PNAS
www.pnas.org

Main Manuscript for

Descending from the trees: Factors favoring transitions to terrestriality in arboreal primates

Timothy M. Eppley [a,b,1], Selwyn Hoeks [c], Colin A. Chapman [d,e,f,g], Jörg U. Ganzhorn [h], Katie Hall [i], Megan A. Owen [a], Dara B. Adams [j,k], Néstor Allgas [l], Katherine R. Amato [m], McAntonin Andriamahaihavana [n], John F. Aristizabal [o,p], Andrea L. Baden [q,r,s], Michela Balestri [t], Adrian A. Barnett [u,v], Júlio César Bicca-Marques [w], Mark Bowler [a,x,y], Sarah A. Boyle [z], Meredith Brown [aa], Damien Caillaud [bb], Cláudia Calegaro-Marques [cc], Christina J. Campbell [dd], Marco Campera [t], Fernando A. Campos [ee], Tatiane S. Cardoso [ff], Xyomara Carretero-Pinzón [gg], Jane Champion [aa], Óscar M. Chaves [hh], Chloe Chen-Kraus [ii], Ian C. Colquhoun [jj], Brittany Dean [aa], Colin Dubrueil [aa], Kelsey M. Ellis [kk], Elizabeth M. Erhart [ll], Kayley J. E. Evans [aa], Linda M. Fedigan [aa], Annika M. Felton [mm], Renata G. Ferreira [nn], Claudia Fichtel [oo], Manuel L. Fonseca [pp], Isadora P. Fontes [qq,rr], Vanessa B. Fortes [ss], Ivanyr Fumian [tt], Dean Gibson [a], Guilherme B. Guzzo [uu], Kayla S. Hartwell [aa,vv], Eckhard W. Heymann [oo], Renato R. Hilário [ww], Sheila M. Holmes [xx], Mitchell T. Irwin [yy], Steig E. Johnson [aa], Peter M. Kappeler [oo,zz], Elizabeth A. Kelley [ab], Tony King [ac,ad,ae], Christoph Knogge [af], Flávia Koch [oo], Martin M. Kowalewski [ag], Liselot R. Lange [ah,ai], M. Elise Lauterbur [aj,ak], Edward E. Louis, Jr. [al], Meredith C. Lutz [am], Jesús Martínez [an,ao], Amanda D. Melin [aa], Fabiano R. de Melo [ap,aq], Tsimisento H. Mihaminekena [ac,ar], Monica S. Mogilewsky [as], Leandro S. Moreira [tt,aq], Letícia A. Moura [aq,at], Carina B. Muhle [w], Mariana B. Nagy-Reis [au], Marilyn A. Norconk [av], Hugh Notman [aa,aw], M. Teague O'Mara [ax,ay,az], Julia Ostner [ba,bc], Erik R. Patel [bd], Mary S. M. Pavelka [aa], Braulio Pinacho-Guendulain [be,bf], Leila M. Porter [yy], Gilberto Pozo-Montuy [bg], Becky E. Raboy [bh], Vololona Rahalinarivo [bi], Njaratiana A. Raharinoro [n], Zafimahery Rakotomalala [n], Gabriel Ramos-Fernández [bj,bk], C. Delaïd Rasamisoa [a], Jonah Ratsimbazafy [ar], Maholy Ravaloharimanitra [ac], Josia Razafindramanana [bi], Tojotanjona P. Razanaparany [bl,n], Nicoletta Righini [bm], Nicola M. Robson [bn], Jonas da Rosa Gonçalves [bp], Justin Sanamo [bq], Nicole Santacruz [br], Hiroki Sato [bs], Michelle L. Sauther [bt], Clara J. Scarry [bu,bv], Juan Carlos Serio-Silva [bw], Sam Shanee [bx], Poliana G. A. de Souza Lins [by], Andrew C. Smith [bz], Sandra E. Smith Aguilar [ca], João Pedro Souza-Alves [cb,cd], Vanessa Katherinne Stavis [ce,cf], Kim J. E. Steffens [cg], Anita I. Stone [ch], Karen B. Strier [ci], Scott A. Suarez [cj], Maurício Talebi [ck,cl], Stacey R. Tecot [cm], M. Paula Tujague [cn,co,cp], Kim Valenta [cq], Sarie Van Belle [cr], Natalie Vasey [b,vv], Robert B. Wallace [an,cs,ao], Gilroy Welch [vv], Patricia C. Wright [ct,cu], Giuseppe Donati [t,2], Luca Santini [cv,cw,2]

[a] Conservation Science and Wildlife Health, San Diego Zoo Wildlife Alliance, Escondido, CA 92027
[b] Department of Anthropology, Portland State University, Portland, OR 97201
[c] Department of Environmental Science, Institute for Water and Wetland Research, Radboud University, 6500GL Nijmegen, The Netherlands
[d] Department of Anthropology, Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington D.C. 20037
[e] Wilson Center, 1300 Pennsylvania Avenue NW, Washington, D.C. 20004
[f] School of Life Sciences, University of KwaZulu-Natal, Scottsville, Pietermaritzburg, South Africa
[g] Shaanxi Key Laboratory for Animal Conservation, Northwest University, Xi'an 710069, China
[h] Department of Animal Ecology and Conservation, Institute of Zoology, Universität Hamburg, 20146 Hamburg, Germany
[i] Sedgwick County Zoo, Wichita, KS 67212
[j] Department of Anthropology, The Ohio State University, Columbus, OH 43210
[k] Department of Anthropology, Humboldt State University, Arcata, CA 95521
[l] Asociación Neotropical Primate Conservation Perú, Moyobamba, San Martin, Perú
[m] Department of Anthropology, Northwestern University, Evanston 60208

[n] Mention Zoologie et Biodiversité Animale, Faculté des Sciences, Université d'Antananarivo, 101 Antananarivo, Madagascar
[o] Departamento de Ciencias Químico Biológicas, Instituto de Ciencias Biomédicas, Universidad Autónoma de Ciudad Juárez, Ciudad Juárez, México
[p] Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, 111711, Colombia
[q] Department of Anthropology, Hunter College of City University of New York, NY 10065
[r] Department of Anthropology, The Graduate Center of City University of New York, NY 10016
[s] The New York Consortium in Evolutionary Primatology (NYCEP), New York, NY
[t] Department of Social Sciences, Oxford Brookes University, Oxford OX3 0BP, UK
[u] Centre for Research in Evolutionary and Environmental Anthropology, Roehampton University, London SW15 5PJ, UK
[v] Department of Zoology, Federal University of Pernambuco, Recife-PE, 50670-901, Brazil
[w] Laboratório de Primatologia, Escola de Ciências da Saúde e da Vida, Pontifícia Universidade Católica do Rio Grande do Sul, PUCRS, Porto Alegre-RS, 90619-900, Brazil
[x] Department of Engineering, Arts, Science and Technology, University of Suffolk, Ipswich IP4 1QJ, UK
[y] Suffolk Sustainability Institute, Ipswich IP4 1QJ, UK
[z] Department of Biology, Rhodes College, Memphis, TN 38112
[aa] Department of Anthropology & Archaeology, University of Calgary, Calgary, Alberta, T2N 1N4, Canada
[bb] Department of Anthropology, University of California, Davis, CA, 95616
[cc] Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre-RS, 90650-001, Brazil.
[dd] Department of Anthropology, California State University Northridge, Northridge, CA 91325
[ee] Department of Anthropology, University of Texas at San Antonio, San Antonio, TX 78249
[ff] Coordenação de Ciências da Terra e Ecologia, Museu Paraense Emílio Goeldi, Belém-PA, 66077-830, Brazil
[gg] Proyecto Zocay, Colombia
[hh] Escuela de Biología, Universidad de Costa Rica, San José, 11501-2060, Costa Rica

