

Review

Cite this article: Smith, J. A., E. M. Dowding, A. A. Abdelhady, P. Abondio, R. Araújo, T. Aze, M. A. Balisi, L. A. Buatois, H. Carvajal-Chitty, D. Chattopadhyay, M. Coiro, G. P. Dietl, C. González Arango, C. Kevrekidis, J. Kimmig, A. M. Mychajliw, C. Pimiento, O. R. Regalado Fernández, K. M. Schroeder, R. C. M. Warnock, T.-R. Yang, M. Yasuhara, L. G. Akita, B. J. Allen, B. M. Anderson, J. Andréolett, F. M. Archuby, G. A. Ballen, Md.I. Bari, M. J. Benton, E. W. Bergh, L. Brambilla, A. Brombacher, Y. K. S. Chan, A. A. Chiarenza, T. Chinzorig, K. M. Coates, D. R. Cordie, M. Cortés-Sánchez, E. J. Cruz-Vega, J. D. Cybulski, K. De Baets, J. De Entrambasaguas, E. M. Dillon, A. Du, A. M. Dunhill, J. M. Erlandson, M.-B. Forel, W. J. Foster, T. A. Gates, A. Gavryushkina, M. K. Grace, H.-P. Grossart, P. Hänsel, P. G. Harnik, M. J. Hopkins, S. S. B. Hopkins, K. Hu, H.-H. M. Huang, R. B. Irmis, V. A. J. Jaques, X. A. Jenkins, A. M. Jukar, P. H. Kelley, R. G. Kihn, A. A. Klomp maker, Á.T. Kocsis, J. Kriwet, D. Lazarus, C.-C. Liao, C.-H. Lin, J. Louys, J. Lozano-Fernandez, M. C. Lozano-Francisco, J. A. Lueders-Dumont, M. E. Malvé, R. C. Martindale, I. Mazzini, G. Modenini, S. Mondal, M. Mondini, M. D. Monferran, L. P. A. Mulvey, K. Nanglu, J. M. T. Nguyen, R. Norris, A. O'Dea, A. L. Ollendorf, J. Orihuela, J. M. Pandolfi, T. Pereira, A. Piro, R. E. Plotnick, S. M. Plaza-Torres, A. Porto, A. Prieto-Márquez, S. W. Punyasena, T. B. Qüental, N. B. Raja, J. Ranaivosoa, L. Ribas-Deulofeu, F. Rivals, V. J. Roden, A. Rosso, F. Saleh, R. B. Salvador, E. E. Saupe, S. Schneider, J. A. Sclafani, M. R. Smith, A. Souron, M. J. Steinbauer, M. Stewart, C. P. Tambussi, E. Thomas, E. Tschopp, T. Tütken, S. Varela, R. I. Vezzosi, A. Villaseñor, M. F. G. Weinkauf, L. E. Zanno, C. Zhang, Q. Zhao, and W. Kiessling (2025). Identifying the Big Questions in paleontology: a community-driven project. *Paleobiology* 51, 408–431.

<https://doi.org/10.1017/pab.2025.10042>

Received: 02 May 2024

Revised: 19 February 2025

Accepted: 06 May 2025

Handling Editor:

James Crampton

Corresponding author:

Jansen Smith;

Email: smithja@d.umn.edu

*Authors are listed alphabetically in two groups: working group leaders and group members.

[†]Indicates leadership role in a working group.

© The Author(s), 2025. Published by Cambridge University Press on behalf of Paleontological Society. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution, and reproduction in any medium, provided the original work is properly cited.

PALEOBIOLOGY
A PUBLICATION OF THE



CAMBRIDGE
UNIVERSITY PRESS

Identifying the Big Questions in paleontology: a community-driven project

Jansen A. Smith^{1,2*} , Elizabeth M. Dowding^{1†} , Ahmed A. Abdelhady^{3†} , Paolo Abondio^{4†} , Ricardo Araújo^{5†} , Tracy Aze^{6†} , Mairin A. Balisi^{7,8,9†} , Luis A. Buatois^{10†} , Humberto Carvajal-Chitty^{11†} , Devapriya Chattopadhyay^{12†} , Mario Coiro^{13,14†} , Gregory P. Dietl^{15,16†} , Catalina González Arango^{17†} , Charalampos Kevrekidis^{18†} , Julien Kimmig^{19,20†} , Alexis M. Mychajliw^{8,21†} , Catalina Pimiento^{22,23†} , Omar Rafael Regalado Fernández^{24†} , Katlin M. Schroeder^{25†} , Rachel C. M. Warnock^{1†} , Tzu-Ruei Yang^{26,27,28†} , Moriaki Yasuhara^{29,30†} , Lailah Gifty Akita³¹ , Bethany J. Allen^{32,33} , Brendan M. Anderson¹⁵ , Jérémy Andréolett³⁴ , Fernando M. Archuby^{35,36} , Gustavo A. Ballen³⁷ , Md. Ibrahimul Bari³⁸ , Michael J. Benton³⁹ , Eugene W. Bergh⁴⁰ , Luciano Brambilla⁴¹ , Anieke Brombacher⁴² , Yong Kit Samuel Chan⁴³ , Alfio Alessandro Chiarenza⁴⁴ , Tsogtbaatar Chinzorig^{45,46,47} , Kadane M. Coates⁴⁸ , David R. Cordie⁴⁹ , Miguel Cortés-Sánchez⁵⁰ , Eduardo J. Cruz-Vega⁵¹ , Jonathan D. Cybulski^{52,53} , Kenneth De Baets⁵⁴ , Julia De Entrambasaguas^{55,56} , Erin M. Dillon^{52,57} , Andrew Du⁵⁸ , Alexander M. Dunhill⁵⁹ , Jon M. Erlandson⁶⁰ , Marie-Béatrice Forel⁶¹ , William J. Foster⁶² , Terry A. Gates^{45,47} , Alexandra Gavryushkina⁶³ , Molly K. Grace⁶⁴ , Hans-Peter Grossart^{65,66} , Patrick Hänsel¹ , Paul G. Harnik⁶⁷ , Melanie Jane Hopkins⁶⁸ , Samantha S. B. Hopkins^{60,69} , Keyi Hu⁷⁰ , Huai-Hsuan M. Huang⁷¹ , Randall B. Irmis^{72,73} , Victory A. J. Jaques^{74,75} , Xavier A. Jenkins⁷⁶ , Advait M. Jukar^{77,78,79} , Patricia H. Kelley⁸⁰ , Romina G. Kihn^{81,82} , Adiël A. Klomp maker⁸³ , Ádám T. Kocsis¹ , Jürgen Kriwet¹⁴ , David Lazarus⁸⁴ , Chun-Chi Liao⁸⁵ , Chien-Hsiang Lin⁸⁶ , Julien Louys⁸⁷ , Jesus Lozano-Fernandez⁸⁸ , María Carmen Lozano-Francisco⁸⁹ , Jessica A. Lueders-Dumont⁹⁰ , Mariano E. Malvé⁹¹ , Rowan C. Martindale⁹² , Iliara Mazzini⁹³ , Giorgia Modenini⁹⁴ , Subhronil Mondal⁹⁵ , Mariana Mondini^{96,97} , Mateo D. Monferran⁹⁸ , Laura P. A. Mulvey¹ , Karma Nanglu⁹⁹ , Jacqueline M. T. Nguyen^{100,101} , Richard Norris¹⁰² , Aaron O'Dea^{52,103} , Amy L. Ollendorf¹⁰⁴ , Johanset Orihuela¹⁰⁵ , John M. Pandolfi¹⁰⁶ , Telmo Pereira^{107,108,109,110} , Alejandra Piro^{36,111} , Roy E. Plotnick¹¹² , Stephanie M. Plaza-Torres¹¹³ , Arthur Porto¹¹⁴ , Albert Prieto-Márquez¹¹⁵ , Surangi W. Punyasena¹¹⁶ , Tiago B. Qüental¹¹⁷ , Nussaibah B. Raja¹ , Voajanahary Ranaivosoa¹¹⁸ , Lauriane Ribas-Deulofeu¹¹⁹ , Florent Rivals^{120,121,122} , Vanessa Julie Roden¹ , Antonietta Rosso¹²³ , Farid Saleh¹²⁴ , Rodrigo Brincalpe Salvador^{125,126} , Erin E. Saupe¹²⁷ , Simon Schneider¹²⁸ , Judith A. Sclafani¹²⁹ , Martin R. Smith¹³⁰ , Antoine Souron¹³¹ , Manuel J. Steinbauer¹³² , Mathew Stewart⁸⁷ , Claudia P. Tambussi¹³³ , Ellen Thomas^{42,134} , Emanuel Tschopp^{135,136,137} , Thomas Tütken¹³⁸ , Sara Varela¹³⁹ , Raúl I. Vezzosi^{140,141} , Amelia Villaseñor¹⁴² , Manuel F. G. Weinkauf¹⁴³ , Lindsay E. Zanno^{45,47} , Chi Zhang⁸⁵ , Qi Zhao⁸⁵ and Wolfgang Kiessling^{1†}

- ¹GeoZentrum Nordbayern, Friedrich-Alexander-Universität Erlangen-Nürnberg (FAU), Erlangen 91054, Germany
- ²Department of Earth and Atmospheric Sciences, University of Minnesota Duluth, Duluth, Minnesota 55812, U.S.A.
- ³Geology Department, Minia University, Al Minya, Al Minya 61519, Egypt
- ⁴IRCCS Istituto delle Scienze Neurologiche di Bologna, Bologna, Emilia-Romagna 40139, Italy
- ⁵Instituto de Plasmas e Fusão Nuclear & Centro de Recursos Naturais e Ambiente (CERENA), Instituto Superior Técnico, Universidade de Lisboa, Lisbon 1049-001, Portugal
- ⁶School of Biological and Marine Sciences, University of Plymouth, Plymouth, Devon PL4 8AA, U.K.
- ⁷Raymond M. Alf Museum of Paleontology, Claremont, California 91711, U.S.A.
- ⁸La Brea Tar Pits and Museum, Natural History Museums of Los Angeles County, Los Angeles, California 90036, U.S.A.
- ⁹Department of Life and Environmental Sciences, University of California–Merced, Merced, California 95343, U.S.A.
- ¹⁰Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5E2, Canada
- ¹¹Departamento de Estudios Ambientales, Universidad Simón Bolívar, Valle de Sartenejas, Baruta/Miranda 89000, Venezuela
- ¹²Department of Earth and Climate Science, IISER Pune, Pune, MH 411008, India
- ¹³Department of Paleontology and Historical Geology, Senckenberg Research Institute and Natural History Museum, Frankfurt am Main 60395, Germany
- ¹⁴Department of Palaeontology, University of Vienna, Vienna, Vienna 1090, Austria
- ¹⁵Paleontological Research Institution, Ithaca, New York 14850, U.S.A.
- ¹⁶Department of Earth and Atmospheric Sciences, Cornell University, Ithaca, New York 14853, U.S.A.
- ¹⁷Departamento de Ciencias Biológicas, Universidad de los Andes, Bogotá 111711, Colombia
- ¹⁸Museum für Ur- und Ortsgeschichte, Museumszentrum Quadrat, Bottrop, 46236, Germany
- ¹⁹Paläontologie und Evolutionsforschung, Abteilung Geowissenschaften, Staatliches Museum für Naturkunde Karlsruhe, 76133 Karlsruhe, Germany
- ²⁰Harold Hamm School of Geology and Geological Engineering, University of North Dakota, Grand Forks, North Dakota 58202, U.S.A.
- ²¹Department of Biology & Program in Environmental Studies, Middlebury College, Middlebury, Vermont 05753, U.S.A.
- ²²Department of Paleontology, University of Zurich, Zurich 8006, Switzerland
- ²³Department of Biosciences, Swansea University, Swansea SA28PP, U.K.
- ²⁴Curation, Senckenberg Naturmuseum Frankfurt, Frankfurt am Main, Hesse 60395, Germany
- ²⁵Institute for Biospheric Studies, Yale University, New Haven, Connecticut 06520, U.S.A.
- ²⁶National Museum of Natural Science, Taichung 404023, Taiwan
- ²⁷Department of Life Sciences, National Chung Hsing University, Taichung 402202, Taiwan
- ²⁸Department of Earth Sciences, National Cheng Kung University, Tainan, 701401 Taiwan
- ²⁹School of Biological Sciences, Area of Ecology and Biodiversity, Swire Institute of Marine Science, Institute for Climate and Carbon Neutrality, and Musketeers Foundation Institute of Data Science, The University of Hong Kong, Hong Kong SAR, China
- ³⁰State Key Laboratory of Marine Pollution, City University of Hong Kong, Kowloon, Hong Kong SAR, China
- ³¹Department of Marine and Fisheries Sciences, University of Ghana, Legon-Campus, Greater-Accra, Ghana
- ³²Department of Biosystems Science and Engineering, ETH Zurich, Basel, Basel-Stadt 4056, Switzerland
- ³³Computational Evolution Group, Swiss Institute of Bioinformatics, Lausanne, Vaud 1015, Switzerland
- ³⁴Institut de Biologie, École Normale Supérieure, Université PSL, CNRS, INSERM, Paris 75005, France
- ³⁵Centro de Estudios Integrales de la Dinámica Exógena, Universidad Nacional de La Plata, La Plata (1900), Provincia de Buenos Aires, Argentina
- ³⁶Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ciudad Autónoma de Buenos Aires, CABA C1425FQB, Argentina
- ³⁷Instituto de Biociências, Universidade Estadual Paulista “Júlio de Mesquita Filho”, Botucatu SP 18618-689, Brazil
- ³⁸Geology, Indian Institute of Technology Bhubaneswar, Bhubaneswar, Odisha 752050, India; and Geology, JIS University, Kolkata, West Bengal 700109, India
- ³⁹Palaeobiology, Research Group, School of Earth Sciences, University of Bristol, Wills Memorial Building, Queen’s Road, Bristol, BS8 1RJ, U.K.
- ⁴⁰Unit for Environmental Sciences and Management, North-West University, Potchefstroom 2531, South Africa
- ⁴¹Centro de Estudios Interdisciplinarios, Universidad Nacional de Rosario, Rosario, Santa Fe 2000, Argentina
- ⁴²Department of Earth & Planetary Sciences, Yale University, New Haven, Connecticut 06511, U.S.A.
- ⁴³Department of Biological Sciences, National University of Singapore, Singapore, 117558 Singapore
- ⁴⁴Department of Earth Sciences, University College London, London WC1E 6BS, U.K.
- ⁴⁵Department of Biological Sciences, North Carolina State University, Raleigh, North Carolina 27695, U.S.A.
- ⁴⁶Division of Paleozoology, The Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar 15160, Mongolia
- ⁴⁷North Carolina Museum of Natural Sciences, Raleigh, North Carolina 27601, U.S.A.
- ⁴⁸Department of Chemistry, The University of the West Indies, Mona, Kingston JMAAW15, Jamaica
- ⁴⁹Division of Biological Sciences, Edgewood University, Madison, Wisconsin 53711, U.S.A.
- ⁵⁰Department of Prehistory and Archaeology, University of Seville, Seville 41004, Spain
- ⁵¹Geology, The University of Puerto Rico, Mayagüez Campus, Mayagüez, Puerto Rico 00680, U.S.A.
- ⁵²Smithsonian Tropical Research Institute, Balboa 0843, Republic of Panamá
- ⁵³Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, U.S.A.
- ⁵⁴Institute of Evolutionary Biology, University of Warsaw, Faculty of Biology, Warsaw 02-089, Poland
- ⁵⁵Departamento de Ciencias de la Tierra, Universidad de Zaragoza, Zaragoza 50009, Spain
- ⁵⁶Instituto Universitario de Investigación de Ciencias Ambientales de Aragón (IUCA), Zaragoza 50009, Spain
- ⁵⁷Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, California 93106, U.S.A.

- ⁵⁸Department of Anthropology & Geography, Colorado State University, Fort Collins, Colorado 80523, U.S.A.
- ⁵⁹School of Earth and Environment, University of Leeds, Leeds LS2 9JT, U.K.
- ⁶⁰Museum of Natural & Cultural History, University of Oregon, Eugene, Oregon 97403, U.S.A.
- ⁶¹Muséum national d'Histoire naturelle, Centre de Recherche en Paléontologie–Paris (CR2P), 75005 Paris, France
- ⁶²Institute for Geology, Universität Hamburg, Hamburg 20146, Germany
- ⁶³School of Computer and Mathematical Sciences, University of Adelaide, SA 5005, Australia
- ⁶⁴Department of Biology, University of Oxford, Oxford OX1 3SZ, U.K.
- ⁶⁵Plankton and Microbial Ecology, Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), 16775 Stechlin, Germany
- ⁶⁶Institute of Biochemistry and Biology, Potsdam University, 14469 Potsdam, Germany
- ⁶⁷Department of Earth and Environmental Geosciences, Colgate University, Hamilton, New York 13346, U.S.A.
- ⁶⁸Division of Paleontology (Invertebrates), American Museum of Natural History, New York, New York 10024, U.S.A.
- ⁶⁹Department of Earth Sciences, University of Oregon, Eugene, Oregon 97403, U.S.A.
- ⁷⁰School of Earth Sciences and Engineering, Nanjing University, Nanjing, Jiangsu 210023, China
- ⁷¹Department of Geosciences, Princeton University, Princeton, New Jersey 08545, U.S.A.
- ⁷²Natural History Museum of Utah, University of Utah, Salt Lake City, Utah 84108-1214, U.S.A.
- ⁷³Department of Geology & Geophysics, University of Utah, Salt Lake City, Utah 84112-0102, U.S.A.
- ⁷⁴CTLab, Central European Institute of Technology–Brno University of Technology, Brno, Moravia 61200, Czech Republic
- ⁷⁵Institute of Geology and Palaeontology, Charles University, Prague, Bohemia 128 43, Czech Republic
- ⁷⁶Department of Biological Sciences, Idaho State University, Pocatello, Idaho 83201, U.S.A.
- ⁷⁷Department of Natural History, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611 USA
- ⁷⁸Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013, U.S.A.
- ⁷⁹Division of Vertebrate Paleontology, Yale Peabody Museum, New Haven, Connecticut 06520, U.S.A.
- ⁸⁰Earth and Ocean Sciences, University of North Carolina Wilmington, Wilmington, North Carolina 28461-5944, U.S.A.
- ⁸¹Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Santa Rosa, La Pampa 6300, Argentina
- ⁸²Universidad Nacional de La Pampa (UNLPam), Santa Rosa, La Pampa 6300, Argentina
- ⁸³Department of Museum Research and Collections & Alabama Museum of Natural History, University of Alabama, Tuscaloosa, Alabama 35487, U.S.A.
- ⁸⁴Retired, Berlin, Germany
- ⁸⁵Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China
- ⁸⁶Biodiversity Research Center, Academia Sinica, Taipei 11529, Taiwan
- ⁸⁷Australian Research Centre for Human Evolution, Griffith University, Brisbane, Queensland 4111, Australia
- ⁸⁸Department de Genètica, Microbiologia i Estadística, & Institut de Recerca de la Biodiversitat (IRBio), Facultat de Biologia, Universitat de Barcelona, Barcelona, Spain
- ⁸⁹Ecology and Geology, University of Málaga, Málaga 29010, Spain
- ⁹⁰Earth and Environmental Sciences, Boston College, Chestnut Hill, Massachusetts 02467, U.S.A.
- ⁹¹IBIOMAR-CONICET, Puerto Madryn, Chubut U9120, Argentina
- ⁹²Department of Earth and Planetary Sciences, The University of Texas at Austin, Austin, Texas 78712, U.S.A.
- ⁹³CNR - Institute of Environmental Geology and Geoengineering, Area della Ricerca di Roma 1, Via Salaria km 29,300, 00015 Montelibretti, RM, Italy
- ⁹⁴BiGeA Department, University of Bologna, Bologna 40126, Italy
- ⁹⁵Department of Earth Sciences, Indian Institute of Science Education and Research (IISER) Kolkata, Mohanpur, West Bengal 741246, India
- ⁹⁶Laboratorio de Zooarqueología y Tafonomía de Zonas Áridas (LaZTA), Instituto de Antropología de Córdoba (IDACOR), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)–Universidad Nacional de Córdoba, Córdoba 5000, Argentina
- ⁹⁷Facultad de Filosofía y Letras, Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires 1406, Argentina
- ⁹⁸Ciencias de la Tierra, Centro de Ecología Aplicada del Litoral–Universidad Nacional del Nordeste, Corrientes, Corrientes 3400, Argentina
- ⁹⁹Department of Earth and Planetary Sciences, University of California Riverside, California, 92521, U.S.A.
- ¹⁰⁰Australian Museum, Sydney, New South Wales 2010, Australia
- ¹⁰¹Flinders University, Adelaide, South Australia 5042, Australia
- ¹⁰²Scripps Institution of Oceanography, University of California, La Jolla, California 92093-0244, U.S.A.
- ¹⁰³Sistema Nacional de Investigación (SENACYT), Panamá, Republic of Panamá
- ¹⁰⁴Paleontology Division, Applied EarthWorks, Inc., Pasadena, California 91107, U.S.A.
- ¹⁰⁵Department of Earth and Environment, Florida International University, Miami, Florida 33199, U.S.A.
- ¹⁰⁶School of the Environment, The University of Queensland, St. Lucia, Queensland 4072, Australia
- ¹⁰⁷Universidade Autónoma de Lisboa, Lisboa 1169-023, Portugal
- ¹⁰⁸Instituto Politécnico de Tomar, Tomar 2300-313, Portugal
- ¹⁰⁹Centro de Geociências da Universidade de Coimbra, Coimbra 3030-790, Portugal
- ¹¹⁰UNIARQ, Centro de Arqueologia da Universidade de Lisboa, Lisboa 1600-214, Portugal
- ¹¹¹División Paleontología Vertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque S/N, La Plata, Buenos Aires B1900, Argentina
- ¹¹²Department of Earth and Environmental Sciences, University of Illinois Chicago, Chicago, Illinois 60607, U.S.A.
- ¹¹³Department of Geological Sciences, University of Colorado Boulder, Boulder, Colorado 80309, U.S.A.
- ¹¹⁴Florida Museum of Natural History, University of Florida, Gainesville, Florida 32605, U.S.A.
- ¹¹⁵Institut Català de Paleontologia Miquel Crusafont (ICP-CERCA), Universitat Autònoma de Barcelona, c/ Escola Industrial 23, 08201 Sabadell, Barcelona, Spain
- ¹¹⁶Department of Plant Biology, University of Illinois at Urbana-Champaign, Urbana, Illinois 61801, U.S.A.
- ¹¹⁷Departamento de Ecologia, Universidade de São Paulo, São Paulo, SP 05508-090, Brazil

