



Cover image: Pictured is a Tasmanian devil (*Sarcophilus harrisii*), a carnivorous marsupial whose numbers are dwindling due to an infectious facial cancer called Devil Facial Tumor Disease. Webb Miller et al. sequenced the genome of devils from northwest and southeast Tasmania, spanning the range of this threatened species on the Australian island. The authors report that the sequences reveal a worrisome dearth of genetic diversity among devils, suggesting the need for genetically characterized stocks to help breed hardier devils that might be better equipped to fight diseases. See the article by Miller et al. on pages 12348–12353. Image courtesy of Stephan C. Schuster.

From the Cover

- 12348 Decoding the Tasmanian devil genome
- 12283 Illuminating chromosomal architecture
- 12295 Symmetry of cultured cells
- 12319 Caloric restriction and infertility
- 12366 Genetic diversity among ants

Contents

THIS WEEK IN PNAS

- 12187 In This Issue

LETTERS (ONLINE ONLY)

- E341 **Difference between restoring and predicting 3D structures of the loops in G-protein-coupled receptors by molecular modeling**
Gregory V. Nikiforovich, Christina M. Taylor, Garland R. Marshall, and Thomas J. Baranski
- E342 **Reply to Nikiforovich et al.: Restoration of the loop regions of G-protein-coupled receptors**
Dahlia A. Goldfeld, Kai Zhu, Thijs Beuming, and Richard A. Friesner
- E343 **Can the functional MRI responses to physical pain really tell us why social rejection “hurts”?**
Gian Domenico Iannetti and André Mouraux
- E344 **Reply to Iannetti and Mouraux: What functional MRI responses to physical pain tell us about why social rejection “hurts”**
Ethan Kross, Marc G. Berman, Walter Mischel, Edward E. Smith, and Tor D. Wager



Free online through the PNAS open access option.

COMMENTARIES

- 12189 **Methyl fingerprinting of the nucleosome reveals the molecular mechanism of high-mobility group nucleosomal-2 (HMGN2) association**
Catherine A. Musselman and Tatiana G. Kutateladze
→ See companion article on page 12283
- 12191 **Examining the establishment of cellular axes using intrinsic chirality**
Jason C. McSheene and Rebecca D. Burdine
→ See companion article on page 12295
- 12193 **Secrets of palm oil biosynthesis revealed**
Toni Voelker
→ See companion article on page 12527

PROFILE

- 12195 **Profile of B. Rosemary Grant**
Prashant Nair
→ See Inaugural Article on page 20156 in issue 47 of volume 107

INAUGURAL ARTICLE

- 12198 **In vitro assembly of physiological cohesin/DNA complexes**
Itay Onn and Douglas Koshland

PHYSICAL SCIENCES

APPLIED PHYSICAL SCIENCES

- 12206 **Density hysteresis of heavy water confined in a nanoporous silica matrix**
Yang Zhang, Antonio Faraone, William A. Kamitakahara, Kao-Hsiang Liu, Chung-Yuan Mou, Juscelino B. Leão, Sung Chang, and Sow-Hsin Chen

CHEMISTRY

- 12212 **Rational growth of branched nanowire heterostructures with synthetically encoded properties and function**
 Xiaocheng Jiang, Bozhi Tian, Jie Xiang, Fang Qian, Gengfeng Zheng, Hongtao Wang, Liqiang Mai, and Charles M. Lieber
- 12217 **Nonresonant femtosecond laser vaporization of aqueous protein preserves folded structure**
John J. Brady, Elizabeth J. Judge, and Robert J. Levis

ENVIRONMENTAL SCIENCES

- 12223 **Observations of nucleation of new particles in a volcanic plume**
Julien Boulon, Karine Sellegri, Maxime Hervo, and Paolo Laj

GEOPHYSICS

- 12227 **Aerosol–cloud–precipitation system as a predator–prey problem**
 Ilan Koren and Graham Feingold

PHYSICS

- 12233 **Moiré bands in twisted double-layer graphene**
Rafi Bistritzer and Allan H. MacDonald
- 12238 **Unprecedented anisotropic metallic state in undoped iron arsenide BaFe_2As_2 revealed by optical spectroscopy**
M. Nakajima, T. Liang, S. Ishida, Y. Tomioka, K. Kihou, C. H. Lee, A. Iyo, H. Eisaki, T. Kakeshita, T. Ito, and S. Uchida

SOCIAL SCIENCES

PSYCHOLOGICAL AND COGNITIVE SCIENCES

- 12491 **Bayesian sampling in visual perception**
Rubén Moreno-Bote, David C. Knill, and Alexandre Pouget
- 12509 **Relation of addiction genes to hypothalamic gene changes subserving genesis and gratification of a classic instinct, sodium appetite**
 Wolfgang B. Liedtke, Michael J. McKinley, Lesley L. Walker, Hao Zhang, Andreas R. Pfenning, John Drago, Sarah J. Hochendoner, Donald L. Hilton, Andrew J. Lawrence, and Derek A. Denton

BIOLOGICAL SCIENCES

BIOCHEMISTRY

- 12198 **In vitro assembly of physiological cohesin/DNA complexes**
 Itay Onn and Douglas Koshland

- 12243 **Exoplasmic cysteine Cys384 of the HDL receptor SR-BI is critical for its sensitivity to a small-molecule inhibitor and normal lipid transport activity**

Miao Yu, Katherine A. Romer, Thomas J. F. Nieland, Shangzhe Xu, Veronica Saenz-Vash, Marsha Penman, Ayce Yesilaltay, Steven A. Carr, and Monty Krieger

- 12249 **tRNA-dependent peptide bond formation by the transferase PacB in biosynthesis of the pacidamycin group of pentapeptidyl nucleoside antibiotics**

Wenjun Zhang, Ioanna Ntai, Neil L. Kelleher, and Christopher T. Walsh

- 12254 **Solution structures of DEAD-box RNA chaperones reveal conformational changes and nucleic acid tethering by a basic tail**

Anna L. Mallam, Inga Jarmoskaite, Pilar Tijerina, Mark Del Campo, Soenke Seifert, Liang Guo, Rick Russell, and Alan M. Lambowitz

- 12260 **Identification of unique mechanisms for triterpene biosynthesis in *Botryococcus braunii***

Tom D. Niehaus, Shigeru Okada, Timothy P. Devarenne, David S. Watt, Vitaliy Sviripa, and Joe Chappell

- 12266 **Tumor suppressor p53 regulates bile acid homeostasis via small heterodimer partner**

Dae-Hwan Kim and Jae W. Lee

- 12271 **NMR basis for interprotein electron transfer gating between cytochrome *c* and cytochrome *c* oxidase**

Koichi Sakamoto, Masakatsu Kamiya, Mizue Imai, Kyoko Shinzawa-Itoh, Takeshi Uchida, Keiichi Kawano, Shinya Yoshikawa, and Koichiro Ishimori

- 12277 **Epsin N-terminal homology domains bind on opposite sides of two SNAREs**

Jing Wang, Michael Gossing, Pengfei Fang, Jana Zimmermann, Xu Li, Gabriele Fischer von Mollard, Liwen Niu, and Maikun Teng

BIOPHYSICS AND COMPUTATIONAL BIOLOGY

- 12283 **Architecture of the high mobility group nucleosomal protein 2-nucleosome complex as revealed by methyl-based NMR**

Hidenori Kato, Hugo van Ingen, Bing-Rui Zhou, Hanqiao Feng, Michael Bustin, Lewis E. Kay, and Yawen Bai
→ See Commentary on page 12189

- 12289 **Stereospecific gating of functional motions in Pin1**

 Andrew T. Namanja, Xiaodong J. Wang, Bailing Xu, Ana Y. Mercedes-Camacho, Kimberly A. Wilson, Felicia A. Etkorn, and Jeffrey W. Peng

- 12295 **Micropatterned mammalian cells exhibit phenotype-specific left-right asymmetry**

Leo Q. Wan, Kacey Ronaldson, Miri Park, Grace Taylor, Yue Zhang, Jeffrey M. Gimble, and Gordana Vunjak-Novakovic
→ See Commentary on page 12191

- 12301 **Maps of protein structure space reveal a fundamental relationship between protein structure and function**

Margarita Osadchy and Rachel Kolodny

- 12307 **Dispersed disease-causing neomorphic mutations on a single protein promote the same localized conformational opening**

Weiwei He, Hui-Min Zhang, Yeeting E. Chong, Min Guo, Alan G. Marshall, and Xiang-Lei Yang

- 12313  **Voltage-gated sodium channel (Na_v) protein dissection creates a set of functional pore-only proteins**
David Shaya, Mohamed Kreir, Rebecca A. Robbins, Stephanie Wong, Justus Hammon, Andrea Brüggemann, and Daniel L. Minor, Jr.

