LETTER

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Averting biodiversity collapse in tropical forest protected areas

A list of the authors and their affiliations appears at the end of the paper.

The rapid disruption of tropical forests probably imperils global biodiversity more than any other contemporary phenomenon[1–3]. With deforestation advancing quickly, protected areas are increasingly becoming final refuges for threatened species and natural ecosystem processes. However, many protected areas in the tropics are themselves vulnerable to human encroachment and other environmental stresses[4–9]. As pressures mount, it is vital to know whether existing reserves can sustain their biodiversity. A critical constraint in addressing this question has been that data describing a broad array of biodiversity groups have been unavailable for a sufficiently large and representative sample of reserves. Here we present a uniquely comprehensive data set on changes over the past 20 to 30 years in 31 functional groups of species and 21 potential drivers of environmental change, for 60 protected areas stratified across the world's major tropical regions. Our analysis reveals great variation in reserve 'health': about half of all reserves have been effective or performed passably, but the rest are experiencing an erosion of biodiversity that is often alarmingly widespread taxonomically and functionally. Habitat disruption, hunting and forest-product exploitation were the strongest predictors of declining reserve health. Crucially, environmental changes immediately outside reserves seemed nearly as important as those inside in determining their ecological fate, with changes inside reserves strongly mirroring those occurring around them. These findings suggest that tropical protected areas are often intimately linked ecologically to their surrounding habitats, and that a failure to stem broad-scale loss and degradation of such habitats could sharply increase the likelihood of serious biodiversity declines.

Tropical forests are the biologically richest ecosystems on Earth[1–3]. Growing concerns about the impacts of anthropogenic pressures on tropical biodiversity and natural ecosystem services have led to increases in the number and extent of protected areas across the tropics[10]. However, much remains unknown about the likelihood of biodiversity persisting in such protected areas. Remote-sensing technologies offer a bird's-eye view of tropical forests and provide many important insights[6,11–13], but are largely unable to discern crucial on-the-ground changes in forest biodiversity and ecological functioning[14].

To appraise both the ecological integrity and threats for tropical protected areas on a global scale, we conducted a systematic and uniquely comprehensive assessment of long-term changes within 60 protected areas stratified across the world's major tropical forest regions (Supplementary Fig. 1). To our knowledge, no other existing data set includes such a wide range of biodiversity and threat indicators for such a large and representative network of tropical reserves. Our study was motivated by three broad issues: whether tropical reserves will function as 'arks' for biodiversity and natural ecosystem processes; whether observed changes are mainly concordant or idiosyncratic among different protected areas; and what the principal predictors of reserve success or failure are, in terms of their intrinsic characteristics and drivers of change.

To conduct our study we amassed expert knowledge from 262 detailed interviews, focusing on veteran field biologists and environmental scientists who averaged nearly 2 decades of experience (mean ± s.d., 19.1 ± 9.6 years) at each protected area. Each interviewed researcher completed a detailed 10-page questionnaire, augmented by a telephone or face-to-face interview (see Supplementary Information). The questionnaires focused on longer-term (approximately 20–30-year) changes in the abundance of 31 animal and plant guilds (trophically or functionally similar groups of organisms), which collectively have diverse and fundamental roles in forest ecosystems (Table 1). We also recorded data on 21 potential drivers of environmental change both inside each reserve and within a 3-km-wide buffer zone immediately surrounding it (Table 1).

Our sample of protected areas spans 36 nations and represents a geographically stratified and broadly representative selection of sites across the African, American and Asia-Pacific tropics (Supplementary Fig. 1). The reserves ranged from 160 ha to 3.6 million ha in size, but most (85%) exceeded 10,000 ha in area (median = 99,350 ha; lower decile = 7,000 ha; upper decile = 750,000 ha). The protected areas fall under various International Union for Conservation of Nature (IUCN) reserve classifications. Using data from the World Database on Protected Areas (http://www.wdpa.org), we found no significant difference ($P = 0.13$) in the relative frequency of high-protection (IUCN Categories I–IV), multiple-use (Categories V–VI) and

Table 1 | The 31 animal and plant guilds, and the 21 environmental drivers assessed both inside and immediately outside each protected area.

Guilds	Potential environmental drivers
Broadly forest-dependent guilds	
Apex predators	Changes in natural-forest cover
Large non-predatory species	Selective logging
Primates	Fires
Opportunistic omnivorous mammals	Hunting
Rodents	Harvests of non-timber forest products
Bats	Illegal mining
Understory insectivorous birds	Roads
Raptorial birds	Automobile traffic
Larger frugivorous birds	Exotic plantations
Larger game birds	Human population density
Lizards and larger reptiles	Livestock grazing
Venomous snakes	Air pollution
Non-venomous snakes	Water pollution
Terrestrial amphibians	Stream sedimentation
Stream-dwelling amphibians	Soil erosion
Freshwater fish	River & stream flows
Dung beetles	Ambient temperature
Army or driver ants	Annual rainfall
Aquatic invertebrates	Drought severity or intensity
Large-seeded old-growth trees	Flooding
Epiphytes	Windstorms
Other functional groups	
Ecological specialists	
Species requiring tree cavities	
Migratory species	
Disturbance-favouring guilds	
Lianas and vines	
Pioneer and generalist trees	
Exotic animal species	
Exotic plant species	
Disease-vectoring invertebrates	
Light-loving butterflies	
Human diseases	