- ¹¹⁸Mention Bassins Sedimentaires Evolution Conservation, Université d'Antananarivo, Faculté des Sciences, Antananarivo101, Madagascar
- ¹¹⁹Institute of Oceanography, National Taiwan University, Taipei 106, Taiwan
- ¹²⁰ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain
- ¹²¹Institut Català de Paleoeologia Humana i Evolució Social (IPHES-CERCA), Tarragona 43007, Spain
- ¹²²Departament d'Història i Història de l'Art, Universitat Rovira i Virgili, 43002 Tarragona, Spain
- ¹²³Department of Biological, Geological and Environmental Sciences, University of Catania, 95129 Catania, Italy
- ¹²⁴Institute of Earth Sciences, University of Lausanne, 1015, Lausanne, Switzerland
- ¹²⁵Finnish Museum of Natural History, University of Helsinki, Helsinki, Uusimaa 00100, Finland
- ¹²⁶The Arctic University Museum of Norway, UiT–The Arctic University of Norway, Tromsø, Troms og Finnmark 9006, Norway
- ¹²⁷Department of Earth Sciences, University of Oxford, Oxford OX1 3AN, U.K.
- ¹²⁸CASP, Cambridge CB3 0UD, U.K.
- ¹²⁹Earth and Planetary Sciences, University of California Davis, Davis, California 95616, U.S.A.
- ¹³⁰Earth Sciences, University of Durham, Durham DH1 3LE, U.K.
- ¹³¹Université de Bordeaux, CNRS, Ministère de la Culture, PACEA, UMR 5199, F-33600 Pessac, France
- ¹³²Bayreuth Center of Ecology and Environmental Research (BayCEER) & Bayreuth Center of Sport Science (BaySpo), University of Bayreuth, Bayreuth 95448, Germany
- ¹³³Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), UNC, CONICET, X5016GCA Córdoba, Argentina
- ¹³⁴Earth & Environmental Sciences, Wesleyan University, Middletown, Connecticut 06459, U.S.A.
- ¹³⁵Department of Animal Biodiversity, Universität Hamburg, Hamburg 20146, Germany
- ¹³⁶Department of Vertebrate Paleontology, American Museum of Natural History, New York City, New York 10024, U.S.A.
- ¹³⁷Freie Universität Berlin, Institute for Geological Sciences, 12249 Berlin, Germany
- ¹³⁸AG für Angewandte und Analytische Paläontologie, Institut für Geowissenschaften, Johannes Gutenberg-Universität Mainz, Mainz 55128, Germany
- ¹³⁹Department of Ecology and Animal Biology, Universidade de Vigo, Vigo, Galicia 36310, Spain
- ¹⁴⁰Laboratorio de Paleontología de Vertebrados, Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CONICET, Gob. E.R., UADER), España 149, Diamante E3105BWA, Argentina
- ¹⁴¹Cátedra de Paleontología, Facultad de Ciencia y Tecnología, Universidad Autónoma de Entre Ríos, Diamante, Entre Ríos E3105BWA, Argentina
- ¹⁴²Anthropology, University of Arkansas, Fayetteville, Arkansas 72764, U.S.A.
- ¹⁴³Institute of Geology and Palaeontology, Univerzita Karlova, Prague 128 43, Czech Republic

Abstract

Paleontology provides insights into the history of the planet, from the origins of life billions of years ago to the biotic changes of the Recent. The scope of paleontological research is as vast as it is varied, and the field is constantly evolving. In an effort to identify “Big Questions” in paleontology, experts from around the world came together to build a list of priority questions the field can address in the years ahead. The 89 questions presented herein (grouped within 11 themes) represent contributions from nearly 200 international scientists. These questions touch on common themes including biodiversity drivers and patterns, integrating data types across spatiotemporal scales, applying paleontological data to contemporary biodiversity and climate issues, and effectively utilizing innovative methods and technology for new paleontological insights. In addition to these theoretical questions, discussions touch upon structural concerns within the field, advocating for an increased valuation of specimen-based research, protection of natural heritage sites, and the importance of collections infrastructure, along with a stronger emphasis on human diversity, equity, and inclusion. These questions offer a starting point—an initial nucleus of consensus that paleontologists can expand on—for engaging in discussions, securing funding, advocating for museums, and fostering continued growth in shared research directions.

Resumen

La paleontología permite conocer la historia del planeta, desde los orígenes de la vida hace miles de millones de años hasta los cambios bióticos de épocas recientes. El ámbito de la investigación paleontológica es tan vasto como variado y está en constante evolución. En un esfuerzo por identificar las “grandes preguntas” de la paleontología, expertos de todo el mundo se reunieron para elaborar una lista de cuestiones prioritarias que el campo puede abordar en los próximos años. Las 89 preguntas aquí presentadas (agrupadas en 11 temas) representan las contribuciones de casi 200 científicos internacionales. Estas preguntas se refieren a temas comunes, entre los que se incluyen los motores y patrones de la biodiversidad, la integración de diferentes tipos de datos a lo largo de escalas espacio-temporales, la aplicación de datos paleontológicos para resolver cuestiones contemporáneas de biodiversidad y clima, y la utilización eficaz de métodos y tecnologías innovadoras para obtener nuevos conocimientos paleontológicos. Además de estos interrogantes teóricos, los debates abordan inquietudes estructurales dentro del campo, y

abogan por una mayor valoración de la investigación basada en especímenes, la protección de los sitios del patrimonio natural y la importancia de la infraestructura de las colecciones; junto con un mayor énfasis en la diversidad humana, la equidad y la inclusión. Estas preguntas representan un punto de partida—un núcleo inicial de consenso que los paleontólogos pueden ampliar—para fomentar debates, obtener financiación, abogar por el apoyo a los museos y estimular el crecimiento continuo en direcciones de investigación compartidas.

Riassunto

La paleontologia offre spunti fondamentali per comprendere la storia del pianeta, dalle origini della vita miliardi di anni fa fino ai cambiamenti biotici più recenti. L'ambito della ricerca paleontologica è tanto vasto quanto diversificato e rappresenta un campo in continua evoluzione. In questo studio, esperti provenienti da tutto il mondo si sono riuniti per redigere un elenco di “Grandi Domande” prioritarie che la paleontologia potrà affrontare nei prossimi anni. Le 89 domande qui presentate, raggruppate in 11 temi, rappresentano il contributo di circa 200 scienziati internazionali. Queste domande riguardano tematiche come i meccanismi e i pattern di biodiversità, l'integrazione di varie tipologie di dati su scale spazio-temporali multiple, l'applicazione delle conoscenze paleontologiche ai problemi attuali della crisi climatica e della biodiversità, e l'uso efficace di metodi e tecnologie innovative per ottenere nuove intuizioni paleontologiche. Oltre a questi temi teorici, la discussione si focalizza su problematiche strutturali del campo, promuovendo una maggiore valorizzazione della ricerca basata sugli esemplari, la protezione dei siti di interesse culturale e paleontologico, e l'importanza delle infrastrutture per preservare le collezioni, insieme a una crescente enfasi su un apporto multiculturale, equo e inclusivo. Queste domande costituiscono un punto di partenza—un nucleo di consenso iniziale che i paleontologi possono espandere—per avviare discussioni, ottenere finanziamenti, promuovere i musei e favorire una crescita continua verso direzioni condivise di ricerca.

Non-technical Summary

Paleontologists study the history of life on Earth, from its beginnings billions of years ago to the present day. To unify the discipline and develop a shared research agenda, nearly 200 scientists from more than 30 countries worked together to identify key questions for the future of paleontology. The resulting questions address topics including biodiversity, data integration, application of paleontology to societal issues, and utilizing new technology. Discussions also focus on topics related to improving the field, such as valuing specimen-based research, protecting fossil collecting sites, advocating for museums, and promoting diversity and inclusion among practitioners. These questions are a starting point for paleontologists for future developments of the discipline.

Introduction

Paleontology offers an important scientific contribution by asking questions about life throughout the billions of years of Earth's history. The field itself has expanded from one based principally on collecting and documenting fossils to a hypothesis-driven, evidence-based field of inquiry using increasingly complex data, analytical approaches, and computational techniques. Paleontologists examine a range of topics about the history of life, including extinction, the evolution of organisms, biodiversity, the impact of climate changes, and the complex dynamics between life and other components of the Earth system. These comprehensive studies of life in the past provide critical context for understanding life on the planet today and the possible responses to ongoing environmental changes.

As in all scientific disciplines, the questions pursued by paleontologists fall on a spectrum, from large overarching questions that are central to the discipline to questions that are more specific and focus on smaller scales or pressing topics or contribute a component for addressing broader questions. The large overarching questions are likely to be persistent, but we can begin to address these grand themes by asking specific questions at various levels of resolution. For example, while a consensus exists on the principal features of the broad trajectory of life preserved in the fossil record, continued and closer examination of the record is required to resolve the details of evolutionary processes, environmental perturbations, and random effects that led to the modern configuration of life on Earth. As the resolution of studies becomes more specific, questions can range from “To which taxon does this specimen belong?” to questions such as “What is the role of abiotic and biotic interactions in driving biodiversity patterns?” Whereas “smaller” questions like the former are foundational to studying paleontology and merit support on their own, it is questions such as the latter

(i.e., a “Big Question”) that are the scope of this paper, as they indicate the current state of the discipline and its aims for future scientific development.

Through the Big Questions project detailed herein, we seek to provide a road map for how paleontological research might develop in the coming years, as prioritized by members of the paleontological community. A Big Question (BQ) is defined here as an open-ended question of high scientific importance that can be answered within a reasonable time frame. Defined in this way, BQs become priority questions that can be used to emphasize the importance of the discipline to the larger research community, as well as to direct scientific effort and research funding (Sutherland *et al.* 2009; Willis and Bhagwat 2010; Parsons *et al.* 2014; Seddon *et al.* 2014). For our purposes, we considered a reasonable time frame to be several years, although some questions may require a longer duration to address (e.g., the duration of a career). The amount of time needed to answer a BQ with precision and accuracy is variable and dependent on many factors, including technological advances and available resources.

The answer to a BQ should represent a substantive leap forward in the community's understanding of an issue or address a knowledge gap. “Scientific importance” requires examination of the perceived value of a BQ within the paleontological community, the broader scientific community, and its transference to society at large. Incorporating a diverse set of individuals engaged in paleontological research increases the confidence with which we can present research directions that can justifiably be defined as scientifically important to the international paleontological community. As such, the Big Questions project represents a democratic perspective of the paleontological discipline by individuals conducting germane research; we acknowledge that this effort was influenced by the opinions of those who participated, who represent a small percentage of the global paleontological community.

As the discipline of paleontology continues to grow in scope and application, paleontologists have a responsibility to routinely reflect on, criticize, discuss, and refine research directions, the best practices for conducting professional activities, and the cohesion of the discipline across geopolitical boundaries. Here we present the outputs of such an effort, providing an examination of the current state of paleontological research as expressed by the questions pursued in this discipline.

Methods

Project Contributors

The Big Questions project is a community initiative, coordinated through the PaleoSynthesis Project, that sought to engage a broad range of scientists working in paleontology and related disciplines (e.g., archaeology, biology, climate science, geology). Members of the Big Questions coordination team (J.A.S., W.K.) invited participation from the community through three solicitations requesting the submission of BQs in 2020 and 2021 (Fig. 1). The first solicitation was distributed in June 2020 using the PaleoNet listserver and to members of societies including the Palaeontological Association, Paleontological Society, and Paläontologische Gesellschaft. To reach a broader audience, the coordination team issued a second call in January 2021, again using PaleoNet, but expanding to include social media (Facebook; Twitter, now X) and listservers for the Ecological Society of America (Ecolog-L) and the Conservation Paleobiology Network (CPN-L).

In March 2021, the first virtual, plenary meeting was held for those individuals who indicated they would like to contribute to the project. As an outcome, participants in the meeting recognized that the group was dominated by individuals from the United States and Europe (Table 1). Consequently, a third solicitation was distributed in late March 2021 using the same approach as the second solicitation, this time with versions in English, French, Italian, Chinese, and Spanish (reflecting widely spoken language proficiencies in the existing group of participants). Participants involved via the first two solicitations were encouraged to use their personal networks to invite participants from places and with backgrounds not already represented in the project.

Working Group Assignments

As a part of the first two solicitations, participants were asked to submit questions they felt were outstanding in the field of paleontology

(Table 2). The coordination team then created 12 themes that captured as much of the variation as possible from the submitted questions. Individuals who joined the Big Questions project during the third solicitation were asked to self-select the best category for their questions, as the 12 themes had already been established. All assignments (from all solicitations) were checked for consistency, and when a question pertained to multiple themes, it was assigned to each relevant theme (Fig. 2). Ten of the groups focused on scientific questions (one of which was dropped due to overlaps with questions in related groups; Table 2) and two groups centered on structural issues relating to how paleontology is practiced, as scientific questions and scientific practice are not distinct domains.

All participating individuals were asked to rank their top five theme preferences (Table 2) and assigned to their highest available preference, while attempting to balance numbers and diverse group composition using inferences regarding aspects to participants' identities (e.g., career stage, country, gender identity). Such inferences are undoubtedly flawed (e.g., institutional affiliation may not reflect a participant's nationality), but were an attempt to form diverse groups using incomplete information. Participants were given the additional option to join one of the groups addressing structural issues ("Fundamental Issues," "Looking Inward and Outward"). All participants were given the option to volunteer as a working group leader, and one to three leaders were selected for each group from those volunteers, with consideration for representation of the diverse backgrounds of individuals participating in the project.

Refinement of Big Questions

Under the direction of working group leaders, the working groups were tasked with refining the set of questions assigned to their themes (Supplementary Material 1) into a condensed set of 8–12 preliminary questions. As a guide for this process, all were asked to consider the following discrete criteria (from Sutherland et al. 2009) for what a BQ entails:

1. Addresses an important gap in knowledge
2. More than just a general topic area (e.g., climate change)
3. Answerable through a realistic research design
4. Has a spatial and temporal scale that can be addressed by a research team
5. Has a factual answer that does not depend on value judgments

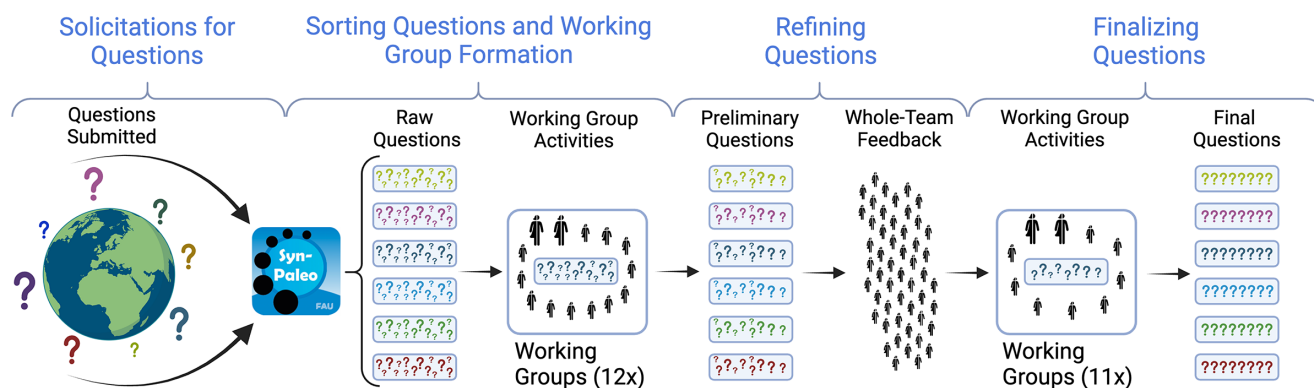


Figure 1. The question pathway in the Big Questions project. Questions were submitted by the global community in one of three solicitations. Submitted questions were assigned to working groups ($n = 12$) composed of self-identified topic experts who chose to participate in the project. Working groups were guided by one to three leaders (larger icons) and refined their assigned questions to a preliminary list. These preliminary questions were assessed by the entire Big Questions team to improve question quality and reduce redundancies in questions from different groups. Using whole-team feedback, working groups (reduced to 11 due to overlaps; Table 2) produced a refined set of final big questions. Created with BioRender.com.

Table 1. Countries and administrative regions represented in the Big Questions project by affiliations of the authorship team at the time of manuscript submission, with respect to when individuals joined the project. Note: as countries and administrative regions represented are derived from the institutional affiliations of the authors, this is likely an underestimate of the number of countries and administrative regions represented by individuals in this project

Country/administrative region (AR)	First solicitation	Second solicitation	Third solicitation	Authorship team
	Number of affiliations (% of solicitation total)	Number of affiliations (% of solicitation total)	Number of affiliations (% of solicitation total)	Number of affiliations (% of authorship total)
Argentina	3 (5.8%)		10 (13.9%)	13 (8.0%)
Australia	1 (1.9%)	2 (5.1%)	2 (2.8%)	5 (3.1%)
Austria		2 (5.1%)		2 (1.2%)
Brazil			2 (2.8%)	2 (1.2%)
Canada			1 (1.4%)	1 (0.6%)
China			4 (5.6%)	4 (2.5%)
Colombia		1 (2.6%)		1 (0.6%)
Czech Republic	2 (3.8%)	1 (2.6%)		3 (2.0%)
Egypt		1 (2.6%)		1 (0.6%)
France			2 (2.8%)	2 (1.2%)
Germany	14 (26.9%)	4 (10.3%)	1 (1.4%)	19 (11.7%)
Ghana	1 (1.9%)			1 (0.6%)
Hong Kong SAR, China	1 (1.9%)			1 (0.6%)
India			4 (5.6%)	4 (2.5%)
Italy	1 (1.9%)	2 (5.1%)	1 (1.4%)	4 (2.5%)
Jamaica		1 (2.6%)		1 (0.6%)
Madagascar			2 (2.8%)	2 (1.2%)
Mongolia			1 (1.4%)	1 (0.6%)
New Zealand			1 (1.4%)	1 (0.6%)
Norway		1 (2.6%)		1 (0.6%)
Panama	2 (3.8%)	1 (2.6%)	2 (2.8%)	5 (3.1%)
Poland	1 (1.9%)			1 (0.6%)
Portugal	1 (1.9%)		2 (2.8%)	3 (2.0%)
Singapore			1 (1.4%)	1 (0.6%)
South Africa			1 (1.4%)	1 (0.6%)
Spain	5 (9.6%)	2 (5.1%)	3 (4.2%)	10 (6.1%)
Switzerland			4 (5.6%)	4 (2.5%)
Taiwan		1 (2.6%)	5 (6.9%)	6 (3.7%)
United Kingdom	2 (3.8%)	3 (7.7%)	4 (5.6%)	9 (5.5%)
United States	18 (34.6%)	16 (41.0%)	19 (26.4%)	53 (32.5%)
Venezuela		1 (2.6%)		1 (0.6%)
Affiliations added	52	39	72	163
Countries/AR added	13	7	11	31

6. Tends not to be situationally dependent (i.e., answerable with “it all depends”)
7. Is not likely to be answerable with “yes” or “no”

Groups accomplished this goal through a combination of strategies, chosen by group leaders, including one or more of: (1) separating questions into subthemes and condensing on common ideas; (2) formation of subgroups to evaluate subsets of questions; (3) virtual

meetings to discuss refinements; and (4) drafting of questions to combine those that existed or cover omitted topics.

