Science Advances

THE
AMAZON

AAAS

Special Collection
OPEN ACCESS

SPECIAL COLLECTION: The Amazon

Select research published in *Science Advances*

The Amazon region covers about 40 percent of South America and influences the many countries and cultures that it covers, from Bolivia to Brazil, Columbia, Ecuador, Guyana, Peru, Suriname, and Venezuela. The region holds among the world's great riches in both plant and animal biodiversity and provides the planet with vital resources for sustained planetary health. This collection of research articles, and the overview provided by pre-eminent scholar and Amazonian expert Dr. Thomas Lovejoy, bring together powerful documentation of the threats to the region's resources and the potential consequences of their loss.

Credit: Koh/istock

ScienceAdvances | AAAS OPEN ACCESS

Science Advances is the digital, open access expansion of *Science* magazine. We publish significant, innovative original research that advances the frontiers of science across a broad arrange of disciplines.

Editor-in- Chief
Jeremy Berg, Ph.D.

Managing Editor
Philippa Benson, Ph.D.

IN THIS COLLECTION

Science Advances Editorial Board Members

DEPUTY EDITORS
Lynden Archer
Cornell University
Aaron Clauset
University of Colorado Boulder
Sarah Fortune
Harvard University
Kip V. Hodges
Arizona State University
Jeremy Jackson
Smithsonian /Scripps
Zakya Kafafi
Lehigh University
Kevin S. LaBar
Duke University, Center for Cognitive Neuroscience
Shahid Naeem
Columbia University
Ali Shilatifard
Northwestern University
Warren Warren
Duke University
Philip Yeagle
University of Connecticut

ASSOCIATE EDITORS
Pulickel Ajayan
Rice University
Mark Aldenderfer
University of California, Merced
Laura D. Attardi
Stanford University
Amanda Barnard
CSIRO
Scott Barrett
Columbia University
Simon Charles Benjamin
University of Oxford
Emily Bernhardt
Duke University
Gregory C. Beroza
Stanford University
Paul Bierman
University of Vermont
Ed Billups
Rice University
Barbara Block
Stanford University
Mike Brown
California Institute of Technology
Joseph S. Broz
SRI International
Julia Chan
University of Texas at Dallas
Navdeep S. Chandel
Northwestern University
Sherry Chemler
The University at Buffalo
Vadim Cherezov
University of Southern California
Julia Clarke
University of Texas at Austin
David Cory
University of Waterloo
Richard D. Cummings
Harvard Medical School
Lélia Delamarre Genentech
South San Francisco
Luciano Di Croce
Center for Genomic Regulation
Dale Dorsett
St. Louis University
Robert B. Dunbar
Stanford University
Patrik Ernfors
Karolinska Institutet
Gleb Finkelstein
Duke University
Maria Flytzani-Stephanopoulos
Tufts University
Tamás Freund
Hungarian Academy of Sciences
Kevin Furlong
Penn State University
John C. Fyfe
Canadian Centre for Climate Modelling and Analysis
Glenn A. Gaetani
Woods Hole Oceanographic Institution
Chris Garrett
University of Victoria
Elizabeth Goldschmidt
US Army Research Lab
Joerg Graf
University of Connecticut
Reuben Harris
University of Minnesota, Twin Cities
Mark E. Hay
Georgia Institute of Technology
Sarah Heilshorn
Stanford University
Christophe Herman
Baylor College of Medicine
Michael Hochberg
University of Montpellier (ISEM)
Jennifer Jacquet
New York University
David James
Northwestern University
Patricia H. Janak
Johns Hopkins University
Jan Karlseder
The Salk Institute for Biological Studies
Meredith Kelly
Dartmouth College
Laeeq Khan
Ohio University
Rachel Klima
Applied Physics Lab, Johns Hopkins University
Naomi Krogman
University of Alberta
Raphael Kudela
UC Santa Cruz
Eugenia Kumacheva
University of Toronto
Robert L. Last
Michigan State University
David Lea
UC Santa Barbara
Cin-Ty A. Lee
Rice University
Lisa A. Levin
Scripps Institution of Oceanography, UCSD
Laura Na Liu
University of Heidelberg
Virginia Lorenz
University of Illinois
David Lou
Nanyang Technological University
Thomas Lovejoy
George Mason University, United Nations Foundation
Yonglong Lu
Chinese Academy of Science
George Malliaras
University of Cambridge
Yuji Matsuda
Kyoto University
Robin C. May
University of Birmingham
Mark McNiven
Mayo Clinic
Robert E. Megginson
University of Michigan
Carmen Menoni
Colorado State University
Andreas S. Meyer-Lindenberg
Heidelberg University
John Miao
UCLA
Jack J. Middelburg
Utrecht University
Penelope Morel
University of Pittsburgh
Trudy Morrison
University of Massachusetts
Margaret Murnane
University of Colorado
Harini Nagendra
Azim Premji University
Kia (Anna Christina)
Nobre Oxford Centre for Human Brain Activity
Ryo Okamoto
Osaka University
Stanley Osher
UCLA
Rebecca Page
University of Arizona
Wendy Panero
Ohio State
Gregory A. Petsko
Weill Cornell Medical College
Julie Phillippi
University of Pittsburgh
Barry Pogson
Australian National University
Wilson Poon
University of Edinburgh
Raul Rabadan
Columbia University
Markus Raschke
University of Colorado
Ray Rezaie
Oklahoma Medical Research Foundation
John A. Rogers
Northwestern University
Lizabeth Romanski
University of Rochester
Anthony B. Rylands
Conservation International
Akira Sawa
Johns Hopkins School of Medicine
John Schellnhuber
Potsdam Institute for Climate Impact Research
Christoph F. Schmidt
Göttingen University
Blair Schoene
Princeton University
Takao Someya
The University of Tokyo
Daniel A. Starr
UC Davis
Pierre Taberlet
LECA, Grenoble
Cedric Tan
University of Oxford
Alexandre Tkatchenko
University of Luxembourg
Geri E.Unger
Hawk Mountain Sanctuary Association
Madeleine van Oppen
University of Melbourne
Joachim von Braun
Bonn University
Leslie Vosshall
The Rockefeller University
Kang Wang
UCLA
Ofer Firstenberg Weizmann
Institute of Science
Johnathan R. Whetstine
Harvard University
Julie Winkler
Michigan State University
Rachel A. W. Wood
University of Edinburgh
Benjamin Xu
National Institutes of Health
Xueming Yang
Chinese Acaddemy of Sciences
Dennis Zaritsky
University of Arizona
Xiaoyang Zhu
Columbia University

© 2017 by The American Association for the Advancement of Science. All Rights Reserved.

The Amazon region

The Amazon region - roughly equivalent to the 48 contiguous U.S. states – includes an enormous forest brimming with biodiversity and many other habitats, from expansive wetlands to canopy communities. Research to date has already documented the value of the region to planetary health, although much remains to be studied. However, the information now available is sufficient to allow scientists and policy makers to address critical questions about the health and sustainability of region today: what is the role of the Amazon as a global carbon stock, how is the region faring under human pressures, and what are the implications of continued habitat and biodiversity loss. This collection of five papers published in *Science Advances* are powerful samples of the science needed to understand and, perhaps, address current threats to Amazonian biodiversity and habitats.

We include an impressive analysis by **Haddad** *et al.* (2015) synthesizing experiments of habitat fragmentation conducted over 35 years (the oldest of which is in the Amazon north of Manaus, started 1979), across five continents and a variety of scales and biomes. The results show that biodiversity within forest fragments is reduced up to 75% and that 70% of the remaining forest in the world is within 1 km of an edge. The **Ter Steege** *et al.* (2015) study shows that under projected trends of continuing deforestation, up to 57% of all Amazon tree species are likely to become globally threatened, including rare species. Research by **Chazdon** *et al.* (2016) on the regrowth of secondary forests found that natural regeneration of second-growth forests, in tandem with sustainably managed forests and curtailed deforestation, could provide a low-cost route to high-carbon sequestration.

We've also included two 2017 papers that highlight situations of habitat and biodiversity loss fueled by expanding human populations and other anthropogenic drivers. The first, a study of forest disturbance by **Tyukavina** *et al.*, documents the extensive combined loss of primary and non-primary forest between 2000 and 2013 across the Brazilian Amazon. The second, by **Estrada** *et al.*, that about 60% of primates worldwide are threatened with extinction and 75% have declining populations, among them many in the Amazon. Because of its size and importance to the overall health of the planet, protection of Amazonian habitats and abundant plant and animal life is increasingly important. This is particularly true as we better understand the role the region in terms of global carbon stocks and hydrological cycles.

I hope that this collection will serve readers as a starting point for further exploration of the Amazon's resources and the potential consequences of continued habitat destruction and declining of biodiversity. In addition, I hope the collection will drive new questions that can help students, stake-holders, policy-makers, and the public appreciate and eventually preserve the wondrous resources of the Amazon.

Thomas E. Lovejoy
University Professor of
Environmental Science and Policy
George Mason University

DOI: 10.1126/sciadv.aar3677

ECOLOGY

10.1126/sciadv.1501639

Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics

Robin L. Chazdon,[1,2]* Eben N. Broadbent,[3] Danaë M. A. Rozendaal,[1,4,5] Frans Bongers,[5] Angélica María Almeyda Zambrano,[3] T. Mitchell Aide,[6] Patricia Balvanera,[7] Justin M. Becknell,[8] Vanessa Boukili,[1] Pedro H. S. Brancalion,[9] Dylan Craven,[10,11,12] Jarcilene S. Almeida-Cortez,[13] George A. L. Cabral,[13] Ben de Jong,[14] Julie S. Denslow,[15] Daisy H. Dent,[16,17] Saara J. DeWalt,[18] Juan M. Dupuy,[19] Sandra M. Durán,[20] Mario M. Espírito-Santo,[21] María C. Fandino,[22] Ricardo G. César,[9] Jefferson S. Hall,[10] José Luis Hernández-Stefanoni,[19] Catarina C. Jakovac,[5,23] André B. Junqueira,[24,25,26] Deborah Kennard,[27] Susan G. Letcher,[28] Madelon Lohbeck,[5,29] Miguel Martínez-Ramos,[7] Paulo Massoca,[23] Jorge A. Meave,[30] Rita Mesquita,[23] Francisco Mora,[7,30] Rodrigo Muñoz,[30] Robert Muscarella,[31,32] Yule R. F. Nunes,[21] Susana Ochoa-Gaona,[14] Edith Orihuela-Belmonte,[14†] Marielos Peña-Claros,[5] Eduardo A. Pérez-García,[30] Daniel Piotto,[33] Jennifer S. Powers,[34] Jorge Rodríguez-Velazquez,[7] Isabel Eunice Romero-Pérez,[30] Jorge Ruíz,[35,36] Juan G. Saldarriaga,[37] Arturo Sanchez-Azofeifa,[20] Naomi B. Schwartz,[31] Marc K. Steininger,[38] Nathan G. Swenson,[39] Maria Uriarte,[31] Michiel van Breugel,[10,40,41] Hans van der Wal,[42,43] Maria D. M. Veloso,[21] Hans Vester,[44] Ima Celia G. Vieira,[45] Tony Vizcarra Bentos,[23] G. Bruce Williamson,[23,46] Lourens Poorter[5]

Regrowth of tropical secondary forests following complete or nearly complete removal of forest vegetation actively stores carbon in aboveground biomass, partially counterbalancing carbon emissions from deforestation, forest degradation, burning of fossil fuels, and other anthropogenic sources. We estimate the age and spatial extent of lowland second-growth forests in the Latin American tropics and model their potential aboveground carbon accumulation over four decades. Our model shows that, in 2008, second-growth forests (1 to 60 years old) covered 2.4 million km^2 of land (28.1% of the total study area). Over 40 years, these lands can potentially accumulate a total aboveground carbon stock of 8.48 Pg C (petagrams of carbon) in aboveground biomass via low-cost natural regeneration or assisted regeneration, corresponding to a total CO$_2$ sequestration of 31.09 Pg CO$_2$. This total is equivalent to carbon emissions from fossil fuel use and industrial processes in all of Latin America and the Caribbean from 1993 to 2014. Ten countries account for 95% of this carbon storage potential, led by Brazil, Colombia, Mexico, and Venezuela. We model future land-use scenarios to guide national carbon mitigation policies. Permitting natural regeneration on 40% of lowland pastures potentially stores an additional 2.0 Pg C over 40 years. Our study provides information and maps to guide national-level forest-based carbon mitigation plans on the basis of estimated rates of natural regeneration and pasture abandonment. Coupled with avoided deforestation and sustainable forest management, natural regeneration of second-growth forests provides a low-cost mechanism that yields a high carbon sequestration potential with multiple benefits for biodiversity and ecosystem services.

INTRODUCTION

Carbon emissions from tropical deforestation and degradation currently contribute an estimated 8 to 15% of annual global anthropogenic carbon emissions, further exacerbating global warming (*1*). National and global efforts to mitigate carbon emissions due to land-use change, such as the United Nations Reduced Emissions from Deforestation and Degradation program, focus primarily on reducing deforestation and degradation of intact tropical forests and enhancement of carbon stocks within disturbed forests, with less emphasis on reforestation and forest restoration (*2*, *3*). Although deforestation in the world's tropical regions continues to reduce overall forest cover (*4*), second-growth forests (SFs) are expanding in many deforested areas of the Neotropics (*5*, *6*). SFs emerge spontaneously in post-cultivation fallows, on abandoned farms and pastures, in the understory of ecological restoration plantings, and following assisted natural regeneration on private or communal lands (*6*, *7*). Natural regeneration of forests is widely considered to be an effective low-cost mechanism for carbon sequestration, particularly in tropical regions (*1*, *2*, *8*, *9*). Recent global estimates suggest that if tropical deforestation were halted entirely, if mature forests remain undisturbed, and if new forests were allowed to continue regrowing on deforested land, 24 to 35% of all carbon emissions from fossil fuels and industrial production from 2000 to 2010 could be mitigated (*10*). Combined with reforesting unused agricultural land, these actions have been estimated to yield a global net carbon sequestration potential of 3 to 5 Pg C (petagrams of carbon) per year (*1*, *9*).

Robust estimates of the carbon sequestration potential of naturally regrowing forests have been hampered by the lack of spatially explicit information on the extent and age distribution of SFs (including shifting cultivation fallows) and on the effects of climate and other environmental factors on local rates of biomass recovery. Assessments of carbon sequestration potential must account for effects of forest successional status, as well as effects of climate, land use, soils, and landscape context (*6*). Four key sources of uncertainty have impeded robust projections of the carbon sequestration potential of naturally regenerating tropical forests: (i) the age, longevity, and spatial distribution of regenerating forests and fallows; (ii) the potential for forest regeneration on previously forested land that is currently used for agriculture, pasture, or other nonforest land uses; (iii) the changes over time in aboveground carbon (AGC) storage in SFs under different environmental conditions (rainfall and soil fertility) and land-use history; and (iv) dynamics of agricultural land use and length of fallow cycles (*11*–*13*).

We reduce several of these uncertainties and estimate, for the first time, the carbon sequestration potential of SF regeneration over the entire Latin American tropical lowlands. We derive our projections using an extensive data set on biomass recovery during forest succession (*14*) and a map of estimated aboveground biomass (AGB) in 2008 derived from wall-to-wall remote sensing coverages (*15*). We estimate carbon sequestration potential under different scenarios of forest regeneration and pasture abandonment. These projections can help guide national policies to mitigate carbon emissions through nature-based approaches, including passive and active restoration approaches, intensification of pasture stocking rates (*16*), payment for environmental services programs, offsets as components of active restoration planning, or legal compliance with forest legislation (*17*). Our study addresses four main questions: (i) What is the area and estimated age distribution of SFs in the lowland Neotropics? (ii) What is the total predicted carbon storage potential of naturally regenerating forests over four decades across biomes and countries? (iii) How much carbon is sequestered under different scenarios of natural regeneration of pastures and persistence of SFs? (iv) How does the carbon sequestration potential of SF regeneration vary across countries?

To determine the carbon sequestration potential of regenerating forests, we first modeled the area and age distribution of existing SFs up to 100 years old. We used a 2008 map of Neotropical AGB in woody vegetation (*15*) to infer stand age using an equation relating biomass to climate and forest age on the basis of 43 successional chronosequences and 1148 plots across the lowland Neotropics (*14*). This map provides the most accurate spatially explicit data on forest biomass currently available and is based on a large network of field plots coupled with satellite LiDAR (light detection and ranging) to parameterize MODIS (Moderate Resolution Imaging Spectroradiometer) satellite data at a spatial resolution of 500 m (*15*). Additionally, we incorporated data on the spatial extent of croplands and pastures across Latin America on the basis of the most recent coverages available at this geographic scale. We then projected future AGB accumulation of SFs ($\leq$60 years) from 2008 to 2048. Our projections account for regional variation in climatic water availability, which strongly influences rates of biomass recovery across our study area (*14*).

Our projections do not assume any tree planting or assisted regeneration practices beyond creating conditions that permit natural regeneration, such as fencing or fire protection. To account for natural or assisted regeneration on former pastures and the potential re-clearing of SFs, we model carbon storage scenarios where only 80, 60, 40, 20, and 0% of young SFs (YSFs; 1 to 20 years) and mid-SFs (MSFs; 20 to 60 years) and 0 to 40% of pasture areas are permitted to regenerate naturally. Randomly selected second-growth areas are prevented from natural regeneration, and existing carbon stocks in these pixels are reduced to the mean level of agricultural lands in our 2008 baseline to simulate forest conversion to agriculture. We do not model any changes in extent of existing croplands, as we only consider changes in carbon storage resulting from regeneration of existing SFs or pasture areas.

RESULTS

Estimated areas of forest and farmland and initial carbon stocks

Our analysis showed that, in 2008, 20.1% of the 8.7 million km^2 of forest and farmland in our study area (1.75 million km^2) was farmland, dominated by 1.2 million km^2 of pasture. Modeled areas of YSFs and MSFs ($\leq$60 years) composed 28.1% (2.4 million km^2) of the study area, whereas old SFs (60 to 100 years) composed 5.3% (461,519 km^2). Only 46.5% of the study area (4.0 million km^2) consisted of old-growth forest (OGF, arbitrarily defined as >100 years; Fig. 1A and Table 1). Modeled areas of YSFs and MSFs were distributed across all biomes and countries

---

[1]Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269–3043, USA. [2]International Institute for Sustainability, Estrada Dona Castorina 124, Rio de Janeiro, CEP 22460-320, Brazil. [3]Spatial Ecology and Conservation Lab, Department of Geography, University of Alabama, Tuscaloosa, AL 35487, USA. [4]Department of Biology, University of Regina, 3737 Wascana Parkway, Regina, Saskatchewan S4S 0A2, Canada. [5]Forest Ecology and Forest Management Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, Netherlands. [6]Department of Biology, University of Puerto Rico, P.O. Box 23360, San Juan, PR 00931-3360, Puerto Rico. [7]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, CP 58089, Morelia, Michoacán, México. [8]Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA. [9]Department of Forest Sciences, "Luiz de Queiroz" College of Agriculture, University of São Paulo, Av. Pádua Dias, 11, 13418-900 Piracicaba, São Paulo, Brazil. [10]SI ForestGEO, Smithsonian Tropical Research Institute, Roosevelt Avenue, 401 Balboa, Ancon, Panama. [11]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany. [12]Institute for Biology, Leipzig University, Johannisallee 21, 04103 Leipzig, Germany. [13]Departamento de Botânica-CCB, Universidade Federal de Pernambuco, Pernambuco, CEP 50670-901, Brazil. [14]Department of Sustainability Science, El Colegio de la Frontera Sur, Av. Rancho Polígono 2-A, Ciudad Industrial, Lerma 24500, Campeche, Mexico. [15]Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA 70118, USA. [16]Smithsonian Tropical Research Institute, Roosevelt Avenue, 401 Balboa, Ancon, Panama. [17]Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK. [18]Department of Biological Sciences, Clemson University, 132 Long Hall, Clemson, SC 29634, USA. [19]Centro de Investigación Científica de Yucatán A.C. Unidad de Recursos Naturales, Calle 43 # 130, Colonia Chuburná de Hidalgo, C.P. 97200, Mérida, Yucatán, México. [20]Earth and Atmospheric Sciences Department, University of Alberta, Edmonton, Alberta T6G 2EG, Canada. [21]Departamento de Biologia Geral, Universidade Estadual de Montes Claros, Montes Claros, Minas Gerais, CEP 39401-089, Brazil. [22]Fondo Patrimonio Natural para la Biodiversidad y Areas Protegidas, Calle 72 No. 12-65 piso 6, 110231 Bogota, Colombia. [23]Biological Dynamics of Forest Fragments Project, Environmental Dynamics Research Coordination, Instituto Nacional de Pesquisas da Amazonia, Manaus, Amazonas, CEP 69067-375, Brazil. [24]Centre for Crop Systems Analysis, Wageningen University, P.O. Box 430, 6700 AK Wageningen, Netherlands. [25]Knowledge, Technology and Innovation Group, Wageningen University, P.O. Box 8130, 6700 EW Wageningen, Netherlands. [26]Coordenação de Tecnologia e Inovação, Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, Aleixo, 69060-001 Manaus, Brazil. [27]Department of Physical and Environmental Sciences, Colorado Mesa University, 1100 North Avenue, Grand Junction, CO 81501, USA. [28]Department of Environmental Studies, Purchase College (SUNY), 735 Anderson Hill Road, Purchase, NY 10577, USA. [29]World Agroforestry Centre (ICRAF), P.O. Box 30677-00100, Nairobi, Kenya. [30]Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico City, C.P. 04510, México. [31]Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, USA. [32]Section of Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Aarhus 8000, Denmark. [33]Centro de Formação em Ciências Agroflorestais, Universidade Federal do Sul da Bahia, Itabuna-BA, 45613-204, Brazil. [34]Departments of Ecology, Evolution, and Behavior and Plant Biology, University of Minnesota, Saint Paul, MN 55108, USA. [35]School of Social Sciences, Geography Area, Universidad Pedagogica y Tecnologica de Colombia, 150003 Tunja, Colombia. [36]Department of Geography, 4841 Ellison Hall, University of California, Santa Barbara, Santa Barbara, CA 93106, USA. [37]Cr 5 No 14-05, P.O. Box 412, Cota, Cundinamarca, Colombia. [38]Department of Geographical Sciences, University of Maryland, College Park, MD 20742, USA. [39]Department of Biology, University of Maryland, College Park, MD 20742, USA. [40]Yale-NUS College, 12 College Avenue West, Singapore 138610, Singapore. [41]Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Singapore. [42]Departamento de Agricultura, Sociedad y Ambiente, El Colegio de la Frontera Sur, Unidad Villahermosa, 86280 Centro, Tabasco, México. [43]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 1090 Amsterdam, Netherlands. [44]Bonhoeffer College, Bruggertstraat 60, 7545 AX Enschede, Netherlands. [45]Museu Paraense Emilio Goeldi, C.P. 399, CEP 66040-170, Belém, Pará, Brazil. [46]Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803–1705, USA.
*Corresponding author. Email: robin.chazdon@uconn.edu
†Present address: National Institute of Ecology and Climate Change, Periférico 5000, Col. Insurgentes Cuicuilco, Delegación Coyoacán, C.P. 04530, México.

but were most extensive (2.2 million km^2) in six countries: Brazil, Mexico, Colombia, Venezuela, Bolivia, and Peru (Fig. 2A and table S2). In 2008, the entire study region was estimated to have a total aboveground C stock of 85.1 Pg. Farmland accounted for 10.2% of the total 2008 C stock (8.7 Pg), with 6.2 Pg C in pastures (Table 1). YSFs and MSFs accounted for 18.3% (15.6 Pg C) of this total, old SFs accounted for 6.4% (5.4 Pg C), and OGFs accounted for 65.1% (55.4 Pg C; Fig. 1B and Table 1).

Carbon sequestration scenarios

In Fig. 2B, we map the carbon sequestration scenario where 100% of YSFs (1 to 20 years) and MSFs (20 to 60 years) in the 2008 baseline map are allowed to regenerate for 40 years at rates predicted by post-abandonment chronosequence studies (*14*). These age classes rapidly accumulate biomass and are the most prevalent across the study region. Under the 100% regeneration assumption, AGC stock increased 2.0-fold in YSFs and 1.2-fold in MSFs, yielding a potential total carbon sequestration of 8.48 Pg C over 40 years (Fig. 1C and Table 1), corresponding to a total sequestration of 31.09 Pg CO_2. This total is equivalent to carbon emissions from fossil fuel use and industrial processes in all of Latin America and the Caribbean from 1993 to 2014 (*18*).

Uncertainty estimates for total potential AGC sequestration in YSFs and MSFs from 2008 to 2048 range from 6.7 to 10.9 Pg C. Neotropical countries vary markedly in carbon sequestration potential (Fig. 1E) as a

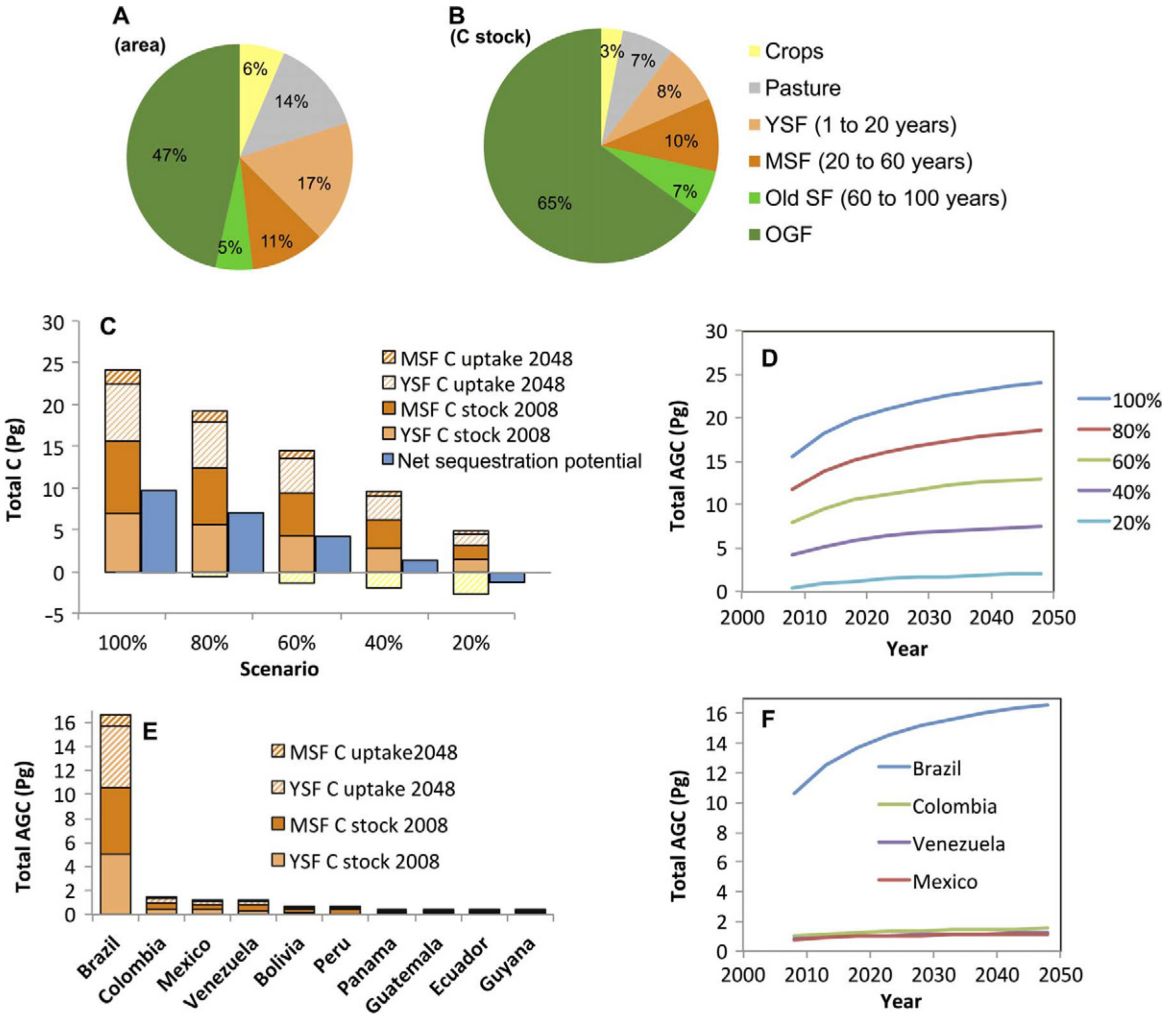


Fig. 1. Area and carbon distributions in SFs in the lowland Neotropics. (**A** and **B**) Percentages of modeled forest area (A) and AGC stock (B) in different land cover and forest age classes in 2008: cropland, pasture, forest ≤20 years (YSF), forest 20 to 60 years (MSF), forest 60 to 100 years (old SF), and forest >100 years (arbitrarily used as cutoff for OGF). (**C**) AGC stocks of YSFs and MSFs in 2008 (filled bars), and their net carbon sequestration from 2008 to 2048 (hatched bars). The total size of the bar indicates the total carbon stocks of those forests in 2048. Stacked bars are shown for five scenarios, where 100, 80, 60, 40, and 20% of the area are allowed to recover. The hatched yellow bar below the zero line indicates the carbon loss under these scenarios due to forest conversion to pasture or cropland in 2008, and the blue bar indicates the net sequestration potential of the different scenarios (carbon sequestration from 2008 to 2048 minus conversion-driven carbon loss in 2008). (**D**) Total AGC of YSFs and MSFs over the period 2008–2048 under different regeneration scenarios. (**E**) AGC of YSFs and MSFs in 2008, and their net carbon sequestration from 2008 to 2048 given 100% recovery, for each country separately. The total size of the bar indicates the total carbon stocks (AGC) of those forests in 2048. (**F**) Total AGC of YSFs and MSFs from 2008 to 2048 for the four countries with the largest carbon sequestration potential in naturally regenerating forests (see table S2 for more details).

result of differences in the extent and geographical distribution of SFs in wet and dry forest biomes (table S2). Brazil, by far, has the highest carbon storage potential in YSFs and MSFs (6.04 Pg C; 71.3%), followed by Colombia, Mexico, and Venezuela (Fig. 1, E and F). Ten countries accounted for 95.1% of the potential net carbon sequestration in YSFs and MSFs from 2008 to 2048 (Fig. 1E). National differences in potential sequestration increase over time (Fig. 1F). Mean annual rates of carbon storage of YSFs and MSFs were greatest from 2008 to 2013, when they potentially stored an average of 0.526 Pg C per year. These rates declined in 2043–2048, where they sequestered an average of 0.081 Pg C per year. Within only the first 5 years, the potential AGC stored from regeneration of YSFs and MSFs (100% scenario; 2.6 Pg C) can mitigate 9.64 Pg CO_2 emissions, which is more than the total CO_2 emissions from fossil fuel consumption and industrial processes from all countries in Latin America and the Caribbean from 2010 to 2014 (8.67 Pg) (*18*).

When less SF area is allowed to persist, the net carbon storage in YSFs and MSFs declines proportionately from 8.48 Pg C (100% recovery) to −1.16 Pg C (Fig. 1C). In the scenario where only 20% of the SF is allowed to persist and regenerate, carbon gains are lower than carbon losses because of forest clearing for agriculture, resulting in a net negative carbon sequestration outcome (Fig. 1C). When 40% of pastures are allowed to regenerate, an additional 2.0 Pg C can be sequestered, regardless of the level of SF persistence (Fig. 3). Similar levels of carbon storage can be achieved through different combinations of SF conservation and forest regeneration following pasture abandonment.

DISCUSSION

Natural regeneration provides a low-cost, nature-based solution for carbon sequestration with enormous potential in the Neotropics. This potential has been overlooked by the 2014 Intergovernmental Panel on Climate Change report, which suggests that the most cost-effective sequestration options in forestry are reducing deforestation, sustainable forest management, and afforestation (*19*). These findings have major implications for policies affecting forest land use, legal instruments, and economic incentives for SF regeneration, restoration, and conservation in Latin America (*20*). Combined with halting new deforestation and sustainably managing tropical forests, the significant carbon sequestration potential delivered by SFs provides essential solutions for reaching national and international carbon mitigation targets and supports ambitious forest restoration goals motivated by the Convention on Biological Diversity Aichi Targets (2010), the Bonn Challenge (2011), and the New York Declaration on Forests (2014), which calls for ending natural forest loss and restoring 350 million ha of forest worldwide by 2030.

Table 1. Area and AGC stocks in 2008, and mean values of projected AGC sequestration over 40 years for six land cover types: YSF (≤20 years), MSF (20 to 60 years), old SF (60 to 100 years), OGF (>100 years, arbitrarily set), pasture, and crops. Carbon gains for old SF and OGF are not shown, because they cannot be estimated accurately. Values of net carbon assume zero deforestation of SFs.

Land use	2008		Net C gain (2008–2048)
	Area (km^2)	AGC (Pg)	AGC (Pg)
YSF	1,512,668	6.9796	6.8402
MSF	925,936	8.6028	1.6366
Old SF	461,518	5.4407	—
OGF	4,043,058	55.3859	—
Pasture	1,186,260	6.1718	4.9925
Crops	558,306	2.5356	2.6330
Total	8,687,747	85.1163	16.1023

Our model of SF age and geographic distribution within the lowland Latin American tropics yields 28% of total forest and agricultural area in YSFs and MSFs in 2008. This percentage is higher than the estimate of 23% by the United Nations Food and Agriculture Organization, which is not derived from mapping or modeling based on remote sensing–based products (*21*). This discrepancy highlights the challenges in estimating the cover of tropical SFs (*6*). Techniques for mapping the age and extent of SFs at pixel sizes below 25 ha are urgently needed to provide more spatially accurate assessments of SF extent and carbon sequestration potential at the country and regional levels (*22*, *23*). Landsat-based coverages of land-use change can potentially provide such information, provided that SFs are distinguished from tree and oil palm plantations (*7*, *24*). As forest patches are often considerably smaller than 25 ha, one limitation of our study is that mean pixel age may reflect the mixture of different forest ages and land cover types within each pixel. This spatial mixing may result in overrepresentation of mid-age values and an overestimation of the areal extent of secondary forests.

The carbon sequestration potential revealed by our study is likely an underestimate of the actual potential, for several reasons. Belowground carbon stocks in soils and roots will add 25% or more to total carbon storage (*25*), but knowledge regarding determinants of successional dynamics of belowground carbon sequestration is insufficient to include in our projections (*26*). Our study area excludes montane areas of Latin America, where SF is regenerating spontaneously on abandoned farmland (*5*). Our estimates could be further improved using higher-resolution spatial data, which are rapidly becoming available (*27*), explicitly taking local landscape matrix conditions into account (*6*), accounting for belowground carbon dynamics (*28*), and incorporating effects of previous land use on biomass recovery (*28*, *29*). Future projections using more recent baseline data will rely on newer spatial analyses of forest biomass and agricultural land use across Latin America when these become available. Similarly, forest regrowth in the African and Asian tropics offers substantial carbon sequestration opportunities that are not included in our study (*30*–*32*). Our projections of carbon sequestration during forest succession, however, do not consider potential negative effects of climate change and extended droughts on rates of biomass accumulation (*33*).

Protecting SFs from deforestation poses many challenges, including the lack of legal definitions for SF (or lack of enforcement of existing definitions) and the absence of effective policy instruments and economic incentives for landowners (*20*). Currently, SFs are highly dynamic within Neotropical lowlands; the estimated time for half of the secondary forest to be removed within a 25 km × 25 km cell in the Brazilian Amazon averaged 5.4 years (*12*). Scenarios of carbon sequestration based on varying rates of forest and pasture regeneration can inform national-level commitments to restore forests through both active and passive pathways. Maps of potential carbon sequestration (Fig. 2B and figs. S1 to S3) provide spatially explicit guidance and realistic expectations for Latin American countries that are developing their

Intended Nationally Determined Contributions (INDCs) as part of their United Nations Framework Convention on Climate Change agreements. For example, Brazil's INDC aims to restore and reforest 12 million ha of Atlantic Forest by 2030 and restore an additional 15 million ha of degraded pasturelands by 2030 (*34*).

Governments, multinational organizations, nongovernmental organizations, and local stakeholders can leverage this climate change mitigation potential by enabling spontaneous or assisted natural regeneration in areas with suitable ecological conditions, by providing incentives to enhance agricultural productivity on degraded lands, and by avoiding further clearance of young and old forests. Our map indicates regions that are optimal for long-term carbon storage because of the natural regeneration of forests, presenting low-cost and high-yield carbon mitigation solutions. Carbon sequestration can be achieved through protection and enhancement of young second-growth areas and agricultural intensification on some parts of the land, judiciously

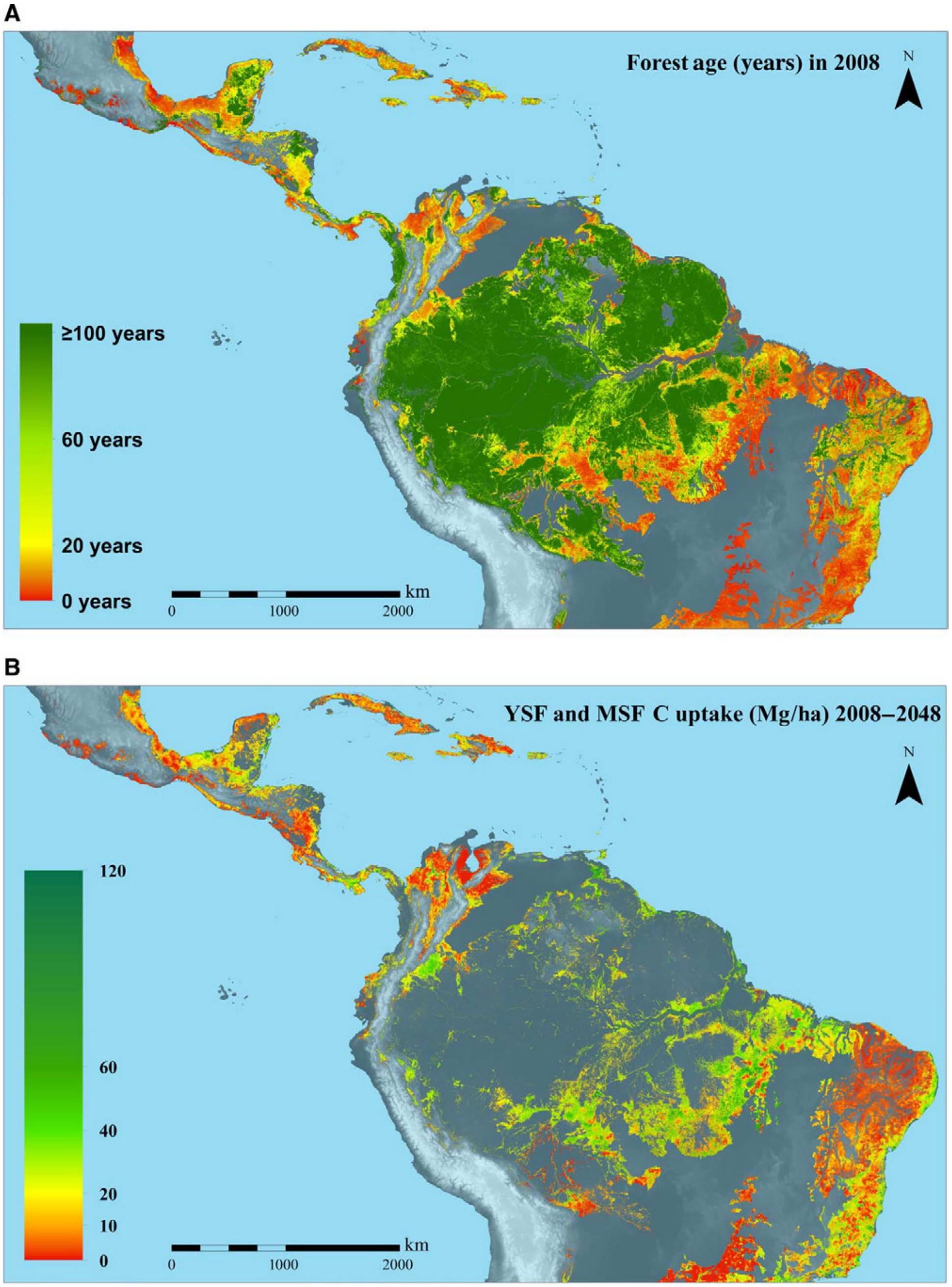


Fig. 2. Age and carbon sequestration maps of a lowland Neotropical forest. (**A** and **B**) Modeled mean forest age in 2008 (A), and the total potential sequestered carbon in OGFs, 2008–2048 for all YSFs (≤20 years) and MSFs (20 to 60 years) in 2008 (B). The gray areas are areas with no data: above 1000-m altitude, savannas, rivers, lakes, OGFs, or urban areas. The biomes covered are moist and dry tropical forests.

sparing other lands for restoration and forest regeneration (Fig. 3) (*35*). Natural regeneration on agricultural land must comply with country- and region-specific agendas for maintaining livelihoods and food security and development of sustainable agricultural land use, including agroforestry. Regenerating forests can complement protection of existing OGFs by extending buffer zones and increasing connectivity of forest habitats.

The enormous potential of SFs has been poorly appreciated, despite their growing extent in tropical landscapes (*1*). In addition to their dual role in both climate change adaptation and mitigation (*36*, *37*), regenerating tropical forests play an important role in biodiversity conservation, increasing connectivity in fragmented landscapes, hydrological regulation, nutrient cycling, and the provision of timber, food, fuel, and fodder to local people (*6*, *37*). The potential carbon sequestration capacity of natural regeneration of YSFs provides a significant low-cost opportunity for carbon sequestration in the tropics while simultaneously benefiting biodiversity and production of multiple ecosystem services, and should be incorporated explicitly into national and international carbon mitigation commitments.

MATERIALS AND METHODS

Experimental design

The study area was located within three major lowland forest biomes (*38*); 83.2% of forest is in the moist broadleaf biome, whereas 16.8% is in dry broadleaf and caatinga biomes combined, with each of these biomes having different percentages of secondary forest (see table S1). Across these forest biomes, we estimated the carbon sequestration potential of regrowing forests. Our analysis focused on carbon stored in AGB. We did not estimate biomass stored in soils, belowground biomass, or dead woody debris owing to major uncertainties in these components across biomes, climate zones, and successional stages.

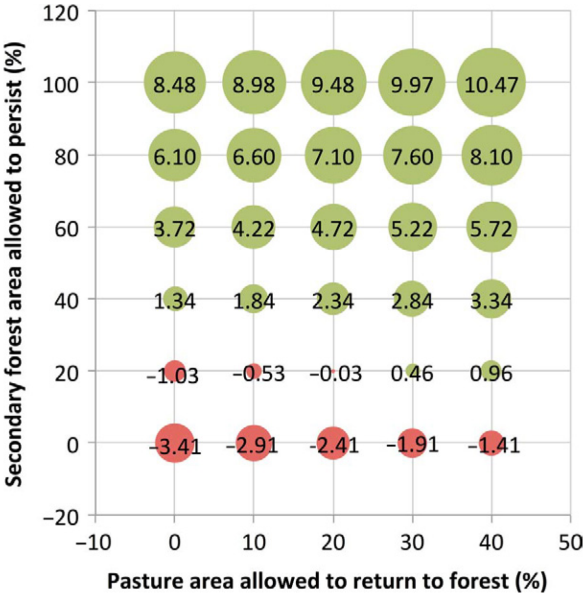


Fig. 3. Potential AGC sequestration (in petagrams) for scenarios of combinations of land use over four decades (2008–2048). Land-use change combinations incorporate the percentage area of land allowed to regenerate following pasture abandonment (0 to 40% cessation of pasture use) and the percentage of YSF (≤20 years) and MSF (20 to 60 years) areas allowed to persist and continue regeneration (0 to 100% forest persistence). The size of the circles indicates the potential amount of carbon sequestered. Values in the cells indicate the magnitude of net carbon sequestered over 40 years (in petagrams), with all possible combinations of the two factors. These scenarios account for carbon loss due to SF clearing, which can lead to negative net carbon sequestration (red circles).

Our approach involved three steps and was based on the most recent and detailed map of Neotropical forest biomass and the largest data set on successional chronosequences compiled to date, including 1148 second-growth plots established in 43 forest sites across the Neotropics (*14*). In the first step, we estimated the areal extent of existing cleared areas and SFs ≤100 years old with potential to regrow. To do so, we used a map of Neotropical forest AGB in 2008 (*15*) and inferred the ages of these forests, using an equation relating biomass to forest age, and used a map of agricultural lands, including pasture areas in 2000 (10-km pixel size) (*39*) available at www.earthstat.org/data-download and cropland in 2005 (1-km pixel size) (*40*) available at www.geo-wiki.org, which provided the percentage of land area with pasture or crops, respectively. In the second step, we assumed that all these regrowth and agricultural areas were allowed to regenerate spontaneously (no active restoration) and projected their biomass accumulation for 40 years into the future, using an equation relating forest age to biomass. In the third step, we relaxed the assumption that all of these areas will regenerate and persist over these projected time scales and modeled carbon sequestration scenarios where 80 to 20% of SF areas undergo regeneration over 40 years. We also simulated carbon sequestration via natural regeneration over 40 years in up to 40% of pasture areas. A detailed description of the 43 study sites is provided by Poorter *et al.* (*14*).

Mapping areas of different forest ages

We modeled mean forest age and cleared forest (agricultural land use) in the Neotropics based on a 500-m-resolution map of forest biomass (*15*). Our analysis did not incorporate edge effects, such as increased tree mortality or variation in seed rain with distance from forest sources (*41*). Further, our approach did not distinguish among logged forests, tree plantations, forests degraded from wildfire, or other disturbances, as spatially explicit data for these cover types are not available across our entire study region. Rather, we limited projections in our study to forests having an initial predicted age of 60 years or less, which we divided into young secondary forests (≤20 years of age) and mid-successional secondary forests (between 20 and 60 years of age). General statistics were provided for forests up to 100 years of predicted age for the initial year 2008. This threshold likely excludes most selectively logged or high-graded forests, whereas natural forest areas that experienced intensive logging are likely to have a stand biomass similar to YSFs and are assumed to undergo similar biomass recovery processes (*6*). However, estimates of forest extent and age would only be slightly affected, as plantations currently cover only 4000 km^2 in Central America, 150,000 km^2 in South America, and 7000 km^2 in the Caribbean (*42*), which is less than 1% of the estimated extent of YSFs (Fig. 1A). To calculate our maps of forest age and AGB from 2008 to 2048, we used the approach described below.

Our study region focused on the Neotropics, between 23.39°N and −23.411°S [that is, the extent of the pantropical AGB map provided by Baccini *et al.* (*15*)], and on lowland areas below an altitude of 1000 m based on the distribution of our chronosequence sites (*14*), as defined by the GTOPO30 digital elevation model available for download at https://lta.cr.usgs.gov/GTOPO30, corresponding to the geographic limits of the locations of our 43 study areas. To distinguish the different forest types, we used a map of world ecoregions (based on potential natural vegetation) obtained from The Nature Conservancy (*38*) and selected the three principal biomes in which our 43 study sites were located: (i) tropical and subtropical moist broadleaf forests (henceforth referred to as moist forest), (ii) tropical and subtropical dry broadleaf forests, and (iii) caatinga [henceforth (ii) and (iii) are combined and referred to as dry forest]. We then masked all open water bodies, including oceans, lakes, and rivers, using datamask images from Hansen *et al.* (*7*), which were acquired at a resolution of 30 m × 30 m and which were used to calculate the percentage land cover within each of the 500 m × 500 m study pixels. Urban areas were masked using high-resolution urban maps (*43*, *44*); see Potere *et al.* (*45*) for a discussion on accuracy assessment. Wetlands were masked using a modified version of the Global Lakes and Wetlands Database created by Lehner and Döll (*46*), available at http://www.worldwildlife.org/pages/global-lakes-and-wetlands-database, which we refined through removal of areas having agriculture or OGF.

The final study area was calculated as the hectares of each pixel occupying terrestrial land surface following adjustment for latitudinal variation in pixel areal extent, which varied from approximately 23.27 ha per pixel at the equator to 21.41 ha per pixel at the northern or southern limit of our study region. All pixels were masked if any portion of the pixel intersected an urban area. We overlaid this map with the map of cropland and pasturelands described above. Here, we refer to both land uses as farmlands.

Estimating 2008 AGB

To obtain AGB (in megagrams per hectare) for each pixel in our study region, we used the Baccini *et al.* (*15*) map for the year 2008, provided by the Woods Hole Research Center (WHRC), which is the most recently updated highest spatial resolution map of AGB currently available in our study region. AGB (in megagrams per hectare) was obtained at a pixel size of ~500 m × 500 m (25 ha). We inferred forest age from forest biomass and local climatic conditions on the basis of a Michaelis-Menten (MM) equation that relates biomass to mean forest age within the pixel and climatic conditions. The MM equation contains an asymptote parameter a that defines the AGB of OGFs and the parameter a_{50} that defines the age at which 50% of old-growth AGB is reached

$$\mathrm{AGB} = (a \times \mathrm{Age}) / (a_{50} + \mathrm{Age}) \tag{1}$$

We used two different data sets to estimate the parameter values for a and a_{50}. The WHRC map has extensive and continuous climatic and old-growth coverage across the Neotropics, and pixels in national parks were used to estimate the climatic dependence of the old-growth asymptote parameter a, which indicates the maximum AGB. By focusing on national parks only, we minimized reductions in AGB caused by anthropogenic disturbances. The database on secondary forest plots [1148 plots established in 43 chronosequences across the major environmental gradients in the Neotropics (*14*)] was used to estimate the climatic dependence of parameter a_{50} that determines the shape of the curve, which is mostly determined by young secondary forests. The WHRC map uses, among others, the allometric equation of Chave *et al.* (*47*) to calculate tree biomass on the basis of stem diameter and wood density. For this reason, we also used the same equation to calculate the biomass for the secondary forest plots of Poorter *et al.* (*14*), versus the updated Chave *et al.* 2014 equation (*48*); this approach ensures consistency with previous carbon estimates across our study area.

We estimated the climate dependence of a (for example, old-growth asymptote) and a_{50} (for example, age at which 50% old-growth asymptote is reached) separately, using a statistical approach to select the most parsimonious subset of four bioclimatic variables from (i) all 19 bioclimatic variables described at www.worldclim.org/bioclim, which were obtained at a 30-s resolution (approximately 1 km × 1 km) from WorldClim (*49*) (www.worldclim.org/current), and (ii) climatic water deficit (CWD; in millimeters per year), which was obtained from http://chave.ups-tlse.fr/pantropical_allometry.htm. CWD is the amount of water lost during dry months (defined as months where evapotranspiration exceeds rainfall) and is calculated as the total rainfall minus evapotranspiration during dry months. This number is, by definition, negative, and sites with CWD of 0 are not seasonally water stressed. We also used (iii) total soil cation exchange capacity (CEC; in centimoles of positive charge per kilogram of soil), which was used as an indicator of soil fertility. CEC was obtained from the Harmonized World Soil Database from http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/.

To model the climatic dependence of old-growth asymptote a, we developed a geographic (for example, biome) weighted regression approach, which enabled consideration of spatial variation in AGB not accounted for in our selected predictor variables. We made a random selection of 1,639,712 pixels that occurred in less-disturbed areas (that is, parks), had 100% land cover, and were within our biome and elevation (<1000-m altitude) criteria. For this analysis, we used the national parks from the World Database on Protected Areas (WDPA) downloaded in July 2015 from www.protectedplanet.net, and pixels that intersected with protected areas with effective protection from data provided by WDPA were selected. As such, we likely selected pixels that had the maximum old-growth biomass given the climatic conditions. Because of the difference in total area of our study biomes and to avoid having the climatic dependence of a being driven disproportionally by one biome, we randomly selected 10% of identified pixels within moist forest areas (n = 1,142,833) but included all identified pixels in dry forest (n = 349,082) and caatinga (n = 147,797) biomes. We first used a forward stepwise regression of AGB on biome and all bioclimatic variables to identify a parsimonious subset of significant predictor variables, which were mean annual rainfall (in millimeters per year), CWD, soil CEC, and temperature seasonality (expressed as the SD * 100, and defined as variable "BIO4" in WorldClim).

To identify fully intact old-growth pixels, which required excluding pixels with mixed land cover or with low AGB due to other limiting factors (for example, flooding and fire), we ran each model two times, removing pixels identified as outliers (for example, negative residuals ≥0.5 STD) during the first run. The final models for moist, dry, and caatinga old-growth AGB were highly significant (r^2 = 0.39, n = 874,222; r^2 = 0.66, n = 239,764; and r^2 = 0.55, n = 101,050, respectively) and highlighted the different controls over AGB in these regions, with moist forest AGB being predicted primarily by CWD and BIO4, dry forest AGB being predicted primarily by CWD and CEC, and caatinga AGB being predicted by CWD and mean annual precipitation. To validate the final map of old-growth AGB, we used an independent group of randomly selected points widely distributed across all biomes within our study region that we manually verified through recent (year 2013+) high-resolution (<5 m × 5 m pixels) satellite imagery to be representative of intact forest at that location, and ran a linear regression between our predicted AGB values at that location and those extracted from the WHRC AGB map. This validation found our old-growth AGB prediction model to be highly significant ($r^2 = 0.70$, $n = 500$). The final model and coefficients for moist, dry, and caatinga are as follows

$$a\,(\text{Moist}) = 370 - 0.0133 * \text{Precipitation} + 0.1586 * \text{CWD} - 0.1235 * \text{CEC} - 0.0191 * \text{BIO4} \quad (2)$$

$$a\,(\text{Dry}) = 330 + 0.0053 * \text{Precipitation} + 0.1984 * \text{CWD} - 1.6974 * \text{CEC} - 0.0084 * \text{BIO4} \quad (3)$$

$$a\,(\text{Caatinga}) = 158 + 0.0398 * \text{Precipitation} + 0.0941 * \text{CWD} - 0.8300 * \text{CEC} - 0.0018 * \text{BIO4} \quad (4)$$

To model the climatic dependence of a_{50}, we included the effects of mean annual precipitation, rainfall seasonality (expressed as a coefficient of variation, and defined as variable "BIO15" in WorldClim), and CWD (*14*). We then used nonlinear regression to fit Eq. 1 to the secondary forest data, using Eqs. 2 to 4 for asymptote a, depending on their biome

$$a_{50} = 26.4368 - 0.004927 \times \text{CWD} + 0.001321 \times \text{Rainfall} - 0.290429 \times \text{Rainfall seasonality} \quad (5)$$

We then inverted Eq. 1 to estimate for each pixel its age from AGB

$$\text{Age} = (a_{50} \times \text{AGB}) / (a - \text{AGB}) \quad (6)$$

where age is in years and AGB is the pixel AGB provided by WHRC 2008. We used Eq. 6 to make an age map of Neotropical forests. Some age estimates were greater than 300 years, because the observed AGB pixel values were close to, or exceeded, those of predicted old-growth values. For those pixels, the age was set to 300 years and AGB values were set to the pixel AGB provided by WHRC 2008. It is important to note that age estimates pertain to the mean value of each pixel, as we cannot resolve forest ages at subpixel resolution. The biomass map we used is, nevertheless, the highest-resolution map currently available, and therefore provides the best estimate. With the arrival of higher-resolution 30 m × 30 m land-use and biomass maps, the accuracy of our predictions may be further improved.

