flexibility (81, 82), and inter-individual variation may be the mechanism underlying niche expansion (83).

Predation pressure is difficult to quantify and evaluate. The number of potential predator species provides a proxy with which to measure this risk (84, 85), and some site-/species-focused studies have noted that relaxation of predation pressure led to more ground-based activity (20, 32, 39). Interestingly, terrestrial predator species richness was associated with more terrestrial activity in our within-species model. Although we were unable to account for predator population abundance or the potential ecological and co-occurrence factors affecting these taxa (86), it appears that anthropogenic factors may play a role. Human population density and distance to roads may be considered as general proxies for various aspects of human encroachment, including feral dogs (*Canis familiaris*), which are known to prey upon wildlife (34, 35, 73). Of the two anthropogenic factors, conspecifics were more terrestrial at sites farther from roads.

Species-Specific Factors as Potential Facilitators of Terrestriality.

Frugivory was associated with decreased ground use in both the complete and intraspecific models, supporting previous assertions that diet is a driving force of terrestriality (38, 87). This link may be associated with folivores or species with a broad dietary spectrum using the ground more often to forage on different preferred foods (17, 88), or because they have gastrointestinal

and dental adaptations allowing them to use terrestrial resources more efficiently (89). Despite the general reduced ground use by frugivores, periods of reduced fruit availability may lead facultative frugivores to search the ground for novel food resources to meet their seasonal nutritional needs (21, 90, 91). Many primates with broad dietary niches come to the ground to engage in geophagy and to access mineral licks (92, 93) and potentially fermented foods (94). However, given the supplementary nature of this feeding habit (95) that often involves short terrestrial travel, it has not been considered a key causative factor in any major shift in strata use. Primates may also descend to the ground to forage for arthropod prey (19, 21).

Group size had an effect in both the complete and within-species models. Large groups can facilitate terrestriality as they can potentially reduce predation risk. Folivores are in principle less constrained by group size compared to frugivores due to the less clumped spatiotemporal availability of preferred resources, although this is not always the case (96, 97). However, although it is conceivable that large groups foster terrestrial activity, it is also possible that groups that use the ground more often tend to form larger groups to reduce predation risk, leaving the causal relationship unclear. In both *Brachyteles hypoxanthus* in Caratinga (Brazil) and *Hapalemur meridionalis* in Mandena (Madagascar), it was the case that the largest group was considerably more terrestrial than smaller groups (17, 39).

Biomechanical (e.g., size-related and anatomical) challenges may impose various biological, ecological, and physiological constraints within both the arboreal and terrestrial strata (8). Such morphological factors could be species-specific consequences that evolve after, or in parallel with, the initial niche expansion into terrestrial activity. However, contrary to our hypothesis, we found a negative effect of body mass between species (i.e., smaller species showed increased terrestriality). Original hypotheses about the relationship between body size and terrestriality were proposed by Fleagle (7, 59) to explain the range of niche use in the entire Primate order, including the larger-bodied catarrhines. The primates included in this study, platyrrhines and lemuriformes, represent a more restricted range of body mass variation, and therefore it is possible that a different relationship between terrestriality and body mass is present for the entire order. We cannot evaluate the role that the relatively recent extinction of the larger and more terrestrial lemur species (98) may have had in releasing the competition for terrestrial resources with the extant smaller lemur species.

Although posthabitation months were used to control for a possible positive observer effect, our complete and within-species model showed that primates studied for shorter periods more strongly associated with ground use. Though this contrasts from some single-species studies (15, 39, 65), we believe our negative effect is more likely the result of the nonrandom distribution of study periods with respect to seasons, or the nonrandom distribution of species with respect to their average level of arboreality within our dataset.

Conclusions

We have shown that there are multiple factors that may lead arboreal primates to use the ground and that this transition is influenced by site-specific ecological pressures. Specifically, habitats with sparser canopies may be responsible for the evolutionary transition of nonhuman primates to terrestrial lifestyles (11, 19), whereas the more proximate causes of strata shift appear to be hotter environmental conditions (71) and dietary shifts away

from frugivory. Considering species-specific traits, larger groups and smaller body mass facilitated ground use.