Following refinement of the preliminary questions by each group, all questions were compiled for cross-group comments. Participants were asked to suggest revisions, evaluate the importance of each question, and identify overlaps. The coordination team then compiled and summarized responses according to the importance of questions and overlaps. Group leaders coordinated

Table 2. Working group themes and numbers of questions related to these groups at three stages of the project. The number of individuals assigned to each group is also provided, with the number of group leaders in parentheses. *The theme “Ecosystems, Environments, and their Records” was included originally, but after the whole-team feedback phase (Fig. 1), considerable overlaps with questions from other groups were apparent, and all questions from this theme were ultimately distributed elsewhere or subsumed by questions in other groups. †Total is greater than the number of submitted questions (*n* = 528), because a question that was relevant to more than one group was assigned to each group for consideration

Working group themes	Number of assigned participants (group leaders)	Initial questions assigned to group	Preliminary questions	Final questions
Adaptations, Innovations, Origins (AIO)	17 (2)	50	4	7
Biodiversity Drivers (BD)	17 (2)	74	9	9
Biodiversity Dynamics in Space and Time (BST)	17 (2)	47	8	7
Climate Change Past and Present (CPP)	16 (2)	52	10	9
Conservation Paleobiology (CPB)	17 (2)	76	6	8
Ecosystems, Environments, and Their Records	16 (2)	55	16	0*
Extinction Dynamics (ED)	17 (2)	60	11	9
Phylogenetics, Taxonomy, and Systematics (PTS)	17 (3)	66	11	10
Scaling Ecological and Evolutionary Processes and Patterns (SEP)	16 (1)	75	11	9
The Adequacy of the Fossil Record (AFR)	16 (2)	51	11	8
Fundamental Issues (FI)	22 (2)	75	9	5
Looking Inward and Outward (LIO)	24 (1)	14	11	8
Total questions:		695†	117	89

efforts within and among groups to refine the questions further on the basis of this compiled information (Tables 3–13). Finally, each working group drafted text to contextualize their questions, forming the first version of this article.

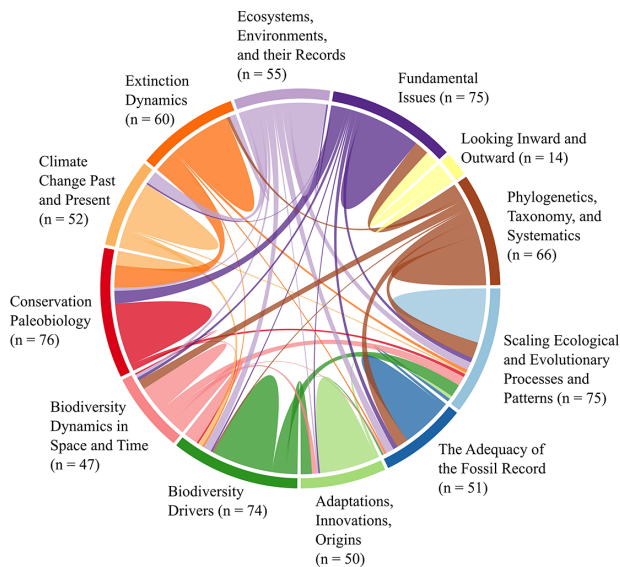


Figure 2. Assignments of originally submitted questions to different working groups. Each question was assigned to at least one group, and many were also assigned to a second group with topic overlap. Width of the outer circle represents the number of questions assigned to each working group (counts also provided in parentheses). Bands connecting different working groups represent the questions assigned to each of the groups, with thicker bands indicating a larger number of questions shared between groups. Created in R Statistical Software (v. 4.3.1; R Core Team 2023) using the circlize package (Gu et al. 2014) and the Paired palette from RColorBrewer (Neuwirth 2022).

The Big Questions in Paleontology

The three solicitations for submission of Big Questions resulted in 528 contributed questions. (Supplementary Material 1: Raw Questions). The number of questions assigned to a given theme ranged from 14 to 76 (Table 2). Groups refined these questions (Supplementary Material 1: Preliminary Questions) to a preliminary list including 4 – 16 questions from each group (Table 2).

After feedback from all BQ participants, working groups again refined their questions, producing 5 – 10 final questions from each group (Table 2; Fig. 1). The BQs are available in Tables 3–13 (in non-ordered lists from each group), clustered in related themes, starting with questions pertaining to topics that might affect any paleontological study (e.g., preservation, scaling, taxonomy). In the eleven sections that follow, explanatory text accompanies the set of questions from each working group, with questions referred to in the text by working group acronyms (see section headers and tables for acronyms) and non-ordered, unranked numbering. Given the strong relationships among different areas of research in paleontology, there are overlaps in the topics of some questions, which can be taken to indicate important, cross-cutting themes within the discipline (Fig. 2).

The Adequacy of the Fossil Record (AFR; Table 3)

The fossil record is our primary window into the origin and evolution of life on Earth, providing the only direct line of evidence for these events. Yet, the fossil record is composed primarily of organisms with anatomical, behavioral, and ecological attributes that enhance their preservation potential (AFR1, Table 3; Kidwell and Flessa 1996; Behrensmeyer et al. 2000; Sansom et al. 2010; Klompmaker et al. 2017; Saleh et al. 2020, 2021). Preservation biases are also often exacerbated by other biases introduced throughout the life of specimens (AFR2; e.g., Seilacher et al. 1985;

Table 3. Big Questions for the working group on “The Adequacy of the Fossil Record”

Unique ID	Big Question
AFR1	How can we best quantify preservation and collecting biases?
AFR2	How do we develop methods to identify, minimize, and correct data entry biases?
AFR3	How do we account for data loss in historical collections and publications?
AFR4	How do we standardize taxonomic, stratigraphic, and ecological reporting during data acquisition?
AFR5	How can we improve the collection of biomolecules from fossils, and what are the limits for biomolecular analysis?
AFR6	How can we correlate marine and terrestrial strata more precisely?
AFR7	In what ways can we use isotopic systems and geochemical methods to help identify preservation biases?
AFR8	Which opportunities and threats for fossil discovery will arise as a result of the changing climate?

Behrensmeyer *et al.* 2000; Louys *et al.* 2017; Krone *et al.* 2024)—for example, those relating to acquisition and curation, collecting, digitization, geography and geopolitics, publication, specimen preservation, storage, and transport (Flessa *et al.* 1992; Whitaker and Kimmig 2020; Raja *et al.* 2022; Johnson *et al.* 2023). Methods development for evaluating and mitigating these biases continues to be an important area of research (AFR1–AFR3; e.g., Dunhill *et al.* 2014; Stewart *et al.* 2021; De Baets *et al.* 2022; Na *et al.* 2023; Antell *et al.* 2024; Hohmann *et al.* 2024). Adding to the challenge presented by these biases, maintenance of existing collections and capacity for new collections are threatened by a lack of funding, curatorial staff, and adequate storage facilities, both physical and digital (AFR3; Allmon *et al.* 2018; Marshall *et al.* 2018).

Differences in data collection and reporting methods can compound biases in paleontological studies, as researchers have specific purposes when they acquire data (AFR4), and these idiosyncrasies can limit future uses of the data. To reduce duplication of data, reduce research costs, and increase versatility, it is imperative to document and clearly communicate data acquisition and management practices (e.g., as through the extended specimen concept; Lendemer *et al.* 2020; Hardisty *et al.* 2022; Monfils *et al.* 2022). Establishing best practices in these areas will benefit paleontology as we move toward a “big data” future (i.e., data characterized by great variety, volume, and/or velocity; Balazka and Rodighiero 2020), and digitization of existing and new specimens is becoming increasingly common (AFR2; Berents *et al.* 2010; Allmon *et al.* 2018).

Methodological, imaging, and analytical advances—geochemical approaches in particular (e.g., nontraditional stable isotopes, synchrotron, handheld XRF)—have created new opportunities for evaluating preservational processes (e.g., Gueriau *et al.* 2016; Teng *et al.* 2017). For example, advances in organic geochemistry have increased the capacity to extract biomolecules and biomarkers from fossil and sedimentary archives (e.g., Schweitzer *et al.* 2008; Briggs and Summons 2014; Vinther 2015; Falk and Wolkenstein 2017; Demarchi 2020; Wiemann *et al.* 2020; McNamara *et al.* 2021). However, it remains to be seen how deep in time biomolecules can be found and with what accuracy and resolution the methods can be applied through geological time (AFR5). Inorganic geochemistry has also advanced fundamentally in the last decades, as stable isotope (traditional and nontraditional) and clumped isotope

systems provide new insights in studies of $p\text{CO}_2$, pH, paleophysiology, mass extinctions, and the paleobiology and paleoenvironment of fossil taxa (e.g., Casey and Post 2011; Cook *et al.* 2015; Kimmig and Holmden 2017; Martin *et al.* 2017; Chen *et al.* 2018; Kral *et al.* 2022; Jung *et al.* 2024). Geochemical advances and continuing improvements to technology and equipment also are expanding the scope of paleontology by enhancing our understanding of diagenesis, morphology, paleoecology, and paleoclimate (AFR6, AFR7; e.g., Smith *et al.* 2021; Abdelhady *et al.* 2024; Comans *et al.* 2024).

The changing global environment also presents new challenges and opportunities for sampling the fossil record (AFR8). For example, as sea level rises and extreme weather events become more common, some existing fossil collecting sites along the coasts may be submerged (e.g., chalk deposits in Europe), while the same processes might lead to the exposure of new sites (e.g., Reimann *et al.* 2018; Voudoukas *et al.* 2022). It is also likely that rising temperatures causing the loss of permafrost and glacial ice will expose previously inaccessible outcrops that offer new opportunities for research, even as the changing climate alters erosional processes that may influence fossil exposure and quality (AFR8; e.g., Clark *et al.* 2021).

Scaling Ecological and Evolutionary Processes and Patterns (SEP; Table 4)

The scale of an investigation influences the observation and interpretation of ecological and evolutionary processes (SEP1–SEP4, Table 4). In paleontology, scale often relates to the temporal and spatial dimensions of taxa, patterns, or processes (SEP2, SEP3).

Table 4. Big Questions for the working group on “Scaling Ecological and Evolutionary Processes and Patterns”

Unique ID	Big Question
SEP1	Which evolutionary and ecological processes (local to global) can be best evaluated using the fossil record?
SEP2	In the fossil record, how do we interpret and measure ecological and evolutionary trends at different taxonomic, spatial, and temporal scales to infer directionality or causality?
SEP3	How do we address the spatial, temporal, and taxonomic incompleteness of the fossil record to be able to interpret ecological and evolutionary processes and patterns at different scales?
SEP4	How can we identify and counteract spatial and temporal transmutations (a change in the relationship between variables caused by crossing data scales, leading to interpretive error) within ecological and evolutionary models?
SEP5	Given incompleteness of the fossil record and spatiotemporal averaging, how do we estimate rates of change in taxonomic composition, community structure, ecosystem function, niches, traits, life modes, turnover, etc., using the fossil record?
SEP6	What drives metacommunity composition and community assembly over time and space?
SEP7	How do external environmental drivers (e.g., plate tectonics, global temperature, sea level) influence the structure of biological systems at different spatiotemporal scales?
SEP8	What are the signatures of emergent processes at macroevolutionary timescales (e.g., species sorting, species selection, clade competition)?
SEP9	How do biological systems impact the abiotic systems and the feedback between them at different scales?

Ecological and evolutionary processes occur at multiple spatiotemporal scales, but identifying or demonstrating their significance at all scales is challenging and rare (SEP4; Jablonski 2008; Price and Schmitz 2016; Rapacciuolo and Blois 2019; Louys et al. 2021; Liow et al. 2023). Evaluating the effects of scaling in the fossil record is further complicated by the need to identify and address the incompleteness of the record (SEP3, SEP5; Peters and Heim 2011; Benson et al. 2021; and see “The Adequacy of the Fossil Record”). The data captured in the fossil record are imperfect and biased, providing only a glimpse of longer and shorter processes, patterns, and interactions (SEP3, SEP5–SEP7; Faith et al. 2021; Flannery-Sutherland et al. 2022; Dunne et al. 2023).

Paleontological research into the ecological and evolutionary drivers of observed patterns is flourishing, as emergent research areas—for example, conservation paleobiology (Dietl et al. 2015; Dillon et al. 2022), geobiology (Knoll et al. 2012), and phylogenetic paleoecology (Lamsdell et al. 2017)—bridge subdisciplines and broach connections between the micro- and macroevolutionary scales (SEP2, SEP5 – 7; e.g., Machado et al. 2023; Rolland et al. 2023). Paleontologists must grapple with demonstrating links to the biology of modern organisms (i.e., neontology) in studies at various scales in the fossil record (Dietl et al. 2019; Rapacciuolo and Blois 2019). Unifying paleo- and neontological data can reveal more about the natural world than either could in isolation (e.g., Hlusko et al. 2016; Smith et al. 2023c); however, the efficacy of cross-scale analyses needs continued examination. Macroecology (Brown 1995; McGill 2019) may provide one option to incorporate a conceptual basis for this work as, for example, studies of the metacommunity concept—a set of local communities that are linked by dispersal of multiple, potentially interacting species (Leibold et al. 2004)—provide a framework for examining scale-based problems. A tenet of this concept is that the study of local patterns and processes is not sufficient to understand the structure and dynamics of a metacommunity (Leibold et al. 2004). Studying metacommunity composition and community assembly over space and time acknowledges the fluidity and connection of communities and seeks common patterns across metacommunities (SEP6; e.g., Muscente et al. 2018, 2022; Eden et al. 2022; Gibert et al. 2022). The relationship between the processes on evolutionary scales, their relative influence, and fluctuations through time continue to be important topics (SEP2, SEP4, SEP8).

Over the course of Earth’s history, the biosphere has had a profound impact on the geosphere in ways that we are still working to fully comprehend (SEP9). Studying the interaction from an abiotic perspective highlights the feedback mechanisms and interactions within the Earth–life system, as traces of life are ubiquitous from Earth’s mantle to the atmosphere (Pawlik et al. 2020; Giuliani et al. 2022).

Phylogenetics, Taxonomy, and Systematics (PTS; Table 5)

The fossil record contains unique information on the diversity of previous life-forms and their relationships to one another, which provides retrospective context for cataloging and understanding life on the planet today. Phylogenetics is often perceived simply as a tool for inferring evolutionary relationships or organizing biodiversity but also can be seen more broadly as a framework for hypothesis testing and reconstructing past events that are not directly observable in the fossil record (Bromham 2016). This can include estimating species divergence times, studying trait evolution, or quantifying diversification dynamics. Although speciation and extinction have a long history of study, these processes

Table 5. Big Questions for the working group on “Phylogenetics, Taxonomy, and Systematics”

Unique ID	Big Question
PTS1	What causes the mechanism of speciation or character evolution to change over time?
PTS2	Which abiotic and biotic factors determine species longevity (stratigraphic duration)?
PTS3	Which aspects of the macroevolutionary process are identifiable in the molecular or fossil records using phylogenetic methods, and under which circumstances?
PTS4	How can traditional taxonomy be used to inform the process of selecting the best operational taxonomic unit for a particular phylogenetic analysis (e.g., diversification, disparification, phylogeny)?
PTS5	How can taxonomic practice help to harmonize boundaries between taxa in fossil and extant groups?
PTS6	How can we collect and integrate developmental data observable in the fossil record (e.g., timing of organogenesis, gene expression) into phylogenetic approaches?
PTS7	How much phylogenetic information can be gained from combining different types of data (e.g., morphology, stratigraphy, biogeography, environmental)?
PTS8	How can we improve the performance of phylogenetic inference through the development of better methods?
PTS9	How do we improve the representation of uncertainty and bias from the fossil and geological records in phylogenetic inference?
PTS10	What can we learn about environmental and geological processes using phylogenetic methods?

are complex, and some aspects require further study to improve our understanding (PTS1, PTS2, Table 5). By adopting new methodologies, improving data collection practices, and integrating various types of data centered around current, carefully constructed taxonomies, we can unlock the full potential of hypothesis testing using phylogenetic approaches (PTS3).

Phylogenies are often constructed using molecular data, but there are many benefits to including information from other sources, such as the fossil record (PTS4, PTS5; Parham et al. 2012; Lee and Palci 2015; Mongiardino Koch et al. 2021; Wright et al. 2022). Other data sources, such as developmental biology (Wright 2015), may also prove useful in phylogenetic inference (PTS6). The field requires a multidisciplinary perspective informed by computer and data science, ecology, geology, geochronology, phylogenomics, and statistics (Parham et al. 2012; Liow et al. 2023). Phylogenomics and deep learning can help to discern and organize biodiversity, but their accuracy will always depend on the quality of their input data, which necessitates reliable systematics and taxonomic identifications (e.g., Bortolus 2008). The accuracy of phylogenetic analyses that include fossils relies on information about taxonomies and their associated uncertainties (Bortolus 2008; Parham et al. 2012; Soul and Friedman 2015; Barido-Sottani et al. 2023). Taxonomy and comparative anatomy are invaluable in understanding diversification history and character evolution, establishing homologies, quantifying variability, and generating testable hypotheses using phylogenetics and species delimitation methods (Barido-Sottani et al. 2023). These research fields must be supported in their own right (Agnarsson and Kuntner 2007; Löbl et al. 2023; Smith et al. 2023b).

Integrating different data types requires explicit process-based models (PTS7, PTS8), such as the fossilized birth–death model,

which models speciation, extinction, and fossilization simultaneously (Stadler 2010; Heath *et al.* 2014). Combined with models of molecular and morphological evolution, this framework allows for statistical inference of dated phylogenies that include extant and fossil taxa. Most existing models treat speciation and character evolution as independent (Warnock and Wright 2020), but further refinement of this framework can illuminate the tempo and mechanisms of speciation (PTS1). Comprehensive analyses also require approaches that capture uncertainty and biases while concurrently allowing for varied approaches to weighting of molecular and morphological data (PTS9). We can construct explicit Bayesian hierarchical models to incorporate different data types while accounting for uncertainty in a principled and intuitive way (e.g., Höhna *et al.* 2016; Bouckaert *et al.* 2019; Ronquist *et al.* 2021). It is also imperative to assess the trade-off between data availability, computational efficiency, and model complexity. Simulations play an important role in confronting this challenge and parameter identifiability issues associated with phylogenetic models by helping to explore the performance of available methods, potential limitations of data, and the expectations under null hypotheses (Barido-Sottani *et al.* 2019; Louca and Pennell 2020; Höhna *et al.* 2022; Mulvey *et al.* 2024).

