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Title	Land use change consistently reduces α# but not ß# and γ# diversity of bees
Authors	Tsang, Toby P. N.;De Santis, A. A. Amado;Armas#Quiñonez, Gabriela;Ascher, John S.;Ávila#Gómez, Eva Samanta;Báldi, András;Ballare, Kimberly M.;Balzan, Mario V.;Banaszak# Cibicka, Weronika;Bänsch, Svenja;Basset, Yves;Bates, Adam J.;Baumann, Jessica M.;Beal#Neves, Mariana;Bennett, Ashley;Bezerra, Antonio Diego M.;Blochtein, Betina;Bommarco, Riccardo;Brosi, Berry;Burkle, Laura A.;Carvalheiro, Luísa G.;Castellanos, Ignacio;Cely#Santos, Marcela;Cohen, Hamutahl;Coulibaly, Drissa;Cunningham, Saul A.;Cusser, Sarah;Dajoz, Isabelle;Delaney, Deborah A.;Del#Val, Ek;Egerer, Monika;Eichhorn, Markus P.;Enríquez, Eunice;Entling, Martin H.;Escobedo#Kenefic, Natalia;Ferreira, Pedro Maria Abreu;Fitch, Gordon;Forrest, Jessica R. K.;Fournier, Valérie;Fowler, Robert;Freitas, Breno M.;Gaines#Day, Hannah R.;Geslin, Benoît;Ghazoul, Jaboury;Glaum, Paul;Gonzalez#Andujar, Jose L.;González#Chaves, Adrian;Grab, Heather;Gratton, Claudio;Guenat, Solène;Gutiérrez#Chacón, Catalina;Hall, Mark A.;Hanley, Mick E.;Hass, Annika;Hennig, Ernest Ireneusz;Hermy, Martin;Hipólito, Juliana;Holzschuh, Andrea;Hopfenmüller, Sebastian;James Hung, Keng#Lou;Hylander, Kristoffer;Izquierdo, Jordi;Jamieson, Mary A.;Jauker, Birgit;Javorek, Steve;Jha, Shalene;Klatt, Björn K.;Kleijn, David;Klein, Alexandra# Maria;Kovács#Hostyánszki, Anikó;Krauss, Jochen;Kuhlmann, Michael;Landaverde#González, Patricia;Latty, Tanya;Leong, Misha;Lerman, Susannah B.;Liu, Yunhui;Pereira Machado, Ana Carolina;Main, Anson;Mallinger, Rachel;Mandelik, Yael;Ferreira Marques, Bruno;Matteson, Kevin;McCune, Frédéric;Meng, Ling#Zeng;Metzger, Jean Paul;Montoya# Pfeiffer, Paula María;Morales, Carolina;Morandin, Lora;Morrison, Jane;Mudri#Stojnić, Sonja;Nalinrachatakan, Pakorn;Norfolk, Olivia;Otieno, Mark;Park, Mia G.;Philpott, Stacy M.;Pisanty, Gideon;Plascencia, Montserrat;Potts, Simon G.;Power, Eileen F.;Prendergast, Kit;Quistberg, Robyn D.;de Lacerda Ramos, Davi;Rech, André Rodrigo;Reynolds, Victoria;Richards, Miriam H.;Roberts, Stuart P. M.;Sabatino, Malena;Samnegård, Ulrika;Sardiñas, Hillary;Sánchez#Echeverría, Karina;Teixeira Saturni, Fernanda;Scheper, Jeroen;Sciligo, Amber R.;Sidhu, C. Sheena;Spiesman, Brian J.;Sritongchuay, Tuanjit;Steffan# Dewenter, Ingolf;Stein, Katharina;Stewart, Alyssa B.;Stout, Jane C.;Taki, Hisatomo;Tangtorwongsakul, Pornpimon;Threlfall, Caragh G.;Faleiro Tinoco, Carla;Tscharntke, Teja;Turo, Katherine J.;Vaidya, Chatura;Vandame, Rémy;Vergara,

	Carlos H.;Viana, Blandina F.;Vides#Borrell, Eric;Warrit, Natapot;Webb, Elisabeth;Westphal, Catrin;Wickens, Jennifer B.;Williams, Neal M.;Williams, Nicholas S. G.;Wilson, Caleb J.;Wu, Panlong;Youngsteadt, Elsa;Zou, Yi;Ponisio, Lauren C.;Bonebrake, Timothy C.
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University College Cork, Ireland
Coláiste na hOllscoile Corcaigh

Land use change consistently reduces α but not β and γ diversity of bees

Toby P. N. Tsang[1,2], A. A. Amado De Santis[3,4], Gabriela Armas-Quiñonez[5], John S. Ascher[6], Eva Samanta Ávila-Gómez[7], András Báldi[8], Kimberly M. Ballare[9,10], Mario V. Balzan[11], Weronika Banaszak-Cibicka[12], Svenja Bänsch[13], Yves Basset[14], Adam J. Bates[15], Jessica M. Baumann[16], Mariana Beal-Neves[17], Ashley Bennett[18], Antonio Diego M. Bezerra[19], Betina Blochtein[17], Riccardo Bommarco[20], Berry Brosi[21], Laura A. Burkle[22], Luísa G. Carvalheiro[23], Ignacio Castellanos[24], Marcela Cely-Santos[25], Hamutahl Cohen[26], Drissa Coulibaly[27], Saul A. Cunningham[28], Sarah Cusser[29], Isabelle Dajoz[30], Deborah A. Delaney[31], Ek Del-Val[32], Monika Egerer[33], Markus P. Eichhorn[34,35], Eunice Enríquez[5], Martin H. Entling[36], Natalia Escobedo-Kenefic[5], Pedro Maria Abreu Ferreira[17], Gordon Fitch[37], Jessica R. K. Forrest[38], Valérie Fournier[39], Robert Fowler[40], Breno M. Freitas[41], Hannah R. Gaines-Day[42], Benoît Geslin[43,44], Jaboury Ghazoul[45], Paul Glaum[46,47], Jose L. Gonzalez-Andujar[48], Adrian González-Chaves[23,49], Heather Grab[50], Claudio Gratton[51], Solène Guenat[52], Catalina Gutiérrez-Chacón[53], Mark A. Hall[54], Mick E. Hanley[55], Annika Hass[13], Ernest Ireneusz Hennig[56], Martin Hermy[57], Juliana Hipólito[58,59], Andrea Holzschuh[60], Sebastian Hopfenmüller[60,61], Keng-Lou James Hung[62], Kristoffer Hylander[63], Jordi Izquierdo[64], Mary A. Jamieson[65], Birgit Jauker[66], Steve Javorek[67], Shalene Jha[68], Björn Klatt[69,70,71], David Kleijn[72], Alexandra-Maria Klein[73], Anikó Kovács-Hostyánszki[8], Jochen Krauss[60], Michael Kuhlmann[74], Patricia Landaverde-González[5,75], Tanya Latty[76], Misha Leong[77], Susannah B. Lerman[78], Yunhui Liu[79], Ana Carolina Pereira Machado[80,81], Anson Main[82,83], Rachel Mallinger[84], Yael Mandelik[85], Bruno Ferreira Marques[86], Kevin Matteson[87], Frédéric McCune[39], Ling-Zeng Meng[88], Jean Paul Metzger[89], Paula María Montoya-Pfeiffer[90], Carolina Morales[91], Lora Morandin[92], Jane Morrison[64,93], Sonja Mudri-

Stojnić[94], Pakorn Nalinrachatakan[95], Olivia Norfolk[96], Mark Otieno[97], Mia G. Park[98,99], Stacy M. Philpott[100], Gideon Pisanty[85,101], Montserrat Plascencia[102], Simon G. Potts[103], Eileen F. Power[104], Kit Prendergast[105,106], Robyn D. Quistberg[100], Davi de Lacerda Ramos[107], André Rodrigo Rech[108], Victoria Reynolds[109], Miriam H. Richards[110], Stuart P. M. Roberts[103,111] , Malena Sabatino[112], Ulrika Samnegård[113], Hillary Sardinas[114], Karina Sánchez-Echeverría[115], Fernanda Teixeira Saturni[116], Jeroen Scheper[72], Amber R. Sciligo[117], C. Sheena Sidhu[118], Brian J. Spiesman[119], Tuanjit Sritongchuay[120], Ingolf Steffan-Dewenter[60], Katharina Stein[121], Alyssa B. Stewart[122], Jane C. Stout[104], Hisatomo Taki[123], Pornpimon Tangtorwongsakul[124], Caragh G. Threlfall[125], Carla Tinoco[126], Teja Tscharntke[127], Katherine J. Turo[128,129], Chatura Vaidya[130], Rémy Vandame[131], Carlos H. Vergara[132], Blandina F. Viana[58], Eric Vides-Borrell[131], Natapot Warrit[95], Elisabeth Webb[133], Catrin Westphal[13], Jennifer B. Wickens[103], Neal M. Williams[134], Nicholas S. G. Williams[16], Caleb J. Wilson[65,135], Panlong Wu[80,136], Elsa Youngsteadt[137], Yi Zou[138], Lauren C. Ponisio[139], Timothy C. Bonebrake[1]

[1]School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong, Hong Kong SAR, China

[2]Department of Biological Sciences, University of Toronto-Scarborough, Toronto, Ontario, Canada

[3]Centro de Estudios Territoriales Ambientales y Sociales (CETAS-UNJu), Jujuy, Argentina

[4]Instituto de Ecorregiones Andinas (INECOA), Universidad Nacional de Jujuy - CONICET, Facultad de Ciencias Agrarias, S. S. de Jujuy, Argentina

[5]Centro de Estudios Conservacionistas, Facultad de Ciencias Químicas y Farmacia, Universidad de San Carlos de Guatemala

[6]Department of Biological Sciences, National University of Singapore, 16 Science Drive 4 S3 Level 4, Singapore 117558

[7]Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo, Carretera Pachuca-Tulancingo km 4.5, C. P. 42184, Mineral de la Reforma, Hidalgo, México

[8]Lendület Ecosystem Services Research Group, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Hungary

