Extensive climate-induced range shifts in butterflies across the globe

Shawan Chowdhury[1*], Upama Aich[1,2], Laura H Antão[3,4], Stefan Pinkert[5,6,7], Perpetra Akite[8], Gilberto SS Almeida[9], Tatsuya Amano[10,11], Andras Ambrus[12], Jade AT Badon[13], Seung-Yun Baek[14], Maksims Balalaikins[15], Michal Barták[16,17], Vijay Barve[18], Michał Bełcik[19], Timothy Bonebrake[20], Simona Bonelli[21], Diana E Bowler[22], Michael F Braby[23,24], Roger Caritg[25], Sei-Woong Choi[26], Wen-Chen Chu[27], Eloisa Clain[28], Steve Collins[29], Johnattan Hernández Cumplido[30], Leonardo Dapporto[31], Gideon G Deme[32,33,34], Matthias Dolek[35], Aleksandra Dolezal[36], Fahmi Idris Firdaus[37], Markus Franzén[38], André VL Freitas[39,40], Richard A Fuller[10,11], Luisa Gensch[41,42,43], Eliza Grames[44], Elia Guariento[45], Bryan Haywood[46], Shiran Hershcovich[47], Kerstin Jantke[48], Eddie John[49], Henrik Kalivoda[50], Azadeh Karimi[51], Ryosuke Katayose[52], Akito Y Kawahara[53], Sujan Khanal[54], Krushnamegh Kunte[55], Lionel L'Hoste[56], Magdalena Lenda[19], Jorge L. León-Cortés[57], Da-Li Lin[58], Yuet Fung Ling[20], Maria Lucia Lorini[9], Dirk Maes[59,60], Dino Martins[61,62,63], Thomas Merckx[64], Xavier Mestdagh[56], Yeray Monasterio[65], Akihiro Nakamura[66], Rachel RY Oh[67,68,69], Lars B Pettersson[70], Jeffrey S Pippen[71], Clara Pladevall[25], Ingrid L Pollet[72], Patrice Pottier[24,73,74], Muhammad A Rafi[75], Danielle L Ramos[76], Tharindu Ranasinghe[77,78], Fanie Rautenbach[79], Martin Reith[80], Abubakar S Ringim[81], Federico Riva[82], David B Roy[22,83], Nils Ryrholm[84], Marjo Saastamoinen[17], Josef Settele[13, 67,68], William Sidemo-Holm[85], Piotr Skorka[19], Nigel E Stork[86], Sanej P Suwal[87], Giedrius Švitra[88], Ann B Swengel[12], Scott R Swengel[12], Nicolas Titeux[56], Robert Tropek[16,89], Olga Tzortzakaki[90], Chris van Swaay[91], Rudi Verovnik[92], Jerome L Wiedmann[93], Martin Wiemers[94], Masaya Yago[95], Hossein Yazdandad[96], Oz B Yehuda[97], Konstantina Zografou[90], Aletta Bonn[67,68,98], Guy Pe'er[67,68†], Jonathan Lenoir[99†]

* corresponding author (shawan.chowdhury@monash.edu)