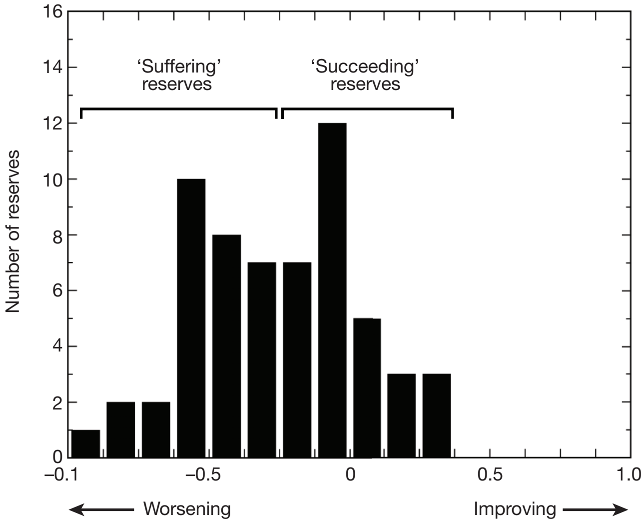

Figure 1 | Distribution of the 'reserve-health index' for 60 protected areas spanning the world's major tropical forest regions. This relative index averages changes in 10 well-studied guilds of animals and plants, including disturbance-avoiding and disturbance-favouring groups, over the past 20 to 30 years.

unclassified reserves between our sample of 60 reserves and all 16,038 reserves found in the same tropical nations (Supplementary Fig. 2). We also found no significant difference ($P = 0.08$) in the geographical isolation of our reserves (travel time to the nearest city with greater than 50,000 residents) relative to a random sample of 60 protected areas stratified across the same 36 nations (Supplementary Fig. 3).

We critically assessed the validity of our interview data by comparing them to 59 independent time-series data sets in which change in a single guild or environmental driver was assessed for one of our protected areas. Collectively, our meta-analysis included some data on 15 of the guilds, 13 of the drivers and 27 of the protected areas in our study (Supplementary Table 1). Most (86.4%) of the independent data sets supported our interview results, and in no case did an independent test report a trend opposite in sign to our interview-based findings.

Our analyses suggest that the most sensitive guilds in tropical protected areas include apex predators, large non-predatory vertebrates, bats, stream-dwelling amphibians, terrestrial amphibians, lizards and larger reptiles, non-venomous snakes, freshwater fish, large-seeded old-growth trees, epiphytes and ecological specialists (all $P < 0.0056$, with effect sizes ranging from -0.36 to -1.05; Supplementary Table 2). Several other groups were somewhat less vulnerable, including primates, understory insectivorous birds, large frugivorous birds, raptorial birds, venomous snakes, species that require tree cavities, and migratory species (all $P < 0.05$, with effect sizes from -0.27 to -0.53). In addition, five groups increased markedly in abundance in the reserves, including pioneer and generalist trees, lianas and vines, invasive animals, invasive plants and human diseases (all $P < 0.0056$, with effect sizes from 0.44 to 1.17).

To integrate these disparate data, we generated a 'reserve-health index' that focused on 10 of the best-studied guilds (data for each available at $\geq 80\%$ of reserves), all of which seem to be sensitive to environmental changes in protected areas. Six of these are generally 'disturbance avoiders' (apex predators, large non-predatory vertebrates, primates, understory insectivorous birds, large frugivorous birds and large-seeded old-growth trees) and the remainder seem to be 'disturbance-favouring' groups (pioneer and generalist trees, lianas and vines, exotic animals and exotic plants). For each protected area, we averaged the mean values for each group, using negative values to indicate increases in abundance of the disturbance-favouring guilds.

The reserve-health index varied greatly among the different protected areas (Fig. 1). About four-fifths of the reserves had negative values, indicating some decline in reserve health. For 50% of all reserves this decline was relatively serious (mean score < -0.25), with the affected organisms being remarkable for their high functional and taxonomic diversity (Fig. 2). These included plants with varying growth forms and life-history strategies, and fauna that differed widely in body size, trophic level, foraging strategies, area needs, habitat use and other attributes. The remaining reserves generally exhibited much more positive outcomes for biodiversity (Fig. 2), although a few disturbance-favouring guilds, such as exotic plants and pioneer and generalist trees, often increased even within these areas.

An important predictor of reserve health was improving reserve management. According to our experts, reserves in which actual, on-the-ground protection efforts (see Supplementary Information) had increased over the past 20 to 30 years generally fared better than those in which protection had declined; a relationship that was consistent across all three of the world's major tropical regions (Fig. 3). Indeed, on-the-ground protection has increased in more than half of the reserves over the past 20 to 30 years, and this is assisting efforts to limit threats such as deforestation, logging, fires and hunting within these reserves (Supplementary Table 3), relative to areas immediately outside (Supplementary Table 4).