Environmental and geological processes influence the course of evolution (e.g., Arakaki *et al.* 2011; Hannisdal and Peters 2011; De Baets *et al.* 2016; Kocsis *et al.* 2021). Incorporating these processes into phylogenetics will elucidate their interaction with biological events, linking large-scale processes, such as the extent and timing of climatic change, continental breakup, or changes in depositional rates through time with evolutionary phenomena (PTS10).

Biodiversity Dynamics in Space and Time (BST; Table 6)

Quantifying and interpreting biodiversity dynamics over time is a long-standing theme in paleontology (Phillips 1860; Sepkoski *et al.* 1981; Benson *et al.* 2021), leading to questions such as whether there are constraints on global biodiversity (BST1, Table 6; Alroy *et al.*

Table 6. Big Questions for the working group on “Biodiversity Dynamics in Space and Time”

Unique ID	Big Question
BST1	What is the global diversity trend through time, and how is diversity constrained, if at all?
BST2	How have large-scale spatial diversity patterns (e.g., latitudinal diversity gradient, distribution of diversity hotspots) changed across deep time?
BST3	What are important drivers of global trends in taxonomic diversity or ecological disparity, and has their relative importance changed through time?
BST4	What is the relationship between deep-time biodiversity (e.g., taxonomic richness, ecomorphological disparity) and ecosystem function (the combination of all biological interactions and physical processes occurring in an ecosystem)?
BST5	What are the drivers of origination in space and time?
BST6	What is a common basis (e.g., taxonomic units, morphological traits) that can be used consistently to bridge modern and fossil biodiversity research?
BST7	In what ways is the “Anthropocene” creating a unique signature in biodiversity over geologic time (both direct and indirect effects; e.g., changes in climate and in connectivity)?

2008; Harmon and Harrison 2015; Rabosky and Hurlbert 2015; Close *et al.* 2020). Given the challenge of fully documenting modern biodiversity (Mora *et al.* 2011), we cannot expect to know absolute biodiversity in the past, but we can estimate relative changes in biodiversity. Genuine trajectories of biodiversity through time can be uncovered only if we can account for spatial differences and temporal changes in preservation potential, as well as other biases particular to the fossil record (e.g., Smiley 2018; Krone *et al.* 2024; and see “The Adequacy of the Fossil Record”). By dissecting the components of these trajectories, we can identify drivers of originations and extinctions in deep time (BST5; and see “Adaptations, Innovations, Origins”). To fully understand biodiversity, we must first agree on the most effective methods for measuring biodiversity over different timescales (BST6; see “Scaling Ecological and Evolutionary Processes and Patterns”). Such a consensus can help address pressing questions, including whether modern biodiversity is an outlier in geological time (BST7).

Spatial aspects of biodiversity, such as the latitudinal diversity gradient (Humboldt 1808), are as important as temporal patterns. An extensive literature explores causes of the latitudinal diversity gradient, including its dynamics over geological timescales (Jablonski *et al.* 2006; Allen *et al.* 2020, 2023; Zacari *et al.* 2021; Fenton *et al.* 2023; Quintero *et al.* 2023). Evidence points to a close link between the intensity of the latitudinal diversity gradient and paleoclimate (Mannion *et al.* 2014; Yasuhara *et al.* 2020; Yasuhara and Deutsch 2022), but exactly how the latitudinal diversity gradient changed over time remains an open question (BST2).

Biodiversity patterns are the result of extinctions, originations, and the intricate interactions between living organisms and their environment. Identifying the specific factors that drive global changes in biodiversity and disentangling the individual and combined effects of these factors require careful research and analysis (BST3; and see “Biodiversity Drivers”). Approaches leveraging new tools—including mechanistic models (e.g., Saupe *et al.* 2019), machine learning (e.g., Raja *et al.* 2021), and network analysis (e.g., Muscente *et al.* 2018, 2022; Woodhouse *et al.* 2023)—can identify key drivers of global and regional biodiversity and biodiversity hotspots through time (Cermeño *et al.* 2022) or at least provide testable hypotheses. We are only beginning to understand and quantify the role of biodiversity as a driver of ecosystem function in the paleontological record (BST4), underscoring the need for consistent units of measure across spatiotemporal scales (BST6; McGuire *et al.* 2023).

Biodiversity Drivers (BD; Table 7)

In paleontology, documenting patterns of biodiversity is a central theme, but understanding the factors that drive these patterns is a large task (Jablonski 2008, 2017; Ezard *et al.* 2016; Di Martino *et al.* 2018). We can, however, begin to address this challenge by decomposing the task into more manageable questions and hypotheses that extend across taxonomic levels. Comparing taxa with differing ecological characteristics (BD1, Table 7) may help disentangle prevailing drivers—including anthropogenic drivers—under shared and disparate environmental conditions or times of perturbation (BD2; Harnik 2011; Klompmaker *et al.* 2013; Hull *et al.* 2015; Trubovitz *et al.* 2023). To compare the potential drivers across taxonomic groups and to do so on different spatial and temporal scales, it is crucial to standardize, harmonize, and clearly communicate study design and methods (Hayek *et al.* 2019). Doing so will help us establish broader principles that transcend specific taxonomic, spatial, and temporal contexts (BD3).

Table 7. Big Questions for the working group on “Biodiversity Drivers”

Unique ID	Big Question
BD1	How do the ecological niches of species influence their response to perturbation?
BD2	How does the prevailing climate state experienced by species and communities influence their response to perturbation?
BD3	How do methodological choices influence the outcome of studies investigating the relative importance of abiotic and biotic drivers in driving biodiversity dynamics?
BD4	How do the rate and magnitude of environmental change impact diversification?
BD5	How did biological evolution affect the evolution of other Earth systems (e.g., lithosphere, atmosphere, and hydrosphere)?
BD6	How has the relative importance of biotic and abiotic drivers of biodiversity and extinction changed through time?
BD7	What is the relative role of biotic and abiotic drivers in increasing ecosystem complexity?
BD8	To what extent do population-based characteristics determine resilience to extinction through geological time?
BD9	How do changes in community structure observed at the population level relate to evolutionary changes in ecosystems through time?

Abiotic and biotic conditions change through time at varying rates and magnitudes, and their effects on biodiversity and ecosystem dynamics warrant further study (BD4, BD7). It has been suggested that abiotic drivers act over broad spatiotemporal scales (e.g., Court Jester model; Barnosky 2001), whereas biotic drivers are more applicable on local and shorter scales (e.g., Red Queen model; Benton 2009; Vermeij and Roopnarine 2013; Wisz et al. 2013). The relative significance of these sets of drivers remains uncertain (BD6; e.g., Eichenseer et al. 2019; Bush and Payne 2021; Spiridonov and Lovejoy 2022), underscoring the importance of conceptual models for how biodiversity responds to them (Vrba 1985, 1992, 1993; Mancuso et al. 2022). There is evidence that diversification patterns observed at higher taxonomic levels (e.g., family) are not always replicated at lower levels (e.g., species; Jablonski 2007; Hendricks et al. 2014; Balisi and Van Valkenburgh 2020). Across each of these variables, the effects of scale on which hypothesis is supported (i.e., biotic or abiotic drivers) merit further consideration—in some instances, relationships may be reversed when comparing shorter ecological and longer evolutionary timescales (BD3; e.g., De Baets et al. 2021). Further exploration with differing spatiotemporal scales, taxonomic groups, and ecologies is needed, as it remains a challenge to dissect the complex interplay between ecology, microevolution, and macroevolution on geological timescales (BD8, BD9; e.g., Liow and Taylor 2019; Liow et al. 2023). Examining the reciprocal effects of biological evolution as an actor, as well as in feedbacks and as a primary driver in other Earth systems, is a promising research direction (BD5).

Adaptations, Innovations, Origins (AIO; Table 8)

The evolutionary history of many species (and higher taxa) is demarcated by adaptive novelties and innovations along with repeated migration, dispersal, and colonization events as species have evolved and survived through morphological adaptation, ontogenetic shifts, and novel behaviors (AIO1, Table 8; e.g.,

Table 8. Big Questions for the working group on “Adaptations, Innovations, Origins”

Unique ID	Big Question
AIO1	What were the geological and biological drivers of the origin of life and major groups of organisms such as eukaryotes, plants, animals, and fungi?
AIO2	How were major life transitions (e.g., origins of biomineralization, early Paleozoic diversifications, terrestrialization, evolution of planktonic lifestyle) in Earth's history associated with major changes in the geological and/or biological environment?
AIO3	How is our understanding of the origination of novelties and innovations affected by fossil preservation, the global quality of the fossil record, and stratigraphic completeness?
AIO4	What are best practices for integrating different analytical tools and techniques to improve our interpretation of the ecological context and timing of the origin of adaptations and features?
AIO5	How have changes in ontogeny (i.e., life-history traits such as larval/juvenile ecology, growth, and developmental patterns, including heterochronies) influenced macroevolution or themselves been influenced by environmental change?
AIO6	Which common patterns of morphological or behavioral responses to environmental change on evolutionary timescales can be identified and how do these compare with modern systems on ecological timescales?
AIO7	Which observable differences in the origin and fixation of features at different scales of biological hierarchy can be identified, and what generated these patterns?

Nylin et al. 2018; Stigall 2019). Colonizing regions in new environments and adapting to cope with the challenges induced by new environmental pressures has led to the development and emergence of advantageous novelties over time. These novelties increase the capacity of individuals to survive, thrive, and reproduce (AIO1, AIO2; e.g., Patton et al. 2021; Tihelka et al. 2022; Woehle et al. 2022). Observing modern species and their responses to stimuli provides paleontologists with a means to connect microevolutionary processes and patterns to those observed over evolutionary timescales in the fossil record (AIO6), which are obscured by taphonomic processes (AIO3). Improving data integration across scales, leveraging new methods, and better accounting for biases can help us answer long-standing questions on topics relating to phylogenomic conflict (Parins-Fukuchi et al. 2021), evolutionary patterns (e.g., phyletic gradualism vs. punctuated equilibrium; Gould and Eldredge 1972; Hunt 2007; Hunt et al. 2015; Tsuboi et al. 2024), and phylogenetic relationships (Wright et al. 2022).

The interdependence among ecological determinants and biological features requires thorough examination to reveal the inextricable relationship between micro- and macroevolutionary processes, environmental change, and preservation (AIO4–AIO6; e.g., Lamsdell et al. 2020; Almécija et al. 2021; and see “The Adequacy of the Fossil Record”). To develop these research directions (AIO5–AIO7), hypotheses on the emergence of major features (e.g., Naranjo-Ortiz and Gabaldón 2019; Murdock 2020), changes in morphology (e.g., Anderson and Ruxton 2020; Hopkins and To 2022), ontogeny (e.g., Chevalier et al. 2021; Friend et al. 2021; Lanzetti et al. 2022), and behavior (e.g., Berbee et al. 2020; Yamamoto and Caterino 2023) require contextualization with spatiotemporal, taphonomic, and preservational constraints (AIO3, AIO4). Answering these questions can facilitate the examination of

overarching patterns in biotic developmental and community responses to perturbation throughout the history of life and can possibly be projected to the future (AIO6). Studies on the emergence of adaptations, innovative features, ontogenetic strategies, behaviors, and the development of novelties can provide paleontology with crucial insights into the processes of evolution and extinction, as well as the interactions between individuals, species, and communities (AIO5–AIO7; Barido-Sottani *et al.* 2020; Brocklehurst and Benson 2021; Stansfield *et al.* 2021; Dunhill *et al.* 2024).

Extinction Dynamics (ED; Table 9)

The understanding that species are ephemeral and will eventually become extinct is now a fundamental principle of paleontology (Cuvier 1813; Darwin 1859; MacLeod 2014; Marshall 2017)—and potentially scales up from species to faunas and paleocommunities (e.g., Muscente *et al.* 2022). This concept is integral to the study of the history of life on Earth, as it helps to explain changes in biodiversity observed in the fossil record (Jablonski 1991; McKinney 1997). At the same time, extinction is a major theme in modern bioscience relating to impacts of anthropogenic stressors (e.g., climate change, habitat change, pollution; McKinney 1997; Dirzo *et al.* 2014). As is usual for comparisons of the modern and fossil records, attempting to bridge the differences in study characteristics (e.g., evolutionary history of ecosystems; spatiotemporal completeness, extent, and resolution; taxonomic completeness; Foote 2000; Eichenseer *et al.* 2019; Foster *et al.* 2023; Pohl *et al.* 2023; Finnegan *et al.* 2024) over which extinction can be observed necessitates reflection on which data types are suitable to facilitate cross-scale studies and comparisons (ED1, Table 9; Lotze *et al.* 2011; Andréoletti and Morlon 2024).

The “BigFive” mass extinctions originally were defined using the concept of statistical outliers (Raup and Sepkoski 1982) at a high taxonomic level, using a specific rate metric, and based on

skeletonized marine organisms. An updated definition of mass extinction is long overdue, as is a dialogue on how pattern and process should be included in the definition (ED2; Marshall 2023). This definition would precipitate the reexamination of whether mass extinctions are associated with consistent vulnerabilities of specific morphological and ecological traits (ED3, ED4; Foster *et al.* 2023) and whether their phases and recovery patterns are comparable (ED6, ED7; Hull *et al.* 2015).

Another aspect of extinction dynamics, pertaining to the ecological impact of the event, is whether functional diversity is maintained across mass extinction events (ED5; Bambach *et al.* 2007; Foster and Twitchett 2014; Aberhan and Kiessling 2015; Dunhill *et al.* 2018; Muscente *et al.* 2018; Cribb *et al.* 2023). Mass extinctions are often attributed to abiotic changes (e.g., changes in temperature, oxygen content, pH), and finding thresholds relating to magnitudes and rates of such changes remains a priority (ED8; Song *et al.* 2021). Species also are likely to experience secondary extinction cascades due to the loss of critical biotic interactions (e.g., predator–prey relationships) in trophic or other biological interaction networks (Roopnarine 2006; Dunne and Williams 2009). If we are to truly understand the dynamics of extinction events in the fossil record and use them to predict extinction risk in our human-dominated world (Barnosky *et al.* 2011; Braje and Erlandson 2013; Song *et al.* 2021; Vahdati *et al.* 2022), we need to understand the interplay between primary and secondary extinction events via the inclusion of biotic interactions in studies of extinction selectivity (e.g., Sanders *et al.* 2018; Mulvey *et al.* 2022; Dunhill *et al.* 2024).

Climate Change Past and Present (CPP; Table 10)

Paleontologists often reconstruct past climates using fossils or geochemical proxies, and this remains a major theme in the biogeosciences (CPP1, Table 10). For example, examining stable oxygen isotopes in fossils can reveal climate change across temporal scales, from the life span of individual organisms (e.g., Nützel *et al.* 2010; Alberti *et al.* 2013) to the eon scale (e.g., Song *et al.* 2019;

Table 9. Big questions for the working group on “Extinction Dynamics”

Unique ID	Big Question
ED1	Which data types can be used to most effectively compare past extinctions to the current biodiversity crisis?
ED2	With our changing understanding of extinctions, how should the definition of “mass extinction” be updated to reflect a unified concept?
ED3	Which, if any, biotic traits associated with survival through a mass extinction (e.g., body size, trophic mode, species associations) are universal across taxa and/or time?
ED4	Which, if any, ecological impacts of extinction are generalizable across time?
ED5	To what extent are ecological functions maintained following the extinction of species?
ED6	To what extent are the phases of events (e.g., collapse, recovery) during extinctions consistent across different biotic crises?
ED7	Which, if any, patterns in the process and timing of recovery following extinction events are universal across clades?
ED8	At what threshold can climate or other abiotic change cause an extinction?
ED9	What is the role of cascading biological effects in extinction dynamics?

Table 10. Big Questions for the working group on “Climate Change Past and Present”

Unique ID	Big Question
CPP1	How can fossils best be used to reconstruct climate change over different timescales?
CPP2	Which climate factors are the proximate drivers of extinction?
CPP3	How can we best use the fossil record to predict climate change impacts on the modern biota?
CPP4	What is the “ecosystem sensitivity” of ecosystem structure in response to climate change?
CPP5	How have the spatial distributions of organisms shifted in response to climate change?
CPP6	How have organisms’ tolerances changed in response to climate change?
CPP7	Which cascading effects of climate change can be identified from the fossil record?
CPP8	What adaptation and management options for conservation biology can be derived from past biosphere responses to climate change?
CPP9	How has climate change affected the evolution of life?

Grossman and Joachimski 2022). However, smoothly integrating data across these temporal scales remains challenging (CPP1). Assessing biotic responses to changing climates is becoming a major theme in paleontology, with several pertinent questions (CPP2–CPP9; e.g., Rita et al. 2019; Piazza et al. 2020; Nätscher et al. 2023). Nevertheless, it is critical to avoid circular reasoning where climate reconstructions based on fossil proxies subsequently are used to interpret fossils.

A host of variables—including direct and indirect measures of nutrient levels, temperature, $p\text{CO}_2$, precipitation, salinity, pH, and, oxygen and other isotopes—can be used to examine the influence of climate on biodiversity (Bijma et al. 2013; Saupe et al. 2019; Jane et al. 2021; Jackson and O’Dea 2023; Lin et al. 2023; Yasuhara and Deutsch 2023; Malanoski et al. 2024). Elucidating the relative importance of these variables on biodiversity can guide conservation efforts (CPP2, CPP8), although best practices for bridging the mismatch in temporal scales studied in paleontology and those of interest to policymakers remain elusive (CPP3; Smith et al. 2018; Pimiento and Antonelli 2022; Groff et al. 2023; Kiessling et al. 2023; and see “Scaling Ecological and Evolutionary Processes and Patterns”). Bridging these gaps can benefit from studies leveraging conservatism of physiology (Reddin et al. 2020), simulations (e.g., Hunt 2012; Barido-Sottani et al. 2019; Raja et al. 2021; Smith et al. 2023a), and the pursuit of higher-resolution paleontological datasets (Smith et al. 2023c). The application of paleontological observations to conservation practice remains primarily aspirational (Groff et al. 2023); however, leveraging the need for temporal context to understand climate change is a promising avenue for integrating paleontological data (Smith et al. 2018; Dietl et al. 2019; Kiessling et al. 2019, 2023).

Climate sensitivity has been defined as the global mean temperature increase when atmospheric CO_2 equivalent concentration is doubled (IPCC 2021), and we can use this framework to define “ecosystem sensitivity” (CPP4). For example, how much will ecological structure—a concept challenging to objectively measure (e.g., Parrott 2010; LaRue et al. 2023)—change on average with a given increase in temperature? A more straightforward assessment of shifts in spatial distribution is also possible, as there is modern (Lenoir et al. 2020) and past (Wing et al. 2005; McElwain 2018) evidence of species ranges tracking climate. Still, the signal is complex (Reddin et al. 2018, 2020), primarily due to sampling constraints and limited temporal resolution, and merits further examination (CPP5). In isolation from or in combination with range shifts, the degree to which species can adapt their niches over time is crucial to predicting how they will respond to ongoing climate change (CPP6). Fossil data support niche stability at low taxonomic levels (Hopkins et al. 2014; Saupe et al. 2014; Stigall 2014; Antell et al. 2020); however, thermal tolerances have evolved across the domains of life (Storch et al. 2014), suggesting that the rate and relative frequency at which tolerances evolve are key features in niche evolution.

The impacts of climate change on biotic systems are numerous (Pörtner 2021), but cascading effects are less well known (CPP7; e.g., Pecl et al. 2017; Słowiński et al. 2018). For example, differential range shifts of species in response to climate may lead to novel communities, with new biotic interactions and elevated potential for secondary extinctions (ED9; Pecl et al. 2017; Chiarenza et al. 2023). Identifying cascading effects in the fossil record is likely difficult but important to reveal the interplay of abiotic and biotic drivers under climate change (O’Keefe et al. 2023).

Conservation Paleobiology (CPB; Table 11)

Conservation paleobiology, which seeks to apply the methods and theories of paleontology to the conservation and restoration of biodiversity and ecosystem services (Dietl et al. 2015), has emerged as a pathway for paleontologists to engage with conservation issues. A key theme in these questions is the integration of multiple types of data and methods across scales (CPB2, CPB4, CPB6, Table 11) to provide insights about biodiversity change (CPB3–CPB5, CPB8). Questions in this section crosscut many of the other sections—especially “Climate Change Past and Present”—as conservation paleobiology is an emergent area of research in paleontology that is informed by the entire discipline.