[†]Senior authors

[1]School of Biological Sciences, Monash University, Melbourne, VIC, Australia
[2]Centre for Evolutionary Biology, School of Biological Sciences, The University of Western Australia, Perth, 6009, Australia
[3]Research Center for Ecological Change, Organismal and Evolutionary Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland FI-00014
[4]Department of Biology, University of Turku, Turku, Finland FI-20014
[5]Conservation Ecology, Philipps-Universität Marburg, Karl-von-Frisch-Straße 8, 35043 Marburg, Germany
[6]Ecology and Evolution, Yale University, 310 Prospect Street, New Haven, CT 06511, USA
[7]Center for Biodiversity and Global Change, Yale University, 310 Prospect Street, New Haven, CT 06511, USA
[8]Department of Zoology, Entomology and Fisheries Sciences, Makerere University Kampala, Kampala, Uganda
[9]Department of Natural Sciences, Institute of Biosciences, Federal University of the State of Rio de Janeiro, Rio de Janeiro, Brazil
[10]School of the Environment, The University of Queensland, Brisbane, Queensland, Australia
[11]Centre for Biodiversity and Conservation Science, The University of Queensland, Brisbane, Queensland, Australia
[12]Independent researcher
[13]Institute of Biological Sciences, University of the Philippines Los Baños, Laguna 4031, Philippines
[14]Institute of Global Innovation Research, Tokyo University of Agriculture and Technology, Fuchu, Japan
[15]Daugavpils University, Institute of Life Sciences and Technology
[16]Department of Ecology, Faculty of Science, Charles University, Prague, Czechia
[17]Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland
[18]Natural History Museum of Los Angeles County, Los Angeles, California, 90007 USA
[19]Institute of Nature Conservation, Polish Academy of Sciences, Mickiewicza 33, Kraków 31-120, Poland.
[20]School of Biological Sciences, The University of Hong Kong, Hong Kong, China
[21]Department of Life Science and Systems Biology, University of Turin

[22]UK Centre for Ecology and Hydrology, Wallingford, UK
[23]Australian National Insect Collection, National Research Collections Australia, GPO Box 1700, Canberra, ACT 2601, Australia
[24]Division of Ecology and Evolution, Research School of Biology, RN Robertson Building, 46 Sullivans Creek Road, The Australian National University, Acton, ACT 2601, Australia
[25]Andorra Research & Innovation, Av. Rocafort 21-23, AD600 Sant Julià de Lòria, Andorra
[26]Mokpo National University, 1666 Youngsan-ro, Chungkye-myon, Muan, Jeonnam 58554, South Korea
[27]Taiwan Biodiversity Research Institute, Ministry of Agriculture, Taiwan
[28]Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, CdMx, México
[29]African Butterfly Research Institute, Nairobi, Kenya
[30]Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, CdMx, México
[31]Department of Biology, University of Florence, Sesto Fiorentino, Florence, Italy
[32]Turku Collegium for Science, Medicine and Technology, University of Turku
[33]Biodiversity Unit, University of Turku, 20014, Turku, Finland;
[34]Department of Zoology, Faculty of Natural Sciences, University of Jos, Nigeria
[35]Büro Geyer und Dolek, Alpenblick 12, 82237 Wörthsee, Germany
[36]Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada
[37]School of Life Sciences and Technology, Institut Teknologi Bandung, Bandung, Indonesia
[38]IFM Biology, Conservation Ecology Group, Linköping University, Linkoping, Sweden
[39]Laboratório de Ecologia e Sistemática de Borboletas, Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil;
[40]Museu de Diversidade Biológica, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil
[41]Max Planck Institute for Meteorology, Hamburg, Germany
[42]International Max Planck Research School on Earth System Modelling, Hamburg, Germany
[43]Research Unit Sustainability and Climate Risks, Center for Earth System Research and Sustainability (CEN), University of Hamburg, Germany
[44]Department of Biological Sciences, Binghamton University, Binghamton, NY 13902, USA
[45]Institute for Alpine Environment, Eurac Research, Drususallee 1, 39100 Bolzano / Bozen, Italy
[46]Nature Glenelg Trust, South Australia, Australia
[47]Butterfly Pavilion in Westminster, Colorado, USA
[48]Center for Earth System Research and Sustainability (CEN), University of Hamburg, Germany
[49]Cyprus Butterfly Study Group, Nicosia, Cyprus
[50]Institute of Landscape Ecology SAS,Štefánikova 3, P.O.BOX 254, 814 99 Bratislava, Slovakia
[51]Department of Environment, Faculty of Natural Resources and Environment, Ferdowsi University of Mashhad, 9177948974 Mashhad, Iran
[52]Graduate School of Agricultural Science, Tokyo University of Agriculture and Technology, Fuchu, Japan
[53]McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA
[54]Institute of Forestry, Pokhara, Nepal
[55]National Centre for Biological Sciences (NCBS), Tata Institute of Fundamental Research (TIFR), GKVK Campus, Bellary Road, Bengaluru 560065, India
[56]Luxembourg Institute of Science and Technology, Environmental Sensing and Modelling unit, Biodiversity Monitoring and Assessment group, 41 rue du Brill, L-4422 Belvaux, Luxembourg
[57]El Colegio de la Frontera Sur, Departamento de Conservación de la Biodiversidad, Carr. Panamericana & Periférico Sur S/N, San Cristóbal de las Casas, Chiapas, 29290, México
[58]Institute of Ecology and Evolutionary Biology, National Taiwan University, Taiwan
[59]Research Institute for Nature and Forest (INBO), Herman Teirlinckgebouw, Havenlaan 88 PO Box 73, B-1000 Brussels, Belgium
[60]Radboud Institute for Biological and Environmental Sciences (RIBES), Radboud University, PO Box 9010, NL-6500 GL Nijmegen, The Netherlands