Although significant climate changes in both the Americas (99) and Madagascar (100) likely facilitated faunal turnover and speciation, it is not clear why terrestriality did not evolve there to the same extent as it is seen in catarrhines. Fossil records are sparse and the real extent of niche diversification that occurred in lemurs and platyrrhines over their evolutionary history is far from being understood (7). Examining primate behavioral and ecological flexibility alongside current environmental conditions, however, provides insight into evolutionary transitional periods that resulted in shifts to novel ecological niches. As human activity drives climate change, degrades primate habitats, and shifts plant phenological patterns, primate populations are facing unprecedented challenges that threaten their persistence (52, 70, 101–104). We expect that an increased use of the ground strata by species inhabiting hot, sparsely canopied sites and that exhibit a more generalized diet can buffer species against extinction. Productive future lines of research that will further clarify factors driving the evolution of terrestriality include comparing behavioral repertoires in terrestrial versus arboreal environments, evaluating potential ecological and life history drivers of annual variation in terrestrial behaviors, and if habitat structure explains variation in population-level terrestriality. All nonhuman primates, however, will be faced with challenges created by anthropogenic changes and for species less inclined to terrestrial activity, fast and effective conservation strategies will need to be implemented to ensure their survival.

Materials and Methods

Coauthors contributed raw monthly behavioral ecology data from 47 primate taxa, specifically 15 lemur species representing two families (Lemuridae and Indridae), and 32 platyrrhine species representing 4 families (Atelidae, Callitrichidae, Cebidae, and Pitheciidae) (Dataset S1). This collated dataset includes 150,961 observation hours across 2,227 months from species at 68 research sites, specifically 20 sites in Madagascar and 48 sites throughout the Americas (Fig. 2 and SI Appendix, Table S1). Our dataset includes 16 primate species (specifically 10 lemur and 6 platyrrhine monkey species) for which we have data from multiple sites.

For each species, we provide monthly proportional data to account for different data-collection methods used in each study. Since nocturnal species are exposed to different ecological pressures compared to diurnal primates, we only focused on diurnal primates. Datasets included had a minimum of 12 h/mo to increase the chances that rare events, in our case terrestriality by arboreal species, would be recorded (105). We considered the monthly proportion of time spent terrestrially as our dependent variable.

Ecological Drivers. We extracted site- and time-specific climate and habitat values in Google Earth Engine (earthengine.google.com) using the spatial coordinates and the year and month of the observations (106). We extracted monthly maximum temperatures and monthly total precipitation from the *ERA5 Monthly Aggregates* dataset (107). The latter is used as a conservative proxy for seasonality (108), incorporating the rainfall variation at research sites for the months included in our dataset. We obtained the relative canopy cover using a circular buffer around the coordinates of each study site from the Landsat Tree Cover Continuous Fields dataset (109) (SI Appendix, Fig. S1). Specifically, the buffer area was equal to twice the size of each study species' reported mean home range area.

We estimated the number of potential terrestrial mammalian predators per species per site from the number of carnivore species per location using International Union for the Conservation of Nature (IUCN) range maps (110). For each species per location, we only considered predators with a mean body mass greater than or equal to one-quarter of the mean body mass of the focal primate. This ratio was based on the minimum predator-prey ratio observed in terrestrial mammals (appendix S1 in ref. 111). The body mass threshold is very