Uncertainty analysis

We performed an uncertainty analysis by calculating the bootstrapped SDs of all parameter estimates and then used a Monte Carlo procedure with 10,000 uniformly random selected parameter combinations within 1 SD of all mean parameter estimates for each pixel in our study region. We then calculated the mean and SD of the predicted age of each combination for each pixel. The mean value was used to create our final map of forest age in 2008, and we calculated the total uncertainty by calculating the total AGB in young secondary forests (≤20 years of age) and mid-secondary forests (between 20 and 60 years of age) as projected, as well as at the lower and upper SD value, and summed these across pixels to provide a measure of uncertainty associated with the total carbon sequestration potential of SFs. The pixel size of our final AGB map is 500 m × 500 m, and we acknowledge that our pixel mean age in many cases will be composed of different aged forests and, in some cases, a mixture of land cover types, such as pasture, secondary forest, and OGF. Although we did not incorporate uncertainty related to mixed pixel land covers across our entire study region, we did conduct tests using hypothetical mixtures of land cover types for selected pixels, and our results showed that variation in carbon gain from 2008 to 2048 resulting from different proportions of forest age was less than the uncertainty resulting from the per-pixel forest age estimation, calculated as the Monte Carlo mean and SD of each pixel's predicted forest age. At the local or regional scale, however, such within-pixel variations can be considerable and may result in deviations from the overall pattern.

For most analyses, forest age was grouped into four classes: YSF (≤20 years), MSF (between 20 and 60 years), old SF (between 60 and 100 years), and OGF (>100 years). We set the threshold age for OGFs arbitrarily at 100 years, because we did not have data for older second-growth plots. After 100 years, the forest is well developed in terms of species richness, structure, and biomass, although species composition and soil characteristics may take much longer to recover.

Projecting AGB accumulation in SFs

For subsequent analyses related to our AGB projections, we focused on young (1 to 20 years) and intermediate (20 to 60 years) second-growth pixels identified in 2008. For each pixel, we predicted the AGB accumulation over 40 years, from 2008 to 2048. We focused on 40 years, because calculating AGB in forests older than 100 years (that is, 60 years plus the projected 40 years) would be extrapolating beyond the maximum SF age of the chronosequences we used to develop the equations (*15*). To calculate AGB from age for our future age distribution maps, we used Eq. 1.

We used the projected biomass accumulation to biomass stocks and sequestration for moist and dry forest types, countries (tables S1 and S2, respectively), and years (see Fig. 1D for increase in carbon stock in young plus mid-age secondary forests for the whole Latin American study region and Fig. 1E for increase in carbon stock in young plus mid-age secondary forests in the four countries with the largest increase over the four decades). To calculate mean annual carbon sequestration rates, we used net AGB change, multiplied it by 0.5 [which is the average carbon value in dry biomass and widely used in the literature, such as by Baccini *et al.* (*15*) on which our initial AGB estimates are based], and divided it over the time interval considered. Because annual rates of AGC storage vary greatly with secondary forest age, we provided mean annual sequestration rates separately for YSF for 2008 and MSF for the periods 2008–2013 and 2043–2048.

Analysis of natural regeneration scenarios

Natural regeneration will not always occur at its full potential because of ecological, geographical, and socioeconomic constraints. To evaluate the effects of reduced secondary regrowth to carbon mitigation (Fig. 1C), we used six scenarios in which the available area allowed to follow natural regeneration was set to 100, 80, 60, 40, 20, or 0%, and assumed no spatial variation in rates of biomass recovery beyond the effects of climate. The carbon stock in the nonselected pixels (secondary forest pixels that were supposed to be transformed into agricultural land) was set to the average carbon stock found in agricultural land pixels, which was calculated as the area-weighted average of crop land pixels and pasture land pixels (49.9 Mg C ha^{-1}).

To evaluate the effects on carbon sequestration of a combination of scenarios of reduced secondary regrowth and reduced regrowth of agricultural land (Fig. 3), we combined six scenarios of secondary forest regeneration, both YSF and MSF (100, 80, 60, 40, 20, or 0%), with five scenarios of areas of forest regeneration on pasture land (40, 30, 20, 10, or 0%), which we considered realistic on the basis of recent data of forest regrowth on abandoned pastures in Para, Brazil (*50*). These scenarios can also simulate cases where natural regeneration is compromised by former land use or lack of seed dispersal (*6*). We applied these filters as described above to create Fig. 1C. The carbon stock in recovering pasture pixels recovers following the modeled calculations described for those pixels. The carbon stock in the nonselected agricultural land pixels remained as the carbon stock that they had in 2008.

All analyses related to the development of the age-to-AGB relationship were performed in R 3.1.2, and all analyses related to the spatial and temporal modeling and mapping were performed in the Interactive Data Language (version 8.2).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/2/5/e1501639/DC1

fig. S1. Carbon sequestration potential during 2008–2048 for crop areas of a lowland Neotropical forest.

fig. S2. Carbon sequestration potential during 2008–2048 for pasture areas of a lowland Neotropical forest.

fig. S3. Carbon sequestration potential during 2008–2048 for areas of YSFs and MSFs (in 2008), crops, and pasture combined.

table S1. Area, carbon stocks, and sequestration potential of different land cover types in lowland moist and dry tropical forest biomes.

table S2. Area, carbon stocks, and sequestration potential of Latin American countries.

table S3. Ranked area, carbon stocks, and sequestration potential of different land cover types in lowland moist and dry tropical forest biomes of the top 10 Latin American countries.

REFERENCES AND NOTES

1. R. A. Houghton, B. Byers, A. A. Nassikas, A role for tropical forests in stabilizing atmospheric CO_2. *Nat. Clim. Chang.* **5**, 1022–1023 (2015).
2. Y. Pan, R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, A. Shvidenko, S. L. Lewis, J. G. Canadell, P. Ciais, R. B. Jackson, S. W. Pacala, A. D. McGuire, S. Piao, A. Rautiainen, S. Sitch, D. Hayes, A large and persistent carbon sink in the world's forests. *Science* **333**, 988–993 (2011).
3. S. J. Wright, The carbon sink in intact tropical forests. *Glob. Chang. Biol.* **19**, 337–339 (2013).
4. FAO, *Global Forest Resources Assessment 2015. How Are the World's Forests Changing?* (FAO, Rome, Italy, 2015).
5. T. M. Aide, M. L. Clark, H. R. Grau, D. López-Carr, M. A. Levy, D. Redo, M. Bonilla-Moheno, G. Riner, M. J. Andrade-Núñez, M. Muñiz, Deforestation and reforestation of Latin America and the Caribbean (2001–2010). *Biotropica* **45**, 262–271 (2013).
6. R. L. Chazdon, *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation* (University of Chicago Press, Chicago, IL, 2014), 485 pp.
7. M. C. Hansen, P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, J. R. G. Townshend, High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013).
8. J. G. Canadell, M. R. Raupach, Managing forests for climate change mitigation. *Science* **320**, 1456–1457 (2008).
9. R. A. Houghton, in *Global Forest Monitoring from Earth Observation*, F. Achard, M. C. Hansen, Eds. (CRC Press, Boca Raton, FL, 2013), pp. 15–38.
10. R. C. Goodman, M. Herold, Why maintaining tropical forests is essential and urgent for a stable climate, in *CGD Climate and Forest Paper Series #11* (Center for Global Development Climate and Forest, Washington, DC, 2014), 56 pp.
11. M. van Breugel, J. S. Hall, D. Craven, M. Bailon, A. Hernandez, M. Abbene, P. van Breugel, Succession of ephemeral secondary forests and their limited role for the conservation of floristic diversity in a human-modified tropical landscape. *PLOS One* **8**, e82433 (2013).
12. A. P. D. Aguiar, I. C. G. Vieira, T. O. Assis, E. L. Dalla-Nora, P. M. Toledo, R. A. Oliveira Santos-Junior, M. Batistella, A. S. Coelho, E. K. Savaget, L. E. O. C. Aragão, C. A. Nobre, J. P. H. Ometto, Land use change emission scenarios: Anticipating a forest transition process in the Brazilian Amazon. *Glob. Chang. Biol.* **22**, 1821–1840 (2016).
13. M. K. Steininger, Net carbon fluxes from forest clearance and regrowth in the Amazon. *Ecol. Appl.* **14**, S313–S322 (2004).
14. L. Poorter, F. Bongers, T. M. Aide, A. M. Almeyda Zambrano, P. Balvanera, J. M. Becknell, V. Boukili, P. H. S. Brancalion, E. N. Broadbent, R. L. Chazdon, D. Craven, J. S. de Almeida-Cortez, G. A. L. Cabral, B. H. J. de Jong, J. S. Denslow, D. H. Dent, S. J. DeWalt, J. M. Dupuy, S. M. Durán, M. M. Espírito-Santo, M. C. Fandino, R. G. César, J. S. Hall, J. L. Hernandez-Stefanoni, C. C. Jakovac, A. B. Junqueira, D. Kennard, S. G. Letcher, J.-C. Licona, M. Lohbeck, E. Marín-Spiotta, M. Martínez-Ramos, P. Massoca, J. A. Meave, R. Mesquita, F. Mora, R. Muñoz, R. Muscarella, Y. R. F. Nunes, S. Ochoa-Gaona, A. A. de Oliveira, E. Orihuela-Belmonte, M. Peña-Claros, E. A. Pérez-García, D. Piotto, J. S. Powers, J. Rodríguez-Velázquez, I. E. Romero-Pérez, J. Ruíz, J. G. Saldarriaga, A. Sanchez-Azofeifa, N. B. Schwartz, M. K. Steininger, N. G. Swenson, M. Toledo, M. Uriarte, M. van Breugel, H. van der Wal, M. D. M. Veloso, H. F. M. Vester, A. Vicentini, I. C. G. Vieira, T. V. Bentos, G. B. Williamson, D. M. A. Rozendaal, Biomass resilience of Neotropical secondary forests. *Nature* **530**, 211–214 (2016).
15. A. Baccini, S. J. Goetz, W. S. Walker, N. T. Laporte, M. Sun, D. Sulla-Menashe, J. Hackler, P. S. A. Beck, R. Dubayah, M. A. Friedl, S. Samanta, R. A. Houghton, Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nat. Clim. Chang.* **2**, 182–185 (2012).
16. B. B. N. Strassburg, A. E. Latawiec, L. G. Barioni, C. A. Nobre, V. P. da Silva, J. F. Valentim, M. Vianna, E. D. Assad, When enough should be enough: Improving the use of current agricultural lands could meet production demands and spare natural habitats in Brazil. *Glob. Environ. Chang.* **28**, 84–97 (2014).
17. B. Soares-Filho, R. Rajão, M. Macedo, A. Carneiro, W. Costa, M. Coe, H. Rodrigues, A. Alencar, Cracking Brazil's Forest Code. *Science* **344**, 363–364 (2014).
18. J. G. J. Olivier, G. Janssens-Maenhout, M. Muntean, J. A. H. W. Petes, *Trends in Global CO_2 Emissions: 2015 Report*, PBL Netherlands Environmental Assessment Agency, The Hague; European Commission, Joint Research Centre (JRC), Institute for Environment and Sustainability (IES). JRC98184, PBL1803; http://edgar.jrc.ec.europa.eu/news_docs/jrc-2015-trends-in-global-co2-emissions-2015-report-98184.pdf [accessed November 2015].
19. IPCC, "Annex II: Glossary [Mach, K. J., S. Planton and C. von Stechow (Eds.)]", *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (IPCC, Geneva, Switzerland, 2014), 151 pp.
20. I. C. G. Vieira, T. Gardner, J. Ferreira, A. C. Lees, J. Barlow, Challenges of governing second-growth forests: A case study from the Brazilian Amazonian State of Pará. *Forests* **5**, 1737–1752 (2014).
21. FAO, *Global Forest Resources Assessment 2010* (Food and Agricultural Organization of the United Nations, Rome, Italy, 2010), 378 pp.
22. J. A. Gallardo-Cruz, J. A. Meave, E. J. González, E. E. Lebrija-Trejos, M. A. Romero-Romero, E. A. Pérez-García, R. Gallardo-Cruz, J. L. Hernández-Stefanoni, C. Martorell, Predicting tropical dry forest successional attributes from space: Is the key hidden in image texture? *PLOS One* **7**, e30506 (2012).
23. M. E. Fagan, R. S. DeFries, S. E. Sesnie, J. P. Arroyo-Mora, C. Soto, A. Singh, P. A. Townsend, R. L. Chazdon, Mapping species composition of forests and tree plantations in Northeastern Costa Rica with an integration of hyperspectral and multitemporal Landsat imagery. *Remote Sens.* **7**, 5660–5696 (2015).
24. R. Petersen, E. D. Goldman, N. Harris, S. Sargent, D. Aksenov, A. Manisha, E. Esipova, V. Shevade, T. Loboda, N. Kuksina, I. Kurakina, *Mapping Tree Plantations with Multispectral Imagery: Preliminary Results for Seven Tropical Countries* (World Resources Institute, Washington, DC); www.wri.org/publication/mapping-treeplantations.
25. S. Luyssaert, I. Inglima, M. Jung, A. D. Richardson, M. Reichstein, D. Papale, S. L. Piao, E.-D. Schulze, L. Wingate, G. Matteucci, L. Aragao, M. Aubinet, C. Beer, C. Bernhofer, K. G. Black, D. Bonal, J.-M. Bonnefond, J. Chambers, P. Ciais, B. Cook, K. J. Davis, A. J. Dolman, B. Gielen, M. Goulden, J. Grace, A. Granier, A. Grelle, T. Griffis, T. Grünwald, G. Guidolotti, P. J. Hanson, R. Harding, D. Y. Hollinger, L. R. Hutyra, P. Kolari, B. Kruijt, W. Kutsch, F. Lagergren, T. Laurila, B. E. Law, G. Le Maire, A. Lindroth, D. Loustau, Y. Malhi, J. Mateus, M. Migliavacca, L. Misson, L. Montagnani, J. Moncrieff, E. Moors, J. W. Munger, E. Nikinmaa, S. V. Ollinger, G. Pita, C. Rebmann, O. Roupsard, N. Saigusa, M. J. Sanz, G. Seufert, C. Sierra, M.-L. Smith, J. Tang, R. Valentini, T. Vesala, I. A. Janssens, CO_2 balance of boreal, temperate, and tropical forests derived from a global database. *Glob. Chang. Biol.* **13**, 2509–2537 (2007).

26. J. S. Powers, M. D. Corre, T. E. Twine, E. Veldkamp, Geographic bias of field observations of soil carbon stocks with tropical land-use changes precludes spatial extrapolation. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 6318–6322 (2011).
27. A. K. Skidmore, N. Pettorelli, N. C. Coops, G. N. Geller, M. Hansen, R. Lucas, C. A. Mücher, B. O'Connor, M. Paganini, H. M. Pereira, M. E. Schaepman, W. Turner, T. Wang, M. Wegmann, Environmental science: Agree on biodiversity metrics to track from space. *Nature* **523**, 403–405 (2015).
28. E. Marín-Spiotta, D. F. Cusack, R. Ostertag, W. L. Silver, in *Post-Agricultural Succession in the Neotropics*, R. W. Myster, Ed. (Springer, New York, 2008), pp. 22–72.
29. E. V. Wandelli, P. M. Fearnside, Secondary vegetation in central Amazonia: Land-use history effects on aboveground biomass. *For. Ecol. Manage.* **347**, 140–148 (2015).
30. S. A. Mukul, J. Herbohn, J. Firn, Tropical secondary forests regenerating after shifting cultivation in the Philippines uplands are important carbon sinks. *Sci. Rep.* **6**, 22483 (2016).
31. K. J. Anderson-Teixeira, M. M. H. Wang, J. C. McGarvey, D. S. LeBauer, Carbon dynamics of mature and regrowth tropical forests derived from a pantropical database (TropForC-db). *Glob. Chang. Biol.* **22**, 1690–1709 (2016).
32. M. Greve, B. Reyers, A. M. Lykke, J.-C. Svenning, Spatial optimization of carbon-stocking projects across Africa integrating stocking potential with co-benefits and feasibility. *Nat. Commun.* **4**, 2975 (2013).
33. M. Uriarte, J. R. Lasky, V. K. Boukili, R. L. Chazdon, A trait-mediated, neighbourhood approach to quantify climate impacts on successional dynamics of tropical rainforests. *Funct. Ecol.* **30**, 157–167 (2016).
34. Federal Republic of Brazil, http://www4.unfccc.int/submissions/INDC/Published%20Documents/Brazil/1/BRAZIL%20iNDC%20english%20FINAL.pdf [accessed October 28, 2015].
35. A. E. Latawiec, B. B. N. Strassburg, P. H. S. Brancalion, R. R. Rodrigues, T. Gardner, Creating space for large-scale restoration in tropical agricultural landscapes. *Front. Ecol. Environ.* **13**, 211–218 (2015).
36. B. Locatelli, C. P. Catterall, P. Imbach, C. Kumar, R. Lasco, E. Marín-Spiotta, B. Mercer, J. S. Powers, N. Schwartz, M. Uriarte, Tropical reforestation and climate change: Beyond carbon. *Restor. Ecol.* **23**, 337–343 (2015).
37. J. A. Stanturf, P. Kant, J.-P. B. Lillesø, S. Mansourian, M. Kleine, L. Graudal, P. Madsen, *Forest Landscape Restoration as a Key Component of Climate Change Mitigation and Adaptation* (IUFRO World Series, Vienna, Austria, 2015), vol. 34, 72 pp.
38. D. M. Olson, E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, K. R. Kassem, Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience* **51**, 933–938 (2001).
39. N. Ramankutty, A. T. Evan, C. Monfreda, J. A. Foley, Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochem. Cycles* **22**, GB1003 (2008).
40. S. Fritz, L. See, I. McCallum, L. You, A. Bun, E. Moltchanova, M. Duerauer, F. Albrecht, C. Schill, C. Perger, P. Havlik, A. Mosnier, P. Thornton, U. Wood-Sichra, M. Herrero, I. Becker-Reshef, C. Justice, M. Hansen, P. Gong, S. Abdel Aziz, A. Cipriani, R. Cumani, G. Cecchi, G. Conchedda, S. Ferreira, A. Gomez, M. Haffani, F. Kayitakire, J. Malanding, R. Mueller, T. Newby, A. Nonguierma, A. Olusegun, S. Ortner, D. R. Rajak, J. Rocha, D. Schepaschenko, M. Schepaschenko, A. Terekhov, A. Tiangwa, C. Vancutsem, E. Vintrou, W. Wenbin, M. van der Velde, A. Dunwoody, F. Kraxner, M. Obersteiner, Mapping global cropland and field size. *Glob. Chang. Biol.* **21**, 1980–1992 (2015).
41. R. Chaplin-Kramer, I. Ramler, R. Sharp, N. M. Haddad, J. S. Gerber, P. C. West, L. Mandle, P. Engstrom, A. Baccini, S. Sim, C. Mueller, H. King, Degradation in carbon stocks near tropical forest edges. *Nat. Commun.* **6**, 10158 (2015).
42. T. Payn, J.-M. Carnus, P. Freer-Smith, M. Kimberley, W. Kollert, S. Liu, C. Orazio, L. Rodriguez, L. N. Silva, M. J. Wingfield, Changes in planted forests and future global implications. *For. Ecol. Manage.* **352**, 57–67 (2015).
43. A. Schneider, M. A. Friedl, D. Potere, A new map of global urban extent from MODIS satellite data. *Environ. Res. Lett.* **4**, 044003 (2009).
44. A. Schneider, M. A. Friedl, D. Potere, Mapping global urban areas using MODIS 500-m data: New methods and datasets based on 'urban ecoregions'. *Remote Sens. Environ.* **114**, 1733–1746 (2010).
45. D. Potere, A. Schneider, S. Angel, D. L. Civco, Mapping urban areas on a global scale: Which of the eight maps now available is more accurate? *Int. J. Remote Sens.* **30**, 6531–6558 (2009).
46. B. Lehner, P. Döll, Development and validation of a global database of lakes, reservoirs and wetlands. *J. Hydrol.* **296**, 1–22 (2004).
47. J. Chave, C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Fölster, F. Fromard, N. Higuchi, T. Kira, J.-P. Lescure, B. W. Nelson, H. Ogawa, H. Puig, B. Riéra, T. Yamakura, Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **145**, 87–99 (2005).
48. J. Chave, M. Réjou-Méchain, A. Búrquez, E. Chidumayo, M. S. Colgan, W. B. C. Delitti, A. Duque, T. Eid, P. M. Fearnside, R. C. Goodman, M. Henry, A. Martínez-Yrízar, W. A. Mugasha, H. C. Muller-Landau, M. Mencuccini, B. W. Nelson, A. Ngomanda, E. M. Nogueira, E. Ortiz-Malavassi, R. Pélissier, P. Ploton, C. M. Ryan, J. G. Saldarriaga, G. Vieilledent, Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Chang. Biol.* **20**, 3177–3190 (2014).
49. R. J. Hijmans, S. E. Cameron, J. L. Parra, P. G. Jones, A. Jarvis, Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
50. EMBRAPA-INPE, Levantamento de informacoes de use e cobertura da terra na Amazonia. *Sumario Executivo* (2011).

Acknowledgments: This paper is a product of the 2ndFOR collaborative research network on secondary forests. We thank the owners of the secondary forest sites for access to their forests, all the people who have established and measured the plots, and the institutions and funding agencies that supported them. We thank E. Marín-Spiotta, M. Toledo, and J. Zimmerman for the use of plot data. E. Arets provided assistance with carbon mitigation calculations. N. Pitman provided constructive comments on an earlier version of this manuscript. This is publication #685 in the Technical Series of the Biological Dynamics of Forest Fragments Project BDFFP-INPA-SI. **Funding:** The following agencies provided financial support for this research: the Australian Department of Foreign Affairs and Trade, Consultative Group for International Agricultural Research (CGIAR) Forests, Trees, and Agroforestry (FTA) Program, the Center for International Forestry Research, Colciencias grant 1243-13-16640, Consejo Nacional de Ciencia y Tecnología (SEP-CONACYT 2009-129740 and SEP-CONACYT 2015-255544 for ReSerBos, CONACYT 33851-B, SEMARNAT-CONACYT 2002 C01-0597, SEP-CONACYT CB-2005-01-51043, and PAPIIT-DGAPA IN213714 and IND211114), PAPIIT-UNAM (IN221503-3), CONACYT (CB-2009-01-128136), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 563304/2010-3, 562955/2010-0, and PQ 307422/2012-7), Instituto Tamanduá, FOMIX-Yucatan (YUC-2008-C06-108863), ForestGEO, Fundação de Amparo à Pesquisa de Minas Gerais (FAPEMIG CRA APQ-0001-11), Fundación Ecológica de Cuixmala, the Heising-Simons Foundation, HSBC, ICETEX, Instituto Internacional de Educação do Brasil, Instituto Nacional de Serviços Ambientais da Amazônia–Instituto Nacional de Pesquisas da Amazônia, the Inter-American Institute for Global Change (Tropi-dry network CRN3-025), the Motta Family Foundation, NSF (NSF-DEB 0639114, 0639393, 1147429, 0129104, 1050957, 1147434, CAREER GRANT DEB-1053237, NSF BCS-1349952, and NSF-CNH-RCN grant 1313788 for Tropical Reforestation Network: Building a Socioecological Understanding of Tropical Reforestation), NUFFIC, USAID (BOLFOR), INCT Biodiversidade e Uso da Terra na Amazônia (CNPq 574008/2008-0), the Silicon Valley Foundation, Stichting Het Kronendak, the Tropenbos Foundation, and Wageningen University (INREF Terra Preta programme and FOREFRONT programme). This study was partly funded by European Union's Seventh Framework Programme (FP7/2007-2013) under grant agreement no. 283093 [Role Of Biodiversity In climate change mitigatioN (ROBIN)]. **Author contributions**: R.L.C., E.N.B., D.M.A.R., L.P., F.B., and A.M.A.Z. designed the study and contributed to the manuscript; R.L.C. led the writing and editing of the manuscript; E.N.B., D.M.A.R., and A.M.A.Z. conducted data analysis and produced maps; all authors contributed data and provided comments on the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials or are derived from publicly available sources. Additional data related to this paper are available from the authors upon request.

Submitted 13 November 2015
Accepted 12 April 2016
Published 13 May 2016
10.1126/sciadv.1501639

Citation: R. L. Chazdon, E. N. Broadbent, D. M. A. Rozendaal, F. Bongers, A. M. A. Zambrano, T. M. Aide, P. Balvanera, J. M. Becknell, V. Boukili, P. H. S. Brancalion, D. Craven, J. S. Almeida-Cortez, G. A. L. Cabral, B. de Jong, J. S. Denslow, D. H. Dent, S. J. DeWalt, J. M. Dupuy, S. M. Durán, M. M. Espírito-Santo, M. C. Fandino, R. G. César, J. S. Hall, J. L. Hernández-Stefanoni, C. C. Jakovac, A. B. Junqueira, D. Kennard, S. G. Letcher, M. Lohbeck, M. Martínez-Ramos, P. Massoca, J. A. Meave, R. Mesquita, F. Mora, R. Muñoz, R. Muscarella, Y. R. F. Nunes, S. Ochoa-Gaona, E. Orihuela-Belmonte, M. Peña-Claros, E. A. Pérez-García, D. Piotto, J. S. Powers, J. Rodríguez-Velazquez, I. Eunice Romero-Pérez, J. Ruíz, J. G. Saldarriaga, A. Sanchez-Azofeifa, N. B. Schwartz, M. K. Steininger, N. G. Swenson, M. Uriarte, M. van Breugel, H. van der Wal, M. D. M. Veloso, H. Vester, I. C. G. Vieira, T. V. Bentos, G. B. Williamson, L. Poorter, Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Sci. Adv.* **2**, e1501639 (2016).

PRIMATOLOGY

Impending extinction crisis of the world's primates: Why primates matter

Alejandro Estrada,[1]* Paul A. Garber,[2]* Anthony B. Rylands,[3] Christian Roos,[4] Eduardo Fernandez-Duque,[5] Anthony Di Fiore,[6] K. Anne-Isola Nekaris,[7] Vincent Nijman,[7] Eckhard W. Heymann,[8] Joanna E. Lambert,[9] Francesco Rovero,[10] Claudia Barelli,[10] Joanna M. Setchell,[11] Thomas R. Gillespie,[12] Russell A. Mittermeier,[3] Luis Verde Arregoitia,[13] Miguel de Guinea,[7] Sidney Gouveia,[14] Ricardo Dobrovolski,[15] Sam Shanee,[16,17] Noga Shanee,[16,17] Sarah A. Boyle,[18] Agustin Fuentes,[19] Katherine C. MacKinnon,[20] Katherine R. Amato,[21] Andreas L. S. Meyer,[22] Serge Wich,[23,24] Robert W. Sussman,[25] Ruliang Pan,[26] Inza Kone,[27] Baoguo Li[28]

Nonhuman primates, our closest biological relatives, play important roles in the livelihoods, cultures, and religions of many societies and offer unique insights into human evolution, biology, behavior, and the threat of emerging diseases. They are an essential component of tropical biodiversity, contributing to forest regeneration and ecosystem health. Current information shows the existence of 504 species in 79 genera distributed in the Neotropics, mainland Africa, Madagascar, and Asia. Alarmingly, ~60% of primate species are now threatened with extinction and ~75% have declining populations. This situation is the result of escalating anthropogenic pressures on primates and their habitats—mainly global and local market demands, leading to extensive habitat loss through the expansion of industrial agriculture, large-scale cattle ranching, logging, oil and gas drilling, mining, dam building, and the construction of new road networks in primate range regions. Other important drivers are increased bushmeat hunting and the illegal trade of primates as pets and primate body parts, along with emerging threats, such as climate change and anthroponotic diseases. Often, these pressures act in synergy, exacerbating primate population declines. Given that primate range regions overlap extensively with a large, and rapidly growing, human population characterized by high levels of poverty, global attention is needed immediately to reverse the looming risk of primate extinctions and to attend to local human needs in sustainable ways. Raising global scientific and public awareness of the plight of the world's primates and the costs of their loss to ecosystem health and human society is imperative.

INTRODUCTION

Nonhuman primates (primates hereafter) are of central importance to tropical biodiversity and to many ecosystem functions, processes, and services. They are our closest living biological relatives, offering critical insights into human evolution, biology, and behavior and playing important roles in the livelihoods, cultures, and religions of many societies. Unsustainable human activities are now the major force driving primate species to extinction. Here, we combine the most frequently used standard for species conservation status [the International Union for Conservation of Nature (IUCN) Red List] with data from peer-reviewed scientific literature and from the United Nations databases to evaluate human-induced threats to primate survival. We examine trends in forest loss resulting from regional and global economic pressures and discuss the impacts of hunting, illegal trade, and other anthropogenic threats on primate populations. We also model agricultural expansion into the 21st century and identify expected spatial conflict within primate range areas. We assess the current level of scientific knowledge available for individual primate taxa, and we highlight the ecological, social, cultural, economic, and scientific importance of primates, as well as the global consequences of their population declines. We also consider future research needs and advances in technology for monitoring human-induced environmental changes that affect primate populations. Finally, we propose a conceptual

---

[1]Institute of Biology, National Autonomous University of Mexico, CP 04510, Mexico City, Mexico. [2]Department of Anthropology, Program in Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana, IL 61801, USA. [3]Conservation International, 2011 Crystal Drive, Suite 500, Arlington, VA 22202, USA. [4]Gene Bank of Primates and Primate Genetics Laboratory, German Primate Center, Leibniz Institute for Primate Research, Kellnerweg 4, 37077 Göttingen, Germany. [5]Department of Anthropology, Yale University, New Haven, CT 06511, USA. [6]Department of Anthropology, University of Texas, Austin, TX 78705, USA. [7]Department of Social Sciences, Oxford Brookes University, Oxford OX3 0BP, U.K. [8]Abteilung Verhaltensökologie und Soziobiologie, Deutsches Primatenzentrum, Leibniz-Institut für Primatenforschung, Kellnerweg 4, D-37077 Göttingen, Germany. [9]Department of Anthropology, University of Colorado at Boulder, 1350 Pleasant Street UCB 233, Boulder, CO 80309, USA. [10]Tropical Biodiversity Section, MUSE—Museo delle Scienze, Corso del Lavoro e della Scienza 3, 38122 Trento, Italy. [11]Department of Anthropology, and Behaviour, Ecology and Evolution Research Centre, Durham University, South Road, Durham DH1 3LE, U.K. [12]Departments of Environmental Sciences and Environmental Health, Rollins School of Public Health, Emory University, 400 Dowman Drive, Math and Science Center, Suite E510, Atlanta, GA 30322, USA. [13]Naturhistorisches Museum Bern, Bernastrasse 15, CH-3005 Bern, Switzerland. [14]Department of Ecology, Federal University of Sergipe, São Cristóvão, SE 49100-000, Brazil. [15]Department of Zoology, Federal University of Bahia, Salvador, BA 40170-290, Brazil. [16]Neotropical Primate Conservation, 23 Portland Road, Manchester M32 0PH, U.K. [17]Asociación Neotropical Primate Conservation Perú, 1187 Avenida Belaunde, La Esperanza, Yambrasbamba, Bongará, Amazonas, Peru. [18]Department of Biology, Rhodes College, 2000 North Parkway, Memphis, TN 38112, USA. [19]Department of Anthropology, University of Notre Dame, Notre Dame, IN 46556, USA. [20]Department of Sociology and Anthropology, Saint Louis University, St. Louis, MO 63108, USA. [21]Department of Anthropology, Northwestern University, 1810 Hinman Avenue, Evanston, IL 60208, USA. [22]Programa de Pós-Graduação em Zoologia, Departamento de Zoologia, Universidade Federal do Paraná, C.P. 19020, Curitiba, PR 81531-990, Brazil. [23]School of Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3 3AF, U.K. [24]Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, Netherlands. [25]Department of Anthropology, Washington University, St. Louis, MO 63130, USA. [26]School of Anatomy, Physiology and Human Biology, University of Western Australia (M309), 35 Stirling Highway, Crawley, Western Australia 6009, Australia. [27]Centre Suisse des Recherches Scientifiques, Université de Cocody, Abidjan, Côte d'Ivoire. [28]Xi'an Branch of Chinese Academy of Sciences, College of Life Sciences, Northwest University, No. 229, Taibai North Road, Xi'an 710069, China.
*Corresponding author. Email: aestradaprimates@gmail.com (A.E.); p-garber@illinois.edu (P.A.G.)

model to guide the development of global, regional, and local approaches to promote primate conservation while at the same time attending to human needs. The goal of this review is not to produce a list of threats but rather to urge attention to the multiple global and regional anthropogenic factors that imperil primates worldwide and to encourage the development of sustainable and effective solutions that enhance primate survival in the medium and long term.

IMPENDING DEFAUNATION OF THE WORLD'S PRIMATES

The order Primates is one of the most species-rich groups of mammals, surpassed only by the orders Chiroptera (bats, 1151 species) and Rodentia (rodents, 2256 species) (*1*, *2*). The most recent taxonomic compilation (April 2016) lists 701 extant taxa belonging to 504 species from 79 genera and 16 families (tables S1 to S4 and Supplementary Text) (*2*–*5*). Primates occur in four regions—the Neotropics (171 species), mainland Africa (111 species), Madagascar (103 species), and Asia (119 species) (Fig. 1)—and are present naturally in 90 countries; however, two-thirds of all species occur in just four countries—Brazil, Madagascar, Indonesia, and the Democratic Republic of the Congo (DRC) (figs. S1 and S2A). These countries represent high-priority areas for primate conservation. The large majority of primates inhabit tropical moist lowland forests, but they also occur in tropical dry forests, mangrove vegetation above high-tide levels, moist montane forests, high-elevation (from 1000 to >4000 m) deciduous and broadleaf temperate forests, savannas, grasslands, inland wetlands, rocky areas, and even deserts (*2*, *4*). The body mass of living primates ranges from 30 g in Madame Berthe's mouse lemur (*Microcebus berthae*) to about 200 kg in male western and eastern gorillas (*Gorilla gorilla* and *Gorilla beringei*, respectively) (Supplementary Text) (*2*, *4*, *5*).

Using information from the IUCN and our current assessment, we estimate that ~60% of primate species, from all 16 extant families, are threatened with extinction because of unsustainable human activities (Figs. 1 and 2 and tables S1 to S4). Threats to primates are widespread: 87% of species in Madagascar are threatened, as are 73% in Asia, 37% in mainland Africa, and 36% in the Neotropics (Fig. 1 and figs. S2B and S3A). The populations of 75% of primate species are decreasing globally (Fig. 1 and fig. S3B). Considering the large number of species currently threatened and experiencing population declines, the world will soon be facing a major extinction event if effective action is not implemented immediately.

FACTORS THAT THREATEN PRIMATE POPULATIONS

The IUCN indicates that the main threats to primate species are loss of habitat due to agriculture (76% of species), logging and wood harvesting (60%), and livestock farming and ranching (31%), as well as direct loss due to hunting and trapping (60%) (fig. S4A). Other threats, such as habitat loss due to road and rail construction, oil and gas drilling, and mining, affect 2 to 13% of primate species, and there are also emerging threats, such as pollution and climate change (fig. S4B and table S5). Globally, agriculture is the principal threat, but secondary threats vary by region. For example, livestock farming and ranching negatively affect 59% of primate species in the Neotropics. In contrast, in mainland Africa, Madagascar, and Asia, hunting and trapping affect 54 to 90% of the

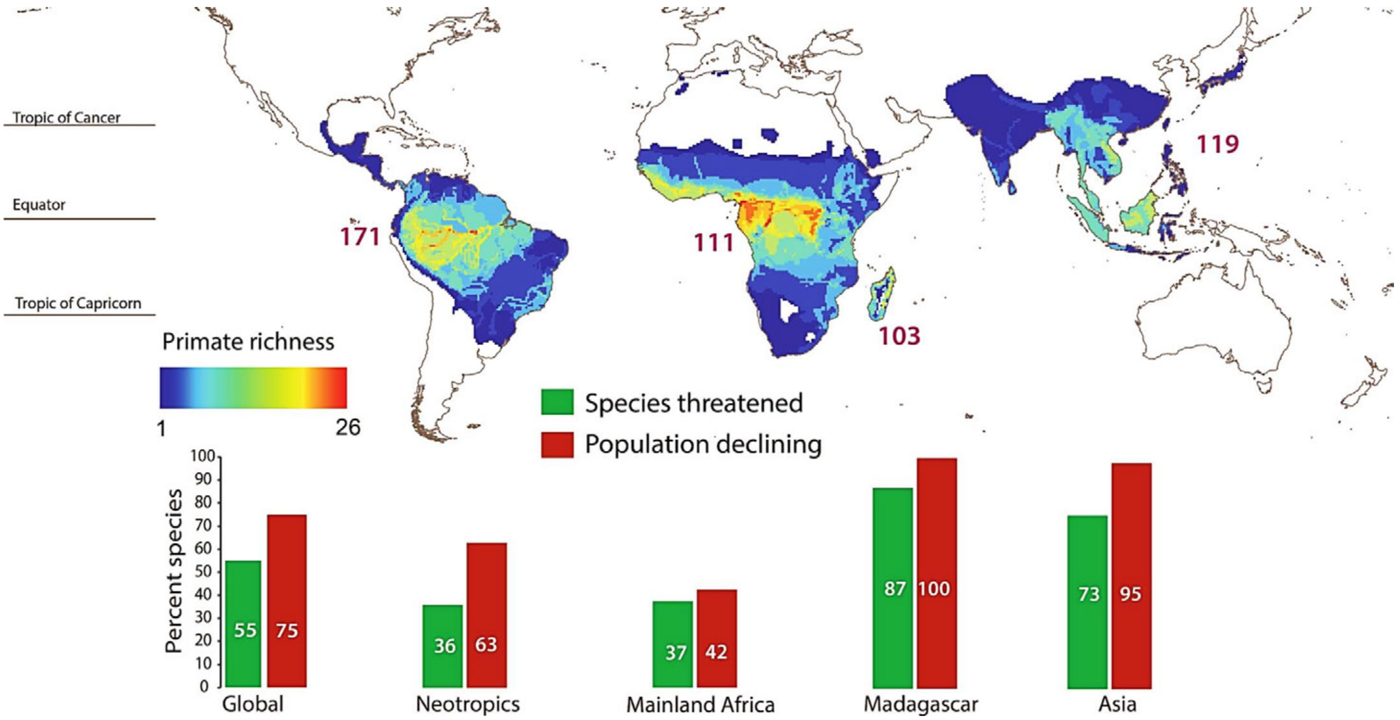


Fig. 1. Global primate species richness, distributions, and the percentage of species threatened and with declining populations. Geographic distribution of primate species. Numbers in red by each region refer to the number of extant species present. The bars at the bottom show the percent of species threatened with extinction and the percent of species with declining populations in each region. Percentage of threatened species and percentage of species with declining populations in each region from tables S1 to S4. Geographical range data of living, native species from the IUCN Red List (www.iucnredlist.org) are overlaid onto a 0.5° resolution equal-area grid. In cases in which a species' range was split into multiple subspecies, these were merged to create a range map for the species. Mainland Africa includes small associated islands.

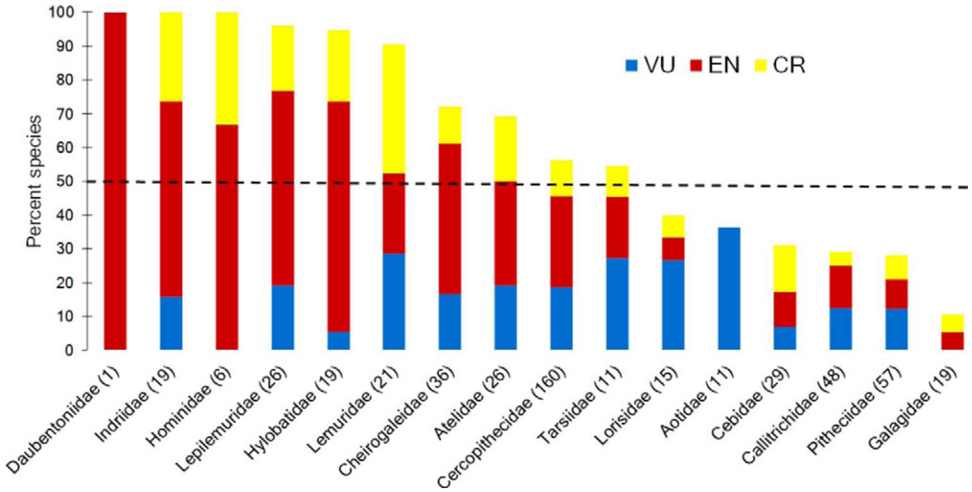


Fig. 2. Percent of species threatened with extinction in each primate family. Assessment of threat level is according to the IUCN Categories and Criteria VU (Vulnerable), EN (Endangered), and CR (Critically Endangered). Number in parentheses after each family indicates the number of species recognized in the family. Data for each species are indicated in tables S1 to S4. Notably, there are threatened species in all 16 primate families. Ten families have more than 50% of their species threatened (broken line at 50%). Note that the graph is only for the Threatened IUCN categories. Families not showing 100% values may have some species classified as Near Threatened (NT), Least Concern (LC), Data Deficient (DD), and Not Evaluated (NE) (see tables S1 to S3). Upon revision of the taxonomy of Malagasy lemurs, a number of taxa once thought to be widespread are now highly threatened; a similar scenario is envisioned for the galagids, where there appears to be a large number of newly recognized species with limited ranges. Taxonomy is based on previous works (*1*–*3*).

species. Logging is the third greatest threat to primates in all regions (fig. S4A).

Land-cover changes, global market demands, and industry-driven deforestation

Global market demands for nonarboreal (for example, soybeans, sugar cane, and rice) and arboreal crops (for example, oil palm and natural rubber), livestock (particularly cattle), and tropical hardwoods have resulted in a process of rapid and widespread industry-driven deforestation in the Neotropics, mainland Africa, Madagascar, and Asia (Supplementary Text and fig. S5, A to F) (*6*). For example, between 1990 and 2010, agricultural expansion in primate range regions was estimated at 1.5 million km^2 (an area three times that of France) and forest cover loss at 2 million km^2 (Fig. 3 and fig. S6, A to C). Increasing global demand for oil palm products is a major driver of recent severe declines in Sumatran and Bornean orangutan (*Pongo abelii* and *Pongo pygmaeus*, respectively) numbers and a serious risk for African apes because large segments of existing populations occur outside protected areas (*7*–*10*). Moreover, future oil palm development is likely to threaten forested areas in South America and Africa (*10*), which is projected to result in severe negative consequences for primate populations in those regions (fig. S5C). The expansion of rubber plantations in southwest China has caused the near extinction of the northern white-cheeked crested gibbon (*Nomascus leucogenys*) and the Hainan gibbon (*Nomascus hainanus*) (*11*). Similarly, deforestation due to the establishment of rubber plantations in India is reported to have severely affected the Bengal slow loris (*Nycticebus bengalensis*), the western hoolock gibbon (*Hoolock hoolock*), and Phayre's langur (*Trachypithecus phayrei*) (*11*, *12*). Modeling the overlap between primate species' distributions and forecasted future agricultural production for the 21st century indicates that regions predicted to undergo the greatest agricultural expansion over the next decades comprise 68% of the global area currently occupied by primates (Fig. 4). This will result in unprecedented spatial conflict with 75% of primate species worldwide (Supplementary Text). Therefore, the implementation of policies to divert agricultural expansion to areas where it is likely to result in the least environmental impacts is essential to reduce spatial conflicts between primate-rich areas and the expanding agricultural frontier (*13*).

Logging, mining, and fossil fuel extraction

Globalized financial markets and a worldwide commodity boom have led to an ever-growing demand for tropical timber and a concomitant expansion of industrial logging, resulting in deforestation and creating a potent economic impetus for road building in forested areas (Supplementary Text) (*14*). Countries in primate range regions are responding to global market demands by expanding logging activities to increase economic growth. In 2010, the Neotropics accounted for 48% of the production of industrial hardwood, followed by Southeast Asia (23%), sub-Saharan Africa (16%), and South Asia (13%) (fig. S5E). In Madagascar, the large-scale harvesting of rosewood (*Dalbergia*) since 2009 has negatively affected several protected areas (*15*). The immediate and long-term effects of legal and illegal logging are a reduction of canopy cover, the destruction of forest undergrowth, and the decline of large tree species important to primates as sources of food and shelter (*16*).

Mining for minerals and diamonds is also a growing threat to tropical ecosystems and their primates. Although it involves relatively small areas, mining contributes to deforestation, forest degradation, and the pollution and poisoning of streams and soil (*17*). In central Africa, the population densities of apes in mined forests [75.7 (45.35 to 126.33) nests/km^2] are markedly lower than in forested sites where mining is absent [234 (185 to 299) nests/km^2] (*18*). In Madagascar, illicit gold and sapphire mining by itinerant miners has affected many forests, including protected ones (*19*). Mining of gold, nickel, and copper on Dinagat island, in the Philippines, is endangering the survival of the Philippine tarsier (*Carlito syrichta*) (*20*). Bushmeat hunting associated with the mining of coltan, tin, gold, and diamonds in the DRC is the main threat

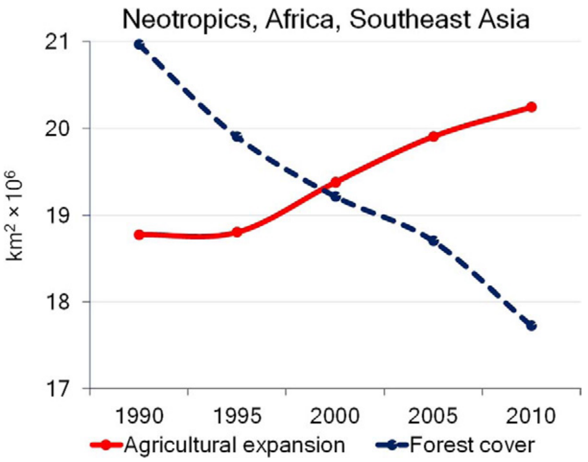


Fig. 3. Agricultural expansion and declines in forest cover for the period 1990–2010 in primate range regions. A rapid expansion of agriculture in primate range regions has been paralleled by a sharp decline in forest cover in the 20-year period considered. Trends for each individual region are shown in fig. S6 (A to C). Data for Africa include Madagascar (source of raw data, FAOSTAT: faostat.fao.org/site/377/DesktopDefault.aspx?PageID=377#ancor. Consulted June 2016).

to Grauer's gorilla (*G. beringei graueri*) (*21*); recent surveys indicate a 77% decline in its numbers, from 17,000 in 1995 to just 3800 in 2014/2015 (*22*). In Perú, the mining of zinc and copper threatens the endemic and Critically Endangered yellow-tailed woolly monkey (*Lagothrix flavicauda*) (*23*). Development associated with fossil fuel extractions also jeopardizes primate survival. By 2035, global demand for oil and natural gas is projected to increase by >30 and 53% respectively, and primate-rich areas, such as the western Amazon and the western Pacific Ocean (Malaysia, Borneo) will be adversely affected. It is estimated that oil and gas concessions in the western Amazon, and in remote forested areas of Colombia, Ecuador, Brazil, Perú, and Bolivia, already cover about 733,414 km^2 (twice the size of Germany) (*24*).

Other anthropogenic stressors

The expansion of industrialized agriculture, logging, mining, oil/gas extraction, and the building of dams and power-line corridors in tropical forest areas is expected to increase human transportation road networks by some 25 million km by 2050 (Supplementary Text) (*25*). Consequences of the unrestricted road and rail building include increased forest losses from human population migration, illegal colonization, and logging; increased bushmeat hunting; and the illegal wildlife trade (Supplementary Text) (*26*). The construction of conventional dams and megadams for generating electricity to attract energy-intensive industry and stimulate local productivity in the world's most biodiverse river basins—the Amazon, Congo, and Mekong—also poses a severe threat to local primate persistence (*27*). For example, the development of 12 megadams in the state of Sarawak, Malaysia, is expected to result in the loss of at least 2425 km^2 of forest cover, affecting populations of the Endangered Müller's gibbon (*Hylobates muelleri*) (*28*).

Currently, primates feeding on crops (commonly termed "crop raiding") is not considered a major cause of global primate population declines by the IUCN because much of the conflict is local in its occurrence, impact, and the types of crops and primate species affected (*9*, *29*–*33*). There are areas of the world, such as parts of North Africa and Asia, where humans tolerate primates as crop pests because of religious beliefs, cultural traditions, and economic benefit (*29*). For example, in the Lindu highlands and Buton island of Sulawesi, humans are tolerant of crop feeding macaques due to the role the macaques hold in the local folklore and because they can help in the harvesting of certain crops, such as cashews, where the monkeys eat only the fruit and let the nut fall to the ground to be collected by farmers (*29*). In other cases, crop feeding by primates (for example, howler monkeys) is tolerated without any economic reward (*30*). Where human and nonhuman primates come into more severe conflict due to crop raiding [for example, chimpanzees (*Pan troglodytes*), gorillas (*Gorilla* spp.), and baboons (*Papio* spp.) in Africa and orangutans (*Pongo* spp.) in Southeast Asia] (*9*, *31*–*33*), culturally and economically appropriate management interventions can mitigate the impact (*9*, *33*). Human-primate conflict due to primates feeding on crops remains a persistent problem and is likely to increase because primate-suitable habitat is converted into agricultural fields or gardens in response to local and global market demands (Fig. 4).

Civil unrest also affects primate populations because of saturation bombing, the use of defoliating chemicals (*34*, *35*), and the increase in bushmeat hunting. Poaching of bonobos (*Pan paniscus*) and gorillas, for example, markedly increased in the DRC and Rwanda as a result of ongoing civil wars (*34*). In Cambodia, armed conflicts have severely affected populations of the black-shanked douc (*Pygathrix nigripes*) (*35*). Land mines, the legacy of wars in the 1960s and 1970s, continue to endanger apes in Southeast Asia and Africa (*34*, *36*).

Forest fragmentation and degradation and the limited resilience of primates

Long-term deforestation has resulted in the fragmentation of 58% of subtropical and 46% of tropical forests (*37*, *38*), forcing primates to live in isolated forest patches, including protected areas. This has led to decreasing numbers, population restructuring, and the loss of genetic diversity, as shown for pied tamarins (*Saguinus bicolor*), northern muriquis (*Brachyteles hypoxanthus*), Udzungwa red colobus monkeys (*Piliocolobus gordonorum*), several species of Chinese colobines (*Rhinopithecus* and *Trachypithecus*), Cross River gorillas (*G. gorilla diehli*), and Bornean orangutans (*39*–*45*). Edge effects predominate in many areas of disturbed forests, exacerbating habitat degradation (*37*). Agricultural expansion as well as legal and illegal logging cause further desiccation of vegetation, and human-induced forest fires devastate large areas in primate range regions yearly, resulting in increased tree mortality and losses of up to one-third of canopy cover (*46*, *47*). Although the effects of habitat loss, fragmentation, and degradation upon primates are mediated by variations in species-specific traits (rarity, trophic levels, dispersal mode, reproductive biology, life history, diet, and ranging behavior), the common response across taxa is population decline (Fig. 1).