However, our findings show that protecting biodiversity involves more than just safeguarding the reserves themselves. In many instances, the landscapes and habitats surrounding reserves are under imminent threat[5,6,15] (Fig. 4 and Supplementary Tables 3 and 4). For example, 85% of our reserves suffered declines in surrounding forest cover in the last 20 to 30 years, whereas only 2% gained surrounding forest. As shown by general linear models (Supplementary Table 5), such changes can seriously affect reserve biodiversity. Among the

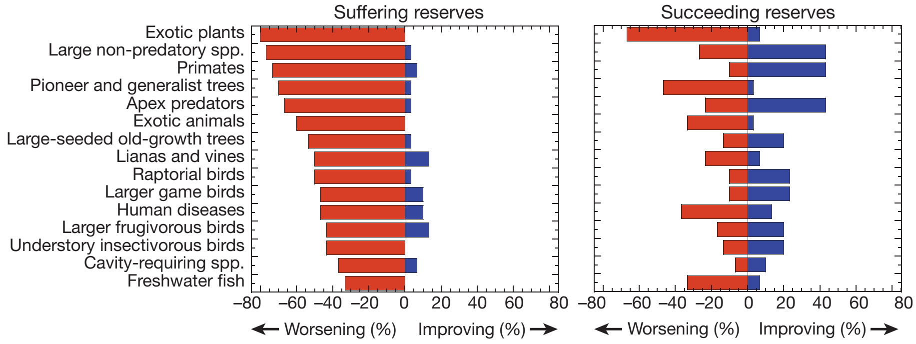

Figure 2 | Percentages of reserves that are worsening versus improving for key disturbance-sensitive guilds, contrasted between 'suffering' and 'succeeding' reserves (which are distinguished by having lower (< -0.25) versus higher (≥ -0.25) values for the reserve-health index, respectively). For disturbance-favouring organisms such as exotic plants and plants, pioneer and generalist trees, lianas and vines, and human diseases, the reserve is considered to be worsening if the group increased in abundance. For any particular guild, reserves with missing or zero values (no trend) are not included.

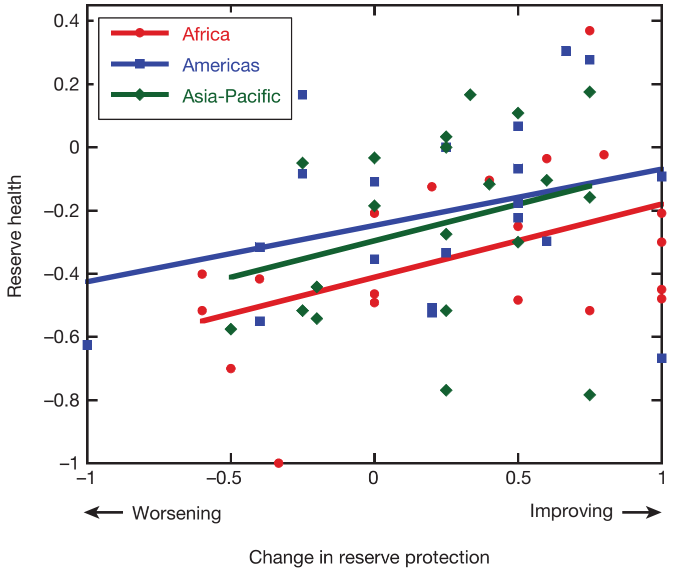

Figure 3 | Effects of improving on-the-ground protection on a relative index of reserve health. This positive relationship held across all three tropical continents (a general linear model showed that the protection term was the most effective predictor of reserve health (Akaike's information criterion weight, 0.595; deviance explained, 11.4%), with the addition of 'continent' providing only a small improvement in model fit (Akaike's information criterion weight, 0.317; deviance explained, 16.3%).

potential drivers of declining reserve health, three of the most important predictors involved ecological changes outside reserves (declining forest cover, increasing logging and increasing fires outside reserves; Supplementary Fig. 6). The remainder involved changes within reserves (particularly declining forest cover and increasing hunting, as well as increasing logging and harvests of non-timber forest products; Supplementary Table 5).

Thus, changes both inside and outside reserves determine their ecological viability, with forest disruption (deforestation, logging and fires), and overexploitation of wildlife and forest resources (hunting and harvests of non-timber forest products) having the greatest direct negative impacts. Other environmental changes, such as air and water pollution, increases in human population densities and climatic change (changes in total rainfall, ambient temperature, droughts and windstorms) generally had weaker or more indirect effects over the last 20 to 30 years (Supplementary Table 5).

Environmental degradation occurring around a protected area could affect biodiversity in many ways, such as by increasing reserve isolation, area and edge effects[15–19]. However, we discovered that its effects are also more insidious: they strongly predispose the reserve itself to similar kinds of degradation. Nearly all (19 of 21) of the environmental drivers had positive slopes when comparing their direction and magnitude inside versus outside reserves (Fig. 5). Among these, 13 were significant even with stringent Bonferroni corrections ($P < 0.0071$) and 17 would have been significant if tested individually ($P < 0.05$). As expected, the associations were strongest for climate parameters but were also strong for variables describing air and water pollution, stream sedimentation, hunting, mining, harvests of non-timber forest products and fires. To a lesser extent, trends in forest cover, human populations, road expansion and automobile traffic inside reserves also mirror those occurring outside reserves (Fig. 5).