CELL BIOLOGY

- 12319  **Prevention of maternal aging-associated oocyte aneuploidy and meiotic spindle defects in mice by dietary and genetic strategies**
Kaisa Selesniemi, Ho-Joon Lee, Ailene Muhlhauser, and Jonathan L. Tilly
- 12325 **Histone H4 lysine 16 hypoacetylation is associated with defective DNA repair and premature senescence in Zmpste24-deficient mice**
Vaidehi Krishnan, Maggie Zi Ying Chow, Zimei Wang, Le Zhang, Baohua Liu, Xinguang Liu, and Zhongjun Zhou
- 12331 **Serine 105 phosphorylation of transcription factor GATA4 is necessary for stress-induced cardiac hypertrophy in vivo**
Jop H. van Berlo, John W. Elrod, Bruce J. Aronow, William T. Pu, and Jeffery D. Molkentin

ECOLOGY

- 12337 **Recent ecological responses to climate change support predictions of high extinction risk**
Ilya M. D. Maclean and Robert J. Wilson
- 12343 **Soils on exposed Sunda Shelf shaped biogeographic patterns in the equatorial forests of Southeast Asia**
J. W. Ferry Slik, Shin-Ichiro Aiba, Meredith Bastian, Francis O. Brearley, Charles H. Cannon, Karl A. O. Eichhorn, Gabriella Fredriksson, Kuswata Kartawinata, Yves Laumonier, Asyraf Mansor, Antti Marjokorpi, Erik Meijaard, Robert J. Morley, Hidetoshi Nagamasu, Reuben Nilus, Eddy Nurtjahya, John Payne, Andrea Permana, Axel D. Poulsen, Niels Raes, Soedarsono Riswan, Carel P. van Schaik, Douglas Sheil, Kade Sidiyasa, Eizi Suzuki, Johan L. C. H. van Valkenburg, Campbell O. Webb, Serge Wich, Tsuyoshi Yoneda, Rahmad Zakaria, and Nicole Zweifel

ENVIRONMENTAL SCIENCES

- 12348 **Genetic diversity and population structure of the endangered marsupial *Sarcophilus harrisii* (Tasmanian devil)**
Webb Miller, Vanessa M. Hayes, Aakrosh Ratan, Desiree C. Petersen, Nicola E. Wittekindt, Jason Miller, Brian Walenz, James Knight, Ji Qi, Fangqing Zhao, Qingyu Wang, Oscar C. Bedoya-Reina, Neerja Katiyar, Lynn P. Tomsho, Lindsay McClellan Kasson, Rae-Anne Hardie, Paula Woodbridge, Elizabeth A. Tindall, Mads Frost Bertelsen, Dale Dixon, Stephen Pycroft, Kristofer M. Helgen, Arthur M. Lesk, Thomas H. Pringle, Nick Patterson, Yu Zhang, Alexandre Kreiss, Gregory M. Woods, Menna E. Jones, and Stephan C. Schuster

EVOLUTION

- 12354  **An ATP-binding cassette subfamily G full transporter is essential for the retention of leaf water in both wild barley and rice**
Guoxiong Chen, Takao Komatsuda, Jian Feng Ma, Christiane Nawrath, Mohammad Pourkheirandish, Akemi Tagiri, Yin-Gang Hu, Mohammad Sameri, Xinrong Li, Xin Zhao, Yubing Liu, Chao Li, Xiaoying Ma, Aidong Wang, Sudha Nair, Ning Wang, Akio Miyao, Shun Sakuma, Naoki Yamaji, Xiuting Zheng, and Eviatar Nevo

- 12360 **Female gamete competition in an ancient angiosperm lineage**
Julien B. Bachelier and William E. Friedman

- 12366 **Cryptic sexual populations account for genetic diversity and ecological success in a widely distributed, asexual fungus-growing ant**
Christian Rabeling, Omar Gonzales, Ted R. Schultz, Maurício Bacci, Jr., Marcos V. B. Garcia, Manfred Verhaagh, Heather D. Ishak, and Ulrich G. Mueller

GENETICS

- 12372  **Systematic investigation of genetic vulnerabilities across cancer cell lines reveals lineage-specific dependencies in ovarian cancer**
Hiu Wing Cheung, Glenn S. Cowley, Barbara A. Weir, Jesse S. Boehm, Scott Rusin, Justine A. Scott, Alexandra East, Levi D. Ali, Patrick H. Lizotte, Terence C. Wong, Guozhi Jiang, Jessica Hsiao, Craig H. Mermel, Gad Getz, Jordi Barretina, Shuba Gopal, Pablo Tamayo, Joshua Gould, Aviad Tsherniak, Nicolas Stransky, Biao Luo, Yin Ren, Ronny Drapkin, Sangeeta N. Bhatia, Jill P. Mesirov, Levi A. Garraway, Matthew Meyerson, Eric S. Lander, David E. Root, and William C. Hahn

- 12378  **Variants of the protein PRDM9 differentially regulate a set of human meiotic recombination hotspots highly active in African populations**
Ingrid L. Berg, Rita Neumann, Shriparna Sarbajna, Linda Odenthal-Hesse, Nicola J. Butler, and Alec J. Jeffreys

- 12384 **Homozygously deleted gene DACH1 regulates tumor-initiating activity of glioma cells**
Akira Watanabe, Hideki Ogiwara, Shogo Ehata, Akitake Mukasa, Shumpei Ishikawa, Daichi Maeda, Keisuke Ueki, Yasushi Ino, Tomoki Todo, Yasuhiro Yamada, Masashi Fukayama, Nobuhito Saito, Kohei Miyazono, and Hiroyuki Aburatani

- 12390 **Mutation of the conserved polyadenosine RNA binding protein, ZC3H14/dNab2, impairs neural function in *Drosophila* and humans**
ChangHui Pak, Masoud Garshasbi, Kimia Kahrizi, Christina Gross, Luciano H. Apponi, John J. Noto, Seth M. Kelly, Sara W. Leung, Andreas Tzschach, Farkhondeh Behjati, Seyede Sedigheh Abedini, Marzieh Mohseni, Lars R. Jensen, Hao Hu, Brenda Huang, Sara N. Stahley, Guanglu Liu, Kathryn R. Williams, Sharon Burdick, Yue Feng, Subhabrata Sanyal, Gary J. Bassell, Hans-Hilger Ropers, Hossein Najmabadi, Anita H. Corbett, Kenneth H. Moberg, and Andreas W. Kuss

IMMUNOLOGY

- 12396  **Controversies in clinical cancer dormancy**
Jonathan W. Uhr and Klaus Pantel
- 12401 **Defining the quantitative limits of intravital two-photon lymphocyte tracking**
Johannes Textor, Antonio Peixoto, Sarah E. Henrickson, Mathieu Sinn, Ulrich H. von Andrian, and Jürgen Westermann
- 12407 **Targeted *Sos1* deletion reveals its critical role in early T-cell development**
Robert L. Kortum, Connie L. Sommers, Clayton P. Alexander, John M. Pinski, Wenmei Li, Alex Grinberg, Jan Lee, Paul E. Love, and Lawrence E. Samelson