Some primates are more behaviorally and ecologically resilient than others when faced with habitat loss, fragmentation, and degradation. Bornean orangutans, for example, can survive, at least temporarily, in logged forests, *Acacia* plantations, and oil palm plantations (*48*). Baboons (*Papio*), Hanuman langurs (*Semnopithecus*), and macaques (*Macaca*) are particularly adaptable and can survive even in urban areas (*49*). Chimpanzees appear to evaluate risks when crop-foraging and adjust their foraging patterns in deciding whether to exploit fragmented forests near humans (*50*). Bonobos tend to avoid areas of high human activity, fragmented forests, or both, and although this may suggest flexibility, the presence of humans appears to significantly reduce their access to potentially available habitat (*51*). Still, persistence in isolated

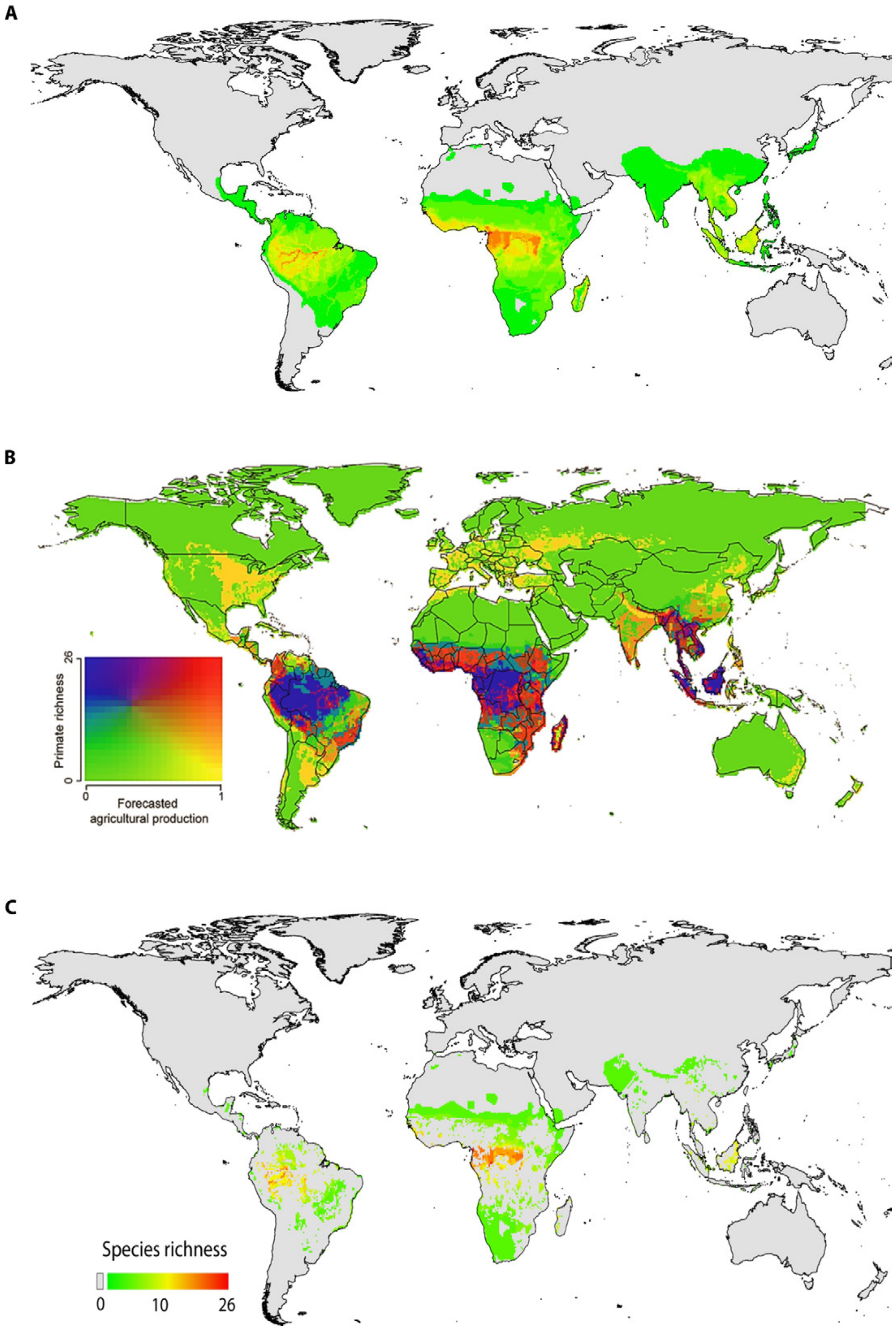


Fig. 4. Global patterns of forecasted agricultural expansion for the 21st century in primate range regions and estimated range contraction. (**A**) Estimated current global primate distributions. (**B**) The predicted 21st century expansion of agriculture estimates a spatial overlap with about 75% of primate species habitat worldwide. Red areas indicate higher spatial overlap between agricultural expansion and primate habitat. Blue areas indicate limited spatial conflict. Agricultural expansion represents a synthesis of the expected increase in the location and area devoted to agricultural production, according to the land-cover map produced by the Integrated Model to Assess the Global Environment and potential productivity obtained from the Global Agro-Ecological Zones (Supplementary Text) (*13*). (**C**) Estimated range contraction in primate distributions by the end of the 21st century under a worst-case scenario of agricultural expansion. See Supplementary Text for methods.

forest fragments, logged forests, agroecosystems, and urban areas is unlikely to be a sustainable option for most species due to hunting, further habitat reduction and fragmentation, reduced carrying capacity, parasite and disease transmission from humans and domestic animals, dog predation, human-primate conflict due to crop raiding, isolation, and continued changes in land use (*52*).

Primates in degraded forests face nutritional shortfalls and lower gut microbial diversity (*53–55*). They also show an increased prevalence of parasites and pathogens. For example, the increased exposure of lemurs (*Avahi laniger*, *Eulemur rubriventer*, *Hapalemur aureus*, *Microcebus rufus*, *Propithecus edwardsi*, and *Prolemur simus*) and chimpanzees (*P. troglodytes*) to human populations has increased their risk of infection by diarrhea-causing enteric pathogens (*56*, *57*). The close phylogenetic relationship between humans and other primates also creates an exceptionally high potential for pathogen exchange (*58*), as evidenced by disease emergence in humans as an unintentional effect of the hunting and butchering of wild primates (for example, human outbreaks of Ebola and the global HIV/AIDS pandemic) (*59*). In addition, exponential human population growth (fig. S7, A and B) and associated human-induced forest loss increase opportunities for wild primates to become exposed to human and domesticated animal pathogens (*60*). Primates escaping or released from the pet trade or sanctuaries can carry pathogens with a potential of transmission to resident populations (*61*). Moreover, ecotourism and research, despite contributing in positive ways to primate conservation, have the unintended consequence of exposing wild primates to human pathogens (*62*, *63*).

Hunting

Human population growth and increasing per capita wealth have led to an increase in commercialized bushmeat hunting relative to subsistence hunting in many parts of the world. This has become a major driving force for primate population decline, especially in Africa and Southeast Asia (*45*, *64*). Although bushmeat hunting is difficult to track, reports indicate that about 150,000 primate carcasses from 16 species were traded annually as bushmeat in urban and rural markets at 89 sites in Nigeria and Cameroon (Supplementary Text) (*64*). In Borneo, between 1950 and 3100 orangutans are estimated to be killed annually (including 375 to 1550 females), a level that far exceeds the maximum sustainable offtake for population viability (*45*). Because only a relatively small number of primates live inside protected areas [for example, 21 to 27.5% of all great apes (*51*, *65*)], populations outside protected areas are declining rapidly; the consequent increase in rarity raises the price of primate meat, making it more worthwhile for poachers to risk encroaching into protected areas to hunt (*66*).

Legal and illegal trade

Many primate species are increasingly threatened by legal and illegal unsustainable trade. Primates are traded for consumption, biomedical research, and zoo and wildlife collections; as pets; for the sale of body parts (bodies, skins, hair, and skulls) used in traditional medicine; as talismans and trophies; and for magical purposes (*67*, *68*). The Convention on International Trade in Endangered Species (CITES) database for 2005–2014 reported a global primate trade of some 450,000 live individuals plus an additional 11,000 individuals in the form of body parts. Asian species accounted for 93% of this trade (12 genera), Neotropical species for 4% (13 genera), and African species for 3% (33 genera) (table S6 and fig. S8, A to C). However, these figures are conservative because CITES only reports statistics formally provided by each country. For example, although CITES reported fewer than 400 night monkeys (*Aotus*) traded internationally between 2005 and 2014 (table S6), in the tri-border area between Perú, Brazil, and Colombia, it was estimated that ~4000 night monkeys (*Aotus nancymaae*, *Aotus vociferans*, and *Aotus nigriceps*) were traded to a single biomedical research facility between 2007 and 2008 alone, for a price of approximately $100,000 (*69*). The expansion of road networks in frontier forests facilitates the extraction and trade of primates to cities and beyond borders (*25*). Together with increasing opportunities from e-commerce, this has given suppliers and smugglers unprecedented access to new markets (*70*, *71*). Wildlife laundering (mixing protected species with legal shipments of similar species) also occurs when wild-collected primates are passed off as captive bred (Supplementary Text) (*72*).

Climate change

Although empirical evidence for the impact of climate change on primates is scarce, a recent global assessment suggests that numerous primates will experience changing climatic conditions during the 21st century, with the Amazon, the Atlantic Forest of Brazil, Central America, and East and Southeast Asia being considered hotspots of climate change–induced primate vulnerability (*73*). Primate taxa with limited geographic distributions and species characterized by slow life history traits (for example, late age at first reproduction and long interbirth intervals) are highly vulnerable to shifting ecological conditions and are likely to be most affected (*74*, *75*). Although some species may cope with these changes either by migrating to more suitable conditions or by adapting in situ, dispersal or range shift is not always possible and may have highly negative consequences (Supplementary Text) (*76*). Forest fragmentation induced by climate change can affect the availability of dispersal routes (*77*). Climate change may also force individuals out of protected areas, making them more vulnerable to hunting and other anthropogenic impacts (*78*), and range shifts among interacting species can affect food supplies and introduce new predators, pathogens, and/or competitors (*79*). Interactions between climate change and other extinction drivers also need to be considered. For instance, projections of land-cover change show that the Bornean orangutan might lose 15 to 30% of its habitat by 2080, mainly due to deforestation and oil palm agriculture, but when coupled with climate change, even more habitat is likely to become unsuitable (*80*). Additionally, more frequent and severe climate change can induce floods, droughts, fires, hurricanes, and El Niño–Southern Oscillation events (*81*) that can affect the food supply available to primate populations, with negative impacts on health, fertility, and mortality (*82*).

Extinction risk and phylogenetic signal

The effect of anthropogenic threats on primates may be compounded by phylogenetic relatedness. Multispecies analyses have shown that extinction risk is not spread randomly across mammalian taxa. Rather, the prevalence of threatened taxa in some clades but not in others implies a strong phylogenetic pattern in susceptibility (*83*, *84*). Our own comparative analysis of 340 primate species suggests that closely related species are more likely to face the same threat status relative to species selected randomly from the phylogeny (Fig. 5, fig. S9, A to C, and Supplementary Text). This result is likely due to the fact that related taxa share intrinsic aspects of their biology, such as body mass, life history, reproductive physiology, geographical distribution, dietary requirements, and behaviors (*85–87*). For example, several colobines (*Trachypithecus*, *Presbytis*, and *Simias*) in Southeast Asia are highly threatened island endemics and share biological traits known to increase their exposure and vulnerability to threats and extinction risks, such as relatively large body mass, diurnal behavior, and restricted geographic ranges.

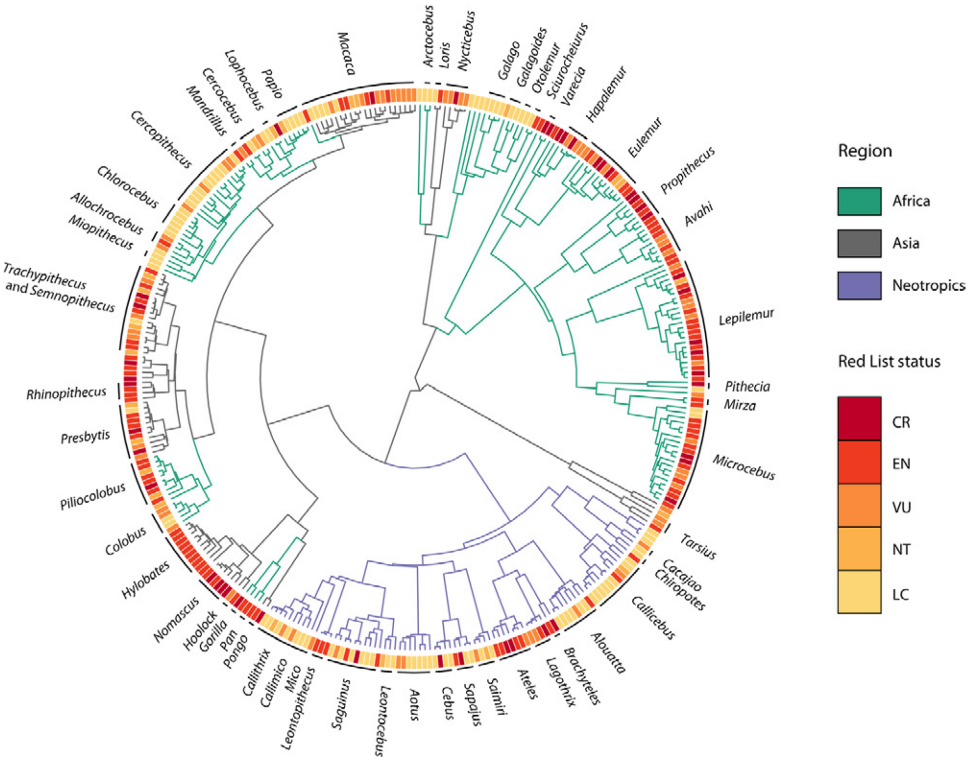


Fig. 5. Phylogenetic signal as a predictor of extinction risk in the world's primates. Distribution of threat values (IUCN Red List categories) for 340 primate species. Representative genera labeled. After taxonomic updates, our working phylogeny included 350 of the 367 species considered in the molecular supertree (*73*), of which 340 are not Data Deficient. Closely related species are more likely to have the same threat status than species taken randomly from the phylogeny [$D = 0.31$; $P (D < 1) < 0.001$], supporting a strong phylogenetic signal (see Supplementary Text for details of methodology). Data for Africa include Madagascar. IUCN Red List Categories: CR (Critically Endangered), EN (Endangered), VU (Vulnerable), NT (Near Threatened), and LC (Least Concern).

WHY PRIMATES MATTER

Social and cultural importance

Beyond sharing a close evolutionary history with humans, primates contribute importantly to the biological and cultural richness and the natural heritage of the countries in which they occur. Many primates play key roles in ecosystem dynamics and sustainability and are central figures in local and regional traditional knowledge, folklore, history, and even economies (*88*). For example, throughout South and Southeast Asia, monkeys figure strongly in Hindu and Buddhist mythology (for example, the Hanuman langur is the monkey god Hanuman in the Ramayana) and have centuries-old sympatric relationships with humans at temples and holy shrines. Today, many of these "monkey temples" are tourist sites, where the monkeys are protected, and provide an important source of income for local populations (*88*). Many traditional societies protect or tolerate primates and have integrated them into their historical narratives as sacred cultural figures and persons, as pets, and as food. For example, the Amazonian Guajá people integrate monkeys into their kinship and religious systems while also relying on primates as a sustainable food source (*89*). As primates become locally rare or extinct, we risk losing complex ecological, social, and cultural relationships that have developed between humans and primates over millennia (Supplementary Text) (*88*, *90*).

Ecological importance

Primates are prey, predator, and mutualist species in food webs and thereby influence ecosystem structure, function, and resilience. Their evolution, feeding ecology, and geographic distribution are closely linked to the diversification of angiosperms, a principal source of food (pollen, nectar, fruits, and seeds) (*91*) for many animals and humans (*92*–*94*). Many primates have been identified or suspected as important pollinators due to their opportunistic nondestructive feeding on flowers and nectar (*94*, *95*). As consumers of different plant parts (for example, fruits, flowers, seeds, gums, and leaves), primates can affect plant propagule dissemination, cause tree mortality, and may negatively affect the reproductive investment of some plants (*95*). However, numerous primates are highly frugivorous, and their relatively large size enables them to disperse small and large seeds over long distances, enhancing forest regeneration (*95*). In the absence of zoochorous seed dispersal by primates, plant populations can experience decreased genetic heterozygosity and increased genetic subpopulation differentiation, increased negative density dependence, and decreased recruitment (*96*–*99*). For example, Madagascar's lemurs display complex relationships with large seed–producing trees, and lemur extinction may be facilitating a decline in the viability of certain Malagasy tree species (*100*). The population collapse of large atelids and cebids in heavily hunted forests of Amazonia has severely degraded long-term forest dynamics and the sustainability of many hardwood tree species with implications for the carbon-storing potential of forests (*101*, *102*). Similarly, the hunting of gibbons in northern Thailand has had a negative effect on the demography of the lapsi tree (*Choerospondias axillaris*), which depends on gibbons to disperse its seeds into light gaps (*103*). The loss of primate seed dispersers has demonstrable impacts on human populations in the same ecosystems. For example, 48% of the plants whose seeds are dispersed by primates in the western regions of Côte d'Ivoire and 42% in Uganda have economic or cultural utility to local human inhabitants (*92*). In southern Nigeria, rural people rely on gathering primate-dispersed fruit and seed species (*104*), suggesting the considerable importance of primate conservation to local human food security.

Primates as model animals

Primates are highly valued model animals, advancing our understanding of the evolutionary history of our species and providing insight into human behavior, cognition, parenting, cooperation, adult social bonds, forms of social conflict and resolution, learning and memory, and the evolution of tool use and language (*105*–*108*). Although there exist important ethical issues that need to be considered when using primates in medical research (*109*), primate models have furthered our understanding of atherosclerosis, respiratory diseases, HIV/AIDS, treatment responses to psychoactive drugs, psychopathologies, sociality, mental health disorders, communication, immunology, brain functioning, pharmacology, endocrine regulation of reproduction, genetics and genomics, and disease risk and parasite dynamics, among many other subjects (*109*). Wild primate populations may hold valuable clues to the origins and evolution of important pathogens and processes of natural disease transmission by serving as sentinels for early disease detection, identification, and surveillance, thus benefiting humans. Because emerging infectious diseases also pose serious threats to both endangered and nonendangered primate species, studies of these diseases in one primate population may benefit conservation efforts for others (*59*).

ADDRESSING CONSERVATION NEEDS

Deforestation, hunting, illegal trade, and wood extraction are leading to a worldwide impoverishment of primate fauna. Drivers of primate loss are dynamic and interact with each other at local, regional, and global scales, leading to a trajectory of biosimplification that is most keenly felt as marked reductions in population sizes and, all too soon, extinctions (Fig. 6). The global scale of primate population declines and the predicted increase in the intensity of major anthropogenic threats (Fig. 1) suggest that conserving wild primates is an immediate but daunting challenge. Without widespread systemic changes in human behavior, populations will continue to decline over the next few decades, with species currently listed by the IUCN as Threatened becoming extinct and species now classified as Near Threatened or Least Concern facing increased extinction risk. Many primates are iconic (for example, gorillas, chimpanzees, orangutans, spider monkeys, and lemurs; Fig. 7), but given the scale of their decline, it is clear that neither their charisma nor their flagship status is sufficient to safeguard them from the threat of human-induced extirpation throughout their native ranges. Extinction rarely results from deficient scientific knowledge of the steps required to protect the species. Instead, it is embedded in political uncertainty, socioeconomic instability, organized criminality, corruption, and policies that favor short-term profits over long-term sustainability (*110*). Meaningful primate conservation will require a major revolution in commitment and policy. Alleviating pressures upon primate habitats requires decreasing the per capita demand of industrialized nations for tropical hardwoods, beef, palm oil, soy, rubber, minerals, and fossil fuels, among other goods, while simultaneously promoting sustainable resource-use practices (Fig. 6) (*111*).

Improving the human condition

The human capital in primate range localities is of utmost importance to primate conservation. High rates of human population growth (5.1 billion people in 2010 to 7.3 billion in 2050 in primate range countries), high levels of poverty and inequality, the loss of natural capital due to extensive and rapid land-cover changes driven by global market demands, poor governance, and the need for food security, health, and literacy are key factors to consider (Supplementary Text and fig. S7, A to C). Solutions to the challenge of primate conservation must include reducing human birth rates and population growth, improving health, reducing poverty and gender biases in education, developing sustainable land-use initiatives, and preserving traditional livelihoods (Fig. 6) (*112*). Locally, people and governments need to become stakeholders in this effort and perceive that they can benefit from protecting primate populations and their forests while at the same time satisfying their basic needs. This will require education, rethinking, and investment from government, nongovernmental organizations (NGOs), and the private sector. There is no single solution to this global problem. Primate ecotourism may be an effective approach in some localities (for example, gorilla ecotourism in Rwanda, DRC, and Uganda) (*113*). In others, minilivestock breeding may be a productive route to improve food security (*114*). Because bushmeat is an important source of food and income for inhabitants from poverty-ridden primate range countries, as well as an important aspect of indigenous culture, in some countries, nonprimate game ranching and game farming may contribute to food security and indirectly to primate conservation (*115*).

Expansion of protected areas

Although the percentage of the land surface devoted to protected areas has steadily increased in primate range countries (fig. S7D), highlighting protected areas as the only plausible conservation tool may contribute to local poverty by denying poor people power over and access to the natural resources that support their livelihoods (*116*). Protected areas must be sufficiently large and provide suitable primate habitats, and species of concern must be present in sufficient numbers within those areas (*117*). Unfortunately, countries in the Neotropics, Africa, and Asia are currently downgrading, downsizing, and degazetting protected areas due to growing industrial-scale natural resource extraction, and a significant number of protected areas are experiencing substantial deforestation (*118*, *119*). Despite these trends, protected areas can and do provide long-term sanctuary for wildlife. For example, a study in the Udzungwa mountains of Tanzania showed that colobine primate populations were stable in the protected areas but declined severely in the unprotected forests (*120*). An 8-year study (2007–2014) using camera traps to annually monitor terrestrial mammals and birds in 15 protected areas in the Neotropics, Africa, and Southeast Asia showed strong evidence of stability and even increases in populations, including those of 23 primate species (19 cercopithecines in Africa and Asia, 3 African apes, and 1 lemur) (*121*). A complementary conservation approach is the REDD+ program, where payments are made to tropical countries to reduce emissions from deforestation and forest degradation (*122*). REDD+ could be a productive approach to increasing primate habitat and connectivity via reforestation and to providing important economic and ecological value for local populations. However, as of yet, no examples of implemented programs and their success on primate conservation are available (*123*).

Land-sharing and land-sparing

Because forests are among the few economic assets available to the rural poor in the tropics, securing their ownership and sustainable commercial use can help poor families cope with and move out of poverty (*124*). In a land-sharing approach (mixing protection and production in an agroecological matrix), community-managed forests are one option to integrate forest management into national poverty reduction programs in

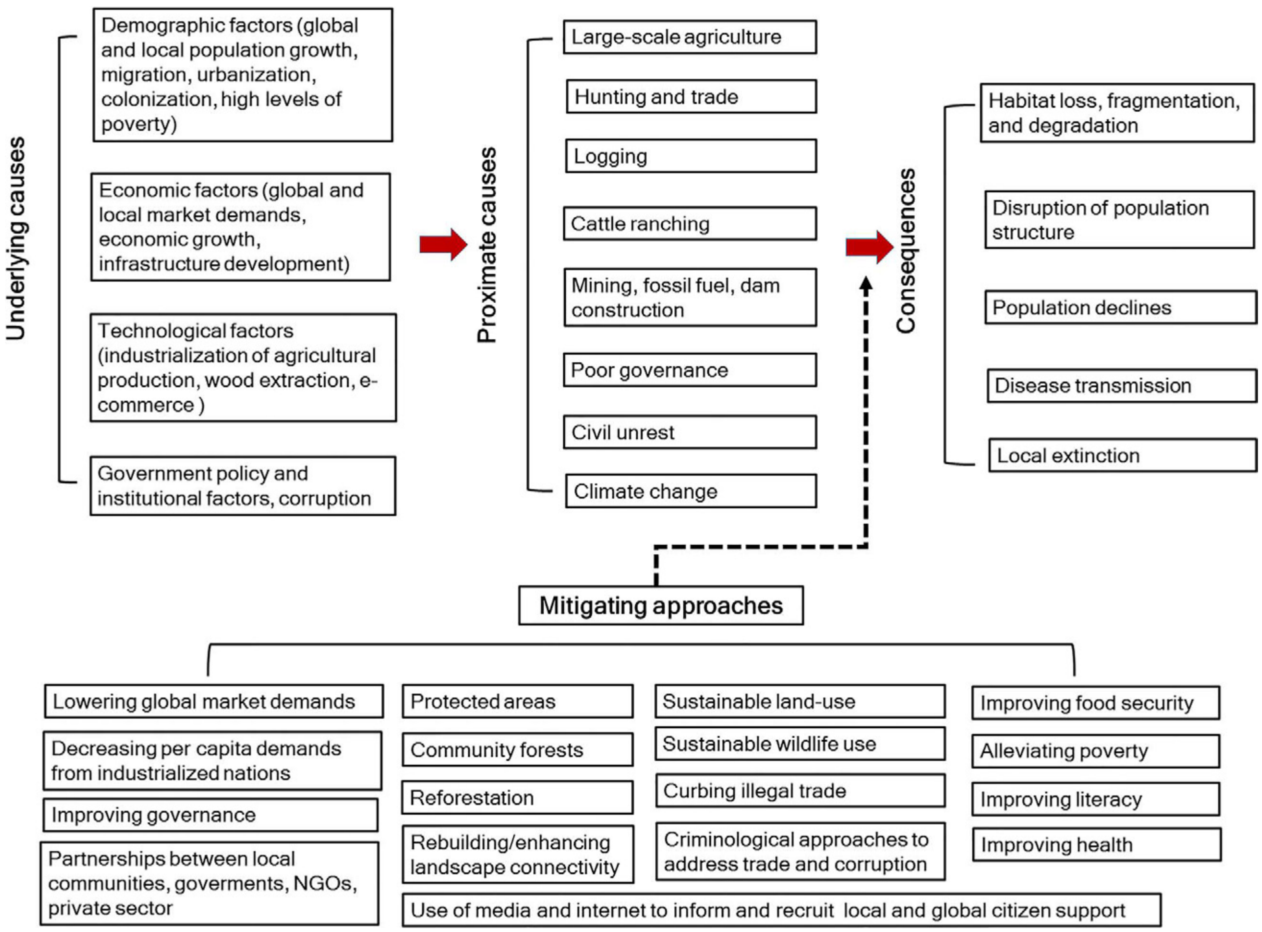


Fig. 6. Factors driving primate population declines and possible mitigating approaches. Four broad social and economic processes drive the proximate causes of threat to primates and human actions that directly affect primate habitats and populations. Mitigating approaches aim at lowering the impact of proximate causes of primate declines. Infrastructure development also includes road and rail expansion.

rural areas, favoring primate species with small area requirements. These forests also have lower and less variable annual deforestation rates than protected ones (*124*). In both land-sparing (favoring species with large area requirements) and land-sharing approaches, promoting biodiversity and the use of lattice-work corridors to connect landscapes along latitudinal and elevational gradients may promote a diversity of habitats for the long-term persistence of primate species that differ in their ecological requirements and may mitigate some of the deleterious effects of climate change (*125*, *126*). A recent study of the fauna, including lemurs, of a 90-km-long biodiversity corridor connecting two national parks in Madagascar showed the need to differentiate among passive dispersers (species that settle randomly around the source population), active dispersers (species that settle only in favorable habitats), and gap-avoiding dispersers (species that avoid dispersing across nonhabitat areas). Thus, a better understanding of the natural history of different primates is critical to identify which taxa might be sustained within forested corridors and those for which no substitute or alternative habitat exists (*127*).

Use of new and traditional technology to monitor primate population vulnerability

A new science of monitoring primate habitats, population status, and anthropogenic threats is currently emerging. It includes taking advantage of global telecommunication systems and wireless Internet, satellite- and airborne-based imagery, drone technology, ever more powerful handheld devices (for example, smart phones and tablets), and camera traps (Supplementary Text) (*120*, *128*). Combined with geographic information system and ground surveys, some of this technology has been used in evaluating sustainable land-use spatial planning and human-primate conflicts [for example, Javan gibbons (*Hylobates moloch*)] (*129*) and in providing case-by-case assessments of species vulnerability to climate change, as shown for Borneo's orangutans (Supplementary Text) (*80*). These same technologies can also be used by local citizen scientists for species and habitat monitoring, thus enhancing the effectiveness of mitigation measures (*128*). Recent technological advances in molecular biology—particularly high-throughput sequencing of DNA extracted from noninvasive samples (for example, feces, urine, and hair)—can accelerate assessments of population size and structure, genetic diversity and evidence of outbreeding, diet (plant, vertebrate, and invertebrate DNA consumption), and parasite and gut microbial diversity for wild primates (*130*–*134*). These advances have allowed researchers to identify species and origins of primate parts confiscated in the illegal bushmeat or pet trade (*135*) and are helpful in the genetic assessment and management of captive populations designed to establish viable, hybrid-free, "backup" populations to refresh the genetic pool of wild populations via reintroduction (*136*, *137*).

Fig. 7. Photos of selected primates from each major world region. Conservation status and photo credits include the following: (**A**) Golden snub-nosed monkey (*Rhinopithecus roxellana*), Endangered, P. A. Garber. (**B**) Ring-tailed lemur (*Lemur catta*), Endangered, R. A. Mittermeier. (**C**) Udzungwa red colobus (*P. gordonorum*), Endangered (Photo Credit: Thomas Struhsaker, Duke University). (**D**) Javan slow loris (*Nycticebus javanicus*), Critically Endangered (Photo Credit: Andrew Walmsley, Andrew Walmsley Photography). (**E**) Sumatran orangutan (*P. abelii*), Critically Endangered (Photo Credit: Perry van Duijnhoven). (**F**) Azara's night monkey (*Aotus azarae*), Least Concern [Photo Credit: Claudia Valeggia (Yale University)/Owl Monkey Project, Formosa-Argentina].

Although these innovations open new avenues for primate study, successful, long-term programs that monitor primate population abundance also rely on simpler and less expensive methods that engage students and local research assistants, such as traditional census methods. There are relatively few multigeneration studies of primate population dynamics, largely because primates are long-living animals and population changes occur over time periods longer than the duration of most studies and research grants. However, a recent study from the Udzungwa Mountains of Tanzania combined locally based monitoring routines and advanced statistical approaches to investigate population abundance, even when information was missing for some monitoring periods (*120*). Another study showed the value of basic field procedures (transect surveys) in monitoring Sumatran orangutan populations, with results that doubled the estimated population from 6600 to 14,613, even though the population was still assessed as declining rapidly due to deforestation (*138*).

Mitigating illegal trade

It has been noted that to mitigate wildlife poaching, interventions need to go beyond regulation by encouraging capacity building in local communities to conserve wildlife, reexamining sustainable offtake mechanisms, such as regulated trade, ranching, and wildlife farming (*139*), and to use social media and the Internet to reduce demand and, ultimately, to curb trade (Supplementary Text and Fig. 6) (*71*, *140*). Although the use of social media to raise local, regional, and global awareness of the plight of the world's primate fauna and of the ecological, social, cultural, and economic importance of primates is, no doubt, essential, it is just as important to develop local, action-oriented conservation education programs, especially those targeting young people and community decision makers. These are powerful conservation tools, combining knowledge and action acquired from successful ongoing programs in Madagascar (*141*), West Java, Indonesia (*142*), and Colombia (*143*) (see details in Supplementary Text). Criminological investigation that focuses on bushmeat trade and the trafficking of primates for pets, body parts, and trophies is also important for tracing the supply chains and criminal networks involved in illegal trade (see the "Focus of future research efforts" section).

Reintroductions and long-term forest protection as conservation tools

Where primate species are locally extinct, reintroductions are an option but can be expensive, and long-term protection of forests is arguably a more cost-effective means of preserving primates than reintroduction (*144*). Nonetheless, reintroductions raise public and political awareness and provide placement solutions for rescued animals in line with welfare concerns. The use of wild-born, rescued, and rehabilitated primates instead of captive-bred animals in reintroduction programs reduces costs and can increase success (*145*). A range of primate species have been successfully introduced in some places, including orangutans, lar gibbons (*Hylobates lar*), southern yellow-cheeked gibbons (*Nomascus gabriellae*), Indonesian slow lorises (*Nycticebus*), Delacour's langurs (*Trachypithecus delacouri*), western gorillas, woolly monkeys (*Lagothrix lagotricha*), golden lion tamarins (*Leontopithecus rosalia*), and pygmy marmosets (*Cebuella pygmaea*) (*146–150*). Still, evidence of outbreeding and introgression in, for example, Bornean orangutan populations due to the reintroduction of rescued animals of different species and subspecies into wild populations highlights the care that must be taken using these kinds of conservation interventions (*151*).

Reducing the urban footprint on primate habitats

Worldwide, urban policies need to be targeted at reducing people's ecological footprints in primate range regions. For instance, promoting the recycling of cell phones, laptops, and other electronic devices could diminish the demand for coltan mining from the Congo Basin in Central Africa, which threatens primates in the region, including gorillas and chimpanzees (*22*, *152*). Decreasing the world's per capita demand for tropical hardwoods, food and nonfood products, minerals, and fossil fuels, among other goods, from primate range regions would help alleviate pressures on primate habitats (*112*).

FOCUS OF FUTURE RESEARCH EFFORTS

The scientific research effort on primates, as measured by the number of published articles on individual primate species on the Web of Science from January 1965 to March 2016, yielded ~47,000 records pertaining to both wild and captive primates. Overall, 16% involve studies of Neotropical monkeys, 36% of African primates, and 48% of Asian primates. Sixty-six percent of the publication records focused on a single family, the Cercopithecidae, principally *Macaca* in Asia and *Papio* in Africa (fig. S10). These results reflect the important role of some taxa in this family (for example, *Macaca mulatta* and *Papio anubis*) as models for studies of human health, behavior, and physiology. Studies of primates in the African Hominidae (chimpanzees, bonobos, and gorillas) constituted another 10% of the total records, and species in the Neotropical families Callitrichidae, Cebidae, and Atelidae combined constituted 13%. Species in the remaining 11 primate families accounted for only 11% of the total records (fig. S10). Thus, despite considerable research efforts over the past 40 years, scientific data for a great majority of primate species are still limited. Moreover, decade-long studies have been conducted on very few species, and studies spanning several generations are even fewer. Such paucity of knowledge suggests that there is an urgent need to generate species- and habitat-specific knowledge about population size, life history and ecology, habitat loss, forest fragmentation, climate change, potential for disease transmission, and human-primate interactions, including detailed population/species recovery plans.

Cultural mapping and the fostering of mutually beneficial partnerships with government and people in local communities, coupled with ethnoprimatological field work, are effective tools to identify specific problems and workable in situ solutions for primate conservation (*153*). For example, a decade-long study in the Central African Republic revealed that traditional forest uses (for example, hunting and gathering) have been replaced by new activities, such as logging, bushmeat hunting, and even conservation programs, and that local human populations are both materially and culturally impoverished by animal declines (*153*). Another study showed that the use of lorises (*Nycticebus* and *Loris*) in traditional medicine and the pet trade in Sri Lanka, Cambodia, and Indonesia followed culturally specific patterns (*154*), and therefore, a deep understanding of local customs is required to develop effective conservation policies.

Because the unprecedented market globalization of the illegal wildlife, bushmeat, and amulet trade is rapidly depleting natural primate populations (*110*), criminological intelligence network analyses, within and outside range states, is critically needed. To be effective, this effort needs to integrate local and global attitudes about environmental insecurity and biodiversity exploitation. For example, local people's perceptions of the risk associated with illegal lemur hunting in Madagascar do not reflect the perception of policy makers (*155*). Attention to poaching as a serious conservation crime will yield a better understanding of whether local people engage in such activities to ensure food security and/or to generate income and may illuminate how best to incentivize sustainable alternatives, such as food subsidies or employment as rangers and conservation guards (*156*). Given the severity of this problem, the social and organized crime contexts of primate bushmeat and live trade need to be included in an integrated model (*157*) that also addresses corruption in supervising government entities in charge of monitoring and prosecuting illegal trade (Fig. 6) (*110*).

Finally, studies that document the interactions of anthropogenic drivers of environmental change with species-specific biological and behavioral traits (for example, body mass, reproductive rate, dietary flexibility, and nutritional needs) within a phylogenetic comparative framework are needed to further our understanding of the imminent threats faced by individual taxa, especially for species that have few close taxonomic relatives. Over the past two decades, a resynthesis and reorganization of new and previously collected data have increased the number of recognized primate species from 180 to 376 in 2005 and from 376 to 504 in 2016 (*158–161*). The recognition of the urgent need to understand the diversity of threatened primates inspired a workshop in 2000 in Orlando, Florida, sponsored by Disney's Animal Kingdom. This workshop gave rise to landmark conservation assessments and action plans for each of the major primate regions (*162–166*).

CONCLUDING COMMENTS

Despite the impending extinction facing many of the world's primates, we remain adamant that primate conservation is not yet a lost cause, and we are optimistic that the environmental and anthropogenic pressures leading to population declines can still be reversed. However, this is contingent on implementing effective scientific, political, and management decisions immediately. Unless we act, human-induced environmental threats in primate range regions will result in a continued and accelerated reduction in primate biodiversity. Primate taxa will be lost through a combination of habitat loss and degradation, population isolation in fragmented landscapes, population extirpation by hunting and trapping, and rapid population decline due to human and domestic animal-borne diseases, increasing human encroachment, and climate change. Perhaps the starkest conclusion of this review is that collectively—as researchers, educators, administrators, and politicians—we are failing to preserve primate species and their habitats. We face a formidable challenge moving forward, as success requires that sustainable solutions address the social, cultural, economic, and ecological interdependencies that are the basis of primate conservation. Our review suggests that by refocusing and publicizing our efforts to academics, government agencies, NGOs, businesses, and the public at large, we can build a comprehensive understanding of the consequences of primate population declines and encourage urgent and effective conservation policies. These policies will differ among countries, regions, habitats, and primate species based on the site-specific nature of each problem. We have one last opportunity to greatly reduce or even eliminate the human threats to primates and their habitats, to guide conservation efforts, and to raise worldwide awareness of their predicament. Primates are critically important to humanity. After all, they are our closest living biological relatives.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/1/e1600946/DC1

fig. S1. Primate habitat countries ranked by the number of species present.
fig. S2. Countries with primate species in the Neotropics, Africa (including Madagascar), and Asia and percent of countries with threatened species.
fig. S3. IUCN threat categories and population status of primate species.
fig. S4. Percent of primate species listed under each proximate threat, according to the IUCN.
fig. S5. Growth trends in cattle stock, agricultural activity, and deforestation in primate range regions.
fig. S6. Agricultural expansion and declines in forest cover for the period 1990–2010 in the Neotropics, Africa, and Asia.
fig. S7. Human population growth in primate range regions.
fig. S8. Global primate trade for the period 2005–2014, as reported by parties to the CITES Secretariat.
fig. S9. Phylogenetic patterns associated with extinction risk for primate species in the Neotropics, Africa, and Asia.
fig. S10. Number of published articles found in the Web of Science for primate species in each family.
table S1. Primate species in the Neotropics grouped by family.
table S2. Primate species in mainland Africa grouped by family.
table S3. Primate species in Madagascar grouped by family.
table S4. Primate species in Asia grouped by family.
table S5. Summary of sources of threat and the number of primate species affected, according to the IUCN Red List.
table S6. Global international trade in primates for the period 2005–2014, as reported by parties to the CITES Secretariat.
Supplementary Text
References (*167*–*209*)

REFERENCES AND NOTES

1. D. E. Wilson, D. M. Reeder, Eds., *Mammal Species of the World* (Johns Hopkins Univ. Press, ed. 3, 2005).
2. International Union for Conservation of Nature, IUCN Red List of threatened species. Version 2015–4; www.iucnredlist.org [accessed 20 January 2016].
3. Integrated Taxonomic Information System (ITIS), Order Primates; www.itis.gov.
4. R. A. Mittermeier, A. B. Rylands, D. E. Wilson, Eds., *Handbook of the Mammals of the World: 3. Primates* (Lynx Edicions, 2013).
5. C. Campbell, A. Fuentes, K. MacKinnon, S. Bearder, R. Stumpf, Eds., *Primates in Perspective* (Oxford Univ. Press, ed. 2, 2010).
6. W. F. Laurance, J. Sayer, K. G. Cassman, Agricultural expansion and its impacts on tropical nature. *Trends Ecol. Evol.* **29**, 107–116 (2014).
7. H. S. Nantha, C. Tisdell, The orangutan–oil palm conflict: Economic constraints and opportunities for conservation. *Biodivers. Conserv.* **18**, 487–502 (2009).
8. S. A. Wich, J. Garcia-Ulloa, H. S. Kühl, T. Humle, J. S. H. Lee, L. P. Koh, Will oil palm's homecoming spell doom for Africa's great apes? *Curr. Biol.* **24**, 1659–1663 (2014).
9. A. Lanjouw, H. Rainer, A. White, Apes overview, in *State of the Apes: Industrial Agriculture and Ape Conservation*, H. Rainer, A. White, A. Lanjouw, Eds. (Arcus/Cambridge Univ. Press, 2015), pp. 164–192.
10. V. Vijay, S. L. Pimm, C. N. Jenkins, S. J. Smith, The impacts of oil palm on recent deforestation and biodiversity loss. *PLOS ONE* **11**, e0159668 (2016).
11. P.-F. Fan, H.-L. Fei, A.-D. Luo, Ecological extinction of the critically endangered northern white-cheeked gibbon *Nomascus leucogenys* in China. *Oryx* **48**, 52–55 (2014).
12. M. K. Mazumder, Diversity, habitat preferences, and conservation of the primates of southern Assam India: The story of a primate paradise. *J. Asia Pac. Biodivers.* **7**, 347–354 (2014).
13. R. Dobrovolski, R. Loyola, G. A. B. Da Fonseca, J. A. F. Diniz-Filho, M. B. Araújo, Globalizing conservation efforts to save species and enhance food production. *Bioscience* **64**, 539–545 (2014).
14. Y. Malhi, T. A. Gardner, G. R. Goldsmith, M. R. Silman, P. Zelazowski, Tropical forests in the Anthropocene. *Annu. Rev. Environ. Resour.* **39**, 125–159 (2014).
15. M. A. Barrett, J. L. Brown, M. K. Morikawa, J.-N. Labat, A. D. Yoder, CITES designation for endangered rosewood in Madagascar. *Science* **328**, 1109–1110 (2010).
16. S. L. Lewis, D. P. Edwards, D. Galbraith, Increasing human dominance of tropical forests. *Science* **349**, 827–832 (2015).
17. N. L. Alvarez-Berríos, T. Mitchell Aide, Global demand for gold is another threat for tropical forests. *Environ. Res. Lett.* **10**, 014006 (2015).
18. A. Lanjouw, in State of the Apes: Extractive Industries and Ape Conservation, H Rainer, A. White, A. Lanjouw, Eds. (Arcus/Cambridge Univ. Press, 2014), pp. 127–161.
19. R. Duffy, Gemstone mining in Madagascar: Transnational networks, criminalisation and global integration. *J. Mod. Afr. Stud.* **45**, 185–206 (2007).
20. R. M. Brown, J. A. Weghorst, K. V. Olson, M. R. Duya, A. J. Barley, M. V. Duya, M. Shekelle, I. Neri-Arboleda, J. A. Esselstyn, N. J. Dominy, P. S. Ong, G. L. Moritz, A. Luczon, M. L. Diesmos, A. C. Diesmos, C. D. Siler, Conservation genetics of the Philippine tarsier: Cryptic genetic variation restructures conservation priorities for an island archipelago primate. *PLOS ONE* **9**, e104340 (2014).
21. P. T. Mehlman, Current status of wild gorilla populations and strategies for their conservation, in *Conservation in the 21st Century: Gorillas as a Case Study*, T. S. Stoinski, H. D. Steklis, P. T. Mehlman, Eds. (Springer, 2008), pp. 3–54.
22. A. J. Plumptre, S. Nixon, R. Critchlow, G. Vieilledent, R. Nishuli, A. Kirkby, E. A. Williamson, J. S. Hall, D. Kujirakwinja, *Status of Grauer's Gorilla and Chimpanzees in Eastern Democratic Republic of Congo: Historical and Current Distribution and Abundance* (Wildlife Conservation Society, Fauna & Flora International and Institut Congolais pour la Conservation de la Nature, 2015).
23. N. Shanee, S. Shanee, Yellow-tailed woolly monkey (*Lagothrix flavicauda*): Conservation status, anthropogenic threats, and conservation initiatives, in *The Woolly Monkey: Behaviour, Ecology, Conservation and Systematics*, T. R. Defler, P. R. Stevenson, Eds. (Springer, 2014), pp. 283–299.
24. M. Finer, B. Babbitt, S. Novoa, F. Ferrarese, S. E. Pappalardo, M. De Marchi, M. Saucedo, A. Kumar, Future of oil and gas development in the western Amazon. *Environ. Res. Lett.* **10**, 024003 (2015).
25. W. F. Laurance, G. R. Clements, S. Sloan, C. S. O'Connell, N. D. Mueller, M. Goosem, O. Venter, D. P. Edwards, B. Phalan, A. Balmford, R. Van Der Ree, I. B. Arrea, A global strategy for road building. *Nature* **513**, 229–232 (2014).
26. W. F. Laurance, S. Sloan, L. Weng, J. A. Sayer, Estimating the environmental costs of Africa's massive "development corridors". *Curr. Biol.* **25**, 3202–3208 (2015).
27. K. Winemiller, P. McIntyre, L. Castello, E. Fluet-Chouinard, T. Giarrizzo, S. Nam, I. Baird, W. Darwall, N. Lujan, I. Harrison, M. L. Stiassny, R. A. Silvano, D. B. Fitzgerald, F. M. Pelicice, A. A. Agostinho, L. C. Gomes, J. S. Albert, E. Baran, M. Petrere Jr., C. Zarfl, M. Mulligan, J. P. Sullivan, C. C. Arantes, L. M. Sousa, A. A. Koning, D. J. Hoeinghaus, M. Sabaj, J. G. Lundberg, J. Armbruster, M. L. Thieme, P. Petry, J. Zuanon, G. Torrente Vilara, J. Snoeks, C. Ou, W. Rainboth, C. S. Pavanelli, A. Akama, A. van Soesbergen, L. Saenz, Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* **351**, 128–129 (2016).
28. J. Kitzes, R. Shirley, Estimating biodiversity impacts without field surveys: A case study in northern Borneo. *Ambio* **45**, 110–119 (2016).
29. E. P. Riley, N. E. C. Priston, Macaques in farms and folklore: Exploring the human-nonhuman primate interface in Sulawesi Indonesia. *Am. J. Primatol.* **72**, 848–854 (2010).
30. Ó. M. Chaves, J. C. Bicca-Marques, Crop-feeding by brown howler monkeys (*Alouatta guariba clamitans*) in forest fragments: The conservation value of cultivated species. *Int. J. Primatol.* **11**, e0145819 (2016).
31. K. J. Hockings, M. R. McLennan, S. Carvalho, M. Ancrenaz, R. Bobe, R. W. Byrne, R. I. M. Dunbar, T. Matsuzawa, W. C. McGrew, E. A. Williamson, M. L. Wilson, B. Wood, R. W. Wrangham, C. M. Hill, Apes in the Anthropocene: Flexibility and survival. *Trends Ecol. Evol.* **30**, 215–222 (2015).
32. N. Seiler, M. M. Robbins, Factors influencing ranging on community land and crop raiding by mountain gorillas. *Anim. Conserv.* **19**, 176–188 (2015).
33. G. Fehlmann, M. J. O'Riain, C. Kerr-Smith, A. J. King, Adaptive space use by baboons (Papio ursinus) in response to management interventions in a human-changed landscape. *Anim. Conserv.* (2016).
34. L. R. Douglas, K. Alie, High-value natural resources: Linking wildlife conservation to international conflict, insecurity, and development concerns. *Biol. Conserv.* **171**, 270–277 (2014).
35. C. Loucks, M. B. Mascia, A. Maxwell, K. Huy, K. Duong, N. Chea, B. Long, N. Cox, T. Seng, Wildlife decline in Cambodia, 1953–2005: Exploring the legacy of armed conflict. *Conserv. Lett.* **2**, 82–92 (2009).
36. J. A. McNeely, Conserving forest biodiversity in times of violent conflict. *Oryx* **37**, 142–152 (2003).
37. N. M. Haddad, L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, J. R. Townshend, Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015).
38. B. Mercer, Tropical Forests: A Review (The Prince's Charities' International Sustainability Unit, 2015).
39. I. P. Farias, W. G. Santos, M. Gordo, T. Hrbek, Effects of forest fragmentation on genetic diversity of the Critically Endangered primate, the pied tamarin (*Saguinus bicolor*): Implications for conservation. *J. Hered.* **106**, 512–521 (2015).
40. P. B. Chaves, C. S. Alvarenga, C. B. Possamai, L. G. Dias, J. P. Boubli, K. B. Strier, S. L. Mendes, V. Fagundes, Genetic diversity and population history of a critically

endangered primate, the northern muriqui (Brachyteles hypoxanthus). *PLOS ONE* **6**, e20722 (2011).

41. M. J. Ruiz-Lopez, C. Barelli, F. Rovero, K. Hodges, C. Roos, W. E. Peterman, N. Ting, A novel landscape genetic approach demonstrates the effects of human disturbance on the Udzungwa red colobus monkey (*Procolobus gordonorum*). *Heredity* **116**, 167–176 (2016).
42. Z. Liu, G. Liu, C. Roos, Z. Wang, Z. Xiang, P. Zhu, B. Wang, B. Ren, F. Shi, H. Pan, M. Li, Implications of genetics and current protected areas for conservation of 5 endangered primates in China. *Conserv. Biol.* **29**, 1508–1517 (2015).
43. R. A. Bergl, B. J. Bradley, A. Nsubuga, L. Vigilant, Effects of habitat fragmentation, population size and demographic history on genetic diversity: The Cross River gorilla in a comparative context. *Am. J. Primatol.* **70**, 848–859 (2008).
44. R. Sharma, N. Arora, B. Goossens, A. Nater, N. Morf, J. Salmona, M. W. Bruford, C. P. van Schaik, M. Krützen, L. Chikhi, Effective population size dynamics and the demographic collapse of Bornean orang-utans. *PLOS ONE* **7**, e49429 (2012).
45. E. Meijaard, D. Buchori, Y. Hadiprakarsa, S. S. Utami-Atmoko, A. Nurcahyo, A. Tjiu, D. Prasetyo, L. C. Nardiyono, M. Ancrenaz, F. Abadi, I. N. G. Antoni, D. Armayadi, A. Dinato, P. G. Ella, T. P. Indrawan, C. M. Kussaritano, C. W. P. Priyono, Y. Purwanto, D. Puspitasari, M. S. W. Putra, A. Rahmat, H. Ramadani, J. Sammy, D. Siswanto, M. Syamsuri, N. Andayani, H. Wu, J. A. Wells, K. Mengersen, Quantifying killing of orangutans and human-orangutan conflict in Kalimantan, Indonesia. *PLOS ONE* **6**, e27491 (2011).
46. J. M. Silveira, J. Louzada, J. Barlow, R. Andrade, L. Mestre, R. Solar, S. Lacau, M. A. Cochrane, A multi-taxa assessment of biodiversity change after single and recurrent wildfires in a Brazilian Amazon forest. *Biotropica* **48**, 170–180 (2016).
47. S. F. Gouveia, F. Villalobos, R. Dobrovolski, R. Beltrão-Mendes, S. F. Ferrari, Forest structure drives global diversity of primates. *J. Anim. Ecol.* **83**, 1523–1530 (2014).
48. E. Meijaard, S. Wich, M. Ancrenaz, A. J. Marshall, Not by science alone: Why orangutan conservationists must think outside the box. *Ann. N. Y. Acad. Sci.* **1249**, 29–44 (2012).
49. M. F. Jaman, M. A. Huffman, The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. *Primates* **54**, 49–59 (2013).
50. S. Krief, M. Cibot, S. Bortolamiol, A. Seguya, J.-M. Krief, S. Masi, Wild chimpanzees on the edge: Nocturnal activities in croplands. *PLOS ONE* **9**, e109925 (2014).
51. J. R. Hickey, J. Nackoney, N. P. Nibbelink, S. Blake, A. Bonyenge, S. Coxe, J. Dupain, M. Emetshu, T. Furuichi, F. Grossmann, P. Guislain, J. Hart, C. Hashimoto, B. Ikembelo, O. Ilambu, B.-I. Inogwabini, I. Liengola, A. L. Lokasola, A. Lushimba, F. Maisels, J. Masselink, V. Mbenzo, N. M. Mulavwa, P. Naky, N. M. Ndunda, P. Nkumu, V. Omasombo, G. E. Reinartz, R. Rose, T. Sakamaki, S. Strindberg, H. Takemoto, A. Vosper, H. S. Kühl, Human proximity and habitat fragmentation are key drivers of the rangewide bonobo distribution. *Biodivers. Conserv.* **22**, 3085–3104 (2013).
52. A. Estrada, B. E. Raboy, L. C. Oliveira, Agroecosystems and primate conservation in the tropics: A review. *Am. J. Primatol.* **74**, 696–711 (2012).
53. K. Amato, C. J. Yeoman, A. Kent, N. Righini, F. Carbonero, A. Estrada, H. Rex Gaskins, R. M. Stumpf, S. Yildirim, M. Torralba, M. Gillis, B. A. Wilson, K. E. Nelson, B. A. White, S. R. Leigh, Habitat degradation impacts black howler monkey (*Alouatta pigra*) gastrointestinal microbiomes. *ISME J.* **7**, 1344–1353 (2013).
54. C. Barelli, D. Albanese, C. Donati, M. Pindo, C. Dallago, F. Rovero, D. Cavalieri, K. M. Tuohy, H. C. Hauffe, C. De Filippo, Habitat fragmentation is associated to gut microbiota diversity of an endangered primate: Implications for conservation. *Sci. Rep.* **5**, 14862 (2015).
55. A. Gomez, K. Petrzelkova, C. J. Yeoman, K. Vlckova, J. Mrázek, I. Koppova, F. Carbonero, A. Ulanov, D. Modry, A. Todd, M. Torralba, K. E. Nelson, H. R. Gaskins, B. Wilson, R. M. Stumpf, B. A. White, S. R. Leigh, Gut microbiome composition and metabolomic profiles of wild western lowland gorillas (*Gorilla gorilla gorilla*) reflect host ecology. *Mol. Ecol.* **24**, 2551–2565 (2015).
56. D. C. Bublitz, P. C. Wright, F. T. Rasambainarivo, S. J. Arrigo-Nelson, J. R. Bodager, T. R. Gillespie, Pathogenic enterobacteria in lemurs associated with anthropogenic disturbance. *Am. J. Primatol.* **77**, 330–337 (2015).
57. M. B. Parsons, D. Travis, E. V. Lonsdorf, I. Lipende, D. M. A. Roellig, S. Kamenya, H. Zhang, L. Xiao, T. R. Gillespie, Epidemiology and molecular characterization of *Cryptosporidium* spp. in humans, wild primates, and domesticated animals in the greater Gombe ecosystem, Tanzania. *PLOS Neglected Trop. Dis.* **9**, e0003529 (2015).
58. N. Cooper, C. L. Nunn, Identifying future zoonotic disease threats: Where are the gaps in our understanding of primate infectious diseases? *Evol. Med. Public Health* **2013**, 27–36 (2013).
59. S. Calvignac-Spencer, S. A. J. Leendertz, T. R. Gillespie, F. H. Leendertz, Wild great apes as sentinels and sources of infectious disease. *Clin. Microbiol. Infect.* **18**, 521–527 (2012).
60. T. R. Gillespie, C. L. Nunn, F. H. Leendertz, Integrative approaches to the study of primate infectious disease: Implications for biodiversity conservation and global health. *Am. J. Phys. Anthropol.* **137**, 53–69 (2008).
61. W. B. Karesh, R. A. Cook, E. L. Bennett, J. Newcomb, Wildlife trade and global disease emergence. *Emerg. Infect. Dis.* **11**, 1000–1002 (2005).
62. F. Schaumburg, L. Mugisha, B. Peck, K. Becker, T. R. Gillespie, G. Peters, F. H. Leendertz, Drug-resistant human *Staphylococcus aureus* in sanctuary apes pose a threat to endangered wild ape populations. *Am. J. Primatol.* **74**, 1071–1075 (2012).
63. K. Gilardi, T. Gillespie, F. Leendertz, E. Macfie, D. Travis, C. Whittier, E. Williamson, *Best Practice Guidelines for Health Monitoring and Disease Control in Great Ape Populations* (IUCN/SSC Primate Specialist Group, 2015); www.primate-sg.org/best_practice_disease.
64. J. E. Fa, J. Olivero, M. Farfán, A. L. Márquez, J. Duarte, J. Nackoney, A. Hall, J. Dupain, S. Seymour, P. J. Johnson, D. W. Macdonald, R. Real, J. M. Vargas, Correlates of bushmeat in markets and depletion of wildlife. *Conserv. Biol.* **29**, 805–815 (2015).
65. International Union for Conservation of Nature, *Regional Action Plan for the Conservation of Western Lowland Gorillas and Central Chimpanzees 2015–2025* (IUCN SSC Primate Specialist Group, 2014), 56 pp; www.primate-sg.org/WEA2014.pdf.
66. F. Rovero, A. S. Mtui, A. S. Kitegile, M. R. Nielsen, Hunting or habitat degradation? Decline of primate populations in Udzungwa Mountains, Tanzania: An analysis of threats. *Biol. Conserv.* **146**, 89–96 (2012).
67. V. Nijman, K. A. I. Nekaris, G. Donati, M. W. Bruford, J. Fa, Primate conservation: Measuring and mitigating trade in primates. *Endanger. Species Res.* **13**, 159–161 (2011).
68. R. R. N. Alves, W. M. S. Souto, R. R. D. Barboza, Primates in traditional folk medicine: A world overview. *Mamm. Rev.* **40**, 155–180 (2010).
69. A. M. Maldonado, V. Nijman, S. K. Bearder, Trade in night monkeys *Aotus* spp. in the Brazil–Colombia–Peru tri-border area: International wildlife trade regulations are ineffectively enforced. *Endanger. Species Res.* **9**, 143–149 (2009).
70. N. Shanee, A. P. Mendoza, S. Shanee, Diagnostic overview of the illegal trade in primates and law enforcement in Peru. *Am. J. Primatol.* **2015** (2015).
71. K. A.-I. Nekaris, N. Campbell, T. G. Coggins, E. J. Rode, V. Nijman, Tickled to death: Analysing public perceptions of 'cute' videos of threatened species (slow lorises—*Nycticebus* spp.) on Web 2.0 sites. *PLOS ONE* **8**, e69215 (2013).
72. UNODC, *Transnational Organized Crime in East Asia and the Pacific. A Threat Assessment* (United Nations Office on Drugs and Crime, Regional Office for Southeast Asia and the Pacific, 2013).
73. T. L. Graham, H. D. Matthews, S. E. Turner, A global-scale evaluation of primate exposure and vulnerability to climate change. *Int. J. Primatol.* **37**, 158–174 (2016).
74. R. G. Pearson, J. C. Stanton, K. T. Shoemaker, M. E. Aiello-Lammens, P. J. Ersts, N. Horning, D. A. Fordham, C. J. Raxworthy, H. Y. Ryu, J. McNees, H. R. Akçakaya, Life history and spatial traits predict extinction risk due to climate change. *Nat. Clim. Change* **4**, 217–221 (2014).
75. P. R. Sesink Clee, E. E. Abwe, R. D. Ambahe, N. M. Anthony, R. Fotso, S. Locatelli, F. Maisels, M. W. Mitchell, B. J. Morgan, A. A. Pokempner, M. K. Gonder, Chimpanzee population structure in Cameroon and Nigeria is associated with habitat variation that may be lost under climate change. *BMC Evol. Biol.* **15**, 2 (2015).
76. A. Schloss, T. A. Nuñez, J. J. Lawler, Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 8606–8611 (2012).
77. S. F. Gouveia, J. P. Souza-Alves, L. Rattis, R. Dobrovolski, L. Jerusalinsky, R. Beltrão-Mendes, S. F. Ferrari, Climate and land use changes will degrade the configuration of the landscape for titi monkeys in eastern Brazil. *Glob. Chang. Biol.* **22**, 2003–2012 (2016).
78. M. B. Araújo, M. Cabeza, W. Thuiller, L. Hannah, P. H. Williams, Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Glob. Chang. Biol.* **10**, 1618–1626 (2004).
79. J. M. Tylianakis, R. K. Didham, J. Bascompte, D. A. Wardle, Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11**, 1351–1363 (2008).
80. M. J. Struebig, M. Fischer, D. L. Gaveau, E. Meijaard, S. A. Wich, C. Gonner, R. Sykes, A. Wilting, S. Kramer-Schadt, Anticipated climate and land-cover changes reveal refuge areas for Borneo's orang-utans. *Glob. Chang. Biol.* **21**, 2891–2904 (2015).
81. Y. Malhi, J. T. Roberts, R. A. Betts, T. J. Killeen, W. Li, C. A. Nobre, Climate change, deforestation, and the fate of the Amazon. *Science* **319**, 169–172 (2008).
82. R. Wiederholt, E. Post, Tropical warming and the dynamics of endangered primates. *Biol. Lett.* **6**, 257–260 (2010).
83. S. A. Fritz, A. Purvis, Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conserv. Biol.* **24**, 1042–1051 (2010).
84. M. S. Springer, R. W. Meredith, J. Gatesy, C. A. Emerling, J. Park, D. L. Rabosky, T. Stadler, C. Steiner, O. A. Ryder, J. E. Janečka, C. A. Fisher, W. J. Murphy, Macroevolutionary dynamics and historical biogeography of primate diversification inferred from a species supermatrix. *PLOS ONE* **7**, e49521 (2012).
85. L. D. Verde Arregoitia, K. Leach, N. Reid, D. O. Fisher, Diversity, extinction, and threat status in Lagomorphs. *Ecography* **38**, 1155–1165 (2015).