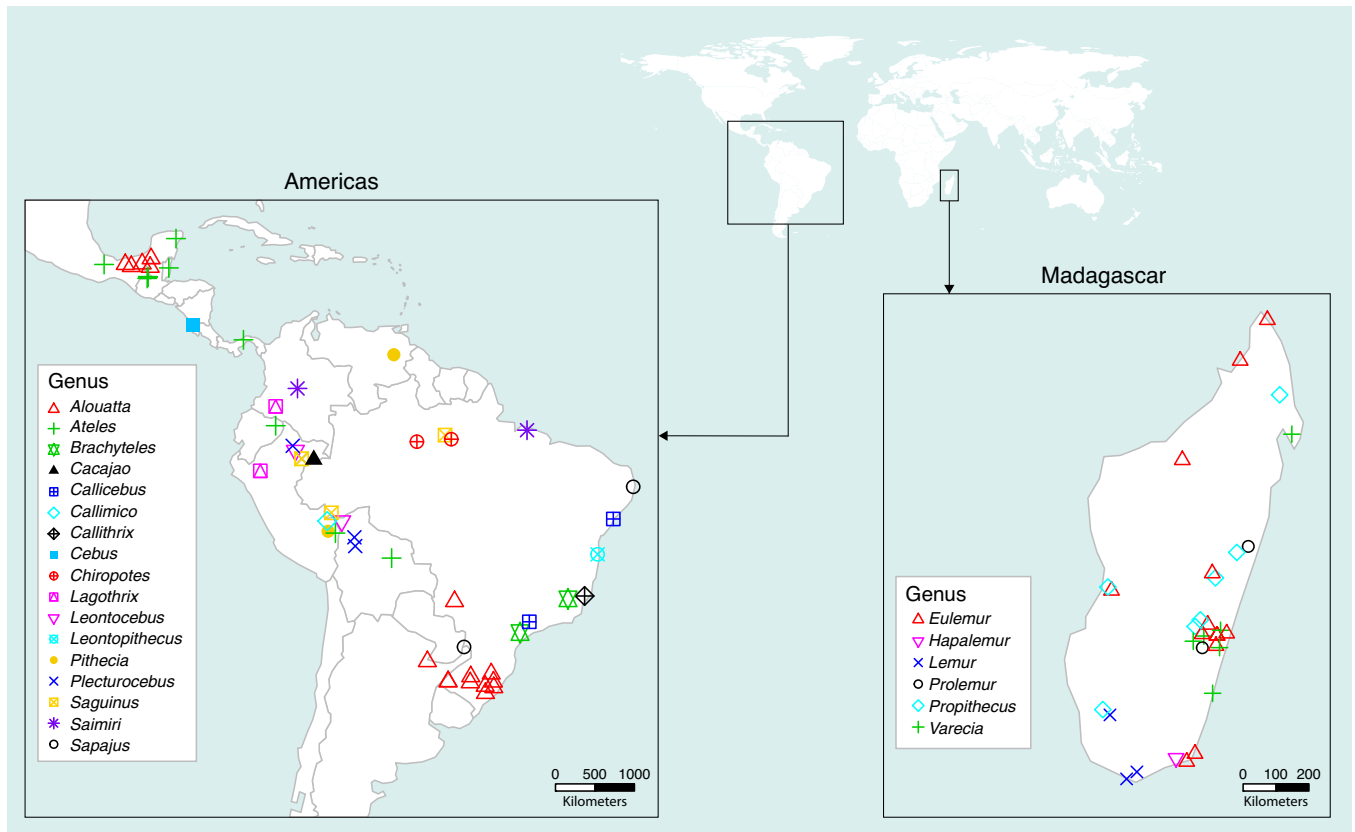


Fig. 2. Spatial distribution of primate genera included in our behavioral ecology dataset.

conservative and may lead to the inclusion of species that do not typically prey on adult primates; however, considering primates' slow life histories and the additive risks to juveniles/infants, smaller predators can potentially trigger a fear reaction (112, 113). This approach is also limited by the nature of IUCN range maps and the consideration of predator-prey body mass ratios, which likely overestimates the presence of predators as large predators may have been extirpated by local hunting and habitat loss. However, this approach allowed us to estimate the spatial gradients of predator species richness at this scale of analysis for all sites and species, thereby avoiding potential author or publication reporting biases (compare with ref. 114). Although primates may also be preyed upon by birds of prey, snakes, and other primates, carnivores are considered their main terrestrial predators (115, 116).

Using IUCN range maps (110), we also estimated the number of sympatric primate species per site: that is, species richness (*SI Appendix, Figs. S2 and S3*). Given the potential increased effect of interspecific competition in sites with less canopy cover (potentially more fragmented), we examined the interaction between these two factors.

Finally, we considered two proxies of anthropogenic disturbance: human population density and distance to roads. The former accounts for the presence of humans, whereas the latter is a proxy of inverse of remoteness (i.e., inverse of accessibility to humans). We obtained the human population density data from the Socioeconomic Data and Applications Center (<https://sedac.ciesin.columbia.edu/>). We used the Gridded Population of the World dataset, v4 (117) for 2000, 2005, 2010, 2015, and 2020 at 30 arc-second resolution (~1 km) (*SI Appendix, Figs. S4 and S5*). We matched the terrestriality data with the values of human population density using the closest layer in time. Road data for the countries of interest were extracted from the OpenStreetMap database (openstreetmap.org). From the vector files we only retained primary, secondary, and tertiary roads, motorways, trunks, all related "links," and residential roads. Instead, we excluded all unclassified roads, paths, footways, and similar. We then rasterized the vector layer at 1-km resolution and calculated the distance from the nearest road for the entire study area (*SI Appendix, Figs. S6 and S7*). All raster data processing was conducted in R v3.6.3 (118) using the "raster" package (119).