- 12413 **Identification of markers that distinguish IgE- from IgG-mediated anaphylaxis**
Marat V. Khodoun, Richard Strait, Laura Armstrong, Noriko Yanase, and Fred D. Finkelman
- 12419 ***Listeria monocytogenes* engineered to activate the NlrC4 inflammasome are severely attenuated and are poor inducers of protective immunity**
John-Demian Sauer, Sabine Pereyre, Kristina A. Archer, Thomas P. Burke, Bill Hanson, Peter Lauer, and Daniel A. Portnoy
- 12425 **Tumor-associated macrophages regulate tumorigenicity and anticancer drug responses of cancer stem/initiating cells**
Masahisa Jinushi, Shigeki Chiba, Hironori Yoshiyama, Kenkichi Masutomi, Ichiro Kinoshita, Hirotohi Dosaka-Akita, Hideo Yagita, Akinori Takaoka, and Hideaki Tahara
- 12431 **Structure of FcRY, an avian immunoglobulin receptor related to mammalian mannose receptors, and its complex with IgY**
Yongning He and Pamela J. Bjorkman
- 12437 **Autoimmune regulator (AIRE)-deficient CD8⁺CD28^{low} regulatory T lymphocytes fail to control experimental colitis**
Céline Pomié, Rita Vicente, Yirajen Vuddamalay, Brita Ardesjö Lundgren, Mark van der Hoek, Geneviève Enault, Jérémy Kagan, Nicolas Fazilleau, Hamish S. Scott, Paola Romagnoli, and Joost P. M. van Meerwijk
- 12443 **Induction of PP2A B β , a regulator of IL-2 deprivation-induced T-cell apoptosis, is deficient in systemic lupus erythematosus**
José C. Crispín, Sokratis A. Apostolidis, Melissa I. Finnell, and George C. Tsokos

MEDICAL SCIENCES

- 12449 **Tumor-specific silencing of *COP22* gene encoding coatomer protein complex subunit $\zeta 2$ renders tumor cells dependent on its paralogous gene *COPZ1***
Michael Shtutman, Mirza Baig, Elina Levina, Gregory Hurteau, Chang-uk Lim, Eugenia Broude, Mikhail Nikiforov, Timothy T. Harkins, C. Steven Carmack, Ye Ding, Felix Wieland, Ralph Buttyan, and Igor B. Roninson
- 12455 **Tumorigenesis in tuberous sclerosis complex is autophagy and p62/sequestosome 1 (SQSTM1)-dependent**
Andrey Parkhitko, Faina Myachina, Tasha A. Morrison, Khadijah M. Hindi, Neil Auricchio, Magdalena Karbowniczek, J. Julia Wu, Toren Finkel, David J. Kwiatkowski, Jane J. Yu, and Elizabeth Petri Henske
- 12461 **A cyclin-D1 interaction with BAX underlies its oncogenic role and potential as a therapeutic target in mantle cell lymphoma**
Elena Beltran, Vicente Fresquet, Javier Martinez-Useros, Jose A. Richter-Larrea, Ainara Sagardoy, Izaskun Sesma, Luciana L. Almada, Santiago Montes-Moreno, Reiner Siebert, Stefan Gesk, Maria J. Calasanz, Raquel Malumbres, Melissa Rieger, Felipe Prosper, Izidore S. Lossos, Miguel Angel Piris, Martin E. Fernandez-Zapico, and Jose A. Martinez-Climent

MICROBIOLOGY

- 12467 **Mapping the regulon of *Vibrio cholerae* ferric uptake regulator expands its known network of gene regulation**
Bryan W. Davies, Ryan W. Bogard, and John J. Mekalanos
- 12473 **Quantifying the sequence–function relation in gene silencing by bacterial small RNAs**
Yue Hao, Zhongge J. Zhang, David W. Erickson, Min Huang, Yingwu Huang, Junbai Li, Terence Hwa, and Hualin Shi
- 12479 **Ligation of Fc gamma receptor IIB inhibits antibody-dependent enhancement of dengue virus infection**
Kuan Rong Chan, Summer Li-Xin Zhang, Hwee Cheng Tan, Ying Kai Chan, Angelia Chow, Angelina Pei Chiew Lim, Subhash G. Vasudevan, Brendon J. Hanson, and Eng Eong Ooi
- 12485 **Evasion of immunity to *Plasmodium falciparum* malaria by IgM masking of protective IgG epitopes in infected erythrocyte surface-exposed PfEMP1**
Lea Barfod, Michael B. Dalgaard, Suzan T. Pleman, Michael F. Ofori, Richard J. Pleass, and Lars Hviid

NEUROSCIENCE

- 12491 **Bayesian sampling in visual perception**
Rubén Moreno-Bote, David C. Knill, and Alexandre Pouget
- 12497 **The Etv1/Er81 transcription factor orchestrates activity-dependent gene regulation in the terminal maturation program of cerebellar granule cells**
Haruka Abe, Makoto Okazawa, and Shigetada Nakanishi
- 12503 **Contextual learning requires synaptic AMPA receptor delivery in the hippocampus**
Dai Mitsushima, Kouji Ishihara, Akane Sano, Helmut W. Kessels, and Takuya Takahashi

PHYSIOLOGY

- 12509 **Relation of addiction genes to hypothalamic gene changes subserving genesis and gratification of a classic instinct, sodium appetite**
Wolfgang B. Liedtke, Michael J. McKinley, Lesley L. Walker, Hao Zhang, Andreas R. Pfenning, John Drago, Sarah J. Hochendoner, Donald L. Hilton, Andrew J. Lawrence, and Derek A. Denton
- 12515 **Related pituitary cell lineages develop into interdigitated 3D cell networks**
Lionel Budry, Chrystel Lafont, Taoufik El Yandouzi, Norbert Chauvet, Geneviève Conéjero, Jacques Drouin, and Patrice Mollard

PLANT BIOLOGY

- 12521 **Clone history shapes *Populus* drought responses**
Sherosha Raj, Katharina Bräutigam, Erin T. Hamanishi, Olivia Wilkins, Barb R. Thomas, William Schroeder, Shawn D. Mansfield, Aine L. Plant, and Malcolm M. Campbell
- 12527 **Comparative transcriptome and metabolite analysis of oil palm and date palm mesocarp that differ dramatically in carbon partitioning**
Fabienne Bourgis, Aruna Kilaru, Xia Cao, Georges-Frank Ngando-Ebongue, Nouredine Drira, John B. Ohlrogge, and Vincent Arondel

→ See Commentary on page 12193

12533 **Genome-wide landscape of polyadenylation in *Arabidopsis* provides evidence for extensive alternative polyadenylation**
 Xiaohui Wu, Man Liu, Bruce Downie, Chun Liang, Guoli Ji, Qingshun Q. Li, and Arthur G. Hunt

12539 **Derepression of ethylene-stabilized transcription factors (EIN3/EIL1) mediates jasmonate and ethylene signaling synergy in *Arabidopsis***
Ziqiang Zhu, Fengying An, Ying Feng, Pengpeng Li, Li Xue, Mu A, Zhiqiang Jiang, Jong-Myong Kim, Taiko Kim To, Wei Li, Xinyan Zhang, Qiang Yu, Zhi Dong, Wen-Qian Chen, Motoaki Seki, Jian-Min Zhou, and Hongwei Guo

POPULATION BIOLOGY

12227 **Aerosol–cloud–precipitation system as a predator–prey problem**
 Ilan Koren and Graham Feingold

PSYCHOLOGICAL AND COGNITIVE SCIENCES

12545 **Plasticity of human auditory-evoked fields induced by shock conditioning and contingency reversal**
 Christian Kluge, Markus Bauer, Alexander Paul Leff, Hans-Jochen Heinze, Raymond J. Dolan, and Jon Driver

12551 **The human visual system's assumption that light comes from above is weak**
Yaniv Morgenstern, Richard F. Murray, and Laurence R. Harris

SUSTAINABILITY SCIENCE

12554 **Social-ecological interactions, management panaceas, and the future of wild fish populations**
Brett T. van Poorten, Robert Arlinghaus, Katrin Daedlow, and Susanne S. Haertel-Borer

ix Subscription Form

PRESIDENT OF THE ACADEMY

Ralph J. Cicerone

EDITOR-IN-CHIEF

Randy Schekman

ASSOCIATE EDITORS

David Chandler
Alan Fersht
Jack Halpern
Dolores R. Piperno
Solomon H. Snyder
B. L. Turner II
Peter K. Vogt
Susan R. Wessler