86. L. D. Verde Arregoitia, S. P. Blomberg, D. O. Fisher, Phylogenetic correlates of extinction risk in mammals: Species in older lineages are not at greater risk. *Proc. Biol. Sci.* **280**, 20131092 (2013).
87. A. C. Lootvoet, J. Philippon, C. Bessa-Gomes, Behavioral correlates of primates conservation status: Intrinsic vulnerability to anthropogenic threats. *PLOS ONE* **10**, e01135538 (2015).
88. A. Fuentes, Ethnoprimatology and the anthropology of the human-primate interface. *Annu. Rev. Anthropol.* **41**, 101–117 (2012).
89. L. Cormier, A preliminary review of neotropical primates in the subsistence and symbolism of indigenous lowland South American peoples. *Ecol. Environ. Anthropol.* **2**, 14–32 (2006).
90. M. Haslam, L. V. Luncz, R. A. Staff, F. Bradshaw, E. B. Ottoni, T. Falótico, Pre-Columbian monkey tools. *Curr. Biol.* **26**, R521–R522 (2016).
91. R. W. Sussman, D. T. Rasmussen, P. H. Raven, Rethinking primate origins again. *Am. J. Primatol.* **75**, 95–106 (2013).
92. I. Koné, J. E. Lambert, J. Refisch, A. Bakayoko, Primate seed dispersal and its potential role in maintaining useful tree species in the Taï region, Côte-d'Ivoire: Implications for the conservation of forest fragments. *Trop. Conserv. Sci.* **1**, 293–306 (2008).
93. J. Lambert, Primate frugivory in Kibale National Park, Uganda, and its implications for human use of forest resources. *Afr. J. Ecol.* **36**, 234–240 (1998).
94. E. W. Heymann, Florivory, nectarivory, and pollination—A review of primate-flower interactions. *Ecotropica* **17**, 41–52 (2011).
95. C. A. Chapman, T. R. Bonnell, J. F. Gogarten, J. E. Lambert, P. A. Omeja, D. Twinomugisha, M. D. Wasserman, J. M. Rothman, Are primates ecosystem engineers? *Int. J. Primatol.* **34**, 1–14 (2013).
96. T. T. Caughlin, J. M. Ferguson, J. W. Lichstein, P. A. Zuidema, S. Bunyavejchewin, D. J. Levey, Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proc. Biol. Sci.* **282**, 20142095 (2015).
97. L. F. Pacheco, J. A. Simonetti, Genetic structure of a mimosoid tree deprived of its seed disperser, the spider monkey. *Conserv. Biol.* **14**, 1766–1775 (2000).
98. G. Nunez-Iturri, O. Olsson, H. F. Howe, Hunting reduces recruitment of primate-dispersed trees in Amazonian Peru. *Biol. Conserv.* **141**, 1536–1546 (2008).
99. C. Bello, M. Galetti, M. A. Pizo, L. F. S. Magnago, M. F. Rocha, R. A. F. Lima, C. A. Peres, O. Ovaskainen, P. Jordano, Defaunation affects carbon storage in tropical forests. *Sci. Adv.* **1**, e1501105 (2015).
100. S. Federman, A. Dornburg, D. C. Daly, A. Downie, G. H. Perry, A. D. Yoder, E. J. Sargis, A. Richard, M. J. Donoghue, A. L. Baden, Implications of lemuriform extinctions for the Malagasy flora. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 5041–5046 (2016).
101. C. A. Peres, T. Emilio, J. Schietti, S. J. M. Desmoulière, T. Levi, Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 892–897 (2016).
102. P. R. Stevenson, A. M. Aldana, Potential effects of ateline extinction and forest fragmentation on plant diversity and composition in the western Orinoco Basin, Colombia. *Int. J. Primatol.* **29**, 365–377 (2008).
103. J. F. Brodie, O. E. Helmy, W. Y. Brockelman, J. L. Maron, Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecol. Appl.* **19**, 854–863 (2009).
104. E. Efiom, thesis, Consequences of bushmeat hunting in tropical forests, Lund University (2013).
105. B. Hare, From hominoid to hominid mind: What changed and why? *Annu. Rev. Anthropol.* **40**, 293–309 (2011).
106. M. E. Thompson, Comparative reproductive energetics of human and nonhuman primates. *Annu. Rev. Anthropol.* **42**, 287–304 (2013).
107. H. Pontzer, Energy expenditure in humans and other primates: A new synthesis. *Annu. Rev. Anthropol.* **44**, 169–187 (2015).
108. E. Fernandez-Duque, C. R. Valeggia, S. P. Mendoza, The biology of paternal care in human and nonhuman primates. *Annu. Rev. Anthropol.* **38**, 115–130 (2009).
109. K. A. Phillips, K. L. Bales, J. P. Capitanio, A. Conley, P. W. Czoty, B. A. t'Hart, W. D. Hopkins, S.-L. Hu, L. A. Miller, M. A. Nader, P. W. Nathanielsz, J. Rogers, C. A. Shively, M. L. Voytko, Why primate models matter. *Am. J. Primatol.* **76**, 801–827 (2014).
110. United Nations Office on Drugs and Crime, *World Wildlife Crime Report: Trafficking in Protected Species* (United Nations Office on Drugs and Crime, 2016); www.unodc.org/documents/data-and-analysis/wildlife/World_Wildlife_Crime_Report_2016_final.pdf.
111. Millennium Ecosystem Assessment, *Ecosystems and Human Well-Being: Synthesis* (Island Press, 2005).
112. F. Dalerum, Identifying the role of conservation biology for solving the environmental crisis. *Ambio* **43**, 839–846 (2014).
113. C. B. Stanford, *Planet Without Apes* (Harvard Univ. Press, 2012), 272 pp.
114. J. Hardouin, É. Thys, V. Joiris, D. Fielding, Mini-livestock breeding with indigenous species in the tropics. *Livestock Res. Rural Dev.* **15**, 4 (2003).
115. N. van Vliet, D. Cornelis, H. Beck, P. Lindsey, R. Nasi, S. LeBel, J. Moreno, J. Fragoso, F. Jori, Meat from the wild: Extractive uses of wildlife and alternatives for sustainability, in *Current Trends in Wildlife Research*, R. Mateo, B. Arroyo, J. T. García, Eds. (Springer International Publishing, 2016), pp. 225–265.
116. W. A. Adams, J. Hutton, People, parks and poverty: Political ecology and biodiversity conservation. *Conserv. Soc.* **5**, 147–183 (2007).
117. R. Hill, C. Miller, B. Newell, M. Dunlop, I. J. Gordon, Why biodiversity declines as protected areas increase: The effect of the power of governance regimes on sustainable landscapes. *Sustainability Sci.* **10**, 357–369 (2015).
118. M. B. Mascia, S. Pailler, R. Krithivasan, V. Roshchanka, D. Burns, M. J. Mlotha, D. R. Murray, N. Peng, Protected area downgrading, downsizing, and degazettement (PADDD) in Africa, Asia, and Latin America and the Caribbean, 1900–2010. *Biol. Conserv.* **169**, 355–361 (2014).
119. B. D. Spracklen, M. Kalamandeen, D. Galbraith, E. Gloor, D. V. Spracklen, A global analysis of deforestation in moist tropical forest protected areas. *PLOS ONE* **10**, e0143886 (2015).
120. F. Rovero, A. Mtui, A. Kitegile, P. Jacob, A. Araldi, S. Tenan, Primates decline rapidly in unprotected forests: Evidence from a monitoring program with data constraints. *PLOS ONE* **10**, e0118330 (2015).
121. L. Beaudrot, J. A. Ahumada, T. O'Brien, P. Alvarez-Loayza, K. Boekee, A. Campos-Arceiz, D. Eichberg, S. Espinosa, E. Fegraus, C. Fletcher, K. Gajapersad, C. Hallam, J. Hurtado, P. A. Jansen, A. Kumar, E. Larney, M. G. M. Lima, C. Mahony, E. H. Martin, A. McWilliam, B. Mugerwa, M. Ndoundou-Hockemba, J. C. Razafimahaimodison, H. Romero-Saltos, F. Rovero, J. Salvador, F. Santos, D. Sheil, W. R. Spironello, M. R. Willig, N. L. Winarni, A. Zvoleff, S. J. Andelman, Standardized assessment of biodiversity trends in tropical forest protected areas: The end is not in sight. *PLOS Biol.* **14**, e1002357 (2016).
122. O. Venter, L. P. Koh, Reducing emissions from deforestation and forest degradation (REDD+): Game changer or just another quick fix? *Ann. N. Y. Acad. Sci.* **1249**, 137–150 (2012).
123. J. García-Ulloa, L. P. Koh, Payment for ecosystem services the role of REDD+ in primate conservation, in An Introduction to Primate Conservation, S. A. Wich, A. J. Marshal, Eds. (Oxford Univ. Press, 2016), pp. 257–268.
124. L. Porter-Bolland, E. A. Ellis, M. R. Guariguata, I. Ruiz-Mallén, S. Negrete-Yankelevich, V. Reyes-García, Community managed forests and forest protected areas: An assessment of their conservation effectiveness across the tropics. *Forest Ecol. Manag.* **268**, 6–17 (2012).
125. P. A. Townsend, K. L. Masters, Lattice-work corridors for climate change: A conceptual framework for biodiversity conservation and social-ecological resilience in a tropical elevational gradient. *Ecol. Soc.* **20**, 1 (2015).
126. P. A. Stephens, Land sparing, land sharing, and the fate of Africa's lions. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 14753–14754 (2015).
127. T. Ramiadantsoa, O. Ovaskainen, J. Rybicki, I. Hanski, Large-scale habitat corridors for biodiversity conservation: A forest corridor in Madagascar. *PLOS ONE* **10**, e0132126 (2015).
128. S. L. Pimm, S. Alibhai, R. Bergl, A. Dehgan, C. Giri, Z. Jewell, L. Joppa, R. Kays, S. Loarie, Emerging technologies to conserve biodiversity. *Trends Ecol. Evol.* **30**, 685–696 (2015).
129. M. A. Reisland, J. E. Lambert, Sympatric apes in sacred forests: Shared space and habitat use by humans and Endangered Javan gibbons (*Hylobates moloch*). *PLOS ONE* **11**, e014689 (2016).
130. E. K. Mallott, R. S. Malhi, P. A. Garber, High-throughput sequencing of fecal DNA to identify insects consumed by wild Weddell's saddleback tamarins (*Saguinus weddelli*, Cebidae, Primates) in Bolivia. *Am. J. Phys. Anthropol.* **156**, 474–481 (2015).
131. L. Moore, L. Vigilant, A population estimate of chimpanzees (*Pan troglodytes schweinfurthii*) in the Ugalla region using standard and spatially explicit genetic capture–recapture methods. *Am. J. Primatol.* **76**, 335–346 (2014).
132. S. Köndgen, S. Schenk, G. Pauli, C. Boesch, F. H. Leendertz, Noninvasive monitoring of respiratory viruses in wild chimpanzees. *Ecohealth* **7**, 332–341 (2010).
133. B. J. Bradley, M. Stiller, D. M. Doran-Sheehy, T. Harris, C. A. Chapman, L. Vigilant, H. Poinar, Plant DNA sequences from feces: Potential means for assessing diets of wild primates. *Am. J. Primatol.* **69**, 699–705 (2007).
134. T. Minhós, E. Wallace, M. J. F. da Silva, R. M. Sá, M. Carmo, A. Barata, M. W. Bruford, DNA identification of primate bushmeat from urban markets in Guinea-Bissau and its implications for conservation. *Biol. Conserv.* **167**, 43–49 (2013).
135. W. Liu, C. Huang, C. Roos, Q. Zhou, Y. Li, F. Wei, Identification of the species, origin and sex of smuggled douc langur (Pygathrix sp.) remains. *Vietnamese J. Primatol.* **1–2**, 63–69 (2008).
136. C. Hvilsom, P. Frandsen, C. Børsting, F. Carlsen, B. Sallé, B. T. Simonsen, H. R. Siegismund, Understanding geographic origins and history of admixture among chimpanzees in European zoos, with implications for future breeding programmes. *Heredity* **110**, 586–593 (2013).

137. J. Pastorini, M. L. Sauther, R. W. Sussman, L. Gould, F. P. Cuozzo, P. Fernando, C. M. Nievergelt, N. I. Mundy, Comparison of the genetic variation of captive ring-tailed lemurs with a wild population in Madagascar. *Zoo Biol.* **34**, 463–472 (2015).
138. S. A. Wich, I. Singleton, M. G. Nowak, S. S. Utami Atmoko, G. Nisam, S. M. Arif, R. H. Putra, R. Ardi, G. Fredriksson, G. Usher, D. L. A. Gaveau, H. S. Kühl, Land-cover changes predict steep declines for the Sumatran orangutan (*Pongo abelii*). *Sci. Adv.* **2**, e1500789 (2016).
139. D. W. S. Challender, D. C. MacMillan, Poaching is more than an enforcement problem. *Conserv. Lett.* **7**, 484–494 (2014).
140. E. F. Daut, D. J. Brightsmith, M. J. Peterson, Role of non-governmental organizations in combating illegal wildlife—Pet trade in Peru. *J. Nat. Conserv.* **24**, 72–82 (2015).
141. F. L. Dolins, A. Jolly, H. Rasamimanana, J. Ratsimbazafy, A. T. Feistner, F. Ravoavy, Conservation education in Madagascar: Three case studies in the biologically diverse island-continent. *Am. J. Primatol.* **72**, 391–406 (2010).
142. J. Supriatna, A. Ario, Primates as flagships for conserving biodiversity and parks in Indonesia: Lessons learned from West Java and North Sumatra. *Primate Conserv.* **29**, 123–131 (2015).
143. A. Savage, R. Guillen, I. Lamilla, L. Soto, Developing an effective community conservation program for cotton-top tamarins (*Saguinus oedipus*) in Colombia. *Am. J. Primatol.* **72**, 379–390 (2010).
144. H. B. Wilson, E. Meijaard, O. Venter, M. Ancrenaz, H. P. Possingham, Conservation strategies for orangutans: Reintroduction versus habitat preservation and the benefits of sustainably logged forest. *PLOS ONE* **9**, e102174 (2014).
145. M. C. M. Kierulff, C. R. Ruiz-Miranda, P. P. de Oliveira, B. B. Beck, A. Martins, J. M. Dietz, D. M. Rambaldi, A. J. Baker, The golden lion tamarin *Leontopithecus rosalia*: A conservation success story. *Int. Zoo Yearb.* **46**, 36–45 (2012).
146. P. Osterberg, P. Samphanthamit, O. Maprang, S. Punnadee, W. Y. Brockelman, Gibbon (*Hylobates lar*) reintroduction success in Phuket, Thailand, and its conservation benefits. *Am. J. Primatol.* **77**, 492–501 (2015).
147. R. S. Moore, Wihermanto, K. A. I. Nekaris, Compassionate conservation, rehabilitation and translocation of Indonesian slow lorises. *Endang. Species Res.* **26**, 93–102 (2014).
148. G. Le Flohic, P. Motsch, H. DeNys, S. Childs, A. Courage, T. King, Behavioural ecology and group cohesion of juvenile western lowland gorillas (*Gorilla g. gorilla*) during rehabilitation in the Batéké Plateaux National Park, Gabon. *PLOS ONE* **10**, e0119609 (2015).
149. D. Car, V. L. Queirogas, M. A. Pedersoli, Translocation and radio-telemetry monitoring of pygmy marmoset, Cebuella pygmaea (Spix, 1823), in the Brazilian Amazon. *Braz. J. Biol.* **75**, 91–97 (2015).
150. J. F. Millán, S. E. Bennett, P. R. Stevenson, Notes on the behavior of captive and released woolly monkeys (Lagothrix lagothricha): Reintroduction as a conservation strategy on Colombian southern Amazon, in *The Woolly Monkey: Behavior, Ecology, Systematics, and Captive Research*, T. R. Defler, P. R. Stevenson, Eds. (Springer, 2014), pp. 249–266.
151. G. L. Banes, B. M. F. Galdikas, L. Vigilant, Reintroduction of confiscated and displaced mammals risks outbreeding and introgression in natural populations, as evidenced by orang-utans of divergent subspecies. *Sci. Rep.* **6**, 22026 (2016).
152. D. Moran, M. Petersone, F. Verones, On the suitability of input–Output analysis for calculating product-specific biodiversity footprints. *Ecol. Indic.* **60**, 192–201 (2016).
153. N. Malone, A. H. Wade, A. Fuentes, E. P. Riley, M. Remis, C. J. Robinson, Ethnoprimatology: Critical interdisciplinarity and multispecies approaches in anthropology. *Crit. Anthropol.* **34**, 8–29 (2014).
154. A. I. Nekaris, C. R. Shepherd, C. R. Starr, V. Nijman, Exploring cultural drivers for wildlife trade via an ethnoprimatological approach: A case study of slender and slow lorises (*Loris* and *Nycticebus*) in South and Southeast Asia. *Am. J. Primatol.* **72**, 877–886 (2010).
155. M. L. Gore, M. L. Lute, J. H. Ratsimbazafy, A. Rajaonson, Local perspectives on environmental insecurity and its influence on illegal biodiversity exploitation. *PLOS ONE* **11**, e0150337 (2016).
156. M. L. Gore, J. Ratsimbazafy, A. Rajaonson, A. Lewis, J. S. Kahler, Public perceptions of poaching risks in a biodiversity hotspot: Implications for wildlife trafficking interventions. *J. Trafficking Organ. Crime Secur.* **2**, 1–20 (2016).
157. J. S. Brashares, B. Abrahms, K. J. Fiorella, C. D. Golden, C. E. Hojnowski, R. A. Marsh, D. J. McCauley, T. A. Nuñez, K. Seto, L. Withey, Wildlife decline and social conflict. Policies aimed at reducing wildlife-related conflict must address the underlying causes. *Science* **345**, 376–378 (2014).
158. A. B. Rylands, R. A. Mittermeier, Primate taxonomy: Species and conservation. *Evol. Anthropol.* **23**, 8–10 (2014).
159. C. P. Groves, Order Primates, in Mammal Species of the World: A Taxonomic and Geographic Reference, D. E. Wilson, D. M. Reeder, Eds. (Smithsonian Institution Press, ed. 2, 1993), pp. 243–277.
160. C. P. Groves, *Primate Taxonomy* (Smithsonian Institution Press, 2001).
161. C. P. Groves, Order Primates, in *Mammal Species of the World: A Taxonomic and Geographic Reference*, D. E. Wilson, D. M. Reeder, Eds. (Johns Hopkins Univ. Press, ed. 3, 2005), pp. 111–184.
162. A. B. Rylands, H. Schneider, A. Langguth, R. A. Mittermeier, C. P. Groves, E. Rodríguez-Luna, An assessment of the diversity of New World primates. *Neotrop. Primates* **8**, 61–93 (2000).
163. P. Grubb, T. M. Butynski, J. F. Oates, S. K. Bearder, T. R. Disotell, C. P. Groves, T. T. Struhsaker, Assessment of the diversity of African primates. *Int. J. Primatol.* **24**, 1301–1357 (2003).
164. D. Brandon-Jones, A. A. Eudey, T. Geissmann, C. P. Groves, D. J. Melnick, J. C. Morales, M. Shekelle, C.-B. Stewart, Asian primate classification. *Int. J. Primatol.* **25**, 97–164 (2004).
165. R. A. Mittermeier, J. U. Ganzhorn, W. R. Konstant, K. Glander, I. Tattersall, C. P. Groves, A. B. Rylands, A. Hapke, J. Ratsimbazafy, M. I. Mayor, E. E. Louis Jr., Y. Rumpler, C. Schwitzer, R. Rasoloarison, Lemur diversity in Madagascar. *Int. J. Primatol.* **29**, 1607–1656 (2008).
166. M. E. Blair, E. J. Sterling, M. M. Hurley, Taxonomy and conservation of Vietnam's primates: A review. *Am. J. Primatol.* **73**, 1093–1106 (2011).
167. I. Tattersall, Cathemeral activity in primates: A definition. *Folia Primatol.* **49**, 200–202 (1987).
168. D. A. Burney, L. P. Burney, L. R. Godfrey, W. L. Jungers, S. M. Goodman, H. T. Wright, A. J. T. Hull, A chronology for late prehistoric Madagascar. *J. Hum. Evol.* **47**, 25–63 (2004).
169. E. F. Lambin, P. Meyfroidt, Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 3465–3472 (2011).
170. P. K. Thornton, Livestock production: Recent trends, future prospects. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 2853–2867 (2010).
171. A. S. Cohn, A. Mosnier, P. Havlík, H. Valin, M. Herrero, E. Schmid, M. O'Hare, M. Obersteiner, Cattle ranching intensification in Brazil can reduce global greenhouse gas emissions by sparing land from deforestation. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 7236–7241 (2014).
172. A. Casson, *Oil Palm, Soybeans and Critical Habitat Loss: A Review* (WWF Forest Conversion Initiative, 2003).
173. F. Danielsen, H. Beukema, N. D. Burgess, F. Parish, C. A. Brühl, P. F. Donald, D. Murdiyarso, B. E. N. Phalan, L. Reijnders, M. Struebig, E. B. Fitzherbert, Biofuel plantations on forested lands: Double jeopardy for biodiversity and climate. *Conserv. Biol.* **23**, 348–358 (2009).
174. L. P. Koh, J. Ghazoul, Spatially-explicit scenario analysis for reconciling agricultural expansion, forest protection, and carbon conservation in Indonesia. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 11140–11144 (2010).
175. J. M. Linder, African primate diversity threatened by "new wave" of industrial oil palm expansion. *Afr. Primates* **8**, 25–38 (2013).
176. Z. Li, J. M. Fox, Mapping rubber tree growth in mainland Southeast Asia using time-series MODIS 250m NDVI and statistical data. *Appl. Geogr.* **32**, 420–432 (2012).
177. E. Warren-Thomas, P. M. Dolman, D. P. Edwards, Increasing demand for natural rubber necessitates a robust sustainability initiative to mitigate impacts on tropical biodiversity. *Conserv. Lett.* **8**, 230–241 (2015).
178. J. Clay, *World Agriculture and the Environment: A Commodity-by-Commodity Guide to Impacts and Practices* (Island Press, 2004).
179. A. Ahrends, P. M. Hollingsworth, A. D. Ziegler, J. M. Fox, H. Chen, Y. Su, J. Xu, Current trends of rubber plantation expansion may threaten biodiversity and livelihoods. *Glob. Environ. Chang.* **34**, 48–58 (2015).
180. Forestry Economics and Policy Division, Planted Forests. A Statement of Principles (Food and Agriculture Organization of the United Nations, 2010); www.fao.org/forestry/plantedforests.
181. Forestry Economics and Policy Division, *State of the World's Forests 2011* (Food and Agriculture Organization of the United Nations, 2011); (www.fao.org/docrep/013/i2000e/i2000e00.htm.
182. M. C. Hansen, P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, J. R. G. Townshend, High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013).
183. P. J. Fashing, N. Nguyen, P. Luteshi, W. Opondo, J. F. Cash, M. Cords, Evaluating the suitability of planted forests for African forest monkeys: A case study from Kakamega forest, Kenya. *Am. J. Primatol.* **74**, 77–90 (2012).
184. R. Bshary, Diana monkeys, *Cercopithecus diana*, adjust their anti-predator response behaviour to human hunting strategies. *Behav. Ecol. Sociobiol.* **50**, 251–256 (2001).
185. R. Noë, R. Bshary, The formation of red colobus–Diana monkey associations under predation pressure from chimpanzees. *Proc. Biol. Sci.* **264**, 253–259 (1997).
186. L. A. Isbell, Predation on primates: Ecological patterns and evolutionary consequences. *Evol. Anthropol.* **3**, 61–71 (1994).

187. M. J. Remis, C. A. Jost Robinson, Reductions in primate abundance and diversity in a multiuse protected area: Synergistic impacts of hunting and logging in a Congo Basin forest. *Am. J. Primatol.* **74**, 602–612 (2012).
188. J. F. Ranaivoarisoa, J. R. Zaonarivelo, R. Lei, S. E. Johnson, T. M. Wyman, R. A. Mittermeier, E. E. Louis Jr., Rapid survey and assessment of the northern sportive lemur, *Lepilemur septentrionalis*, in northern Madagascar. *Primate Conserv.* **27**, 23–31 (2013).
189. N. F. Kümpel, E. J. Milner-Gulland, J. M. Rowcliffe, G. Cowlishaw, Impact of gun-hunting on diurnal primates in continental Equatorial Guinea. *Int. J. Primatol.* **29**, 1065–1082 (2008).
190. J. F. Oates, *Primates of West Africa: A Field Guide and Natural History* (Conservation International, 2011).
191. C. R. Shepherd, Illegal primate trade in Indonesia exemplified by surveys carried out over a decade in North Sumatra. *Endang. Spec. Res.* **11**, 201–205 (2012).
192. V. Nijman, D. Spaan, E. J. Rode-Margono, Wirdateti, K. A. I. Nekaris, Changes in the primate trade in Indonesian wildlife markets over a 25-year period: Fewer apes and langurs, more macaques, and slow lorises. *Am. J. Primatol.* 10.1002/ajp.22517 (2015).
193. C. Starr, K. A. I. Nekaris, U. Streicher, L. Leung, Traditional use of slow lorises *Nycticebus bengalensis* and *N. pygmaeus* in Cambodia: An impediment to their conservation. *Endang. Spec. Res.* **12**, 17–23 (2010).
194. A. L. S. Meyer, M. R. Pie, F. C. Passos, Assessing the exposure of lion tamarins (*Leontopithecus spp.*) to future climate change. *Am. J. Primatol.* **76**, 551–562 (2014).
195. S. Shanee, Predicting future effects of multiple drivers of extinction risk in Peru's endemic primate fauna, in *Ethnoprimatology: Primate Conservation in the 21st Century*, M. Waller, Ed. (Springer, 2016), pp. 315–349.
196. J. M. Rothman, C. A. Chapman, T. T. Struhsaker, D. Raubenheimer, D. Twinomugisha, P. G. Waterman, Long-term declines in nutritional quality of tropical leaves. *Ecology* **96**, 873–878 (2015).
197. M. A. Barrett, J. L. Brown, R. E. Junge, A. D. Yoder, Climate change, predictive modeling and lemur health: Assessing impacts of changing climate on health and conservation in Madagascar. *Biol. Conserv.* **157**, 409–422 (2013).
198. United Nations Population Fund, State of World Population 2011 (United Nations Population Fund, 2011), www.unfpa.org/sites/default/files/pub-pdf/EN-SWOP2011-FINAL.pdf [accessed September 2015].
199. R. I. McDonald, P. Green, D. Balk, B. M. Fekete, C. Revenga, M. Todd, M. Montgomery, Urban growth, climate change, and freshwater availability. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 6312–6317 (2011).
200. United Nations Development Programme, Human Development Report (United Nations Development Programme, 2014); http://hdr.undp.org/en/content/human-development-report-2014 [accessed 4 September 2015]
201. R. W. Kates, P. Dasgupta, African poverty: A grand challenge for sustainability science. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 16747–16750 (2007).
202. S. Shanee, N. Shanee, Measuring success in a community conservation project: Local population increase in a Critically Endangered primate, the yellow-tailed woolly monkey (Lagothrix *flavicauda*) at la Esperanza, northeastern Peru. *Trop. Conserv. Sci.* **8**, 169–186 (2015).
203. I. Koné, K. Ouattara, A. D. Koffi, A top priority site for primate conservation in Côte d'Ivoire soon designated as a protected area? *Afr. Primates* **10**, 59–60 (2015).
204. R. H. Horwich, R. Das, A. Bose, Conservation and the current status of the golden langur in Assam, India, with reference to Bhutan. *Primate Conserv.* **27**, 77–83 (2013).
205. A. C. van Andel, S. A. Wich, C. Boesch, L. P. Koh, M. M. Robbins, J. Kelly, H. S. Kuehl, Locating chimpanzee nests and identifying fruiting trees with an unmanned aerial vehicle. *Am. J. Primatol.* **77**, 1122–1134 (2015).
206. K. Kakaes, F. Greenword, M. Lippincott, S. Dosemagen, P. Meier, S. A. Wich, Drones and Aerial Observation: New Technologies for Property Rights, Human Rights, and Global Development: A Primer (New America, 2015); http://drones.newamerica.org/primer/DronesAndAerialObservation.pdf
207. K. M. Fornace, C. J. Drakeley, T. William, F. Espino, J. Cox, Mapping infectious disease landscapes: Unmanned aerial vehicles and epidemiology. *Trends Parasitol.* **30**, 514–519 (2014).
208. M. B. Parsons, T. R. Gillespie, E. V. Lonsdorf, D. Travis, I. Lipende, B. Gilagiza, S. Kamenya, L. Pintea, G. M. Vazquez-Prokopec, Global positioning system data-loggers: A tool to quantify fine-scale movement of domestic animals to evaluate potential for zoonotic transmission to an endangered wildlife population. *PLOS ONE* **9**, e110984 (2014).
209. P. O'Donoghue, C. Rutz, Real-time anti-poaching tags could help prevent imminent species extinctions. *J. Appl. Ecol.* **53**, 5–10 (2016).

Acknowledgments: P.A.G. wishes to thank J. A. Garber for inspiring him to devote more of his time, energy, and thoughts to protecting the world's endangered primate populations. We also would like to honor the memory of our esteemed coauthor, colleague, friend, and outstanding primatologist (R.W.S.), who passed away in June 2016. We dedicate this paper to him. **Funding:** No funding was used to support the writing of this review paper. However, S.G. and R.D. acknowledge the support of CNPq and of CAPES, FAPESB, CNPq (process 461665/2014-0), and PRODOC/UFBA (process 5849/2013), respectively. **Author contributions:** A.E. and P.A.G. conceived and designed the review. A.B.R. and C.R. updated and verified the taxonomy of species listed in tables S1 to S3. L.V.A. did the phylogenetic signal analysis and built the phylogenetic trees shown in Fig. 5 and fig. S4. M.d.G. assisted in compiling the species lists and retrieved the data from the Web of Science. M.d.G., K.A.-I.N., and V.N. compiled the CITES data on primate trade. S.G. and R.D. produced Figs. 1 and 4 and fig. S2 and did the analysis on agricultural expansion and primate distributions. All of the other authors contributed data, discussed further analyses, and commented on various versions of the manuscript. S.S. is a project director of the UK Neotropical Primate Conservation and the Asociación Neotropical Primate Conservation, Perú. **Competing interests:** The authors declare that they have no competing interests. No institutional review board or institutional animal and welfare committee approval was needed for this study. **Data and materials availability:** All data are reported as estimates and used for assessments in the paper. This information is presented in the paper and/or in the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 30 April 2016
Accepted 22 November 2016
Published 18 January 2017
10.1126/sciadv.1600946

Citation: A. Estrada, P. A. Garber, A. B. Rylands, C. Roos, E. Fernandez-Duque, A. Di Fiore, K. Anne-Isola Nekaris, V. Nijman, E. W. Heymann, J. E. Lambert, F. Rovero, C. Barelli, J. M. Setchell, T. R. Gillespie, R. A. Mittermeier, L. V. Arregoitia, M. de Guinea, S. Gouveia, R. Dobrovolski, S. Shanee, N. Shanee, S. A. Boyle, A. Fuentes, K. C. MacKinnon, K. R. Amato, A. L. S. Meyer, S. Wich, R. W. Sussman, R. Pan, I. Kone, B. Li, Impending extinction crisis of the world's primates: Why primates matter. *Sci. Adv.* **3**, e1600946 (2017).

APPLIED ECOLOGY

Habitat fragmentation and its lasting impact on Earth's ecosystems

10.1126/sciadv.1500052

Nick M. Haddad,[1]* Lars A. Brudvig,[2] Jean Clobert,[3] Kendi F. Davies,[4] Andrew Gonzalez,[5] Robert D. Holt,[6] Thomas E. Lovejoy,[7] Joseph O. Sexton,[8] Mike P. Austin,[9] Cathy D. Collins,[10] William M. Cook,[11] Ellen I. Damschen,[12] Robert M. Ewers,[13] Bryan L. Foster,[14] Clinton N. Jenkins,[15] Andrew J. King,[9] William F. Laurance,[16] Douglas J. Levey,[17] Chris R. Margules,[18,19] Brett A. Melbourne,[4] A. O. Nicholls,[9,20] John L. Orrock,[12] Dan-Xia Song,[8] John R. Townshend[8]

We conducted an analysis of global forest cover to reveal that 70% of remaining forest is within 1 km of the forest's edge, subject to the degrading effects of fragmentation. A synthesis of fragmentation experiments spanning multiple biomes and scales, five continents, and 35 years demonstrates that habitat fragmentation reduces biodiversity by 13 to 75% and impairs key ecosystem functions by decreasing biomass and altering nutrient cycles. Effects are greatest in the smallest and most isolated fragments, and they magnify with the passage of time. These findings indicate an urgent need for conservation and restoration measures to improve landscape connectivity, which will reduce extinction rates and help maintain ecosystem services.

INTRODUCTION

Destruction and degradation of natural ecosystems are the primary causes of declines in global biodiversity (*1*, *2*). Habitat destruction typically leads to fragmentation, the division of habitat into smaller and more isolated fragments separated by a matrix of human-transformed land cover. The loss of area, increase in isolation, and greater exposure to human land uses along fragment edges initiate long-term changes to the structure and function of the remaining fragments (*3*).

Ecologists agree that habitat destruction is detrimental to the maintenance of biodiversity, but they disagree—often strongly—on the extent to which fragmentation itself is to blame (*4*, *5*). Early hypotheses based on the biogeography of oceanic islands (*6*) provided a theoretical framework to understand fragmentation's effect on extinction in terrestrial landscapes composed of "islands" of natural habitat scattered across a "sea" of human-transformed habitat. Central to the controversy has been a lingering uncertainty about the role of decreased fragment size and increased isolation relative to the widespread and pervasive effects of habitat loss in explaining declines in biodiversity and the degradation of ecosystems (*7*). Observational studies of the effects of fragmentation have often magnified the controversy because inference from nonmanipulative studies is limited to correlation and because they have individually often considered only single aspects of fragmentation (for example, edge, isolation, and area) (*8*). However, together with these correlative observations, experimental studies reveal that fragmentation has multiple simultaneous effects that are interwoven in complex ways and that operate over potentially long time scales (*9*).

Here, we draw on findings of the world's largest and longest-running fragmentation experiments that span 35 years and disparate biomes on five continents. Their rigorous designs and long-term implementation overcome many limitations of observational studies. In particular, by manipulating and isolating individual aspects of fragmentation while controlling for others, and by doing so on entire ecosystems, they provide a powerful way to disentangle cause and effect in fragmented landscapes. Here, we present experimental evidence of unexpected long-term ecological changes caused by habitat fragmentation.

Highlighting one ecosystem type as an example, we first present a global analysis of the fragmentation of forest ecosystems, quantifying for the first time the global hotspots of intensive historical fragmentation. We then synthesize results from the set of long-term experiments conducted in a wide variety of ecosystems to demonstrate consistent impacts of fragmentation, how those impacts change over time, and how they align with predictions from theory and observation. Finally, we identify key knowledge gaps for the next generation of fragmentation experiments.

GLOBAL ANALYSIS OF THE EXTREME MAGNITUDE AND EXTENT OF FRAGMENTATION

New satellite data sets reveal at high resolution how human activities are transforming global ecosystems. Foremost among these observations are those of forest cover because of the high contrast between forest

---

[1]Department of Biological Sciences, North Carolina State University, Raleigh, NC 27695, USA. [2]Department of Plant Biology, Michigan State University, East Lansing, MI 48824–1312, USA. [3]Station d'Ecologie Expérimentale du CNRS a Moulis USR 2936, Moulis, 09200 Saint-Girons, France. [4]Department of Ecology and Evolutionary Biology, UCB 334, University of Colorado, Boulder, CO 80309, USA. [5]Department of Biology, McGill University, Montreal, Quebec H3A 1B1, Canada. [6]Department of Biology, University of Florida, Gainesville, FL 32611, USA. [7]Department of Environmental Science and Policy, George Mason University, Fairfax, VA 22030, USA. [8]Global Land Cover Facility, Department of Geographical Sciences, University of Maryland, College Park, MD 20702, USA. [9]CSIRO Land and Water Flagship, GPO Box 1700, Canberra, Australian Capital Territory 2601, Australia. [10]Department of Biology, Colby College, 5746 Mayflower Hill, Waterville, ME 04901, USA. [11]Department of Biological Sciences, St. Cloud State University, St. Cloud, MN 56301, USA. [12]Department of Zoology, University of Wisconsin, Madison, WI 53706, USA. [13]Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berkshire SL5 7PY, UK. [14]Department of Ecology and Evolutionary Biology and Kansas Biological Survey, University of Kansas, 2101 Constant Avenue, Lawrence, KS 66047–3759, USA. [15]Instituto de Pesquisas Ecológicas, Rod. Dom Pedro I, km 47, Caixa Postal 47, Nazaré Paulista, São Paulo 12960-000, Brazil. [16]Centre for Tropical Environmental and Sustainability Science and College of Marine and Environmental Sciences, James Cook University, Cairns, Queensland 4878, Australia. [17]National Science Foundation, Arlington, VA 22230, USA. [18]Centre for Tropical Environmental and Sustainability Science, School of Earth and Environmental Sciences, James Cook University, Cairns 4878, Australia. [19]Research Center for Climate Change, University of Indonesia, Kota Depok, Java Barat 16424, Indonesia. [20]The Institute for Land, Water and Society, Charles Sturt University, Thurgoona Campus, Albury, New South Wales 2640, Australia.
*Corresponding author. E-mail: nick_haddad@ncsu.edu

and anthropogenic land cover types. Deforestation, which was already widespread in temperate regions in the mid-18th to 20th centuries and increased in the tropics over the past half century, has resulted in the loss of more than a third of all forest cover worldwide (*10*, *11*). Beyond the direct impacts of forest loss and expanding anthropogenic land cover (for example, agricultural fields and urban areas), remnant forests are likely to suffer from being smaller, more isolated, and with a greater area located near the edge of the forest (*12*).

We analyzed the world's first high-resolution map of global tree cover (*13*) to measure the magnitude of forest fragmentation. This analysis revealed that nearly 20% of the world's remaining forest is within 100 m of an edge (Fig. 1, A and B)—in close proximity to agricultural, urban, or other modified environments where impacts on forest ecosystems are most severe (*14*). More than 70% of the world's forests are within 1 km of a forest edge. Thus, most forests are well within the range where human activities, altered microclimate, and nonforest species may influence and degrade forest ecosystems (*15*). The largest contiguous expanses of remaining forests are in the humid tropical regions of the Amazon and Congo River Basins (Fig. 1A). Large areas of more disjunct forest also remain in southeastern Asia, New Guinea, and the boreal biomes.

Historical data enable the study of the process of forest fragmentation over time. We reconstructed the historical forest extent and timing of fragmentation in two forested regions of Brazil that provide a stark contrast in land-use dynamics. The Brazilian Amazon is a rapidly changing frontier (*10*), yet most of its forests remain contiguous and far from an edge despite recent increases in fragmentation (Fig. 1, C and D). In contrast, the Brazilian Atlantic Forest is a largely deforested landscape, cleared for agriculture and logged for timber over the last three centuries (*11*). This remaining forest is dominated by small fragments, with most fragments smaller than 1000 ha and within 1000 m of a forest edge (Fig. 1, E and F) (*16*). In the Brazilian Amazon, the proportion of forest farther than 1 km from the forest edge has decreased from 90% (historical) to 75% (today), and in the Brazilian Atlantic, from 90% to less than 9%.

These two forested regions of Brazil define extremes of the fragmentation process and are representative of the extent of fragmentation in forested landscapes worldwide (Fig. 1), as well as many other biomes including temperate grasslands, savannas, and even aquatic systems (*17*). For example, although a spatial analysis similar to that of forest is not currently possible in grasslands, 37% of the world's grassland eco-regions are classified as "highly fragmented" (*18*, *19*).

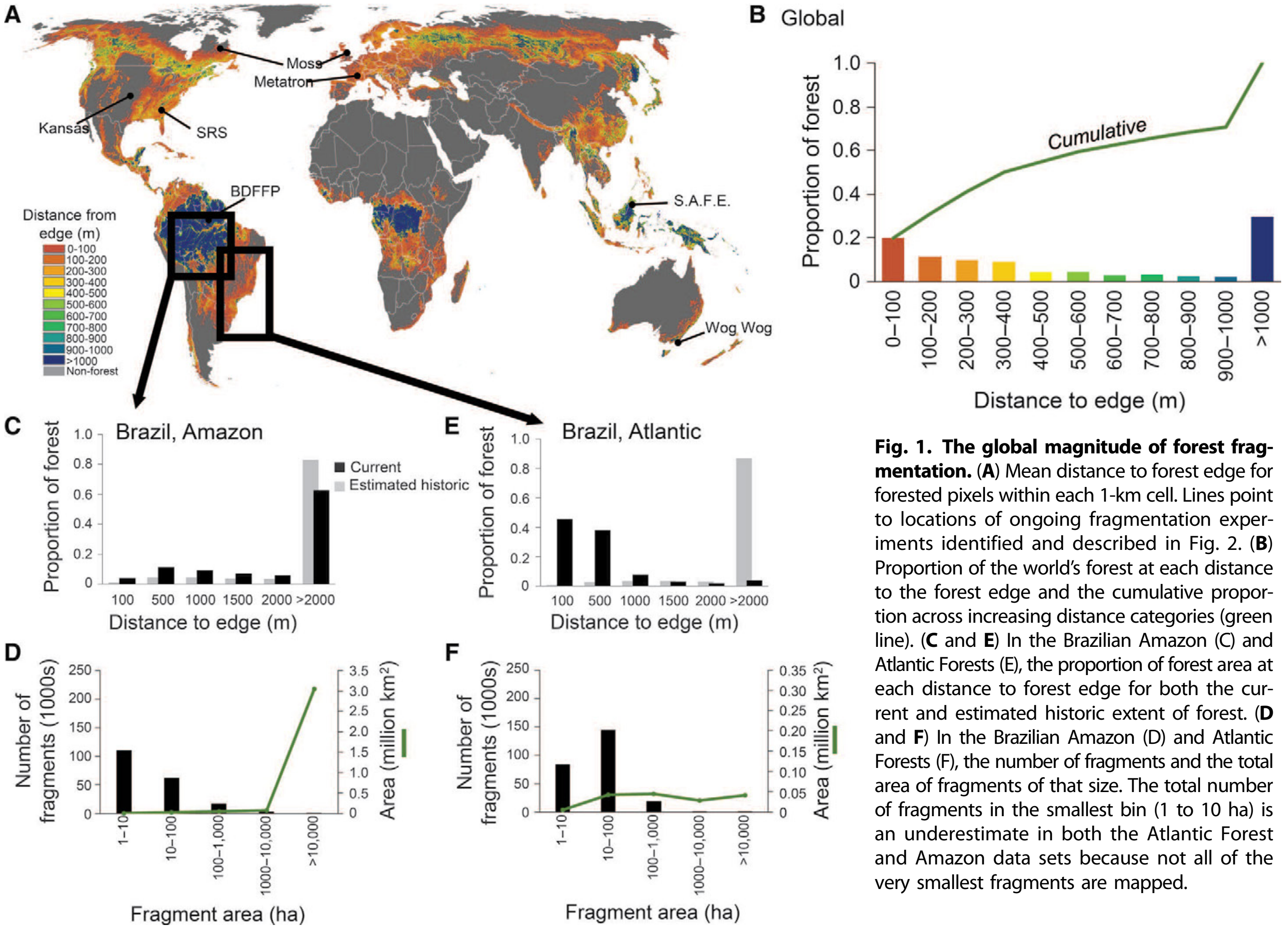


Fig. 1. The global magnitude of forest fragmentation. (**A**) Mean distance to forest edge for forested pixels within each 1-km cell. Lines point to locations of ongoing fragmentation experiments identified and described in Fig. 2. (**B**) Proportion of the world's forest at each distance to the forest edge and the cumulative proportion across increasing distance categories (green line). (**C** and **E**) In the Brazilian Amazon (C) and Atlantic Forests (E), the proportion of forest area at each distance to forest edge for both the current and estimated historic extent of forest. (**D** and **F**) In the Brazilian Amazon (D) and Atlantic Forests (F), the number of fragments and the total area of fragments of that size. The total number of fragments in the smallest bin (1 to 10 ha) is an underestimate in both the Atlantic Forest and Amazon data sets because not all of the very smallest fragments are mapped.

Robust knowledge of how habitat fragmentation affects biodiversity and ecosystem processes is needed if we are to comprehend adequately the implications of this global environmental change.

THE VALUE OF LONG-TERM FRAGMENTATION EXPERIMENTS

Long-term experiments are a powerful tool for understanding the ecological consequences of fragmentation (*20*). Whereas observational studies of fragmented landscapes have yielded important insights (*9*, *21*), they typically lack rigorous controls, replication, randomization, or baseline data. Observational studies have limited ability to isolate the effects of fragmentation from concomitant habitat loss and degradation per se (*4*, *7*, *22*). Remnant fragments are embedded in different types and qualities of surrounding habitat, complicating interpretation because the surrounding habitat also influences biodiversity and ecosystem productivity (*23*).

The long-term fragmentation experiments we analyze here comprise the entire set of ongoing terrestrial long-term experiments. They occur in several biomes (Fig. 2 and Supplementary Materials) and were designed to manipulate specific components of fragmentation—habitat size, isolation, and connectivity—while controlling for confounding factors such as the amount of habitat lost across a landscape (Fig. 2). The largest fragments across these experiments match the size of fragments commonly created by anthropogenic activities (Figs. 1 and 2). Distances to the edge of experimental fragments range to 500 m, encompassing edge distances found in more than half of forests worldwide (Fig. 1B). In each experiment, different fragmentation treatments with replication were established, starting from continuous, nonfragmented landscapes and controlling for background environmental variation either by experimental design (blocking) or by measurement of covariates for use in subsequent analyses. Tests were conducted within fragments that varied experimentally in area or edge, within fragments that were experimentally isolated or connected, or within experimental fragments compared to the same area within continuous habitat. All treatments were replicated. Experiments were created by destroying or creating precise amounts of habitat across replicate landscapes, allowing tests of fragmentation effects independent of habitat loss. The robust

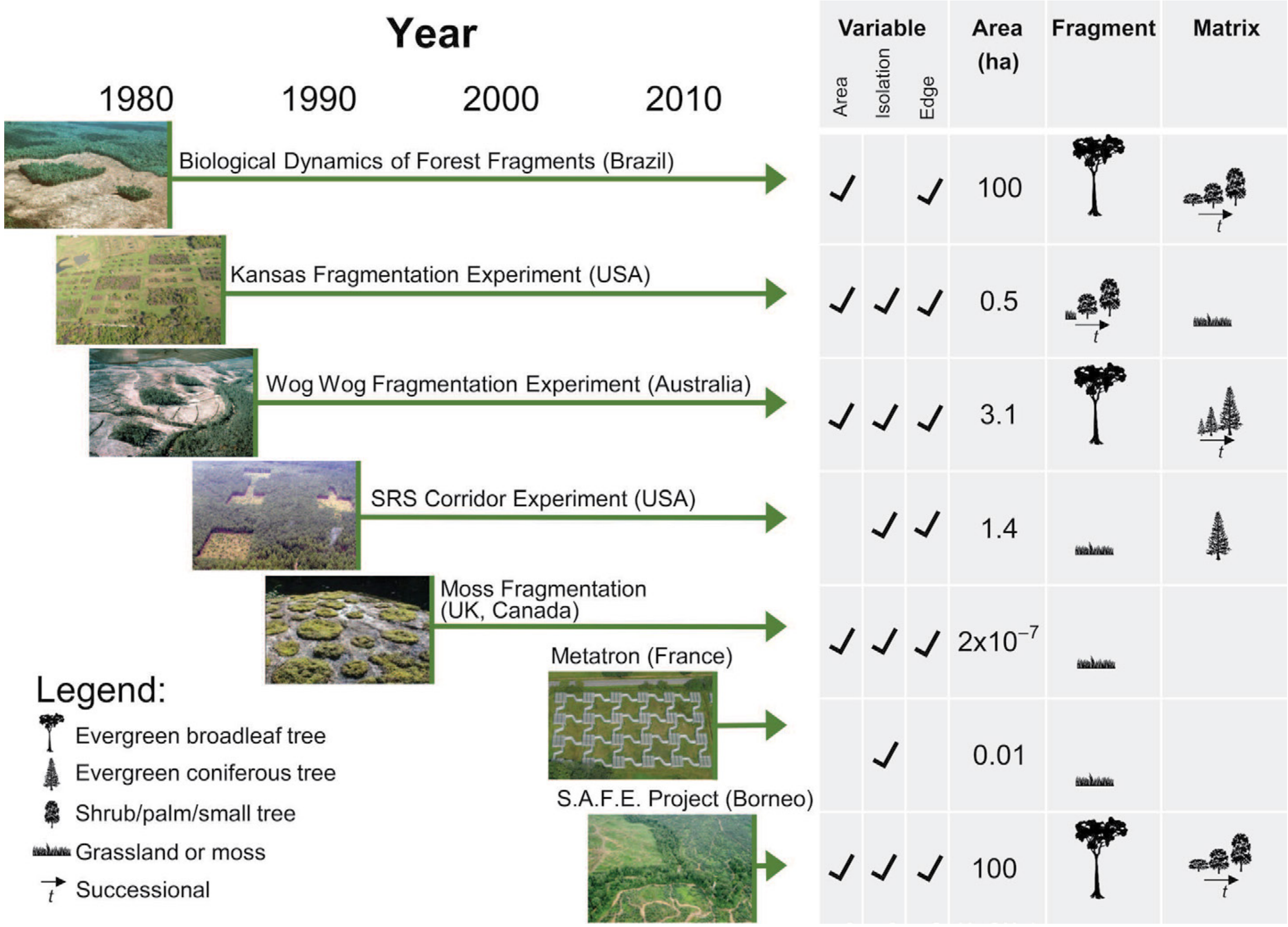


Fig. 2. The world's ongoing fragmentation experiments. All experiments have been running continuously since the time indicated by the start of the associated arrow (with the exception of the moss fragmentation experiment, which represents a series of studies over nearly two decades). The variables under study in each experiment are checked. The area is that of the experiment's largest fragments. Icons under "Fragment" and "Matrix" indicate the dominant community and its relative height, with multiple trees representing succession.

and comparable experimental designs allow for powerful tests of the mechanisms underpinning the ecological impacts of fragmentation, and the long-term nature of ensuing studies has revealed consistent emergent effects.