Our findings signal that the fates of tropical protected areas will be determined by environmental changes both within and around the reserves, and that pressures inside reserves often closely reflect those occurring around them. For many reasons, larger reserves should be more resilient to such changes[15–22], although we found that removing the effects of reserve area statistically did not consistently weaken the correlations between changes inside versus outside protected areas (Supplementary Table 6).

Our study reveals marked variability in the health of tropical protected areas. It indicates that the best strategy for maintaining biodiversity within tropical reserves is to protect them against their major proximate threats, particularly habitat disruption and overharvesting. However, it is not enough to confine such efforts to reserve interiors while ignoring their surrounding landscapes, which are often being rapidly deforested, degraded and overhunted[5,6,13,15] (Fig. 5). A failure to limit interrelated internal and external threats could predispose reserves to ecological decay, including a taxonomically and functionally

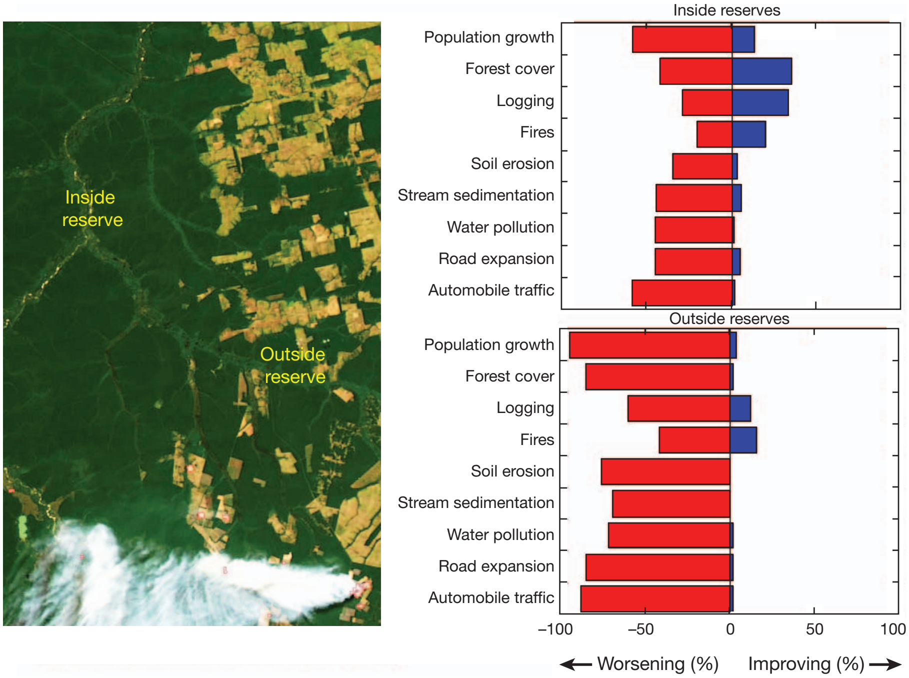

Figure 4 | Comparison of ecological changes inside versus outside protected areas, for selected environmental drivers. The image is an example of the strong distinction in disturbance inside versus outside a reserve. The bars show the percentages of reserves with improving versus worsening conditions.

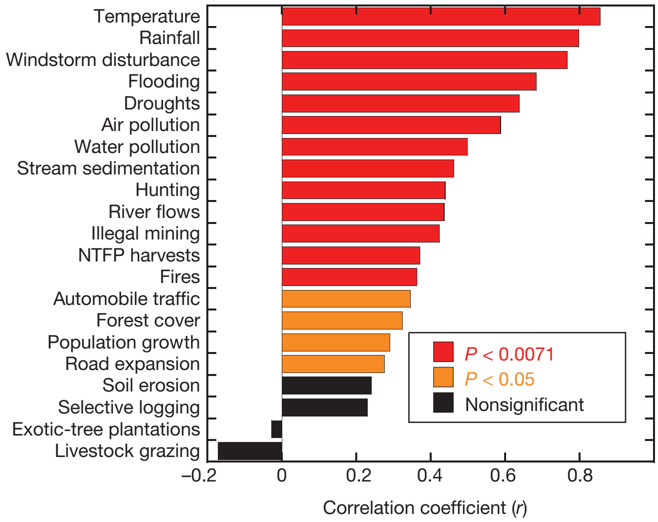

Figure 5 | Pearson correlations comparing the direction and strength of 21 environmental drivers inside versus outside tropical protected areas. NTFP, non-timber forest products.

sweeping array of changes in species communities (Fig. 2) and an erosion of fundamental ecosystem processes[16,18,23].