[9]Department of Integrative Biology, University of Texas at Austin, Austin, TX 78739, USA

[10]USDA Forest Service, Rocky Mountain Research Station, Bozeman, MT 59717, USA

[11]Institute of Applied Sciences, Malta College of Arts, Science and Technology, Paola, PLA9032, Malta

[12]Department of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, 60-625 Poznań, Poland

[13]Functional Agrobiodiversity, University of Göttingen, 37077, Göttingen, Germany

[14]Smithsonian Tropical Research Institute, Panama City, Republic of Panama

[15]School of Animal, Rural & Environmental Sciences, Nottingham Trent University, Nottingham, UK

[16]School of Agriculture, Food and Ecosystem Sciences, The University of Melbourne, Richmond, Victoria, Australia

[17]Programa de Pós-Graduação em Ecologia e Evolução da Biodiversidade, Pontifícia Universidade Católica do Rio Grande do Sul, PUCRS, Av. Ipiranga 6681, prédio 12, bloco C, sala 111, Porto Alegre, RS 90619-900, Brazil

[18]Department of Entomology, Michigan State University, 578 Wilson Road, East Lansing, MI 48824, United States

[19]Departamento de Zootecnia, Centro de Ciências Agrárias, Universidade Federal do Ceará, Fortaleza, CE, Brazil

[20]Swedish University of Agricultural Sciences, Department of Ecology, 75007 Uppsala, Sweden

[21]Department of Biology, University of Washington, Seattle, Washington, USA

[22]Montana State University, Department of Ecology, Bozeman, MT USA 59717

[23]Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia, Brazil

[24]Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Mineral de la Reforma, Hidalgo, Mexico

[25]Department of Environmental Studies, University of California- Santa Cruz

[26]University of California, Division of Agriculture and Natural Resources, UC Cooperative Extension Ventura County. Ventura, CA

[27]University Peleforo GON COULIBALY of Korhogo, Cote d'Ivoire

[28]Fenner School of Environment & Society, The Australian National University, Canberra, Australia, 2601

[29]Santa Barbara Botanic Garden, 1212 Mission Canyon Rd, Santa Barbara, CA 93111, USA

[30]Université Paris-Cité, UMR CNRS 7618, Paris, France

[31]Department of Entomology & Wildlife Biology, University of Delaware, Newark, DE, United States

[32]Insitituto de Investigaciones en Ecosistemas y Sustentabilidad, UNAM

[33]Department of Life Science Systems, TUM School of Life Sciences, Technical University of Munich, Hans Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

[34]School of Biological, Earth and Environmental Sciences, University College Cork, Cork, Ireland

[35]Environmental Research Institute, University College Cork, Cork, Ireland

[36]37iES Landau, Institute for Environmental Sciences, University of Kaiserslautern-Landau (RPTU), Germany

[37]Department of Biology, York University, Toronto, ON, Canada

[38]Department of Biology, University of Ottawa, Ottawa, ON, Canada

[39]Centre de recherche et d'innovation sur les végétaux, Université Laval, Québec City, QC, Canada

[40]University of Sussex, Falmer, Brighton, United Kingdom

[41]Departamento de Zootecnia, Centro de Ciências Agrárias, Universidade Federal do Ceará, Fortaleza, CE, Brazil

[42]Department of Entomology, University of Wisconsin, Madison, Madison, WI, USA

[43]IMBE, Aix Marseille Univ., Avignon Univ., CNRS, IRD, Marseille, France

[44]Université de Rennes (UNIR), UMR 6553 ECOBIO, CNRS, Rennes, France

[45]Ecosystem Management, Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland

[46]Department of Environmental Science and Policy, University of California-Davis, Davis, CA, 95616, USA

[47]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, 48109, USA

[48]Institute for Sustainable Agriculture (IAS), Spanish National Research Council (CSIC), Cordoba, Spain

[49]Laboratório de Ecologia da Paisagem e Conservação, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

[50]Department of Entomology, The Pennsylvania State University, University Park, PA, 16802 USA

[51]Department of Entomology, University of Wisconsin-Madison, 1630 Linden Dr. Madison, Madison, WI, 53706, USA

[52]Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Switzerland

[53]Wildlife Conservation Society –Colombia Program, Av 5N # 22N-11, Cali, Colombia

[54]Hawkesbury Institute for the Environment, Western Sydney University, Richmond, Australia

[55]School of Biological and Marine Sciences, University of Plymouth, Plymouth, PL4 8AA. UK.

[56]Federal Statistical Office, Division Territory and Environment, Section Geoinformation

[57]KU Leuven, University of Leuven (KU Leuven), dept Earth & Environmental Sciences, Celestijnenlaan 200E, 3001 Heverlee

[58]Laboratório de Interações Inseto-Microrganismo, Universidade Federal de Viçosa (UFV), Viçosa, MG, Brazil

[59]Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil

[60]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, 97074 Würzburg, Germany

[61]Stiftung Kulturlandschaft Günztal, 87724 Ottobeuren, Germany

[62]Oklahoma Biological Survey, University of Oklahoma, Norman, Oklahoma, USA

[63]Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden

[64]Department of Agri-Food Engineering and Biotechnology, Universitat Politècnica de Catalunya - Campus del Baix Llobregat, 08860 Castelldefels, Spain

[65]Department of Biological Sciences, Oakland University, Rochester, MI, United States

[66]Department of Animal Ecology, Justus Liebig University Giessen, Giessen, Germany

[67]Agriculture and Agri-Food Canada, Kentville Research and Development Centre, Kentville, Nova Scotia, Canada

[68]Department of Integrative Biology & Lady Bird Johnson Wildflower Center, University of Texas at Austin, Austin, TX 78739, USA

[69]Agroecology, Department of Crop Sciences, Göttingen University, Germany

[70]Biodiversity, Department of Biology, Lund University, Sweden

[71]Halmstad University, School of Business, Innovation and Sustainability, Biology & Environmental Sciences, P.O. Box 823, 30118 Halmstad, Sweden

[72]Plant Ecology and Nature Conservation Group, Wageningen University & Research, 6700 AA Wageningen, The Netherlands

[73]Nature Conservation and Landscape Ecology, University of Freiburg, Germany

[74]Zoological Museum, University of Kiel, Germany, Hegewischstr. 3, D-24105 Kiel

[75]General Zoology, Institute for Biology, Martin-Luther University Halle-Wittenberg, Hoher Weg 8, 06120 Halle (Saale), Germany

[76]School of Life and Environmental Sciences & Sydney Institute of Agriculture, University of Sydney, Sydney, NSW, Australia

[77]California Academy of Sciences, San Francisco, CA, USA

[78]USDA Forest Service Northern Research Station, Amherst, MA, USA

[79]College of Resources and Environmental Sciences, China Agricultural University, Beijing 100193, China

[80]Programas de Pós-Graduação em Ciência Florestal e Biologia Animal, Universidade Federal dos Vales do Jequitinhonha e Mucuri, Campus JK, Diamantina, MG, Brazil

[81]Instituto de Biología, Pontificia Universidad Católica de Valparaíso, Valparaíso, Chile

[82]School of Natural Resources, University of Missouri, Columbia, MO, USA

[83]California Department of Pesticide Regulation, Sacramento, CA, 95812, USA

[84]Department of Entomology and Nematology, University of Florida, Gainesville, Florida, USA

[85]Department of Entomology, The Robert H. Smith Faculty of Agriculture, Food and Environment, The Hebrew University of Jerusalem, Rehovot 7610001, Israel

[86]Programa de Pós Graduação em Ecologia e Evolução - Universidade Federal de Goiás, Goiânia, Brasil

[87]Project Dragonfly/Department of Biology, Miami University, 111 Upham Hall, Oxford, OH 45056, USA

[88]College of Biological & Agricultural Sciences, Honghe University, Mengzi, Yunnan 661199, China

[89]Department of Ecology, Institute of Biosciences, Institute of Advanced Studies, University of São Paulo, SP, Brazil

[90]Laboratório de Abelhas, Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

[91]Instituto de Investigaciones en Biodiversidad y Medio Ambiente (INIBIOMA), Universidad Nacional del Comahue, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Bariloche (8400), Argentina

[92]Pollinator Partnership, San Francisco, CA

[93]Department of Environment, Agriculture and Geography, Bishop's University, 2600 College St., Sherbrooke, QC, J1M 1Z7, Canada

[94]University of Novi Sad, Faculty of Sciences, Department of Biology and Ecology, Trg Dositeja Obradovića 2, 21000 Novi Sad, Serbia

[95]Center of Excellence in Entomology and Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand

[96]Deceased

[97]Water and Agricultural Resource Management, University of Embu, Embu, Kenya

[98]Department of Entomology, Cornell University, Ithaca, New York, USA

[99]Xerces Society for Invertebrate Conservation, Portland, OR, USA

[100]Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

[101]The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

[102]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, CA 95064, USA

[103]Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, Reading University, RG6 6EU, UK

[104]Botany, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

[105]University of Sunshine Coast

[106]School of Molecular and Life Sciences, Curtin University, Kent Street, Bentley, WA, 6102, Australia

[107]University of Brasília, Institute of Biological Sciences, Graduate Program in Ecology – Campus Darcy Ribeiro, Asa Norte, Brasília-DF 70910-900, Brazil

[108]Centre of Advanced Studies on the Functioning of Ecological Systems and Interactions (CAFESIN - MULTIFLOR), Federal University of Jequitinhonha and Mucuri Valleys. CEP 39100-000, Diamantina, Minas Gerais, Brazil

[109]University of Queensland, School of Biological Sciences, Brisbane, Australia

[110]Department of Biological Sciences, Brock University, 1812 Sir Isaac Brock Way, St. Catharines, ON, L2T 1X6, Canada

[111]Université Libre de Bruxelles, Faculté des Sciences, Campus de la Plaine - CP 264/02, Boulevard du Triomphe, ACC.2 ,1050 Bruxelles

[112]Centro de Investigaciones en Abejas Sociales (CIAS), IIPROSAM. CONICET – UNMDP