These experiments mimic anthropogenic fragmentation; they are whole-ecosystem manipulations in which all species and processes experienced the same treatment (*24*). Emergent responses thus reflect the multiple direct and indirect effects of interacting species and processes. Further, because experimentally fragmented ecosystems are open to fluxes of individuals and resources, fragmentation effects can manifest across multiple levels of ecological organization (Fig. 3). Long-term experiments have the power to detect lagged and/or chronic impacts.

The first fragmentation experiments, now more than three decades old, were created to test effects of fragment area on both species persistence and patterns of immigration, reflecting concern in conservation biology about the role of fragmentation in reducing population sizes below viable levels (*25*) (Fig. 2). Subsequent experiments, created two decades ago, shifted focus to modifying habitat isolation, reflecting recognition of the potential to mitigate negative effects of fragmentation by recreating habitat—specifically with corridors—to increase connectivity among fragments (*26*) (Fig. 2). The newest experiments test emerging questions about potentially deleterious synergies between fragmentation and global changes in climate and land use (Fig. 2).

We synthesized results available 31 January 2014 for all studies within these experiments that were conducted in all treatments and replicates, and tested fragmentation effects on dispersal, abundance, extinction, species richness, community composition, and ecosystem functioning. We first calculated effect sizes of fragmentation as log response ratios (Fig. 3). Data from 76 different studies across the five longest-running experiments were drawn from published and unpublished sources (table S1). We synthesized results according to three fragmentation treatments: reduced fragment area [the focus of Biological Dynamics of Forest Fragments Project (BDFFP), Wog Wog, and Kansas; see Fig. 2 for identifiers of experiments], increased fragment isolation [Savannah River Site (SRS) and Moss], and increased proportion of edge (all experiments). Fragmented treatments were compared directly to non- or less-fragmented habitats that were either larger or connected via structural corridors (table S1).

Strong, consistent, and accumulating effects of habitat fragmentation

Our synthesis revealed strong and consistent responses of organisms and ecosystem processes to fragmentation arising from decreased fragment area, increased isolation, and the creation of habitat edges (Fig. 3).

Community and ecosystem responses emerge from observed responses at the level of populations. Reduced area decreased animal

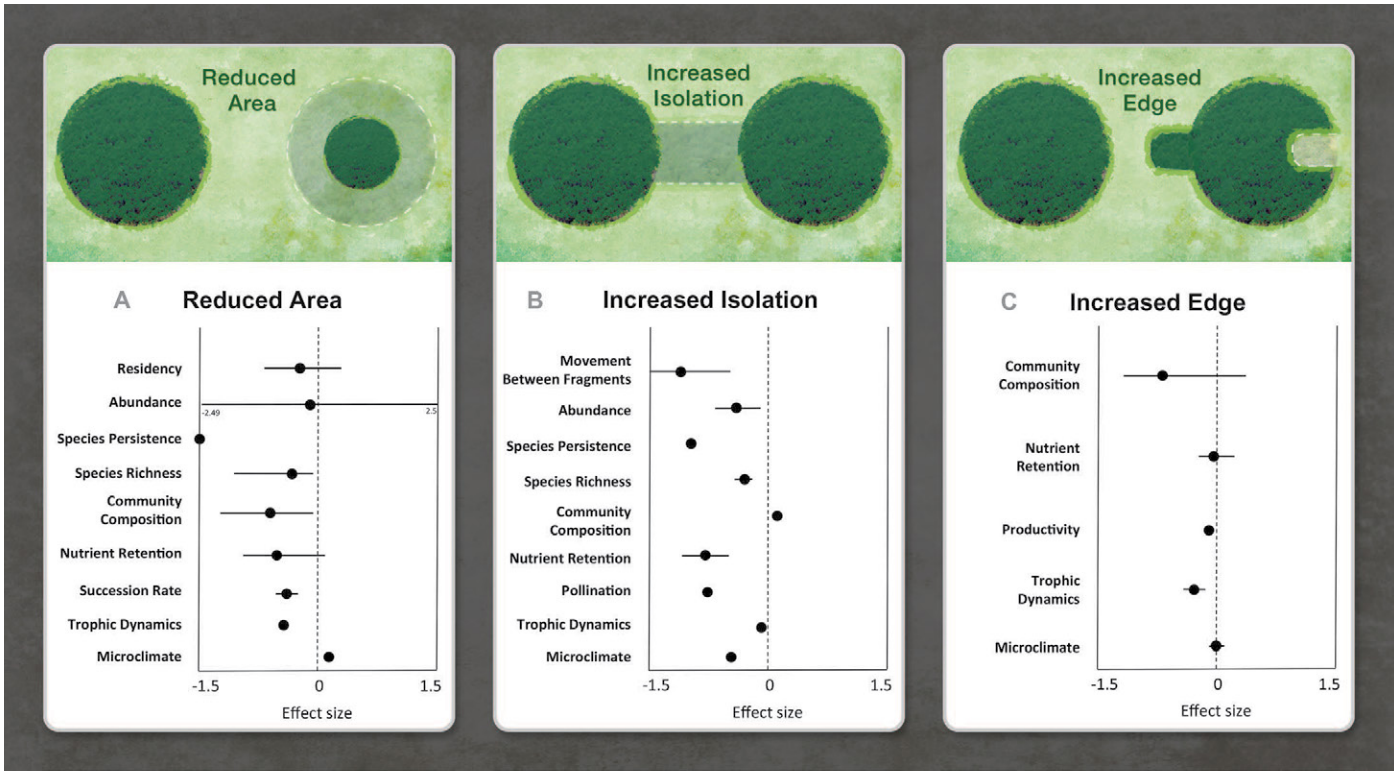


Fig. 3. Fragmentation effects propagate through the whole ecosystem. (**A** to **C**) For each fragmentation treatment [reduced area in BDFFP, Wog Wog, Kansas (A); increased isolation in SRS and Moss (B); and increased edge in all experiments (C)], we summarize major findings for ecological processes at all levels of ecological organization. Each dot represents the mean effect size [computed as log response ratio: ln(mean in more fragmented treatment/mean in non- or less-fragmented treatment)] for an ecological process. Effect sizes are statistical, such that negative or positive values could represent degrading function. Horizontal bars are the range when a dot is represented by more than one study. Details, including individual effect sizes for each study, are reported in table S1.

residency within fragments, and increased isolation reduced movement among fragments, thus reducing fragment recolonization after local extinction (Fig. 3, A and B). Reduced fragment area and increased fragment isolation generally reduced abundance of birds, mammals, insects, and plants (Fig. 3, A and B). This overall pattern emerged despite complex patterns of increases or declines in abundance of individual species (Fig. 3A) with various proximate causes such as release from competition or predation, shifts in disturbance regimes, or alteration of abiotic factors (*14*, *27*–*29*). Reduced area, increased isolation, and increased proportion of edge habitat reduced seed predation and herbivory, whereas increased proportion of edge caused higher fledgling predation that had the effect of reducing bird fecundity (represented together as trophic dynamics in Fig. 3, A to C). Perhaps because of reduced movement and abundance, the ability of species to persist was lower in smaller and more isolated fragments (Fig. 3, A and B).

As predicted by theory (*6*, *30*, *31*), fragmentation strongly reduced species richness of plants and animals across experiments (Fig. 3, A and B), often changing the composition of entire communities (Fig. 3, A to C). In tropical forests, reduced fragment size and increased proportion of edge habitat caused shifts in the physical environment that led to the loss of large and old trees in favor of pioneer trees (Fig. 3, A and C), with subsequent impacts on the community composition of insects (*32*). In grasslands, fragment size also affected succession rate, such that increased light penetration and altered seed pools in smaller fragments impeded the rate of ecological succession relative to that of larger fragments (*33*) (Fig. 3A).

Consistently, all aspects of fragmentation—reduced fragment area, increased isolation, and increased edge—had degrading effects on a disparate set of core ecosystem functions. Degraded functions included reduced carbon and nitrogen retention (Fig. 3, A to C), productivity (Fig. 3C), and pollination (Fig. 3B).

In summary, across experiments spanning numerous studies and ecosystems, fragmentation consistently degraded ecosystems, reducing species persistence, species richness, nutrient retention, trophic dynamics, and, in more isolated fragments, movement.

Long-term consequences of fragmentation

To synthesize all time series of species richness and ecosystem functioning gathered across experiments, we measured effects of fragmentation over the course of each study. The effect of fragmentation was calculated over time as the proportional change in fragmented relative to non- or less-fragmented treatments (Fig. 4).

In most cases, the large and consistent effects of fragmentation revealed by the experiments were predicted from theory. However, we were struck by the persistence of degradation to biodiversity and ecosystem processes and by the increase in many of the effects over time (Fig. 4). For example, extreme rainfall events at Wog Wog appeared to delay the decline in plant species richness for 5 years after fragmentation. In the Kansas Experiment, a lag of 12 years occurred before fragmentation effects on plant succession were detected. Our results thus reveal long-term and progressive effects of fragmentation and provide support for three processes proposed by recent studies in spatial ecology: extinction debt, immigration lag, and ecosystem function debt (Fig. 4).

First, we found strong evidence for temporal lags in extinction [that is, "extinction debt" (*30*)] in fragments. Species richness of plants, arthropods, and birds sampled in the experiments conducted in mature forest fragments and replicated moss landscapes showed decreases of

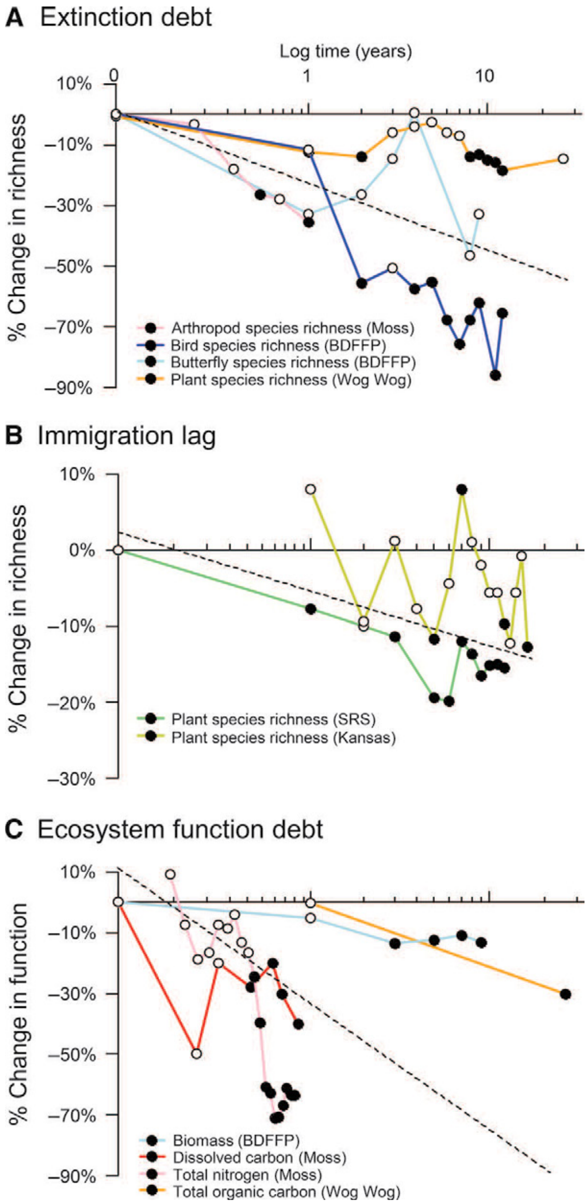


Fig. 4. Delayed effects of fragmentation on ecosystem degradation. (**A**) The extinction debt represents a delayed loss of species due to fragmentation. (**B**) The immigration lag represents differences in species richness caused by smaller fragment area or increased isolation during fragment succession. (**C**) The ecosystem function debt represents delayed changes in ecosystem function due to reduced fragment size or increased isolation. Percent loss is calculated as proportional change in fragmented treatments [for example, (no. of species in fragment − no. of species in control)/(no. of species in control) × 100]. Fragments and controls were either the same area before and after fragmentation, fragments compared to unfragmented controls, or small compared to large fragments. Filled symbols indicate times when fragmentation effects became significant, as determined by the original studies (see table S2). Mean slopes (dashed lines) were estimated using linear mixed (random slopes) models. Mean slope estimates (mean and SE) were as follows: (A) −0.22935 (0.07529); (B) −0.06519 (0.03495); (C) −0.38568 (0.16010).

20 to 75% after fragmentation (Fig. 4A). Some declines were evident almost immediately after fragmentation, whereas others increased in magnitude over the experiment's duration. Across experiments, average loss was >20% after 1 year, >50% after 10 years, and is still increasing in the longest time series measured (more than two decades). The rate of change appears to be slower in larger fragments [in BDFFP, 50% decline in bird species after 5 years in 1-ha fragments, but after 12 years in 100-ha fragments; in Moss, 40% decline in arthropod species richness of small fragments and 26% reduction in large fragments after 1 year (*34*, *35*)]. As predicted by theory (*36*), the extinction debt appears to take longer to pay in larger fragments.

Second, we observed that reduced richness was coincident with an "immigration lag" (*37*), whereby small or isolated fragments are slower to accumulate species during community assembly (*33*, *38*) (Fig. 4B). Immigration lags were observed in experiments conducted in successional systems that were initiated by creating new habitat fragments, rather than by fragmenting existing habitats. After more than a decade, immigration lags resulted in 5% fewer species after 1 year, and 15% fewer species after 10 years in small or isolated fragments compared to large or connected fragments (Fig. 4B).

Third, we observed an ecosystem function debt caused by fragmentation (*39*) in forest and moss fragments (Fig. 4C). An ecosystem function debt is manifest both as delayed changes in nutrient cycling and as changes to plant and consumer biomass. Loss of function amounted to 30% after 1 year, rising to 80% after a decade in small and isolated fragments when compared to larger and more connected fragments (Fig. 4C). Functional debts can result from biodiversity loss, as when loss of nutrients and reduction in decomposition are caused by simplification of food webs. Alternatively, the impact is exhibited through pathways whereby fragmentation changes biotic (for example, tree density in successional systems) or abiotic conditions (for example, light regimes or humidity) in ways that alter and potentially impair ecosystem function [for example, biomass collapse in fragments; Figs. 3 and 4; altered nitrogen and carbon soil dynamics (*40*)].

A new understanding of the effects of fragmentation

By testing existing theory, experiments play a pivotal role in advancing ideas and developing new theory. We draw on experimental evidence to highlight two ways that the understanding of fragmentation has been enriched by the interplay between long-term experiments and development of theory.

First, island biogeography (*6*) was among the earliest theories to predict extinction and immigration rates and patterns of species richness in isolated biotas, which were later used to predict the effects of fragmentation on these variables. Experiments in continental settings tested the theory and gave rise to fresh perspectives. For example, islands are surrounded by sea, a thoroughly inimical matrix for island-dwelling species. Habitat islands, or fragments, are surrounded by a matrix that may not be so unsuitable for some species. In terms of all of the ecological variables studied in our long-term experiments, our results support the conclusion that ecological dynamics in human-modified fragments are a stark contrast to the dynamics in intact habitats that remain. Observational studies that have devoted more detailed consideration to the countryside within which fragments are embedded explain the diversity of ecological responses in remaining fragments (*41*). At the same time as experiments supported the core predictions of classical theories about effects of fragment size and isolation (Figs. 3 and 4), they spurred and tested new theories such as metacommunity theory (*42*) to account for variation in connectivity and habitat quality within and between fragments (*33*, *43*–*45*), spatial dynamics (*14*, *46*), and spatially varying interspecific interactions (*47*).

Second, experiments have demonstrated that the effects of fragmentation are mediated by variation in traits across species. More realistic predictions of community responses to fragmentation emerged after explicit consideration of species traits such as rarity and trophic levels (*48*, *49*), dispersal mode (*50*–*52*), reproductive mode and life span (*29*, *53*), diet (*54*), and movement behavior (*55*, *56*). Increasingly, the simple theoretical prediction that fragmentation reduces species richness is being modified to account for species identity through models that focus on how species vary in their traits (*4*, *21*, *36*, *48*, *57*, *58*). Consideration of traits may help to interpret variation around the overarching pattern that fragmentation consistently reduces species richness across many species and biomes (Figs. 3 and 4).

A NEW GENERATION OF FRAGMENTATION EXPERIMENTS

New foci are emerging for studying ecosystem fragmentation, including (i) synergies between fragmentation and global changes, (ii) eco-evolutionary responses of species to fragmentation, and (iii) ecological responses to fragmentation in production landscapes—that is, ecosystems whose services are under extreme appropriation by humans (*59*).

First, conclusions from experiments thus far are likely to have been conservative because impacts from other environmental changes have been mostly excluded. Most forms of global change known to reduce population sizes and biodiversity will be exacerbated by fragmentation (*58*, *60*), including climate change (*61*), invasive species (*62*, *63*), hunting (*64*), pollution [including light, noise, and chemicals (*65*)], and altered disturbance regimes (*66*).

More complex experiments with unparalleled control and capacity to simultaneously manipulate fragmentation and other global changes are now under way (*53*). The Metatron, created in 2011 in southern France (*67*), enables ecologists to assess effects of variation in temperature and other abiotic factors in addition to habitat isolation. The SAFE Project is being created in the rainforest of Borneo (*68*) and will embed a fragmentation experiment within a production agricultural plantation in which poaching will occur. Other synergies should be investigated experimentally, including the interaction between fragmentation and hunting, fire, infectious disease outbreaks, or nitrogen deposition. Within these experiments, fragmentation and loss of habitat can then be varied independently.

Second, current experiments have stopped short of examining how fragmentation drives evolution through genetic bottlenecks, ecological traps, changing patterns of selection, inbreeding, drift, and gene flow (*69*–*72*). Extensive fragmentation has occurred over many years, and in some regions over millennia (*11*). Changes caused by fragmentation undoubtedly lead to altered patterns of selection and trait evolution. Evolutionary responses to fragmentation have already been suggested (*73*, *74*), and it is likely that such changes will, in turn, feed back to influence population persistence and ecosystem resilience in fragmented landscapes. Linking long-term experiments with the tools of landscape genetics (*75*) may provide powerful insights into the evolutionary dynamics of species inhabiting fragmented landscapes.

Third, new experiments should address the management of natural habitats in production landscapes by monitoring vegetation, networks of interacting species, and ecosystem services at ecologically relevant spatial and temporal scales (*76*–*78*). Some ecosystem services have global consequences, for example, local carbon sequestration affects global atmospheric CO_2. However, in many cases the benefits obtained by people depend on their proximity to habitat fragments (*79*). For example, crop pollination and biological pest control from natural areas adjacent to farms are made available by the very process of habitat fragmentation, bringing people and agriculture closer to those services. Yet, further fragmentation reduces access to many services and ultimately may push landscapes past tipping points, beyond which essential ecosystem services are not merely diminished but lost completely (*80*). This complex relationship creates a double-edged sword, for which locally optimal levels and arrangements of habitat must be sought. New fragmentation experiments should consider how multiple fragments in a landscape interact, creating an ecological network in which the collective benefit of ecosystem services may be greater than the sum of services provided by individual fragments (*81*, *82*). Experimental inferences may then be tested beyond their spatiotemporal domains and, if successful, extrapolated across scales. Such research will be aided by satellite monitoring of ecosystems and human land use across the globe. The most powerful research programs will integrate experiments, observational studies, air- and space-borne imaging, and modeling.

CONCLUSIONS

Fragmentation experiments—some of the largest and longest-running experiments in ecology—provide clear evidence of strong and typically degrading impacts of habitat fragmentation on biodiversity and ecological processes. The findings of these experiments extend to a large fraction of the terrestrial surface of the Earth. Much of the Earth's remaining forest fragments are less than 10 ha in area, and half of the world's forest is within 500 m of the forest edge—areas and distances matched to existing long-term experiments (Figs. 1 and 2) from which consistent effects of fragmentation have emerged (Figs. 3 and 4).

Reduced fragment area, increased isolation, and increased edge initiate changes that percolate through ecosystems (Fig. 3). Fragmentation has the capacity to generate persistent, deleterious, and often unpredicted outcomes, including surprising surges in abundance of some species and the pattern that long temporal scales are required to discern many strong system responses. In light of these conclusions and ongoing debates, we suggest that fragmentation's consistency, pervasiveness, and long-term degrading effect on biodiversity and ecosystem function have not been fully appreciated (*9*).

Without gains in yield and efficiency of agricultural systems (*83*), the expansion of human populations will inevitably continue to reduce and fragment natural areas. The area of Earth's land surface devoted to cropland already occupies 1.53 billion hectares (*83*) and may expand 18% by the middle of this century (*84*), and the area committed to urban centers is predicted to triple to 0.18 billion hectares by 2030 (*85*). The capacity of the surviving forests and other natural habitats to sustain biodiversity and ecosystem services will hinge upon the total amount and quality of habitat left in fragments, their degree of connectivity, and how they are affected by other human-induced perturbations such as climate change and invasive species. Long-term experiments will be even more needed to appreciate, explain, and predict long-term effects. New efforts should work in concert, coordinating a network of experiments across ecosystems and spatial extents.

The effects of current fragmentation will continue to emerge for decades. Extinction debts are likely to come due, although the counteracting immigration debts may never fully be paid. Indeed, the experiments here reveal ongoing losses of biodiversity and ecosystem functioning two decades or longer after fragmentation occurred. Understanding the relationship between transient and long-term dynamics is a substantial challenge that ecologists must tackle, and fragmentation experiments will be central for relating observation to theory.

Experimental results to date show that the effects of fragmentation are strong and markedly consistent across a diverse array of terrestrial systems on five continents. Increasingly, these effects will march in concert with other global changes. New experiments should be coupled with emerging technologies, landscape genetics, and detailed imagery of our planet, and should be coordinated with current ecological theory to understand more deeply the coupled dynamics of ecological and social systems. These insights will be increasingly critical for those responsible for managing and prioritizing areas for preservation and ecological restoration in fragmented landscapes.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/1/2/e1500052/DC1
Materials and Methods
Fig. S1. Map of the BDFFP experiment and location within Brazil.
Fig. S2. Map of the Kansas fragmentation experiment.
Fig. S3. Map of the Wog Wog experiment and location within Australia.
Fig. S4. Map of the SRS experiment showing locations of the eight blocks in the second SRS Corridor Experiment within the SRS, South Carolina, USA.
Fig. S5. Design of the Moss experiment.
Fig. S6. Design of the Metatron experiment with 48 enclosed fragments and adjoining enclosed corridors.
Fig. S7. Map of the SAFE experiment and location within Borneo [after Ewers *et al.* (*68*)].
Table S1. Metadata for Fig. 3 in the main text.
Table S2. Metadata for Fig. 4 in the main text.

REFERENCES AND NOTES

1. H. M. Pereira, P. W. Leadley, V. Proenca, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarres, M. B. Araujo, P. Balvanera, R. Biggs, W. W. L. Cheung, L. Chini, H. D. Cooper, E. L. Gilman, S. Guenette, G. C. Hurtt, H. P. Huntington, G. M. Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U. R. Sumaila, M. Walpole, Scenarios for global biodiversity in the 21st century. *Science* **330**, 1496–1501 (2010).
2. M. R. W. Rands, W. M. Adams, L. Bennun, S. H. M. Butchart, A. Clements, D. Coomes, A. Entwistle, I. Hodge, V. Kapos, J. P. W. Scharlemann, W. J. Sutherland, B. Vira, Biodiversity conservation: Challenges beyond 2010. *Science* **329**, 1298–1303 (2010).
3. D. B. Lindenmayer, J. Fischer, *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis* (Island Press, Washington, DC, 2006).
4. R. K. Didham, V. Kapos, R. M. Ewers, Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* **121**, 161–170 (2012).
5. L. Fahrig, Rethinking patch size and isolation effects: The habitat amount hypothesis. *J. Biogeogr.* **40**, 1649–1663 (2013).
6. R. H. MacArthur, E. O. Wilson, *The Theory of Island Biogeography* (Princeton University Press, Princeton, NJ, 1967).
7. L. Fahrig, Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487–515 (2003).
8. S. K. Collinge, *The Ecology of Fragmented Landscapes* (The Johns Hopkins University Press, Baltimore, MD, 2009).
9. I. Ibanez, D. S. W. Katz, D. Peltier, S. M. Wolf, B. T. C. Barrie, Assessing the integrated effects of landscape fragmentation on plants and plant communities: The challenge of multiprocess–multiresponse dynamics. *J. Ecol.* **102**, 882–895 (2014).
10. M. C. Hansen, P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, J. R. G. Townshend, High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013).

11. M. Williams, *Deforesting the Earth*: *From Prehistory to Global Crisis* (University of Chicago Press, Chicago, 2003).
12. D. Skole, C. Tucker, Tropical deforestation and habitat fragmentation in the Amazon: Satellite data from 1978 to 1988. *Science* **260**, 1905–1910 (1993).
13. J. O. Sexton, X. P. Song, M. Feng, P. Noojipady, A. Anand, C. Q. Huang, D. H. Kim, K. M. Collins, S. Channan, C. DiMiceli, J. R. Townshend, 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. Digital Earth* **6**, 427–448 (2013).
14. W. F. Laurance, T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, E. Sampaio, Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conserv. Biol.* **16**, 605–618 (2002).
15. E. N. Broadbent, G. P. Asner, M. Keller, D. E. Knapp, P. J. C. Oliveira, J. N. Silva, Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv.* **141**, 1745–1757 (2008).
16. M. C. Ribeiro, J. P. Metzger, A. C. Martensen, F. J. Ponzoni, M. M. Hirota, The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biol. Conserv.* **142**, 1141–1153 (2009).
17. T. P. Hughes, D. R. Bellwood, C. Folke, R. S. Steneck, J. Wilson, New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol. Evol.* **20**, 380–386 (2005).
18. T. Ricketts, E. Dinerstein, D. Olson, C. Loucks, W. Eichbaum, K. Kavanagh, P. Hedao, P. Hurley, K. Carney, R. Abell, S. Walters, *A Conservation Assessment of the Terrestrial Ecoregions of North America* (Island Press, Washington, DC, 1999).
19. R. P. White, S. Murray, M. Rohweder, *Grassland Ecosystems* (World Resources Institute, Washington, DC, 2000).
20. K. McGarigal, S. A. Cushman, Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecol. Appl.* **12**, 335–345 (2002).
21. H. M. Martinson, W. F. Fagan, Trophic disruption: A meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. *Ecol. Lett.* **17**, 1178–1189 (2014).
22. J. I. Watling, M. A. Donnelly, Fragments as islands: A synthesis of faunal responses to habitat patchiness. *Conserv. Biol.* **20**, 1016–1025 (2006).
23. K. M. Flinn, M. Vellend, P. L. Marks, Environmental causes and consequences of forest clearance and agricultural abandonment in central New York, USA. *J. Biogeogr.* **32**, 439–452 (2005).
24. D. A. Saunders, R. J. Hobbs, C. R. Margules, Biological consequences of ecosystem fragmentation: A review. *Conserv. Biol.* **5**, 18–32 (1991).
25. M. E. Soulé, *Viable Populations for Conservation* (Cambridge University Press, Cambridge, UK, 1987).
26. E. O. Wilson, E. O. Willis, in *Ecology and Evolution of Communities*, M. L. Cody, J. M. Diamond, Eds. (The Belknap Press, Cambridge, MA, 1975), pp. 522–534.
27. H. L. Vasconcelos, E. M. Bruna, Arthropod responses to the experimental isolation of Amazonian forest fragments. *Zoologia* **29**, 515–530 (2012).
28. N. M. Haddad, L. A. Brudvig, E. I. Damschen, D. M. Evans, B. L. Johnson, D. J. Levey, J. L. Orrock, J. Resasco, L. L. Sullivan, J. J. Tewksbury, S. A. Wagner, A. J. Weldon, Potential negative ecological effects of corridors. *Conserv. Biol.* **28**, 1178–1187 (2014).
29. C. D. Collins, R. D. Holt, B. L. Foster, Patch size effects on plant species decline in an experimentally fragmented landscape. *Ecology* **90**, 2577–2588 (2009).
30. D. Tilman, R. M. May, C. L. Lehman, M. A. Nowak, Habitat destruction and the extinction debt. *Nature* **371**, 65–66 (1994).
31. I. Hanski, A. Moilanen, M. Gyllenberg, Minimum viable metapopulation size. *Am. Nat.* **147**, 527–541 (1996).
32. W. F. Laurance, P. Delamonica, S. G. Laurance, H. L. Vasconcelos, T. E. Lovejoy, Conservation: Rainforest fragmentation kills big trees. *Nature* **404**, 836 (2000).
33. W. M. Cook, J. Yao, B. L. Foster, R. D. Holt, L. B. Patrick, Secondary succession in an experimentally fragmented landscape: Community patterns across space and time. *Ecology* **86**, 1267–1279 (2005).
34. A. Gonzalez, Community relaxation in fragmented landscapes: The relation between species richness, area and age. *Ecol. Lett.* **3**, 441–448 (2000).
35. G. Ferraz, G. J. Russell, P. C. Stouffer, R. O. Bierregaard, S. L. Pimm, T. E. Lovejoy, Rates of species loss from Amazonian forest fragments. *Proc. Natl. Acad. Sci. U.S.A.* **100**, 14069–14073 (2003).
36. J. L. Orrock, J. I. Watling, Local community size mediates ecological drift and competition in metacommunities. *Proc. Biol. Sci.* **277**, 2185–2191 (2010).
37. S. T. Jackson, D. F. Sax, Balancing biodiversity in a changing environment: Extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* **25**, 153–160 (2010).
38. J. Clobert, J. F. Le Galliard, J. Cote, S. Meylan, M. Massot, Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **12**, 197–209 (2009).
39. P. Staddon, Z. Lindo, P. D. Crittenden, F. Gilbert, A. Gonzalez, Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecol. Lett.* **13**, 543–552 (2010).
40. S. A. Billings, E. A. Gaydess, Soil nitrogen and carbon dynamics in a fragmented landscape experiencing forest succession. *Landsc. Ecol.* **23**, 581–593 (2008).
41. C. D. Mendenhall, D. S. Karp, C. F. J. Meyer, E. A. Hadly, G. C. Daily, Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature* **509**, 213–217 (2014).
42. A. Gonzalez, J. H. Lawton, F. S. Gilbert, T. M. Blackburn, I. Evans-Freke, Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* **281**, 2045–2047 (1998).
43. H. M. Alexander, B. L. Foster, F. Ballantyne, C. D. Collins, J. Antonovics, R. D. Holt, Metapopulations and metacommunities: Combining spatial and temporal perspectives in plant ecology. *J. Ecol.* **100**, 88–103 (2012).
44. C. R. Margules, The Wog Wog habitat fragmentation experiment. *Environ. Conserv.* **19**, 316–325 (1992).
45. E. I. Damschen, L. A. Brudvig, Landscape connectivity strengthens local–regional richness relationships in successional plant communities. *Ecology* **93**, 704–710 (2012).
46. W. M. Cook, K. T. Lane, B. L. Foster, R. D. Holt, Island theory, matrix effects and species richness patterns in habitat fragments. *Ecol. Lett.* **5**, 619–623 (2002).
47. K. F. Davies, B. A. Melbourne, C. R. Margules, Effects of within- and between-patch processes on community dynamics in a fragmentation experiment. *Ecology* **82**, 1830–1846 (2001).
48. K. F. Davies, C. R. Margules, K. F. Lawrence, Which traits of species predict population declines in experimental forest fragments? *Ecology* **81**, 1450–1461 (2000).
49. K. F. Davies, C. R. Margules, J. F. Lawrence, A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* **85**, 265–271 (2004).
50. J. Yao, R. D. Holt, P. M. Rich, W. S. Marshall, Woody plant colonization in an experimentally fragmented landscape. *Ecography* **22**, 715–728 (1999).
51. E. I. Damschen, L. A. Brudvig, N. M. Haddad, D. J. Levey, J. L. Orrock, J. J. Tewksbury, The movement ecology and dynamics of plant communities in fragmented landscapes. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 19078–19083 (2008).
52. L. L. Sullivan, B. L. Johnson, L. A. Brudvig, N. M. Haddad, Can dispersal mode predict corridor effects on plant parasites? *Ecology* **92**, 1559–1564 (2011).
53. Z. Lindo, J. Whiteley, A. Gonzalez, Traits explain community disassembly and trophic contraction following experimental environmental change. *Glob. Chang. Biol.* **18**, 2448–2457 (2012).
54. 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).
55. J. E. Diffendorfer, M. S. Gaines, R. D. Holt, Habitat fragmentation and movements of three small mammals (Sigmodon, Microtus, and Peromyscus). *Ecology* **76**, 827–839 (1995).
56. K. S. Van Houtan, S. L. Pimm, J. M. Halley, R. O. Bierregaard Jr., T. E. Lovejoy, Dispersal of Amazonian birds in continuous and fragmented forest. *Ecol. Lett.* **10**, 219–229 (2007).
57. I. Hanski, Extinction debt at different spatial scales. *Anim. Conserv.* **16**, 12–13 (2013).
58. R. Dirzo, H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, B. Collen, Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
59. C. Kueffer, C. N. Kaiser-Bunbury, Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. *Front. Ecol. Environ.* **12**, 131–137 (2014).
60. W. F. Laurance, D. C. Useche, Environmental synergisms and extinctions of tropical species. *Conserv. Biol.* **23**, 1427–1437 (2009).
61. M. Krosby, J. Tewksbury, N. M. Haddad, J. Hoekstra, Ecological connectivity for a changing climate. *Conserv. Biol.* **24**, 1686–1689 (2010).
62. R. K. Didham, J. M. Tylianakis, N. J. Gemmell, T. A. Rand, R. M. Ewers, Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* **22**, 489–496 (2007).
63. L. Gibson, A. J. Lynam, C. J. A. Bradshaw, F. L. He, D. P. Bickford, D. S. Woodruff, S. Bumrungsri, W. F. Laurance, Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science* **341**, 1508–1510 (2013).
64. C. A. Peres, Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conserv. Biol.* **15**, 1490–1505 (2001).
65. K. J. Gaston, T. W. Davies, J. Bennie, J. Hopkins, Review: Reducing the ecological consequences of night-time light pollution: Options and developments. *J. Appl. Ecol.* **49**, 1256–1266 (2012).
66. M. A. Cochrane, W. F. Laurance, Fire as a large-scale edge effect in Amazonian forests. *J. Trop. Ecol.* **18**, 311–325 (2002).
67. D. Legrand, O. Guillaume, M. Baguette, J. Cote, A. Trochet, O. Calvez, S. Zajitschek, F. Zajitschek, J. Lecomte, Q. Benard, J. F. Le Galliard, J. Clobert, The Metatron: An experimental system to study dispersal and metaecosystems for terrestrial organisms. *Nat. Methods* **9**, 828–833 (2012).
68. R. M. Ewers, R. K. Didham, L. Fahrig, G. Ferraz, A. Hector, R. D. Holt, V. Kapos, G. Reynolds, W. Sinun, J. L. Snaddon, E. C. Turner, A large-scale forest fragmentation experiment: The Stability of Altered Forest Ecosystems Project. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **366**, 3292–3302 (2011).
69. A. R. Templeton, K. Shaw, E. Routman, S. K. Davis, The genetic consequences of habitat fragmentation. *Ann. Mo. Bot. Gard.* **77**, 13–27 (1990).
70. A. Young, T. Boyle, T. Brown, The population genetic consequences of habitat fragmentation for plants. *Trends Ecol. Evol.* **11**, 413–418 (1996).

71. M. S. Gaines, J. E. Diffendorfer, R. H. Tamarin, T. S. Whittam, The effects of habitat fragmentation on the genetic structure of small mammal populations. *J. Hered*. **88**, 294–304 (1997).
72. J. L. Orrock, Conservation corridors affect the fixation of novel alleles. *Conserv*. *Genet*. **6**, 623–630 (2005).
73. T. Merck, H. Van Dyck, B. Karlsson, O. Leimar, The evolution of movements and behaviour at boundaries in different landscapes: A common arena experiment with butterflies. *Proc*. *Biol*. *Sci*. **270**, 1815–1821 (2003).
74. S. P. Ripperger, M. Tschapka, E. K. V. Kalko, B. Rodriguez-Herrera, F. Mayer, Life in a mosaic landscape: Anthropogenic habitat fragmentation affects genetic population structure in a frugivorous bat species. *Conserv*. *Genet*. **14**, 925–934 (2013).
75. S. Manel, R. Holderegger, Ten years of landscape genetics. *Trends Ecol. Evol.* **28**, 614–621 (2013).
76. M. Keller, D. S. Schimel, W. W. Hargrove, F. M. Hoffman, A continental strategy for the National Ecological Observatory Network. *Front*. *Ecol*. *Environ*. **6**, 282–284 (2008).
77. H. Tallis, H. Mooney, S. Andelman, P. Balvanera, W. Cramer, D. Karp, S. Polasky, B. Reyers, T. Ricketts, S. Running, K. Thonicke, B. Tietjen, A. Walz, A global system for monitoring ecosystem service change. *Bioscience* **62**, 977–986 (2012).
78. J. O. Sexton, R. D. Ramsey, D. L. Bartos, Habitone analysis of quaking aspen in the Utah Book Cliffs: Effects of site water demand and conifer cover. *Ecol*. *Model*. **198**, 301–311 (2006).
79. A. K. Fremier, F. A. J. DeClerck, N. A. Bosque-Perez, N. E. Carmona, R. Hill, T. Joyal, L. Keesecker, P. Z. Klos, A. Martinez-Salinas, R. Niemeyer, A. Sanfiorenzo, K. Welsh, J. D. Wulfhorst, Understanding spatiotemporal lags in ecosystem services to improve incentives. *Bioscience* **63**, 472–482 (2013).
80. T. H. Keitt, Habitat conversion, extinction thresholds, and pollination services in agroecosystems. *Ecol*. *Appl*. **19**, 1561–1573 (2009).
81. P. Opdam, E. Steingrover, S. van Rooij, Ecological networks: A spatial concept for multi-actor planning of sustainable landscapes. *Landsc. Urban Plan.* **75**, 322–332 (2006).
82. M. Cabeza, A. Moilanen, Design of reserve networks and the persistence of biodiversity. *Trends Ecol*. *Evol*. **16**, 242–248 (2001).
83. J. A. Foley, N. Ramankutty, K. A. Brauman, E. S. Cassidy, J. S. Gerber, M. Johnston, N. D. Mueller, C. O'Connell, D. K. Ray, P. C. West, C. Balzer, E. M. Bennett, S. R. Carpenter, J. Hill, C. Monfreda, S. Polasky, J. Rockstrom, J. Sheehan, S. Siebert, D. Tilman, D. P. M. Zaks, Solutions for a cultivated planet. *Nature* **478**, 337–342 (2011).
84. D. Tilman, Global environmental impacts of agricultural expansion: The need for sustainable and efficient practices. *Proc. Natl. Acad. Sci. U.S.A.* **96**, 5995–6000 (1999).
85. K. C. Seto, B. Guneralp, L. R. Hutyra, Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 16083–16088 (2012).

Acknowledgments: For comments, we thank R. Dunn, P. Ehrlich, L. Frishkoff, F. Gould, A. Leidner, C. Mendenhall, A. Tal, J. Watling, and the Fukami and Peay labs at Stanford. For symbols in figures, we thank the Integration and Application Network, University of Maryland Center for Environmental Science. **Funding:** R.M.E. is supported by ERC (European Research Council) Project number 281986. A.G. is supported by the Natural Sciences and Engineering Research Council, the Canada Research Chair program, and the Quebec Centre for Biodiversity Science. C.N.J. was supported by the Brazilian agency CAPES through the Ciência Sem Fronteiras program. R.D.H. thanks the University of Florida Foundation. J.C. is supported by the labex TULIP and the ANR Infrastructure grant AnaEE-France. Global forest cover data and analysis were provided under support from the NASA Making Earth System Data Records for Use in Research Environments (MEaSUREs; NNH06ZDA001N) and Land Cover and Land Use Change (NNH07ZDA001N-LCLUC) programs. For long-term support of experiments, we thank the Andrew W. Mellon Foundation (BDFFP); the Kansas Biological Survey and National Science Foundation (NSF) (DEB 01-08302 and DEB-0950100; Kansas Experiment); NSF and U.S. Department of Agriculture Forest Service–Savannah River (SRS Corridor Experiment); NSF DEB 0841892 and Environment and Heritage NSW, Forestry Corporation NSW, and CSIRO Ecosystem Sciences (Wog Wog); and the Sime Darby Foundation (SAFE).

Submitted 15 January 2015
Accepted 17 February 2015
Published 20 March 2015
10.1126/sciadv.1500052

Citation: N. M. Haddad, L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, J. R. Townshend, Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015).

ECOLOGY

10.1126/sciadv.1500936

Estimating the global conservation status of more than 15,000 Amazonian tree species

Hans ter Steege,[1,2]* Nigel C. A. Pitman,[3,4] Timothy J. Killeen,[5] William F. Laurance,[6] Carlos A. Peres,[7] Juan Ernesto Guevara,[8,9]
Rafael P. Salomão,[10] Carolina V. Castilho,[11] Iêda Leão Amaral,[12] Francisca Dionízia de Almeida Matos,[12]
Luiz de Souza Coelho,[12] William E. Magnusson,[13] Oliver L. Phillips,[14] Diogenes de Andrade Lima Filho,[12]
Marcelo de Jesus Veiga Carim,[15] Mariana Victória Irume,[12] Maria Pires Martins,[12] Jean-François Molino,[16] Daniel Sabatier,[16]
Florian Wittmann,[17] Dairon Cárdenas López,[18] José Renan da Silva Guimarães,[15] Abel Monteagudo Mendoza,[19]
Percy Núñez Vargas,[20] Angelo Gilberto Manzatto,[21] Neidiane Farias Costa Reis,[22] John Terborgh,[4] Katia Regina Casula,[22]
Juan Carlos Montero,[12,23] Ted R. Feldpausch,[14,24] Euridice N. Honorio Coronado,[14,25] Alvaro Javier Duque Montoya,[26]
Charles Eugene Zartman,[12] Bonifacio Mostacedo,[27] Rodolfo Vasquez,[19] Rafael L. Assis,[28] Marcelo Brilhante Medeiros,[29]
Marcelo Fragomeni Simon,[29] Ana Andrade,[30] José Luís Camargo,[30] Susan G. W. Laurance,[6]
Henrique Eduardo Mendonça Nascimento,[12] Beatriz S. Marimon,[31] Ben-Hur Marimon Jr.,[31] Flávia Costa,[13]
Natalia Targhetta,[28] Ima Célia Guimarães Vieira,[10] Roel Brienen,[14] Hernán Castellanos,[32] Joost F. Duivenvoorden,[33]
Hugo F. Mogollón,[34] Maria Teresa Fernandez Piedade,[28] Gerardo A. Aymard C.,[35] James A. Comiskey,[36] Gabriel Damasco,[8]
Nállarett Dávila,[37] Roosevelt García-Villacorta,[38,39] Pablo Roberto Stevenson Diaz,[40] Alberto Vincentini,[13] Thaise Emilio,[13,41]
Carolina Levis,[13,42] Juliana Schietti,[13] Priscila Souza,[13] Alfonso Alonso,[43] Francisco Dallmeier,[43] Leandro Valle Ferreira,[10]
David Neill,[44] Alejandro Araujo-Murakami,[45] Luzmila Arroyo,[45] Fernanda Antunes Carvalho,[13] Fernanda Coelho Souza,[13]
Dário Dantas do Amaral,[10] Rogerio Gribel,[46] Bruno Garcia Luize,[47] Marcelo Petrati Pansonato,[13] Eduardo Venticinque,[48]
Paul Fine,[8] Marisol Toledo,[23] Chris Baraloto,[49,50] Carlos Cerón,[51] Julien Engel,[52] Terry W. Henkel,[53] Eliana M. Jimenez,[54]
Paul Maas,[55] Maria Cristina Peñuela Mora,[56] Pascal Petronelli,[49] Juan David Cardenas Revilla,[12] Marcos Silveira,[57]
Juliana Stropp,[58,59] Raquel Thomas-Caesar,[60] Tim R. Baker,[14] Doug Daly,[61] Marcos Ríos Paredes,[62] Naara Ferreira da Silva,[28]
Alfredo Fuentes,[63] Peter Møller Jørgensen,[64] Jochen Schöngart,[17] Miles R. Silman,[65] Nicolás Castaño Arboleda,[18]
Bruno Barçante Ladvocat Cintra,[28] Fernando Cornejo Valverde,[66] Anthony Di Fiore,[67] Juan Fernando Phillips,[68]
Tinde R. van Andel,[1] Patricio von Hildebrand,[69] Edelcilio Marques Barbosa,[12] Luiz Carlos de Matos Bonates,[12]
Deborah de Castro,[28] Emanuelle de Sousa Farias,[70] Therany Gonzales,[71] Jean-Louis Guillaumet,[72] Bruce Hoffman,[73]
Yadvinder Malhi,[74] Ires Paula de Andrade Miranda,[12] Adriana Prieto,[75] Agustín Rudas,[75] Ademir R. Ruschell,[76] Natalino Silva,[77]
César I.A. Vela,[78] Vincent A. Vos,[79,80] Eglée L. Zent,[81] Stanford Zent,[81] Angela Cano,[40] Marcelo Trindade Nascimento,[82]
Alexandre A. Oliveira,[83] Hirma Ramirez-Angulo,[84] José Ferreira Ramos,[12] Rodrigo Sierra,[85] Milton Tirado,[85]
Maria Natalia Umaña Medina,[86] Geertje van der Heijden,[87] Emilio Vilanova Torre,[84] Corine Vriesendorp,[3] Ophelia Wang,[88]
Kenneth R. Young,[89] Claudia Baider,[83,90] Henrik Balslev,[91] Natalia de Castro,[28] William Farfan-Rios,[65] Cid Ferreira,[12]
Casimiro Mendoza,[92,93] Italo Mesones,[8] Armando Torres-Lezama,[84] Ligia Estela Urrego Giraldo,[26] Daniel Villarroel,[45]
Roderick Zagt,[94] Miguel N. Alexiades,[95] Karina Garcia-Cabrera,[65] Lionel Hernandez,[96] Isau Huamantupa-Chuquimaco,[20]
William Milliken,[97] Walter Palacios Cuenca,[98] Susamar Pansini,[99] Daniela Pauletto,[100] Freddy Ramirez Arevalo,[101]
Adeilza Felipe Sampaio,[99] Elvis H. Valderrama Sandoval,[101,102] Luis Valenzuela Gamarra[19]

Estimates of extinction risk for Amazonian plant and animal species are rare and not often incorporated into land-use policy and conservation planning. We overlay spatial distribution models with historical and projected deforestation to show that at least 36% and up to 57% of all Amazonian tree species are likely to qualify as globally threatened under International Union for Conservation of Nature (IUCN) Red List criteria. If confirmed, these results would increase the number of threatened plant species on Earth by 22%. We show that the trends observed in Amazonia apply to trees throughout the tropics, and we predict that most of the world's >40,000 tropical tree species now qualify as globally threatened. A gap analysis suggests that existing Amazonian protected areas and indigenous territories will protect viable populations of most threatened species if these areas suffer no further degradation, highlighting the key roles that protected areas, indigenous peoples, and improved governance can play in preventing large-scale extinctions in the tropics in this century.

INTRODUCTION

Amazonian forests have lost ~12% of their original extent and are projected to lose another 9 to 28% by 2050 (*1*, *2*). The consequences of ongoing forest loss in Amazonia (here all rainforests of the Amazon basin and Guiana Shield) are relatively well understood at the ecosystem level, where they include soil erosion (*3*, *4*), diminished ecosystem services (*5*–*8*), altered climatic patterns (*5*, *7*, *9*–*11*), and habitat degradation. By contrast, little is known about how historical forest loss has affected the population sizes of plant and animal species in the basin and how ongoing deforestation will affect these populations in the future.