Many paleontologists are seeking ways to more directly connect their science to practice (CPB1, CPB2, CPB8; Dillon et al. 2022). Although there are several success stories of paleontological data application (e.g., Everglades restoration; Marshall et al. 2014), only 10.8% of published conservation paleobiology studies have had a demonstrable effect on conservation practice (comparable to other areas of conservation science; see Groff et al. 2023). A cultural shift in the norms and practices of the paleontological community is required to produce research results that more closely align with the needs and concerns of practitioners (Dietl et al. 2023). How to get there is a big question (CPB1). At the same time, questions that form the theoretical basis for conservation paleobiology (CPB3–CPB7) remain research priorities, offering opportunities for scientific progress while highlighting gaps in our understanding of biodiversity and ecosystem function and, by extension, ecosystem services (Dillon et al. 2022). For example, it remains a significant challenge to untangle the different drivers that push ecosystems

Table 11. Big Questions for the working group on “Conservation Paleobiology”

Unique ID	Big Question
CPB1	What translational science strategies could be adopted to ensure that conservation paleobiology research remains relevant and aligned with the priorities of environmental resource managers and conservation practitioners?
CPB2	How do we integrate multiple types of paleontological data (e.g., molecular, environmental, ecological) with planning and decision support tools for guiding ecosystem management?
CPB3	How can our understanding of past episodes of environmental change be used to develop scenarios of biological responses to modern and future environmental stressors?
CPB4	How can we use paleontological data to define meaningful ecological baselines that are relevant to conservation across spatial and temporal scales?
CPB5	How can the fossil record inform our ability to diagnose and mitigate the effects of multiple interacting human and nonhuman drivers of environmental change on biodiversity and ecosystem functioning?
CPB6	How can we compare rates of biodiversity change (e.g., extinction, adaptation, geographic range shifts) across ecological, historical, and paleontological timescales?
CPB7	How can recent sedimentary records expand the temporal scope over which ecological resilience can be evaluated?
CPB8	In what ways can paleoenvironmental reconstructions improve the accuracy and scope of ecosystem services risk assessments?

beyond their natural limits and to understand the resulting responses over time (CPB5). The extent to which paleoecological records can be utilized to broaden the temporal perspective for detecting critical transitions in ecosystems and signals of changing resilience (CPB7) is also not fully understood. Nor is it known how, and under which circumstances, looking to the past can contribute productively to setting baselines for ecosystem recovery (CPB4) or anticipating a climate-changed future (CPB3). Such knowledge could support conservation management and planning efforts designed to help reduce the loss of biodiversity and ecosystem services (CPB8) in the face of environmental change. Theoretical development in these areas is foundational for paleontology and is essential for the discipline to grow as an applied area of research to provide insights about future changes in the human-dominated world (Dietl and Flessa 2011; Dietl *et al.* 2015, 2019; Barnosky *et al.* 2017; Dillon *et al.* 2022; Pimiento and Antonelli 2022; Groff *et al.* 2023; Kiessling *et al.* 2023; Kowalewski *et al.* 2023; Zuschin 2023).

Fundamental Issues (FI; Table 12)

Every scientific discipline relies on a dedicated community and supportive infrastructure. To protect paleontology’s foundational resources, infrastructure updates are needed (FI1, FI3, FI5, Table 12). Best practices for collecting, curating, and archiving paleontological data and heritage are developing, but a consensus remains a work in progress (FI1). Assigning specimens an accurate taxonomy in a sound systematic framework is critical for their utility and inclusion in a shareable resource (e.g., GBIF, iDigBio, the Paleobiology Database, FI3; Marshall *et al.* 2018). The accuracy and resolution of taxonomic identifications strongly affect biodiversity measurements and interpretation, but this fundamental work is consistently undervalued in the current system for rewarding academics (FI3; Agnarsson and Kuntner 2007; Mabry *et al.* 2022; Salvador *et al.* 2022; Smith *et al.* 2023b). As a result, taxonomic expertise is under threat (e.g., Agnarsson and Kuntner 2007; Salvador *et al.* 2022). Even so, novel methods for taxonomic analysis (e.g., machine learning; Romero *et al.* 2020; De Baets 2021; Punyasena *et al.* 2022; Abdelhady *et al.* 2024; Adaïmé *et al.* 2024) hold the potential to make taxonomic work more efficient, reproducible, and sustainable. Reliable taxonomic, locality, and stratigraphic information are essential for building physical (e.g., samples) and digital

(e.g., metadata, imagery) storage infrastructure that allows comparison and integration among researchers and scientific disciplines (Löbl *et al.* 2023). These improvements require a community effort that is supported by sustainable long-term funding—particularly in the Global South (e.g., Valenzuela-Toro and Viglino 2021; Raja *et al.* 2022). This funding can enable expanded accessibility, use, and combination of data, all of which are critical for facilitating interdisciplinary research (Allmon *et al.* 2018; Kaufman *et al.* 2018; Smith *et al.* 2023b). Through interdisciplinary research and study programs, the field can continue to expand (FI3). For example, studies of prehistory demonstrate long-standing human collection and use of fossils from the middle Pleistocene onward, creating new opportunities to understand human behavior through interactions with fossils (Cortés-Sánchez *et al.* 2020). Interdisciplinarity will continue to generate new creative approaches with valuable perspectives from other disciplines (e.g., archaeology, biology) while providing new insights on long-pursued questions in paleontology (FI2–FI4).

Paleontology is also economically and societally important (FI4, FI5). Economic contributions include resource exploration, regional tourism (Perini and Calvo 2008; Kibria *et al.* 2019), and diverse products based on paleontological research (e.g., books, clothing, film and television works, theme parks, toys, video games). Aside from these outputs, paleontology requires greater valorization within the scientific community and broader public (FI4, FI5; Plotnick *et al.* 2023). Geosites are non-renewable areas important for understanding Earth’s history through the observation of biological and geological phenomena. Protecting and conserving important outcrops (e.g., Atkinson *et al.* 2005; Maran 2014; Mexicana 2020; Neto De Carvalho *et al.* 2021; Carvalho and Leonardi 2022) and access to them necessitate transparent discussion among all who interact with and care about the sites (e.g., paleontologists, landowners, traditional custodians of the land, universities, industrial companies, museums, government). Additionally, collection spaces are the physical repositories of our geoh heritage (e.g., museums, geological surveys) and require sustained support from governments, academics, and the public. The primary evidence that paleontologists rely on (physical specimens) is under threat due to restructuring in funding models and museum closures, which removes from the public a pathway for engagement with geoh heritage. Public engagement provides a valuable means to increase the profile of paleontology. This work and the people involved in it require significant investment to draw together science, economy, and culture to care for Earth and life’s heritage (FI1, FI4, FI5).

As scientists, we have a responsibility to communicate with the public about our work, yet many researchers receive no formal training on how to perform this duty (e.g., Salvador *et al.* 2021), and these activities are secondary in hiring and promotion decisions (FI2, FI4; e.g., Davies *et al.* 2021; Raja and Dunne 2022). Without an informed public, policymakers cannot craft legislation that benefits the greatest number of people, and individuals cannot make accurate data-driven decisions. The roles of paleontologists continue to diversify, with a large proportion of graduates working outside academia in settings with variable skill requirements (FI2; e.g., industry, conservation, education, government; Keane *et al.* 2021). Paleontologists need skills to make them academically, economically, and socially valuable so they can share information about the long-term changes and variability that life on Earth has experienced with increased proficiency.

Looking Inward and Outward (LIO; Table 13)

Whereas paleontologists are keenly aware of the taphonomic biases constraining our view of past biodiversity, we have not systematically studied the biases linked to the identities and practices shaping how

Table 12. Big Questions for the working group on “Fundamental Issues”

Unique ID	Big Question
FI1	How can we efficiently collect, store, and combine different paleontological data types in an openly accessible and inclusive way?
FI2	What are best practices for training paleontologists to have a broad set of skills (e.g., data analyses, research skills, soft skills) that are transferable to an increasingly wider range of job requirements inside and outside academia?
FI3	How can we best motivate taxonomic and systematic work and facilitate crosstalk and collaboration with other paleontological disciplines?
FI4	How can paleontologists communicate findings and foster critical thinking skills so that the public can understand the utility of paleontological information and differentiate valid scientific ideas from other ideas?
FI5	What are the best practices for the protection and valorization of geosites and unique fossil heritage?

Table 13. Big Questions for the working group on “Looking Inward and Outward”

Unique ID	Big Question
LIO1	How is our understanding of past ecological and evolutionary processes shaped by biases in publication by location, authorship, language use, and funding availability?
LIO2	Which processes drive turnover in diversity trends (e.g., gender identities, different geographic regions) of academic paleontologists over time, and how could increased diversity lead to increasingly diverse products and outcomes?
LIO3	Which socioeconomic and identity factors—and their intersections—underlie variability in publication rate, professional advancement, and grant awards among the global paleontology community, both historically and in the present day?
LIO4	To what extent are paleontological specimen collecting and repository practices built on a legacy of colonial economic structures and how can we avoid recapitulating these interactions today across individual and institutional collaborations?
LIO5	How should qualities of fossil origin (e.g., country, sovereignty, collection process, local collaborative involvement, political conflict) be considered when designing research and navigating potential trade-offs in ethics and scientific value?
LIO6	Which settings (e.g., economic, cultural, physical) govern the biogeography of where paleontological fieldwork occurs and who (e.g., gender/ethnic identity) carries out—and benefits from—that work?
LIO7	Which institutional and mentorship attributes, such as accountability mechanisms, facilitate equitable collaboration among paleontologists, avoid bias, and promote the retention of students from backgrounds and identities currently underrepresented in paleontology?
LIO8	How do we integrate and sustain a commitment to diversity, equity, and inclusion initiatives into the foundations of hiring, promotion, and funding schemes in paleontology?

we collect, analyze, and interpret the fossil record. Presently, socioeconomic factors disproportionately influence the sampling coverage of both modern ecosystems and past biodiversity (Cisneros et al. 2022; Monarrez et al. 2022; Raja et al. 2022). Many perspectives and data are missing, which contributes to an incomplete understanding of past and present global biodiversity and restricts the development of ecological and evolutionary theory (LIO1, Table 13; Mohammed et al. 2022; Raja et al. 2022). Identifying and addressing these biases and challenges in paleontology (e.g., dominance of the English language; Cisneros et al. 2022; Raja et al. 2022) and incorporating as many diverse perspectives as possible will lead to a better understanding of all aspects of life on Earth (LIO2, LIO3).

Though many people globally have undertaken the study of past life, including within Indigenous traditions and local communities (Mayor 2007; Benoit et al. 2024), the earliest data points of Western academic paleontology are tied to the expansion of colonial empires (Monarrez et al. 2022; Scarlett 2022). Current research infrastructure is often built on these colonial legacies, including specimens held in museum collections (LIO4; Bradley et al. 2014; Cisneros et al. 2022; Mohammed et al. 2022; Monarrez et al. 2022; Raja et al. 2022). Digitization efforts are making museum collections and exhibits more accessible internationally to those with internet access, but digital representations do not necessarily provide the same research and engagement opportunities as physical specimens and have their own complications (e.g., compliance with sharing

policies, digital quality and resolution, large file sizes, internet access and bandwidth; Falkingham 2012; Lewis 2019). Natural history specimens and geosites are often considered to be natural heritage items (including status as UNESCO sites, <https://whc.unesco.org/en/list>), and calls for repatriation are growing in number (Bradley et al. 2014; Vogel 2019), making evaluating this issue in paleontology a priority (LIO4; see “Fundamental Issues”).

Researchers, institutions, and funding bodies must make proactive decisions to avoid contributing further to colonial legacies by evaluating the power dynamics of international collaborations while contending with the curation of specimens collected in the past (LIO5; e.g., Dunne et al. 2022). These decisions can run counter to incentives for publication on “novelty” and unique specimens, which are often gleaned from fieldwork in key geographic regions (e.g., Myanmar; LIO6; Dunne et al. 2022; Raja et al. 2022).

More broadly, fieldwork is not equally accessible to everyone despite its high value as a component of science education (e.g., Shinbrot et al. 2022). As in all the sciences with fieldwork components, paleontologists must grapple with safety and equity considerations, including mechanisms for reporting sexual harassment and assault (Clancy et al. 2014), explicit discussions about the safety of people of marginalized identities in field conditions (Demery and Pipkin 2021; Rudzki et al. 2022), and accessibility and inclusive design of field experiences for people with disabilities (LIO6; Stokes et al. 2019).

The exclusion and attrition of groups of people with particular identities and affinities (i.e., minoritized or marginalized groups) from academia have previously been described as a passive, leaky pipeline; however, this metaphor downplays the challenges posed by racism, colonial legacies, and systemic bias at institutional levels, which are now more accurately described as a “hostile obstacle course” (e.g., Bernard and Cooperdock 2018; Valenzuela-Toro and Viglino 2021; Berhe et al. 2022; Carter et al. 2022). Recognizing that these challenges exist, paleontologists must identify and embrace practices that create a more inclusive and equitable culture (LIO7; Valenzuela-Toro and Viglino 2021; Carter et al. 2022; Cisneros et al. 2022; Raja et al. 2022). Current diversity, equity, and inclusion tasks fall disproportionately on minoritized individuals, yet often are not considered in tenure and promotion assessments (LIO8; Jimenez et al. 2019). Although individual actions are important, support for diversity, equity, and inclusion must come from the highest levels of leadership (e.g., those making funding decisions) to signal their value (Dutt 2021; Chen et al. 2022). In implementing these changes, we can iteratively add to our dataset of changing outcomes in paleontology to evaluate whether such actions are effective (LIO2) and how this affects our understanding of both past and future worlds (LIO1).

Concluding Remarks

The present state of paleontological research is complex and constantly changing. Considering the limited number of paleontologists employed professionally in comparison to other scientific fields (e.g., Keane et al. 2021; Plotnick et al. 2025), it is prudent to develop a shared research agenda that the paleontological community can jointly address (Fig. 3). The questions presented here are unavoidably influenced by the perspectives of those participating and by the initial set of questions submitted. However, we have attempted to minimize this influence through our strategy for an inclusive approach to question submission, project participation, and authorship. Doing so gives us confidence that these BQs faithfully represent a forward-looking agenda for the discipline of paleontology.

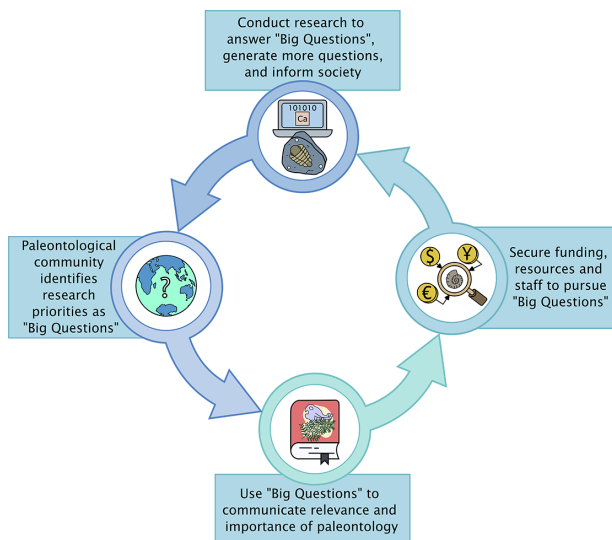


Figure 3. The Big Questions project can be used as a tool to guide research in paleontology and to advocate for the importance of funding paleontological research.

Whether this list of questions is taken as a whole, separated by theme, or examined piecemeal as individual questions, we encourage all in the paleontological community to use these BQs as a tool for communicating the importance of paleontology and securing research funding. Indeed, as the questions presented here have emerged from a community-wide effort, they likely are more representative of the state of the field than if the exercise was conducted with a top-down approach by a select few individuals, and this element may add credibility and power to arguments for funding in paleontology, broadly. As in other endeavors to define priority questions (e.g., Sutherland *et al.* 2009; Seddon *et al.* 2014), we expect a variety of uses (e.g., development of research projects, spurring discussion on the importance of different BQs) and audiences (e.g., other scientists, funding bodies, students, the general public). We anticipate these BQs will be used by researchers as framing and inspiration for new research directions and as a tool they can use to justify paleontological research to funding organizations (Fig. 3). The BQs reiterate the substantive contributions of museums and physical collection spaces, making clear a need for sustained funding of the repositories of our geoheritage. The BQs highlight the breadth and vitality of paleontology and the important and substantive role the discipline will continue to play in pushing the frontiers of understanding throughout the life sciences.

Many of the questions included here are directed at pursuing long-standing hypotheses on how life has evolved and responded to environmental change. A large portion also pertains to the application of paleontological data to the biodiversity and environmental crises that permeate the modern world. Questions in each of these areas share common considerations, including the effects of scale on observations and the ever-present challenge of assessing the adequacy of the fossil record to address these questions. Reflecting larger ongoing discussions in science and society, there is also an emphasis on conducting paleontological research more inclusively and equitably as a community. Through efforts like this Big Questions project that bring together groups of people with many backgrounds, expertises, and motivations, we aspire to grow and strengthen the global paleontological community. Our collective understanding of the history and future of life on Earth will only be

improved by creating a cohesive discipline where all interested individuals can contribute.

Acknowledgments. The Big Questions in Paleontology project was possible because of the participation of many members of the global paleontology community, and we thank all who contributed at any stage of the project. The project was coordinated through the PaleoSynthesis Project hosted at Friedrich-Alexander Universität Erlangen-Nürnberg, with funding from the Volkswagen Foundation (Az 96 796). We thank the editor (J. Crampton) and two anonymous reviewers for their comments on a previous version of this article.

Competing Interests. The authors declare no competing interests.

Data Availability Statement. Supplementary Material is available on Zenodo at: <https://doi.org/10.5281/zenodo.14278550>.

Literature Cited

- Abdelhady, A. A., B. Seuss, S. Jain, K. H. Abdel-Raheem, A. Elsheikh, M. S. Ahmed, A. M. Elewa, and A. M. Hussain. 2024. New and emerging technologies in paleontology and paleobiology: a horizon scanning review. *Journal of African Earth Sciences* 210:105155.
- Aberhan, M., and W. Kiessling. 2015. Persistent ecological shifts in marine molluscan assemblages across the end-Cretaceous mass extinction. *Proceedings of the National Academy of Sciences USA* 112:7207–7212.
- Adaimé, M.-É., S. Kong, and S. W. Punyasena. 2024. Deep learning approaches to the phylogenetic placement of extinct pollen morphotypes. *PNAS Nexus* 3:pgad419.
- Agnarsson, I., and M. Kuntner. 2007. Taxonomy in a changing world: seeking solutions for a science in crisis. *Systematic Biology* 56:531–539.
- Alberti, M., F. T. Fürsich, and D. K. Pandey. 2013. Seasonality in low latitudes during the Oxfordian (Late Jurassic) reconstructed via high-resolution stable isotope analysis of the oyster *Actinostreon marshi* (J. Sowerby, 1814) from the Kachchh Basin, western India. *International Journal of Earth Sciences* 102:1321–1336.
- Allen, B. J., P. B. Wignall, D. J. Hill, E. E. Saupe, and A. M. Dunhill. 2020. The latitudinal diversity gradient of tetrapods across the Permo-Triassic mass extinction and recovery interval. *Proceedings of the Royal Society B* 287:20201125.
- Allen, B. J., M. E. Clapham, E. E. Saupe, P. B. Wignall, D. J. Hill, and A. M. Dunhill. 2023. Estimating spatial variation in origination and extinction in deep time: a case study using the Permian–Triassic marine invertebrate fossil record. *Paleobiology* 49:509–526.
- Allmon, W. A., G. P. Dietl, J. R. Hendricks, and R. M. Ross. 2018. Bridging the two fossil records: paleontology's "big data" future resides in museum collections. Pp. 35–44 in G. D. Rosenberg and R. M. Clary, eds. *Museums at the forefront of the history and philosophy of geology: history made, history in the making*. Geological Society of America, Boulder, Colo.
- Almécija, S., A. S. Hammond, N. E. Thompson, K. D. Pugh, S. Moyà-Solà, and D. M. Alba. 2021. Fossil apes and human evolution. *Science* 372:eabb4363.
- Alroy, J., M. Aberhan, D. J. Bottjer, M. Foote, F. T. Fürsich, P. J. Harries, A. J. Hendy, *et al.* 2008. Phanerozoic trends in the global diversity of marine invertebrates. *Science* 321:97–100.
- Anderson, S. C., and G. D. Ruxton. 2020. The evolution of flight in bats: a novel hypothesis. *Mammal Review* 50:426–439.
- Andréoletti, J., and H. Morlon. 2024. Comparing extinction rates: past, present, and future. Pp. 348–365 in S. M. Scheiner, ed. *Encyclopedia of biodiversity*, 3rd ed. Academic Press, Oxford.
- Antell, G. S., W. Kiessling, M. Aberhan, and E. E. Saupe. 2020. Marine biodiversity and geographic distributions are independent on large scales. *Current Biology* 30:115–121.
- Antell, G. T., R. B. J. Benson, and E. E. Saupe. 2024. Spatial standardization of taxon occurrence data—a call to action. *Paleobiology* 50:177–193.
- Arakaki, M., P.-A. Christin, R. Nyffeler, A. Lendel, U. Eggli, R. M. Ogburn, E. Spriggs, M. J. Moore, and E. J. Edwards. 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proceedings of the National Academy of Sciences USA* 108:8379–8384.