[ii] Department of Anthropology, Yale University, New Haven, CT 06511
[jj] Department of Anthropology and The Centre for Environment & Sustainability, University of Western Ontario, London, Ontario, N6A 3K7, Canada
[kk] Department of Anthropology, Miami University, Oxford, OH 45056
[ll] Department of Anthropology, Texas State University, San Marcos, TX 78666
[mm] Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences (SLU), Alnarp, Sweden
[nn] Pós-Graduação em Psicobiologia, Universidade Federal do Rio Grande do Norte, Natal-RN, 59078-970, Brazil
[oo] Behavioral Ecology and Sociobiology Unit, German Primate Center, 37077 Göttingen, Germany
[pp] Laboratorio de Ecología de Bosques Tropicales y Primatología, Departamento de Ciencias Biológicas, Universidad de los Andes, Bogotá, 111711, Colombia
[qq] Programa de Pós-graduação em Desenvolvimento e Meio Ambiente, Universidade Federal de Sergipe, São Cristóvão-SE, 49100-000, Brazil
[rr] Secretaria Municipal de Meio Ambiente, Aracaju-SE, 49015-190, Brazil
[ss] Laboratório de Primatologia, Departamento de Zootecnia e Ciências Biológicas, Universidade Federal de Santa Maria, Palmeira das Missões-RS, 98300-000, Brazil
[tt] Fundação de Apoio à Pesquisa (FUNAPE), Universidade Federal de Goiás, Goiânia-GO, 74690-612, Brazil
[uu] Museu de Ciências Naturais, Universidade de Caxias do Sul, Caxias do Sul-RS, 95070-560, Brazil
[vv] Foundation for Wildlife Conservation, Belize
[ww] Departamento de Meio Ambiente e Desenvolvimento, Universidade Federal do Amapá, Macapá-AP, 68903-419, Brazil
[xx] Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden
[yy] Department of Anthropology, Northern Illinois University, DeKalb, IL 60115
[zz] Department of Sociobiology and Anthropology, University of Göttingen, 37077 Göttingen, Germany

[ab] Saint Louis Zoo, Saint Louis, MO 63110
[ac] The Aspinall Foundation, 101 Antananarivo, Madagascar
[ad] The Aspinall Foundation, Port Lympne Reserve, Hythe CT21-4LR, UK
[ae] Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury CT2 7NZ, UK
[af] Instituto de Pesquisas Ecológicas (IPÊ), Nazaré Paulista-SP, 12960-000, Brazil
[ag] Estacion Biologica Corrientes (CCT Nordeste) – CONICET, Corrientes, W3401XAL, Argentina
[ah] Association for Research and Conservation in the Amazon (ARCAmazon), Puerto Maldonado, Madre de Dios, Peru
[ai] Junglekeepers Peru, Puerto Maldonado, Madre de Dios, Peru
[aj] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85719
[ak] Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11790
[al] Omaha's Henry Doorly Zoo and Aquarium, Omaha, NE 68107
[am] Animal Behavior Graduate Group, University of California, Davis, CA 95616
[an] Wildlife Conservation Society, La Paz, Bolivia
[ao] Red Boliviana de Primatología (RedBolPrim), Bolivia
[ap] Department of Forestry Engineering, Federal University of Viçosa, Viçosa-MG, 36570-900, Brazil
[aq] Muriqui Instituto de Biodiversidade (MIB), Caratinga-MG, 35300-037, Brazil
[ar] Groupe d'Etude et de Recherches sur les Primates de Madagascar (GERP), 101 Antananarivo, Madagascar
[as] School of the Environment, Portland State University, Portland, OR 97201
[at] Universidade Federal do Espírito Santo (UFES), Vitória-ES, 29075-910, Brazil
[au] Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada
[av] Department of Anthropology, Kent State University, Kent, OH 44240
[aw] Centre for Social Sciences (Anthropology), Athabasca University, Athabasca, Alberta, T9S 3A3, Canada
[ax] Department of Biological Sciences, Southeastern Louisiana University, Hammond, LA 70402

[ay] Department of Migration, Max Planck Institute of Animal Behavior, 78315 Radolfzell, Germany
[az] Smithsonian Tropical Research Institute, Panamá, 0843-03092, República de Panamá
[ba] Department of Behavioral Ecology, University of Goettingen, 37077 Goettingen, Germany
[bc] Research Group Primate Social Evolution, German Primate Center, Leibniz Institute for Primate Research, 37077 Goettingen, Germany
[bd] Lemur Conservation Foundation, Myakka City, FL 34251
[be] Departamento de Ciencias de la Salud, Universidad Autónoma Metropolitana (UAM), Unidad Lerma, México
[bf] Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIIDIR), Unidad Oaxaca, Instituto Politécnico Nacional, Oaxaca, México
[bg] Conservación de la Biodiversidad del Usumacinta A.C., Balancán, Tabasco, México
[bh] Department of Biology, University of Maryland, College Park, MD 20742
[bi] Mention Anthropobiologie et Développement Durable, Faculté des Sciences, University of Antananarivo, 101 Antananarivo, Madagascar
[bj] Department of Mathematical Modelling of Social Systems, Institute for Research on Applied Mathematics and Systems, Universidad Nacional Autónoma de México, Mexico City, México
[bk] Center for Complexity Sciences, Universidad Nacional Autónoma de México, Mexico City, México
[bl] Graduate School of Asian and African Area Studies, Kyoto University, Kyoto, 615-8510, Japan
[bm] Instituto de Investigaciones en Comportamiento Alimentario y Nutrición, Universidad de Guadalajara, México
[bn] Department of Life Sciences, Imperial College London, London SW7 2AZ, UK
[bp] Instituto de Desenvolvimento Sustentável Mamirauá, Tefé-AM, 69553-225, Brazil
[bq] Département Sciences de la Nature et de l’Environnement, Facultés des Sciences, Université d’Antsiranana, 201 Antsiranana, Madagascar
[br] College of Veterinary Medicine, Cornell University, Ithaca, NY 14853
[bs] Primate Research Institute, Kyoto University, Aichi 484-8506, Japan
[bt] Department of Anthropology, University of Colorado-Boulder, Boulder, CO 80302

[bu] Department of Anthropology, California State University, Sacramento, Sacramento, CA 95819

[bv] Interdepartmental Doctoral Program in Anthropological Sciences, Stony Brook University, Stony Brook, NY, 11794

[bw] Red de Biología y Conservación de Vertebrados, Instituto de Ecología AC, Xalapa, Veracruz, México

[bx] Neotropical Primate Conservation, Seaton, Cornwall PL11 3JQ, UK

[by] Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Federal do Mato Grosso, Cuiabá-MT, 78060-900, Brazil

[bz] School of Life Sciences, Anglia Ruskin University, Cambridge CB1 1PT, UK

[ca] Instituto de Investigaciones Sociológicas de la Universidad Autónoma Benito Juárez de Oaxaca, Oaxaca, México

[cb] Departamento de Zoologia, Universidade Federal de Pernambuco, Recife-PE, 50670-901, Brazil

[cd] Laboratório de Ecologia, Comportamento e Conservação (LECC), Universidade Federal de Pernambuco, Recife-PE, 50670-901, Brazil