As a result, the conservation status of the >15,000 species that compose the Amazonian tree flora—one of the most diverse plant communities on Earth—remains unknown. To date, only a tiny proportion of Amazonian tree species have been formally assessed for the International Union for Conservation of Nature (IUCN) Red List. Two previous studies have attempted to estimate the extinction threat to Amazonian plants using theory, data, and vegetation maps to model reductions in range size, but they disagreed on whether the proportion of

---

[1] Biodiversity Dynamics, Naturalis Biodiversity Center, Darwin building, Darwinweg 4, Leiden 2300 AA, The Netherlands. [2] Ecology and Biodiversity Group, Utrecht University, Padualaan 8, Utrecht, Netherlands. [3] Science and Education, The Field Museum, 1400 S. Lake Shore Drive, Chicago, IL 60605–2496, USA. [4] Center for Tropical Conservation, Duke University, Nicholas School of the Environment, Durham, NC 27708, USA. [5] Agteca-Amazonica, Santa Cruz, Bolivia. [6] Centre for Tropical Environmental and Sustainability Science, College of Marine and Environmental Sciences, James Cook University, Cairns, Queensland 4870, Australia. [7] School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK. [8] Department of Integrative Biology, University of California, Berkeley, CA 94720–3140, USA. [9] Museo Ecuatoriano de Ciencias Naturales, Av. Río Coca E6-115 e Isla Floreana, Quito, Ecuador. [10] Coordenação de Botânica, Museu Paraense Emilio Goeldi, Av. Magalhaes Barata 376, C.P. 399, Belém, PA 66040–170, Brazil. [11] EMBRAPA – Centro de Pesquisa Agroflorestal de Roraima, BR 174, km 8 – Distrito Industrial, Boa Vista, RR 69301–970, Brazil. [12] Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM 69060–001, Brazil. [13] Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM 69060–001, Brazil. [14] School of Geography, University of Leeds, Woodhouse Lane, Leeds LS2 9JT, UK. [15] Instituto de Pesquisas Científicas e Tecnológicas do Amapá - IEPA, Av. Feliciano Coelho, 1509. Trem, Macapá, Amapá 68901–025, Brazil. [16] UMR AMAP, Institut de Recherche pour le Développement (IRD), TA 40/PS2, Boulevard de la Lironde, Montpellier Cedex 5 34398, France. [17] Biogeochemistry, Max Planck Institute for Chemistry, Hahn-Meitner Weg 1, Mainz 55128, Germany. [18] Herbario Amazónico Colombiano, Instituto SINCHI, Calle 20 No 5, Bogotá, DF 44, Colombia. [19] Jardín Botánico de Missouri, Oxapampa, Pasco, Peru. [20] Herbario Vargas, Universidad Nacional de San Antonio Abad del Cusco, Avenida de la Cultura, Nro 733, Cusco, Cuzco, Peru. [21] Departamento de Biologia, Universidade Federal de Rondônia, Rodovia BR 364 s/n Km 9,5 - Sentido Acre, Unir, Porto Velho, Rondônia 76.824-027, Brazil. [22] Programa de Pós-Graduação em Desenvolvimento Regional e Meio Ambiente PGDRA, Universidade Federal de Rondônia, Rodovia BR 364 s/n Km 9,5 - Sentido Acre, Unir, Porto Velho, Rondônia 76.824-028, Brazil. [23] Instituto Boliviano de Investigacion Forestal, Universidad Autónoma Gabriel René Moreno, Km 9 Carretera al Norte, El Vallecito, FCA-UAGRM, Santa Cruz, Bolivia. [24] College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4RJ, UK. [25] Instituto de Investigaciones de la Amazonía Peruana, Av. José A. Quiñones km. 2.5, Iquitos, Loreto, Peru. [26] Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Calle 64 x Cra 65, Medellín, Antioquia 1027, Colombia. [27] Facultad de Ciencias Agrícolas, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia. [28] Coordenação de Dinâmica Ambiental, Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM 69060–001, Brazil. [29] Prédio da Botânica e Ecologia, Embrapa Recursos Genéticos e Biotecnologia, Parque Estaccao Biologica, Av. W5 Norte, Brasilia, DF 70770–917, Brazil. [30] Projeto Dinâmica Biológica de Fragmentos Florestais, Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM 69060–001, Brazil. [31] Departamento de Ciências Biológicas, Universidade do Estado de Mato Grosso, Nova Xavantina, MT, Brazil. [32] Universidad Nacional Experimental de Guayana, Calle Chile, urbaniz Chilemex, Puerto Ordaz, Bolivar, Venezuela. [33] Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, Sciencepark 904, Amsterdam, Noord Holland 1098 XH, The Netherlands. [34] Endangered Species Coalition, 8530 Geren Rd., Silver Spring, MD 20901, USA. [35] Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), UNELLEZ-Guanare, Guanare, Portuguesa 3350, Venezuela. [36] Inventory and Monitoring Program, National Park Service, 120 Chatham Lane, Fredericksburg, VA 22405, USA. [37] Biologia Vegetal, Universidade Estadual de Campinas, Caixa Postal 6109, Campinas, SP 13.083-970, Brazil. [38] Institute of Molecular Plant Sciences, University of Edinburgh, Mayfield Rd, Edinburgh EH3 5LR, UK. [39] Royal Botanic Garden of Edinburgh, 20a Inverleith Row, Edinburgh EH3 5LR, UK. [40] Laboratorio de Ecología de Bosques Tropicales y Primatología, Universidad de los Andes, Bogotá, DF, Colombia. [41] Comparative Plant and Fungal Biology, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK. [42] Forest Ecology and Forest Management Group, University of Wageningen, Lumen, building no.100, Droevendaalsesteeg 3, Wageningen 6708 PB, Netherlands. [43] Center for Conservation Education and Sustainability, Smithsonian Conservation Biology Institute, National Zoological Park, MRC 0705, Washington, DC 20013–7012, USA. [44] Ecosistemas, Biodiversidad y Conservación de Especies, Universidad Estatal Amazónica, Km. 2 1/2 vía a Tena (Paso Lateral), Puyo, Pastaza, Ecuador. [45] Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel Rene Moreno, Avenida Irala 565 Casilla Post al 2489, Santa Cruz, Bolivia. [46] Diretoria de Pesquisas Científicas, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, RJ, Brazil. [47] Coordenação de Tecnologia e Inovação, Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM 69060–001, Brazil. [48] Centro de Biociências, Departamento de Ecologia, Universidade Federal do Rio Grande do Norte - UFRN, Campus Universitário - Lagoa Nova, Natal, RN 59072–970, Brazil. [49] UMR Ecologie des Forêts de Guyane, Institut National de la Recherche Agronomique (INRA), Campus agronomique, Kourou Cedex 97379, French Guiana. [50] International Center for Tropical Botany (ICTB), Florida International University, 11200 SW 8th Street, OE 167, Miami, FL 33199, USA. [51] Escuela de Biología Herbario Alfredo Paredes, Universidad Central, Ap. Postal 17.01.2177, Quito, Pichincha, Ecuador. [52] UMR Ecologie des Forêts de Guyane, CNRS, Kourou Cedex, French Guiana. [53] Department of Biological Sciences, Humboldt State University, 1 Harpst Street, Arcata, CA 95521, USA. [54] Grupo de Ecología de Ecosistemas Terrestres Tropicales, Universidad Nacional de Colombia Sede Amazonía, Leticia, Amazonas, Colombia. [55] Taxonomy and Systematics, Naturalis Biodiversity Center, Darwin building, Darwinweg 4, Leiden 2300 AA, The Netherlands. [56] Universidad Regional Amazónica IKIAM, Km 7 via Muyuna, Tena, Napo, Ecuador. [57] Museu Universitário, Universidade Federal do Acre, Rio Branco, AC 69915–559, Brazil. [58] Land Resource and Management Unit, Joint Research Centre of the European Commission, Via Enrico Fermi 2749, TP 440, Ispra, VA I-21027, Italy. [59] Institute of Biological and Health Sciences, Federal University of Alagoas, Av. Lourival Melo Mota, s/n, Tabuleiro do Martins, Maceio, AL 57072–970, Brazil. [60] Iwokrama International Programme for Rainforest Conservation, Georgetown, Guyana. [61] New York Botanical Garden, 2900 Southern Blvd, Bronx, New York, NY 10458–5126, USA. [62] Servicios de Biodiversidad EIRL, Iquitos, Loreto, Peru. [63] Herbario Nacional de Bolivia, Universitario UMSA, Casilla 10077 Correo Central, La Paz, Bolivia. [64] Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166–0299, USA. [65] Biology Department and Center for Energy, Environment and Sustainability, Wake Forest University, 1834 Wake Forest Rd, Winston Salem, NC 27106, USA. [66] Andes to Amazon Biodiversity Program, Madre de Dios, Madre de Dios, Peru. [67] Department of Anthropology, University of Texas at Austin, SAC 5.150, 2201 Speedway Stop C3200, Austin, TX 78712, USA. [68] Fundación Puerto Rastrojo, Cra 10 No. 24–76 Oficina 1201, Bogotá, DF, Colombia. [69] Fundación Estación de Biología, Cra 10 No. 24–76 Oficina 1201, Bogotá, DF, Colombia. [70] Laboratório de Ecologia de Doenças Transmissíveis da Amazônia (EDTA), Instituto Leônidas e Maria Deane, Fiocruz, Rua Terezina, 476, Adrianópolis, Manaus, AM 69057–070, Brazil. [71] ACEER Foundation, Jirón Cusco N° 370, Puerto Maldonado, Madre de Dios, Peru. [72] Departement EV, Muséum national d'histoire naturelle de Paris, 16 rue Buffon, Paris 75005, France. [73] Amazon Conservation Team, Doekhieweg Oost #24, Paramaribo, Suriname. [74] Environmental Change Institute, Oxford University Centre for the Environment, Dyson Perrins Building, South Parks Road, Oxford, England OX1 3QY, UK. [75] Instituto de Ciencias Naturales, UNAL, Universidad Nacional de Colombia, Apartado 7945, Bogotá, DF, Colombia. [76] Embrapa Amazonia Oriental, Trav. Dr. Enéas Pinheiro s/nº, Belém, PA, Brazil. [77] Universidade Federal Rural da Amazônia, Belém, PA, Brazil. [78] Facultad de Ciencias Forestales y Medio Ambiente, Universidad Nacional de San Antonio Abad del Cusco, San Martín 451, Puerto Maldonado, Madre de Dios, Peru. [79] Universidad Autónoma del Beni, Riberalta, Beni, Bolivia. [80] Regional Norte Amazónico, Centro de Investigación y Promoción del Campesinado, Riberalta, Beni, Bolivia. [81] Laboratory of Human Ecology, Instituto Venezolano de Investigaciones Científicas - IVIC, Ado 20632, Caracas 1020A, Venezuela. [82] Laboratório de Ciências Ambientais, Universidade Estadual do Norte Fluminense, Av. Alberto Lamego 2000, Campos dos Goyatacazes, RJ 28013–620, Brazil. [83] Instituto de Biociências - Dept. Ecologia, Universidade de Sao Paulo - USP, Rua do Matão, Trav. 14, no. 321, Cidade Universitária, São Paulo, SP 05508–090, Brazil. [84] Instituto de Investigaciones para el Desarrollo Forestal (INDEFOR), Universidad de los Andes, Conjunto Forestal, C.P. 5101, Mérida, Mérida, Venezuela. [85] GeoIS, El Día 369 y El Telégrafo, 3° Piso, Quito, Pichincha, Ecuador. [86] Department of Biology, University of Maryland, College Park, MD 20742, USA. [87] Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI 53202, USA. [88] Environmental Science and Policy, Northern Arizona University, Flagstaff, AZ 86011, USA. [89] Geography and the Environment, University of Texas at Austin, 305 E. 23rd Street, CLA building, Austin, TX 78712, USA. [90] Agricultural Services, Ministry of Agro-Industry and Food Security, The Mauritius Herbarium, Reduit, Mauritius. [91] Department of Bioscience, Aarhus University, Building 1540 Ny Munkegade, Aarhus C, Aarhus DK-8000, Denmark. [92] FOMABO, Manejo Forestal en las Tierras Tropicales de Bolivia, Sacta, Cochabamba, Bolivia. [93] Escuela de Ciencias Forestales (ESFOR), Universidad Mayor de San Simon (UMSS), Sacta, Cochabamba, Bolivia. [94] Tropenbos International, Lawickse Allee 11 PO Box 232, Wageningen 6700 AE, The Netherlands. [95] School of Anthropology and Conservation, University of Kent, Marlowe Building, Canterbury, Kent CT2 7NR, UK. [96] Centro de Investigaciones Ecológicas de Guayana, Universidad Nacional Experimental de Guayana, Calle Chile urbaniz Chilemex, Puerto Ordaz, Bolivar, Venezuela. [97] Comparative Plant and Fungal Biology, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, UK. [98] Herbario Nacional del Ecuador, Universidad Técnica del Norte, Quito, Pichincha, Ecuador. [99] Programa de Pós-Graduação em Desenvolvimento Regional e Meio Ambiente PGDRA, Universidade Federal de Rondônia, Rodovia BR 364 s/n Km 9,5 - Sentido Acre, Unir, Porto Velho, Rondônia 76.824-029, Brazil. [100] Instituto de Biodiversidade e Floresta, Universidade Federal do Oeste do Pará, Rua Vera Paz, Campus Tapajós, Santarém, PA 68015–110, Brazil. [101] Facultad de Biologia, Universidad Nacional de la Amazonia Peruana, Pevas 5ta cdra, Iquitos, Peru. [102] Department of Biology, University of Missouri, St. Louis, MO 63121, USA.

*Corresponding author. E-mail: hans.tersteege@naturalis.nl

threatened plant species in the Amazon is low (5 to 9%) (*12*) or moderate (20 to 33%) (*13*).

Here, we build on that work by using a spatially explicit model of tree species abundance (*14*) based on 1485 forest inventories (fig. S1) to quantify how historical deforestation across Amazonia (*1*, *2*, *15*) has reduced the population sizes of 4953 relatively common tree species. We use a separate model to estimate population declines for an additional 10,247 rarer tree species. For both models, we also estimate the population losses expected for 2050 under two deforestation scenarios (*1*, *2*) and ask to what extent projected losses can be prevented by Amazonia's existing protected area network. In contrast to previous studies, which presented results in the currency of statistical probability of extinction, we interpret our results using the criteria of the IUCN Red List of Threatened Species, the most commonly used yardstick for species conservation status.

RESULTS

Effects of historical forest loss on tree populations

The original lowland forests of Amazonia are estimated to have covered 5.74 million km^2 (fig. S2), 11.4% of which had been deforested by 2013 (*1*, *2*) (figs. S3 and S4A and appendix S1). Most of the estimated

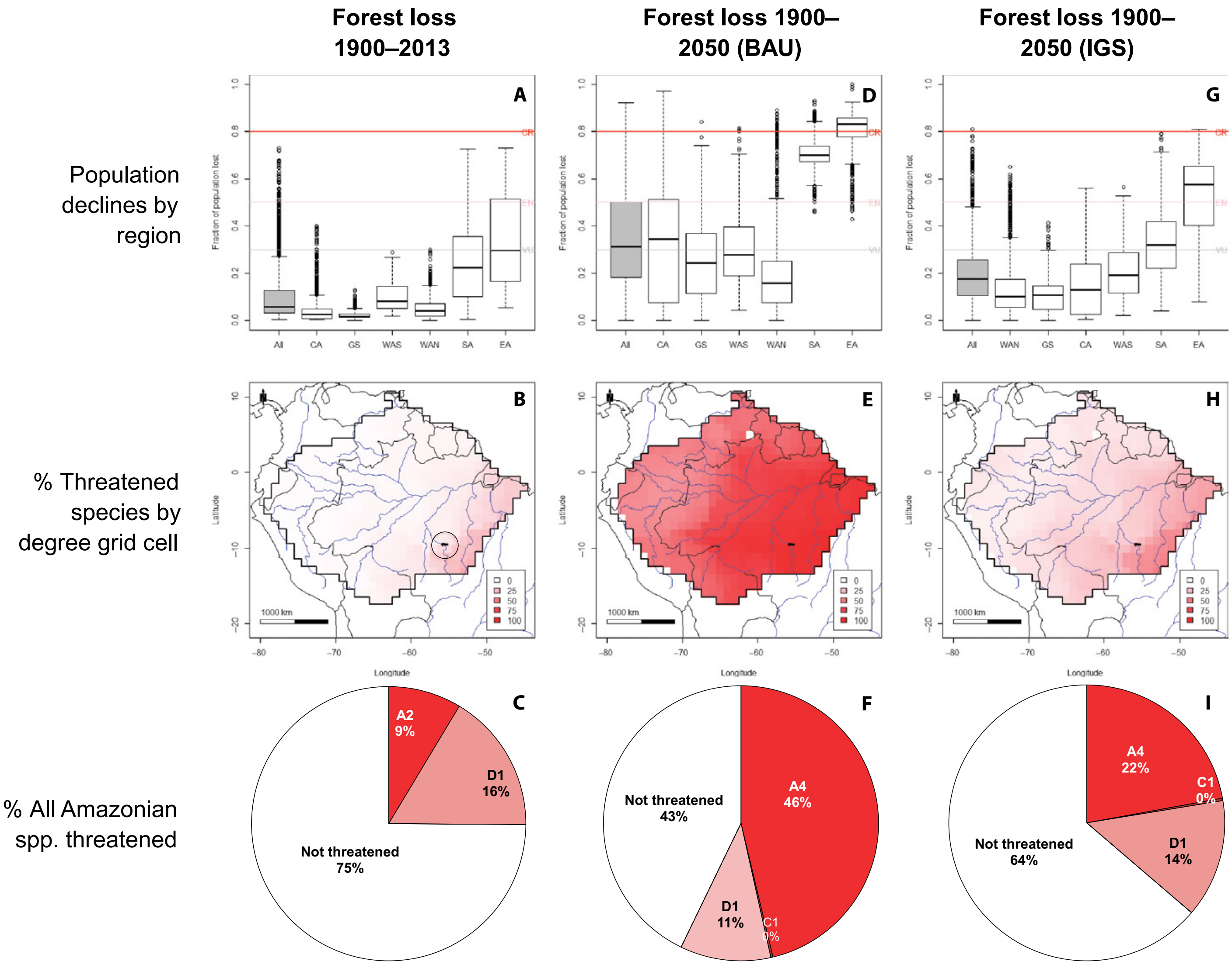


Fig. 1. Estimated population declines and threat status of Amazonian tree species under historical deforestation and two projected deforestation scenarios. Historical deforestation (**A** to **C**). Projected deforestation (**D** to **I**). Top row: Percent population loss of 4953 tree species in the entire Amazon and in six Amazonian regions. Middle row: Percent species in a DGC estimated as globally threatened based on projected (including historical) forest loss (IUCN A2 and A4; *n* = 4953). Bottom row: Proportion of all 15,200 Amazonian tree species estimated to be globally threatened based on four different IUCN threat criteria. BAU: projected (including historical) deforestation through 2050 based on a BAU scenario (*1*, *2*); IGS: projected (including historical) deforestation through 2050 based on an IGS (*1*, *2*). Cristalino State Park is the small black polygon in southeastern Amazonia, encircled in (B). CA, Central Amazonia; GS, Guiana Shield; WAS, Southwestern Amazonia; WAN, Northwestern Amazonia; SA, Southern Amazonia; EA, Eastern Amazonia; CR, critically endangered; EN, endangered; VU, vulnerable.

3.2×10^{10} individual trees lost to date (appendixes S2 and S3) were in southern and eastern Amazonia (Fig. 1A).

Overlaying these deforestation data with the output of our spatial model of the distribution and abundance of 4953 relatively common tree species allowed us to estimate the impact of forest loss on the Amazonian populations of these species. Forest loss up to 2013 (figs. S3 and S4A) caused a mean decline of 11% in the number of individuals of tree species across Amazonia (median, 6%) (Fig. 1A and fig. S4D) and mean declines of 2 to 32% in individual Amazonian regions. Of 4953 common species, 342 (7.5%) have lost a large enough proportion of their original populations (≥30%) to qualify as globally threatened under IUCN criterion A2 (Fig. 1A and appendix S2). A separate analysis performed to model the distribution and extinction risk of 10,247 rare tree species in the Amazon suggested that 9% of them (a total of 967 species) have lost enough individuals to qualify as globally threatened under the same criterion (fig. S5A and table S1). Together, these analyses suggest that 9% of all Amazonian tree species likely qualify as threatened as a result of historical forest loss through 2013 (Fig. 1C). Adding the 2579 rare species that may qualify as threatened because they have an estimated <1000 individuals (IUCN criterion D1) increases the proportion of all threatened species to 25% (Table 1).

The data in fig. S4 (A and D) suggest a one-to-one relationship between percent historical forest loss and mean percent loss of individuals to date. Consequently, population losses of the common species are highest in regions where deforestation rates are highest, the so-called “Arc of Deforestation” in southern and eastern Amazonia. The same patterns were observed for rare species.

Effects of projected forest loss on tree populations

We repeated the above analyses for two scenarios of projected forest loss (which include historical loss). The business-as-usual (BAU) scenario model (*1*) estimates that, by 2050, ~40% of the original Amazon forest will be destroyed (figs. S4B and S6 and appendix S1). The improved governance scenario (IGS) model (*1*) estimates forest loss by 2050 at 21% (figs. S4C and S7 and appendix S1). Under these two scenarios, only 31 to 42% of grid cells maintain >95% forest cover. As is the case for historical deforestation, future deforestation is projected to be most severe in southern and eastern Amazonia (34 to 66% and 42 to 76% forest cover loss, respectively).

For common species, mean population declines under the BAU scenario are estimated to be 35% (median, 32%), and absolute declines range from 0 to 83% (Fig. 1D, fig. S4E, and appendixes S2 and S3). Under the BAU scenario, 2567 (51%) of all common species likely qualify as threatened under IUCN criterion A4 (Fig. 1D). Under IGS, average losses are lower, with a mean of 20% (median, 18%) and a range of 0 to 82% (fig. S4F and appendixes S2 and S3); 774 (16%) of common species likely qualify as threatened (Fig. 1G). Again, the severest threat is found in southern and eastern Amazonia (Fig. 1G and fig. S4D).

Both scenarios also pose severe threats to rare species. Under the BAU scenario, 4466 (43%) of all rare species are predicted to lose ≥30% of their population by 2050 (fig. S5B and table S1), compared to 2590 (25%) of all rare species under IGS (fig. S5C and table S1). Under the BAU scenario, rare species are expected to be most severely hit in southern and eastern Amazonia, where the median population loss is 100% and more than 65 and 86% of the species, respectively, have population losses of more than 80% (table S1).

Combining the analyses of common and rare species suggests that 3364 to 7033 Amazonian tree species likely qualify as globally threatened as a result of a combination of historical and projected forest loss (Fig. 1, F and I). An additional 1657 to 2151 species in the data set are likely to qualify as globally threatened because they have very small population sizes (IUCN criteria C1 and D1). When all criteria are included, we find that 36 to 57% of Amazonian tree species likely qualify as globally threatened (Table 1).

To what degree will protected areas and indigenous territories prevent declines of Amazonian tree populations?

Over the last 50 years, Amazonian countries have formalized a large network of protected areas and indigenous territories (fig. S8 and appendix S1) that now cover 52.2% of the basin: 9% in strict conservation reserves (SCRs) (fig. S9A) and 44.3% in sustainable use and indigenous reserves (SUIRs) (fig. S9B). Our models suggest that all of the 4953 common species are protected to some degree by SCRs and SUIRs (for convenience, we refer to both as protected areas) (fig. S9, C and D). Every common species is estimated to have more than 5500 adult individuals within protected areas, with 23%, on average, of these individuals occurring in SCRs and 77% in SUIRs. However, Performance is poor in some Amazonian regions. For example, the

Table 1. Number of Amazonian tree species estimated to qualify as globally threatened under four IUCN threat status criteria. Numbers of threatened species are nonoverlapping (that is, species listed for C1 did not qualify for A4). BAU = projected (including historical) deforestation through 2050 based on a BAU scenario (*1*, *2*); IGS = projected (including historical) deforestation through 2050 based on an IGS (*1*, *2*).

	Forest loss 1900–2013	Forest loss 1900–2050 (BAU)	Forest loss 1900–2050 (IGS)
Total number of species	15,200	15,200	15,200
Number of species with >30% observed population decline to date (IUCN A2)	1309	—	—
Number of species with >30% projected population decline over three generations (IUCN A4)	—	7033	3364
Number of species with >10% projected population decline over three generations and <10,000 individuals (IUCN C1)	—	38	44
Number of species with <1000 individuals (IUCN D1)	2505	1619	2107
Total number of threatened species	3814	8690	5515
Percentage of all species threatened	25	57	36

scarcity of SCRs in central and eastern Amazonia means that, on average, only 2% of individuals of common species in these regions are in SCRs (fig. S9, C and D). Our simulation models also suggest that 580 of the 10,247 rare species have more than 70% of their individuals in SCRs (fig. S10A and table S2), compared to 4005 in SUIRs.

Preventing deforestation within protected areas between now and 2050 could significantly reduce the number of threatened Amazonian tree species because both 2050 deforestation scenarios assume significant deforestation within protected areas (figs. S11 to S13): one-third of projected BAU deforestation and 16% of projected IGS deforestation. If the deforestation that is projected to occur within protected areas under the BAU scenario and IGS is not factored in, the number of common species that likely qualify as threatened under IUCN criterion A4 will fall by 29 to 44%. For example, 63% of wild Brazil nut trees (*Bertholletia excelsa*) are expected to be lost by 2050 under the BAU scenario. Under a modified IGS that allows for no deforestation within protected areas, this percentage drops to 32%, and *B. excelsa* no longer qualifies as endangered (appendix S2).

DISCUSSION

Our analyses suggest that historical and ongoing forest loss may cause population declines of >30% in one-quarter to one-half of all Amazonian tree species by 2050. These declines affect species in all Amazonian regions, including iconic Amazonian trees such as Brazil nut (*B. excelsa*), wild populations of major food crops such as cacao (*Theobroma cacao*; 50% population decline with the BAU scenario) and açai palm (*Euterpe oleracea*; 72% decline with the BAU scenario), and 167 of the 227 hyperdominant taxa that account for half of all Amazonian trees (*14*). Although these declines comprise both historical population losses and population losses projected to occur in the future, they could be used to classify these species as threatened now under IUCN criterion A4b.

Thousands of other Amazonian tree species are likely to qualify as globally threatened because they have very small populations (Table 1). Although our methods and results are preliminary (see the Supplementary Materials), the statistical independence that we find between the estimated population size of a species and its fractional decline in numbers (fig. S14) suggests that the primary findings will remain stable as sampling improves.

A 22% increase in the global red list for plants

Our estimates of the threat status of all Amazonian tree species constitute the largest threat assessment ever carried out. In fact, the number of species assessed in our analyses (15,200) is nearly as large as the number of all plant species evaluated by the IUCN over its 50-year history (19,738) [Table 3b in the IUCN Red List (*16*)]. If the 194 countries that have adopted the Global Strategy for Plant Conservation are to meet target 2 ("A preliminary assessment of the conservation status of all known plant species" by 2020), it will require large scaling-up approaches such as the one described here [see also Miller *et al.* (*17*)].

Such approaches are urgently needed for South America's tropical flora. Over the last 10 years, only 1275 plant species from tropical South America were added to the IUCN Red List, despite strong evidence that the number should be at least an order of magnitude higher (*18*–*21*). In general, our results provide strong support to predictions that at least one in four plant species in the South American tropics now deserve listing as globally threatened (*20*). They also show that most of the species that likely qualify as threatened in the region remain absent from global and national red lists. For example, of the 2567 common species that qualify as threatened under our BAU analysis, only 351 (14%) had previously been assessed using IUCN criteria and only 6% are listed as threatened. Adding all of our threatened Amazonian tree species to the IUCN Red List would increase the number of globally threatened plants on Earth by 22% and the number of globally threatened tree species by 36%.

We are aware, however, that our results are too preliminary to constitute a red list for Amazonian trees. Red-listing these species will require case-by-case assessments by the IUCN/Species Survival Commission Global Tree Specialist Group and country-level teams, taking into account other data sources and threat criteria. What we show here are the size, urgency, and feasibility of this task. A recent Brazilian effort to evaluate the threat status of 4617 plant species in Brazil reported a per-species cost of ~US$50 (*19*). This suggests that individually assessing the named species that we suspect to be threatened and making their threat status visible to the conservation community would cost <US$1,000,000.

Most tropical tree species may be globally threatened

Despite strong spatial clustering in both deforestation scenarios and species distributions, our analyses reveal a simple rule of thumb that works at both regional and basinwide scales: *n*% forest loss yields an average of ~*n*% population loss (Fig. 1 and fig. S4, A and D). This implies that tree species in other forest biomes of tropical South America have lost much larger proportions of their population than in the core closed-canopy Amazonian moist forest: for example, the Atlantic forest (84 to 88% forest loss) (*22*), the Cerrado (53%) (*23*), the Caatinga (37%) (*23*), and dry forests in general (>60%) (*24*).

Given that Africa has lost ~55% of its tropical forests and Asia has lost ~35%, mostly since 1900 (*25*), our analyses suggest that most tree species in the Old World tropics have lost more than 30% of their individuals over the last 150 years and thus qualify as globally threatened under IUCN criterion A4. In turn, because >90% of all tree species on Earth are tropical (*26*), trees may deserve to join cycads (63%), amphibians (41%), and corals (33%) on the list of groups with the highest proportions of globally threatened species.

Although many tropical tree species have symbiotic relationships with animals and co-occur with thousands of species of nonarboreal plants, high rates of threat cannot be inferred for these organisms in the same way because of their much shorter life spans. Bird *et al.* (*27*) compared estimated range maps of Amazonian bird species with maps of projected deforestation across three bird generations and found that only 5.5 to 18.8% of species qualified as threatened under IUCN criterion A4. Three bird generations in their model averaged 14.8 years, compared to 150 years in our tree model.

Linking forest loss, species threat status, and protected areas management in the Amazon

Heavy forest clearing in southern and eastern Amazonia has put an especially high proportion of tree species at risk of extinction (Fig. 1A). In the worst hit areas of the Arc of Deforestation, a third of tree species have already lost >30% of their population to deforestation, and more than half likely qualify as globally threatened based on projected (and historical) forest loss (Fig. 1B).

By linking spatial trends in forest loss to trends in the population sizes of individual Amazonian plant species in this way, models such as ours should soon make it possible to translate remote sensing–based data on Amazonian deforestation into site-specific and species-specific guidance for conservation managers. It will also be possible to model how individual species will be affected by infrastructure projects (*28*) such as major hydroelectric dams (*29*), degazetting of protected areas (*30*), and other drivers of Amazonian forest loss. This could have serious implications for large-scale development projects, which are increasingly required to protect IUCN-listed taxa and their habitat [for example, *Performance Standard 6. Biodiversity Conservation and Sustainable Management of Natural Resources* (*31*)].

These models can also generate predictions about which plant species occur in which protected areas and, thus, to what extent these species are protected and where. For example, floristic surveys at Cristalino State Park, in one of Brazil's most severely deforested regions, have recorded at least 551 tree species (*32*). Appendix S4 lists another 766 species that have a high probability of occurring at Cristalino State Park according to our model and shows that as many as 1214 of the 1317 species known or expected from Cristalino State Park likely qualify as globally threatened under the BAU scenario. Similar analyses could help ensure that Amazonian protected areas with especially high numbers of globally threatened tree species receive the level of protection and funding they merit.

Many practical and scientific obstacles stand in the way of a stable, comprehensive red list for Amazonian tree species (see the Supplementary Materials). We have shown in this study that such a list will include several thousand species, many of which are now considered common, and will include a very large majority of the tree species occurring in the Amazon's worst hit regions. As Amazonian forest loss continues, new approaches such as these will be needed to help guide management away from BAU scenarios and ensure a long-term future for the world's richest tree flora. Indeed, sustaining the recent historical trend of reduced Amazonian deforestation through 2050 will keep as many tree species from becoming critically endangered as there are critically endangered plant species on the IUCN Red List today.

MATERIALS AND METHODS

Amazonian base map

To overlay spatial data on deforestation, protected areas, and tree species distribution and abundance, we first made a base map of Amazonia. The borders of the base map were the same as those in our previous study (*14*). We gridded this landscape into 0.1-degree grid cells (01DGCs) (*33*) and eliminated all 01DGCs that were more than 50% water (*33*), nonforest vegetation such as open wetlands or savannahs (*1*), or elevations of >500 m (*34*). This reduced the total area by 17%. We then quantified the area of all individual 01DGCs, which varies with latitude because of distance from the equator (~124 km^2 at the equator, ~106 km^2 at 14°S, and ~120 km^2 at 8°N). The final forest map consists of 46,986 01DGCs or 5.79 million km^2 (fig. S1).

Tree density

Our tree inventory data come from the Amazon Tree Diversity Network (ATDN) (*14*). The methods we used to estimate tree density, abundance, and distribution are similar to those used in our previous study (*14*) but are based on >20% more tree plots than in that study. The ATDN now comprises 1766 (1-ha) tree inventory plots scattered throughout Amazonia (fig. S1).

The total number of trees in Amazonia with ≥10 cm diameter at breast height was estimated as in our previous study (*14*) but with a larger subset of plots (1625) and at the 1-degree grid cell (DGC) level. We constructed a locally weighted (loess) regression model for tree density (stems/ha) on the basis of the observed tree density in 1625 plots, with latitude, longitude, and their interaction as independent variables. The span was set at 0.5 to yield a relatively smooth average. The model was used to estimate the average tree density in each DGC (D_{DGC}, stems/ha) (fig. S15). This average density per hectare was then multiplied by the total forested area of each DGC to obtain the total number of trees in the DGC. The total number of trees estimated was 3.2×10^{11}. This is 17.9% lower than the estimate in our previous study (*14*) because this number corrects for the actual lowland forest cover in each DGC.

Modeled population sizes and species distributions: Common species

Analyses of tree species composition were performed with a subset of 1560 plots in which all 775,532 free-standing trees ≥10 cm diameter at breast height had been identified with a valid name at the species (86.0%), genus (97.2%), or family (99.0%) level before our study. Most plots (1282) measured exactly 1 ha, 392 were smaller (0.25 to 0.99), 91 were larger (1.01 to 4), and 4 were plotless samples (point-centered quarter) for which the number of trees was equivalent to that typically found in 0.5 to 1 ha. Most issues of species identification and nomenclature were handled as in our previous study (*14*), but there were some exceptions. Species with a "cf." identification were accepted as belonging to the named species, whereas those with "aff." were tabulated at the genus level. All data associated with names that were clearly wrong (for example, those of small herbs) were disregarded.

Although we assume identification error to be within acceptable limits for common species [see discussion in our previous paper (*14*)], we retained only plots in which ≥60% of individuals were identified to species (1480 plots) (fig. S16). The number of trees belonging to each species in the DGC was estimated as follows. Abundances of all valid species were converted into relative abundances for each plot: $\text{RA}_i = n_i/N$, where n_i is the number of individuals of species i and N is the total number of trees in the plot (including unidentified trees) (*14*). For each of the 4953 species with a valid name in the 1485 plots, we constructed an inverse distance weighting (IDW) model for RA_i, with a power of 2, a maximum number of plots used for each local estimation of 150, and a maximum distance parameter of 4°. We did not use a LOESS model (*14*) because this had the undesirable effect of predicting very small occurrences of species far from localities where the species was actually recorded. For a similar reason, we used a cutoff of 4° with IDW modeling because, otherwise, species would have very low densities over the entire Amazon. These adjustments have a significant effect on the ranges of species [that is, ranges here are smaller than in our previous study (*14*)] but a negligible effect on their total number of individuals. The number of individuals of species i in a given DGC was then simply the total number of trees in the DGC multiplied by the fraction of the species i. Although we used a slightly different approach and a slightly larger data set compared to those in our previous study (*14*), our results are very similar to the results of that study.

Modeled population sizes and species distributions: Rare species

To estimate the total number of tree species present in Amazonia, we extrapolated the rank-abundance distribution of the 4953 named species as in our previous study (*14*). This yielded an additional 10,247 species, for a total of 15,200 estimated tree species in Amazonia. For shorthand, in this paper, we refer to the 4953 named species as "common species" and to the 10,247 other taxa as "rare species."

Because our tree plot data cannot tell us how these very rare species are distributed, we carried out a separate modeling exercise to estimate the degree to which their ranges overlap with deforestation or protected areas. In doing this, we relied on two simplifying assumptions: (i) these rare species have small circular geographic ranges whose sizes are correlated to their population sizes (*13*) and (ii) these species are not randomly distributed across the Amazon but instead are more likely to occur in DGCs with higher overall tree diversity. This stratification is consistent with the theoretical notion that there is a one-to-one relationship between Fisher's α at large sample sizes and rare species (in large samples, the number of singletons actually equals Fisher's α, the number of doubletons equals ~α/2, and the number of tripletons equals ~α/3…) (*35*). To estimate how many rare species occur in each DGC, we made an updated map of tree diversity (Fisher's α) in Amazonia (*36*) at 0.1° resolution and used this map to stratify the position of rare species. For each rare species, a DGC was chosen randomly, with a probability proportional to the DGC's Fisher's α. Range size was calculated for all 10,247 species as in the study of Hubbell *et al.* (*13*). Each circular range was overlain on deforestation and protected area maps (pixels at 0.1° resolution). The fraction of the population intersecting these maps was then calculated as the number of pixels of deforestation (or protected area) divided by the total number of pixels of forest within that circular section. This was repeated 500 times to provide the mean expectation and confidence limits.

Protected areas and deforestation

Spatial data and categories of Amazonian protected areas were gathered from the World Database of Protected Areas (*37*) and updated with individual country park service sources (for example, http://geo.sernanp.gob.pe/geoserver) and—for indigenous territories of Guyana, Peru, and Bolivia—with data from Red Amazónica de Información Socioambiental Georeferenciada (http://raisg.socioambiental.org/). We did not include indigenous territories from Suriname, Venezuela, and Ecuador because these areas are not yet officially designated. Protected areas were classified as SCRs (IUCN categories Ia to IV) or SUIRs (IUCN categories V to VII and all other types) (table S3). Where the data indicated an overlap between SCRs and SUIRs, the overlap was designated as SCR.

Historical deforestation up to 2013 was based on data from Soares-Filho *et al.* (*1*, *2*) and Hansen *et al.* (*15*). To estimate projected deforestation in 2050 (including historical deforestation), we used both BAU scenario and IGS based on the work of Soares-Filho *et al.* (*1*, *2*). Every 01DGC of the Amazonian base map was classified as protected or unprotected and as forested or deforested, depending on whether >50% of the 01DGC was occupied by a protected area or deforestation.

For common species, we estimated the number of individuals of a given species that fell within areas of deforestation or protection by first multiplying the population size in each DGC by the proportion of its 01DGCs that were classified as deforested or protected. This analysis assumes that the individuals of a species are homogeneously distributed within each DGC. We then summed the results for all DGCs to yield the total number of individuals of each species that were lost to deforestation or occurred within a protected area.

For rare species, the proportion of the number of individuals of a given rare species lost in a given DGC was quantified as the proportion of that DGC classified as deforested. Rare species in heavily deforested DGCs thus show a much higher loss than those in less disturbed DGCs, and those in intact DGCs had zero losses. The degree to which rare species' distributions overlap with protected areas was estimated in the same fashion. All analyses were carried out with R software (*38*).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/1/10/e1500936/DC1

Use of the IUCN threat criteria
Caveats regarding deforestation scenarios
Caveats regarding population models
Caveats regarding the interaction between tree species populations and forest loss
Fig. S1. Map of Amazonia showing the location of the 1485 ATDN plots that contributed data to this report.
Fig. S2. Map of lowland forests in the Amazon.
Fig. S3. Total deforestation of the Amazon by 2013.
Fig. S4. Deforestation and tree population declines in the Amazon.
Fig. S5. Deforestation and tree population declines of rare species in the Amazon.
Table S1. Deforestation and tree population declines of rare species in the Amazon.
Fig. S6. Projected (including historical) deforestation in the Amazon by 2050 in the BAU scenario.
Fig. S7. Projected (including historical) deforestation in the Amazon by 2050 in the IGS.
Fig. S8. Protected areas and indigenous territories in the Amazon.
Fig. S9. How much of the Amazon is protected and how many individual trees do protected areas protect?
Fig. S10. Rare species in protected areas and indigenous territories.
Table S2. Rare species in protected areas and indigenous territories.
Fig. S11. Protected areas and indigenous territories in the Amazon with deforestation according to BAU scenario 2050.
Fig. S12. Protected areas and indigenous territories in the Amazon with deforestation according to IGS 2050.
Fig. S13. How much forest loss has taken place and will take place in Amazonian protected areas?
Fig. S14. Decline in relative population size shows no relationship with original population size in (A) BAU scenario and (B) IGS.
Fig. S15. Interpolated stem density for the Amazon.
Fig. S16. Interpolated identification level of plots in the Amazon.
Fig. S17. Projected and observed deforestation in Amazonia from 2002 to 2013.
Table S3. IUCN categories, designations, and conversion into SCRs (1) and SUIRs (2).
Appendix S1. Data by DGC.
Appendix S2. Data by species.
Appendix S3. Data of individuals by region.
Appendix S4. Tree species estimated to occur in Cristalino State Park in Brazil but not yet recorded there (*32*) and their estimated threat status according to historical and projected deforestation.
Appendix S5. Plot metadata.
References (*39*–*83*)

REFERENCES AND NOTES

1. B. S. Soares-Filho, D. C. Nepstad, L. M. Curran, E. Voll, G. C. Cerqueira, R. A. Garcia, C. A. Ramos, A. McDonald, P. Lefebvre, P. Schlesinger, Eds., *LBA-ECO LC-14 Modeled Deforestation Scenarios, Amazon Basin: 2002-2050* (Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN, 2013); http://daac.ornl.gov//LBA/guides/LC14_Amazon_Scenarios.html
2. B. S. Soares-Filho, D. C. Nepstad, L. M. Curran, G. C. Cerqueira, R. A. Garcia, C. A. Ramos, E. Voll, A. McDonald, P. Lefebvre, P. Schlesinger, Modelling conservation in the Amazon basin. *Nature* **440**, 520–523 (2006).
3. P. M. Fearnside, Deforestation in Brazilian Amazonia: History, rates, and consequences. *Conserv. Biol.* **19**, 680–688 (2005).
4. N. J. H. Smith, P. Alvim, A. Homma, I. Falesi, A. Serrão, Environmental impacts of resource exploitation in Amazonia. *Glob. Environ. Change* **1**, 313–320 (1991).

5. E. A. Davidson, A. C. de Araújo, P. Artaxo, J. K. Balch, I. F. Brown, M. M. C. Bustamante, M. T. Coe, R. S. DeFries, M. Keller, M. Longo, J. W. Munger, W. Schroeder, B. S. Soares-Filho, C. M. Souza, S. C. Wofsy, The Amazon basin in transition. *Nature* **481**, 321–328 (2012).
6. L. E. O. C. Aragão, Y. Malhi, R. M. Roman-Cuesta, S. Saatchi, L. O. Anderson, Y. E. Shimabukuro, Spatial patterns and fire response of recent Amazonian droughts. *Geophys. Res. Lett.* **34**, L07701 (2007).
7. Y. Malhi, J. T. Roberts, R. A. Betts, T. J. Killeen, W. Li, C. A. Nobre, Climate change, deforestation, and the fate of the Amazon. *Science* **319**, 169–172 (2008).
8. D. Nepstad, D. McGrath, C. Stickler, A. Alencar, A. Azevedo, B. Swette, T. Bezerra, M. DiGiano, J. Shimada, R. Seroa da Motta, E. Armijo, L. Castello, P. Brando, M. C. Hansen, M. McGrath-Horn, O. Carvalho, L. Hess, Slowing Amazon deforestation through public policy and interventions in beef and soy supply chains. *Science* **344**, 1118–1123 (2014).
9. C. D'Almeida, C. J. Vörösmarty, G. C. Hurtt, J. A. Marengo, S. L. Dingman, B. D. Keim, The effects of deforestation on the hydrological cycle in Amazonia: A review on scale and resolution. *Int. J. Climatol.* **27**, 633–647 (2007).
10. L. E. O. C. Aragão, Environmental science: The rainforest's water pump. *Nature* **489**, 217–218 (2012).
11. D. V. Spracklen, S. R. Arnold, C. M. Taylor, Observations of increased tropical rainfall preceded by air passage over forests. *Nature* **489**, 282–285 (2012).
12. K. J. Feeley, M. R. Silman, Extinction risks of Amazonian plant species. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 12382–12387 (2009).
13. S. P. Hubbell, F. He, R. Condit, L. Borda-de-Água, J. Kellner, H. ter Steege, How many tree species are there in the Amazon and how many of them will go extinct? *Proc. Natl. Acad. Sci. U.S.A.* **105**, 11498–11504 (2008).
14. H. ter Steege, N. C. A. Pitman, D. Sabatier, C. Baraloto, R. P. Salomão, J. E. Guevara, O. L. Phillips, C. V. Castilho, W. E. Magnusson, J.-F. Molino, A. Monteagudo, P. N. Vargas, J. C. Montero, T. R. Feldpausch, E. N. Honorio Coronado, T. J. Killeen, B. Mostacedo, R. Vasquez, R. L. Assis, J. Terborgh, F. Wittmann, A. Andrade, W. F. Laurance, S. G. W. Laurance, B. S. Marimon, B.-H. Marimon Jr., I. C. G. Vieira, I. L. Amaral, R. Brienen, H. Castellanos, D. C. López, J. F. Duivenvoorden, H. F. Mogollón, F. D. de Almeida Matos, N. Dávila, R. García-Villacorta, P. R. S. Diaz, F. Costa, T. Emilio, C. Levis, J. Schietti, P. Souza, A. Alonso, F. Dallmeier, A. J. D. Montoya, M. T. F. Piedade, A. Araujo-Murakami, L. Arroyo, R. Gribel, P. V. A. Fine, C. A. Peres, M. Toledo, G. A. Aymard C., T. R. Baker, C. Cerón, J. Engel, T. W. Henkel, P. Maas, P. Petronelli, J. Stropp, C. E. Zartman, D. Daly, D. Neill, M. Silveira, M. R. Paredes, J. Chave, D. de Andrade Lima Filho, P. M. Jørgensen, A. Fuentes, J. Schöngart, F. C. Valverde, A. Di Fiore, E. M. Jimenez, M. C. P. Mora, J. F. Phillips, G. Rivas, T. R. van Andel, P. von Hildebrand, B. Hoffman, E. L. Zent, Y. Malhi, A. Prieto, A. Rudas, A. R. Ruschell, N. Silva, V. Vos, S. Zent, A. A. Oliveira, A. C. Schutz, T. Gonzales, M. T. Nascimento, H. Ramirez-Angulo, R. Sierra, M. Tirado, M. N. U. Medina, G. van der Heijden, C. I. A. Vela, E. V. Torre, C. Vriesendorp, O. Wang, K. R. Young, C. Baider, H. Balslev, C. Ferreira, I. Mesones, A. Torres-Lezama, L. E. U. Giraldo, R. Zagt, M. N. Alexiades, L. Hernandez, I. Huamantupa-Chuquimaco, W. Milliken, W. P. Cuenca, D. Pauletto, E. V. Sandoval, L. V. Gamarra, K. G. Dexter, K. Feeley, G. Lopez-Gonzalez, M. R. Silman, Hyperdominance in the Amazonian tree flora. *Science* **342**, 1243092 (2013).
15. M. Hansen, P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, J. R. G. Townshend, High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013).
16. IUCN, IUCN Red List (2014); http://cmsdocs.s3.amazonaws.com/summarystats/2014_3_Summary_Stats_Page_Documents/2014_3_RL_Stats_Table_3b.pdf
17. J. S. Miller, G. A. Krupnick, H. Stevens, H. Porter-Morgan, B. Boom, P. Acevedo-Rodríguez, J. Ackerman, D. Kolterman, E. Santiago, C. Torres, J. Velez, Toward target 2 of the Global Strategy for Plant Conservation: An expert analysis of the Puerto Rican flora to validate new streamlined methods for assessing conservation status. *Ann. Mo. Bot. Gard.* **99**, 199–205 (2013).
18. B. León, J. Roque, C. Ulloa Ulloa, N. Pitman, P. M. Jørgensen, A. Cano, Libro rojo de las plantas endémicas del Perú. *Rev. Peruana Biol.* **13**, 1–976 (2006).
19. G. Martinelli, M. Avila Moraes, in *Livro vermelho da flora do Brasil* (Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil, 2013).
20. N. C. A. Pitman, P. M. Jørgensen, Estimating the size of the world's threatened flora. *Science* **298**, 989 (2002).
21. N. C. A. Pitman, P. M. Jørgensen, R. S. R. Williams, S. León-Yánez, R. Valencia, Extinction-rate estimates for a modern neotropical flora. *Conserv. Biol.* **16**, 1427–1431 (2002).
22. M. C. Ribeiro, J. P. Metzger, A. C. Martensen, F. J. Ponzoni, M. M. Hirota, The Brazilian Atlantic forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biol. Conserv.* **142**, 1141–1153 (2009).
23. R. Beuchle, R. C. Grecchia, Y. E. Shimabukuro, R. Seligerc, H. D. Eva, E. Sano, F. Achard, Land cover changes in the Brazilian Cerrado and Caatinga biomes from 1990 to 2010 based on a systematic remote sensing sampling approach. *Appl. Geogr.* **58**, 116–127 (2015).
24. C. A. Portillo-Quintero, G. A. Sánchez-Azofeifa, Extent and conservation of tropical dry forests in the Americas. *Biol. Conserv.* **143**, 144–155 (2010).
25. N. S. Sodhi, M. R. C. Posa, T. M. Lee, D. Bickford, L. P. Koh, B. W. Brook, The state and conservation of Southeast Asian biodiversity. *Biodivers. Conserv.* **19**, 317–328 (2010).
26. P. V. A. Fine, An evaluation of the geographic area hypothesis using the latitudinal gradient in North American tree diversity. *Evol. Ecol. Res.* **3**, 413–428 (2001).
27. J. P. Bird, G. M. Buchanan, A. C. Lees, R. P. Clay, P. F. Develey, I. Yépez, S. H. M. Butchart, Integrating spatially explicit habitat projections into extinction risk assessments: A reassessment of Amazonian avifauna incorporating projected deforestation. *Divers. Distrib.* **18**, 273–281 (2012).
28. P. Fearnside, W. F. Laurance, M. A. Cochrane, S. Bergen, P. Sampaio, C. Barber, S. D'Angelo, T. Fernandes, The future of Amazonia: Models to predict the consequences of future infrastructure in Brazil's multi-annual plans. *Novos Cad.* **15**, 25–52 (2012).
29. M. Benchimol, C. A. Peres, Edge-mediated compositional and functional decay of tree assemblages in Amazonian forest islands after 26 years of isolation. *J. Ecol.* **103**, 408–420 (2015).
30. E. Bernard, L. A. O. Penna, E. Araújo, Downgrading, downsizing, degazettement, and reclassification of protected areas in Brazil. *Conserv. Biol.* **28**, 939–950 (2014).
31. International Finance Corporation, *Performance Standard 6. Biodiversity Conservation and Sustainable Management of Natural Resources* (International Finance Corporation, Washington, DC, 2012).
32. D. C. Zappi, D. Sasaki, W. Milliken, J. Iva, G. S. Henicka, N. Biggs, S. Frisby, Plantas vasculares da região do Parque Estadual Cristalino, norte de Mato Grosso, Brasil. *Acta Amazonica* **41**, 29–38 (2011).
33. Environmental Systems Research Institute, *ESRI Data & Maps 1999. An ESRI White Paper* (Environmental Systems Research Institute, Redlands, CA, 1999).
34. Jet Propulsion Laboratory, (NASA, 2009), vol. 2008; www2.jpl.nasa.gov/srtm/
35. R. A. Fisher, A. S. Corbet, C. B. Williams, The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* **12**, 42–58 (1943).
36. H. ter Steege, N. Pitman, D. Sabatier, H. Castellanos, P. Van Der Hout, D. C. Daly, M. Silveira, O. Phillips, R. Vasquez, T. Van Andel, J. Duivenvoorden, A. A. De Oliveira, R. Ek, R. Lilwah, R. Thomas, J. Van Essen, C. Baider, P. Maas, S. Mori, J. Terborgh, P. N. Vargas, H. Mogollón, W. Morawetz, A spatial model of tree α-diversity and tree density for the Amazon. *Biodivers. Conserv.* **12**, 2255–2277 (2003).
37. protectedplanet.net, World Database of Protected Areas (UNEP, WCMC, IUCN, WCPA, 2010), vol. 2014; www.protectedplanet.net
38. R Development Core Team (R Foundation for Statistical Computing, Vienna, Austria, 2011).
39. IUCN, *IUCN Red List Categories and Criteria. Version 3.1* (IUCN, Gland, Switzerland, ed. 2, 2012).
40. T. R. Baker, R. T. Pennington, S. Magallon, E. Gloor, W. F. Laurence, M. Alexiades, E. Alvarez, A. Araujo, E. J. M. M. Arets, G. Aymard, A. A. de Oliveira, I. Amaral, L. Arroyo, D. Bonal, R. J. W. Brienen, J. Chave, K. G. Dexter, A. Di Fiore, E. Eler, T. R. Feldpausch, L. Ferreira, G. Lopez-Gonzales, G. van der Heijden, N. Higuchi, E. Honorio, I. Huamantupa, T. J. Killeen, S. Laurance, C. Leaño, S. L. Lewis, Y. Malhi, B. S. Marimon, B. Hur Marimon Jr., A. M. Mendoza, D. Neill, M. C. Peñuela-Mora, N. Pitman, A. Preito, C. A. Quesada, F. Ramírez, H. Ramírez Angulo, A. Rudas, A. R. Ruschel, R. P. Salomão, A. S. de Andrade, J. N. M. Silva, M. Silveira, M. F. Simon, W. Spironello, H. ter Steege, J. Terborgh, M. Toledo, A. Torres-Lezama, R. Vasquez, I. C. Guimaraes Vieira, E. Vilanova, V. A. Vos, O. L. Phillips, Fast demographic traits promote high diversification rates of Amazonian trees. *Ecol. Lett.* **17**, 527–536 (2014).
41. J. W. F. Slik, V. Arroyo-Rodríguez, S.-I. Aiba, P. Alvarez-Loayza, L. F. Alves, P. Ashton, P. Balvanera, M. L. Bastian, P. J. Bellingham, E. van den Berg, L. Bernacci, P. da Conceição Bispo, L. Blanc, K. Böhning-Gaese, P. Boeckx, F. Bongers, B. Boyle, M. Bradford, F. Q. Brearley, M. Breuer-Ndoundou Hockemba, S. Bunyavejchewin, D. C. L. Matos, M. Castillo-Santiago, E. L. M. Catharino, S.-L. Chai, Y. Chen, R. K. Colwell, R. L. Chazdon, C. Clark, D. B. Clark, D. A. Clark, H. Culmsee, K. Damas, H. S. Dattaraja, G. Dauby, P. Davidar, S. J. DeWalt, J.-L. Doucet, A. Duque, G. Durigan, K. A. O. Eichhorn, P. V. Eisenlohr, E. Eler, C. Ewango, N. Farwig, K. J. Feeley, L. Ferreira, R. Field, A. T. de Oliveira Filho, C. Fletche, O. Forshed, G. Franco, G. Fredriksson, T. Gillespie, J.-F. Gillet, G. Amarnath, D. M. Griffith, J. Grogan, N. Gunatilleke, D. Harris, R. Harrison, A. Hector, J. Homeier, N. Imai, A. Itoh, P. A. Janse, C. A. Joly, B. H. J. de Jong, K. Kartawinata, E. Kearsley, D. L. Kelly, D. Kenfack, M. Kessler, K. Kitayama, R. Kooyman, E. Larney, Y. Laumonier, S. Laurance, W. F. Laurance, M. J. Lawes, I. L. do Amaral, S. G. Letche, J. Lindsell, X. Lu, A. Mansor, A. Marjokorpi, E. H. Martin, H. Meilb, F. P. L. Melo, D. J. Metcalfe, V. P. Medjibe, J. P. Metzger, J. Millet, D. Mohandass, J. C. Montero, M. de Morisson Valeriano, B. Mugerwa, H. Nagamasu, R. Nilus, S. Ochoa-Gaonau, O. Onrizal, N. Page, P. Parolin, M. Parre, N. Parthasarathy, E. Paudel, A. Permana, M. T. F. Piedade, N. C. A. Pitman, L. Poorter, A. D. Poulsen, J. Poulsen, J. Powers, R. C. Prasad, J.-P. Puyravaud, J.-C. Razafimahaimodiso, J. Reitsma, J. R. dos Santos, W. R. Spironello, H. Romero-Saltos, F. Rovero, A. H. Rozak, K. Ruokolainen, E. Rutishauser, F. Saiter, P. Saner, B. A. Santos, F. Santos, S. K. Sarker, M. Satdichanh, C. B. Schmitt, J. Schöngart, M. Schulze, M. S. Suganuma, D. Sheil, E. da Silva Pinheiro, P. Sist, T. Stevart, R. Sukumar, I.-F. Sun, T. Sunderland, H. S. Suresh, E. Suzukic, M. Tabarelli, J. Tang, N. Targhetta, I. Theilade, D. W. Thomas, P. Tchouto, J. Hurtado, R. Valencia, J. L. C. H. van Valkenburg, T. Van Do, R. Vasquez, H. Verbeeck, V. Adekunle, S. A. Vieira, C. O. Webb, T. Whitfeld, S. A. Wich, J. Williams, F. Wittmann, H. Wöll, X. Yang,

C. Y. A. Yao, S. L. Yap, T. Yonedac, R. A. Zahawi, R. Zakaria, R. Zang, R. L. de Assis, B. G. Luize, E. M. Venticinque, An estimate of the number of tropical tree species. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 7472–7477 (2015).