- Atkinson, T. P., R. J. Buta, and D. C. Kopaska-Merkel. 2005. Saving the Union Chapel Mine: how a group of determined amateurs teamed up with professionals to save a world-class trackway site in Alabama. Pp. 191–200 in R. J. Buta, A. K. Rindsberg, and D. C. Kopaska-Merkel, eds. *Pennsylvanian footprints in the Black Warrior Basin of Alabama. Alabama Paleontological Society Monograph 1*. Alabama Paleontological Society, Birmingham.
- Balazka, D., and D. Rodighiero. 2020. Big data and the Little Big Bang: an epistemological (R)evolution. *Frontiers in Big Data* 3:1–31.
- Balisi, M. A., and B. Van Valkenburgh. 2020. Iterative evolution of large-bodied hypercarnivory in canids benefits species but not clades. *Communications Biology* 3:1–9.
- Bambach, R. K., A. M. Bush, and D. H. Erwin. 2007. Autecology and the filling of ecospace: key metazoan radiations. *Paleontology* 50:1–22.
- Barido-Sottani, J., W. Pett, J. E. O'Reilly, and R. C. Warnock. 2019. FossilSim: an R package for simulating fossil occurrence data under mechanistic models of preservation and recovery. *Methods in Ecology and Evolution* 10:835–840.
- Barido-Sottani, J., N. M. Van Tiel, M. J. Hopkins, D. F. Wright, T. Stadler, and R. C. Warnock. 2020. Ignoring fossil age uncertainty leads to inaccurate topology and divergence time estimates in time calibrated tree inference. *Frontiers in Ecology and Evolution* 8:fevo.2020.00183.
- Barido-Sottani, J., A. Pohle, K. De Baets, D. Murdock, and R. C. Warnock. 2023. Putting the F into FBD analysis: tree constraints or morphological data? *Paleontology* 66:e12679.
- Barnosky, A. D. 2001. Distinguishing the effects of the Red Queen and Court Jester on Miocene mammal evolution in the northern Rocky Mountains. *Journal of Vertebrate Paleontology* 21:172–185.
- Barnosky, A. D., N. Matzke, S. Tomiya, G. O. Wogan, B. Swartz, T. B. Quental, C. Marshall, et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471:51.
- Barnosky, A. D., E. A. Hadly, P. Gonzalez, J. Head, P. D. Polly, A. M. Lawing, J. T. Eronen, et al. 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* 355:eaah4787.
- Behrensmeyer, A. K., S. M. Kidwell, and R. A. Gastaldo. 2000. Taphonomy and paleobiology. *Paleobiology* 26:103–147.
- Benoit, J., C. R. Penn-Clarke, R. Rust, D. P. Groenewald, P. Vickers-Rich, and C. W. Helm. 2024. Indigenous knowledge of palaeontology in Africa. *Geological Society of London Special Publication* 543:SP543–2022–2236.
- Benson, R. B., R. Butler, R. A. Close, E. Saupe, and D. L. Rabosky. 2021. Biodiversity across space and time in the fossil record. *Current Biology* 31: R1225–R1236.
- Benton, M. J. 2009. The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. *Science* 323:728–732.
- Berbee, M. L., C. Strullu-Derrien, P.-M. Delaux, P. K. Strother, P. Kenrick, M.-A. Selosse, and J. W. Taylor. 2020. Genomic and fossil windows into the secret lives of the most ancient fungi. *Nature Reviews Microbiology* 18:717–730.
- Berents, P., M. Hamer, and V. Chavan. 2010. Towards demand driven publishing: approaches to the prioritization of digitization of natural history collections data. *Biodiversity Informatics* 7:113–119.
- Berhe, A. A., R. T. Barnes, M. G. Hastings, A. Mattheis, B. Schneider, B. M. Williams, and E. Marin-Spiotta. 2022. Scientists from historically excluded groups face a hostile obstacle course. *Nature Geoscience* 15:2–4.
- Bernard, R. E., and E. H. G. Cooperdock. 2018. No progress on diversity in 40 years. *Nature Geoscience* 11:292–295.
- Bijma, J., H.-O. Pörtner, C. Yesson, and A. D. Rogers. 2013. Climate change and the oceans—What does the future hold? *Marine Pollution Bulletin* 74:495–505.
- Bortolus, A. 2008. Error cascades in the biological sciences: the unwanted consequences of using bad taxonomy in ecology. *AMBIO: A Journal of the Human Environment* 37:114–118.
- Bouckaert, R., T. G. Vaughan, J. Barido-Sottani, S. Duchêne, M. Fourment, A. Gavryushkina, J. Heled, et al. 2019. BEAST 2.5: an advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 15: e1006650.
- Bradley, J., P. Adgemis, and L. Haralampou. 2014. “Why can't they put their names?": colonial photography, repatriation and social memory. *History and Anthropology* 25:47–71.
- Braje, T. J., and J. M. Erlandson. 2013. Human acceleration of animal and plant extinctions: a Late Pleistocene, Holocene, and Anthropocene continuum. *Anthropocene* 4:14–23.
- Briggs, D. E., and R. E. Summons. 2014. Ancient biomolecules: their origins, fossilization, and role in revealing the history of life. *BioEssays* 36: 482–490.
- Brocklehurst, N., and R. J. Benson. 2021. Multiple paths to morphological diversification during the origin of amniotes. *Nature Ecology and Evolution* 5: 1243–1249.
- Bromham, L. 2016. Testing hypotheses in macroevolution. *Studies in History and Philosophy of Science A* 55:47–59.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- Bush, A. M., and J. L. Payne. 2021. Biotic and abiotic controls on the Phanerozoic history of marine animal biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 52:269–289.
- Carter, A. M., E. H. Johnson, and E. R. Schroeter. 2022. Long-term retention of diverse paleontologists requires increasing accessibility. *Frontiers in Ecology and Evolution* 10. <https://doi.org/10.3389/fevo.2022.876906>.
- Carvalho, I. de S., and G. Leonardi. 2022. The invisibles of science and the paleontological heritage: the Brazilian study case. *Geoheritage* 14:107.
- Casey, M. M., and D. M. Post. 2011. The problem of isotopic baseline: reconstructing the diet and trophic position of fossil animals. *Earth-Science Reviews* 106:131–148.
- Cermeño, P., C. García-Comas, A. Pohl, S. Williams, M. J. Benton, C. Chaudhary, G. Le Gland, et al. 2022. Post-extinction recovery of the Phanerozoic oceans and biodiversity hotspots. *Nature* 607:507–511.
- Chen, C. Y., S. S. Kahanamoku, A. Tripathi, R. A. Alegado, V. R. Morris, K. Andrade, and J. Hosbey. 2022. Systemic racial disparities in funding rates at the National Science Foundation. *eLife* 11:e83071.
- Chen, J., I. P. Montañez, Y. Qi, S. Shen, and X. Wang. 2018. Strontium and carbon isotopic evidence for decoupling of pCO₂ from continental weathering at the apex of the late Paleozoic glaciation. *Geology* 46:395–398.
- Chevalier, T., T. Colard, A. Colombo, L. Golovanova, V. Doronichev, and J.-J. Hublin. 2021. Early ontogeny of humeral trabecular bone in Neandertals and recent modern humans. *Journal of Human Evolution* 154:102968.
- Chiarenza, A. A., A. M. Waterson, D. N. Schmidt, P. J. Valdes, C. Yesson, P. A. Holroyd, M. E. Collinson, et al. 2023. 100 million years of turtle paleoniche dynamics enable the prediction of latitudinal range shifts in a warming world. *Current Biology* 33:109–121.e3.
- Cisneros, J. C., N. B. Raja, A. M. Ghilardi, E. M. Dunne, F. L. Pinheiro, O. R. Regalado Fernández, M. A. F. Sales, et al. 2022. Digging deeper into colonial palaeontological practices in modern day Mexico and Brazil. *Royal Society Open Science* 9:210898.
- Clancy, K. B., R. G. Nelson, J. N. Rutherford, and K. Hinde. 2014. Survey of academic field experiences (SAFE): trainees report harassment and assault. *PLoS ONE* 9:e102172.
- Clark, J., J. Bayarsaikhan, A. V. Miller, S. Vanderwarf, I. Hart, G. Caspari, and W. T. T. Taylor. 2021. Mongolia's frozen heritage: a summary of the archaeology of the cultural cryosphere. *Journal of Glacial Archaeology* 5:103–120.
- Close, R. A., R. B. Benson, E. E. Saupe, M. E. Clapham, and R. J. Butler. 2020. The spatial structure of Phanerozoic marine animal diversity. *Science* 368:420–424.
- Comans, C. M., S. M. Smart, E. R. Kast, Y. Lu, T. Lüdecke, J. N. Leichter, D. M. Sigman, T. Ikejiri, and A. Martínez-García. 2024. Enameloid-bound $\delta^{15}\text{N}$ reveals large trophic separation among Late Cretaceous sharks in the northern Gulf of Mexico. *Geobiology* 22:e12585.
- Cook, P. K., M.-A. Languille, E. Dufour, C. Mocuta, O. Tombret, F. Fortuna, and L. Bertrand. 2015. Biogenic and diagenetic indicators in archaeological and modern otoliths: potential and limits of high definition synchrotron micro-XRF elemental mapping. *Chemical Geology* 414:1–15.
- Cortés-Sánchez, M., M. D. Simón-Vallejo, J.-C. Corral, M. del C. Lozano-Francisco, J. L. Vera-Peláez, F. J. Jiménez-Espejo, A. García-Alix, et al. 2020. Fossils in Iberian prehistory: a review of the palaeozoological evidence. *Quaternary Science Reviews* 250:106676.
- Cribb, A. T., K. K. Formoso, C. H. Woolley, J. Beech, S. Brophy, P. Byrne, V. C. Cassady, et al. 2023. Contrasting terrestrial and marine ecospace dynamics after the end-Triassic mass extinction event. *Proceedings of the Royal Society B* 290:20232232.
- Cuvier, G. 1813. *Essay on the theory of the Earth*. Routledge, Oxford, U.K.
- Darwin, C. 1859. *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life*. Appleton and Company, New York.

- Davies, S. W., H. M. Putnam, T. Ainsworth, J. K. Baum, C. B. Bove, S. C. Crosby, I. M. Côté, et al. 2021. Promoting inclusive metrics of success and impact to dismantle a discriminatory reward system in science. *PLoS Biology* 19:e3001282.
- De Baets, K. 2021. Performance of machine-learning approaches in identifying ammonoid species based on conch properties. *Peer Community in Paleontology* 1:100010.
- De Baets, K., A. Antonelli, and P. C. Donoghue. 2016. Tectonic blocks and molecular clocks. *Philosophical Transactions of the Royal Society B* 371:20160098.
- De Baets, K., J. W. Huntley, D. Scarponi, A. A. Klompmaker, and A. Skawina. 2021. Phanerozoic parasitism and marine metazoan diversity: dilution versus amplification. *Philosophical Transactions of the Royal Society B* 376:20200366.
- De Baets, K., E. Jarochowska, S. Z. Buchwald, C. Klug, and D. Korn. 2022. Lithology controls ammonoid size distributions. *Palaios* 37:744–754.
- Demarchi, B. 2020. *Amino acids and proteins in fossil biominerals: an introduction for archaeologists and palaeontologists*. Wiley, Hoboken, N.J.
- Demery, A.-J. C., and M. A. Pipkin. 2021. Safe fieldwork strategies for at-risk individuals, their supervisors and institutions. *Nature Ecology and Evolution* 5:5–9.
- Dietl, G. P., and K. W. Flessa. 2011. Conservation paleobiology: putting the dead to work. *Trends in Ecology and Evolution* 26:30–37.
- Dietl, G. P., S. M. Kidwell, M. Brenner, D. A. Burney, K. W. Flessa, S. T. Jackson, and P. L. Koch. 2015. Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. *Annual Review of Earth and Planetary Sciences* 43:79–103.
- Dietl, G. P., J. A. Smith, and S. R. Durham. 2019. Discounting the past: the undervaluing of paleontological data in conservation science. *Frontiers in Ecology and Evolution* 7:108.
- Dietl, G. P., S. R. Durham, C. Clark, and R. Prado. 2023. Better together: building an engaged conservation paleobiology science for the future. *Ecological Solutions and Evidence* 4:e12246.
- Dillon, E. M., J. Q. Pier, J. A. Smith, N. B. Raja, D. Dimitrijević, E. L. Austin, J. D. Cybulski, et al. 2022. What is conservation paleobiology? Tracking 20 years of research and development. *Frontiers in Ecology and Evolution* 10:1117.
- Di Martino, E., J. B. C. Jackson, P. D. Taylor, and K. G. Johnson. 2018. Differences in extinction rates drove modern biogeographic patterns of tropical marine biodiversity. *Science Advances* 4:eaaq1508.
- Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. *Science* 345:401–406.
- Dunhill, A. M., B. Hannisdal, and M. J. Benton. 2014. Disentangling rock record bias and common-cause from redundancy in the British fossil record. *Nature Communications* 5:4818.
- Dunhill, A. M., W. J. Foster, J. Sciberras, and R. J. Twitchett. 2018. Impact of the Late Triassic mass extinction on functional diversity and composition of marine ecosystems. *Palaeontology* 61:133–148.
- Dunhill, A. M., K. Zarczynny, J. O. Shaw, J. W. Atkinson, C. T. Little, and A. P. Beckerman. 2024. Extinction cascades, community collapse, and recovery across a Mesozoic hyperthermal event. *Nature Communications* 15:8599.
- Dunne, E. M., N. B. Raja, P. P. Stewens, Zin-Maung-Maung-Thein, and K. Zaw. 2022. Ethics, law, and politics in palaeontological research: the case of Myanmar amber. *Communications Biology* 5:1–10.
- Dunne, E. M., S. E. Thompson, R. J. Butler, J. Rosindell, and R. A. Close. 2023. Mechanistic neutral models show that sampling biases drive the apparent explosion of early tetrapod diversity. *Nature Ecology and Evolution* 7:1480–1489.
- Dunne, J. A., and R. J. Williams. 2009. Cascading extinctions and community collapse in model food webs. *Philosophical Transactions of the Royal Society B* 364:1711–1723.
- Dutt, K. 2021. Addressing racism through ownership. *Nature Geoscience* 14:58–58.
- Eden, R., A. Manica, and E. G. Mitchell. 2022. Metacommunity analyses show an increase in ecological specialisation throughout the Ediacaran period. *PLoS Biology* 20:e3001289.
- Eichenseer, K., U. Balthasar, C. W. Smart, J. Stander, K. A. Haaga, and W. Kiessling. 2019. Jurassic shift from abiotic to biotic control on marine ecological success. *Nature Geoscience* 12:638–642.
- Ezard, T. H. G., T. B. Quntal, and M. J. Benton. 2016. The challenges to inferring the regulators of biodiversity in deep time. *Philosophical Transactions of the Royal Society B* 371:20150216.
- Faith, J. T., A. Du, A. K. Behrensmeier, B. Davies, D. B. Patterson, J. Rowan, and B. Wood. 2021. Rethinking the ecological drivers of hominin evolution. *Trends in Ecology and Evolution* 36:797–807.
- Falk, H., and K. Wolkstein. 2017. Natural product molecular fossils. *Progress in the Chemistry of Organic Natural Products* 104:1–126.
- Falkingham, P. 2012. Acquisition of high resolution three-dimensional models using free, open-source, photogrammetric software. *Palaeontologia Electronica* 15:1T:15p.
- Fenton, I. S., T. Aze, A. Farnsworth, P. Valdes, and E. E. Saupe. 2023. Origination of the modern-style diversity gradient 15 million years ago. *Nature* 614:708–712.
- Finnegan, S., P. G. Harnik, R. Lockwood, H. K. Lotze, L. McClenachan, and S. S. Kahanamoku. 2024. Using the fossil record to understand extinction risk and inform marine conservation in a changing world. *Annual Review of Marine Science* 16:307–333.
- Flannery-Sutherland, J. T., D. Silvestro, and M. J. Benton. 2022. Global diversity dynamics in the fossil record are regionally heterogeneous. *Nature Communications* 13:2751.
- Flessa, K., M. Kowalewski, and S. E. Walker. 1992. Post-collection taphonomy: shell destruction and the Chevrolet. *Palaios* 7:553–554.
- Foote, M. 2000. Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. *Paleobiology* 26:578–605.
- Foster, W. J., and R. J. Twitchett. 2014. Functional diversity of marine ecosystems after the Late Permian mass extinction event. *Nature Geoscience* 7:233–238.
- Foster, W. J., B. J. Allen, N. H. Kitzmann, J. Münchmeyer, T. Rettelbach, J. D. Witts, R. J. Whittle, et al. 2023. How predictable are mass extinction events? *Royal Society Open Science* 10:221507.
- Friend, D. S., B. M. Anderson, and W. D. Allmon. 2021. Geographic contingency, not species sorting, dominates macroevolutionary dynamics in an extinct clade of neogastropods (Volutospina; Volutidae). *Paleobiology* 47:236–250.
- Gibert, C., A. Zaccà, F. Fluteau, G. Ramstein, O. Chavasseau, G. Thiery, A. Souron, et al. 2022. A coherent biogeographical framework for Old World Neogene and Pleistocene mammals. *Palaeontology* 65:e12594.
- Giuliani, A., R. N. Drysdale, J. D. Woodhead, N. J. Planavsky, D. Phillips, J. Hergt, W. L. Griffin, S. Oesch, H. Dalton, and G. R. Davies. 2022. Perturbation of the deep-Earth carbon cycle in response to the Cambrian Explosion. *Science Advances* 8:eabj1325.
- Gould, S. J., and N. Eldredge. 1972. Punctuated equilibria: an alternative to phyletic gradualism. *Models in Paleobiology* 1972:82–115.
- Groff, D. V., C. M. MacKenzie, J. Q. Pier, A. B. Shaffer, and G. P. Dietl. 2023. Knowing but not doing: quantifying the research-implementation gap in conservation paleobiology. *Frontiers in Ecology and Evolution* 11:1058992.
- Grossman, E. L., and M. M. Joachimski. 2022. Ocean temperatures through the Phanerozoic reassessed. *Scientific Reports* 12:1–13.
- Gu, Z., L. Gu, R. Eils, M. Schlesner, and B. Brors. 2014. Circlize implements and enhances circular visualization in R. *Bioinformatics* 30:2811–2812.
- Gueriau, P., S. Bernard, and L. Bertrand. 2016. Advanced synchrotron characterization of paleontological specimens. *Elements* 12:45–50.
- Hannisdal, B., and S. E. Peters. 2011. Phanerozoic Earth system evolution and marine biodiversity. *Science* 334:1121–1124.
- Hardisty, A. R., E. R. Ellwood, G. Nelson, B. Zimkus, J. Buschbom, W. Addink, R. K. Rabeler, et al. 2022. Digital extended specimens: enabling an extensible network of biodiversity data records as integrated digital objects on the Internet. *BioScience* 72:978–987.
- Harmon, L. J., and S. Harrison. 2015. Species diversity is dynamic and unbounded at local and continental scales. *American Naturalist* 185:584–593.
- Harnik, P. G. 2011. Direct and indirect effects of biological factors on extinction risk in fossil bivalves. *Proceedings of the National Academy of Sciences USA* 108:13594–13599.
- Hayek, L.-A. C., M. A. Buzas, and E. Thomas. 2019. Identifying disruptions to the ecological balance of nature: a foraminiferal example across the initiation of the Paleocene–Eocene thermal maximum. *Paleobiology* 45:98–113.
- Heath, T. A., J. P. Huelsenbeck, and T. Stadler. 2014. The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences USA* 111:E2957–E2966.