[61]Institut Botànic de Barcelona, Consejo Superior de Investigaciones Científicas and Ajuntament de Barcelona, Barcelona, Catalonia 08038, Spain
[62]Mpala Research Centre, Nanyuki 555-10400, Kenya
[63]Turkana Basin Institute, Stony Brook University, NY 11794
[64]WILD, Biology Department, Vrije Universiteit Brussel, Pleinlaan 2, 1050 Brussels, Belgium
[65]Asociación Española para la Protección de las Mariposas y su Medio (ZERYNTHIA)
[66]Yunnan Key Laboratory of Forest Ecosystem Stability and Global Change, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan 666303, China
[67]Helmholtz Centre for Environmental Research - UFZ, Leipzig, Germany
[68]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
[69]Department of Geography, National University of Singapore, Singapore
[70]Biodiversity and Evolution, Department of Biology, Lund University, Ecology Building, SE-223 62 Lund, Sweden
[71]Georgetown University, Washington, DC 20057, United States
[72]Acadia University, Biology Department, Wolfville NS, B4P 2R6 Canada
[73]Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, The University of New South Wales, Sydney, New South Wales, Australia
[74]Department of Biological and Environmental Sciences, Faculty of Science, University of Gothenburg, Gothenburg, Sweden
[75]National Insect Museum, National Agricultural Research Center, Islamabad, Pakistan
[76]Plant Technology and Environmental Monitoring Ltd, Technological Park of São José dos Campos, São José dos Campos, Brazil
[77]Butterfly Conservation Society of Sri Lanka, 762/A, Yatihena, Malwana, 11670, Sri Lanka
[78]Wild Island Foundation, 6A, Mendis Lane, Moratuwa, 10400, Sri Lanka
[79]Applied Microbial and Health Biotechnology Institute, Cape Peninsula University of Technology, South Africa
[80]Forest Guardian Scholarships (Gadyen Forè)
[81]Department of Animal and Environmental Biology, Federal University Dutse, Jigawa State, Nigeria
[82]Instituut voor Milieuvraagstukken, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands
[83]Centre for Ecology and Conservation, University of Exeter, Penryn TR10 9EZ, UK
[84]Department of Electronics, Mathematics and Natural Sciences, Faculty of Engineering and Sustainable Development, University of Gävle, S-801 76 Gävle, Sweden
[85]Centre for Environmental and Climate Science, Lund University, Lund, Sweden
[86]School of Environment and Sciences, Griffith University, Nathan campus, Queensland, Australia
[87]Nature Conservation and Study Centre & Butterfly Watchers, Nepal
[88]Lithuanian Entomological Society, Lithuania
[89]Institute of Entomology, Biology Centre, Czech Academy of Sciences, Ceske Budejovice, Czechia
[90]Department of Biological Applications and Technology, University of Ioannina, 45100 Ioannina, Greece
[91]De Vlinderstichting, P.O. Box 506, NL-6700 AM Wageningen, Netherlands
[92]University of Ljubljana, Biotechnical Faculty, Department of Biology, Jamnikarjeva 101, 1000 Ljubljana, Slovenia
[93]Ohio Lepidopterists, Vice President, NABA editor for Ohio, United States
[94]Senckenberg Deutsches Entomologisches Institut, Eberswalder Str. 90, 15374 Müncheberg, Germany
[95]The University Museum, The University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-0033, Japan
[96]Department of Environmental Sciences and Engineering, Faculty of Natural Resources and Marine Sciences, Tarbiat Modares University, 46417-76489 Noor, Iran
[97]Achva Academic College, MP. Shikmim, 7980400, Israel
[98]Institute of Biodiversity, Ecology and Evolution, Friedrich Schiller University Jena, Jena, Germany
[99]UMR CNRS 7058 Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN), Université de Picardie Jules Verne, Amiens, France