[113]Department of Biology, Lund University, 223 62 Lund, Sweden

[114]Department of Environmental Science, Policy and Management, University of California, Berkeley

[115]Laboratorio de Ecología de Interacciones Bióticas. Facultad de Biología. Universidad Michoacana de San Nicolás de Hidalgo. Morelia, Michoacán, México

[116]Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, 321, Travessa 14, 05508-900 São Paulo, SP, Brazil

[117]The Organic Center, Washington D.C., USA

[118]Jasper Ridge Biological Preserve, Stanford University

[119]Department of Entomology, Kansas State University, Manhattan, KS 66506

[120]UFZ-Helmholtz Centre for Environmental Research, Department of Computational Landscape Ecology, Permoserstr. 15, 04318 Leipzig, Germany

[121]Faculty of Forest and Environment, Eberswalde University for Sustainable Development, Eberswalde, Germany

[122]Department of Plant Science, Faculty of Science, Mahidol University, Bangkok, 10400 Thailand

[123]Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki, 305-8687, Japan

[124]Conservation Ecology Program, King Mongkut's University of Technology Thonburi, Bangkok 10150, Thailand

[125]School of Life and Environmental Sciences, Faculty of Science, The University of Sydney, Camperdown, Australia

[126]Department of Ecology, Universidade Federal de Goiás, 74001-970 Goiânia, Brazil

[127]Functional Agrobiodiversity and Agroecology, University of Göttingen, Göttingen, Germany

[128]Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, New Jersey, USA

[129]Department of Entomology, The Ohio State University, Columbus, Ohio, USA

[130]Department of Integrative Biology, University of Texas at Austin, Austin, TX 78712, USA

[131]El Colegio de la Frontera Sur, Departamento Agricultura Sociedad y Ambiente, San Cristóbal de Las Casas, Chiapas, Mexico

[132]Departamento de Ciencias Químico-Biológicas, Universidad de las Américas Puebla, Cholula, Puebla, México

[133]U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri, Columbia, MO 65211, USA

[134]Department of Entomology and Nematology, University of California, One Shields Ave., Davis, CA 95616, USA

[135]Department of Entomology, University of Kentucky, Lexington, KY, USA

[136]School of Ecology and Environment, Inner Mongolia University, Hohhot 010021, China

[137]Department of Applied Ecology, North Carolina State University, Raleigh, NC, USA

[138]Department of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University, Suzhou, China

[139]Institute for Ecology and Evolution, University of Oregon, Eugene, Oregon, USA

Name	ORCID
Toby P. N. Tsang	0000-0002-8176-7777
Gabriela Armas-Quiñonez	0009-0003-7973-0005
John S. Ascher	0000-0002-7887-2461
András Báldi	0000-0001-6063-3721
Kimberly M. Ballare	0000-0002-1824-3364
Weronika Banaszak-Cibicka	0000-0003-3465-2712
Svenja Bänsch	0000-0001-7332-7213
Yves Basset	0000-0002-1942-5717
Mariana Beal-Neves	0000-0001-5900-563X
Antonio Diego M. Bezerra	0000-0002-8070-5582
Betina Blochtein	0000-0001-8452-1716
Riccardo Bommarco	0000-0001-8888-0476
Berry Brosi	0000-0002-9233-1151
Laura A. Burkle	0000-0002-8413-1627

Luísa G. Carvalheiro	0000-0001-7655-979X
Ignacio Castellanos	0000-0003-4480-656X
Marcela Cely-Santos	0000-0001-9792-8793
Drissa Coulibaly	0000-0002-8495-5773
Saul A. Cunningham	0000-0003-0703-6893
Sarah Cusser	0000-0002-0100-026X
Isabelle Dajoz	0000-0003-0862-1517
Ek Del-Val	0000-0003-3862-1024
Monika Egerer	0000-0002-3304-0725
Markus P. Eichhorn	0000-0002-3381-0822
Martin H Entling	0000-0002-3947-6407
Pedro Maria Abreu Ferreira	0000-0002-4088-4571
Gordon Fitch	0000-0002-2471-1160
Jessica R. K. Forrest	0000-0002-5273-9339
Valérie Fournier	0000-0003-0711-5241
Robert Fowler	0000-0002-5246-8831
Breno M. Freitas	0000-0002-9932-2207
Hannah R. Gaines-Day	0000-0002-9798-0601
Benoît Geslin	0000-0002-2464-7998
Jaboury Ghazoul	0000-0002-8319-1636
Paul Glaum	0000-0002-7451-8369
Jose L. Gonzalez-Andujar	0000-0003-2356-4098
Adrian González-Chaves	0000-0002-5233-8957
Heather Grab	0000-0002-1073-8805
Claudio Gratton	0000-0001-6262-9670
Solène Guenat	0000-0002-2077-405X
Mark A. Hall	0000-0003-4273-980X

Mick E Hanley	0000-0002-3966-8919
Annika Hass	0000-0002-3377-4622
Martin Hermy	0000-0002-5403-0139
Juliana Hipólito	0000-0002-0721-3143
Andrea Holzschuh	0000-0002-5235-4746
Sebastian Hopfenmüller	0009-0004-5138-6342
Keng-Lou James Hung	0000-0002-1557-3958
Jordi Izquierdo	0000-0002-3949-1295
Mary A. Jamieson	0000-0002-1716-0372
Birgit Jauker	0000-0001-50279351
David Kleijn	0000-0003-2500-7164
Alexandra-Maria Klein	0000-0003-2139-8575
Anikó Kovács-Hostyánszki	0000-0001-5906-4816
Jochen Krauss	0000-0003-2304-9117
Michael Kuhlmann	0000-0003-3664-6922
Patricia Landaverde-González	0000-0001-9636-3292
Andrew P. Landsman	0000-0002-4750-819X
Misha Leong	0000-0003-0225-0022
Susannah B. Lerman	0000-0002-2331-8439
Ana Carolina Pereira Machado	0000-0002-0432-2627
Anson R. Main	0000-0001-9539-760X
Yael Mandelik	0000-0002-9576-119X
Frédéric McCune	0000-0002-2710-6580
Ling-Zeng Meng	0000-0002-0566-1647
Jean Paul Metzger	0000-0002-0087-5240
Paula María Montoya-Pfeiffer	0000-0002-6648-1535
Jane Morrison	0000-0002-4055-4679

Pakorn Nalinrachatakan	0000-0001-7962-5844
Olivia Norfolk	0000-0002-2909-304X
Mia G. Park	0000-0002-1250-7664
Stacy M. Philpott	0000-0002-8338-3806
Gideon Pisanty	0000-0003-2076-430X
Simon G. Potts	0000-0002-2045-980X
Kit Prendergast	0000-0002-1164-6099
André Rodrigo Rech	0000-0003-4685-7483
Victoria Reynolds	0000-0002-6071-9303
Malena Sabatino	0000-0001-8726-601X
Karina Sánchez-Echeverría	0009-0004-9990-3994
Jeroen Scheper	0000-0002-4314-996X
Amber R. Sciligo	0000-0003-2437-8799
C. Sheena Sidhu	0000-0002-7190-3544
Ingolf Steffan-Dewenter	0000-0003-1359-3944
Katharina Stein	0000-0003-3111-6172
Alyssa B. Stewart	0000-0002-7266-1081
Sonja Mudri-Stojnić	0000-0002-0118-0475
Hisatomo Taki	0000-0002-2399-0049
Pornpimon Tangtorwongsakul	0000-0003-1321-6970
Caragh G. Threlfall	0000-0002-4197-8588
Teja Tscharntke	0000-0002-4482-3178
Katherine J. Turo	0000-0003-1578-4592
Chatura Vaidya	0000-0002-1655-9496
Rémy Vandame	0000-0001-6931-1067
Carlos H. Vergara	0000-0002-5234-525X
Eric Vides-Borrell	0000-0003-4416-0797

Natapot Warrit	0000-0002-6338-1782
Catrin Westphal	0000-0002-2615-1339
Nicholas S. G. Williams	0000-0001-6291-9483
Caleb J. Wilson	0000-0002-5546-4801
Lauren C. Ponisio	0000-0002-3838-7357
Timothy C. Bonebrake	0000-0001-9999-2254

Corresponding: Toby P. N. Tsang, Lauren C. Ponisio, Timothy C. Bonebrake

Email: paknok.tsang@utoronto.ca, lponisio@uoregon.edu, tbone@hku.hk

Running title: Land use change reduces bee diversity

Abstract

Land use change threatens global biodiversity and compromises ecosystem functions, including pollination and food production. Reduced taxonomic α diversity is often reported under land use change, yet the impacts could be different at larger spatial scales (i.e., γ diversity), either due to reduced β diversity amplifying diversity loss or increased β diversity dampening diversity loss. Additionally, studies often focus on taxonomic diversity, while other important biodiversity components, including phylogenetic diversity, can exhibit differential responses. Here, we evaluated how agricultural and urban land use alter the taxonomic and phylogenetic α, β, γ diversity of an important pollinator taxon – bees. Using a multi-continental dataset of 3,117 bee assemblages from 157 studies, we found that taxonomic α-diversity was reduced by 16-18% in both agricultural and urban habitats relative to natural habitats. Phylogenetic α diversity decreased by 11-12% in agricultural and urban habitats. Compared with natural habitats, taxonomic and phylogenetic β diversity increased by 11% and 6% in urban habitats respectively but exhibited no systematic change in agricultural habitats. We detected a 22% decline in taxonomic γ diversity and a 17% decline in phylogenetic γ diversity in agricultural habitats, but γ diversity of urban habitats was not significantly different from natural habitats. These findings highlight the threat of agricultural expansions to large-scale bee diversity due to systematic γ diversity decline. In addition, while both urbanization and agriculture lead to consistent declines in α diversity, their impacts on β or γ diversity vary, highlighting the need to study the effects of land use change at multiple scales.