42. A. Regalado, Brazil says rate of deforestation in Amazon continues to plunge. *Science* **329**, 1270–1271 (2010).
43. D. Nepstad, B. S. Soares-Filho, F. Merry, A. Lima, P. Moutinho, J. Carter, M. Bowman, A. Cattaneo, H. Rodrigues, S. Schwartzman, D. G. McGrath, C. M. Stickler, R. Lubowski, P. Piris-Cabezas, S. Rivero, A. Alencar, O. Almeida, O. Stella, The end of deforestation in the Brazilian Amazon. *Science* **326**, 1350–1351 (2009).
44. M. Finer, M. Orta-Martínez, A second hydrocarbon boom threatens the Peruvian Amazon: Trends, projections, and policy implications. *Environ. Res. Lett.* **5**, 014012 (2010).
45. V. H. Gutiérrez-Vélez, R. DeFries, M. Pinedo-Vásquez, M. Uriarte, C. Padoch, W. Baethgen, K. Fernandes, Y. Lim, High-yield oil palm expansion spares land at the expense of forests in the Peruvian Amazon. *Environ. Res. Lett.* **6**, 044029 (2011).
46. A. Petherick, Pipe dream. *Nat. Climate Change* **3**, 859–860 (2013).
47. L. M. Dávalos, A. C. Bejarano, M. A. Hall, H. L. Correa, A. Corthals, O. J. Espejo, Forests and drugs: Coca-driven deforestation in tropical biodiversity hotspots. *Environ. Sci. Technol.* **45**, 1219–1227 (2011).
48. R. Müller, D. Müller, F. Schierhorn, G. Gerold, P. Pacheco, Proximate causes of deforestation in the Bolivian lowlands: An analysis of spatial dynamics. *Reg. Environ. Change* **12**, 445–459 (2012).
49. G. P. Asner, W. Llactayo, R. Tupayachi, E. R. Luna, Elevated rates of gold mining in the Amazon revealed through high-resolution monitoring. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 18454–18459 (2013).
50. M. Finer, C. N. Jenkins, S. L. Pimm, B. Keane, C. Ross, Oil and gas projects in the Western Amazon: Threats to wilderness, biodiversity, and indigenous peoples. *PLOS One* **3**, e2932 (2008).
51. G. P. Asner, M. Keller, M. Lentini, F. Merry, C. Souza Jr., in *Amazonia and Global Change*, M. Keller, M. Bustamante, J. Gash, P. S. Dias, Eds. (John Wiley and Sons, Washington, DC, 2009), pp. 25–42.
52. L. Castello, D. G. McGrath, L. L. Hess, M. T. Coe, P. A. Lefebvre, P. Petry, M. N. Macedo, V. F. Renó, C. C. Arantes, The vulnerability of Amazon freshwater ecosystems. *Conserv. Lett.* **6**, 217–229 (2013).
53. M. Finer, C. N. Jenkins, Proliferation of hydroelectric dams in the Andean Amazon and implications for Andes-Amazon connectivity. *PLOS One* **7**, e35126 (2013).
54. L. E. O. C. Aragão, Y. E. Shimabukuro, The incidence of fire in Amazonian forests with implications for REDD. *Science* **328**, 1275–1278 (2010).
55. S. L. Lewis, P. M. Brando, O. L. Phillips, G. M. F. van der Heijden, D. Nepstad, The 2010 Amazon drought. *Science* **331**, 554 (2011).
56. O. L. Phillips, L. E. O. C. Aragão, S. L. Lewis, J. B. Fisher, J. Lloyd, G. López-González, Y. Malhi, A. Monteagudo, J. Peacock, C. A. Quesada, G. van der Heijden, S. Almeida, I. Amaral, L. Arroyo, G. Aymard, T. R. Baker, O. Bánki, L. Blanc, D. Bonal, P. Brando, J. Chave, Á. C. A. de Oliveira, N. D. Cardozo, C. I. Czimczik, T. R. Feldpausch, M. A. Freitas, E. Gloor, N. Higuchi, E. Jiménez, G. Lloyd, P. Meir, C. Mendoza, A. Morel, D. A. Neill, D. Nepstad, S. Patiño, M. C. Peñuela, A. Prieto, F. Ramírez, M. Schwarz, J. Silva, M. Silveira, A. S. Thomas, H. ter Steege, J. Stropp, R. Vásquez, P. Zelazowski, E. A. Dávila, S. Andelman, A. Andrade, K.-J. Chao, T. Erwin, A. Di Fiore, E. Honorio C., H. Keeling, T. J. Killeen, W. F. Laurance, A. P. Cruz, N. C. A. Pitman, P. N. Vargas, H. Ramírez-Angulo, A. Rudas, R. Salamão, N. Silva, J. Terborgh, A. Torres-Lezama, Drought sensitivity of the Amazon rainforest. *Science* **323**, 1344–1347 (2009).
57. P. M. Brando, J. K. Balch, D. C. Nepstad, D. C. Morton, F. E. Putz, M. T. Coe, D. Silvério, M. N. Macedo, E. A. Davidson, C. C. Nóbrega, A. Alencar, B. S. Soares-Filho, Abrupt increases in Amazonian tree mortality due to drought–fire interactions. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 6347–6352 (2014).
58. J. Brodie, E. Post, W. F. Laurance, Climate change and tropical biodiversity: A new focus. *Trends Ecol. Evol.* **27**, 145–150 (2012).
59. A. Lima, T. S. F. Silva, L. E. Oliveira e Cruz de Aragão, R. M. de Feitas, M. Adami, A. R. Formaggio, Y. E. Shimabukuro, Land use and land cover changes determine the spatial relationship between fire and deforestation in the Brazilian Amazon. *Appl. Geogr.* **34**, 239–246 (2012).
60. F. Tierra, *Ampliación responsable de la frontera agrícola. Propuestas para Politicas Públicas, No. 1* (Tierra, La Paz, Bolivia, 2014); http://ftierra.org/index.php?option=com_mtree&task=att_download&link_id=53&cf_id=43
61. Cambio (Cambio, Periodico de estado plurinacional de Bolivia, 2014); www.cambio.bo/?q=bolivia-proyecta-ampliar-su-frontera-agr%C3%ADcola-10-millones-de-hect%C3%A1reas
62. J. L. Dammert B. (Iniciativa para la Conservación en la Amazonía Andina (ICAA), United States Agency for International Development (USAID)/ International Resources Group (IRG), Sociedad Peruana de Derecho Ambiental (SPDA), Corporación de Gestión y Derecho Ambiental (ECOLEX), Social Impact (SI), Patrimonio Natural (PN) y Conservation Strategy Fund (CSF), 2013), vol. 2015; www.amazonia-andina.org/amazonia-activa/biblioteca/publicaciones/cambio-uso-suelos-agricultura-gran-escala-amazonia-andina.
63. IdHeMAd Amazônia (Instituto do Homem e Meio Ambiente da Amazônia, Brazil, 2013), vol. 2014; http://imazon.org.br/
64. B. Soares-Filho, R. Rajão, M. Macedo, A. Carneiro, W. Costa, M. Coe, H. Rodrigues, A. Alencar, Cracking Brazil's forest code. *Science* **344**, 363–364 (2014).
65. B. Soares-Filho, P. Moutinho, D. Nepstad, A. Anderson, H. Rodrigues, R. Garcia, L. Dietzsch, F. Merry, M. Bowman, L. Hissa, R. Silvestrini, C. Maretti, Role of Brazilian Amazon protected areas in climate change mitigation. *Proc. Natl. Acad. Sci. U.S.A.* **107**, 10821–10826 (2010).
66. J. M. Adeney, N. L. Christensen Jr., S. L. Pimm, Reserves protect against deforestation fires in the Amazon. *PLOS One* **4**, e5014 (2009).
67. A. Nelson, K. M. Chomitz, Effectiveness of strict vs. multiple use protected areas in reducing tropical forest fires: A global analysis using matching methods. *PLOS One* **6**, e22722 (2011).
68. C. A. Peres, J. W. Terborgh, Amazonian nature reserves: An analysis of the defensibility status of existing conservation units and design criteria for the future. *Conserv. Biol.* **9**, 34–46 (1995).
69. J. Ferreira, L. E. O. C. Aragão, J. Barlow, P. Barreto, E. Berenguer, M. Bustamante, T. A. Gardner, A. C. Lees, A. Lima, J. Louzada, R. Pardini, L. Parry, C. A. Peres, P. S. Pompeu, M. Tabarelli, J. Zuanon, Brazil's environmental leadership at risk. *Science* **346**, 706–707 (2014).
70. J. Hardner, paper presented at the Conference on Economics and Conservation in the Tropics: A Strategic Dialogue, vol. 31, San Francisco, CA, 2008.
71. D. P. Kanak, I. Henderson, *Closing the REDD+ Gap: The Global Forest Finance Facility* (Global Canopy Programme, Oxford, UK, 2012).
72. C. A. Peres, Conservation in sustainable-use tropical forest reserves. *Conserv. Biol.* **25**, 1124–1129 (2011).
73. D. C. Morton, Y. Le Page, R. DeFries, G. J. Collatz, G. C. Hurtt, Understorey fire frequency and the fate of burned forests in southern Amazonia. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**, 20120163 (2013).
74. P. Moser, W. L. Oliveira, M. B. Medeiros, J. R. Pinto, P. V. Eisenlohr, I. L. Lima, G. P. Silva, M. F. Simon, Tree species distribution along environmental gradients in an area affected by a hydroelectric dam in Southern Amazonia. *Biotropica* **46**, 367–376 (2014).
75. ANEEL (SIGEL, Agência Nacional de Elergia Elétrica, 2013), vol. 2014; www.aneel.gov.br/
76. Y. Malhi, L. E. O. C. Aragão, D. Galbraith, C. Huntingford, R. Fisher, P. Zelazowski, S. Sitch, C. McSweeney, P. Meir, Exploring the likelihood and mechanism of a climate-change–induced dieback of the Amazon rainforest. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 20610–20615 (2009).
77. E. Pos, J. E. G. Andino, D. Sabatier, J.-F. Molino, N. Pitman, H. Mogollón, D. Neill, C. Cerón, G. Rivas, A. Di Fiore, R. Thomas, M. Tirado, K. R. Young, O. Wang, R. Sierra, R. García-Villacorta, R. Zagt, W. Palacios, M. Aulestia, H. ter Steege, Are all species necessary to reveal ecologically important patterns? *Ecol. Evol.* **4**, 4626–4636 (2014).
78. H. ter Steege, *Amazon Tree Diversity Network* (Universiteit Utrecht, Utrecht, Netherlands, 2011), vol. 2014; http://web.science.uu.nl/Amazon/ATDN/
79. G. P. Asner, D. E. Knapp, E. N. Broadbent, P. J. C. Oliveira, M. Keller, J. N. Silva, Selective logging in the Brazilian Amazon. *Science* **310**, 480–482 (2005).
80. H. ter Steege, I. Welch, R. J. Zagt, Long-term effect of timber harvesting in the Bartica Triangle, Central Guyana. *For. Ecol. Manage.* **170**, 127–144 (2002).
81. J. Grogan, A. G. Blundell, R. M. Landis, A. Youatt, R. E. Gullison, M. Martinez, R. Kómetter, M. Lentini, R. E. Rice, Over-harvesting driven by consumer demand leads to population decline: Big-leaf mahogany in South America. *Conserv. Lett.* **3**, 12–20 (2010).
82. J. Mark, A. C. Newton, S. Oldfield, M. Rivers, *The International Timber Trade: A Working List of Commercial Timber Tree Species* (Botanic Gardens Conservation International, Richmond, UK, 2014).
83. W. F. Laurance, H. E. M. Nascimento, S. G. Laurance, A. C. Andrade, P. M. Fearnside, J. E. L. Ribeiro, R. L. Capretz, Rain forest fragmentation and the proliferation of successional trees. *Ecology* **87** 469–482 (2006).

Acknowledgments: This report is the result of the work of hundreds of different scientists and research institutions in the Amazon over the last 80 years. Without their hard work, this analysis would have been impossible. **Funding:** This work was supported by Alberta Mennega Stichting; ALCOA Suriname; Amazon Conservation Association; Banco de la República; CELOS Suriname; CAPES (PNPG); Conselho Nacional de Desenvovimento Científico e Tecnológico of Brazil (CNPq) Projects CENBAM, PELD (558069/2009-6), PRONEX-FAPEAM (1600/2006), Áreas Úmidas, MAUA; PELD (403792/2012-6), PPBio, PVE 004/2012, Universal (479599/2008-4), and Universal 307807-2009-6; FAPEAM projects DCR/2006, Hidroveg with FAPESP, and PRONEX with CNPq; FAPESP; Colciencias; CONICIT; Duke University; Ecopetrol; FEPIM 044/2003; The Field Museum; Conservation International/DC (TEAM/Instituto Nacional de Pesquisas da Amazônia Manaus), Gordon and Betty Moore Foundation; Guyana Forestry Commission; Investissement d'Avenir grant of the French ANR (CEBA: ANR-10-LABX-0025); IVIC; Margaret Mee Amazon Trust; Miquel fonds; MCTI–Museu Paraense Emílio Goeldi–Proc. 407232/2013-3–PVE-MEC/MCTI/CAPES/CNPq; National Geographic Society (7754-04 and 8047-06 to P.M.J.; 6679-99, 7435-03, and 8481-08 to T.W.H.); NSF-0726797 to K.R.Y.; NSF Dissertation Improvement; Netherlands Foundation for the Advancement of Tropical Research WOTRO (grants WB85-335 and W84-581); Primate Conservation Inc.; Programme Ecosystèmes Tropicaux (French Ministry of Ecology and Sustainable Development); Shell Prospecting and

Development Peru; Smithsonian Institution's Biological Diversity of the Guiana Shield Program; Stichting het van Eeden-fonds; The Body Shop; The Ministry of the Environment of Ecuador; TROBIT; Tropenbos International; U.S. National Science Foundation (NSF-0743457 and NSF-0101775 to P.M.J.; NSF-0918591 to T.W.H.); USAID; Variety Woods Guyana; Wenner-Gren Foundation; WWF-Brazil; WWF-Guianas; XIIéme Contrat de Plan Etat Région-Guyane (French Government and European Union) and grants to RAINFOR from the European Union, UK Natural Environment Research Council, and the Gordon and Betty Moore Foundation. We thank D. Zappi for providing the Cristalino State Park checklist. O.L.P. was supported by a European Research Council Advanced Grant and a Royal Society Wolfson Research Merit Award. **Author contributions:** H.t.S. and N.C.A.P. conceived the study and designed the analyses. H.t.S. carried out most analyses. H.t.S., N.C.A.P., T.J.K., W.F.L., C.A.P., and J.E.G. wrote the manuscript. All of the other authors contributed data, discussed further analyses, and commented on various versions of the manuscript. This is contribution 679 of the technical series of the BDFFP (INPA/STRI). **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials in appendix S1 and S5. Additional data related to this paper may be requested from the authors.

Submitted 15 July 2015
Accepted 7 October 2015
Published 20 November 2015
10.1126/sciadv.1500936

Citation: H. ter Steege, N. C. A. Pitman, T. J. Killeen, W. F. Laurance, C. A. Peres, J. E. Guevara, R.P. Salomão, C. V. Castilho, I. L. Amaral, F. D. de Almeida Matos, L. de Souza Coelho, W. E. Magnusson, O. L. Phillips, D. de Andrade Lima Filho, M. de Jesus Veiga Carim, M. V. Irume, M. P. Martins, J.-F. Molino, D. Sabatier, F. Wittmann, D. C. López, J. R. da Silva Guimarães, A. M. Mendoza, P. N. Vargas, A. G. Manzatto, N. F. C. Reis, J. Terborgh, K. R. Casula, J. C. Montero, T. R. Feldpausch, E. N. Honorio Coronado, A. J. D. Montoya, C. E. Zartman, B. Mostacedo, R. Vasquez, R. L. Assis, M. B. Medeiros, M. F. Simon, A. Andrade, J. L. Camargo, S. G. W. Laurance, H. E. M. Nascimento, B. S. Marimon, B.-H. Marimon Jr., F. Costa, N. Targhetta, I. C. G. Vieira, R. Brienen, H. Castellanos, J. F. Duivenvoorden, H. F. Mogollón, M. T. F. Piedade, G. A. Aymard C., J. A. Comiskey, G. Damasco, N. Dávila, R. García-Villacorta, P. R. S. Diaz, A. Vincentini, T. Emilio, C. Levis, J. Schietti, P. Souza, A. Alonso, F. Dallmeier, L. V. Ferreira, D. Neill, A. Araujo-Murakami, L. Arroyo, F. A. Carvalho, F. C. Souza, D. D. do Amaral, R. Gribel, B. G. Luize, M. P. Pansonato, E. Venticinque, P. Fine, M. Toledo, C. Baraloto, C. Cerón, J. Engel, T. W. Henkel, E. M. Jimenez, P. Maas, M. C. P. Mora, P. Petronelli, J. D. C. Revilla, M. Silveira, J. Stropp, R. Thomas-Caesar, T. R. Baker, D. Daly, M. R. Paredes, N. F. da Silva, A. Fuentes, P. M. Jørgensen, J. Schöngart, M. R. Silman, N. C. Arboleda, B. B. L. Cintra, F. C. Valverde, A. Di Fiore, J. F. Phillips, T. R. van Andel, P. von Hildebrand, E. M. Barbosa, L. C. de Matos Bonates, D. de Castro, E. de Sousa Farias, T. Gonzales, J.-L. Guillaumet, B. Hoffman, Y. Malhi, I. P. de Andrade Miranda, A. Prieto, A. Rudas, A. R. Ruschell, N. Silva, C. I. A. Vela, V. A. Vos, E. L. Zent, S. Zent, A. Cano,M. T. Nascimento, A. A. Oliveira, H. Ramirez-Angulo, J. F. Ramos, R. Sierra,M. Tirado, M. N. U. Medina, G. van der Heijden, E. V. Torre, C. Vriesendorp, O. Wang, K. R. Young, C. Baider, H. Balslev, N. de Castro, W. Farfan-Rios, C. Ferreira, C. Mendoza, I. Mesones, A. Torres-Lezama, L. E. U. Giraldo, D. Villarroel, R. Zagt, M. N. Alexiades, K. Garcia-Cabrera, L. Hernandez, I. Huamantupa-Chuquimaco, W. Milliken, W. P. Cuenca, S. Pansini, D. Pauletto, F. R. Arevalo, A. F. Sampaio, E. H. Valderrama Sandoval, L. V. Gamarra, Estimating the global conservation status of more than 15,000 Amazonian tree species. *Sci. Adv.* **1**, e1500936 (2015).

ENVIRONMENTAL SCIENCES

Types and rates of forest disturbance in Brazilian Legal Amazon, 2000–2013

Alexandra Tyukavina,[1]* Matthew C. Hansen,[1] Peter V. Potapov,[1] Stephen V. Stehman,[2] Kevin Smith-Rodriguez,[1] Chima Okpa,[1] Ricardo Aguilar[1]

Deforestation rates in primary humid tropical forests of the Brazilian Legal Amazon (BLA) have declined significantly since the early 2000s. Brazil's national forest monitoring system provides extensive information for the BLA but lacks independent validation and systematic coverage outside of primary forests. We use a sample-based approach to consistently quantify 2000–2013 tree cover loss in all forest types of the region and characterize the types of forest disturbance. Our results provide unbiased forest loss area estimates, which confirm the reduction of primary forest clearing (deforestation) documented by official maps. By the end of the study period, nonprimary forest clearing, together with primary forest degradation within the BLA, became comparable in area to deforestation, accounting for an estimated 53% of gross tree cover loss area and 26 to 35% of gross aboveground carbon loss. The main type of tree cover loss in all forest types was agroindustrial clearing for pasture (63% of total loss area), followed by small-scale forest clearing (12%) and agroindustrial clearing for cropland (9%), with natural woodlands being directly converted into croplands more often than primary forests. Fire accounted for 9% of the 2000–2013 primary forest disturbance area, with peak disturbances corresponding to droughts in 2005, 2007, and 2010. The rate of selective logging exploitation remained constant throughout the study period, contributing to forest fire vulnerability and degradation pressures. As the forest land use transition advances within the BLA, comprehensive tracking of forest transitions beyond primary forest loss is required to achieve accurate carbon accounting and other monitoring objectives.

INTRODUCTION

Rates of deforestation in Brazil significantly slowed after 2004 according to the Brazilian national satellite–based deforestation monitoring system PRODES (www.obt.inpe.br/prodes) (*1*). The major underlying cause of deforestation has been beef and soybean production in response to growing global and national demands (*2*, *3*). Deforestation in the region in the early 2000s was reported to be predominantly due to pasture expansion (*4*), with increasing forest-to-cropland conversion in Mato Grosso (*5*). Success in slowing deforestation is attributed to a number of factors, including declining commodity prices, the role of government policies and implementation, civil society activism, and private industry engagement (*6*–*8*). Despite the recent deforestation reduction, Brazil remains the single largest contributor to natural forest loss among tropical countries (*9*). Extant demands for commodities sourced through tropical deforestation will test the ability of Brazil to achieve further reductions in forest loss.

The PRODES (*1*) data set and a global forest loss map from the University of Maryland (UMD) (*10*) agree on the general decreasing deforestation trend in Brazil for the past decade but disagree in terms of the absolute forest cover loss rates, presumably due to differences in methodology. Although PRODES quantifies large-scale deforestation of disturbed and undisturbed primary forest, other forest change dynamics (including secondary forest clearing, logging, and fire) are omitted. Conversely, the UMD map quantifies any tree cover loss, including forest plantation rotations, fire, logging, and natural disturbances. PRODES ignores all changes outside of the old-growth forests of the dense humid tropical forest biome, whereas the UMD product maps all tree cover dynamics, including secondary forest and dry tropical woodland clearing. Additionally, minimum mapping units of 6.25 and 0.09 ha for PRODES and UMD, respectively, result in product differences.

Most regional- and continental-scale studies on the types of deforestation are based on tabular data sources and modeling (*4*, *11*, *12*). Remote sensing data, specifically time series of medium– and high–spatial resolution optical imagery, can be used to attribute types of stand-replacement forest clearing (deforestation), for example, clearing for pasture, cropland, mining, infrastructure, and urban expansion. This has been realized in the form of postdeforestation land-use mapping by the Brazilian systems TerraClass (www.inpe.br/cra/projetos_pesquisas/dados_terraclass.php) and TerraClass Cerrado (www.dpi.inpe.br/tccerrado/) and the nongovernmental land-cover and land-use mapping initiative MapBiomas (http://mapbiomas.org). The use of remotely sensed data in assessing the degree and type of partial canopy loss (forest degradation) has been demonstrated in monitoring wildfires and selective logging (*13*, *14*). Given these demonstrated capabilities, a more comprehensive accounting of forest disturbance dynamics is possible for the Brazilian Amazon.

All wall-to-wall deforestation or postdisturbance land-use maps derived using remotely sensed data contain errors, which results in the biased area estimates derived via map pixel counting (*15*–*17*). This study follows good practice recommendations (*15*–*17*) to use a probability sample for unbiased area estimation from remotely sensed data. Our study includes the following objectives: (i) produce unbiased estimates of annual forest disturbance rates between 2000 and 2013 for the states of the BLA using a sample-based approach; (ii) characterize the types of forest disturbance and predisturbance forest types; (iii) assess carbon implications of the observed forest loss dynamics; and (iv) compare sample-based estimates with the existing deforestation, forest degradation, and postdeforestation land-use maps.

RESULTS

BLA total tree cover loss

Most tree cover loss in the BLA between 2000 and 2013 occurred in dense primary humid tropical forests (Fig. 1 and table S1). The rates of human clearing in all forest types decreased after 2005 (Fig. 2B). The relative

---

[1] Department of Geographical Sciences, University of Maryland, College Park, MD 20742, USA. [2] Department of Forest and Natural Resource Management, State University of New York, Syracuse, NY 13210, USA.
*Corresponding author. Email: atyukav@umd.edu

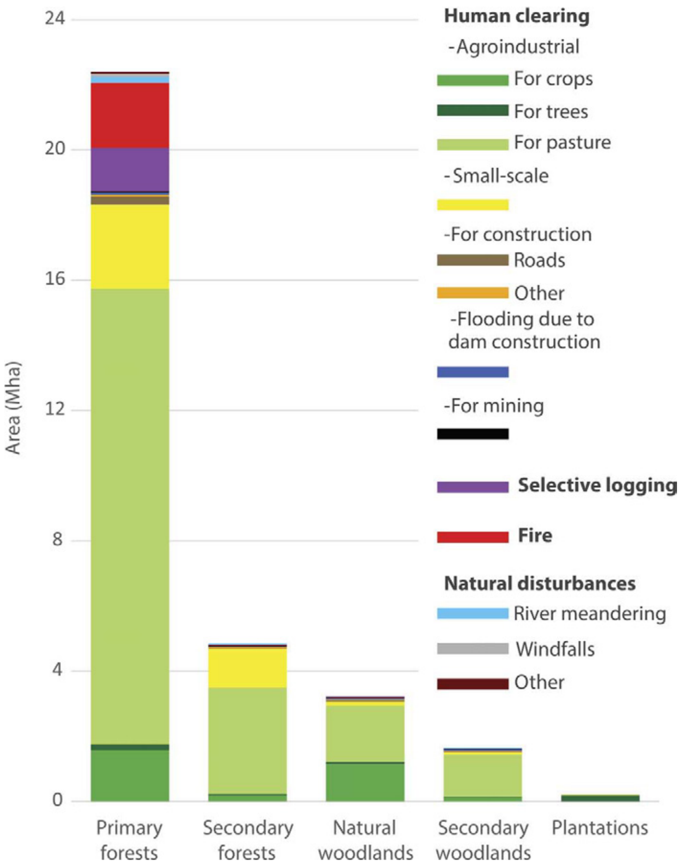


Fig. 1. Sample-based estimates of the total 2000–2013 tree cover loss area in BLA. Estimates are disaggregated by predisturbance forest type and disturbance type. Selective logging and fire categories do not represent complete tree cover loss but rather the area affected by these processes. See table S1 for SEs of the estimates.

difference between the maximum and minimum tree cover loss years was 73% in primary forests (maximum, 2003; minimum, 2013), 75% in natural woodlands (maximum, 2004; minimum, 2008–2009), and 66% in other forests (maximum, 2002; minimum, 2012) (table S2B). Fire disturbance had three peaks (2005, 2007, and 2010). By 2013, human clearing of other forest types, together with natural forest loss and non–stand-replacement disturbances (fire and selective logging) in all forest types (including primary), was comparable in area to that of clearing of primary forests (0.70 ± 0.08 Mha versus 0.63 ± 0.07 Mha, where the ± term is the SE of the estimate) (table S3 and Fig. 2B). That is, by 2013, deforestation in woodlands and secondary forests, together with natural tree cover loss and degradation in all forest types, had reached a magnitude of area similar to that of deforestation in dense primary humid tropical forests, which is the main target of current national-level mitigation efforts.

State-level tree cover loss estimates

At the state level, the largest contributors to tree cover loss are Mato Grosso and Pará, which together comprise 60% of the total 13-year loss area (table S4 and Fig. 3A). These two states are also the leading contributors to primary forest loss (Fig. 3B), whereas Maranhão, Mato Grosso, and Tocantins, which are partially located within Cerrado woodlands (Fig. 4), make up 99% of tree cover loss in natural woodlands (table S4).

Agroindustrial forest clearing for pasture is the largest contributor to primary forest loss at the state level (Fig. 3B), except for Roraima and Amapá, where small-scale clearing prevails over agroindustrial. Small-scale clearing is the second largest disturbance type in other frontier states (Acre, Amazonas, and Rondônia). Mato Grosso has a substantial portion of primary forest loss to croplands (18%; table S4), followed by fire (14%). Primary forest fires are also widespread in Maranhão (16%), Tocantins (15%), Amazonas (10%), Pará (5%), Rondônia (5%), and Roraima (4%). Most selective logging occurs within Mato Grosso and Pará, the two largest primary forest clearing contributors, and is estimated at 8 and 7% of the total primary forest loss of these states, respectively. Natural forest disturbances, namely, river meandering and windfalls, contribute more than 1% of primary forest loss only in Amazonas (8% river meandering and 3% windfalls) and Roraima (2% windfalls).

Natural woodlands are converted to cropland more often than primary forests are converted to cropland (Fig. 3C). Conversion to cropland is a major type of loss dynamic in the natural woodlands of Mato Grosso (50%) and the second largest (after pasture conversion) loss type in the natural woodlands of Maranhão (37%) and Tocantins (24%).

Secondary forests and woodlands are primarily cleared for agroindustrial pastures and small-scale agricultural activities (Fig. 3D). Clearing for plantations is a significant contributor to loss dynamics in some areas (45% in Amapá and 2 to 3% in Amazonas, Maranhão, Mato Grosso, Pará, and Rondônia).

Construction of the Luis Eduardo Magalhães (Lajeado) Dam in Tocantins, which was completed in 2002, resulted in extensive inundation and contributed 5% of the total 2000–2013 tree cover loss in the state (4% of loss in primary forests, 3% in natural woodlands, and 10% in secondary forests and woodlands).

Annual state-level tree cover loss estimates (Fig. 5 and table S5) show a peak loss in primary forests and natural woodlands in 2003 and 2004 in most states and a less pronounced peak in secondary forests and woodlands in 2002 in Mato Grosso, Maranhão, and Tocantins. The largest annual loss amplitude is observed in Mato Grosso (1.62 ± 0.12 Mha in 2004 versus 0.12 ± 0.04 Mha in 2009).

Carbon implications

Our results indicate that, by 2013, clearing of woodlands and secondary forests and non–stand-replacement disturbances (fires and selective logging) exceeded human clearing of primary forests in area (53% versus 47%) (table S3 and Fig. 2B). We used our sample data to estimate the implications of this result on gross carbon loss. From all sample pixels of tree cover loss (3908 pixels), we derived the range of mean predisturbance aboveground carbon (AGC) density estimates from three carbon maps (Table 1). AGC loss was assumed to be 100%, resulting from stand-replacement forest disturbances (human and natural), 4 to 37% (average 21%) from selective logging (*18*), and 10 to 50% (average 30%) from fire (*19*). The results of this estimation process indicate that 26 to 35% of 2013 gross AGC loss likely resulted from disturbance types other than human clearing of primary forests. The lowest contribution of other disturbance types to gross AGC loss was in 2003 (13 to 18%), corresponding to an annual peak of primary forest clearing, and the highest contribution was in 2010 (38 to 49%), the drought year with fire disturbance peak (Fig. 6). If deforestation (clearing of primary forests) continues to decline, carbon emissions from other forest and disturbance types, including natural woodlands, will constitute a substantial proportion of gross carbon loss in the BLA.

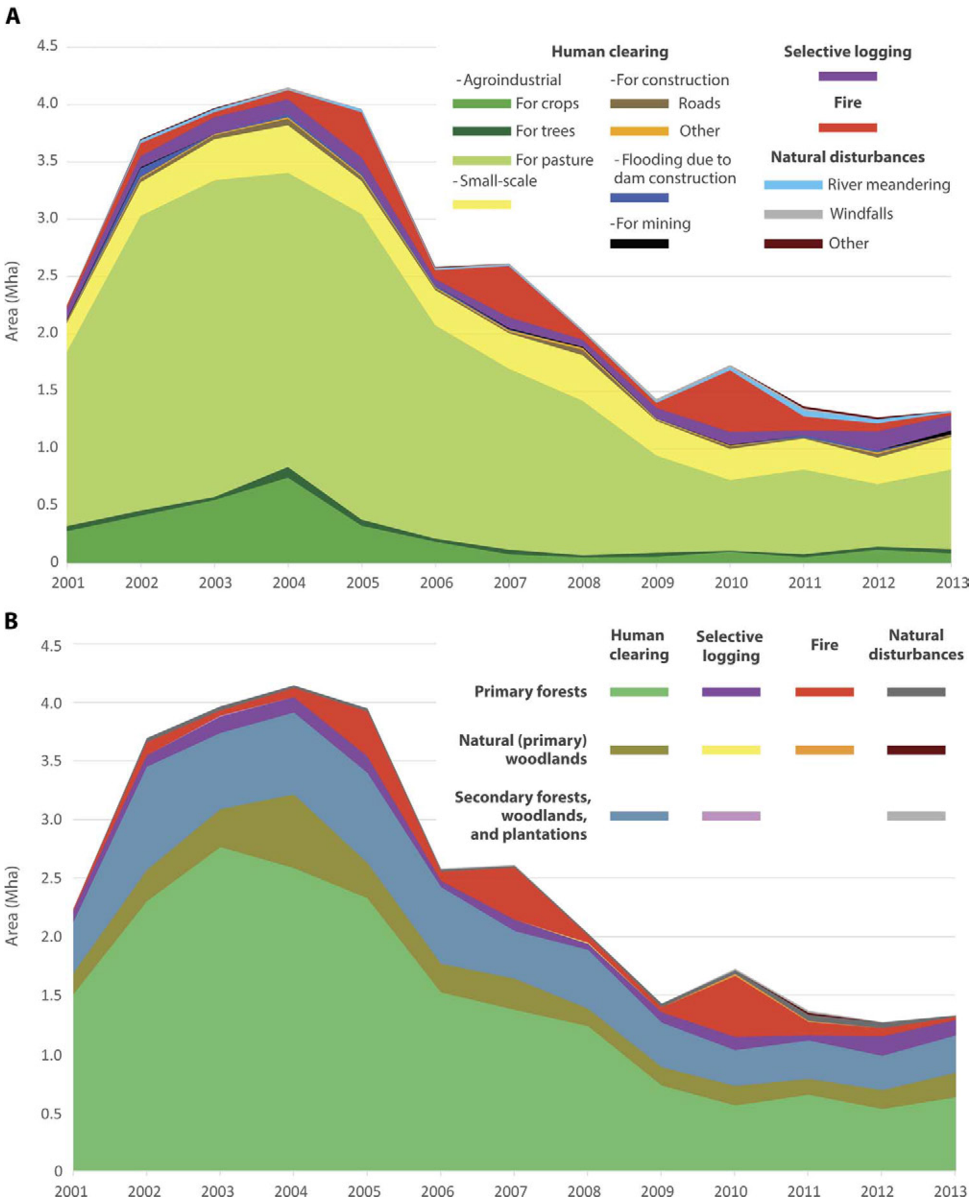


Fig. 2. Sample-based estimates of annual tree cover loss area in BLA. Estimates are disaggregated by (**A**) disturbance type and (**B**) predisturbance forest type and disturbance type group. Selective logging and fire categories do not represent complete tree cover loss but rather the area affected by these processes. See tables S2 and S3 for SEs of the estimates.

Comparison with deforestation and tree cover loss maps

PRODES and Souza *et al.* (*20*) both map deforestation in primary humid tropical forests of the Brazilian Amazon, which corresponds to the human clearing of primary forests in our study. Although all three studies document decreased annual deforestation rates after 2005 and agree in the overall area of deforestation, annual estimates vary up to 65% (Table 2 and Fig. 7). The largest relative disagreement is 2009, when Souza *et al.* (*20*) detect substantially larger deforestation areas than PRODES and the current study. The peak of deforestation is 2003 according to our study and 2004 according to others.

PRODES is successful in reproducing our unbiased sample-based annual loss area estimates, but PRODES is not spatially accurate. Only 79% of the sample-based estimated area of human clearing of primary forest was within the PRODES forest mask. Thus, the forest mask imposed by PRODES results in omitting 21% of the estimated area of primary forest cover loss.

The UMD map detects more tree cover loss in the BLA each year, compared to PRODES and Souza *et al.* (*20*) (Fig. 7). The explanation for this difference is that the UMD map is not limited to mapping deforestation of primary forests but includes all tree cover loss dynamics. The UMD map underestimates total tree cover loss at the beginning of the study period (before 2010) and overestimates total tree cover loss at the end, that is, displays a temporal pattern of bias, which is absent in PRODES and Souza *et al.* (*20*). This may be due to the following reasons: (i) loss date attribution uncertainty (*10*); (ii) a possible increase of model sensitivity to loss events at the end of the study period caused by the after-effects of the two large droughts (2005 and 2010); and (iii) the new model including Landsat 8 data in 2013, which has proven to increase sensitivity to small-scale disturbances.

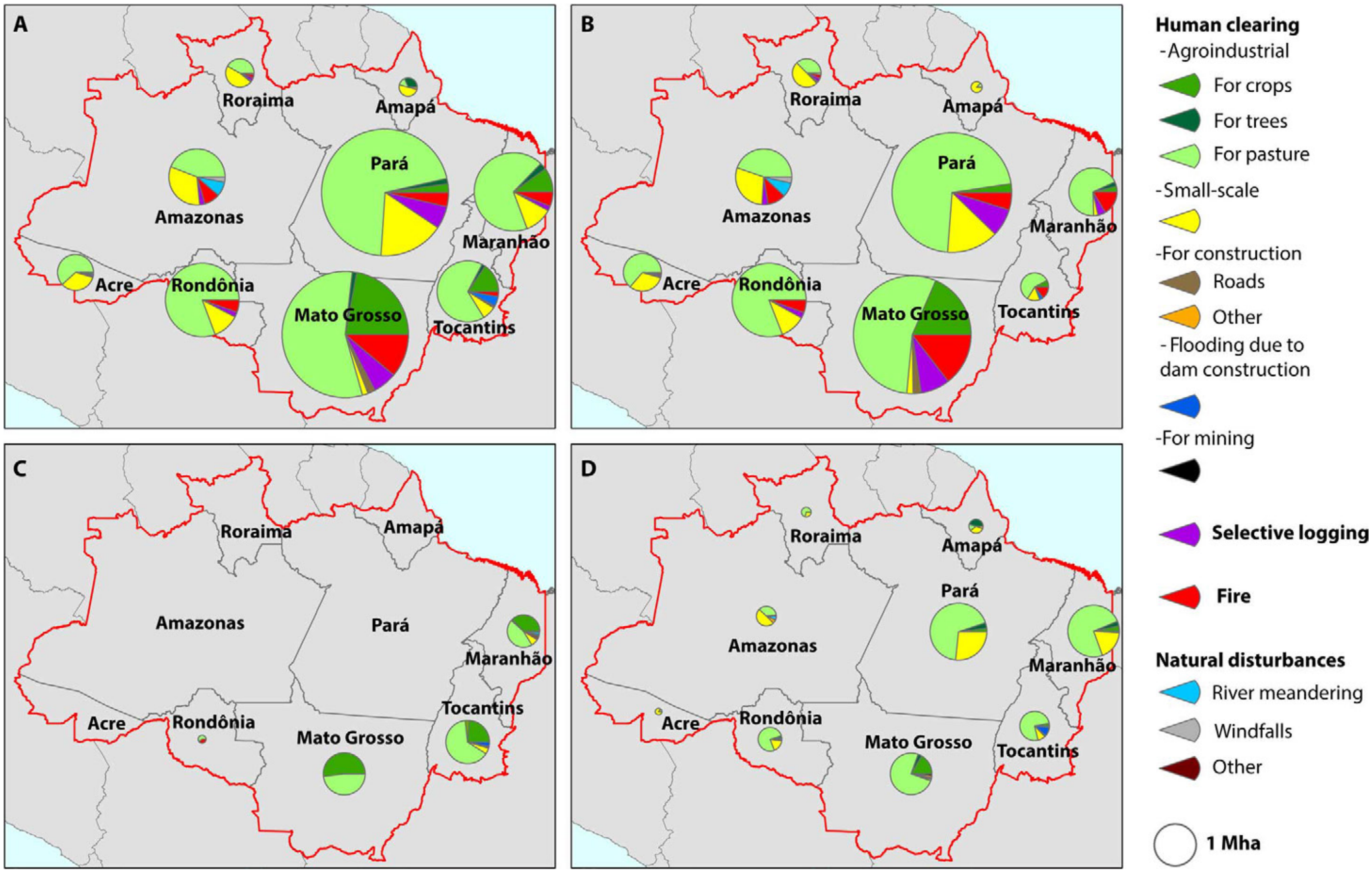


Fig. 3. The 2000–2013 state-level tree cover loss area estimates. Estimates are disaggregated by disturbance type in (**A**) all forests, (**B**) primary forests, (**C**) natural woodlands, and (**D**) secondary forests, woodlands, and plantations. See table S4 for SEs of the estimates.

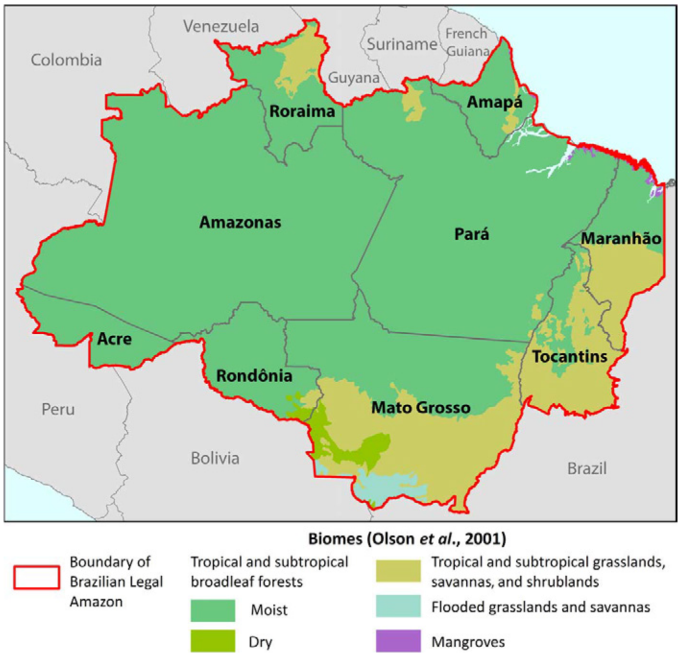


Fig. 4. Study area—BLA.

Comparison with forest degradation maps

Results of the current sample-based analysis indicate fire peaks in 2005, 2007, and 2010 (Fig. 8), which is consistent with earlier Moderate Resolution Imaging Spectroradiometer (MODIS)–based observations (*21*). Two of these fire peaks, 2005 and 2010, occur within years of extreme drought (*22*, *23*). Drought conditions, together with forest fragmentation edge effects and selective logging, increase humid tropical forest susceptibility to fire, which often originates from human activities outside of the forest (*24*, *25*). Selective logging rates remain constant in the region between 2000 and 2013 (Fig. 8). We compared our selective logging and fire area estimates with mapping results from the Brazilian national forest degradation monitoring system DEGRAD and from Souza *et al.* (*20*) (Fig. 8).

DEGRAD detects areas affected by selective logging and fire during 2007–2013 (see www.obt.inpe.br/degrad/ and Materials and Methods for more information on DEGRAD methodology). The larger degradation area detected by DEGRAD compared to the sample-based analysis (combined selective logging and fire) is likely due to (i) differences in methodology and definitions (DEGRAD marks the entire forest patches as degraded when disturbance signs are present, whereas we consider only a 120-m buffer around visible logging damage and fire scars as degraded). This difference was partially offset by analyzing DEGRAD only within the sampling region of the current study, leaving out 49% of

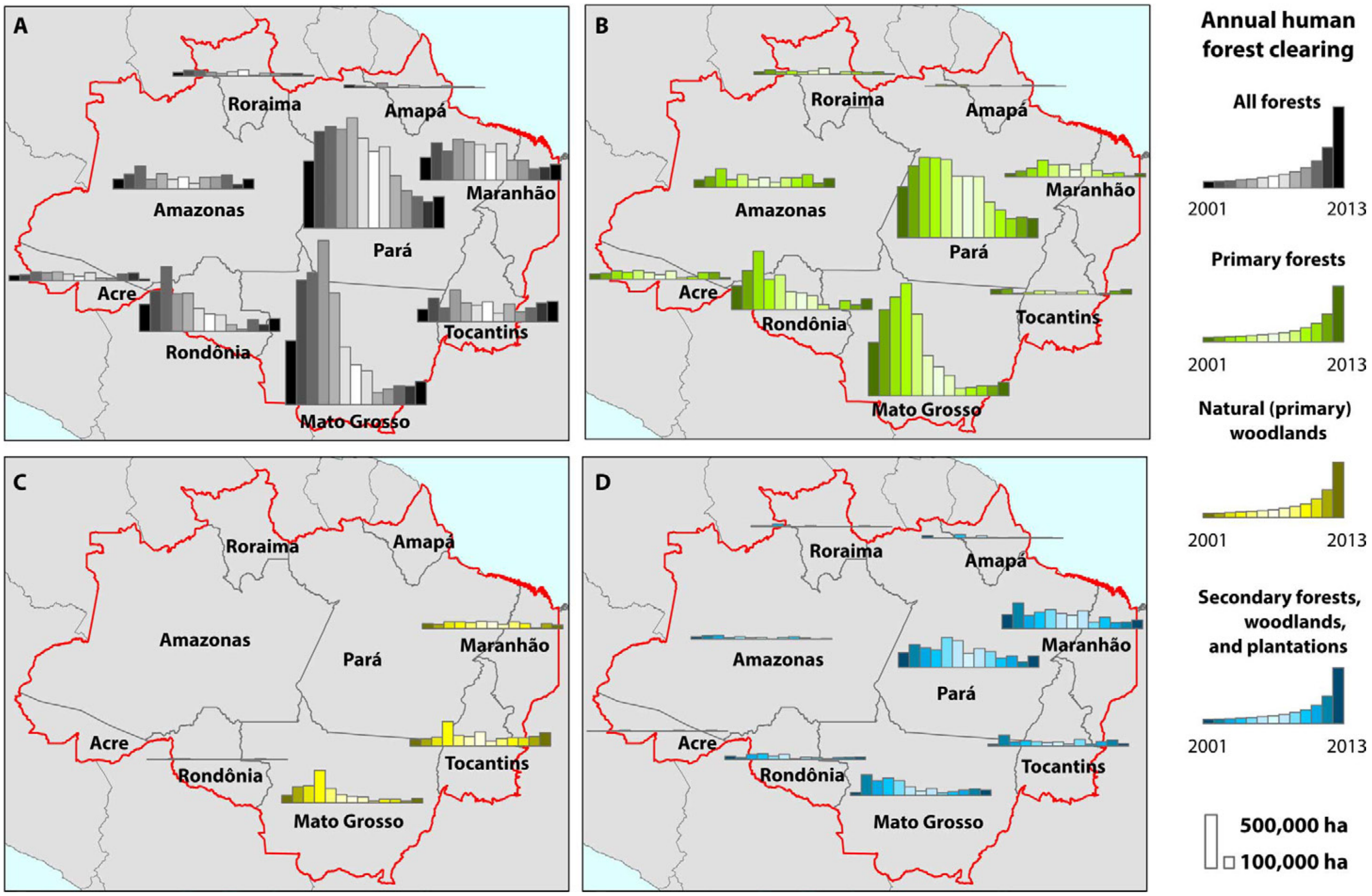


Fig. 5. Annual human forest clearing by state. (**A**) In all forests, (**B**) in primary forests, (**C**) in natural (primary) woodlands, and (**D**) in secondary forests, woodlands, and plantations. See table S5 for SEs of the estimates.

Table 1. Mean AGC density in predisturbance forest types (MgC/ha). For carbon data source description, see Materials and Methods.

	Sample size (*n*)	Predisturbance (year 2000) AGC density (MgC/ha)			
		Baccini *et al.* (*48*)	Saatchi *et al.* (*50*)	Avitabile *et al.* (*51*)	Range
Primary forests	2702	99.3	94.9	77.4	77.4–99.3
Natural (primary) woodlands	387	27.5	28.4	18.9	18.9–28.4
Secondary forests, woodlands, and plantations	819	48.4	48.3	44.8	44.8–48.4

DEGRAD area. (ii) DEGRAD includes some pre-2007 degradation in the 2007–2013 map: 26% (41 of 160) of the samples marked as pre-2007 fire or logging degradation were identified as 2007–2013 degradation in DEGRAD.

Peaks of degradation detected by DEGRAD are 1 year later compared to the peak fire years from our sample and independent MODIS estimates (Fig. 8). The 1-year lag in DEGRAD is confirmed by a sample-level degradation date analysis: 72% (89 of 124) of the sampled pixels identified as 2007–2013 degradation in both our sample analysis and DEGRAD had DEGRAD year of disturbance 1 year later. The lag in degradation detection is probably due to the use of single-date imagery in the DEGRAD system: Year 2008 DEGRAD map was based on imagery from 7 April to 3 October 2008 (91% of the scenes were acquired before September), whereas our sample-based analysis indicates that ~70% of fires in 2000–2013 occurred in September to December (Table 3).

Souza *et al.* (*20*) 2000–2010 forest degradation estimates are also based on a single-date Landsat imagery analysis and have a similar 1-year lag in degradation date detection (Fig. 8), detecting peaks of forest degradation in 2006 and 2008 instead of 2005 and 2007 and missing the 2010 peak.

The differences between the three estimates are probably due to different degradation definitions, which are often difficult to formalize (for example, how the boundaries of the burnt areas are defined or what distance from visible logging extractions is considered degraded), different methodological approaches [automated image classification of Souza *et al.* (*20*) versus visual image interpretation of DEGRAD versus visual sample interpretation of the current study], different input data [a single Landsat image per year by Souza *et al.* (*20*) and DEGRAD versus a continuum of 16-day Landsat composites in our study], and slightly different study areas.

Comparison with land-cover and land-use maps

We have compared our sample-based estimates of forest disturbance types to the existing land-cover and land-use maps for the BLA, namely, TerraClass, TerraClass Cerrado, and MapBiomas. The TerraClass system (www.inpe.br/cra/projetos_pesquisas/dados_terraclass.php) maps land uses following deforestation detected by PRODES by 2004, 2008, 2010, 2012, and 2014 (*26*). We compared sampled pixels identified as human clearing of primary forests in our analysis with the temporally closest TerraClass map (see Materials and Methods and Table 4). Similar to our results, TerraClass identified pasture as the most widespread post-deforestation land use: 87% of area identified as TerraClass pasture corresponds to the agroindustrial clearing for pasture disturbance type in our sample analysis, indicating a high degree of agreement between the two products. Of the sample pixels falling within TerraClass pasture, 7% are labeled as small-scale clearing disturbance, a difference that does not necessarily represent a thematic disagreement. Only 6% of the area TerraClass labels as pasture disagrees with our sample interpretation, falling into cropland, tree plantation, construction, dam, and mining disturbance types. More than 85% of the TerraClass area of annual agriculture was in agreement with our agroindustrial clearing for crops disturbance type. A large percent of small-scale clearing area from our current study corresponds to TerraClass forest (46% of the area), which is likely explained by the median size of small-scale clearing in our study being 5 ha and minimum mapping unit of PRODES being 6.25 ha. Small-scale clearings also correspond to TerraClass pastures (26%), secondary regrowth and reforestation (15%), mosaic of land uses (5%), and other classes (8%). Numerous forest loss sample pixels are identified as no deforestation or secondary vegetation in TerraClass (columns "Forest," "Nonforested areas," and "Secondary regrowth and reforestation"), probably because of the differences in deforestation date identification between our sample-based analysis and PRODES, which is the deforestation baseline for TerraClass.

TerraClass Cerrado (www.dpi.inpe.br/tccerrado/) maps 2013 land uses for the Cerrado region of Brazil. We compared sample pixels identified as 2001–2012 human clearing of natural woodlands in our analysis with the 2013 TerraClass Cerrado map (see Materials and Methods and Table 5). Of the sample pixels falling within TerraClass Cerrado pasture, 79% were labeled as pasture in our sample interpretation; of TerraClass cropland, 95% of sample pixels were labeled as cropland. At the same time, TerraClass Cerrado omits 21% of the area identified as human clearing of natural woodlands in the current study, marking them as natural vegetation (Table 5). TerraClass and TerraClass Cerrado confirm our finding that natural woodlands are converted to croplands

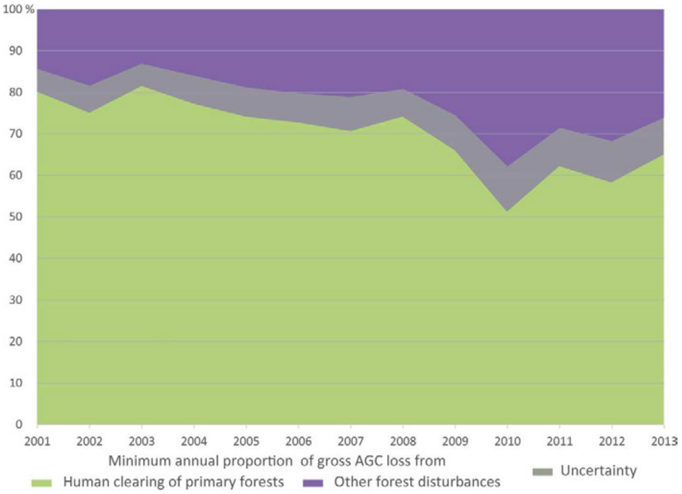


Fig. 6. Estimated annual percent of gross AGC loss from human clearing of primary forests versus other forest disturbances. Other disturbances include human clearing of woodlands and secondary forests, fires, and selective logging. Uncertainty is based on the range of mean AGC estimates per forest type from Table 1.

Table 2. Comparison between annual deforestation estimates. (A) Current study (human clearing of primary forests), (B) PRODES, and (C) Souza *et al.* (*20*). Total difference between (A) and (C), and (B) and (C) is calculated only for 2001–2010 because of the absence of Souza *et al.* (*20*) estimates for 2011–2013.