EDITORIAL BOARD

Animal, Nutritional, and Applied Microbial Sciences

David L. Denlinger
R. Michael Roberts
Linda J. Saif
Ryuzo Yanagimachi

Anthropology

Richard G. Klein
C. Owen Lovejoy
James F. O'Connell

Applied Mathematical Sciences

Peter J. Bickel
David L. Donoho
Stephen E. Fienberg

Applied Physical Sciences

Francisco de la Cruz
Jerry P. Gollub
Tom C. Lubensky
David A. Weitz

Astronomy

Neta A. Bahcall

Biochemistry

Michael R. Botchan
Jennifer A. Doudna
Edward D. Korn
Stephen C. Kowalczykowski
John Kuriyan
Michael A. Marletta
Kiyoshi Mizuuchi
Charles M. Radding
Venkatraman Ramakrishnan
Tom A. Rapoport
James A. Wells
William T. Wickner

Biophysics and Computational Biology

David Baker
Adriaan Bax
Axel T. Brunger
William A. Eaton
Angela M. Gronenborn
Barry H. Honig
Robert Langer
Michael Levitt
Gregory A. Petsko
John W. Sedat

Cellular and Developmental

Biology

C. David Allis
Donald D. Brown
Eric H. Davidson
Brigid L. M. Hogan
Eric N. Olson
Michael Rosbash
David D. Sabatini
Gertrud M. Schüpbach

Cellular and Molecular

Neuroscience

David E. Clapham
Pietro V. De Camilli
Richard L. Huganir
L. L. Iversen
Yuh-Nung Jan
Eve Marder
Jeremy Nathans
Charles F. Stevens
Thomas C. Südhof
Joseph S. Takahashi

Chemistry

Stephen J. Benkovic
Harry B. Gray
Michael L. Klein
Raphael D. Levine
Tobin J. Marks
Jerrold Meinwald
David A. Tirrell
Nicholas J. Turro

Computer and Information Sciences

Butler W. Lampson
William H. Press

Earth, Atmospheric, and Planetary Sciences

Thure E. Cerling
W. G. Ernst
Andrew H. Knoll
Mark H. Thieme

Economic Sciences

Roy Radner
Jose A. Scheinkman

Engineering Sciences

Alexis T. Bell
Mark E. Davis
Mildred S. Dresselhaus
Evelyn L. Hu
William R. Schowalter

Environmental Sciences and Ecology

Robert E. Dickinson
Paul G. Falkowski
David M. Karl
Robert May
William W. Murdoch
David W. Schindler

Evolutionary Biology

Francisco J. Ayala
May R. Berenbaum
Sean B. Carroll
W. Ford Doolittle
Douglas J. Futuyma
Daniel L. Hartl
Richard E. Lenski
Masatoshi Nei
Gene E. Robinson

Genetics

Kathryn V. Anderson
Thomas W. Cline
Stanley N. Cohen
Barry Ganetzky
Iva Š. Greenwald
Jeffrey C. Hall
Philip C. Hanawalt
Mary-Claire King
Jasper Rine
Reed B. Wickner

Human Environmental Sciences

Ruth S. DeFries
Susan Hanson

Immunology

Peter Cresswell
Douglas T. Fearon
Tak Wah Mak
Philippa Marrack
William E. Paul
Ralph M. Steinman
Tadatsugu Taniguchi
Arthur Weiss

Mathematics

Richard V. Kadison
Robion C. Kirby
Kenneth A. Ribet

Medical Genetics, Hematology, and Oncology

Dennis A. Carson
C. Thomas Caskey
Joseph L. Goldstein
Mark T. Groudine
Tony Hunter
Philip W. Majerus
Inder M. Verma
Owen N. Witte

Medical Physiology and Metabolism

Robert J. Lefkowitz
David J. Mangelsdorf
Salvador Moncada
David W. Russell

Microbial Biology

John M. Coffin
R. John Collier
Emil C. Gotschlich
E. Peter Greenberg
Diane E. Griffin
Peter M. Howley
Ralph R. Isberg
Elliott D. Kieff
Robert A. Lamb
Peter Palese
Thomas E. Shenk

Thomas J. Silhavy
Thomas E. Wellems

Physics

Curtis G. Callan, Jr.
Anthony Leggett
Paul C. Martin

Physiology and Pharmacology

Richard W. Aldrich
Susan G. Amara
David Julius
Arthur Karlin
Ramón Latorre

Plant Biology

David Baulcombe
Anthony R. Cashmore
Maarten J. Chrispeels
Enrico Coen
Joseph R. Ecker
Robert Haselkorn
June B. Nasrallah

Plant, Soil, and Microbial Sciences

James C. Carrington
Vicki L. Chandler
Brian J. Staskawicz

Psychological and Cognitive Sciences

Wilson S. Geisler
J. Anthony Movshon
Dale Purves
Edward E. Smith

Social and Political Sciences

Alejandro Portes
Brian Skyrms
Kenneth W. Wachter

Sustainability Science

Barry R. Bloom
William C. Clark
Partha Sarathi Dasgupta
Robert W. Kates
Pamela A. Matson
Elinor Ostrom
Stephen Polasky
Hans Joachim Schellnhuber

Systems Biology

Marc W. Kirschner
Eric D. Siggia
Wing Hung Wong

Systems Neuroscience

Thomas D. Albright
Robert Desimone
Fred H. Gage
Charles D. Gilbert
Marcus E. Raichle
Leslie G. Ungerleider

Submission to PNAS

Authors (members and nonmembers) may submit their manuscripts directly to PNAS at www.pnascentral.org. Authors must recommend three appropriate Editorial Board members, three NAS members who are expert in the paper's scientific area, and five qualified referees. No Academy member sponsor is required.

PNAS (ISSN-0027-8424) is published weekly in print by the National Academy of Sciences.

Correspondence: PNAS, 700 11th Street, NW, Suite 450, Washington, DC 20001 USA. E-mail: PNAS@nas.edu.

Copyright: Volumes 90–105, copyright © 1993–2008 by the National Academy of Sciences of the United States of America, all rights reserved. Volumes 1–89 and 106–108, copyright as a collective work only; author(s) retains copyright to individual articles. **Requests for Permission:** See www.pnas.org/misc/rightperm.shtml for details.

Address requests to reproduce material published in Volumes 1–89 to the original author(s); e-mail other requests to PNASpermissions@nas.edu, fax 1-202-334-2739, or PNAS Permissions Editor, 700 11th Street, NW, Suite 450, Washington, DC 20001 USA. Please cite the exact material to be reprinted and state specifically where it will be used.

Photocopies: PNAS is registered with the Copyright Clearance Center (CCC), 222 Rosewood Drive, Danvers, MA 01923 USA, fax 1-978-750-4470, or www.copyright.com. Authorization to photocopy items for the internal or personal use of specific clients is granted by the National Academy of Sciences provided that the proper fee is paid directly to CCC. **Microforms:** Contact UMI at www.umi.com or P.O. Box 1346, Ann Arbor, MI 48106-1346 USA.

Advertising: Mark Chesnek, 700 11th Street, NW, Suite 450, Washington, DC 20001 USA. Phone 1-202-334-2696, fax 1-202-334-1346, e-mail mchesnek@nas.edu.

Subscriptions: Send payments to PNAS, c/o AIP, P.O. Box 503284, St. Louis, MO 63150-3284 USA. For subscription help, e-mail subs@aip.org, phone 1-516-576-2270, or visit www.pnas.org/subscriptions. **2011 Rates:** US, individual—\$375 (first class delivery available at a surcharge of \$375); non-US, individual—\$585; US/non-US, institutional online only, \$1,305–7,215. Subscriptions are entered on a calendar-year basis.