Keywords

Biodiversity monitoring, global warming, global change, macroclimate, species redistribution, tropical ecosystems

Abstract

Ongoing global change is leading to the widespread redistribution of species[1,2]. Assessments of shifts in species geographic ranges, however, remain taxonomically biased and geographically limited[2], especially for insects. We conducted a global synthesis on butterfly range shifts using a combination of multi-lingual review in 15 languages and expert assessments, compiling data on range shifts for 1758 species (10% of described butterfly species) from 109 countries over the last three decades. In 5 of these countries, over 50% of butterfly species shifted their ranges. Overall, most species showed horizontal range expansion (81%), while 27% contracted their range and 22% shifted in elevation. Expansions were primarily reported in tropical species-rich regions, while 19% of species displayed multiple, concurrent range shifts in different countries, highlighting the complexity of these responses. In addition, there was also variation across families - while one-third of the documented species are nymphalids, pierids and papilionids had the highest proportion of species, experiencing range shift. We pinpoint nine drivers of species redistribution, with climate change and severe weather as most prominent. We suggest a future-focused conservation strategy that emphasises monitoring expansion in underrepresented regions and megadiverse countries, leveraging citizen science, and integrating range shifts into conservation planning.

Main

Anthropogenic pressures, such as land-use change, agricultural intensification, and global warming, are reshaping species distributions worldwide[1,2,3,4]. Species shifting their distributions to track suitable conditions is one of the key signatures of ongoing global change effects[1,2,5,6,7,8], being widely documented across the tree of life and across realms[2,9,10]. These shifts may trigger cascading consequences across ecosystems, resulting in the reorganisation of communities, decoupling of coevolved interactions, and undermining conservation strategies[2,10,11].

Ranges can change either longitudinally or latitudinally, either expanding or contracting, as new habitat is gained or lost at the margins[12,13,14,15]. Types of range shifts are not mutually exclusive, and a single species can show multiple spatiotemporal movements in different parts of its range, resulting in complex dynamics. The colonisation or extirpation rates of range-shifting species largely depend on the interaction between their traits (diet, habitat use, mobility) and the prevailing landscape configuration, which ultimately constrain or facilitate the colonisation of newly available habitats[9,16,17]. If only a small amount of habitat is suitable across the landscape, the establishment of a stepping stone population might be uncertain or slow, or the founding population may go extinct[18,19,20]. Accordingly, some species can track their available habitat, while others suffer from climate debts[6,21].