Area of deforestation (Mha)														
	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	Total
(A) Sample	1.51	2.30	2.77	2.59	2.33	1.52	1.38	1.24	0.73	0.56	0.65	0.53	0.63	18.72
(B) PRODES	1.82	2.17	2.54	2.78	1.90	1.43	1.17	1.29	0.75	0.70	0.64	0.46	0.59	18.22
(C) Souza *et al.* (*20*)	1.72	2.33	2.22	2.44	2.22	1.60	1.38	1.24	1.20	0.55	—	—	—	16.91
Difference between estimates (%)														
	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	Total
Sample versus PRODES (A − B)/A × 100%	−20.5	6.0	8.2	−7.4	18.3	6.3	15.3	−4.4	−2.3	−25.2	1.4	13.5	6.3	2.7
Sample versus Souza (A − C)/A × 100%	−14.2	−1.4	19.6	5.5	4.5	−4.9	0.1	−0.3	−64.2	1.7	—	—	—	0.04
PRODES versus Souza (B − C)/B × 100%	5.3	−7.8	12.5	12.0	−17.0	−11.9	−18.0	3.9	−60.5	21.5	—	—	—	−2.3

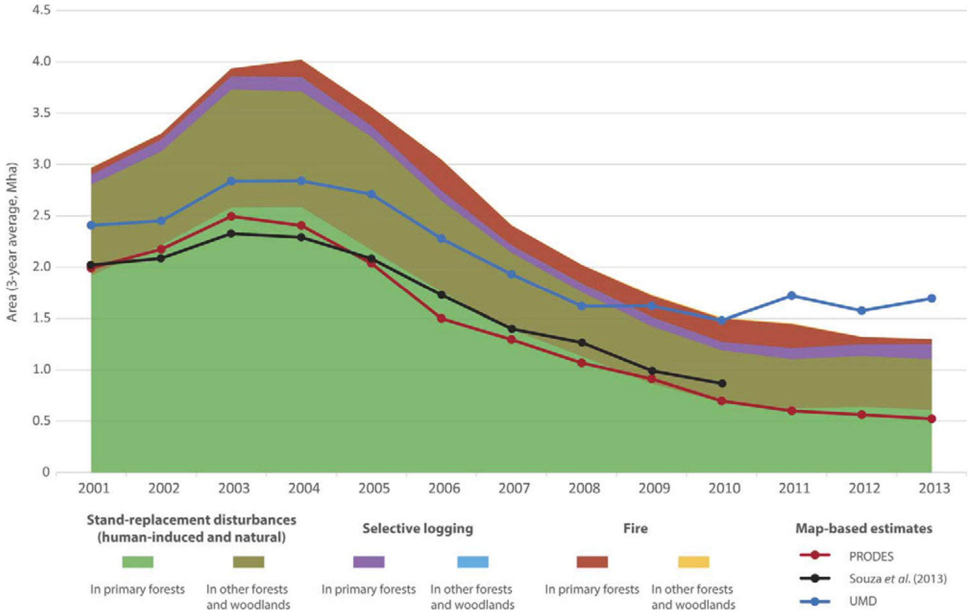


Fig. 7. Comparison of sample- and map-based annual deforestation estimates. Three-year averages of sample-based annual tree cover loss estimates by disturbance type (stand-replacement disturbances, selective logging, and fire) and forest type (primary forests and other forests and woodlands) compared with 3-year averages of annual map-based deforestation estimates from PRODES and Souza *et al.* (*20*) and tree cover loss estimates from UMD map.

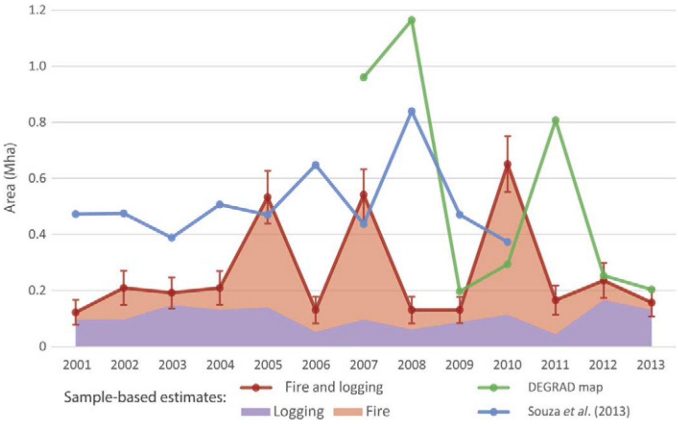


Fig. 8. Comparison of forest degradation estimates. Sample-based fire and selective logging estimates are compared with DEGRAD map within sampling region and Souza *et al.* (*20*) degradation estimate. Error bars represent ±SE.

more often than primary forests are converted to croplands (Tables 4 and 5): The pasture/cropland conversion ratio is 2:1 in TerraClass Cerrado (natural woodlands of Cerrado region) and 11:1 in TerraClass (primary forests of BLA).

MapBiomas (http://mapbiomas.org) maps major types of land cover and land use (forest, cropland, pasture, planted forests, coastal forests, water, and others) annually between 2008 and 2015 for the Amazon, Cerrado, and Pantanal biomes, which enables comparison with our sampled pixels, identified as 2001–2013 human clearing of all forest types (see Materials and Methods and Table 6). Of the sample pixels falling within MapBiomas pasture, 86% were labeled as pasture in our sample interpretation; of MapBiomas cropland, 64% of sample pixels were labeled as cropland. Thirty percent of the area identified as human clearing of all forest types in the current study falls within the MapBiomas "Other" category, which represents nonforested types of land cover and therefore does not disagree with our interpretation in terms of forest cover absence. A major disagreement between our sample-based result and MapBiomas is the 26% of the human forest clearing area that MapBiomas labels as "Forest." This disagreement is probably due to the different forest definitions used and possible commission errors in the MapBiomas annual forest layers (MapBiomas has yet to undergo a formal accuracy assessment).

DISCUSSION

Forest monitoring systems using remote sensing have traditionally been map-based. Wall-to-wall maps are useful for a variety of applications, including regional forest management and law enforcement, planning of ground-based measurement campaigns, and informing ecosystem and biodiversity modeling. Sample-based validation data provide critical information necessary to quantify classification errors and biases present in the maps and to produce unbiased area estimates and their associated uncertainties expressed as confidence intervals (*17*). Here, we demonstrate how sample reference data can be used for multiple research objectives, complementing map-based monitoring, including (i) unbiased area estimation, satisfying Intergovernmental Panel on Climate Change emissions reporting requirements, which specify the absence of over- or underestimation so far as can be judged, and reduction of uncertainties as far as practicable (*27*); (ii) verification of temporal trends from the maps or revealing their biases over time; and (iii) attribution of additional thematic information (for example, forest disturbance type or predisturbance forest type).

Brazil conducts the most advanced operational forest monitoring system, integrating near–real-time deforestation monitoring [DETER and DETER-B (*28*)], annual deforestation [PRODES (*1*)], forest degradation (DEGRAD), and postdeforestation land-use (TerraClass) mapping within primary forests. However, the increasing contribution of tree cover loss in other (nonprimary) forest types to gross tree cover and carbon loss suggests that national monitoring systems should

Table 3. Monthly distribution of sample pixels identified as fire disturbance, 2000–2013. "End of year—uncertain date" indicates that the fire scar was observed in the first 16-day composite of the year and there were no cloud-free 16-day composites at the end of the previous year; in this case, fire was attributed to the end of the previous year.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	End of year—uncertain date
Number of pixels	2	2	5	3	5	1	6	45	93	18	31	9	15

Table 4. Comparison between types of human clearing in primary forests (2001–2013) identified from the sample and postdeforestation land-use types from TerraClass. Cell entries of the confusion matrix denote the number of sample pixels in each category (a mixed loss pixel was recorded as 0.5). The 113.5 sample pixels with TerraClass showing later loss date than the current analysis (for example, 2004 instead of 2001–2003) were excluded from the analysis and are not displayed in the table.

Human clearing of primary forests (current study)		TerraClass										
		Pasture	Annual agriculture (cropland)	Mosaic of land uses	Secondary regrowth and reforestation	Forest	Nonforested areas	Water	No data	Mining	Urban areas	Total
Agroindustrial clearing	Pasture	944	11.5	35	129	250	56	1.5	80.5	0	0	1507.5
	Crops	52	86	0	6	10	17.5	0	4.5	0	0	176
	Trees	4	3	1	8	2	2	0	0	0	0	20
Small-scale clearing		73.5	0	13.5	43.5	130	10	3	7.5	0	0	281
Construction	Roads	5.5	0	0.5	2.5	15.5	3	0	0	0	0	27
	Other	2.5	0	1	0.5	1	0.5	0	0	0	0	5.5
Dam construction		3	0	0	0	4	2	0	0	0	0	9
Mining		2	0	0	0	0.5	0	0	0	0	0	2.5
Total		1086.5	100.5	51	189.5	413	91	4.5	92.5	0	0	2028.5

expand beyond the ever-decreasing primary forest resource that is currently monitored by PRODES. For example, secondary forests have rapid carbon and nutrient accumulation potential (*29*), which may be offset by their widespread reclearing. Cerrado woodlands and savannas have high species richness and endemism, high rates of land conversion to agriculture, and low level of protection, which pose an imminent threat for biodiversity, water recycling to the atmosphere, and other deleterious impacts (*30*–*32*). Brazil has prototyped a deforestation monitoring system for other biomes outside of the Amazon region (PMDBBS system, http://siscom.ibama.gov.br/monitora_biomas/). This effort included producing a baseline map of 2002 vegetation for Caatinga, Cerrado, Mata Atlântica, Pampa, and Pantanal biomes and mapping 2002–2008 and 2008–2009 vegetation changes using data from Landsat and CBERS (China-Brazil Earth Resources Satellite) satellites. However, the maps were updated for the years 2010 and 2011 only for the Cerrado biome; no updates are available for the following years. TerraClass postdeforestation land-use mapping was expanded to include the Cerrado region but only for the year 2013. Moderate-resolution (MODIS-based) monitoring of vegetation changes in the Cerrado region has been prototyped in several studies (*33*, *34*), but not yet implemented operationally, as with DETER in primary forests.

National forest monitoring should not focus only on forest clearing and conversion to nonforest land uses ("deforestation"). Non–stand-replacement disturbances, such as selective logging, paired with climate change and increased vulnerability to fire, may lead to significant carbon emissions and biodiversity losses and eventually to conversion of forests to other land covers. DEGRAD is one example of such a national-scale degradation monitoring effort, even though limited by a single-date image analysis approach. Our results suggest that the use of the entire record of satellite observations, rather than a single best image for a given year, may yield better results in tree cover loss date attribution and improve near–real-time forest disturbance monitoring (*35*). An independent nongovernmental MapBiomas system is moving in this direction by using the entire archive of Landsat observations to map annual land-cover and land-use transitions in all biomes of Brazil.

As illustrated in this study, quantifying forest disturbance dynamics is a complex task. Comprehensive tracking of predisturbance state (primary versus secondary), disturbance factor (for example, fire versus mechanical clearing), and subsequent land use (for example, soybean versus mining) is a challenge. The work of the Brazilian National Institute for Space Research (INPE) on documenting these dynamics is at the forefront of all similar national capabilities, as evidenced by the host of INPE products seeking to track comprehensive forest change. Our study demonstrates the increased need for such systematic monitoring because the relative amounts of tree cover loss due to different factors have changed dramatically since 2000. For applications such as carbon monitoring, the omission of forest disturbance types

Table 5. Comparison between types of human clearing in natural woodlands (2001–2012) identified from the sample and 2013 land use according to TerraClass Cerrado. Cell entries of the confusion matrix denote the number of sample pixels (1 and 0.5 loss) in each category.

Human clearing of natural woodlands (current study)		TerraClass Cerrado							
		Pasture	Agriculture (annual and perennial)	Mosaic of land uses	Forestry	Natural vegetation	Water	No data	Total
Agroindustrial clearing	Pasture	115	3	0	1	41	0	0	160
	Crops	25.5	73.5	0	3	9.5	0	1	112.5
	Trees	2	0	0	2	1	0	0	5
Small-scale clearing		3.5	0	0	0	3.5	0	0	7
Construction	Roads	0	0.5	1	0	4	0	0	5.5
	Other	0	0	1	0	1	0	0	2
Dam construction		0	0	0	0	1	4	0	5
Mining		0	0	0	0	0	0	0	0
Total		146	77	2	6	61	4	1	297

Table 6. Comparison between types of human clearing in all forest types (2001–2013) identified from the sample and land cover/land use according to MapBiomas. Cell entries of the confusion matrix denote the number of sample pixels (1 and 0.5 loss) in each category.

Human clearing of all forest types (current study)		MapBiomas								
		Pasture	Agriculture	Forest	Planted forest	Coastal forest	Water	Other	No data	Total
Agroindustrial clearing	Pasture	997.5	73.5	536	0	0	1	717	0	2325
	Crops	87.5	132.5	28.5	0	0	0	101	0	349.5
	Trees	3	1	30	0	0	0	20	0	54
Small-scale clearing		61.5	0	271.5	0	0	0	121	1	455
Construction	Roads	9.5	1	15	0	0	0	13	0	38.5
	Other	4	0	1	0	0	0	10	0	15
Dam construction		0	0	0	0	0	18	4	0	22
Mining		1.5	0	0	0	0	1	6	0	8.5
Total		1164.5	208	882	0	0	20	992	1	3267.5

other than large-scale clearing may lead to inaccurate emission estimation. To address this issue, national forest monitoring systems could produce wall-to-wall characterizations of forest type, loss, and gain. Such maps could then be used to construct strata for the allocation of a probability sample, resulting in unbiased, precise estimators of forest cover loss dynamics and associated carbon losses and gains (*17*, *36*, *37*).

MATERIALS AND METHODS

Study area

The study area is the BLA; Brazilian states of Acre, Amapá, Amazonas, Mato Grosso, Pará, Rondônia, Roraima, and Tocantins; and the western part of the state of Maranhão (Fig. 4). The boundaries of BLA were obtained from the database of the Woods Hole Research Center (http://whrc.org/publications-data/datasets/large-scale-biosphere-atmosphere-experiment/) and modified to exclude the east of Maranhão in accordance with the PRODES study area.

Most of the BLA (81.2%) lies within the tropical moist broadleaf forest biome (Fig. 4); 16.3% within tropical grasslands, savannas, and shrublands, including Guianan savanna in the north of the region and Cerrado woodlands in the south; 1.2% within Chiquitano tropical dry broadleaf forests; 1.0% within Pantanal flooded savannas; and 0.3% within coastal mangroves (*38*). Although most states in the BLA are dominated by humid tropical forests, significant parts of Tocantins, Maranhão, and Mato Grosso are occupied by Cerrado woodlands.

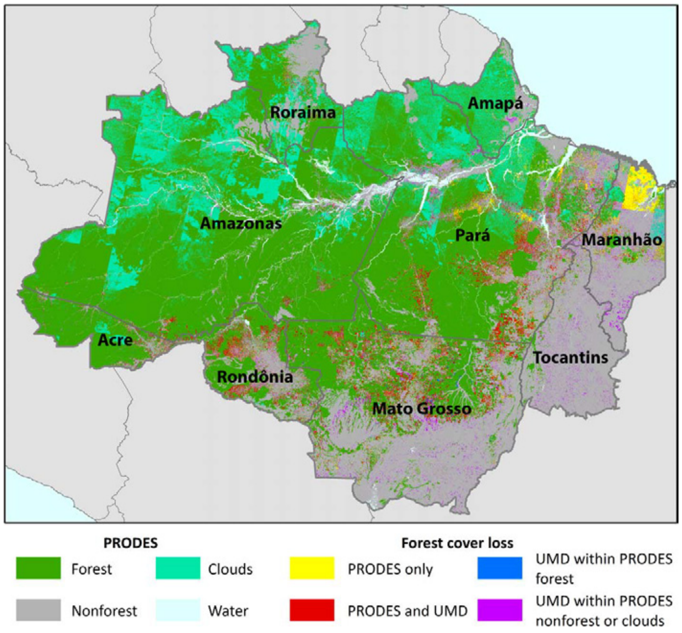


Fig. 9. PRODES forest mask and 2001–2013 forest cover loss and UMD 2001–2013 tree cover loss within BLA.

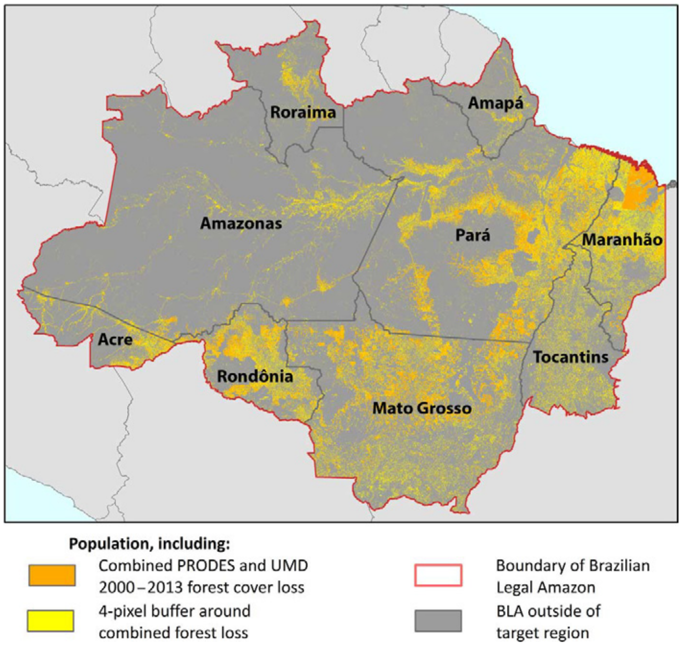


Fig. 10. Population from which the simple random sample of 10,000 pixels was selected.

PRODES and UMD data sets

PRODES is a deforestation monitoring system operated by INPE. PRODES maps deforestation within an ever-decreasing "nominally intact" forest mask (Fig. 9) (*39*); clearing of secondary forest regrowth is not mapped. The PRODES forest mask includes primarily dense humid tropical forests; Cerrado woodlands are mostly considered nonforest (Fig. 9). The PRODES methodology is a scene-based semiautomated classification, involving (i) generation of fractional images using linear spectral mixture modeling, (ii) image segmentation, (iii) unsupervised classification of segments, and (iv) visual interpretation and correction of mapping results (*39*). Scene-based approaches are more affected by cloud artifacts, which are labeled as no data areas in PRODES (Fig. 9). The minimum size of the image segment in PRODES mapping method (minimum mapping unit) is 6.25 ha (*1*), which likely introduces omission of deforestation associated with clearing of smaller forest patches.

The UMD global tree cover loss product (*10*) maps the loss of any woody vegetation taller than 5 m (with % canopy cover of >0), regardless of it being natural intact vegetation or secondary regrowth. Hence, the UMD product characterizes tree cover dynamics both within and outside of the PRODES forest mask (Fig. 9). The UMD mapping method is a more data-intensive pixel-based approach that uses all available cloud-free pixels (*40*), allowing it to map tree cover loss within PRODES no-data (cloudy) areas (Fig. 9).

Sampling design

We aggregated all forest loss areas detected by PRODES and UMD products from 2001 to 2013 as "combined forest loss" to define the region of interest. Combined forest loss was buffered by 120 m (four Landsat pixels) to include areas with likely forest loss omission in both products. The population from which the sample was selected consisted of the combined PRODES and UMD forest loss and associated buffer (Fig. 10). A total of 10,000 sample pixels (30 m × 30 m) were selected from this region via simple random sampling. Sample-based estimates of forest loss area were produced for the entire BLA and for each state separately (Table 7). The SE of the estimated area depends on the absolute size of the sample (see Eq. 2) and not on the percent of the population sampled (*41*). For example, the sample size of 10,000 yielded an SE of 1.3% for the total 2001–2013 forest cover loss estimate in BLA (table S1), which we consider to be sufficiently precise.

A direct estimator of area for simple random sampling (*16*) was used to estimate the area of tree cover loss based on the sample reference values. These area estimates are based on the reference data and sample labeling protocol described in the following subsection. For each sampled pixel, the proportion of area of tree cover loss was recorded as 0, 0.5, or 1. The estimated area of tree cover loss type *i* within a region of interest was computed as

$$\hat{A}_i = A_{\text{tot}}\bar{y}_i \tag{1}$$

where $\bar{y}_i$ is the sample mean proportion of tree cover loss of type *i* (that is, mean of the *n* sample pixel values of 0, 0.5, or 1), A_{tot} is the area of the region of interest, and *n* is the number of sample pixels in the region of interest.

Area estimates can be produced for the full population or regions of interest such as states. For the full population, the sample size is $n =$ 10,000. Sample sizes for each state are listed in Table 7. The SE of the estimated area is

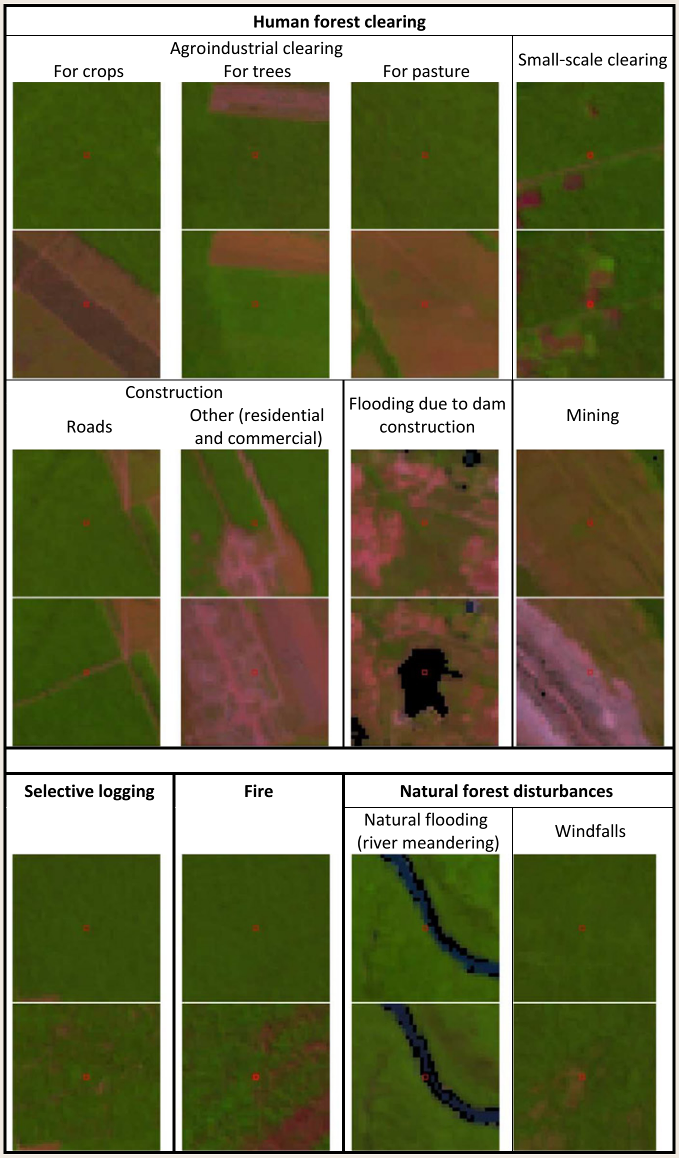
$$\text{SE}(\hat{A}_i) = A_{\text{tot}}\frac{s_i}{\sqrt{n}} \tag{2}$$

where s_i is the sample SD of tree cover loss type *i* in the region of interest (that is, the SD of the tree cover loss values of 0, 0.5, and 1 for the *n* pixels sampled in that region). The estimates for regions of interest such as states are considered "domain" or "subpopulation" estimates, and the estimators implemented are those recommended by Cochran [(*41*), section 2.12].

Table 7. Sample size (number of pixels) and area of target region by state in BLA.

State	Sample size, n	Area of target region, A_{tot} (Mha)
Acre	310	2.74
Amapá	151	1.29
Amazonas	877	7.15
Maranhão	1,278	11.50
Mato Grosso	2,550	22.75
Pará	3,030	26.37
Rondônia	909	7.81
Roraima	210	1.88
Tocantins	685	5.88
BLA total	10,000	87.36

Table 8. Types of forest disturbance. Images are subsets of pre- and postdisturbance (top and bottom, respectively) for annual Landsat composites (band combination, 5-4-3). Small red rectangles represent sampled pixels.



Reference data and sample labeling protocol

Reference values for each sampled pixel were derived via visual interpretation of annual Landsat composite images for 1999–2013 and, when available, high-resolution imagery from Google Earth. Reference data and final interpretation results for each sampled pixel are available at glad.umd.edu/brazil. Landsat annual composites represent median normalized reflectance values from all available cloud/shadow-free pixels for a given year. Methods for cloud screening, image normalization, and per-pixel compositing are described by Potapov *et al.* (*40*). In addition to annual Landsat composites, 16-day composite images from 1999–2013 were examined for sampled pixels identified as having experienced forest degradation (from fire and selective logging) in the initial sample screening. This was done to get a more precise estimate of the timing of these events: Low-intensity disturbances such as fires occur in local dry seasons and during droughts. If these disturbances occurred late in the year, their annual allocation might be incorrectly assigned to the following year using median annual composites.

Each sampled pixel was initially visually assessed independently by two experts. Sample pixels with disagreement between experts were subsequently revisited until a consensus was reached. All sampled pixels were identified as yes/no tree cover loss. Pixels with tree cover loss were further attributed with (i) loss year (2001–2013), (ii) likely disturbance type, and (iii) predisturbance forest type. Mixed sample pixels, located on the boundary of tree cover loss patches, were marked as edge pixels and treated as "0.5 loss" in area calculations, with 404 of 10,000 sample pixels (4%) identified as boundary pixels. We identified only the first stand-replacement forest disturbance event during the study period (2000–2013) and the associated land-cover transition. For example, if a forested sample pixel was initially converted to pasture, and later transformed to cropland, our analysis would assign it as a forest-to-pasture conversion. If a sample pixel experienced tree cover loss at the beginning of the study period followed by tree-cover regrowth and a second tree cover loss event, we would record only the first loss event and ignore the subsequent dynamics. However, this example case would be labeled as a forestry land use, that is, the clearing of trees to be replaced by tree cover in the management of a plantation.

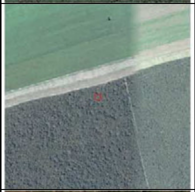
Types of forest disturbance were subdivided into stand-replacement (human forest clearing and natural forest disturbances) and non–stand-replacement (degradation), which consists of fire and selective logging (Table 8). For stand-replacement disturbances, a sample pixel was considered "loss" if the entire pixel or half of the pixel (in case of mixed boundary pixels) experienced complete tree cover loss. Human forest clearing includes large-scale agroindustrial clearing for nonwoody crops, tree plantations, and pasture; small-scale clearing; clearing for mining, road construction, and other construction; and flooding of forests after the construction of dams (Table 8). Agroindustrial forest clearing is reliably distinguished from all other clearing types at Landsat resolution based on the size, shape, and spatial pattern of a clearing. However, distinguishing agroindustrial clearing for row crops from newly established pastures may be challenging in the absence of high-resolution imagery on Google Earth. Georeferenced ground images from Panoramio provide additional information for interpreters in these cases. Small-scale clearing was identified by its size and postclearing land use (combination of cropland, pasture, orchards, and residences) for older clearings and by size only for the fresh clearings. Median area of loss patches identified as small-scale clearing is 5 ha. Only 24% of small-scale clearing sample pixels fall within the most recent INCRA (National Institute of Colonization and Agrarian Reform) settlement map, which indicates that these small-scale clearings are created not only by smallholders (rural settlers) but also by agro-industrial enterprises. Natural forest disturbances include windfalls, river meandering, and other natural disturbances. The latter category is very rare and implies that the type of natural disturbance could not be identified reliably (for example, it was not clear whether tree cover was lost due to a windfall or as an after-effect of a drought).

For non–stand-replacement disturbances, which included forest degradation due to fire and selective logging, a sample pixel was marked as affected by forest disturbance if it experienced canopy damage or was located within a 120-m buffer around visible fire or logging damage. The 120-m buffer (four Landsat pixels) is the minimum number of 30-m Landsat pixels, containing a 100-m buffer, corresponding to the area initially affected by felling of individual trees in conventional selective logging (*42*) and containing the most edge effects associated with increased tree mortality and altered forest structure (*43*). If a sample pixel experienced degradation (due to fire or logging) before being cleared within a study period, we considered clearing to be the major type of forest disturbance and recorded only clearing to avoid double-counting. Tropical forest fires have a distinct pattern of concentric circles (Table 8) because of diurnal variation in precipitation and humidity (*44*), which enables their identification on Landsat imagery. Selective logging is marked by the presence of logging roads and a semiregular pattern of gaps caused by tree extraction (Table 8).

Major predisturbance forest types were defined as dense (>60% canopy cover) tropical forests (both humid and dry), woodlands and parklands (10 to 60% canopy cover), and tree plantations (Table 9). Dense tropical forests were further subdivided into primary and secondary, which in Landsat imagery have different spectral responses (primary forests are usually characterized by low spectral reflectance in the shortwave infrared range) and texture (primary forests have larger crowns creating a recognizable texture, whereas secondary forests look comparatively uniform). Primary and secondary forests can be unambiguously distinguished in submeter imagery when available from Google Earth by the size of tree crowns. Primary forests identified this way using satellite imagery include primary intact and primary degraded (for example, previously selectively logged) and may include some old-growth secondary forests (for example, cleared during the rubber boom of 1879–1912). Field data show that tropical secondary forests regain the density, basal area, aboveground biomass (AGB), and species richness similar to those of primary forests after 40 years (*45*), and selectively logged primary forests fully restore their AGB in about 25 years (*46*). This evidence suggests that primary degraded and old-growth secondary forests, indistinguishable in circa 2000 satellite imagery from primary intact forests, have carbon storage and biodiversity value analogous to those of primary intact forests, and that possible inclusion of such forests into our "primary forest" category will not affect the main conclusions of the study.

Woodlands and parklands were also subdivided into natural (primary) and secondary. Natural woodlands and parklands correspond to the uniform woody vegetation patches in the "Tropical grasslands, savannas, and shrublands" biome (*38*). The biome map also helped distinguish between dense secondary forests in the tropical forest biome and natural woodlands. Secondary woodlands and parklands represent sparse secondary regrowth in both tropical forests and savannas. Tree plantations are characterized by regular patch shapes, high reflectance in the shortwave infrared range and uniform texture in Landsat imagery, and systematic planting recognizable in high-resolution imagery.

Table 9. Predisturbance forest types. Images are subsets of pre- and postdisturbance (top and bottom, respectively) for annual Landsat composites on the left (band combination, 5-4-3) and Google Earth imagery on the right. Small red rectangles represent sampled pixels.

Predisturbance forest type		Predisturbance Landsat	Predisturbance high-resolution imagery from Google Earth
Dense (>60% canopy cover) tropical forests	Primary		
	Secondary		
Woodlands (40 to 60% canopy cover) and parklands (10 to 40% canopy cover)	Natural (primary)		
	Secondary		
Forest plantations and other tree crops			

Quality of reference data

The quality of sample visual interpretation depends on multiple factors, such as the availability of reference satellite data, distinguishability of various classes with the available satellite data (discussed in the previous subsection), image interpretation experience of validation experts, and usability of validation interface. Here, we will discuss several indicators of the quality of the reference sample data, which is a basis of the current analysis.

The primary source of reference data to identify the presence or absence of forest loss in each sampled pixel was annual Landsat cloud-free composites, produced using the entire archive of Landsat ETM+ data for the study period. Eighty-one percent of the sampled pixels had at least one cloud-free observation in each year (2000–2013), 9% had one missing annual observation, 4% had two missing observations, 2% had three missing observations, 3% had four missing observations, and 2% had five or more missing observations. Additionally, 44% of all sample pixels had at least one very high resolution (VHR; resolution, <1 m) image on Google Earth, 34% had SPOT image (resolution, 2.5 m), and 22% had only Landsat. These higher-resolution imagery sources (VHR and SPOT) facilitated identification of forest loss cause and predisturbance forest type. Sampled pixels with detected forest loss had higher availability of high-resolution imagery on Google Earth (58% VHR, 38% SPOT, and 4% Landsat only), which is probably due to the fact that high-resolution imaging systems target settlements and areas of human development more often than undisturbed forested areas.

Visual interpretation of each sample pixel was first performed by each of the two experts independently; initial agreement between the interpreters on the sampled pixel belonging to the yes/no/boundary forest loss category was 87%. The remaining 13% of sampled pixels were iteratively reinterpreted until consensus was reached. From the sampled pixels with initial forest loss agreement, 80% had loss year agreement and another 12% had a 1-year difference in loss date between the two interpreters. Sampled pixels with initial forest loss agreement had 78% agreement for loss type and 82% agreement for predisturbance forest type. High rates of initial interpretation agreement illustrate that interpretation criteria, described in the previous subsection, were applied by the experts consistently.

Auxiliary data: DEGRAD

DEGRAD is a forest degradation monitoring system operated by INPE (www.obt.inpe.br/degrad/). DEGRAD data for the BLA exist for 2007–2013 and identify three types of degradation: mild (small gaps from selective logging), moderate (later stages of selective logging, skid trails, and other logging infrastructure are visible in the imagery, but large trees and the structure of canopy are still preserved), and intensive (significant loss of large trees and understory due to heavy selective logging, often accompanied by recurring fires). The DEGRAD methodology is based on visual interpretation of a single good image during the year. Hand-drawn polygons of forest degradation outline the forest area in which degradation events were observed. Of the degradation area mapped by DEGRAD, 49% is outside of our sampling region, which includes forest canopy damages, detectable in Landsat imagery and mapped by PRODES and UMD, and a surrounding 120-m buffer. To ensure an adequate comparison of our sample-based fire and logging estimates with DEGRAD, we analyzed DEGRAD only within our sampling region.

Auxiliary data: TerraClass and TerraClass Cerrado

TerraClass is another project operated by INPE (www.inpe.br/cra/projetos_pesquisas/dados_terraclass.php) with the objective of mapping land uses following deforestation in primary forests of the BLA (*26*). TerraClass is currently available for the years 2004, 2008, 2010, 2012, and 2014. Each year's map assigns the type of land use to all areas that were deforested by that year according to PRODES using single-date Landsat imagery. Current year's deforestation does not have an assigned postdeforestation land use (for example, year 2004 TerraClass has "Deforestation 2004" class). Therefore, to compare our sample-based disturbance types (which reflect only the first transition of forested vegetation to other land covers) to TerraClass postdeforestation land uses (which may change over time), we overlaid sample pixels identified in our study as 2001–2003 forest loss with 2004 TerraClass; 2004–2007 loss sample pixels with 2008 TerraClass; and 2008–2009 with 2010, 2010–2011 with 2012, and 2012–2013 loss sample pixels with 2014 TerraClass. Only the sample pixels identified as human clearing of primary forests were used in the comparison to ensure the best match with deforestation as mapped by PRODES. All TerraClass pasture categories (pastures, pastures with shrubs, pastures with bare soil, and pastures with tree regeneration) were combined into one pasture category to facilitate the comparison; secondary vegetation and reforestation classes were also combined (Table 4). Combining pasture categories into one class was reported to decrease confusion between TerraClass postdeforestation land-use classes from 23 to 10% based on a sample validation using SPOT reference data (*26*).

TerraClass Cerrado is a similar Landsat-based system mapping land uses following the conversion of natural vegetation into other land uses in the woodland region of Cerrado (www.dpi.inpe.br/tccerrado/). TerraClass Cerrado is available only for the year 2013. We compared the 2013 TerraClass Cerrado land-use map with the sample pixels labeled as human clearing of natural woodlands in 2001–2012 of our current study (Table 5); year 2013 was eliminated from the comparison due to the possible omission of late 2013 forest loss in TerraClass, which uses single-date Landsat imagery.

Auxiliary data: MapBiomas

MapBiomas is a nongovernmental land-cover and land-use mapping project, operated by a consortium of nongovernmental organizations, universities, and geospatial companies in Brazil (http://mapbiomas.org/), using modern cloud computing and data storage technologies. Currently, the project is still under development. Collection 1 annual land-cover and land-use maps are available for the years 2008 to 2015; accuracy assessment information is not yet available. Maps are produced from multitemporal Landsat image composites using a combination of spectral mixture analysis (to map forests) and supervised Random Forest classification (to map pasture, cropland, and planted forests) and a set of priority rules to combine individual thematic layers.

Because in the current study we identified only the first land-cover transition after stand-replacement forest disturbance, we compared our forest loss sample pixels with the temporally closest MapBiomas map: 2001–2007 forest loss samples were compared with 2008 MapBiomas classes; 2008 loss with 2009 MapBiomas; 2009 with 2010; 2010 with 2011; 2011 with 2012; 2012 with 2013; and 2013 forest loss samples with 2014 MapBiomas land-cover and land-use classes. MapBiomas is available for all biomes, and therefore, we were able to compare it with sampled pixels identified in the current study as human clearing of all forest types (primary and secondary dense humid tropical forests, natural and secondary woodlands, and planted forests).

Auxiliary data: AGC density

To estimate the contribution of different types of forest disturbances to gross carbon loss, we used circa year 2000 biomass maps, rather than maps of "premodern" (circa 1970s) biomass (*47*), because we do not estimate pre-2000 forest disturbance rates in the present study. The following circa year 2000 AGB/AGC density maps were intersected with our sample pixels: (i) the new 30-m Baccini *et al.* (*48*) data set, obtained from the Global Forest Watch website (www.climate.globalforestwatch.org), of a continuous 30-m resolution layer of AGB density estimates, produced using Landsat imagery and Geoscience Laser Altimeter System (GLAS)–estimated biomass following an approach for MODIS-based mapping (*49*); (ii) Saatchi *et al.* (*50*) 1-km resolution AGB density map, derived using a combination of lidar, optical, and microwave remotely sensed data; and (iii) Avitabile *et al.* (*51*) 1-km resolution AGB density map, integrating Saatchi's and Baccini's maps (*49*, *50*) and correcting for biases present in these maps (*52*, *53*) by using an independent set of reference data.

Predisturbance (year 2000) carbon densities for each forest type (Table 1) were derived by averaging values from each map corresponding to all tree cover loss sample pixels of this forest type. Estimates of AGB density from Baccini's, Saatchi's, and Avitabile's maps (Mg/ha) were converted to AGC density (MgC/ha) using a 0.5 coefficient. The range of mean AGC densities from all three map sources was further used to compare annual proportions of AGC loss from human clearing of primary forests and from other forest disturbances (Fig. 6).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/4/e1601047/DC1

table S1. Total 2001–2013 forest cover loss in BLA by disturbance type and forest type (Mha ± SE).
table S2A. Annual forest cover loss in BLA by disturbance type in all forests (Mha ± SE).
table S2B. Annual tree cover loss in BLA by forest type (Mha ± SE), all disturbance types.
table S3. Annual tree cover loss in BLA by major disturbance types and types of forest cover (Mha ± SE).
table S4. Disturbance types by state and forest type (Mha ± SE), corresponding to Fig. 3.
table S5. Annual human forest clearing by state and forest type (Mha ± SE), corresponding to Fig. 5.

REFERENCES AND NOTES

1. Instituto Nacional de Pesquisas Espaciais, *Monitoramento da Cobertura Florestal da Amazônia por Satélites: Sistemas PRODES, DETER, DEGRAD E QUEIMADAS 2007-2008* (Instituto Nacional de Pesquisas Espaciais, 2008).
2. J. Karstensen, G. Peters, R. M. Andrew, Attribution of CO_2 emissions from Brazilian deforestation to consumers between 1990 and 2010. *Environ. Res. Lett.* **8**, 024005 (2013).
3. P. M. Fearnside, A. M. R. Figueiredo, S. C. M. Bonjour, Amazonian forest loss and the long reach of China's influence. *Environ. Dev. Sustain.* **15**, 325–338 (2013).
4. E. Barona, N. Ramankutty, G. Hyman, O. T. Coomes, The role of pasture and soybean in deforestation of the Brazilian Amazon. *Environ. Res. Lett.* **5**, 024002 (2010).
5. D. C. Morton, R. S. DeFries, Y. E. Shimabukuro, L. O. Anderson, E. Arai, F. del Bon Espirito-Santo, R. Freitas, J. Morisette, Cropland expansion changes deforestation dynamics in the southern Brazilian Amazon. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 14637–14641 (2006).
6. D. Boucher, S. Roquemore, E. Fitzhugh, Brazil's success in reducing deforestation. *Trop. Conserv. Sci.* **6**, 426–445 (2013).
7. D. Nepstad, D. Mcgrath, C. Stickler, A. Alencar, A. Azevedo, B. Swette, T. Bezerra, M. Digiano, J. Shimada, R. Seroa da Motta, E. Armijo, L. Castello, P. Brando, M. C. Hansen, M. Mcgrath-Horn, O. Carvalho, L. Hess, Slowing Amazon deforestation through public policy and interventions in beef and soy supply chains. *Science* **344**, 1118–1123 (2014).
8. J. Assunção, C. Gandour, R. Rocha, Deforestation slowdown in the Brazilian Amazon: Prices or policies? *Environ. Dev. Econ.* **20**, 697–722 (2015).
9. A. Tyukavina, A. Baccini, M. C. Hansen, V Potapov, S. V Stehman, R. A. Houghton, A. M. Krylov, S. Turubanova, S. J. Goetz, Aboveground carbon loss in natural and managed tropical forests from 2000 to 2012. *Environ. Res. Lett.* **10**, 074002 (2015).
10. M. C. Hansen, V Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, J. R. G. Townshend, High-resolution global maps of 21-st century forest cover change. *Science* **342**, 850–853 (2013).
11. R. A. Houghton, Carbon emissions and the drivers of deforestation and forest degradation in the tropics. *Curr. Opin. Environ. Sustain.* **4**, 597–603 (2012).
12. N. Hosonuma, M. Herold, V. De Sy, R. S. DeFries, M. Brockhaus, L. Verchot, A. Angelsen, E. Romijn, An assessment of deforestation and forest degradation drivers in developing countries. *Environ. Res. Lett.* **7**, 044009 (2012).
13. G. Asner, D. E. Knapp, E. N. Broadbent, J. C. Oliveira, M. Keller, J. N. Silva, Selective logging in the Brazilian Amazon. *Science* **310**, 480–482 (2005).
14. C. M. Souza Jr., D. Roberts, Mapping forest degradation in the Amazon region with Ikonos images. *Int. J. Remote Sens.* **26**, 425–429 (2005).
15. P. Olofsson, G. M. Foody, M. Herold, S. V. Stehman, C. E. Woodcock, M. A. Wulder, Good practices for estimating area and assessing accuracy of land change. *Remote Sens. Environ.* **148**, 42–57 (2014).
16. S. V. Stehman, Estimating area from an accuracy assessment error matrix. *Remote Sens. Environ.* **132**, 202–211 (2013).
17. Global Forest Observations Initiative, *Integration of Remote-Sensing and Ground-Based Observations for Estimation of Emissions and Removals of Greenhouse Gases in Forests: Methods and Guidance from the Global Forest Observations Initiative* (Food and Agriculture Organization, ed. 2, 2016).
18. F. E. Putz, P. A. Zuidema, T. Synnott, M. Peña-Claros, M. A. Pinard, D. Sheil, J. K. Vanclay, P. Sist, S. Gourlet-Fleury, B. Griscom, J. Palmer, R. Zagt, Sustaining conservation values in selectively logged tropical forests: The attained and the attainable. *Conserv. Lett.* **5**, 296–303 (2012).
19. A. Alencar, D. Nepstad, C. Vera, Forest understory fire in the Brazilian Amazon in ENSO and non-ENSO years: Area burned and committed carbon emissions. *Earth Interact.* **10**, 1–17 (2006).
20. C. Souza Jr., J. Siqueira, M. Sales, A. Fonseca, J. Ribeiro, I. Numata, M. Cochrane, C. Barber, D. Roberts, J. Barlow, Ten-year Landsat classification of deforestation and forest degradation in the Brazilian Amazon. *Remote Sens.* **5**, 5493–5513 (2013).
21. D. C. Morton, Y. Le Page, R. DeFries, G. J. Collatz, G. C. Hurtt, Understorey fire frequency and the fate of burned forests in southern Amazonia. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**, 20120163 (2013).
22. S. L. Lewis, M. Brando, O. L. Phillips, G. M. F. Van Der Heijden, D. Nepstad, The 2010 Amazon drought. *Science* **331**, 554 (2011).
23. N. Zeng, J.-H. Yoon, J. A. Marengo, A. Subramaniam, C. A. Nobre, A. Mariotti, J. D. Neelin, Causes and impacts of the 2005 Amazon drought. *Environ. Res. Lett.* **3**, 014002 (2008).
24. M. A. Cochrane, Fire science for rainforests. *Nature* **421**, 913–919 (2003).
25. M. A. Cochrane, W. F. Laurance, Synergisms among fire, land use, and climate change in the Amazon. *AMBIO* **37**, 522–527 (2008).
26. C. A. de Almeida, A. C. Coutinho, J. C. D. M. Esquerdo, M. Adami, A. Venturieri, C. G. Diniz, N. Dessay, L. Durieux, A. R. Gomes, High spatial resolution land use and land cover mapping of the Brazilian Legal Amazon in 2008 using Landsat-5/TM and MODIS data. *Acta Amaz.* **46**, 291–302 (2016).
27. Intergovernmental Panel on Climate Change, *Good Practice Guidance for Land Use, Land-Use Change and Forestry* (IPCC National Greenhouse Gas Inventories Programme, 2003).
28. C. G. Diniz, A. A. de Almeida Souza, D. C. Santos, M. C. Dias, N. C. Da Luz, D. R. V. de Moraes, J. S. A. Maia, A. R. Gomes, I. da Silva Narvaes, D. M. Valeriano, L. E. P. Maurano, M. Adami, DETER-B: The new Amazon near real-time deforestation detection system. *IEEE J. Sel. Top. Appl. Earth Obs. Remote Sens.* **8**, 3619–3628 (2015).
29. T. R. Fieldpausch, M. A. Rondon, E. C. M. Fernandes, S. J. Riha, E. Wandelli, Carbon and nutrient accumulation in secondary forests regenerating on pastures in Central Amazonia. *Ecol. Appl.* **14**, 164–176 (2004).
30. C. A. Klink, R. B. Machado, Conservation of the Brazilian cerrado. *Conserv. Biol.* **19**, 707–713 (2005).
31. J. F. Silva, M. R. Fariñas, J. M. Felfili, C. A. Klink, Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. *J. Biogeogr.* **33**, 536–548 (2006).
32. S. A. Spera, G. L. Galford, M. T. Coe, M. N. Macedo, J. F. Mustard, Land-use change affects water recycling in Brazil's last agricultural frontier. *Glob. Chang. Biol.* **22**, 3405–3413 (2016).
33. P. Ratana, A. R. Huete, L. Ferreira, Analysis of cerrado physiognomies and conversion in the MODIS seasonal–temporal domain. *Earth Interact.* **9**, 1–22 (2005).
34. N. C. Ferreira, L. G. Ferreira, M. E. Ferreira, M. Bustamante, and J. Ometto, Assessing deforestation related carbon emissions in the Brazilian savanna based on moderate resolution imagery, in *2011 IEEE International Geoscience and Remote Sensing Symposium (IGARSS)* (IEEE, 2011), pp. 748–751.
35. M. C. Hansen, A. Krylov, A. Tyukavina, V. Potapov, S. Turubanova, B. Zutta, S. Ifo, B. Margono, F. Stolle, R. Moore, Humid tropical forest disturbance alerts using Landsat data. *Environ. Res. Lett.* **11**, 034008 (2016).
36. P. V. Potapov, J. Dempewolf, Y. Talero, M. C. Hansen, S. V Stehman, C. Vargas, E. J. Rojas, D. Castillo, E. Mendoza, A. Calderón, R. Giudice, N. Malaga, B. R. Zutta, National satellite-based humid tropical forest change assessment in Peru in support of REDD+ implementation. *Environ. Res. Lett.* **9**, 124012 (2014).
37. A. Tyukavina, S. V. Stehman, P.V. Potapov, S. A. Turubanova, A. Baccini, S. J. Goetz, N. T. Laporte, R. A. Houghton, M. C. Hansen, National-scale estimation of gross forest

aboveground carbon loss: A case study of the Democratic Republic of the Congo. *Environ. Res. Lett.* **8**, 1–14 (2013).

38. D. M. Olson, E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'Amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, K. R. Kassem, Terrestrial ecoregions of the world: A new map of life on Earth. *Bioscience* **51**, 933–938 (2001).
39. Y. E. Shimabukuro, J. R. dos Santos, A. R. Formaggio, V. Duarte, B. F. T. Rudorff, The Brazilian Amazon monitoring program: PRODES and DETER projects, in *Global Forest Monitoring from Earth Observation* (CRC Press, 2012), p. 354.
40. P. V. Potapov, S. A. Turubanova, M. C. Hansen, B. Adusei, M. Broich, A. Altstatt, L. Mane, C. O. Justice, Quantifying forest cover loss in Democratic Republic of the Congo, 2000–2010, with Landsat ETM + data. *Remote Sens. Environ.* **122**, 106–116 (2012).
41. W. G. Cochran, *Sampling Techniques* (John Wiley & Sons, ed. 3, 1977).
42. G. P. Asner, M. Keller, J. N. M. Silva, Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon. *Glob. Chang. Biol.* **10**, 765–783 (2004).
43. E. N. Broadbent, G. P. Asner, M. Keller, D. E. Knapp, P. J. C. Oliveira, J. N. Silva, Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv.* **141**, 1745–1757 (2008).
44. L. Giglio, Characterization of the tropical diurnal fire cycle using VIRS and MODIS observations. *Remote Sens. Environ.* **108**, 407–421 (2007).
45. T. M. Aide, J. K. Zimmerman, J. B. Pascarella, L. Rivera, H. Marcano-Vega, Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. *Restor. Ecol.* **8**, 328–338 (2000).
46. S. Gourlet-Fleury, F. Mortier, A. Fayolle, F. Baya, D. Ouédraogo, F. Bénédet, N. Picard, Tropical forest recovery from logging: A 24 year silvicultural experiment from Central Africa. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**, 20120302 (2013).
47. E. M. Nogueira, A. M. Yanai, F. O. R. Fonseca, P. M. Fearnside, Carbon stock loss from deforestation through 2013 in Brazilian Amazonia. *Glob. Chang. Biol.* **21**, 1271–1292 (2015).
48. D. J. Zarin, N. L. Harris, A. Baccini, D. Aksenov, M. C. Hansen, C. Azevedo-Ramos, T. Azevedo, B. A. Margono, A. C. Alencar, C. Gabris, A. Allegretti, P. Potapov, M. Farina, W. S. Walker, V. S. Shevade, T. V. Loboda, S. Turubanova, A. Tyukavina, Can carbon emissions from tropical deforestation drop by 50% in 5 years? *Glob. Chang. Biol.* **22**, 1336–1347 (2016).
49. A. Baccini, S. J. Goetz, W. S. Walker, N. T. Laporte, M. Sun, D. Sulla-Menashe, J. Hackler, P. S. A. Beck, R. Dubayah, M. A. Friedl, S. Samanta, R. A. Houghton, Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. *Nat. Clim. Chang.* **2**, 182–185 (2012).
50. S. S. Saatchi, N. L. Harris, S. Brown, M. Lefsky, E. T. A. Mitchard, W. Salas, Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 9899–9904 (2011).
51. V. Avitabile, M. Herold, G. B. M. Heuvelink, S. L. Lewis, O. L. Phillips, G. P. Asner, J. Armston, P. S. Ashton, L. Banin, N. Bayol, N. J. Berry, P. Boeckx, B. H. J. De Jong, B. DeVries, C. A. J. Girardin, E. Kearsley, J. A. Lindsell, G. Lopez-Gonzalez, R. Lucas, Y. Malhi, A. Morel, E. T. A. Mitchard, L. Nagy, L. Qie, M. J. Quinones, C. M. Ryan, S. J. W. Ferry, T. Sunderland, G. Vaglio Laurin, R. Cazzolla Gatti, R. Valentini, H. Verbeeck, A. Wijaya, S. Willcock, An integrated pan-tropical biomass map using multiple reference datasets. *Glob. Chang. Biol.* **22**, 1406–1420 (2016).
52. E. T. A. Mitchard, T. R. Feldpausch, R. J. W. Brienen, G. Lopez-Gonzalez, A. Monteagudo, T. R. Baker, S. L. Lewis, J. Lloyd, C. A. Quesada, M. Gloor, H. ter Steege, P. Meir, E. Alvarez, A. Araujo-Murakami, L. E. O. C. Aragão, L. Arroyo, G. Aymard, O. Banki, D. Bonal, S. Brown, F. I. Brown, C. E. Cerón, V. C. Moscoso, J. Chave, J. A. Comiskey, F. Cornejo, M. C. Medina, L. Da Costa, F. R. C. Costa, A. Di Fiore, T. F. Domingues, T. L. Erwin, T. Frederickson, N. Higuchi, E. N. H. Coronado, T. J. Killeen, W. F. Laurance, C. Levis, W. E. Mangusson, B. S. Marimon, B. H. Marimon Jr., I. M. Polo, P. Mishra, M. T. Nascimento, D. Neill, M. P. Núñez Vargas, W. A. Palacios, A. Parada, G. P. Molina, M. Peña-Claros, N. Pitman, C. A. Peres, L. Poorter, A. Prieto, H. Ramirez-Angulo, Z. Restrepo Correa, A. Roopsind, K. H. Roucoux, A. Rudas, R. P. Salomão, J. Schietti, M. Silveira, P. F. de Souza, M. K. Steininger, J. Stropp, J. Terborgh, R. Thomas, M. Toledo, A. Torrez-Lezama, T. R. van Andel, G. M. F. van der Heijden, I. C. G. Vieira, S. Vieira, E. Vilanova-Torre, V. A. Vos, O. Wang, C. E. Zartman, Y. Malhi, O. L. Philips, Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites. *Glob. Ecol. Biogeogr.* **23**, 1–12 (2014).
53. E. T. A. Mitchard, S. S. Saatchi, A. Baccini, G. P. Asner, S. J. Goetz, N. L. Harris, S. Brown, Uncertainty in the spatial distribution of tropical forest biomass: A comparison of pan-tropical maps. *Carbon Balance Manag.* **8**, 10 (2013).

Acknowledgments: We thank H. Mesquita (Brazilian Forest Service) for valuable insight into Brazilian national forest monitoring data. **Funding:** Support for the study was provided by the Gordon and Betty Moore Foundation (grant 5131), Norwegian Climate and Forests Initiative through the Global Forest Watch project, NASA Land Cover and Land Use Change program (grant NNX08AL99G), and NASA Carbon Monitoring System program (grant NNX13AP48G). **Author contributions:** A.T., M.C.H., P.V.P., and S.V.S. designed the study. A.T., K.S.-R., C.O., and R.A. interpreted sample data. A.T. and S.V.S. performed statistical data analysis. A.T., M.C.H., P.V.P., and S.V.S. wrote and edited the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions of the study are present in the paper and/or the Supplementary Materials. Individual sample interpretation data may be provided by the authors upon request.

Submitted 10 May 2016
Accepted 21 February 2017
Published 12 April 2017
10.1126/sciadv.1601047

Citation: A. Tyukavina, M. C. Hansen, P. V. Potapov, S. V. Stehman, K. Smith-Rodriguez, C. Okpa, R. Aguilar, Types and rates of forest disturbance in Brazilian Legal Amazon, 2000–2013. *Sci. Adv.* **3**, e1601047 (2017).


THIS IS NOT SCIENCE FICTION
This is captivating, impactful *Science* | ScienceMag.org
Check out the *Science* family of journals for
news-making research and analysis for the scientific community.