Exclusive Agent for Subscribers in Japan: USACO Corporation, 17-12 Higashi-Azabu, 2-Chome, Minato-ku, Tokyo 106-0044, Japan. Phone 81 3 3505 3256, fax 81 3 3505 6282, e-mail tokyo-sales@usaco.co.jp. **Change of Address:** PNAS, c/o AIP, Suite 1N01, 2 Huntington Quadrangle, Melville, NY 11747 USA. Phone 1-800-344-6902, fax 1-516-349-9704, e-mail subs@aip.org. Please send notification 6 weeks in advance and list the old and new addresses. **Claims:** Requests for replacement copies will not be honored more than 60 days after the issue date for domestic subscribers and not more than 90 days after the issue date for foreign subscribers. Claims will not be honored for more than two issues per calendar year for the same subscriber. To make a claim, e-mail subs@aip.org or call 1-800-344-6902. **Single Copies:** \$40 per issue in the US, \$50 non-US. To order, e-mail subs@aip.org or call 1-800-344-6902. **Canadian GST:** Registration Number R-133130880.

Postmaster: Send address changes to PNAS, c/o AIP, Suite 1N01, 2 Huntington Quadrangle, Melville, NY 11747 USA. Periodicals postage paid at Washington, DC, and additional mailing offices.

PNAS is available online at www.pnas.org.
PRINTED IN THE USA



Printed on acid-free paper effective Volume 84, Issue 1, and on 80% post-consumer recycled paper effective Volume 107, Issue 1. Printed with soy ink.

PNAS STAFF

Publisher

Kenneth R. Fulton

Executive Editor

Diane M. Sullenberger

Managing Editor

Daniel H. Salsbury

Recruiting Editor

David Stopak

Editorial Staff

James B. Allison

Jenna Al-Malawi

Josiah W. Armour

Teresa V. Callahan

Victoria Chihos

Ryan Conley

Amanda Hopkins

Andrew Huber

Benjamin Jipson

Meredith C. Jones

Etta Kavanagh

Jacob Kendall-Taylor

Jeffrey King

Jay Leamy

Kay McLaughlin

Kathryn Murphy

Tom Myers

Jennifer Nelson

Matthew Parks

May B. Piotrowski

Dane Secor

Sarah Shumway

Production Manager

Dana M. Compton

Production Staff

Kelly A. Gerrity

Sophie Mohin

Kelly A. Newton

Kat Rodenhizer

Audrey Springer

Marketing Manager

Mark Chesnek

Marketing Staff

Jennifer Bradley

Media Staff

Sola Ayeni-Biu

Ann Griswold

Prashant Nair

Ashley Truxon

Senior Finance Officer

Janice Guzman

Business Staff

Metina Booze

Corey P. Colwill

Lesli H. Martin

Authorship

Authorship should be limited to those who have contributed substantially to the work. Authors must indicate their specific contributions to the published work; this information will be published as a footnote to the paper. The corresponding author must have obtained permission from all authors for the submission of each version of the paper and for any change in authorship.

Conflict of Interest

All authors, members, referees, and editors must disclose any association that poses a conflict of interest in connection with the manuscript. Authors must acknowledge all funding sources supporting the work. See www.pnas.org/misc/coi.shtml for details.

Supporting Information

Authors may use Supporting Information to enhance their papers in PNAS by providing additional substantive material for online posting, but the print version of the paper must stand on its own merits.

Cover Images

Authors are encouraged to submit scientifically interesting and visually arresting images for the cover.

Information for Authors

Please see the complete Information for Authors, available online at www.pnas.org.

PNAS Online

PNAS articles are published daily online before print at www.pnas.org in PNAS Early Edition.

The articles in PNAS report original research by independent authors and do not necessarily represent the views of the National Academies.

Soils on exposed Sunda Shelf shaped biogeographic patterns in the equatorial forests of Southeast Asia

J. W. Ferry Slik^{a,1}, Shin-Ichiro Aiba^b, Meredith Bastian^{c,d}, Francis Q. Brearley^e, Charles H. Cannon^{a,f}, Karl A. O. Eichhorn^g, Gabriella Fredriksson^h, Kuswata Kartawinataⁱ, Yves Laumonier^j, Asyraf Mansor^k, Antti Marjokorpi^l, Erik Meijaard^m, Robert J. Morley^{n,o,p}, Hidetoshi Nagamasu^q, Reuben Nilus^r, Eddy Nurtjahya^s, John Payne^t, Andrea Permana^u, Axel D. Poulsen^v, Niels Raes^w, Soedarsono Riswanⁱ, Carel P. van Schaik^u, Douglas Sheil^x, Kade Sidiyasa^y, Eizi Suzuki^z, Johan L. C. H. van Valkenburg^{aa}, Campbell O. Webb^{bb}, Serge Wich^{u,cc}, Tsuyoshi Yoneda^{dd}, Rahmad Zakaria^k, and Nicole Zweifel^u

^aPlant Geography Lab, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China; ^bFaculty of Science, Kagoshima University, Kagoshima 890-0065, Japan; ^cPhiladelphia Zoo, Philadelphia, PA 19104-1196; ^dDepartment of Evolutionary Anthropology, Duke University, Durham, NC 27708-0680; ^eSchool of Science and the Environment, Manchester Metropolitan University, Manchester M15 6BH, United Kingdom; ^fDepartment of Biological Sciences, Texas Tech University, Lubbock, TX 79409; ^gEichhorn Ecology, 3702 BK, Zeist, The Netherlands; ^hInstitute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 1098 SM, Amsterdam, The Netherlands; ⁱHerbarium Bogoriense, Research Center for Biology, Bogor 16911, Indonesia; ^jCenter for International Forestry Research, Bogor 16000, Indonesia; ^kSchool of Biological Sciences, Universiti Sains Malaysia, 11800 USM, Pulau Pinang, Malaysia; ^lStora Enso, FIN-01300, Vantaa, Finland; ^mPeople and Nature Consulting International, Jakarta 15412, Indonesia; ⁿPalynova Limited, Littleport, Ely CB6 1PY, United Kingdom; ^oDepartment of Earth Sciences, Royal Holloway, University of London, Egham TW20 0EX, United Kingdom; ^pInstitute for Geosciences, Christian-Albrechts-Universität, D-24118 Kiel, Germany; ^qKyoto University Museum, Kyoto University, Kyoto 606-8501, Japan; ^rSabah Forestry Department, Forest Research Center, 90715 Sandakan, Sabah, Malaysia; ^sUniversitas Bangka Belitung, Bangka 33782, Indonesia; ^tWorld Wildlife Fund Malaysia, 88800 Kota Kinabalu, Sabah, Malaysia; ^uAnthropological Institute and Museum, Universität Zürich, CH-8057 Zürich, Switzerland; ^vRoyal Botanic Garden Edinburgh, Edinburgh EH3 5LR, United Kingdom; ^wNHN Section, Netherlands Centre for Biodiversity Naturalis, Leiden University, 2300 RA, Leiden, The Netherlands; ^xInstitute of Tropical Forest Conservation, Kabale, Uganda; ^yWanariset-Samboja Herbarium, Samboja 75277, Indonesia; ^zDepartment of Earth and Environmental Sciences, Kagoshima University, Kagoshima 890-0065, Japan; ^{aa}Plant Protection Service, Wageningen University, 6700 HC, Wageningen, The Netherlands; ^{bb}Harvard University Herbaria, Harvard University, Cambridge, MA 02138-2020; ^{cc}Sumatran Orangutan Conservation Program, Medan 20154, Indonesia; and ^{dd}Faculty of Agriculture, Kagoshima University, Kagoshima 890-0065, Japan

Edited by David L. Dilcher, Indiana University, Bloomington, IN, and approved June 16, 2011 (received for review March 1, 2011)