Species-Specific Factors. For each species' specific site, coauthors contributed the monthly proportion of time spent feeding on fruit, the mean body mass, and the mean group size measured in the field. In the absence of mean body mass, we used data from the All the World's Primates database (120). We inferred locomotion type via the Intermembral Index (IMI) (63), which is calculated as $(\text{length of humerus} + \text{length of radius}) / (\text{length of femur} + \text{length of tibia}) \times 100$. Quadrupedal primates typically have an IMI between 67 and 104; of the arboreal quadrupeds, those falling below the lower threshold typically exhibit VCL, and those above the upper threshold are typically categorized as exhibiting brachiation, but also suspensory locomotion (7, 8, 63). Given potential for error when collecting field measurements, and the relative stability of the IMI within genera, we assigned each species to a category based on the IMI averaged at the genus level.

Statistical Analyses. We tested our hypotheses by fitting a zero-inflated model with a β -family and logit link-function and using Bayesian inference. The use of a zero-inflation and β -family allowed accommodating for the highly skewed and zero-inflated distribution of terrestriality values bounded between 0 and 1. We added a group level to study site and one to species to control for multiple estimates in the same locations and multiple estimates per species, respectively. Considering climatic variation and its effect on resource phenology (108), we controlled for seasonality using monthly temperature and total precipitation at each site. We used study duration (i.e., the number of months posthabitation) to control for observer effect within the models. We controlled for phylogenetic effects by using a variance-covariance matrix derived from the phylogeny in Upham et al. (121). An additional observation level random effect was added to control for overdispersion. All fixed factors were scaled to a mean of 0 and SD of 1 to ensure comparability of the effect sizes, as well as improving numerical stability in their estimation. We used weakly informative priors using a normal distribution with an SD of 10 for the intercept, and an SD of 1.5 for all slope coefficients, thereby limiting the range to a plausible gradient of variation considering the logit link-function and scaled coefficients (122). All predictors were tested for multicollinearity prior to the modeling but none showed a correlation coefficient >0.7 , so all variables were retained in the final model (123).

The complete model accounted for both intra- and interspecific variability in terrestriality; thus, we ran two additional models to disentangle the variability within- and between-species. To assess whether the detected effects could also explain the different degrees of terrestriality among conspecific populations (within-species model), we included only anthropogenic and ecological drivers, as well as site-specific species' factors for which we had data (percent frugivory and group size). Prior to fitting this second model, we first subtracted the species' mean from each observation value (species mean deviation) (124). Then, we fitted a model including both ecological drivers and species-specific traits to estimate the variability across species (between-species model), from which we subtracted the species mean deviation from each observation value. For both the within- and between-species model, we rescaled the variable to a mean of 0 and SD of 1 prior to model fitting and used the same weakly informative priors used for the complete model.

We ran 6,000 iterations over 10 Markov chain Monte Carlo chains for each model, with a "burn in" period of 2,000 iterations per chain leading to a total of 40,000 usable posteriors. We also checked models for chain convergence and parameter identifiability. We summarized the posterior distributions of coefficient estimates using 95% credible intervals. We considered credible intervals that did not overlap with zero as strong evidence of directionality. We also reported the probability of direction, a threshold-independent measure of evidence that varies from 50 to 100% and that indicates the probability of a coefficient being different from zero (125). We fitted the models in R v3.6.3 (118) using the 'brms' package (126), for model fitting, 'bayestestR' (125) for Bayesian summary statistics, and 'ape' (127) and 'phytools' (128) for handling the phylogenetic data.

Data, Materials, and Software Availability. All statistical codes and data used in the analyses have been deposited in Figshare (<https://doi.org/10.6084/m9.figshare.19344992.v1>) (129). All other study data are included in the main text and supporting information.

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