[ce] Laboratório de Produtos Naturais e Espectrometria de Massas (LaPNEM), Faculdade de Ciências Farmacêuticas, Alimentos e Nutrição (FACFAN), Universidade Federal de Mato Grosso do Sul (UFMS), Campo Grande-MS, 79070-900, Brazil

[cf] Universidade Federal de Mato Grosso do Sul (UFMS), Campo Grande-MS, 79070-900, Brazil

[cg] Department of Biology, Institute of Zoology, Universität Hamburg, 20146 Hamburg, Germany

[ch] Biology Department, California Lutheran University, Thousand Oaks, CA 91360

[ci] Department of Anthropology, University of Wisconsin-Madison, 1180 Observatory Drive, Madison, WI 53706

[cj] Department of Behavioral Sciences, San Diego Mesa College, San Diego, CA 92111

[ck] Departamento de Ciências Ambientais, Lab Ecologia e Conservação da Natureza and the Programa Análise Ambiental Integrada, Universidade Federal de São Paulo, São Paulo-SP, 04040-003, Brazil

[cl] Instituto Pró-Muriqui, São Paulo-SP, Brazil

[cm] School of Anthropology, University of Arizona, Tucson, AZ 85719

[cn] Facultad de Ciencias Forestales (FCF), Universidad Nacional de Misiones (UNaM), Eldorado, Misiones, Argentina

[co] Instituto de Biología Subtropical (IBS), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Puerto Iguazú, Misiones, Argentina

[cp] Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Puerto Iguazú (3370), Misiones, Argentina

[cq] Department of Anthropology, University of Florida, Gainesville, FL 32603

[cr] Department of Anthropology, University of Austin at Texas, Austin, TX 78712

[cs] Wildlife Conservation Society, Bronx, NY 10460

[ct] Department of Anthropology, Stony Brook University, Stony Brook, NY 11794

[cu] Centre ValBio, Ranomafana, Madagascar

[cv] Department of Biology and Biotechnology "Charles Darwin", Sapienza University of Rome, 00185 Rome, Italy

[cw] National Research Council, Institute of Research on Terrestrial Ecosystems (CNR- IRET), 00015 Monterotondo, Rome, Italy

[1] To whom correspondence may be addressed. **Email:** teppley@sdzwa.org

[2] Contributed equally to this work

Author Contributions: T.M.E., K.H., A.A.B., P.C.W., G.D., and L.S. designed research. T.M.E., C.A.C., J.U.G., M.A.O., D.B.A., N.A., K.R.A., M.A.A., J.F.A., A.L.B., M.B., J.C.B.M., M.B., S.A.B., M.B., D.C., C.C.M., C.J.C., M.C., F.A.C., T.S.C., X.C.P., J.C., O.M.C., C.C.K., I.C.C., B.D., C.D., K.M.E., E.M.E., K.J.E.E., L.M.F., A.M.F., R.G.F., C.F., M.L.F., I.P.F., V.B.F., I.F., D.G., G.B.G., K.S.H., E.W.H., R.R.H., S.M.H., M.T.I., S.E.J., P.M.K., E.A.K., T.K., C.K., F.K., M.M.K., L.R.L., M.E.L., E.E.L., M.C.L., J.M., A.D.M., F.R.M., T.H.M., M.S.M., L.S.M., L.A.M., C.B.M., M.B.N.R., M.A.N., H.N., M.T.O., J.O., E.R.P., M.S.M.P., B.P.G., L.M.P., G.P.M., B.E.R., V.R., N.A.R., Z.R., G.R.F., C.D.R., J.R., M.R., J.R., T.P.R., N.R., N.M.R., J.R.G., J.S., N.S., H.S., M.L.S., C.J.S., J.C.S.S., S.S., P.G.A.S.L., A.C.S., S.E.S.A., J.P.S.A., V.K.S., K.J.E.S., A.I.S., K.B.S., S.A.S., M.T., S.R.T., M.P.T., K.V., S.V.B., N.V., R.B.W., G.W., P.C.W., and G.D. contributed datasets. T.M.E., S.H., G.D., and L.S. analyzed data. T.M.E., S.H., G.D., and L.S. wrote the paper. All authors read and edited this manuscript.

Competing Interest Statement: The authors declare no competing interest.

Classification: Biological Sciences: Anthropology

Keywords: primate communities; primate evolution; evolutionary transitions; niche shift; climate change

This PDF file includes:

- Main Text
- Figures 1 and 2
- Table 1

Abstract

Among mammals, the order Primates is exceptional in having a high taxonomic richness where the taxa are arboreal, semi-terrestrial, or terrestrial. Though 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 provide analogous scenarios to those transitional periods. Therefore, we investigated predominantly arboreal primate genera from the Americas and Madagascar that lack fully terrestrial taxa, to determine whether ecological drivers (habitat canopy cover, predation risk, maximum temperature, primate community assemblage, human population density, and roads) or species-specific traits (body mass, group size, and degree of frugivory) associate with increased terrestriality. We collated 150,634 observation hours across 2,215 months from 47 species at 19 sites in Madagascar and 48 sites in the Americas. Multiple factors were associated with ground use in these otherwise arboreal species, including increased temperatures, a decrease in canopy cover, a dietary shift away from frugivory, and larger group

size. These factors mostly explain intra-specific 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 towards greater ground use.

Significance Statement

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 temperatures 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 species already inhabiting hot, sparsely canopied sites, and exhibiting more generalized diets, are more likely to shift towards greater ground use. Evolutionarily, similar factors may have been responsible for the transition of hominins and some catarrhines to terrestrial lifestyles.

Main Text

Introduction

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, Strepsirrhini of Madagascar, and lorisiform primates of Africa and Asia) (7, 12-14). However, some of these arboreal 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, 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 and, thus, facilitating ground use in primates (17, 20, 31-33). It should be noted, however, native carnivores are often supplanted by non-native carnivores, including dogs, which can still 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 fulfil 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, 40, 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 dietary overlap (54, 55). Therefore, in sites with high primate species richness 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 equilibrium is reached (56). The interaction between habitat canopy cover and primate species richness requires that they are examined together.

Species-specific factors have also been suggested to facilitate niche transition. Limited resource availability may lead to shifts in foraging strategies, including increased terrestriality (11, 16, 38). For instance, 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 semi-terrestrial primates tend to be larger than strictly arboreal primates and tend to live in larger groups (22, 57, 58). Both characteristics are likely adaptations to high predation pressure and resource availability (58-62) and may have facilitated the shift to terrestriality. Additionally, to the extent that a species' forelimb-hindlimb proportions influence the biomechanics of quadrupedalism, species with more proportional limbs are more adapted for cursorial quadrupedalism in a terrestrial environment (7, 8, 63). Such species-specific factors may facilitate the evolutionary transition of hominins and catarrhine primates to terrestrial lifestyles (9, 11, 64).

We focus on primates of the Americas and Madagascar to explore anthropogenic, ecological factors, and species-specific traits that are associated with greater use of the ground in two independent radiations. Regarding ecological and anthropogenic factors, we predicted that terrestriality would be greater in species at sites 1) with more open, degraded, or fragmented forest areas, i.e., less canopy cover; 2) with higher maximum temperatures favoring behavioral thermoregulation; 3) where fewer native terrestrial predators pose a risk; 4) with high primate species richness, and 5) in greater distance from both roads and higher human population densities (Fig. 1). Considering species-specific traits that may promote ground use, we predicted that terrestriality would 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 quadrupedalism (Fig. 1).