The marked biogeographic difference between western (Malay Peninsula and Sumatra) and eastern (Borneo) Sundaland is surprising given the long time that these areas have formed a single landmass. A dispersal barrier in the form of a dry savanna corridor during glacial maxima has been proposed to explain this disparity. However, the short duration of these dry savanna conditions make it an unlikely sole cause for the biogeographic pattern. An additional explanation might be related to the coarse sandy soils of central Sundaland. To test these two nonexclusive hypotheses, we performed a floristic cluster analysis based on 111 tree inventories from Peninsular Malaysia, Sumatra, and Borneo. We then identified the indicator genera for clusters that crossed the central Sundaland biogeographic boundary and those that did not cross and tested whether drought and coarse-soil tolerance of the indicator genera differed between them. We found 11 terminal floristic clusters, 10 occurring in Borneo, 5 in Sumatra, and 3 in Peninsular Malaysia. Indicator taxa of clusters that occurred across Sundaland had significantly higher coarse-soil tolerance than did those from clusters that occurred east or west of central Sundaland. For drought tolerance, no such pattern was detected. These results strongly suggest that exposed sandy sea-bed soils acted as a dispersal barrier in central Sundaland. However, we could not confirm the presence of a savanna corridor. This finding makes it clear that proposed biogeographic explanations for plant and animal distributions within Sundaland, including possible migration routes for early humans, need to be reevaluated.

climate change | human migration | plant distribution | sea-level change

Together with the Amazon Basin, Congo Basin, and New Guinea, Southeast Asia's Sundaland forms one of the world's largest equatorial tropical forests (1). The present-day insular nature of this region is unrepresentative of the historical situation because most of the time the area formed a single landmass as a result of lowered sea levels associated with global cooling events (2–5). Despite this long history of land connections, there exists a marked biogeographic boundary between western (Malay Peninsula and Sumatra) and eastern (Borneo) Sundaland (3, 5, 6). These differences have been explained by a hypothesized north-south-oriented savanna corridor through the center

of Sundaland that blocked dispersal of wet forest species (7–13). Although there is strong evidence for drier conditions within the region during the last glacial period (10, 12–15), the presence of a continuous north-south savanna corridor through the center of Sundaland remains controversial, and most coupled vegetation–climate reconstructions contradict this possibility (4, 16–20). Furthermore, the savanna-corridor hypothesis is based on the climatic conditions during glacial maxima when land area was maximal. This situation existed for only 17% of time during the last 250,000 y (2), making it unlikely that it is solely responsible for the observed biogeographic pattern in Sundaland.

Another explanation for the biogeographic boundary in central Sundaland relates to the soil conditions of the exposed sea floor (12). The current topsoil texture map of the region (21) shows that coarse-textured, often poorly drained soils are a common feature of the central part of the region (Fig. 1). These soils limit plant growth because they are extremely nutrient poor; they currently support peat swamp on poorly drained sites and heath forests on well-drained sites, both with a distinct species composition, generally low productivity, and poor diversity compared with the richer lowland forests on fine-textured, more nutrient-rich and better-drained soils (22). Sediments of the central Sunda Shelf sea bed also consist of these coarse-textured sands (12, 23, 24). Palynological data from east of Natuna Island (25) contain more common Poaceae pollen than any equatorial pollen sites do, suggesting that poorly drained areas of the Sunda Shelf were covered with extensive grass-dominated fresh-water swamps during periods of lowered sea levels. For most of the time, the connection between eastern and western Sundaland

Author contributions: J.W.F.S. designed research; J.W.F.S., S.-I.A., M.B., F.Q.B., C.H.C., K.A.O.E., G.F., K.K., Y.L., A. Mansor, A. Marjokorpi, E.M., H.N., R.N., E.N., J.P., A.P., A.D.P., N.R., S.R., C.P.v.S., D.S., K.S., E.S., J.L.C.H.v.V., C.O.W., S.W., T.Y., R.Z., and N.Z. performed research; J.W.F.S., R.J.M., and N.R. analyzed data; and J.W.F.S. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: ferryslik@hotmail.com.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1103353108/-DCSupplemental.

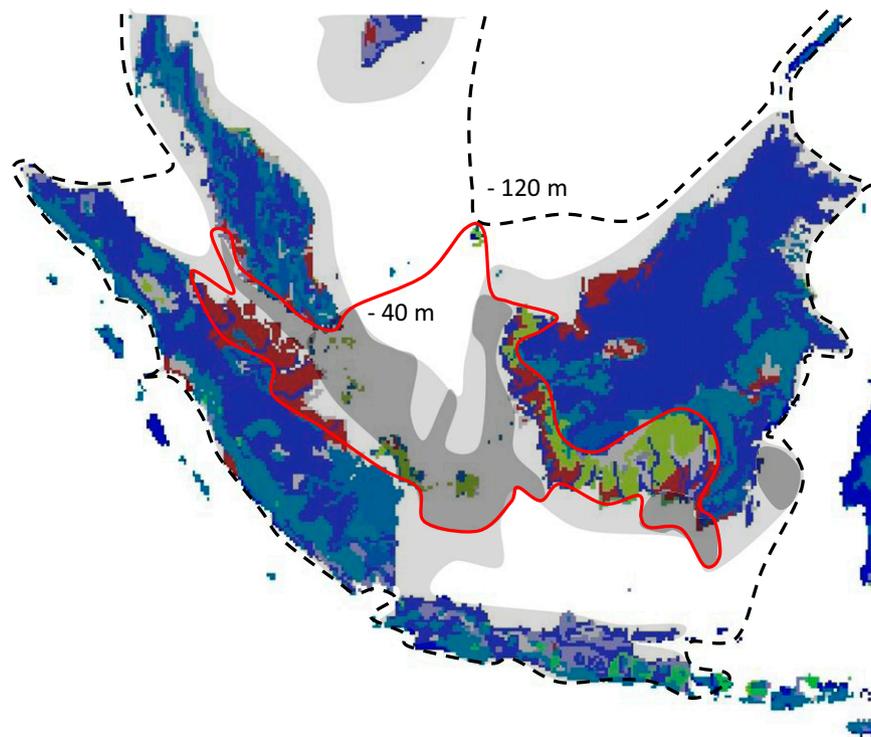


Fig. 1. Composite map of Sundaland. The green and red areas indicate currently exposed land areas with coarse sandy and/or badly drained soils. The light gray areas indicate the exposed sea bed at a sea-level lowering of 40 m, a situation that existed for more than 50% of the time during the last 250,000 y (2). The dark gray areas indicate the coarse sandy soils on this exposed seabed (12). The dashed black line indicates the maximum land area during the Last Glacial Maximum, when sea levels were lowered by ~ 120 m. The red line indicates the potential extent of the sandy soil dispersal barrier in central Sundaland.

ran through this coarse sandy exposed sea bed (Fig. 1) (2), which could have formed an enduring dispersal barrier to taxa ill adapted to these conditions.

Capitalizing on a unique database of 111 forest tree inventories from the region, we try to renew the discussion on the observed biogeographic differences between western and eastern Sundaland by testing both the climate and soil dispersal barrier hypotheses. Because a dispersal barrier based on soil properties assumes a different dispersal-limitation mechanism than one based on climate does, it should result in recognizable floristic signatures. A drier central Sundaland with a savanna corridor (hypothesis 1) should act as a filter blocking drought-intolerant tree species while letting drought-tolerant species pass, whereas a central Sundaland characterized by coarse-textured sandy soils (hypothesis 2) should block tree species adapted to fine-textured soils while letting taxa adapted to coarse soil pass. By looking at the drought and coarse-soil texture tolerance of the genera characteristic of floristic clusters that cross central Sundaland and those that are restricted to either side of it, we can thus gain insight into the processes that shaped the biogeographic patterns.

Results

The final floristic data set of 111 locations and 280 genera resulted in a dendrogram with 11 terminal clusters (Fig. S1), with 10 (5 unique) in Borneo, 5 (none unique) in Sumatra, and 3 (1 unique) in Peninsular Malaysia (Fig. 2). Five floristic clusters crossed the central Sundaland biogeographic barrier, and six were found either west or east of this boundary. For the floristic clusters that crossed the biogeographic boundary, we found 12 indicator genera versus 39 found for the clusters that did not cross (Dataset S1). The indicator genera of the crossing floristic clusters had a significantly higher coarse-soil tolerance than did the indicator genera of clusters that did not cross the biogeographic boundary [0.67 ± 0.15 versus 0.44 ± 0.18 (mean \pm SD), for

crossing and noncrossing indicator genera, respectively; F ratio = 16.9, $P = 0.0002$]. For drought tolerance, on the other hand, no significant difference was found [0.50 ± 0.16 versus 0.56 ± 0.21 (mean \pm SD), for crossing and noncrossing indicator genera, respectively; F ratio = 1.0, $P = 0.327$].