Protected areas are a cornerstone of efforts to conserve tropical biodiversity[3,4,13,21]. It is not our intent to diminish their crucial role but to highlight growing challenges that could threaten their success. The vital ecological functions of wildlife habitats surrounding protected areas create an imperative, wherever possible, to establish sizeable buffer zones around reserves, maintain substantial reserve connectivity to other forest areas and promote lower-impact land uses near reserves by engaging and benefiting local communities[4,15,24–27]. A focus on managing both external and internal threats should also increase the resilience of biodiversity in reserves to potentially serious climatic change[28–30] in the future.

METHODS SUMMARY

Our interview protocol, rationale, questionnaire and data analyses are detailed in the Supplementary Information. We selected protected areas broadly to span the African, American and Asia-Pacific tropics (Supplementary Fig. 1), focusing on sites with mostly tropical or subtropical forest that had at least 10 refereed publications and 4–5 researchers with long-term experience who could be identified and successfully interviewed.

We devised a robust and relatively simple statistical approach to assess temporal changes in the abundance of each guild and in each potential environmental driver across our reserve network (see Supplementary Information). In brief, this involved asking each expert whether each variable had markedly increased, remained stable or markedly declined for each reserve. These responses were scored as 1, 0 and -1, respectively. For each response, the expert was also asked to rank their degree of confidence in their knowledge. After discarding responses with lower confidence, scores from the individual experts at each site were pooled to generate a mean value (ranging from -1.0 to 1.0) to estimate the long-term trend for each variable.

The means for each variable across all 60 sites were then pooled into a single data distribution. We used bootstrapping (resampling with replacement; 100,000 iterations) to generate confidence intervals for the overall mean of the data distribution. If the confidence intervals did not overlap zero, then we interpreted the trend as being non-random. Because we tested many different guilds, we used a stringent Bonferroni correction ($P \leq 0.0056$) to reduce the likelihood of Type I statistical errors, although we also identified guilds that showed evidence of trends ($P \leq 0.05$) if tested individually. For comparison, we estimated effect sizes (bootstrapped mean divided by s.d., with negative values indicating declines) for changes in guild abundances and for potential drivers inside and outside reserves (Supplementary Tables 2–4).

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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William F. Laurance[1,2], D. Carolina Useche[2], Julio Rendeiro[2], Margareta Kalka[2], Corey J. A. Bradshaw[3], Sean P. Sloan[1], Susan G. Laurance[1], Mason Campbell[1], Kate