Results

The 47 arboreal primate species we studied spent little time on the ground (2.4 ± 0.1% of the activity budget, monthly mean ± SE; N = 2,215 months), and for over half of the species (61.7%) terrestrial behavior comprised less than 1% of their total monthly activity. Lemurs spent 3.3 ± 0.1% (monthly mean ± SE; N = 990 months) of their time on the ground, whereas monkeys spent 2.4 ± 0.2% (monthly mean ± SE; N = 1,225 months) of their time on the ground. In all models, lemurs were on average more terrestrial than monkeys (Table 1; SI Appendix, Table S2).

In the complete model, the most important ecological pressure associated with terrestriality was maximum temperature, which showed a positive effect, and habitat canopy cover, which showed a negative effect, on time spent on the ground (SI Appendix, Table S2 and Fig. S8). Considering anthropogenic drivers, distance to roads was positively associated with ground use (SI Appendix, Table S2 and Fig. S8). For species-specific factors, a species' degree of frugivory had a negative effect, whereas group size was positively associated with terrestriality (SI Appendix, Table S2 and Fig. S8).

For the within-species model (Table 1; SI Appendix, Fig. S9), multiple ecological pressures influenced primate ground use. Similar to the complete model, maximum temperature and distance to roads had positive effects and habitat canopy cover had a negative effect. Unlike the complete model, however, predation risk had a negative effect, while the interaction between primate-rich habitats and habitat canopy cover was positive, meaning that the effect of canopy cover on terrestriality is amplified in areas with higher primate species richness. Like the complete model, the only two species-specific factors related to terrestriality were degree of frugivory (negative) and group size (positive).

In the between-species model (Table 1; SI Appendix, Fig. S10), none of the factors were strongly related to terrestriality. The only ecological factors that exhibited a clear effect were habitat canopy cover (positive) and primate species richness (negative). Species in habitats with denser canopy cover and with less sympatric primate species spent a greater proportion of time on the ground. Body mass had a negative effect and group size had a positive effect on terrestrial activity, with 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. However, our between-species analysis reveals that species that descend more often to the ground tend to be smaller and live in closed-canopy habitats. Contrary to previous single-species studies that showed an observer effect (15, 39, 65, but see 33), study duration (the number of post-habituation months) had no effect in our models.

Ecological drivers of terrestriality

Maximum temperatures showed a positive effect on both the complete and intraspecific models. Chronic and rapid temperature increases can quickly drive behavioral shifts (cf. 66, 67). A possible explanation is that lemurs and 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 *E. 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 driver in many evolutionary shifts (72). However, the degree to which this may result in a more terrestrial primate lifestyle is unclear

(11). Interestingly, we found contrasting effects of canopy cover on ground use within- vs. between-species: denser canopy cover was associated with spending less active time on the ground within-species, but more time on the ground between-species. The former is in line with our expectation that terrestrial activity tends to be higher in 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), though their ability to do so may be guided by species-specific characteristics acting as a predisposition, i.e., behavioral and anatomical exaptations (75, 76). The between-species result is more difficult to explain, which could be due to factors that were not considered, such as potential aerial predators.

Primate species richness had a negative effect on terrestriality in the interspecific 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 richness in the intraspecific model affirms 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 interindividual 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 richness was associated with more terrestrial activity in our within-species model. Though we were unable to account for predator population abundance or the potential ecological and co-occurrence drivers 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 only more terrestrial at sites further away 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 as 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), and/or because they have gastrointestinal and dental adaptations allowing them to more efficiently use terrestrial resources (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, though this is not always the case (96, 97). However, though 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 proposed by Fleagle (7, 58) were developed 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.

Conclusion

We have shown that there are multiple factors that may drive 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 hominins and non-human 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. Examining primate behavioral and ecological flexibility along-side current environmental conditions provides scenarios analogous to 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, 99-102). We expect that these human-induced impacts will lead several species that already inhabit hot, sparsely canopied sites and that exhibit more generalized diets to increase their use of the ground strata.

Materials and Methods

We used published and unpublished data to compile monthly data on behavioral observations from 47 primate taxa, specifically 15 lemur species representing two families (Lemuridae and Indriidae), and 32 platyrrhine species representing four families (Atelidae, Callitrichidae, Cebidae, and Pitheciidae). The dataset includes 150,634 observation hours across

2,215 months from species at 67 research sites, specifically 19 sites in Madagascar and 48 sites throughout the Americas (Fig. 2; SI Appendix, Table S1). Our dataset includes 16 primate species (specifically 10 lemur and six 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 hours/month to increase the chances that rare events, in our case terrestriality by arboreal species, would be recorded (103). We considered the monthly proportion of time spent terrestrially as our dependent variable.

Ecological drivers

Geographic coordinates and date of each study allowed us to extract site- and time-specific environmental data. We extracted monthly maximum temperatures from the *ERA5 Monthly Aggregates* dataset (104). We obtained the relative canopy cover using a circular buffer around the coordinates of each study site from the Landsat Tree Cover Continuous Fields (GLCF) dataset (105; SI Appendix, Fig. S1). Specifically, the buffer area was equal to twice the size of each study species reported mean home range. We extracted both climate and habitat values with Google Earth Engine (earthengine.google.com) using the spatial coordinates and the year and month of the observations (106) and processed in R version 3.6.3 (107).

We estimated the number of potential terrestrial mammalian predators per species per site from the number of carnivore species per location using IUCN range maps (108). For each species per location, we only considered predators with a mean body mass greater than or equal to ¼ 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 109). This approach is 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 allows us to estimate the spatial gradients of predator richness at this scale of analysis for all sites and species, thereby avoiding potential author or publication reporting biases (cf. 110). Although primates may also be preyed upon by birds of prey, snakes, and other primates, carnivores are considered their main terrestrial predators (111, 112).

Using IUCN range maps (108), we also estimated the number of sympatric primate species per site (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 number presence of humans, whereas the former 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 (http://sedac.ciesin.columbia.edu/). We used the Gridded Population of the World (GPW) dataset, v.4 dataset (113) for 2000, 2005, 2010, 2015, and 2020 at 30 arcsecond resolution (~1km) (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 1km resolution and calculated the distance from the nearest road for the entire study area (SI Appendix, Figs. S6 and S7).

Species-specific factors

For each species' specific site, co-author(s) 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 (114). We inferred locomotion type via the Inter-Membral Index (IMI; 63), which is calculated as ((length of humerus + length of radius) / (length of femur + length of tibia)) * 100. Quadrupedal primates typically have an IMI between 67 and 104, with those falling below the lower threshold typically exhibiting vertical clinging and leaping (VCL), and those above the upper threshold typically categorized as exhibiting brachiation, but also suspensory locomotion (7, 8, 63). Given intraspecific limb length variability and potential for error when collecting field measurements, we assigned each species to a category based on either the IMI provided by contributing co-authors, or as recorded in the All the World's Primates database (114).

Statistical analyses

We tested our hypotheses by fitting a zero-inflated model with a beta family and logit link-function and using Bayesian inference. The use of a zero-inflation and beta 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. We used study duration (i.e., the number of months post-habituation) 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. (115). We added an additional observation level random effect to control for overdispersion. We scaled all fixed factors to a mean of zero and standard deviation of 1. We used weakly informative priors using a normal distribution with a standard deviation of 10 for the intercept, and a standard deviation of 1.5 for all slope coefficients, thereby limiting the range to a plausible gradient of variation considering the logit link-function and standardized coefficients. All predictors were tested for multi-collinearity prior to the modelling but none showed a correlation coefficient >0.7, so all variables were retained in the final model (116).