Despite the recent increase in reports of range shifts across ecosystems, current knowledge remains taxonomically and geographically biased[22,23,24]. Of the published literature on species redistribution in response to climate change, nearly half comes from Europe[24], with limited insights from tropical regions, where most biodiversity is found[23,25]. A global analysis of 12,415 species confirmed this bias: flowering plants represented nearly 40% of reported range shifts, and among animals, birds and fish were the most assessed groups[2]. These imbalances reduce the global relevance of range shift data and cast doubt on the reliability of so-called 'global' summaries, which often overlook regions experiencing rapid environmental changes[23]. The lack of detailed species distribution data in under-sampled areas and for under-represented taxa hinders our ability to comprehensively detect and understand species redistributions and their consequences on global biodiversity[15,26].

Addressing these taxonomic and geographic shortfalls requires collaborative efforts to integrate existing data, improve monitoring systems, and integrate unconventional data sources, ultimately creating a more comprehensive global view of how biodiversity responds to environmental changes[27,28,29]. Butterflies are an excellent taxonomic group for tackling these limitations and testing diverse approaches, and even some of the first demonstrations of range shifts in response to climate warming came from butterflies (e.g.[9]). They are highly diverse (19,327 species)[30] and widespread, are highly sensitive to environmental changes, and are among the best monitored insect groups[5,31,32,33]. Their reliance on host plants, limited thermal tolerance, relatively high dispersal capacity and short life cycles make them an early warning system for studying the impacts of environmental changes[33,34,35,36]. Yet butterfly range shift data are still surprisingly fragmented, mostly restricted to temperate regions and often on the leading rather than trailing edge[2,14,37].

Here, we quantify global patterns of butterfly range shifts by combining a multi-lingual systematic review including 15 languages and expert knowledge to assess patterns in range expansion, range contraction, and elevational shifts (Table 1). We document patterns across countries and butterfly families, and assess which threats underpin butterfly species modifying their natural range and range dynamics. Finally, we highlight priorities for future research and conservation.

Global pattern in studying butterfly range shifts

Our dataset covers range shift information for 1758 species across 109 countries (Figure 1A-D; Extended Data 1) from every continent where butterflies occur[30], stemming from 565 unique studies and 68 expert assessments. Species belonged to the six major butterfly families (Figure 1E). There were substantial differences in geographic coverage between the three types of range shifts (Figure 1). We found horizontal range expansion for 1426 species from 106 countries (Figure 1B), horizontal range contraction for 479 species from 47 countries (Figure 1C), and elevational range shifts for 380 species from 29 countries (Figure 1D). Furthermore, horizontal range expansions were reported across all continents, with the highest number of reports originating from the Tropics (e.g., Brazil, Benin) (Figure 1B), challenging the most recent synthesis claiming little evidence for poleward range shifts in the tropics[15]. One potential reason for the higher number of range expansion reports from the Tropics could be the inclusion of scientific literature published in languages other than English[28.38], as well as the support from several international experts on butterflies.

Records for range contractions were far less common outside of Europe and North America, with the highest number of horizontal range contraction reports in temperate countries (e.g., Belgium, United Kingdom, Sweden; Figure 1C)[39,40,41].

Finally, elevational range shifts were detected across tropical, temperate and boreal regions but almost exclusively from the Northern Hemisphere (Figure 1D). However, there were substantially fewer reports of elevational range shifts in the Tropics despite temperature declining faster with elevation in tropical regions and steeper adiabatic lapse rates, which would theoretically facilitate faster upslope movements in response to warming[8,10,42]. This imbalance is due to limited or a lack of long-term monitoring programs in tropical and subtropical mountain regions, where biodiversity is highest but infrastructure is scarce[28].

Similar to this geographic variation, we found substantial differences in the taxonomic coverage among the three types of range shifts. Relative to the total number of species per family, nymphalids had the highest percentage of species shifting their ranges, while riodinids had the lowest (Figure 1E). Across range change types and families, both relative to the total number of species and range shifting species, the highest percentages were always reported for horizontal range expansions and the lowest for elevational shifts (Figure 1E).