Abernethy[4], Patricia Alvarez[5], Victor Arroyo-Rodriguez[6], Peter Ashton[7], Julieta Benítez-Malvido[6], Allard Blom[8], Kadiri S. Bobo[9], Charles H. Cannon[10], Min Cao[10], Richard Carroll[8], Colin Chapman[11], Rosamond Coates[12], Marina Cords[13], Finn Danielsen[14], Bart De Dijn[15], Eric Dinerstein[8], Maureen A. Donnelly[16], David Edwards[1], Felicity Edwards[1], Nina Farwig[17], Peter Fashing[18], Pierre-Michel Forget[19], Mercedes Foster[20], George Gale[21], David Harris[22], Rhett Harrison[10], John Hart[23], Sarah Karpanty[24], W. John Kress[25], Jagdish Krishnaswamy[26], Willis Logsdon[1], Jon Lovett[27], William Magnusson[28], Fiona Maisels[4,29], Andrew R. Marshall[30], Deedra McClearn[31], Divya Mudappa[32], Martin R. Nielsen[33], Richard Pearson[34], Nigel Pitman[5], Jan van der Ploeg[35], Andrew Plumptre[36], John Poulsen[37], Mauricio Quesada[6], Hugo Rainey[29], Douglas Robinson[38], Christiane Roetgers[1], Francesco Rovero[39], Frederick Scatena[40], Christian Schulze[41], Douglas Sheil[42], Thomas Struhsaker[5], John Terborgh[5], Duncan Thomas[38], Robert Timm[43], J. Nicolas Urbina-Cardona[44], Karthikeyan Vasudevan[45], S. Joseph Wright[2], Juan Carlos Arias-G.[46], Luzmila Arroyo[47], Mark Ashton[48], Philippe Auzel[11], Dennis Babaasa[49], Fred Babweteera[50], Patrick Baker[51], Olaf Banki[52], Margot Bass[53], Inogwabini Bila-Isia[54], Stephen Blake[29], Warren Brockelman[55], Nicholas Brokaw[56], Carsten A. Brühl[57], Sarayudh Bunyavejchewin[58], Jung-Tai Chao[59], Jerome Chave[60], Ravi Chellam[61], Connie J. Clark[5], José Clavijo[62], Robert Congdon[34], Richard Corlett[63], H. S. Dattaraja[64], Chittaranjan Dave[65], Glyn Davies[66], Beatriz de Mello Beisiegel[67], Rosa de Nazaré Paes da Silva[68], Anthony Di Fiore[69], Arvin Diesmos[70], Rodolfo Dirzo[71], Diane Doran-Sheehy[72], Mitchell Eaton[73], Louise Emmons[25], Alejandro Estrada[12], Corneille Ewango[74], Linda Fedigan[75], François Feer[19], Barbara Fruth[76], Jacalyn Giacalone Willis[77], Uromi Goodale[78], Steven Goodman[79], Juan C. Guix[80], Paul Guthiga[81], William Haber[82], Keith Hamer[83], Ilka Herbinger[84], Jane Hill[30], Zhongliang Huang[85], I Fang Sun[86], Kalan Ickes[87], Akira Itoh[88], Natália Ivanauskas[89], Betsy Jackes[34], John Janovec[90], Daniel Janzen[40], Mo Jiangming[91], Chen Jin[10], Trevor Jones[92], Hermes Justiniano[93], Elisabeth Kalko[94]‡, Aventino Kasangaki[95], Timothy Killeen[96], Hen-biau King[97], Erik Klop[98], Cheryl Knott[99], Inza Koné[100], Enoka Kudavidanage[63], José Lahoz da Silva Ribeiro[101], John Lattke[102], Richard Laval[103], Robert Lawton[104], Miguel Leal[105], Mark Leighton[106], Miguel Lentino[107], Cristiane Leonel[108], Jeremy Lindsell[109], Lee Ling-Ling[110], K. Eduard Linsenmair[111], Elizabeth Losos[112], Ariel Lugo[113], Jeremiah Lwanga[114], Andrew L. Mack[115], Marlucia Martins[116], W. Scott McGraw[117], Roan McNab[118], Luciano Montag[119], Jo Myers Thompson[120], Jacob Nabe-Nielsen[121], Michiko Nakagawa[122], Sanjay Nepal[123], Marilyn Norconk[124], Vojtech Novotny[125], Sean O'Donnell[126], Muse Opiang[127], Paul Ouboter[128], Kenneth Parker[129], N. Parthasarathy[130], Kátia Pisciotta[131], Dewi Prawiradilaga[132], Catherine Pringle[133], Subaraj Rajathurai[134], Ulrich Reichard[135], Gay Reinartz[136], Katherine Renton[137], Glen Reynolds[138], Vernon Reynolds[139], Erin Riley[140], Mark-Oliver Rödel[141], Jessica Rothman[142], Philip Round[143], Shoko Sakai[144], Tania Sanaiotti[28], Tommaso Savini[21], Gertrud Schaab[145], John Seidensticker[146], Alhaji Siaka[147], Miles R. Silman[148], Thomas B. Smith[149], Samuel Soares de Almeida[150]‡, Navjot Sodhi[63]‡, Craig Stanford[151], Kristine Stewart[152], Emma Stokes[29], Kathryn E. Stoner[153], Raman Sukumar[154], Martin Surbeck[76], Mathias Tobler[90], Teja Tscharntke[155], Andrea Turkalo[156], Govindaswamy Umapathy[157], Merlijn van Weerd[35], Jorge Vega Rivera[137], Meena Venkataraman[158], Linda Venn[159], Carlos Verea[160], Carolina Volkmer de Castilho[161], Matthias Waltert[155], Benjamin Wang[149], David Watts[48], William Weber[29], Paige West[13], David Whitacre[162], Ken Whitney[163], David Wilkie[29], Stephen Williams[34], Debra D. Wright[115], Patricia Wright[164], Lu Xiankai[91], Pralad Yonzon[165]‡ & Franky Zamzani[166]