- Hendricks, J. R., E. E. Saupe, C. E. Myers, E. J. Hermesen, and W. D. Allmon. 2014. The generification of the fossil record. *Paleobiology* 40:511–528.
- Hlusko, L. J., C. A. Schmitt, T. A. Monson, M. F. Brasil, and M. C. Mahaney. 2016. The integration of quantitative genetics, paleontology, and neontology reveals genetic underpinnings of primate dental evolution. *Proceedings of the National Academy of Sciences USA* 113:9262–9267.
- Hohmann, N., J. R. Koelewijn, P. Burgess, and E. Jarochowska. 2024. Identification of the mode of evolution in incomplete carbonate successions. *BMC Ecology and Evolution* 24:113.
- Höhna, S., M. J. Landis, T. A. Heath, B. Boussau, N. Lartillot, B. R. Moore, J. P. Huelsenbeck, and F. Ronquist. 2016. RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. *Systematic Biology* 65:726–736.
- Höhna, S., B. T. Kopperud, and A. F. Magee. 2022. CRABS: congruent rate analyses in birth–death scenarios. *Methods in Ecology and Evolution* 13: 2709–2718.
- Hopkins, M. J., and R. To. 2022. Long-term clade-wide shifts in trilobite segment number and allocation during the Palaeozoic. *Proceedings of the Royal Society B* 289:20221765.
- Hopkins, M. J., C. Simpson, and W. Kiessling. 2014. Differential niche dynamics among major marine invertebrate clades. *Ecology Letters* 17:314–323.
- Hull, P. M., S. A. F. Darroch, and D. H. Erwin. 2015. Rarity in mass extinctions and the future of ecosystems. *Nature* 528:345–351.
- Humboldt, A. v. 1808. *Ansichten der Natur*. Cotta, Tübingen, Germany.
- Hunt, G. 2007. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proceedings of the National Academy of Sciences USA* 104:18404–18408.
- Hunt, G. 2012. Measuring rates of phenotypic evolution and the inseparability of tempo and mode. *Paleobiology* 38:351–373.
- Hunt, G., M. J. Hopkins, and S. Lidgard. 2015. Simple versus complex models of trait evolution and stasis as a response to environmental change. *Proceedings of the National Academy of Sciences USA* 112:4885–4890.
- [IPCC] Intergovernmental Panel on Climate Change. 2021. *Climate Change 2021: the physical science basis*. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. P. 2391 in V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, et al., eds. Cambridge University Press, Cambridge.
- Jablonski, D. 1991. Extinctions: a paleontological perspective. *Science* 253:754–757.
- Jablonski, D. 2007. Scale and hierarchy in macroevolution. *Palaeontology* 50: 87–109.
- Jablonski, D. 2008. Biotic interactions and macroevolution: extensions and mismatches across scales and levels. *Evolution: International Journal of Organic Evolution* 62:715–739.
- Jablonski, D. 2017. Approaches to macroevolution: 2. Sorting of variation, some overarching issues, and general conclusions. *Evolutionary Biology* 44: 451–475.
- Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102–106.
- Jackson, J. B. C., and A. O'Dea. 2023. Evolution and environment of Caribbean coastal ecosystems. *Proceedings of the National Academy of Sciences USA* 120: e2307520120.
- Jane, S. F., G. J. A. Hansen, B. M. Kraemer, P. R. Leavitt, J. L. Mincer, R. L. North, R. M. Pilla, et al. 2021. Widespread deoxygenation of temperate lakes. *Nature* 594:66–70.
- Jimenez, M. F., T. M. Lavery, S. P. Bombaci, K. Wilkins, D. E. Bennett, and L. Pejchar. 2019. Underrepresented faculty play a disproportionate role in advancing diversity and inclusion. *Nature Ecology and Evolution* 3:1030–1033.
- Johnson, K. R., I. F. P. Owens, and the Global Collection Group. 2023. A global approach for natural history museum collections. *Science* 379:1192–1194.
- Jung, J., S. F. Zoppe, T. Söte, S. Moretti, N. N. Duprey, A. D. Foreman, T. Wald, et al. 2024. Coral photosymbiosis on Mid-Devonian reefs. *Nature* 636: 647–653.
- Kaufman, D. S. and PAGES 2k special-issue editorial team. 2018. Technical note: open-paleo-data implementation pilot—the PAGES 2k special issue. *Climate of the Past* 14:593–600. <https://doi.org/10.5194/cp-14-593-2018>
- Keane, C., L. Gonzales, and D. Robinson. 2021. *Status of recent geoscience graduates*. American Geosciences Institute, Alexandria, Va.
- Kibria, A., S. B. Akhundjanov, and R. Oladi. 2019. Fossil fuel share in the energy mix and economic growth. *International Review of Economics and Finance* 59:253–264.
- Kidwell, S. M., and K. W. Flessa. 1996. The quality of the fossil record: populations, species, and communities. *Annual Review of Ecology and Systematics* 24:433–464.
- Kiessling, W., N. B. Raja, V. J. Roden, S. T. Turvey, and E. E. Saupe. 2019. Addressing priority questions of conservation science with palaeontological data. *Philosophical Transactions of the Royal Society B* 374:20190222.
- Kiessling, W., J. A. Smith, and N. B. Raja. 2023. Improving the relevance of paleontology to climate change policy. *Proceedings of the National Academy of Sciences USA* 120:e2201926119.
- Kimmig, S. R., and C. Holmden. 2017. Multi-proxy geochemical evidence for primary aragonite precipitation in a tropical-shelf “calcite sea” during the Hirnantian glaciation. *Geochimica et Cosmochimica Acta* 206:254–272.
- Klompaker, A. A., C. E. Schweitzer, R. M. Feldmann, and M. Kowalewski. 2013. The influence of reefs on the rise of Mesozoic marine crustaceans. *Geology* 41:1179–1182.
- Klompaker, A. A., R. W. Portell, and M. G. Frick. 2017. Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential. *Palaeontology* 60:773–794.
- Knoll, A. H., D. E. Canfield, and K. O. Konhauser. 2012. *Fundamentals of geobiology*. Wiley, Hoboken, NJ.
- Kocsis, Á. T., C. J. Reddin, C. R. Scotese, P. J. Valdes, and W. Kiessling. 2021. Increase in marine provinciality over the last 250 million years governed more by climate change than plate tectonics. *Proceedings of the Royal Society B* 288:20211342.
- Kowalewski, M., R. Nawrot, D. Scarponi, A. Tomašových, and M. Zuschin. 2023. Marine conservation palaeobiology: what does the late Quaternary fossil record tell us about modern-day extinctions and biodiversity threats? *Cambridge Prisms: Extinction* 1:e24.
- Kral, A. G., M. Lagos, P. Guagliardo, T. Tütken, and T. Geisler. 2022. Rapid alteration of cortical bone in fresh- and seawater solutions visualized and quantified from the millimeter down to the atomic scale. *Chemical Geology* 609:121060.
- Krone, I. W., K. M. Magoulick, and R. M. Yohler. 2024. All the Earth will not remember: how geographic gaps structure the record of diversity and extinction. *Paleobiology* 50:214–225.
- Lamsdell, J. C., C. R. Congreve, M. J. Hopkins, A. Z. Krug, and M. E. Patzkowsky. 2017. Phylogenetic paleoecology: tree-thinking and ecology in deep time. *Trends in Ecology and Evolution* 32:452–463.
- Lamsdell, J. C., V. E. McCoy, O. A. Perron-Feller, and M. J. Hopkins. 2020. Air breathing in an exceptionally preserved 340-million-year-old sea scorpion. *Current Biology* 30:4316–4321.
- Lanzetti, A., R. Portela-Miguez, V. Fernandez, and A. Goswami. 2022. Testing heterochrony: connecting skull shape ontogeny and evolution of feeding adaptations in baleen whales. *Evolution and Development* 25:257–273.
- LaRue, E. A., R. T. Fahey, B. C., Alvashere, J. W. Atkins, P. Bhatt, B. Buma, A. Chen, et al. 2023. A theoretical framework for the ecological role of three-dimensional structural diversity. *Frontiers in Ecology and the Environment* 21:4–13.
- Lee, M. S., and A. Palci. 2015. Morphological phylogenetics in the genomic age. *Current Biology* 25:R922–R929.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Lendemer, J., B. Thiers, A. K. Monfils, J. Zaspel, E. R. Ellwood, A. Bentley, K. LeVan, et al. 2020. The Extended Specimen Network: a strategy to enhance US biodiversity collections, promote research and education. *BioScience* 70: 23–30.
- Lenoir, J., R. Bertrand, L. Comte, L. Bourgeaud, T. Hattab, J. Murienne, and G. Grenouillet. 2020. Species better track climate warming in the oceans than on land. *Nature Ecology and Evolution* 4:1044–1059.
- Lewis, D. 2019. The fight for control over virtual fossils. *Nature* 567:20–23.
- Lin, C.-H., C.-L. Wei, S. L. Ho, and L. Lo. 2023. Ocean temperature drove changes in the mesopelagic fish community at the edge of the Pacific Warm Pool over the past 460,000 years. *Science Advances* 9:eadf0656.

- Liow, L. H., and P. D. Taylor. 2019. Cope's Rule in a modular organism: directional evolution without an overarching macroevolutionary trend. *Evolution* 73:1863–1872.
- Liow, L. H., J. Uyeda, and G. Hunt. 2023. Cross-disciplinary information for understanding macroevolution. *Trends in Ecology and Evolution* 38:250–260.
- Löbl, I., B. Klausnitzer, M. Hartmann, and F.-T. Krell. 2023. The silent extinction of species and taxonomists—an appeal to science policymakers and legislators. *Diversity* 15:1053.
- Lotze, H. K., J. M. Erlandson, M. J. Hardt, R. D. Norris, K. Roy, T. D. Smith, and C. R. Whitcraft. 2011. How do we know about the past. Pp. 137–161 in J. B. C. Jackson, K. E. Alexander, and E. Sala, eds. *Shifting baselines: the past and the future of ocean fisheries*. Island Press, Washington, D.C.
- Louca, S., and M. W. Pennell. 2020. Extant timetrees are consistent with a myriad of diversification histories. *Nature* 580:502–505.
- Louys, J., S. Kealy, S. O'Connor, G. Price, S. Hawkins, K. P. Aplin, Y. Rizal, et al. 2017. Differential preservation of vertebrates in Southeast Asian caves. *International Journal of Speleology* 46:379–408.
- Louys, J., G. J. Price, and K. J. Trueman. 2021. Space-time equivalence in the fossil record, with a case study from Pleistocene Australia. *Quaternary Science Reviews* 253:106764.
- Mabry, M. E., F. Zapata, D. L. Paul, P. M. O'Connor, P. S. Soltis, D. C. Blackburn, and N. B. Simmons. 2022. Monographs as a nexus for building extended specimen networks using persistent identifiers. *Bulletin of the Society of Systematic Biologists* 1. <https://doi.org/10.18061/bssb.v1i1.8323>.
- Machado, F. A., C. S. Mongle, G. Slater, A. Penna, A. Wisniewski, A. Soffin, V. Dutra, and J. C. Uyeda. 2023. Rules of teeth development align microevolution with macroevolution in extant and extinct primates. *Nature Ecology and Evolution* 7:1729–1739.
- MacLeod, N. 2014. The geological extinction record: history, data, biases, and testing. *Geological Society of America Special Paper* 505:1–28.
- Malanoski, C. M., A. Farnsworth, D. J. Lunt, P. J. Valdes, and E. E. Saupe. 2024. Climate change is an important predictor of extinction risk on macroevolutionary timescales. *Science* 383:1130–1134.
- Mancuso, A. C., R. B. Irmis, T. E. Pedernera, L. C. Gaetano, C. A. Benavente, and B. T. Bredeen III. 2022. Paleoenvironmental and biotic changes in the Late Triassic of Argentina: testing hypotheses of abiotic forcing at the basin scale. *Frontiers in Earth Science* 10. <https://doi.org/10.3389/feart.2022.883788>.
- Mannion, P. D., P. Upchurch, R. B. Benson, and A. Goswami. 2014. The latitudinal biodiversity gradient through deep time. *Trends in Ecology and Evolution* 29:42–50.
- Maran, S. A. 2014. Conservation of paleontological heritage in Serbia: from philosophy to practice. *Bulletin of the Natural History Museum* 7:7–28.
- Marshall, C. R. 2017. Five palaeobiological laws needed to understand the evolution of the living biota. *Nature Ecology and Evolution* 1:0165.
- Marshall, C. R. 2023. Forty years later: the status of the “Big Five” mass extinctions. *Cambridge Prisms: Extinction* 1:e5.
- Marshall, C. R., S. Finnegan, E. C. Clites, P. A. Holroyd, N. Bonuso, C. Cortez, E. Davis, et al. 2018. Quantifying the dark data in museum fossil collections as palaeontology undergoes a second digital revolution. *Biology Letters* 14: 20180431.
- Marshall, F. E., G. L. Wingard, and P. A. Pitts. 2014. Estimates of natural salinity and hydrology in a subtropical estuarine ecosystem: implications for greater everglades restoration. *Estuaries and Coasts* 37:1449–1466.
- Martin, J. E., T. Tacail, and V. Balter. 2017. Non-traditional isotope perspectives in vertebrate palaeobiology. *Palaeontology* 60:485–502.
- Mayor, A. 2007. Place names describing fossils in oral traditions. *Geological Society of London Special Publication* 273:245–261.
- McElwain, J. C. 2018. Paleobotany and global change: important lessons for species to biomes from vegetation responses to past global change. *Annual Review of Plant Biology* 69:761–787.
- McGill, B. J. 2019. The what, how and why of doing macroecology. *Global Ecology and Biogeography* 28:6–17.
- McGuire, J. L., A. M. Lawing, S. Díaz, and N. Chr. Stenseth. 2023. The past as a lens for biodiversity conservation on a dynamically changing planet. *Proceedings of the National Academy of Sciences USA* 120:e2201950120.
- McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* 28:495–516.
- McNamara, M. E., V. Rossi, T. S. Slater, C. S. Rogers, A.-L. Ducrest, S. Dubey, and A. Roulin. 2021. Decoding the evolution of melanin in vertebrates. *Trends in Ecology and Evolution* 36:430–443.
- Mexicana, P. 2020. How is the paleontological heritage of Mexico and other Latin American countries protected? *Paleontología Mexicana* 9:83–90.
- Mohammed, R. S., G. Turner, K. Fowler, M. Pateman, M. A. Nieves-Colón, L. Fanovich, S. B. Cooke, et al. 2022. Colonial legacies influence biodiversity lessons: how past trade routes and power dynamics shape present-day scientific research and professional opportunities for Caribbean scientists. *American Naturalist* 200:140–155.
- Monarrez, P. M., J. B. Zimmt, A. M. Clement, W. Gearty, J. J. Jacisin, K. M. Jenkins, K. M. Kusnerik, et al. 2022. Our past creates our present: a brief overview of racism and colonialism in Western paleontology. *Paleobiology* 48:173–185.
- Monfils, A. K., E. R. Kimmel, D. L. Linton, T. D. Marsico, A. B. Morris, and B. R. Ruhfel. 2022. Collections education: the extended specimen and data acumen. *BioScience* 72:177–188.
- Mongiardino Koch, N., R. J. Garwood, and L. A. Parry. 2021. Fossils improve phylogenetic analyses of morphological characters. *Proceedings of the Royal Society B* 288:20210044.
- Mora, C., D. P. Tittensor, S. Adl, A. G. Simpson, and B. Worm. 2011. How many species are there on Earth and in the ocean? *PLoS Biology* 9:e1001127.
- Mulvey, L. P., R. C. Warnock, and K. De Baets. 2022. Where traditional extinction estimates fall flat: using novel copylogenetic methods to estimate extinction risk in platyhelminths. *Proceedings of the Royal Society B* 289:20220432.
- Mulvey, L. P., M. R. May, J. M. Brown, S. Höhna, A. M. Wright, and R. C. Warnock. 2024. Assessing the adequacy of morphological models using posterior predictive simulations. *Systematic Biology* 74:34–52.
- Murdock, D. J. 2020. The “biomineralization toolkit” and the origin of animal skeletons. *Biological Reviews* 95:1372–1392.
- Muscente, A. D., A. Prabhu, H. Zhong, A. Eleish, M. B. Meyer, P. Fox, R. M. Hazen, and A. H. Knoll. 2018. Quantifying ecological impacts of mass extinctions with network analysis of fossil communities. *Proceedings of the National Academy of Sciences USA* 115:5217–5222.
- Muscente, A. D., R. C. Martindale, A. Prabhu, X. Ma, P. Fox, R. M. Hazen, and A. H. Knoll. 2022. Appearance and disappearance rates of Phanerozoic marine animal paleocommunities. *Geology* 50:341–345.
- Na, L., Q. Li, C. Krause, M. Zhu, and W. Kiessling. 2023. Revisiting the Phanerozoic rock–diversity relationship. *Geological Magazine* 160:1853–1862.
- Naranjo-Ortiz, M. A., and T. Gabaldón. 2019. Fungal evolution: major ecological adaptations and evolutionary transitions. *Biological Reviews* 94:1443–1476.
- Nätscher, P. S., J. Gliwa, K. De Baets, A. Ghaderi, and D. Korn. 2023. Exceptions to the temperature–size rule: no Lilliput Effect in end-Permian ostracods (Crustacea) from Aras Valley (northwest Iran). *Palaeontology* 66:e12667.
- Neto De Carvalho, C., A. N. Baucon, A. N. Bayet-Goll, and J. N. Belo. 2021. The Penha Garcia Ichnological Park at Naturtejo UNESCO Global Geopark (Portugal): a geotourism destination in the footprint of the Great Ordovician Biodiversification Event. *Geoconservation Research* 4:70–79.
- Neuwirth, E. 2022. RColorBrewer: ColorBrewer Palettes, R package version 1.1-3. <https://cran.r-project.org/web/packages/RColorBrewer/index.html>
- Nützel, A., M. Joachimski, and M. L. Correa. 2010. Seasonal climatic fluctuations in the Late Triassic tropics—high-resolution oxygen isotope records from aragonitic bivalve shells (Cassian Formation, northern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology* 285:194–204.
- Nylin, S., S. Agosta, S. Bensch, W. A. Boeger, M. P. Braga, D. R. Brooks, M. L. Forister, et al. 2018. Embracing colonizations: a new paradigm for species association dynamics. *Trends in Ecology and Evolution* 33:4–14.
- O'Keefe, F. R., R. E. Dunn, E. M. Weitzel, M. R. Waters, L. N. Martinez, W. J. Binder, J. R. Southon, et al. 2023. Pre-Younger Dryas megafaunal extirpation at Rancho La Brea linked to fire-driven state shift. *Science* 381:eabo3594.
- Parham, J. F., P. C. J. Donoghue, C. J. Bell, T. D. Calway, J. J. Head, P. A. Holroyd, J. G. Inoue, et al. 2012. Best practices for justifying fossil calibrations. *Systematic Biology* 61:346–359.