Discussion

Soil Dispersal Barrier in Central Sundaland. Our results provide evidence that the exposed sea-bed soils may have played a role as dispersal barrier in central Sundaland. The special character and potential impact on plant species distributions of the currently submerged soils of central Sundaland have been noted before (4, 12) but have not yet been taken seriously as a dispersal barrier. A soil dispersal barrier also makes sense in a historical perspective because, unlike the hypothesized savanna corridor, the soil conditions would have been present in central Sundaland whenever sea levels dropped enough to expose the current shelf area. During the Pleistocene, this was the case for hundreds of thousands of years (2), more than enough time to cause a detectable biogeographic signal. Based on our reinterpretation of recent data (26), a likely vegetation type for the former soils of the submerged Sunda Shelf would have been heath forest on well-drained sandy soils, with kerapah peat swamps on poorly drained interfluves, and with herb-dominated swamp vegetation for areas that experienced some degree of climatic seasonality to the north, e.g., in the vicinity of Natuna. The region of the Java sea is more likely to have borne seasonal climate vegetation based on the palynological record from the southern part of the Makassar Straits, which shows the presence of widespread grass-dominated vegetation throughout the last glacial period (marine isotope stages 2–4, 16–74 ka) with extensive burning, as shown by charcoal records, from ~ 16 to 37 ka (27, 28). Heath forests and kerapah peats in the equatorial region between Sumatra and Borneo, herbaceous swamps in low-lying areas of the Natuna

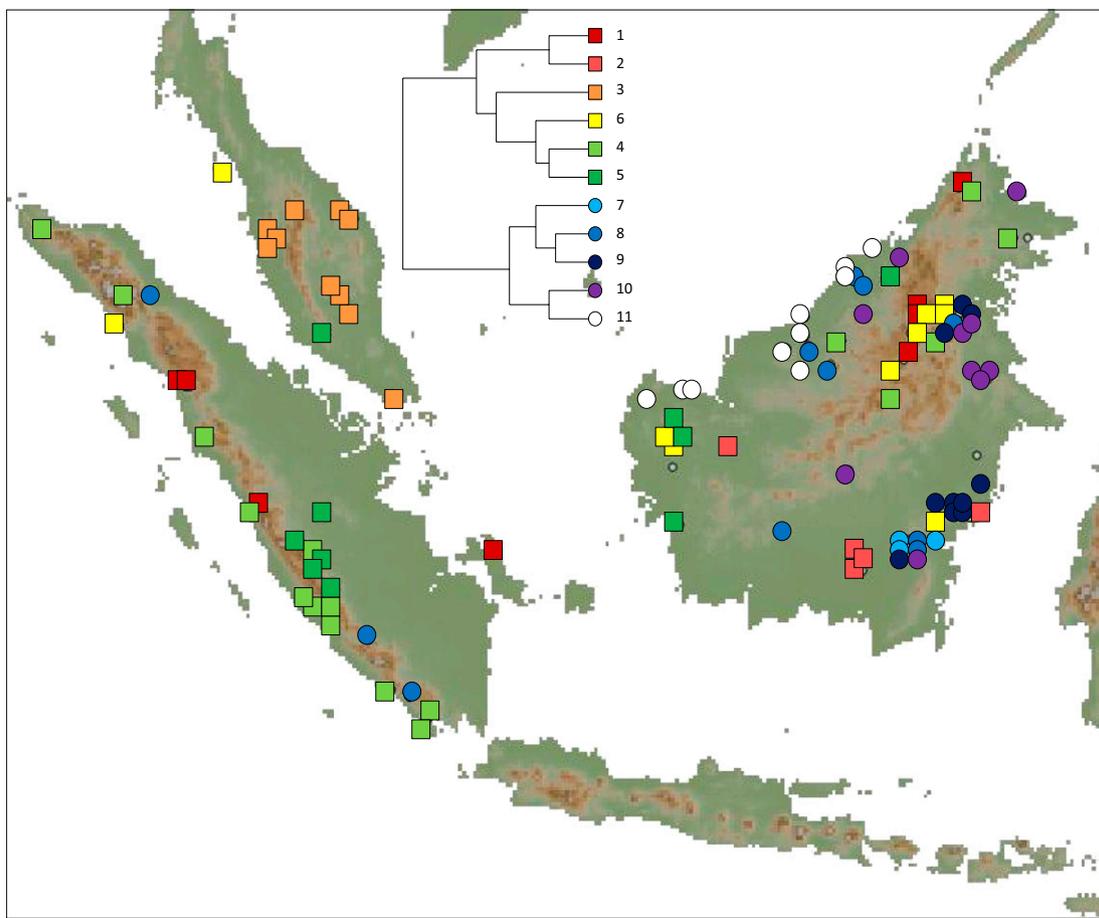


Fig. 2. Spatial distribution of the 111 forest inventory locations with their floristic affinities indicated by the color scheme in the dendrogram and the map.

region, and seasonal climate vegetation in the Java Sea area could have acted as a dispersal barrier for plants and animals not adapted to such soils or vegetation types. Indeed, current heath and swamp forests are characterized by a limited mix of tree species of the surrounding forests, resulting in much reduced diversity and productivity compared with lowland forests on fine-textured and richer soils (22, 29).

What About the Savanna-Corridor Hypothesis? On the other hand, our study provides no support for a continuous savanna corridor in central Sundaland, which is in accordance with most coupled vegetation–climate models (16–20), although the most recent historical vegetation reconstruction for this region (4) includes a savanna corridor in some models. However, this outcome could only be achieved by a priori forcing of a continuous corridor into these models (4). These outcomes do not mean that the savanna corridor did not exist because there is strong evidence for drier, savanna-like or seasonal conditions north and south of central Sundaland in the Pleistocene (10, 12–15, 30, 31). However, if it existed, it left no clear floristic evidence among current tree populations. One reason for this lack of evidence could be that the wetter climates that prevailed during interglacial periods have led to the disappearance of the drought-tolerant taxa from Borneo, Sumatra, and Peninsular Malaysia, thus erasing any floristic evidence for a savanna corridor in these areas. Another reason could be that, even if there was a continuous savanna corridor in central Sundaland, it probably occurred during conditions of maximum sea-level retreat. This situation existed for only short periods of time during the Pleistocene (2), making it unlikely that

it is solely responsible for the observed biogeographic patterns in Sundaland.

Floristic Diversity Patterns in Sundaland. Another interesting outcome of our analysis is the high floristic diversity of Borneo compared with other Sundaland areas, with Borneo harboring 10 of the 11 identified floristic clusters (5 endemic), Sumatra 5 (none endemic), and Peninsular Malaysia only 3 (1 endemic). Even when Sumatra and Peninsular Malaysia are combined, they still only harbor 6 of the 11 identified floristic clusters, 5 of which are shared with Borneo. This pattern, which has recently also been demonstrated for bird species (6), probably largely reflects the longevity of everwet climate forests on Borneo (4, 28). Glacial–interglacial forest expansions and contractions seem to have had the most negative impact on lowland forests of Sumatra and Peninsular Malaysia because, compared with their present day potential extent, their size was small during glacial periods (3, 4). This small forest size might have resulted in the disappearance of some unique lowland floristic associations. Additionally, for parts of Sumatra and especially Peninsular Malaysia, considerably drier conditions existed during glacial periods (10, 12–15), which might have negatively affected their lowland everwet forest types. Borneo, on the other hand, has had a relatively stable everwet climate at its core and in most of the lowland coastal areas with the exception of the south and northeast, which might explain why it maintained so many unique lowland forest types (4, 12, 15, 28, 32).