[1]Centre for Tropical Environmental and Sustainability Science (TESS) and School of Marine and Tropical Biology, James Cook University, Cairns, Queensland 4878, Australia. [2]Smithsonian Tropical Research Institute, Balboa, Ancón, Panama. [3]School of Earth and Environmental Sciences, University of Adelaide, Adelaide, South Australia 5005, Australia. [4]Stirling University, Stirling FK9 4LA, UK. [5]Duke University, Durham, North Carolina 27705, USA. [6]Universidad Nacional Autónoma de México (UNAM), Morelia, Mexico. [7]Royal Botanic Gardens, Kew, Richmond TW9 3AB, UK. [8]World Wildlife Fund (WWF), Washington DC 20037, USA. [9]University of Dschang, Dschang, Cameroon. [10]Xishuangbanna Tropical Botanical Garden, Yunnan 666303, People's Republic of China. [11]McGill University, Montreal H3A 2T7, Canada. [12]Estación de Biologia Tropical Los Tuxtlas, Universidad Nacional Autónoma de México, Veracruz 95701, Mexico. [13]Columbia University, New York, New York 10027, USA. [14]Nordic Foundation for Development and Ecology, DK-1159 Copenhagen, Denmark. [15]Bart De Dijn Environmental Consultancy, Paramaribo, Suriname. [16]Florida International University, Miami, Florida 33199, USA. [17]Philipps-Universität Marburg, Marburg 35043, Germany. [18]California State University, Fullerton, California 92834, USA. [19]Museum Natural d'Histoire Naturelle, 91800 Brunoy, France. [20]US Geological Survey, Smithsonian Institution, Washington DC 20013, USA. [21]King Mongkut's University of Technology Thonburi, Bangkok 10150, Thailand. [22]Royal Botanic Garden, Edinburgh, Scotland EH3 5LR, UK. [23]Tshuapa-Lomami-Lualaba Project, Kinshasa, Democratic Republic of Congo. [24]Virginia Tech University, Blacksburg, Virginia 24061, USA. [25]National Museum of Natural History, Smithsonian Institution, Washington DC 20013, USA. [26]Ashoka Trust for Research in Ecology and the Environment (ATREE), Bangalore 560064, India. [27]University of Twente, Enschede, Netherlands. [28]Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas 69011-970, Brazil. [29]Wildlife Conservation Society, Bronx, New York 10460, USA. [30]University of York, Heslington, York YO10 5DD, UK. [31]La Selva Biological Station, San Pedro, Costa Rica. [32]Nature Conservation Foundation, Mysore 570 002, India. [33]University of Copenhagen, Copenhagen, Denmark. [34]James Cook University, Townsville, Queensland 4811, Australia. [35]Leiden University, Leiden, Netherlands. [36]Wildlife Conservation Society, Kampala, Uganda. [37]Woods Hole Research Center, Falmouth, Massachusetts 02540, USA. [38]Oregon State University, Corvallis, Oregon 97331, USA. [39]Museo delle Scienze, 38122 Trento, Italy. [40]University of Pennsylvania, Philadelphia, Pennsylvania 19104, USA. [41]University of Vienna, 1030 Vienna, Austria. [42]Bwindi Impenetrable National Park, Kabale, Uganda. [43]University of Kansas, Lawrence, Kansas 66045, USA. [44]Pontificia Universidad Javeriana, Bogotá, Colombia. [45]Wildlife Institute of India, Dehradun, India. [46]Unidad de Parques Nacionales Naturales de Colombia, Bogotá, Colombia. [47]Museo de Historia Natural Noel Kempff, Santa Cruz, Bolivia. [48]Yale University, New Haven, Connecticut 06511, USA. [49]Institute of Tropical Forest Conservation, Kabale, Uganda. [50]Budongo Conservation Field Station, Masindi, Uganda. [51]Monash University, Melbourne, Victoria 3800, Australia. [52]Utrecht University, Utrecht, Netherlands. [53]Finding Species, Takoma Park, Maryland 20912, USA. [54]University of Kent, Kent CT2 7NZ, UK. [55]Mahidol University Salaya, Nakhon Pathom 73170, Thailand. [56]University of Puerto Rico, San Juan 00936, Puerto Rico. [57]University Koblenz-Landau, D-76829 Landau, Germany. [58]Department of National Parks, Chatuchak, Bangkok 10900, Thailand. [59]Taiwan Forestry Research Institute, Tapei 10066, Taiwan. [60]Université Paul Sabatier, Toulouse, France. [61]Wildlife Conservation Society, Bangalore 560070, India. [62]Universidad Central de Venezuela, Aragua, Venezuela. [63]National University of Singapore, Singapore 117543. [64]Indian Institute of Science, Bangalore 560012, India. [65]World Wide Fund for Nature (WWF), New Delhi 110003, India. [66]World Wide Fund for Nature (WWF), Surrey GU7 1XR, UK. [67]Instituto Chico Mendes de Conservação de Biodiversidade, Atibaia, São Paulo 12952-011, Brazil. [68]O Conselho Regional de Engenhara, Arquitetura e Agronomia do Pará, Belém, Pará, Brazil. [69]University of Texas, Austin, Texas 78712, USA. [70]National Museum of the Philippines, Manila, Phillipines. [71]Stanford University, Stanford, California 94305, USA. [72]State University of New York at Stony Brook, Stony Brook, New York 11794, USA. [73]University of Colorado, Boulder, Colorado 80309, USA. [74]Wildlife Conservation Society, Kinshasa, Democratic Republic of Congo. [75]University of Calgary, Alberta T2N 1N4, Canada. [76]Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. [77]Montclair State University, Montclair, New Jersey 07043, USA. [78]University of California, San Diego, California 92093, USA. [79]Field Museum of Natural History, Chicago, Illinois 60605, USA. [80]Universitat de Barcelona, 08028 Barcelona, Spain. [81]Kenya Institute for Public Policy Research and