Keywords: Land uses, bees, pollinators, biodiversity decline, agriculture, urban

Introduction

Human activities have transformed global terrestrial environments for anthropogenic land uses, mainly agriculture and urban developments (Ellis, Klein Goldewijk, Siebert, Lightman, & Ramankutty, 2010). These processes reduce biodiversity by creating environments with unsuitable biotic and abiotic conditions and enhancing competitive exclusion (Mayfield et al., 2010), ultimately threatening ecosystem functions (van der Plas, 2019). A common approach in evaluating the ecological impacts of land use change is to compare the number of taxa within assemblages (taxonomic α-diversity) between natural habitats and anthropogenic habitats (Purvis & Hector, 2000). Previous studies have found that taxonomic α-diversity in different taxa can be reduced by 19%-40% in agricultural habitats and 4%-50% in urban habitats on average (Newbold et al., 2015).

However, taxonomic α diversity analyses could fail to capture the potential effects of land use change on homogenizing assemblages, thus underestimating γ diversity loss (i.e., diversity at larger spatial scales) (Socolar, Gilroy, Kunin, & Edwards, 2016). Taxonomic β diversity, relatively understudied compared with taxonomic α diversity, captures compositional variations between assemblages and can determine how α diversity loss upscales to γ diversity (Mori, Isbell, & Seidl, 2018; Socolar et al., 2016). Specifically, reduced and increased β diversity can result in higher and lower γ diversity loss relative to what would be expected based on α diversity losses alone (Socolar et al., 2016). While land use change is expected to homogenize assemblages and reduce β diversity, empirical studies have shown mixed results (Newbold et al., 2016).

Regardless of the spatial scale at which it is measured, a limitation of taxonomic diversity is its inability to effectively reflect ecological differences between species, such as morphology,

307 physiology, and phenology (Purvis & Hector, 2000; Tucker et al., 2017). Recent studies have
308 increasingly emphasized analyzing phylogenetic diversity alongside taxonomic diversity
309 (Cadotte & Tucker, 2018; Tucker et al., 2017). As evolution shapes species traits, phylogenetic
310 approaches can efficiently capture high-dimensional ecological differences, reducing the risks of
311 omitting important traits (Tucker et al., 2017; Tucker, Davies, Cadotte, & Pearse, 2018).
312 Additionally, phylogenetic diversity has exhibited similar or even better performance than
313 taxonomic diversity in explaining ecosystem functions or services across sites (Tucker et al.,
314 2019; van der Plas, 2019).
315 While not always the case, responses of phylogenetic diversity to land use change should
316 largely follow taxonomic diversity change (Tucker & Cadotte, 2013). However, land use could
317 also lead to more phylogenetic diversity loss than would be expected based on the taxonomic
318 diversity loss. This is because land use change can strengthen phylogenetic habitat filtering
319 (Grab et al., 2019; Nowakowski, Frishkoff, Thompson, Smith, & Todd, 2018), causing only a
320 subset of phylogenetically similar species to persist under anthropogenic land uses due to
321 conserved traits (Duarte, 2011). Interestingly, the filtering effects on α- and β-diversity can vary,
322 again demonstrating the importance of analyzing both α and β diversity to better understand net
323 impacts at larger spatial scales (i.e., γ diversity) (Nowakowski et al., 2018).
324 To understand how land use change affects taxonomic and phylogenetic diversity, we focused
325 on a well-studied and ecologically important taxon, bees. Pollination services by bees can be
326 greater in sites with high bee taxonomic and phylogenetic α diversity and landscapes with high
327 taxonomic β diversity between sites (Grab et al., 2019; Weekers et al., 2022; Winfree et al.,
328 2018), compared to lower-diversity sites and landscapes. Ongoing global land use change is
329 known to reduce bee diversity generally (Cariveau & Winfree, 2015; De Palma et al., 2016;

Winfree, Bartomeus, & Cariveau, 2011). However, the exact effects can vary with land use types, with some studies reporting increased bee diversity under land use change (Cariveau & Winfree, 2015; Prendergast, Dixon, & Bateman, 2022; Winfree et al., 2011). Furthermore, the impacts of anthropogenic land uses are often evaluated using taxonomic α diversity, even though other biodiversity metrics could exhibit different patterns (De Palma et al., 2017; Harrison, Gibbs, & Winfree, 2018). Importantly, some bee lineages are especially sensitive to land use change, which could lead to a more substantial decline in phylogenetic diversity relative to taxonomic diversity (Grab et al., 2019; Harrison et al., 2018).

We examined the ecological impacts of land use change on global bee diversity using bee assemblage data from agricultural, urban, and natural habitats across all continents except Antarctica, where bees are absent. Our objectives were to 1) compare taxonomic and phylogenetic α, β and γ diversity between natural, agricultural and urban habitats, 2) investigate whether land use change leads to stronger phylogenetic habitat filtering, and 3) identify the genera particularly affected by the agricultural and urban habitats. For objective 1, we expected that natural habitats would contain greater taxonomic and phylogenetic α, β, and γ diversity. For objective 2, we predicted declines in phylogenetic diversity in urban and agricultural habitats, even after controlling for taxonomic diversity, due to increased phylogenetic habitat filtering.

Materials and Methods

Data collection, cleaning, and filtering

Bee data were collected from various sources, including the PREDICTS database (Hudson et al., 2014), a previous meta-analysis on bee diversity in agricultural systems (Kennedy et al., 2013), literature searches, and expert recommendations (see Section S1 for details and the

353 limitations of our dataset). We corrected species synonyms using a bee species guide and world
354 checklist (Ascher & Pickering, 2022). Missing taxa were further reviewed by a taxonomist co-
355 author (John S. Ascher). For 1% of 2,257 species-level identifications, no matches were found;
356 these were treated as morphospecies instead of species. For morphospecies or genus-level data,
357 we checked the validity of the genus in the checklist and corrected them when necessary.

358 Datasets were divided into different studies (see Table S1 for details of each study) according
359 to their sampling strategies, which were broadly classified as: (1) "flower visitors", if the study
360 sampled flower-visiting bees within an area, (2) "targeted plants" if the study sampled flower-
361 visiting bees of targeted plant species, and (3) "all bees" for any other method, such as pan traps,
362 hand-netting, and vane traps. Thus, if a dataset provided bee data based on different sampling
363 strategies, such as pan traps and hand netting bees from targeted plant species, the data would be
364 separated into different studies. For each site within each study, we aggregated bee species
365 abundance data across sampling dates (hereafter referred to as assemblage). We excluded *Apis*
366 *mellifera* from all assemblages, as they were often from managed colonies.

367 We only included assemblages in our analyses if the following criteria had been met: 1) The
368 sampling strategy had a broad taxonomic focus rather than only focusing on certain groups of
369 bees (e.g., *Bombus* spp., solitary bees). 2) Spatial coordinates were recorded. 3) The number of
370 individuals observed was recorded. 4) At least ten individuals were identified to at least the
371 genus level to ensure reliable rarefaction results (see below). We did not use a threshold higher
372 than ten individuals because this might bias the analyses against impoverished assemblages. The
373 threshold is also consistent with or higher than that used in previous studies based on rarefaction
374 (Blowes et al., 2022; van Klink et al., 2024). 5) The assemblages had sampling completeness of
375 $\geq$ 50% to ensure the reliability of diversity estimates. Sampling completeness was calculated

using the R package iNEXT.3D (Chao et al., 2021). 6) The assemblage had at least 95% of observed individuals identified to at least the genus level to ensure reliable estimations of phylogenetic diversity. We did not set a minimum number of assemblages to include in a study for subsequent analyses.

Definition of land uses

We classified the land use of each assemblage based on the predominant environment within the sampling area. Natural habitats were defined as areas primarily covered by vegetation resulting from natural succession or restoration (i.e., active attempts to bring the site to a more natural state). Agricultural habitats were defined as sites managed for growing resources, including food and animal products. Urban habitats included green spaces covered by planted vegetation (not natural succession) managed for amenity or recreation (e.g., lawns, gardens). See Section S2 for details of the land use classification.

Phylogeny

We used a global genus-level phylogeny to quantify the phylogenetic diversity of each assemblage (Hedtke, Patiny, & Danforth, 2013). Tip names on the phylogenetic tree were corrected using Ascher & Pickering (2022) and further reviewed by a taxonomist co-author (John S. Ascher). We converted the tree to ultrametric using a non-negative least square (Turley, Biddinger, Joshi, & López-Uribe, 2022). The strong cophenetic correlation (Pearson's $r = 0.93$) indicated that the tree's structure was largely conserved. Our data contained taxa from 355

genera, of which 32 were missing from the tree and were added to the closest sister genus available (Table S2). We randomly selected one species in the tree from each genus, then attached all species from each study as polytomies at the mid-point of its corresponding genus branch, as this approach has been demonstrated to capture phylogenetic diversity well when a species-level phylogeny is unavailable (Qian & Jin, 2021). While the use of a genus-level phylogeny might not fully capture phylogenetic patterns of assemblages, previous bee studies have used the same phylogeny and detected phylogenetic diversity changes and phylogenetic habitat filtering (De Palma et al., 2017; Harrison et al., 2018; Hendrix, Forbes, & MacDougall, 2018). We quantified the phylogenetic α-diversity of each assemblage by generating ten phylogenetic trees and found that the values of phylogenetic α-diversity were highly correlated (Pearson's $r > 0.99$). Thus, we only used the first phylogenetic tree for subsequent analyses.

α and γ diversity estimates

In our analyses, α and γ diversity always represent within- and across-sample diversity, respectively, within the same land use type. Thus, comparing α and γ diversity across habitats allows for assessing whether diversity loss is exacerbated at larger spatial scales by land use change (Chase et al., 2019; Socolar et al., 2016). To estimate taxonomic and phylogenetic α and γ diversity, we estimated both metrics with the Hill number equal to 1, as it considers the relative abundance of species within assemblages and is less prone to undersampling than lower Hill numbers (Roswell, Dushoff, & Winfree, 2021).

We estimated α diversity for all assemblages, while γ diversity was estimated only for studies with at least five assemblages from at least one land use. Additionally, γ diversity was only

estimated for studies that indicated sampling effort for each assemblage. We pooled species abundance data across assemblages of the same land uses within each study before conducting the γ diversity rarefaction analyses. To control for differences in sampling completeness between assemblages across studies, we extrapolated all α and γ diversities to their asymptotes (i.e., when sampling completeness equals 1). Each assemblage's taxonomic and phylogenetic diversity was estimated using iNEXT.3D (Chao et al., 2021).