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 (% frugivory and group size). Prior to fitting this second model, we first subtracted the species' mean from each observation value (species mean deviation) (117). 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 zero and standard deviation of 1 prior to model fitting.

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. We fitted the models using the ‘brms’ package (118) in R version 3.6.3 (107).

Acknowledgments

A complete list of acknowledgements can be found in the SI Appendix.

References

1. Q. Ji, *et al.*, The earliest known eutherian mammal. *Nature* **416**, 816–822 (2002).

2. F. S. Szalay, “Ancestral locomotor modes, placental mammals, and the origin of Euprimates: Lessons from history” in *Primate Origins: Adaptations and Evolution*, M. J. Ravosa, M. Dagosto, Eds. (Springer, 2007), pp. 457–487.

3. R. W. Sussman, Primate origins and the evolution of angiosperms. *Am. J. Primatol.* **23**, 209–223 (1991).

4. E. C. Kirk, P. Lemelin, M. W. Hamrick, D. M. Boyer, J. I. Bloch, Intrinsic hand proportions of euarchontans and other mammals: Implications for the locomotor behavior of plesiadapiforms. *J. Hum. Evol.* **55**, 278–299 (2008).

5. D. M. Boyer, S. Toussaint, M. Godinot, Postcrania of the most primitive euprimate and implications for primate origins. *J. Hum. Evol.* **111**, 202–215 (2017).

6. D. L. Gebo, E. J. Sargis, Terrestrial adaptations in the postcranial skeletons of guenons. *Am. J. Phys. Anthropol.* **93**, 341–371 (1994).

7. J. G. Fleagle, *Primate Adaptation and Evolution, 3rd ed.* (Academic Press, 2013).

8. J. G. Fleagle, D. E. Lieberman, “Major transformations in the evolution of primate locomotion” in *Great Transformations in Vertebrate Evolution*, K. P. Dial, N. H. Shubin, E. L. Brainerd, Eds. (University of Chicago Press, 2015), pp. 257–278.

9. K. D. Hunt, Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. *J. Anat.* **228**, 630–685 (2016).

10. A. L. Machnicki, L. B. Spurlock, K. B. Strier, P. L. Reno, C. O. Lovejoy, First steps of bipedality in hominids: evidence from the atelid and *Proconsul* pelvis. *PeerJ* **4**, e1521 (2016).

11. M. L. McCrossin, B. R. Benefit, S. N. Gitau, A. K. Palmer, K. T. Blue, “Fossil evidence for the origins of terrestriality among Old World higher primates” in *Primate Locomotion: Recent Advances*, J. Strasser, J. Fleagle, A. Rosenberger, H. McHenry, Eds. (Springer, 1998), pp. 353–396.

12. J. G. Fleagle, K. E. Reed, Comparing primate communities: a multivariate approach. *J. Hum. Evol.* **30**, 489–510 (1996).

13. E. W. Heymann, Giant fossil New World primates: arboreal or terrestrial? *J. Hum. Evol.* **34**, 99–101 (1998).

14. J. M. Kamilar, L. M. Guidi, The phylogenetic structure of primate communities: variation within and across continents. *J. Biogeogr.* **37**, 801–813 (2010).

15. F. P. Tabacow, S. L. Mendes, K. B. Strier, Spread of a terrestrial tradition in an arboreal primate. *Am. Anthropol.* **111**, 238–249 (2009).

16. A. A. Barnett, *et al.*, Terrestrial foraging by *Cacajao melanocephalus ouakary* (Primates) in Amazonian Brazil: is choice of seed patch size and position related to predation-risk? *Folia Primatol*. **83**, 126–139 (2012).

17. T. M. Eppley, G. Donati, J. U. Ganzhorn, Determinants of terrestrial feeding in an arboreal primate: the case of the southern bamboo lemur (*Hapalemur meridionalis*). *Am. J. Phys. Anthropol.* **161**, 328–342 (2016).

18. J. C. Serio-Silva, R. Ramírez-Julián, T. M. Eppley, C. A. Chapman, “Terrestrial locomotion and other adaptive behaviors in howler monkeys (*Alouatta pigra*) living in forest fragments” in *Movement Ecology of Neotropical Forest Mammals*, R. Reyna, C. A. Chapman, Eds. (Springer Nature, 2019), pp. 125–140.

19. J. P. Souza-Alves, *et al.*, Terrestrial behavior in titi monkeys (*Callicebus*, *Cheracebus*, and *Plecturocebus*): potential correlates, patterns, and differences between genera. *Int. J. Primatol.* **40**, 553–572 (2019).

20. C. M. Monteza-Moreno, M. C. Crofoot, M. N. Grote, P. A. Jansen, Increased terrestriality in a Neotropical primate living on islands with reduced predation risk. *J. Hum. Evol.* **143**, 102768 (2020).

21. R. E. Williamson, *et al.*, Sharing spaces: niche differentiation in diet and substrate use among wild capuchin monkeys. *Anim. Behav.* **179**, 317–338 (2021).

22. C. H. Janson, M. L. Goldsmith, Predicting group size in primates: foraging costs and predation risks. *Behav. Ecol.* **6**, 326–336 (1995).

23. M. R. Shattuck, S. A. Williams, Arboreality has allowed for the evolution of increased longevity in mammals. *Proc. Natl. Acad. Sci. USA* **107**, 4635–4639 (2010).

24. D. L. Cheney, R. W. Wrangham, "Predation" in *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, T. T. Struhsaker, Eds. (University of Chicago Press, 1987), pp. 227–239.

25. L. E. Miller, "An introduction to predator sensitive foraging" in *Eat or Be Eaten: Predator Sensitive Foraging Among Primates*, L. E. Miller, Ed. (Cambridge University Press, 2002), pp. 1–17.

26. C. P. van Schaik, Why are diurnal primates living in groups? *Behaviour* **87**, 120–144 (1983).

27. R. W. Wrangham, J. L. Gittleman, C. A. Chapman CA, Constraints on group size in primates and carnivores: Population density and day-range as assays of exploitation competition. *Behav. Ecol. Sociobiol.* **32**, 199–209 (1993).

28. L. A. Isbell, Predation on primates: ecological patterns and evolutionary consequences. *Evol. Anthropol.* **3**, 61–71 (1994).

29. Z.J. Farris, *et al.*, Threats to a rainforest carnivore community: A multi-year assessment of occupancy and co-occurrence in Madagascar. *Biol. Conserv.* **210**, 116–124 (2017).

30. L. N. Rich, *et al.*, Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. *Glob. Ecol. Biogeogr.* **26**, 918–929 (2017).

31. W. S. McGraw, R. Bshary, Association of terrestrial mangabeys (*Cercocebus atys*) with arboreal monkeys: Experimental evidence for the effects of reduced ground predator pressure on habitat use. *Int. J. Primatol.* **23**, 311–325 (2002).

32. C. J. Campbell, *et al.*, Terrestrial behavior of *Ateles* spp. *Int. J. Primatol.* **26**, 1039–1051 (2005).

33. J. P. Souza-Alves, *et al.*, For emergency only: terrestrial feeding in Coimbra-Filho’s titis reflects seasonal arboreal resource availability. *Primates* **62**, 199–206 (2021).

34. G. Pozo-Montuy, J. C. Serio-Silva, C. A. Chapman, Y. M. Bonilla-Sánchez, Resource use in a landscape matrix by an arboreal primate: evidence of supplementation in black howlers (*Alouatta pigra*). *Int. J. Primatol.* **34**, 714–731 (2013).