Another possibility explaining the low floristic diversity of lowland forests on Sumatra could be related to the underrepresentation of eastern Sumatran locations, which might have

affected our results because this area is one of the largest lowland forest regions within Sundaland. Unfortunately, it is also one of the most deforested areas within Sundaland, which means that getting inventory data from undisturbed forests of this region is almost impossible. Although older inventory studies probably exist, they are difficult to access because they are published in local reports. Therefore, Sumatra might eventually turn out to harbor more floristic diversity than is detected by our study.

Migration of Early Humans Through Sundaland. The presence of a savanna corridor in central Sundaland has been used as an argument for the rapid dispersal of early humans (between ca. 60,000 and 45,000 y ago) from mainland Southeast Asia and central Sundaland to Java and then onward to eastern Indonesia, Papua New Guinea, and Australia (12). However, the presence of swamps and heath forests in central Sundaland, as suggested by our study, would not favor this human-dispersal route because swamps and heath forests, aside from being hard to traverse, are generally low-productivity systems with limited wildlife and other edible products for hunter-gatherers (22). It would be more likely that humans used the coastal routes along Sundaland to reach Java and beyond (33, 34), especially because, during this period, large parts of central Sundaland would have been submerged by sea, leaving only a small land area in central Sundaland as a land connection (2).

Conservation Issues. Our study underlines the conservation importance of lowland forests because they contain floristic associations that are unique and among the most threatened in Southeast Asia. In Borneo, only a fraction of the identified lowland forest types are protected (35). Moreover, they are mostly excluded from the Heart of Borneo program, which is especially focused on hill and montane forests. In Sumatra and Peninsular Malaysia, the ongoing loss of forest is critical (36, 37). In special need of conservation are kerapah swamps, which form one of the oldest plant communities in the region and can be followed back in time to the Oligocene. Throughout the region, there is considerable pressure to convert forests to oil palm, pulp, and other industrial plantations even though many deforested areas, especially in Sumatra, remain unused (38, 39). Additionally, existing lowland forest reserves, especially in Indonesia, provide no guarantee for good forest protection because remote-sensing studies have shown that serious forest degradation, fires, and even clearance are occurring within their boundaries (40, 41). Our results strongly underline the need to focus conservation priorities in Southeast Asia toward better protection of lowland forest systems before most of them have disappeared.

Methods

Floristic Analysis. We used tree inventory data for 111 locations across Sundaland (Fig. 2 and Dataset S2), which were centered on an underlying grid of $\sim 10 \times 10$ km that corresponded to our climate and soil layers (see below). Each of our locations thus represents the pooled trees from plots that fell

within such grid cells. Most of these locations contained many morphospecies, making direct comparisons between locations based on species-level identifications impossible. Therefore, we based our floristic analysis on genera only, which not only improves the identification accuracy but has also been shown to reflect species-level floristic patterns well (42). For each location, we ranked genera from high to low abundance and selected the 30 most abundant genera for the floristic analysis because selection of a fixed number of genera makes floristic comparisons depend less on sample size. In cases where more than 30 genera were selected because of equal genus abundances, we randomly excluded genera from the lowest abundance class until we had selected 30 genera. In some cases, there were fewer than 30 genera present in a location. We decided to retain these locations because they usually represented low-diversity forest types such as heath, peat swamp, and montane forests. Overall, 30 genera represented between 54.8% and 100% of individuals from each inventory [$77.7 \pm 11.3\%$ (mean \pm SD)]. We used relative abundances of genera (number of individuals divided by total number of individuals in each inventory) to make the locations comparable. The final matrix, containing all locations and the relative abundances of their genera, was used in a cluster analysis (data were log 10-transformed to reduce impact of abundant genera) using minimal-variance clustering.

Indicator Genera Analysis. To determine the characteristic genera for each cluster in the floristic analysis, we used an indicator method (43). This method calculates an indicator value (IV) for each genus in predefined clusters (like the clusters identified by a floristic analysis). Only genera that have a high mean abundance and are present in the majority of locations of a cluster (and have low abundance and frequency outside of that cluster) will score a high IV. To test whether the observed IV of a genus in a cluster was significantly higher than could be expected based on a random distribution of individuals over the locations, the observed IV was compared with 999 randomly generated IVs. These random IVs were generated by a reallocation procedure in which the number of individuals per genus was randomly reshuffled over the locations (43). If the observed IV of a genus in a cluster fell within the top 5% of the random IVs (sorted in decreasing order), it was considered to deviate significantly from the random distribution. Indicator taxa were mapped on the dendrogram (Fig. S2).

Testing Indicator Taxa Drought and Coarse-Soil Tolerance. Drought and coarse-soil tolerance of genera were determined by sorting the 111 study locations by their annual rainfall (WorldClim, <http://www.worldclim.org>) and subsoil texture values taken from the Food and Agriculture Organization of the United Nations' TERRASTAT: *Global Land Resources GIS Models and Databases for Poverty and Food Insecurity Mapping* (21) (Fig. S3). Drought tolerance per genus was calculated as the abundance in the 50% driest sites divided by total abundance over all sites. Similarly, coarse-soil tolerance per genus was calculated as the abundance in the 50% coarsest soil sites divided by total abundance over all sites. Therefore, the higher the value (scaled between 0 and 1), the more tolerant a genus is to drought or coarse soil (the whole list is in Dataset S1). We then tested (one-way ANOVA) whether the means of the drought and coarse-soil tolerance values of the indicator taxa differed significantly between floristic clusters that crossed the dispersal barrier versus those that did not cross. Some indicator taxa occurred in several clusters. In those cases, we used only the data (cross or not cross central Sundaland) from the cluster where it scored its highest IV.

ACKNOWLEDGMENTS. We thank PLOTNET, STREK, ITCI, and David Newbery for sharing their plot data with us. A. Mansor and R.Z. thank the Malaysian Remote Sensing Agency for financial assistance and Universiti Sains Malaysia for technical support.

- Richards PW (1996) *The Tropical Rain Forest: An Ecological Study* (Cambridge Univ Press, Cambridge, UK), 2nd Ed.
- Voris HK (2000) Maps of Pleistocene sea levels in Southeast Asia: Shorelines, river systems and time durations. *J Biogeogr* 27:1153–1167.
- Meijaard E (2004) Solving mammalian riddles. A reconstruction of the Tertiary and Quaternary distribution of mammals and their palaeoenvironments in island Southeast Asia. PhD thesis (Australian National University, Canberra, Australia).
- Cannon CH, Morley RJ, Bush ABG (2009) The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. *Proc Natl Acad Sci USA* 106:11188–11193.
- Woodruff DS (2010) Biogeography and conservation in Southeast Asia: How 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. *Biodivers Conserv* 19:919–941.
- Lim HC, Rahman MA, Lim SL, Moyle RG, Sheldon FH (2011) Revisiting Wallace's haunt: Coalescent simulations and comparative niche modeling reveal historical mechanisms that promoted avian population divergence in the Malay Archipelago. *Evolution* 65:321–334.
- Heaney LR (1991) A synopsis of climatic and vegetational change in Southeast Asia. *Clim Change* 19:53–61.
- Brandon-Jones D (1996) The Asian Golobinae (Mammalia: Cercopithecidae) as indicators of Quaternary climatic change. *Biol J Linn Soc Lond* 59:327–350.
- Adams JM, Faure H (1997) Preliminary vegetation maps of the world since the last glacial maximum: An aid to archeological understanding. *J Archaeol Sci* 24:623–647.
- Gathorne-Hardy FJ, Syaokani, Davies RG, Eggleton P, Jones DT (2002) Quaternary rainforest refugia in south-east Asia: Using termites (Isoptera) as indicators. *Biol J Linn Soc Lond* 75:453–466.
- Meijaard E (2003) Mammals of Southeast Asian islands and their Late Pleistocene environments. *J Biogeogr* 30:1245–1257.
- Bird MI, Taylor D, Hunt C (2005) Palaeoenvironments of insular Southeast Asia during the Last Glacial Period: A savanna corridor in Sundaland? *Quat Sci Rev* 24:2228–2242.