β diversity estimates

For each land use in each study, we used multiplicative partitioning (β = γ / mean α) to obtain their β diversity (Jost, 2007). This method is especially suitable to understand the spatial scaling of diversity loss, as it represents the scaling factor relating α and γ diversity (Baselga, 2013; Socolar et al., 2016). The metric also reflects the contribution of β diversity to γ diversity (Contribution of β = (1-α/γ) * 100% = (1-1/β) * 100%).

The corresponding γ and α diversities were taken from rarefaction analyses. As more abundant assemblages should more heavily influence γ diversity estimates, mean α diversity was weighted according to the total abundance of each assemblage (Crist, Veech, Gering, & Summerville, 2003). Consistent with the γ diversity analyses, our analyses included only studies with at least five assemblages in at least one land use.

Climatic and methodological variables

We collected a variety of climatic and methodological variables to control for their effects on bee diversity and to better quantify any effect of land use change (Table 1). For climatic variables, we collected mean annual temperature and annual precipitation, as well as the seasonality of each assemblage from the public database CHELSA v1.2 (Karger et al., 2017). Annual precipitation was square root transformed to reduce the effects of outliers. All data were at 30 arc-second (~1 km) resolution.

For the β and γ diversity analyses, we additionally included methodological variables in the models that might affect both diversity metrics, namely 1) study extent, 2) standard deviations in sampling efforts across assemblages, 3) the number of assemblages, 4) standard deviations in sampling completeness across assemblages, and 5) log-transformed mean sampling completeness across assemblages (Table 1; see Section S3 for details and rationales to include these variables).

Preliminary analyses found high collinearity (Pearson's $R > 0.7$) among climatic variables and among the mean and standard deviations in sampling completeness across assemblages. Thus, we conducted robust PCA separately for all climatic variables and the two methodological variables. We included climatic PC1 and PC2 for subsequent analyses, which captured >81% of the climatic variations within our dataset (Table S3). Increasing PC1 scores primarily reflect colder sites with high seasonality in temperature but low seasonality in precipitation, while increasing PC2 scores reflect warmer and wetter sites with lower temperature seasonality and lower precipitation seasonality.

For the two methodological variables, we extracted the PCA1 score to represent them, as it captured 93.1% variations across assemblages. A higher sampling effort PCA1 score indicates lower mean sampling completeness with higher variation across assemblages (Table S3). Robust PCA was conducted using R-package rrcov (Todorov & Filzmoser, 2009).

General modeling strategy

We used mixed models to identify the effects of land use while controlling for methodological and climatic covariates, as well as other unaccounted-for study differences using random effects. Study-level variation can lead to varying estimates of land use effects. For example, the effects may be stronger in warmer landscapes with fewer natural habitats in the surrounding environments (Ganuza et al., 2022; Kennedy et al., 2013). Methodological factors such as sampling area (Azaele et al., 2015) and methods (Lee & Guénard, 2019) can also alter estimates of land use effects. Here, we focused on the general trend across studies rather than examining how land use change interacts with other environmental or methodological variables. Therefore, apart from a few climatic and methodological covariates, we used study identity as a random effect to control for such study-level variations.

This statistical framework has been used in previous quantitative syntheses assessing land use effects on diversity or abundance by comparing data from studies conducted in different regions based on different methods. It also allows for studies with data on one land use only (De Palma et al., 2016; Millard et al., 2021; Newbold et al., 2015). A summary of how mixed models work is provided in Section S4. Additionally, we provide a simple simulation (Section S5) to justify our approach of including study-level land use effects, despite some studies only providing bee data for a single land use. We emphasize here that mixed models do not estimate study-level land use effects (or in general any random slope) through modelling its relationship in each study individually. Rather, the calculations involve calculating the fixed effects and the variance-covariance matrix, which uses data from all studies (Raudenbush & Bryk, 2002). Below we

484 provided a brief description of the models. For mathematical expressions please refer to Table
485 S4.

486

487 **Objective 1a: α diversity**

488 To examine how taxonomic and phylogenetic α-diversity varied across land uses, we built linear
489 mixed models with Gaussian distributions using log-transformed α-diversity. We specified log-
490 transformed α-diversity as the response to improve normality. For predictors, we included
491 sampling method (three levels: All bees/ Flower visitors/ Targeted plants) and land use (three
492 levels: Natural/Agricultural/Urban) of each site. Climatic PC1 and PC2 scores were also added
493 as predictors to control for the effects of regional climate on bee α-diversity. Our analyses
494 included nominal variables, so we set the intercepts as natural habitats sampled with methods
495 targeting all bees. We further used sampling completeness as a weight in the regression, such
496 that poorly sampled sites (and, therefore, those with higher uncertainty in diversity estimates)
497 had lower weights in the analyses (Carvalheiro et al., 2013).
498 For random effects, study identity was added as a random intercept, with land use effects
499 added as random slopes, so the estimates of land use effects could vary across studies. The
500 random slopes were never correlated with random intercepts to facilitate model convergence
501 (Matuschek, Kliegl, Vasishth, Baayen, & Bates, 2017).
502 Additionally, to control for spatial autocorrelation, we added an assemblage-level random
503 intercept based on the spatial coordinates of each site. The Matérn correlation model was used to
504 construct the correlation matrix and estimate the spatial random effect. All spatial random effects
505 were study-specific, indicating that spatial autocorrelations were modelled within but not across

studies, as they had very different methodologies. Indeed, we detected substantial spatial autocorrelation between sites within the same study but not between sites across different studies (Section S6). We compared models with and without spatial random effects and found that the model including spatial autocorrelation had a significantly improved model fit, as indicated by a reduction of >490 in the conditional AIC.

We built the linear mixed model using R package spaMM, which allows including spatial random effects (Rousset & Ferdy, 2014). We then conducted an omnibus test for differences across land uses based on F tests using R package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017). If the effect of land use was significant, we further conducted pairwise comparisons across the three land uses, with the p-value adjusted by False Discovery Rate corrections.

Objective 1b & 1c: β and γ diversity

The β and γ diversity analyses were conducted at the study level (i.e., each land use from a study contributes one data point). In the models, log-transformed multiplicative β diversity (to improve normality) and untransformed γ diversity were the responses. Land uses, sampling methods, climatic PC1 and PC2 scores, number of sampling sites, standard deviations of sampling efforts, PC1 scores based on sampling completeness, and study extent were added as predictors. Climatic PC1 and PC2 scores were averaged across assemblages of the same land use in each study. Study extent and number of sampling sites were log-transformed, as their effects tend to be non-linear (Beck, Holloway, & Schwanghart, 2013; Marcon, Zhang, & Hérault, 2014; Marion, Fordyce, & Fitzpatrick, 2017; Soininen, McDonald, & Hillebrand, 2007). We added sampling completeness of γ diversity as weights in the models to account for some pooled

assemblages being more unreliable in diversity estimations due to low completeness. Study identity was added as a random intercept.

We started with a model that included the interaction between land use and study extent due to potential differences in distance-decay relationship across land uses. However, the interaction term was non-significant. Therefore, we included no interaction term in the final model. Again, an omnibus test was conducted for the effect of land use, and if significant, pairwise comparisons were conducted across land use. Linear mixed models were built with R package lme4 (Bates, Mächler, Bolker, & Walker, 2015) and p-values were obtained from lmerTest (Kuznetsova et al., 2017). Pairwise comparisons were conducted in emmeans (Lenth, 2024), with the p-values adjusted by False Discovery Rate corrections.

Objective 2: Phylogenetic habitat filtering in natural, agricultural, and urban habitats

If agricultural and urban land uses increase phylogenetic habitat filtering, their negative effect on phylogenetic diversity should still be significant after adding taxonomic diversity as a covariate. Previous studies have used this approach to assess whether environments have lower phylogenetic diversity than expected based on taxonomic diversity (Barreto, Graham, & Rangel, 2019; Sol, Bartomeus, González-Lagos, & Pavoine, 2017). We did not use null model analyses because some of the studies in our meta-data set included studies with a single land use, which did not capture species that fail to persist in different land uses (Lessard, Belmaker, Myers, Chase, & Rahbek, 2012).

We added taxonomic diversity as an additional predictor to the phylogenetic diversity models described in Objective 1a-c. For α and γ diversity, the relationship between phylogenetic and

551 taxonomic diversity is a decelerating relationship, but for β diversity, it is largely linear (Figure
552 S1). Thus, we added log-transformed taxonomic diversity into each model. Note that for α and β
553 diversity models, the responses were also log-transformed. This effectively models a power law
554 relationship, which can range from linear to non-linear. We only conducted pairwise
555 comparisons between land uses if the omnibus test revealed a significant effect.

556

557 **Objective 3: Genus abundance across land uses**

558 To facilitate interpretations of diversity patterns, we further identified genera that have reduced
559 abundance in agricultural and urban habitats relative to natural habitats. We conducted the
560 analyses at the genus- rather than species-level, as the latter would lead to strong temperate
561 region biases, given that more tropical studies relied on morphospecies or genus-level
562 identifications. For this objective, we selected 51 genera that were frequently detected across
563 studies, and thus, the effects of land use can be reliably quantified (see Section S7 for details).
564 Our analyses included genera with different geographical distributions, such as the
565 cosmopolitan genus *Megachile* and the Neotropical genus *Partamona* (Michener, 2007). Thus,
566 different trends across genera could be driven by their varying sensitivity to land use changes
567 and regional differences in the extent of environmental changes and management intensity.
568 Quantifying the contributions of each mechanism would require additional life-history and
569 environmental data. Nevertheless, our results can identify the genera more systematically
570 affected by different land use drivers regardless of the underlying mechanisms
571 We built a model for each genus with their abundance in each assemblage as the response and
572 land use, sampling method, and climatic PC1 and PC2 scores as predictors. Random effects were

identical with the α-diversity models (Objective 1a), with study identity as a random intercept and land use as a random slope to control for between-study differences. Again, a spatial term based on Matérn correlation nested within studies was added to control for spatial autocorrelation. We used negative binomial mixed models to analyze abundance changes across land uses (Warton, 2005). An offset capturing log-transformed sampling effort of each assemblage was also added.