35. Z. J. Farris, S. Chan, R. Rafaliarison, K. Valenta, Occupancy modeling reveals interspecific variation in habitat use and negative effects of dogs on lemur populations. *Int. J. Primatol.* **40**, 706–720 (2019).

36. K. A. Wright, *et al.*, Positional behavior and substrate use in wild adult bearded capuchin monkeys (*Sapajus libidinosus*). *Am. J. Primatol.* **81**, e23067 (2019).

37. A. M. Felton, L. M. Engström, A. Felton, C. D. Knott, Orangutan population density, forest structure and fruit availability in hand-logged and unlogged peat swamp forests in West Kalimantan, Indonesia. *Biol. Conserv.* **114**, 91–101 (2003).

38. A. A. Barnett, *et al.*, Terrestrial activity in Pitheciins (*Cacajao, Chiropotes* and *Pithecia* spp.). *Am. J. Primatol.* **74**, 1106–1127 (2012).

39. I. M. C. Mourthé, *et al.*, Ground use by northern muriquis (*Brachyteles hypoxanthus*). *Am. J. Primatol.* **69**, 706–712 (2007).

40. B. Wong, U. Candolin, Behavioral responses to changing environments. *Behav. Ecol.* **26**, 665–673 (2015).

41. J. C. Bicca-Marques, Ó. M. Chaves, G. P. Hass, Howler monkey tolerance to habitat shrinking: lifetime warranty or death sentence? *Am. J. Primatol*. **82**, e23089 (2020).

42. S. J. Cunningham, A. C. Kruger, M. P. Nxumalo, P. A. Hockey, Identifying biologically meaningful hot-weather events using threshold temperatures that affect life-history. *PLoS ONE* **8**, e82492 (2013).

43. I. Bramer, *et al.*, Advances in monitoring and modelling climate at ecologically relevant scales. *Adv. Ecol. Res.* **58**, 101–161 (2018).

44. D. R. Samson, K. D. Hunt, A thermodynamic comparison of arboreal and terrestrial sleeping sites for dry-habitat chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda. *Am. J. Primatol.* **74**, 811–818 (2012).

45. V. P. Kosheleff, C. N. Anderson, Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. *Am. J. Phys. Anthropol.* **139**, 172–181 (2009).

46. H. Takemoto. Acquisition of terrestrial life by human ancestors influenced by forest microclimate. *Sci. Rep.* **7**, 5741 (2017).

47. J. C. Bicca-Marques, C. Calegaro-Marques, Locomotion of black howlers in a habitat with discontinuous canopy. *Folia Primatol*. **64**, 55–61 (1995).

48. G. Pozo-Montuy, J. C. Serio-Silva, Movement and resource use by a group of *Alouatta pigra* in a forest fragment in Balancán, México. *Primates* **48**, 102–107 (2007).

49. S. F. Ferrari, R. R. Hilário, Use of water sources by buffy-headed marmosets (*Callithrix flaviceps*) at two sites in the Brazilian Atlantic Forest. *Primates* **53**, 65–70 (2012).

50. C. R. Amoroso, P. M. Kappeler, C. Fichtel, C. L. Nunn, Water availability impacts habitat use by red-fronted lemurs (*Eulemur rufifrons*): an experimental and observational study. *Int. J. Primatol.* **41**, 61–80 (2020).

51. Ó. M. Chaves, *et al.*, Flower consumption, ambient temperature and rainfall modulate drinking behavior in a folivorous-frugivorous arboreal mammal. *PLoS ONE* **16**, e0236974 (2021).

52. J. S. Carvalho, *et al.*, A global risk assessment of primates under climate and land use/cover scenarios. *Glob. Change Biol.* **25**, 3163–3178 (2019).

53. IPCC, "Climate Change 2021: The Physical Science Basis" in *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, V. Masson-Delmotte, et al., Eds. (Cambridge University Press, 2021).

54. J. U. Ganzhorn, "Body mass, competition and the structure of primate communities" in *Primate Communities*, J. G. Fleagle, C. H. Janson, K. E. Reed, Eds. (Cambridge University Press, 1999), pp. 141–157.

55. C. H. Janson, C. A. Chapman, "Resources and primate community structure" in *Primate Communities,* J. G. Fleagle, C. H. Janson, K. E. Reed, Eds. (Cambridge University Press, 1999), pp. 237–267.

56. T. P. Bregman, A. C. Lees, N. Seddon, H. E. MacGregor, B. Darski, Species interactions regulate the collapse of biodiversity and ecosystem function in tropical forest fragments. *Ecology* **96**, 2692–2704 (2015).

57. T. H. Clutton-Brock, P. H. Harvey, Primate ecology and social organization. *J. Zool.* **183**, 1–39 (1977).

58. J. G. Fleagle, "Size and adaptation in primates" in *Size and Scaling in Primate Biology,* W. L. Jungers, Ed. (Plenum Press, 1985), pp. 1–19.

59. W. D. Hamilton, Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311 (1971).

60. G. Cowlishaw, Vulnerability to predation in baboon populations. *Behaviour* **131**, 293–304 (1994).

61. L. A. Isbell, Predation on primates: ecological patterns and evolutionary consequences. *Evol. Anthropol.* **3**, 61–71 (1994).

62. M. C. Crofoot, Why mob? Reassessing the costs and benefits of primate predator harassment. *Folia Primatol.* **83**, 252–273 (2012).

63. J. R. Napier, P. H. Napier, *The Natural History of the Primates* (MIT Press, 1985).

64. B. R. Benefit, *Victoriapithecus*: the key to Old World monkey and catarrhine origins. *Evol. Anthropol.* **7**, 155–174 (1999).

65. K. Nowak, A. le Roux, S. A. Richards, C. P. Scheijen, R. A. Hill, Human observers impact habituated samango monkeys' perceived landscape of fear. *Behav. Ecol.* **25**, 1199–1204 (2014).

66. M. A. Maslin, S. Shultz, M. H. Trauth, A synthesis of the theories and concepts of early human evolution. *Phil. Trans. R. Soc. B* **370**, 1663 (2015).

67. E. A. Beever, *et al.*, Behavioral flexibility as a mechanism for coping with climate change. *Front. Ecol. Environ.* **15**, 299–308 (2017).

68. J. G. Boyles, F. Seebacher, B. Smit, A. E. McKechnie, Adaptive thermoregulation in endotherms may alter responses to climate change. *Integr. Comp. Biol.* **51**, 676–690 (2011).

69. J. Terrien, M. Perret, F. Aujard, Behavioral thermoregulation in mammals: a review. *Front. Biosci.* **16**, 1428–1444 (2011).

70. R. Buchholz, *et al.*, Behavioural research priorities for the study of animal response to climate change. *Anim. Behav.* **150**, 127–137 (2019).

71. B. F. Oliveira, B. R. Scheffers, Vertical stratification influences global patterns of biodiversity. *Ecography*, **42**, 249–249 (2019).

72. C. A. Stockwell, A. P. Hendry, M. T. Kinnison, Contemporary evolution meets conservation biology. *Trends Ecol. Evol.* **18**, 94–101 (2003).

73. M. Galetti, I. Sazima, Impact of feral dogs in an urban Atlantic forest fragment in southeastern Brazil. *Nat. Conserv.* **4**, 146–151 (2006).

74. H. M. Prates, J. C. Bicca-Marques, Age-sex analysis of activity budget, diet, and positional behavior in *Alouatta caraya* in an orchard forest. *Int. J. Primatol*. **29**, 703–715 (2008).

75. S. A. Boyle, A. T. Smith, Can landscape and species characteristics predict primate presence in forest fragments in the Brazilian Amazon? *Biol. Conserv.* **143**, 1134–1143 (2010).