Analysis, Nairobi, Kenya. [82]Missouri Botanical Garden, St. Louis, Missouri 63166, USA. [83]University of Leeds, Leeds LS2 9JT, UK. [84]Wild Chimpanzee Foundation, Abidjan 23, Cote d'Ivoire. [85]Dinghushan Biosphere Reserve, Zhaoqing, People's Republic of China. [86]Tunghai University, Taichung 407, Taiwan. [87]Clemson University, Clemson, South Carolina 29634, USA. [88]Osaka City University, Osaka 558-8585, Japan. [89]Instituto Florestal, São Paulo, São Paulo 02377-000, Brazil. [90]Botanical Research Institute of Texas, Fort Worth, Texas 76107, USA. [91]South China Botanical Garden, Guangzhou 510650, People's Republic of China. [92]Anglia Ruskin University, Cambridge CB1 1PT, UK. [93]Fundación para la Conservación del Bosque Chiquitano, Bolivia. [94]University of Ulm, 89069 Ulm, Germany. [95]Mbarara University of Science and Technology, Mbarara, Uganda. [96]Conservation International, Arlington, Virginia 22202, USA. [97]Society of Subtropical Ecology, Taipei, Taiwan. [98]Royal Haskoning, Water and Ecology Group, Groningen, Netherlands. [99]Boston University, Boston, Massachusetts 02215, USA. [100]Centre Suisse de Recherches Scientifiques en Côte d'Ivoire, Abidjan, Côte d'Ivoire. [101]Universidade Estadual de Londrina, Londrina, Paraná, Brazil. [102]Universidad Central de Venezuela, Caracas, Venezuela. [103]The Bat Jungle, Monteverde, Costa Rica. [104]University of Alabama, Huntsville, Alabama 35899, USA. [105]Boîte Postale 7847, Libreville, Gabon. [106]95 Warren Road, Framingham, Massachusetts 01702, USA. [107]Colección Ornitológica Phelps, Caracas, Venezuela. [108]Parque Estadual Horto Florestal, São Paulo, São Paulo 02377-000, Brazil. [109]Royal Society for the Protection of Birds, Sandy SG19 2DL, UK. [110]National Taiwan University, Taipei, Taiwan. [111]University of Würzburg, Biocenter, D97074 Wuerzburg, Germany. [112]Organization for Tropical Studies, Durham, North Carolina 27705, USA. [113]USDA International Institute of Tropical Forestry, Río Piedras, Puerto Rico 00926. [114]Makerere University, Kampala, Uganda. [115]Green Capacity Inc., New Florence, Pennsylvania 15944, USA. [116]Museu Paraense Emílio Goeldi, Belém, Pará 66040-170, Brazil. [117]Ohio State University, Columbus, Ohio 43210, USA. [118]Wildlife Conservation Society, Flores, Guatemala. [119]Universidad Federal do Pará, Belém, Pará 66040-170, Brazil. [120]Lukuru Wildlife Research Foundation, Kinshasa, Democratic Republic of Congo. [121]Aarhus University, 4000 Roskilde, Denmark. [122]Nagoya University, Nagoya, Japan. [123]University of Waterloo, Waterloo, Ontario N2L 3G1, Canada. [124]Kent State University, Kent, Ohio 44242, USA. [125]Institute of Entomology, Ceske Budejovice, Czech Republic. [126]University of Washington, Seattle, Washington 98195, USA. [127]PNG Institute of Biological Research, Goroka, Papua New Guinea. [128]University of Suriname, Paramaribo, Suriname. [129]113-3885 Richet Rd, Prince George, British Columbia V2K 2J2, Canada. [130]Pondicherry University, Puducherry 605-014, India. [131]Fundação Florestal, São Paulo, São Paulo 02377-000, Brazil. [132]Research Centre for Biology, Cibinong 16911, Indonesia. [133]University of Georgia, Athens, Georgia 30602, USA. [134]Strix Wildlife Consultancy, Singapore. [135]Southern Illinois University, Carbondale, Illinois 62901, USA. [136]Zoological Society of Milwaukee, Milwaukee, Wisconsin 53226, USA. [137]Estación de Biologia Chamela, Universidad Nacional Autónoma de México, Jalisco 48980, Mexico. [138]Danum Valley Field Centre, Sabah, Malaysia. [139]Oxford University, Oxford BN26 5UX, UK. [140]San Diego State University, San Diego, California 92182, USA. [141]Museum für Naturkunde, Berlin, Germany. [142]City University of New York, New York 10065, USA. [143]Mahidol University, Bangkok 10400, Thailand. [144]Research Institute for Humanity and Nature, Kyoto, Japan. [145]Karlsruhe University of Applied Sciences, Karlsruhe, Germany. [146]National Zoological Park, Washington DC 20013, USA. [147]Gola Forest Programme, Kenema, Sierra Leone. [148]Wake Forest University, Winston-Salem, North Carolina 27106, USA. [149]University of California, Los Angeles, California 90095, USA. [150]Av. Maalhães Barata 376, Belém, Pará 66040-170, Brazil. [151]University of Southern California, Los Angeles, California 90089, USA. [152]Institute of Applied Ethnobotany, Pompano Beach, Florida 33069, USA. [153]Texas A & M University, Kingsville, Texas 78363, USA. [154]Indian Institute of Science, Bangalore, India. [155]Georg-August-Universität, Göttingen, Germany. [156]Wildlife Conservation Society, Bangui, Central African Republic. [157]Centre for Cellular and Molecular Biology, Hyderabad, India. [158]701, Vesta B, Lodha Paradise, Thane, India. [159]Paluma Environmental Education Centre, Paluma, Queensland 4816, Australia. [160]Universidad Central de Venezuela, Maracay, Venezuela. [161]Embrapa Roraima, Boa Vista, Roraima, Brazil. [162]Treasure Valley Math and Science Center, Boise, Idaho 83714, USA. [163]Rice University, Houston, Texas 77005, USA. [164]Stony Brook University, Stony Brook, New York 11794, USA. [165]Resources Himalaya Foundation, Kathmandu, Nepal. [166]Gunung Palung National Park, West Kalimantan, Indonesia.
‡Deceased.