For one genus (*Dasypoda*), abundance data based on sampling flower visitors of all or targeted plant species were not available. Thus, we dropped sampling method from the model. For 31 genera, the effects of land use were only compared between agricultural and natural habitats, as there was a lack of urban studies containing abundance data of these genera. When three land uses were analyzed, we conducted pairwise comparisons if a significant result was obtained from the omnibus test. As we analyzed multiple genera, results might be affected by multiple comparisons. We further adjusted pairwise comparison p-values using False Discovery Rate corrections.

We extracted the predicted abundance for each model for each land use while holding climatic PC1 and PC2 at their mean values, as well as holding the sampling strategy at "All bees". We then calculated the ratio of predicted abundance between agricultural (or urban) and natural habitats (Agricultural or Urban/Natural). We further log-transformed these ratios to convert them into arithmetic scales (Agresti, 2007). We then used the package phytools (Revell, 2012) to assess if there were phylogenetic signals in the log-transformed ratio based on Pagel's λ.

Briefly, Pagel's λ assesses whether any biological characteristics follow Brownian motion, a standard evolutionary model that assumes the differences in the characteristics accumulate through a random walk over evolutionary time scales (Pagel, 1999). λ equals one when the

596 characteristics are consistent with Brownian motion expectations. Alternatively, λ can be as low
597 as zero when the characteristics deviate from the evolutionary model. While other metrics to
598 measure evolutionary signals exist, Pagel's λ is known to be the most robust metric according to
599 simulation studies (Münkemüller et al., 2012).

600

601 **Results**

602 Our analyses included bee assemblage data from 3,117 assemblages and 437,091 individuals of
603 4,002 taxonomic units from 157 studies. The majority of the data (2,574 assemblages from 120
604 studies) were in temperate regions (i.e., absolute latitude > 23.4°), mainly North America and
605 Europe, while 543 assemblages from 37 studies were in the tropics (Figure 1a). All studies
606 identified specimens to species-level or morphospecies-level whenever possible, except two
607 studies, which identified specimens to genus-level. Sampling methods of individual studies range
608 from point-based sampling (e.g., single vane trap) to aggregating samples within an area as large
609 as 10 ha. In general, most studies were conducted along transects <100m or within plots < 1ha
610 (Table S1). Forty-two studies (27%) provided data on bee assemblages in more than one land
611 use. All diversity models had high conditional R^2 (0.63 – 0.91, Table S5-S8).

612

613 **Objective 1a: α diversity**

614 Taxonomic α-diversity declined by an average of 15.8% in agricultural (P = 0.006; 95% CI:
615 1.9%, 27.6%) and 19.6% in urban habitats (P = 0.006; 95% CI: 3.1%, 33.2%) compared with
616 natural habitats after controlling for climatic and sampling differences (linear mixed models;
617 Figure 1b, Table S5). Using the genus-level phylogeny of bees (Hedtke *et al.*, 2013), we found
618 that phylogenetic α-diversity declined by an average of 11.0% in agricultural habitats (P = 0.005;

95% CI: 2.7%, 18.7%) and 11.6% (P = 0.017; 95% CI: 1.0%, 21.1%) in urban habitats relative to natural habitats (Figure 1c, Table S5). Pairwise comparisons between agricultural and urban habitats were non-significant for both diversity metrics.

Objective 1b: β diversity

The average taxonomic β-diversity was 1.75 (95% CI = 1.66, 1.83), making up 42.7% of the taxonomic γ diversity. Using linear mixed models, we observed a 6.4% decline in taxonomic β-diversity in agricultural habitats relative to natural habitats, although the results were marginally non-significant (P = 0.06; 95% CI = 1.1%, 11.4%; Figure 1c, Table S6). Pairwise comparisons also revealed marginally non-significant differences between urban and natural habitats, with 8.8% higher taxonomic β-diversity in urban habitats (P = 0.06; 95% CI = -0.4%, 18.7%; Figure 1c, Table S6). However, we detected 16.2% higher taxonomic β-diversity in urban compared to agricultural habitats (P = 0.004; 95% CI = 6.5%, 26.8%).

Across studies, phylogenetic β diversity averaged at 1.20 (95% CI = 1.17, 1.22), equivalent to 16.7% contribution of phylogenetic γ diversity. Phylogenetic β-diversity was highest in urban habitats—6.4% higher than natural habitats (P = 0.004; 95% CI = 2.2%, 10.7%; Figure 1c, Table S5) and 8.8% higher than agricultural habitats (P < 0.001; 95% CI: 4.5%, 13.3%). However, we found minimal evidence of differences between agricultural and natural habitats.

Objective 1c: γ diversity

Taxonomic γ diversity was, on average, 25.2% lower in agricultural than in natural habitats (P = 0.008; 95% CI: 10.5%, 39.9%; Figure 1d, Table S7). A 15.6% decline was also observed in

641 urban habitats relative to natural habitats, but the difference was not statistically significant.
642 Differences between urban and agricultural habitats were also non-significant.

643 Similarly, we found that phylogenetic γ diversity declined by 17.8% (P = 0.006; 95% CI:
644 8.7%, 26.7%) in agricultural habitats relative to natural habitats (Figure 1d, Table S7). The
645 pairwise comparison between natural and urban habitats, as well as between agricultural and
646 urban habitats, was non-significant.

647

648 **Objective 2: Phylogenetic habitat filtering in natural, agricultural, and urban habitats**

649 After controlling for their taxonomic counterparts using linear mixed models, phylogenetic α
650 and γ diversity metrics exhibited minimal differences across land uses (Figure 2a, 2c, Table S8).
651 However, we found that phylogenetic β diversity was highest in urban habitats, while
652 agricultural and natural habitats exhibited similar values (Figure 2b, Table S8). Specifically,
653 phylogenetic β diversity in urban habitats was 3.9% higher than in natural habitats (P = 0.03;
654 95% CI: 0.44%, 7.5%) and 4.5% higher than in agricultural habitats (P = 0.03; 95% CI: 0.84%,
655 7.97%).

656

657 **Objective 3: Genus abundance across land uses**

658 Compared with their average abundance in natural habitats, 73% and 61% of common genera
659 exhibited reduced average abundance in agricultural and urban habitats, respectively, echoing the
660 results of diversity analyses (Table S9, Figure S2). Eight genera showed significantly lower
661 abundance in agricultural habitats, four belonging to the family Megachilidae (*Osmia*, *Hoplitis*,
662 *Megachile*, *Anthidium*). Only *Protandrena* (mining bees, ground nesters) had increased

abundance in agricultural habitats relative to natural habitats. For urban habitats, only *Osmia* (mason bees, primarily cavity nesters) exhibited a significant response to land use, with reduced abundance in urban relative to natural habitats. We detected some phylogenetic signals in the responses to agricultural (Pagel's $\lambda = 0.38$, $P = 0.08$) and minimal signals in the responses to urban habitats (Pagel's $\lambda < 0.001$, $P = 1$) (Figure 3). After controlling phylogeny, responses of bee genera to urban and agricultural habitats were weakly correlated (Pearson's $r = 0.09$) (Figure S2).

Discussion

Biodiversity loss observed at local scales (α diversity) can be dampened or amplified at larger spatial scales (γ diversity), depending on changes in the scaling factor (β diversity) (Socolar et al., 2016). We synthesized the trends in how two major land use drivers, namely agriculturalization and urbanization, affect bee taxonomic and phylogenetic α, β, and γ diversity. We found that the trends in α, β, and γ diversity are largely consistent between taxonomic and phylogenetic metrics when responding to the same land use driver. The α diversity declines under the different anthropogenic land uses are consistent with our expectations and previous studies based on other taxa (Millard et al., 2021; Newbold et al., 2015). These results provide additional evidence of the threats of agricultural and urban expansion (Dicks et al., 2021) by demonstrating their negative impacts on phylogenetic α diversity in addition to taxonomic α diversity. The responses of β diversity to land uses are more variable, as urban habitats exhibited higher β diversity than natural habitats, which is in contrast with the general expectation that urbanization drives biotic homogenization (Socolar et al., 2016). At the same time, we found some support for agricultural habitats having reduced taxonomic β but not phylogenetic β

686 diversity. These ultimately lead to reduced taxonomic and phylogenetic γ diversity in agricultural
687 habitats, but not urban habitats, where we failed to detect significant γ diversity loss compared to
688 natural habitats. The β and γ diversity results highlight the threat of agricultural expansions to
689 large-scale bee diversity due to systematic γ diversity decline. Broadly, our results provide
690 empirical evidence showing that, although α diversity responses may be similar across land use
691 drivers, β diversity responses vary, resulting in different γ diversity consequences.

692 The differing responses of β diversity to urban and agricultural land use may be a result of
693 differing environmental heterogeneity within these land use categories. In our dataset, most
694 studies compared assemblages within a single city or landscape, with the mean and 95%
695 percentile of the study extent being 38 km and 478 km, respectively. At these scales, different
696 management practices within cities, such as varying ornamental plants or mowing frequencies
697 due to owner preferences (Aronson et al., 2017; Lerman, Contosta, Milam, & Bang, 2018;
698 Prendergast et al., 2022), can increase environmental heterogeneity and, therefore, result in
699 higher β diversity than natural habitats (Alberti, 2016). Conversely, β diversity exhibited varying
700 trends or marginal declines in agricultural habitats across studies. While agricultural activities
701 reduce environmental heterogeneity, particularly in monocultural croplands (Leong, Ponisio,
702 Kremen, Thorp, & Roderick, 2016), the effects can be more variable in subsistence agriculture
703 systems (Landaverde-González et al., 2017), potentially explaining the marginal results. This
704 ultimately led to detectable declines of γ diversity in agricultural habitats but not urban habitats.
705 Thus, our results indicate that while land use impacts are usually reported to affect α diversity
706 negatively across terrestrial taxa, these conclusions do not necessarily extend to γ diversity,
707 particularly with urbanization (Fenoglio, Rossetti, & Videla, 2020; Liang, He, Theodorou, &
708 Yang, 2023; Newbold et al., 2015; Sol et al., 2017).