76. T. M. Eppley, L. Santini, J. C. Tinsman, G. Donati, Do functional traits offset the effects of fragmentation? The case of large-bodied diurnal lemur species. *Am. J. Primatol.* **82**, e23104 (2020).

77. G. Cowlishaw, R. I. M. Dunbar, *Primate Conservation Biology* (University of Chicago Press, 2000).

78. C. A. Peres, P. M. Dolman, Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia* **122**, 175–189 (2000).

79. D. I. Bolnick, *et al.*, Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proc. R. Soc. B* **277**, 1789–1797 (2010).

80. H. Segre, N. DeMalach, Z. Henkin, R. Kadmon, Quantifying competitive exclusion and competitive release in ecological communities: A conceptual framework and a case study. *PLoS ONE* **11**, e0160798 (2016).

81. M. R. McLennan, N. Spagnoletti, K. J. Hockings, The implications of primate behavioral flexibility for sustainable human–primate coexistence in anthropogenic habitats. *Int. J. Primatol.* **38**, 105–121 (2017).

82. K. B. Strier, What does variation in primate behavior mean? *Am. J. Phys. Anthropol*. **162**, 4–14 (2017).

83. G. C. Costa, D. O. Mesquita, G. R. Colli, L. J. Vitt, Niche expansion and the niche variation hypothesis: does the degree of individual variation increase in depauperate assemblages? *Am. Nat.* **172**, 868–877 (2008).

84. H. D. Vance-Chalcraft, D.A. Soluk, N. Ozburn, Is prey predation risk influenced more by increasing predator density or predator species richness in stream enclosures? *Oecologia* **139**, 117–122 (2004).

85. J. N. Griffin, J. E. Byrnes, B. J. Cardinale, Effects of predator richness on prey suppression: a meta-analysis. *Ecology* **94**, 2180–2187 (2013).

86. C. L. Davis, *et al.*, Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide. *Ecol. Lett.* **21**, 1401–1412 (2018).

87. M. F. Teaford, P. S. Ungar, Diet and the evolution of the earliest human ancestors. *Proc. Natl. Acad. Sci. USA* **97**, 13506–13511 (2000).

88. A. Mekonnen, *et al.*, Dietary flexibility of Bale monkeys (*Chlorocebus djamdjamensis*) in southern Ethiopia: effects of habitat degradation and life in fragments. *BMC Ecol.* **18**, 4 (2018).

89. J. E. Lambert, Primate digestion: interactions among anatomy, physiology, and feeding ecology. *Evol. Anthropol.* **7**, 8–20 (1998).

90. A. M. Ashbury, *et al.*, Why do orangutans leave the trees? Terrestrial behavior among wild Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Kalimantan. *Am. J. Primatol.* **77**, 1216–1229 (2015).

91. J. E. Lambert, J. M. Rothman, Fallback foods, optimal diets, and nutritional targets: primate responses to varying food availability and quality. *Annu. Rev. Anthropol.* **44**, 493–512 (2015).

92. A. Link, N. Galvis, E. Fleming, A. Di Fiore, Patterns of mineral lick visitation by spider monkeys and howler monkeys in Amazonia: are licks perceived as risky areas? *Am. J. Primatol.* **73**, 386–396 (2011).

93. B. P. Semel, *et al.*, Assessing the function of geophagy in a Malagasy rain forest lemur. *Biotropica* **51**, 769–780 (2019).

94. K. R. Amato, *et al.*, Fermented food consumption in wild nonhuman primates and its ecological drivers. *Am. J. Phys. Anthropol.* **175**, 513–530 (2021).

95. P. A. Pebsworth, M. A. Huffman, J. E. Lambert, S. L. Young, Geophagy among nonhuman primates: A systematic review of current knowledge and suggestions for future directions. *Am. J. Phys. Anthropol.* **168**, 164–194 (2019).

96. R. Steenbeek, C. P. van Schaik, Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behav. Ecol. Sociobiol.* **49**, 100–110 (2001).

97. T. V. Snaith, C. A. Chapman, Primate group size and interpreting socioecological models: do folivores really play by different rules? *Evol. Anthropol.* **16**, 94–106 (2007).

98. L. R. Godfrey, W. L. Jungers, G. T. Schwartz, "Ecology and extinction of Madagascar's subfossil lemurs" in *Lemurs: Ecology and Adaptation*, L. Gould, M. L. Sauther, Eds. (Springer, 2006), pp. 41–64.

99. K. J. Hockings, *et al.*, Apes in the Anthropocene: flexibility and survival. *Trends Ecol. Evol.* **30**, 215–222 (2015).

100. A. Estrada, *et al.*, Impending extinction crisis of the world's primates: Why primates matter. *Sci. Adv.* **3**, e1600946 (2017).

101. C. Galán-Acedo, *et al.*, The conservation value of human-modified landscapes for the world's primates. *Nat. Commun.* **10**, 152 (2019).

102. C. A. Chapman, C. A. Peres, Primate conservation: lessons learned in the last 20 years can guide future efforts. *Evol. Anthropol*. **30**, 345–361 (2021).

103. P. J. Weatherhead, How unusual are unusual events? *Am. Nat.* **128**, 150–154 (1986).

104. Copernicus Climate Change Service (C3S). ERA5: Fifth generation of ECMWF atmospheric reanalyses of the global climate. Copernicus Climate Change Service Climate Data Store (CDS) (2017), https://cds.climate.copernicus.eu/cdsapp#!/home

105. J. O. Sexton, *et al.*, Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS vegetation continuous fields with lidar-based estimates of error. *Int. J. Digit. Earth* **6**, 427–448 (2013).

106. N. Gorelick, *et al.*, Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* **202**, 18–27 (2017).

107. R Core Development Team, R: A language and environment for statistical computing. R Foundation for Statistical Computing (2020).

108. IUCN (International Union for Conservation of Nature). The IUCN red list of threatened species. Gland, Switzerland (2017).

109. M. A. Tucker, T. L. Rogers, Examining predator–prey body size, trophic level and body mass across marine and terrestrial mammals. *Proc. R. Soc. B* **281**, 20142103 (2014).

110. T. Barsbai, D. Lukas, A. Pondorfer, Local convergence of behavior across species. *Science* 371, 292–295 (2021).

111. D. Hart, "Predation on primates: a biogeographical analysis" in *Primate Anti-Predator Strategies*, S. L. Gursky, K. A. I. Nekaris, Eds. (Springer, 2007), pp. 27–59

112. C. Fichtel, "Predation" in *The Evolution of Primate Societies*, J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, J. Silk, Eds. (Chicago University Press, 2012), pp. 169–194.

113. CIESIN - Center for International Earth Science Information Network, Columbia University. *Gridded population of the world, version 4 (GPWv4): Population density, revision 11*: NASA Socioeconomic Data and Applications Center (SEDAC) (2018).

114. N. Rowe, M. Myers, *All the World's Primates* (Primate Conservation, Inc., 2017), http://www.alltheworldsprimates.org

115. N. S. Upham, J. A. Esselstyn, W. Jetz, Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. *PLoS Biol.* **17**, e3000494 (2019).

116. C. F. Dormann, *et al.*, Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46 (2013).

117. M. Van de Pol, J. Wright, A simple method for distinguishing within-versus between-subject effects using mixed models. *Anim. Behav.* **77**, 753–758 (2009).