- Parins-Fukuchi, C., G. W. Stull, and S. A. Smith. 2021. Phylogenomic conflict coincides with rapid morphological innovation. *Proceedings of the National Academy of Sciences USA* 118:e2023058118.
- Parrott, L. 2010. Measuring ecological complexity. *Ecological Indicators* 10: 1069–1076.
- Parsons, E. C. M., B. Favaro, A. A. Aguirre, A. L. Bauer, L. K. Blight, J. A. Cigliano, M. A. Coleman, et al. 2014. Seventy-one important questions for the conservation of marine biodiversity. *Conservation Biology* 28:1206–1214.
- Patton, A. H., L. J. Harmon, M. del Rosario Castañeda, H. K. Frank, C. M. Donihue, A. Herrel, and J. B. Losos. 2021. When adaptive radiations collide: different evolutionary trajectories between and within island and mainland lizard clades. *Proceedings of the National Academy of Sciences USA* 118:e2024451118.
- Pawlik, L., B. Buma, P. Šamonil, J. Kvaček, A. Gałazka, P. Kohout, and I. Malik. 2020. Impact of trees and forests on the Devonian landscape and weathering processes with implications to the global Earth's system properties—a critical review. *Earth-Science Reviews* 205:103200.
- Pecl, G. T., M. B. Araújo, J. D. Bell, J. Blanchard, T. C. Bonebrake, I.-C. Chen, T. D. Clark, et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355:eaai9214.
- Perini, M. M., and J. O. Calvo. 2008. Paleontological tourism: an alternative income to vertebrate paleontology. *Arquivos do Museu Nacional* 66:285–289.
- Peters, S. E., and N. A. Heim. 2011. Macrostratigraphy and macroevolution in marine environments: testing the common-cause hypothesis. *Geological Society of London Special Publication* 358:95–104.
- Phillips, J. 1860. *Life on the Earth: its origin and succession*. Macmillan and Company, London and Cambridge.
- Piazza, V., C. V. Ullmann, and M. Aberhan. 2020. Temperature-related body size change of marine benthic macroinvertebrates across the Early Toarcian Anoxic Event. *Scientific Reports* 10:4675.
- Pimiento, C., and A. Antonelli. 2022. Integrating deep-time palaeontology in conservation prioritisation. *Frontiers in Ecology and Evolution* 10:959364.
- Plotnick, R. E., B. M. Anderson, S. J. Carlson, A. M. Jukar, J. Kimmig, and E. Petsios. 2023. Paleontology is far more than new fossil discoveries. *Scientific American*, August 30.
- Plotnick, R. E., B. A. Anderson, S. J. Carlson, A. Jukar, J. Kimmig and E. Petsios. 2025. Employment in paleontology: status and trends in the United States. *Paleobiology*, 1–11.
- Pohl, A., R. G. Stockey, X. Dai, R. Yohler, G. Le Hir, D. Hülse, A. Brayard, S. Finnegan, and A. Ridgwell. 2023. Why the Early Paleozoic was intrinsically prone to marine extinction. *Science Advances* 9:eadg7679.
- Pörtner, H.-O. 2021. Climate impacts on organisms, ecosystems and human societies: integrating OCLTT into a wider context. *Journal of Experimental Biology* 224:jeb238360.
- Price, S. A., and L. Schmitz. 2016. A promising future for integrative biodiversity research: an increased role of scale-dependency and functional biology. *Philosophical Transactions of the Royal Society B* 371:20150228.
- Punyasena, S. W., D. S. Haselhorst, S. Kong, C. C. Fowlkes, and J. E. Moreno. 2022. Automated identification of diverse Neotropical pollen samples using convolutional neural networks. *Methods in Ecology and Evolution* 13: 2049–2064.
- Quintero, I., M. J. Landis, W. Jetz, and H. Morlon. 2023. The build-up of the present-day tropical diversity of tetrapods. *Proceedings of the National Academy of Sciences USA* 120:e2220672120.
- Rabosky, D. L., and A. H. Hurlbert. 2015. Species richness at continental scales is dominated by ecological limits. *American Naturalist* 185:572–583.
- Raja, N. B., and E. M. Dunne. 2022. Publication pressure threatens the integrity of palaeontological research. *Geological Curator* 11:407–418.
- Raja, N. B., A. Lauchstedt, J. M. Pandolfi, S. W. Kim, A. F. Budd, and W. Kiessling. 2021. Morphological traits of reef corals predict extinction risk but not conservation status. *Global Ecology and Biogeography* 30:1597–1608.
- Raja, N. B., E. M. Dunne, A. Matiwane, T. M. Khan, P. S. Nätscher, A. M. Ghilardi, and D. Chattopadhyay. 2022. Colonial history and global economics distort our understanding of deep-time biodiversity. *Nature Ecology and Evolution* 6:145–154.
- Rapacciuolo, G., and J. L. Blois. 2019. Understanding ecological change across large spatial, temporal and taxonomic scales: integrating data and methods in light of theory. *Ecography* 42:1247–1266.
- Raup, D. M., and J. J. Sepkoski Jr. 1982. Mass extinctions in the marine fossil record. *Science* 215:1501–1503.
- R Core Team. 2023. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Reddin, C. J., Á. T. Kocsis, and W. Kiessling. 2018. Marine invertebrate migrations trace climate change over 450 million years. *Global Ecology and Biogeography* 27:704–713.
- Reddin, C. J., P. S. Nätscher, Á. T. Kocsis, H.-O. Pörtner, and W. Kiessling. 2020. Marine clade sensitivities to climate change conform across timescales. *Nature Climate Change* 10:249–253.
- Reimann, L., A. T. Vafeidis, S. Brown, J. Hinkel, and R. S. J. Tol. 2018. Mediterranean UNESCO World Heritage at risk from coastal flooding and erosion due to sea-level rise. *Nature Communications* 9:4161.
- Rita, P., P. Nätscher, L. V. Duarte, R. Weis, and K. De Baets. 2019. Mechanisms and drivers of belemnite body-size dynamics across the Pliensbachian–Toarcian crisis. *Royal Society Open Science* 6:190494.
- Rolland, J., L. F. Henao-Diaz, M. Doebeli, R. Germain, L. J. Harmon, L. L. Knowles, L. H. Liow, J. E. Mank, A. Machac, and S. P. Otto. 2023. Conceptual and empirical bridges between micro- and macroevolution. *Nature Ecology and Evolution* 7:1181–1193.
- Romero, I. C., S. Kong, C. C. Fowlkes, C. Jaramillo, M. A. Urban, F. Obolukuenobe, C. D'Apollito, and S. W. Punyasena. 2020. Improving the taxonomy of fossil pollen using convolutional neural networks and superresolution microscopy. *Proceedings of the National Academy of Sciences USA* 117: 28496–28505.
- Ronquist, F., J. Kudlicka, V. Senderov, J. Borgström, N. Lartillot, D. Lundén, L. Murray, T. B. Schön, and D. Broman. 2021. Universal probabilistic programming offers a powerful approach to statistical phylogenetics. *Communications Biology* 4:1–10.
- Roopnarine, P. D. 2006. Extinction cascades and catastrophe in ancient food webs. *Paleobiology* 32:1–19.
- Rudzi, E. N., S. E. Kuebbing, D. R. Clark, B. Gharaibeh, M. J. Janecka, R. Kramp, K. D. Kohl, et al. 2022. A guide for developing a field research safety manual that explicitly considers risks for marginalized identities in the sciences. *Methods in Ecology and Evolution* 13:2318–2330.
- Saleh, F., J. B. Antcliffe, B. Lefebvre, B. Pittet, L. Laibl, F. P. Peris, L. Lustri, P. Gueriau, and A. C. Daley. 2020. Taphonomic bias in exceptionally preserved biotas. *Earth and Planetary Science Letters* 529:115873.
- Saleh, F., O. G. Bath-Enright, A. C. Daley, B. Lefebvre, B. Pittet, A. Vite, X. Ma, et al. 2021. A novel tool to untangle the ecology and fossil preservation knot in exceptionally preserved biotas. *Earth and Planetary Science Letters* 569:117061.
- Salvador, R. B., B. M. Tomotani, K. L. O'Donnell, D. C. Cavallari, J. V. Tomotani, R. A. Salmon, and J. Kasper. 2021. Invertebrates in science communication: confronting scientists' practices and the public's expectations. *Frontiers in Environmental Science* 9. <https://doi.org/10.3389/fenvs.2021.606416>.
- Salvador, R. B., D. C. Cavallari, D. Rands, and B. M. Tomotani. 2022. Publication practice in taxonomy: global inequalities and potential bias against negative results. *PLoS ONE* 17:e0269246.
- Sanders, D., E. Thébault, R. Kehoe, and F. J. Frank van Veen. 2018. Trophic redundancy reduces vulnerability to extinction cascades. *Proceedings of the National Academy of Sciences USA* 115:2419–2424.
- Sansom, R. S., S. E. Gabbott, and M. A. Purnell. 2010. Decay of vertebrate characters in hagfish and lamprey (Cyclostomata) and the implications for the vertebrate fossil record. *Proceedings of the Royal Society B* 278:1150–1157.
- Saupe, E. E., J. R. Hendricks, A. T. Peterson, and B. S. Lieberman. 2014. Climate change and marine molluscs of the western North Atlantic: future prospects and perils. *Journal of Biogeography* 41:1352–1366.
- Saupe, E. E., C. E. Myers, A. Townsend Peterson, J. Soberón, J. Singarayer, P. Valdes, and H. Qiao. 2019. Spatio-temporal climate change contributes to latitudinal diversity gradients. *Nature Ecology and Evolution* 3:1419–1429.
- Scarlett, J. P. 2022. The harmful legacy of colonialism in natural hazard risk. *Nature Communications* 13:6945.
- Schweitzer, M. H., R. Avci, T. Collier, and M. B. Goodwin. 2008. Microscopic, chemical and molecular methods for examining fossil preservation. *Comptes Rendus Palevol* 7:159–184.

- Seddon, A. W. R., A. W. Mackay, A. G. Baker, H. J. B. Birks, E. Breman, C. E. Buck, E. C. Ellis, *et al.* 2014. Looking forward through the past: identification of 50 priority research questions in palaeoecology. *Journal of Ecology* **102**: 256–267.
- Seilacher, A., W. E. Reif, and F. Westphal. 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. *Philosophical Transactions of the Royal Society B* **311**:5–23.
- Sepkoski, J. J., R. K. Bambach, D. M. Raup, and J. W. Valentine. 1981. Phanerozoic marine diversity and the fossil record. *Nature* **293**:435–437.
- Shinbrot, X. A., K. Treibergs, L. M. A. Hernández, D. Esparza, K. Ghezzi-Kopel, M. Goebel, O. J. Graham, *et al.* 2022. The impact of field courses on undergraduate knowledge, affect, behavior, and skills: a scoping review. *BioScience* **72**:1007–1017.
- Słowiński, M., P. Skubała, I. Zawiska, A. Kruk, M. Obremska, K. Milecka, and F. Ott. 2018. Cascading effects between climate, vegetation, and macroinvertebrate fauna in 14,000-year palaeoecological investigations of a shallow lake in eastern Poland. *Ecological Indicators* **85**:329–341.
- Smiley, T. M. 2018. Detecting diversification rates in relation to preservation and tectonic history from simulated fossil records. *Paleobiology* **44**:1–24.
- Smith, H. E., J. J. Bevirt, J. Zaim, Y. Rizal, Aswan, M. R. Puspaningrum, A. Trihascaryo, *et al.* 2021. High-resolution high-throughput thermal neutron tomographic imaging of fossiliferous cave breccias from Sumatra. *Scientific Reports* **11**:19953.
- Smith, J. A., S. R. Durham, and G. P. Dietl. 2018. Conceptions of long-term data among marine conservation biologists and what conservation paleobiologists need to know. Pp. 23–54 in C. L. Tyler and C. L. Schneider, eds. *Marine conservation paleobiology*. Springer International, Cham.
- Smith, J. A., M. J. Pruden, J. C. Handley, S. R. Durham, and G. P. Dietl. 2023a. Assessing the utility of death assemblages as reference conditions in a common benthic index (M-AMBI) with simulations. *Geological Society of London Special Publication* **529**:131–151.
- Smith, J. A., N. B. Raja, T. Clements, D. Dimitrijević, E. M. Dowding, E. M. Dunne, B. M. Gee, *et al.* 2023b. Increasing the equitability of data citation in paleontology: capacity building for the big data future. *Paleobiology* **50**: 165–176.
- Smith, J. A., M. C. Rillo, Á. T. Kocsis, M. Dornelas, D. Fastovich, H.-H. M. Huang, L. Jonkers, *et al.* 2023c. BioDeepTime: a database of biodiversity time series for modern and fossil assemblages. *Global Ecology and Biogeography* **32**:1680–1689.
- Song, H., P. B. Wignall, H. Song, X. Dai, and D. Chu. 2019. Seawater temperature and dissolved oxygen over the past 500 million years. *Journal of Earth Science* **30**:236–243.
- Song, H., D. B. Kemp, L. Tian, D. Chu, H. Song, and X. Dai. 2021. Thresholds of temperature change for mass extinctions. *Nature Communications* **12**:4694.
- Soul, L. C., and M. Friedman. 2015. Taxonomy and phylogeny can yield comparable results in comparative paleontological analyses. *Systematic Biology* **64**:608–620.
- Spiridonov, A., and S. Lovejoy. 2022. Life rather than climate influences diversity at scales greater than 40 million years. *Nature* **607**:307–312.
- Stadler, T. 2010. Sampling-through-time in birth–death trees. *Journal of Theoretical Biology* **267**:396–404.
- Stansfield, E., P. Mitteroecker, S. Y. Vasilyev, S. Vasilyev, and L. N. Butaric. 2021. Respiratory adaptation to climate in modern humans and Upper Palaeolithic individuals from Sungir and Mladeč. *Scientific Reports* **11**:7997.
- Stewart, M., W. C. Carleton, and H. S. Groucutt. 2021. Climate change, not human population growth, correlates with Late Quaternary megafauna declines in North America. *Nature Communications* **12**:965.
- Stigall, A. L. 2014. When and how do species achieve niche stability over long time scales? *Ecography* **37**:1123–1132.
- Stigall, A. L. 2019. The invasion hierarchy: ecological and evolutionary consequences of invasions in the fossil record. *Annual Review of Ecology, Evolution, and Systematics* **50**:355–380.
- Stokes, A., A. D. Feig, C. L. Atchison, and B. Gilley. 2019. Making geoscience fieldwork inclusive and accessible for students with disabilities. *Geosphere* **15**: 1809–1825.
- Storch, D., L. Menzel, S. Frickenhaus, and H.-O. Pörtner. 2014. Climate sensitivity across marine domains of life: limits to evolutionary adaptation shape species interactions. *Global Change Biology* **20**:3059–3067.
- Sutherland, W. J., W. M. Adams, R. B. Aronson, R. Aveling, T. M. Blackburn, S. Broad, G. Ceballos, *et al.* 2009. One hundred questions of importance to the conservation of global biological diversity. *Conservation Biology* **23**:557–567.
- Teng, F.-Z., N. Dauphas, and J. M. Watkins. 2017. Non-traditional stable isotopes: retrospective and prospective. *Reviews in Mineralogy and Geochemistry* **82**:1–26.
- Tihelka, E., R. J. Howard, C. Cai, and J. Lozano-Fernandez. 2022. Was there a Cambrian explosion on land? The case of arthropod terrestrialization. *Biology* **11**:1516.
- Trubovitz, S., J. Renaudie, D. Lazarus, and P. J. Noble. 2023. Abundance does not predict extinction risk in the fossil record of marine plankton. *Communications Biology* **6**:1–10.
- Tsuboi, M., J. Szepeanacz, S. De Lisle, K. L. Voje, M. Grabowski, M. J. Hopkins, A. Porto, *et al.* 2024. The paradox of predictability provides a bridge between micro- and macroevolution. *Journal of Evolutionary Biology* **37**:1413–1432.
- Vahdati, A. R., J. D. Weissmann, A. Timmermann, M. P. de León, and C. P. Zollikofer. 2022. Exploring Late Pleistocene hominin dispersals, coexistence and extinction with agent-based multi-factor models. *Quaternary Science Reviews* **279**:107391.
- Valenzuela-Toro, A. M., and M. Viglino. 2021. Latin American challenges. *Nature* **598**:374–375.
- Vermeij, G. J., and P. D. Roopnarine. 2013. Reining in the Red Queen: the dynamics of adaptation and extinction reexamined. *Paleobiology* **39**:560–575.
- Vinther, J. 2015. A guide to the field of palaeo colour: melanin and other pigments can fossilise: reconstructing colour patterns from ancient organisms can give new insights to ecology and behaviour. *BioEssays* **37**:643–656.
- Vogel, G. 2019. Natural history museums face their own past. *Science* **363**: 1371–1372.
- Vousdoukas, M. I., J. Clarke, R. Ranasinghe, L. Reimann, N. Khalaf, T. M. Duong, B. Ouwenel, *et al.* 2022. African heritage sites threatened as sea-level rise accelerates. *Nature Climate Change* **12**:256–262.
- Vrba, E. S. 1985. Environment and evolution: alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science* **81**: 229–236.
- Vrba, E. S. 1992. Mammals as a key to evolutionary theory. *Journal of Mammalogy* **73**:1–28.
- Vrba, E. S. 1993. Turnover-pulses, the Red Queen, and related topics. *American Journal of Science* **293**:418.
- Warnock, R. C., and A. M. Wright. 2020. *Understanding the tripartite approach to Bayesian divergence time estimation*. Cambridge University Press, Cambridge.
- Whitaker, A. F., and J. Kimmig. 2020. Anthropologically introduced biases in natural history collections, with a case study on the invertebrate paleontology collections from the middle Cambrian Spence Shale Lagerstätte. *Palaeontologia Electronica* **23**:a58.
- Wiemann, J., J. M. Crawford, and D. E. Briggs. 2020. Phylogenetic and physiological signals in metazoan fossil biomolecules. *Science Advances* **6**: eaba6883.
- Willis, K. J., and S. A. Bhagwat. 2010. Questions of importance to the conservation of biological diversity: answers from the past. *Climate of the Past* **6**: 759–769.
- Wing, S. L., G. J. Harrington, F. A. Smith, J. I. Bloch, D. M. Boyer, and K. H. Freeman. 2005. Transient floral change and rapid global warming at the Paleocene-Eocene boundary. *Science* **310**:993–996.
- Wis, M. S., J. Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C. F. Damgaard, C. F. Dormann, *et al.* 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* **88**:15–30.
- Woehle, C., A.-S. Roy, N. Glock, J. Michels, T. Wein, J. Weissenbach, D. Romero, *et al.* 2022. Denitrification in foraminifera has an ancient origin and is complemented by associated bacteria. *Proceedings of the National Academy of Sciences USA* **119**:e2200198119.
- Woodhouse, A., A. Swain, W. F. Fagan, A. J. Fraass, and C. M. Lowery. 2023. Late Cenozoic cooling restructured global marine plankton communities. *Nature* **614**:713–718.
- Wright, D. F. 2015. Fossils, homology, and “Phylogenetic Paleo-ontology”: a reassessment of primary posterior plate homologies among fossil and living crinoids with insights from developmental biology. *Paleobiology* **41**:570–591.

- Wright, A. M., D. W. Bapst, J. Barido-Sottani, and R. C. M. Warnock.** 2022. Integrating fossil observations into phylogenetics using the fossilized birth–death model. *Annual Review of Ecology, Evolution, and Systematics* 53: 251–273.
- Yamamoto, S., and M. S. Caterino.** 2023. A remarkable new fossil species of *Amplectister* with peculiar hindleg modifications (Coleoptera: Histeridae): further evidence for myrmecophily in Cretaceous clown beetles. *Palaeoworld* 32:481–489.
- Yasuhara, M., and C. A. Deutsch.** 2022. Paleobiology provides glimpses of future ocean: fossil records from tropical oceans predict biodiversity loss in a warmer world. *Science* 375:25–26.
- Yasuhara, M., and C. A. Deutsch.** 2023. Tropical biodiversity linked to polar climate. *Nature* 614:626–628.
- Yasuhara, M., C.-L. Wei, M. Kucera, M. J. Costello, D. P. Tittensor, W. Kiessling, T. C. Bonebrake, et al.** 2020. Past and future decline of tropical pelagic biodiversity. *Proceedings of the National Academy of Sciences USA* 117:12891–12896.
- Zacai, A., C. Monnet, A. Pohl, G. Beaugrand, G. Mullins, D. M. Kroeck, and T. Servais.** 2021. Truncated bimodal latitudinal diversity gradient in early Paleozoic phytoplankton. *Science Advances* 7:eabd6709.
- Zuschin, M.** 2023. Challenges of conservation paleobiology: from baselines to novel communities to the necessity for granting rights to nature. *Palaos* 38: 259–263.