We found no evidence that land use change systematically strengthens phylogenetic habitat filtering, and in fact, we found relaxed filtering in urban habitats for β diversity of bees. Previous bee studies have found variable phylogenetic habitat filtering effects across different types of agricultural and urban environments (Bartomeus, Cariveau, Harrison, & Winfree, 2018; Odanaka & Rehan, 2019; Ramírez, Hernández, Link, & López-Uribe, 2015; Villalta, Bouget, Lopez-Vaamonde, & Baude, 2022), potentially leading to no generalizable patterns when coarse land use classification is used. Studies of phylogenetic habitat filtering for β diversity are rare. The weakly relaxed phylogenetic habitat filtering in urban habitats detected can again be explained by increased environmental heterogeneity in cities compared with natural and agricultural habitats (Alberti, 2016; Aronson et al., 2017). For example, given the strong co-evolutionary history between bees and plants (Brown & Cunningham, 2022), different planting preferences across urban green spaces can attract varying bee lineages, leading to higher phylogenetic β diversity than expected based on taxonomic β diversity. Nevertheless, the weakly relaxed phylogenetic filtering for phylogenetic β diversity did not propagate to γ diversity of bees in urban habitats, as phylogenetic β diversity only contributed to 16.7% of γ diversity across studies.

Apart from their varying impacts on bee diversity, another difference between the two land uses is that the genus-level abundance changes exhibited an intermediate phylogenetic signal in agricultural habitats but minimal signal in urban habitats. The small number of genera in our analyses (≤51) limited our statistical power (Münkemüller et al., 2012), while genus-level analyses can underestimate phylogenetic signals (Rabosky, 2015). Species-level analyses, including rare species, are needed to determine the true extent of phylogeny in governing bees' responses to the two land uses. Nevertheless, the stronger phylogenetic signals in agricultural

habitats suggest a higher importance of evolutionarily conserved traits, such as nesting biology and lecty (Odanaka & Rehan, 2019), in determining species abundance in these environments (Grab et al., 2019). Alternatively, species responses to urban habitats may be more driven by stochasticity (Sattler et al., 2010) or evolutionarily labile traits, such as thermal tolerances (Hamblin, Youngsteadt, López-Uribe, & Frank, 2017).

As phylogenetic and taxonomic diversity respond similarly to agricultural and urban land uses, conservation measures that increase taxonomic diversity in agricultural and urban habitats are expected to increase their phylogenetic counterparts. These findings can facilitate decision-making in management targeting multiple diversity metrics, as the responses of phylogenetic diversity to different environmental drivers are less understood than those of taxonomic diversity (Cadotte & Tucker, 2018). For α diversity, measures such as organic farming, crop diversification, establishing flower strips, and planting gardens have been found to increase pollinator taxonomic α-diversity in meta-analyses or quantitative syntheses (Kennedy et al., 2013; Lichtenberg et al., 2017; Majewska & Altizer, 2020; Scheper et al., 2013). Studies have also evaluated the effectiveness of conservation measures in enhancing taxonomic β diversity (Ponisio, M'Gonigle, & Kremen, 2016), although they are relatively rare compared with studies focusing on taxonomic α diversity. The same environmental drivers could increase taxonomic α diversity but reduce taxonomic β diversity in bees (Steinert, Sydenham, Eldegard, & Moe, 2020), meaning that associated conservation measures can simultaneously mitigate and exacerbate the impacts of land use change, leading to unclear net effects on γ diversity. Thus, we emphasize the importance of conducting additional taxonomic β and γ diversity assessments on the effectiveness of conservation measures to better understand their contributions to mitigating land use impacts.

Many large-scale conservation assessments focusing on the impacts of land uses are based on projecting α diversity models to different land use scenarios (Chaudhary, Verones, de Baan, & Hellweg, 2015; De Palma et al., 2017; Newbold et al., 2015). While α diversity patterns are helpful for conservation planning, they might not apply to biodiversity at larger spatial scales (e.g., national, regional, or landscape-level biodiversity), which might have exacerbated/weakened diversity loss depending on β diversity changes (Socolar et al., 2016). Our findings demonstrate that qualitative conclusions about land use impacts can differ between α and γ diversity analyses. Based on our results, while taxonomic and phylogenetic α diversity of bees might exhibit similar changes in agriculturalization and urbanization hotspots, the consequences for γ diversity can be very different, with more substantial impacts at larger scales expected in agriculturalization hotspots such as West Africa and Southeast Asia (Williams et al., 2021). Given the need to conserve biodiversity and its associated ecosystem functions at multiple scales (Socolar et al., 2016; Winfree et al., 2018), our study confirms the threat of agricultural expansions to global bee diversity. It also highlights the need to understand processes determining β and γ diversity changes and integrate these diversity metrics into conservation assessments.

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Conflict of Interest Statement: We declare there is no conflict of interest.

Data availability: R-scripts and 97% (152 of 157 analyzed studies) diversity and genus abundance data have been uploaded to Zenodo (DOI: 10.5281/zenodo.14201156) and GitHub (https://github.com/tpaknok/BeeLandUse). For the remaining 3% of studies with restricted access, please contact the co-authors listed in Table S1 directly.

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Table 1. Predictors for the models related to each objective. Objectives 1a, 1b, and 1c are to compare α, β, γ, diversity across three land uses, respectively. Objectives 2a, 2b, and 2c are to assess whether agricultural and urban habitats exhibited stronger phylogenetic habitat filtering in α, β, γ diversity, respectively. Objective 3 is to identify genera with altered abundance in agricultural and urban habitats relative to natural habitats. The rationales including different variables and their transformations have been described in the main text.

Variable name	Description	Objectives
Land use	A factor with three levels: Natural / Agricultural / Urban	1-3
Sampling method	A factor with three levels: All bees / Floral visitor only / Floral visitor of targeted plants	1-3
Climate PCA1	PCA1 score based on mean annual temperature, annual precipitation, as well as temperature and precipitation seasonality of each assemblage.	1-3
Climate PCA2	PCA2 score based on the aforementioned climatic variables.	1-3
log(Number of assemblages)	Number of assemblages of each land use within a study.	1b-1c, 2b-2c
Sampling effort S.D.	The standard deviation of sampling efforts between assemblages of the same land use within a study.	1b-1c, 2b-2c
Sampling completeness PCA1	PCA1 score based on the mean and standard deviation of sampling completeness between assemblages of the same land use within a study.	1b-1c, 2b-2c
log(Sampling extent)	Maximum distance between assemblages of the same land use within a study.	1b-1c, 2b-2c
log(Taxonomic diversity)	The taxonomic counterpart of phylogenetic α, β, and γ diversity.	2
Study identity	Added as random effects to account for other differences between studies.	1-3
Spatial autocorrelation term	Controlling for spatial autocorrelation within each study based on the latitude and longitude of each assemblage.	1a, 2a, 3a

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Figure

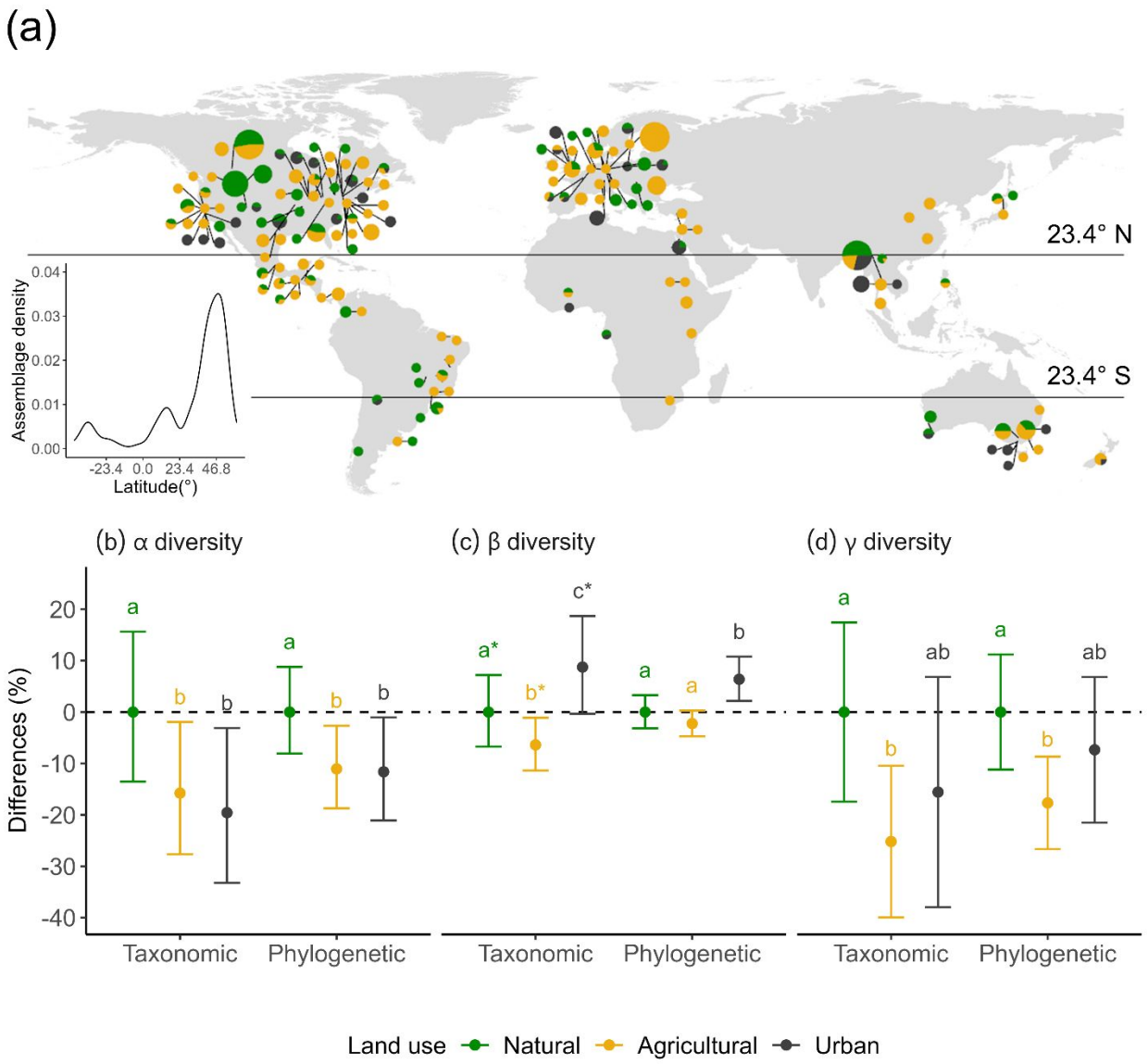


Figure 1. (a) Map showing locations of 157 studies included, and the proportion of natural, agricultural, and urban habitats sampled within the study. Pie size is proportional to the number of sampled sites in each study, ranging from 1 to 368. The density plot indicates the distribution of the studied assemblages (n = 3,117) along the latitudinal gradient. (b-d) Diversity changes relative to values of natural habitats, with each panel showing responses of one diversity metric:

(b) α, (c) β, and (d) γ diversity. Point estimates represent model predictions of each land use based on fixed effects only, while error bars are 95% confidence intervals. The estimations of α diversity were obtained by holding other covariates at the mean or mode values. For β and γ diversity, the estimation reflects a standardized sampling study with all assemblages having 100% sampling completeness, and other covariates at the mean or mode values. Small letters above error bars indicate results from pairwise comparisons, with different letters representing different groups. *indicates that the pairwise comparisons included marginally non-significant results ($p = 0.06$).

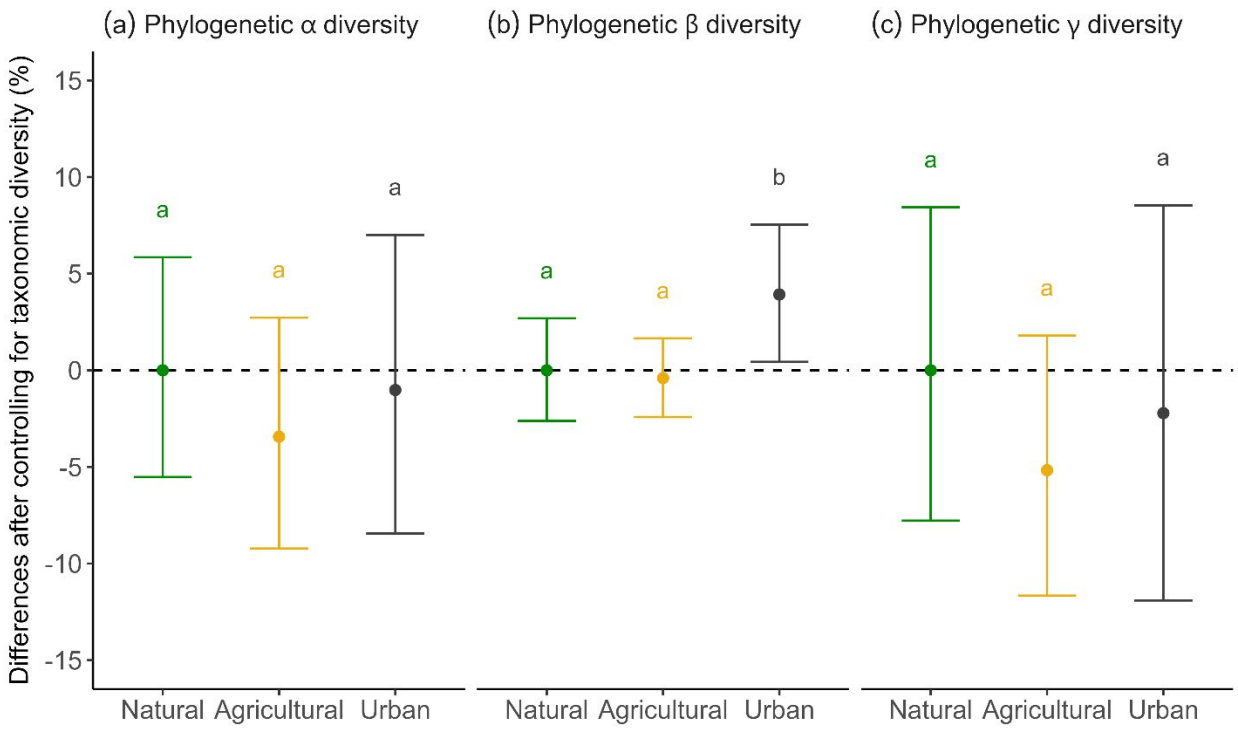
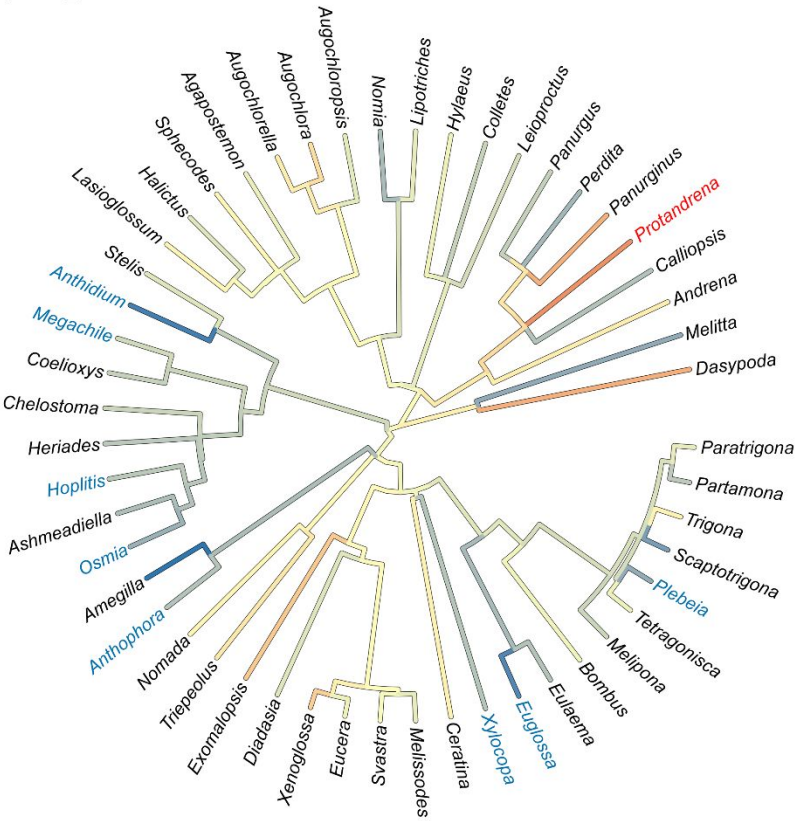


Figure 2. Percent differences in phylogenetic (a) α, (b) β, and (c) γ diversity metrics after controlling for their taxonomic counterparts, using natural habitats as the baseline. Error bars represent 95% confidence intervals, while point estimates present model predictions based on fixed effects only. The estimated α diversity was based on holding all other covariates at the mean or mode values. The estimated β and γ diversity were based on assuming studies with standardized sampling and all assemblages with 100% sampling completeness, while other covariates were at the mean or mode values. Small letters above error groups indicate different grouping based on pairwise comparisons.

(a) Agricultural



(b) Urban

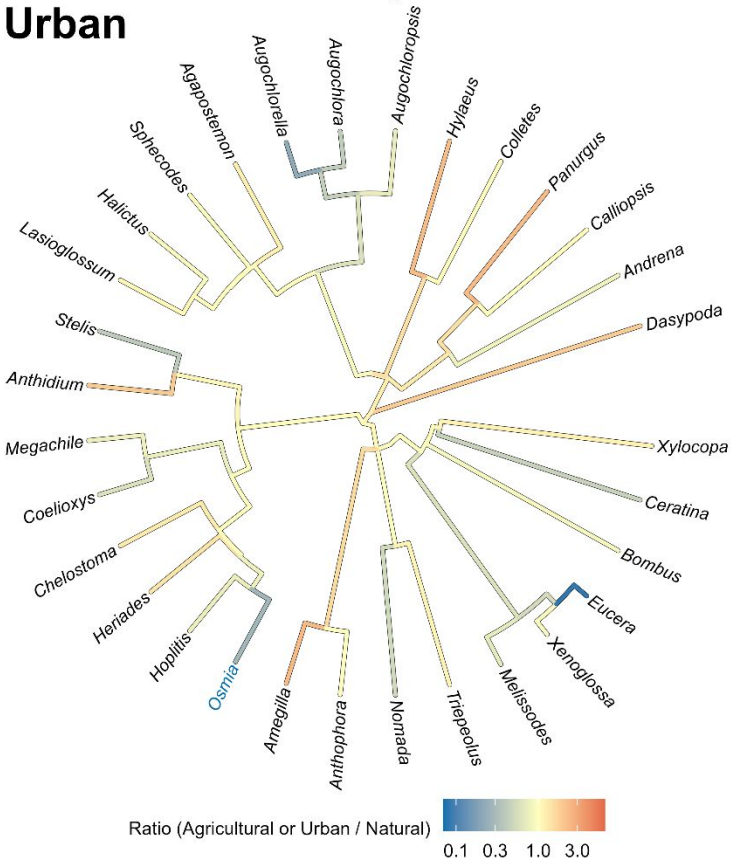


Figure 3. Phylogenetic relationships of all genera examined and their responses to agricultural (a) and urban land uses (b) in terms of abundance. When the ratio equals 1, genus abundance in agricultural or urban habitats is the same as in natural habitats. Genera in red and blue are significantly more and less abundant in anthropogenic land uses, respectively. See Fig. S2 for bar plots representing how individual genera respond to agricultural and urban land uses differently.