118. P. Bürkner, brms: An R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Softw.* **80**, 1–28 (2017).

Figures and Tables

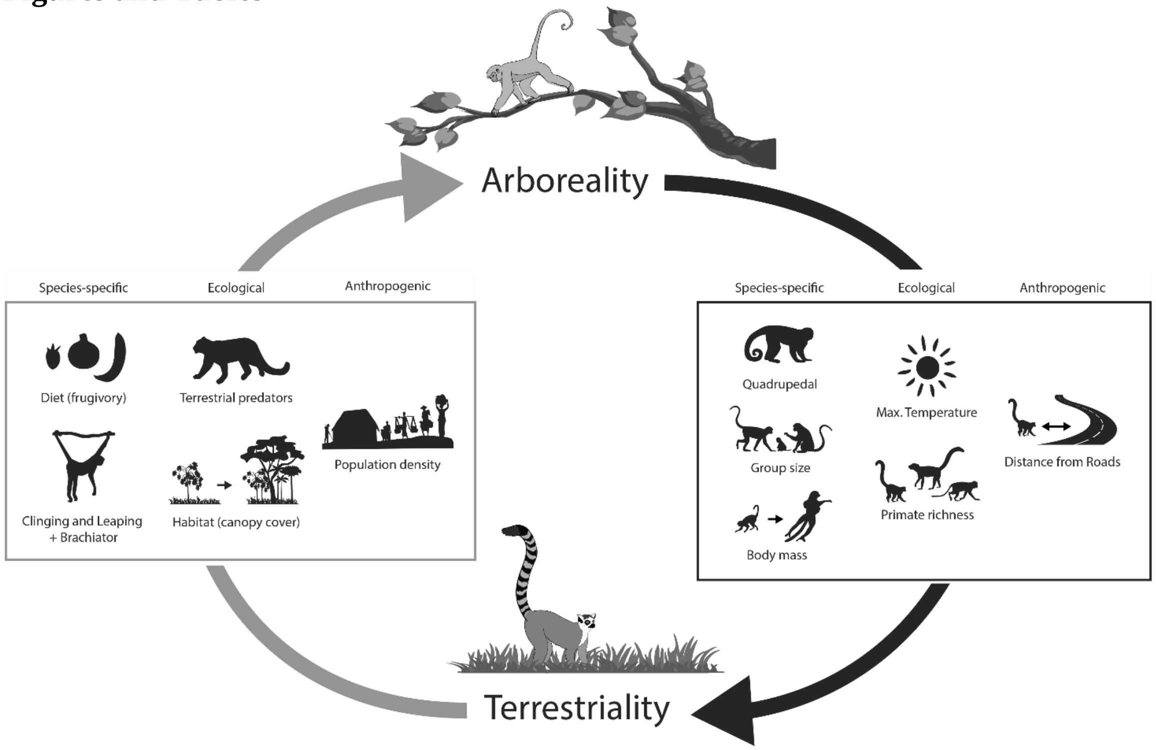

Fig. 1. Hypothesized relationships between species-specific traits, and ecological and anthropogenic factors and ground use by monkeys in the Americas and lemurs in Madagascar.

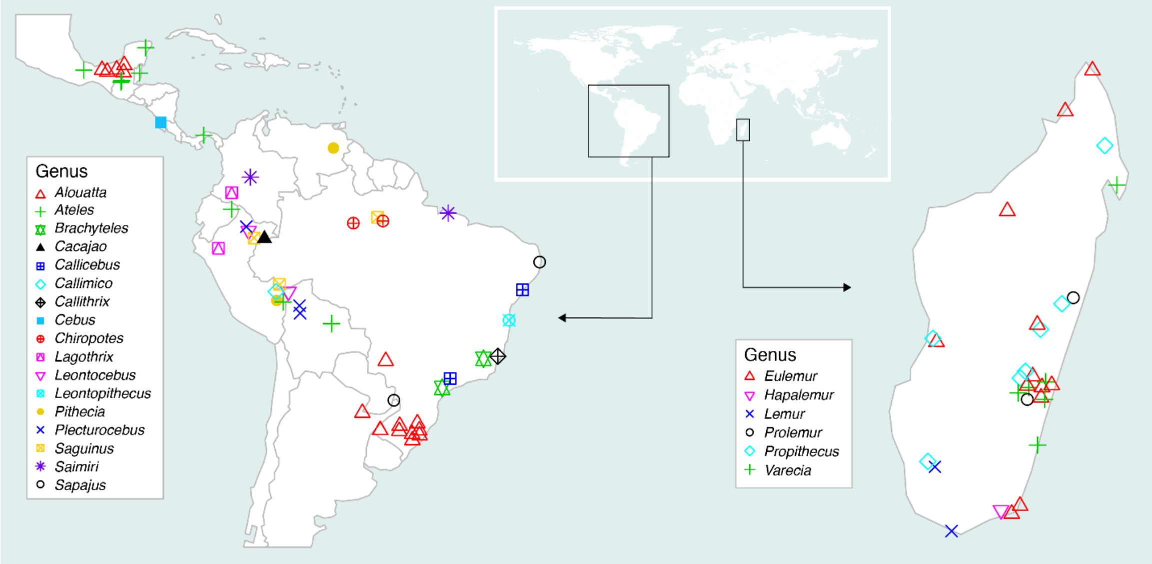

Fig. 2. Spatial distribution of primate genera included in our behavioral ecology dataset.

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.

	Estimate	Error	CI	PD
Within-Species Model				
Intercept	-4.21	1.39	-7.01 – -1.44	100%
Predation risk	0.23	0.15	-0.07 – 0.51	94%
Habitat (canopy cover)	-0.24	0.13	-0.50 – 0.01	96%
Temperature maximum	0.16	0.04	0.08 – 0.23	100%
Primate richness	0.22	0.19	-0.15 – 0.57	88%
Habitat x Primate richness	0.14	0.10	-0.06 – 0.33	92%
Diet (frugivory)	-0.16	0.04	-0.24 – -0.09	100%
Group size	0.09	0.05	-0.01 – 0.18	96%
Post-habituation	-0.03	0.04	-0.11 – 0.05	75%
Human population density	-0.07	0.16	-0.38 – 0.23	68%
Distance to road	0.38	0.17	0.03 – 0.70	99%
Between-Species Model				
Intercept	-3.75	2.28	-8.43 – 0.68	95%
Region (Americas)	-1.12	2.58	-6.25 – 4.35	70%
Predation risk	-0.23	0.42	-1.04 – 0.60	72%
Habitat (canopy cover)	0.59	0.40	-0.21 – 1.36	94%
Temperature maximum	0.00	0.31	-0.58 – 0.61	50%
Primate richness	-0.30	0.21	-0.70 – 0.11	93%
Habitat x Primate richness	-0.02	0.11	-0.23 – 0.20	56%
Diet (frugivory)	-0.22	0.27	-0.75 – 0.30	80%
Body mass	-0.58	0.39	-1.35 – 0.19	93%
Group size	0.38	0.28	-0.18 – 0.92	92%
IM index (Quadrupedal)	0.27	1.33	-2.34 – 2.87	58%
IM index (VCL)	0.27	1.44	-2.47 – 3.17	57%
Human population density	-0.12	0.37	-0.87 – 0.59	62%
Distance to road	0.28	0.42	-0.55 – 1.10	75%

Estimate = Mean of the posterior distribution; Error = Standard deviation of the posterior distribution; CI = 95% credible intervals; PD = probability of direction indicating the probability of a coefficient of being different from zero. IM (Inter-Membral) index intercept is a categorical variable and corresponds to brachiator, whereas VCL (vertical clinging and leaping) and quadrupedalism are the estimated differences from the intercept.