There was also a clear imbalance in which species were reported to be shifting among studies and countries, whereby 65% of species in our dataset had a single record of range shift from a single study (Figure 1A). Only 102 species (6%) had more than 10 reports of different range shifts from at least 10 different studies, with 66% of these range shifts' records being related to horizontal range expansion, while only two species (*Aphantopus hyperantus* and *Parnassius apollo*) had multiple records of elevational range shifts across multiple studies (Figure 1A). For example, *Araschnia levana*, *Boloria selene*, and *Aphantopus hyperantus* had the highest number of records for horizontal range expansion (n = 34), contraction (n = 25), and elevational range shift (n = 13), respectively and in many cases, these records were from different regions. Among the species reported to show elevational shift, we obtained 32% of the species showing uphill movement and 32% of species showing downhill movements (no specific movements mentioned for the other 26% species. For four species (*Vanessa cardui*, *Nymphalis antiopa*, *Gonepteryx rhamni*, and *Anthocharis cardamines*) we obtained records of both uphill and downhill shift records.

Spatial patterns of butterfly range shifts

We revealed strong geographical patterns in the species showing range shifts among countries (Figures 2, 3). When considered against the total butterfly species pool of each country (as reported in Pinkert et al.[30]), five European nations (i.e. Sweden, the Czech Republic, Finland, Luxembourg, and Spain) dominate, with documented range shift records for more than half of their known butterfly fauna (Figure 2). Conversely, for most countries in our data - i.e. for which we have range shift data for at least one butterfly species - the documented shifts affected less than 10% of the country's species. Among the three types of range shifts studied, Sweden showed the highest taxonomic representativeness for reports on range-expanding species (61%), while Czech Republic and Estonia had the highest percentages of horizontal range contraction (63%) and elevational range shifts (35%), respectively. All these European countries have long-term systematic butterfly monitoring sites.

To better address sampling gaps in countries where our dataset covers few butterfly species relative to the total known, we calculated the percentage of butterfly species per country with range shift data, relative to all species in that country that have been reported to shift their range either locally or elsewhere. In 32 countries from all continents, at least 25% of the butterfly species for which we have range shift data somewhere in the world have experienced a range shift in the focal country, and in 10 countries this was true for more than half of the species (Figure 3). Among the range shift types, the highest percentages appeared in Sweden (78% for horizontal range expansions), Czech Republic (85% for horizontal range contractions), and Estonia (44% for elevational range shifts).

Most species (80%) showed a single type of range shift in our dataset—typically horizontal range expansions (70%). However, 342 species (19%), especially in Europe and parts of South America, displayed multiple range shift types, such as both horizontal range expansions and contractions either within a country or across different countries. For example, *Danaus plexippus* experienced range contraction in the United States, but range expansion in Spain, while *Aporia crataegi* experienced both range expansion and contraction in Andorra. These multi-dimensional shifts highlight the complexity of biotic responses to ongoing environmental pressures, and underscore the importance of distinguishing between the different types of range shifts when assessing biodiversity redistribution[22].

Our results provide vital insights into where and how butterfly ranges are changing globally, while also highlighting the urgent need for more equitable and standardised monitoring programs across countries to improve the taxonomic representativeness of each country in such efforts to compile range shift observations globally. High values in Europe reflect both genuine change and the much greater probability of detecting shifts given long-term programs; lower values in many tropical countries likely reflect data scarcity rather than biological stability. Despite representing a significant portion of the world’s butterfly diversity, regions such as Central Africa, Southeast Asia, mainland New Guinea and its surrounding islands, and the Amazon Basin remain markedly underrepresented in our compiled dataset. For example, many authors, especially from the tropics, categorised species as range expanding or contracting when the species was new to a certain region or went extinct from that region, repetitively (Table 1). This is concerning because tropical species are especially vulnerable: they already live near thermal limits, have restricted ranges, and are isolated from cool refugia[43,44]. Elevational range shifts are also more commonly reported for tropical insects than poleward range shifts[45], which contrasts with Colwell & Feeley[15]. Recent work suggests a major erosion of the geographic availability in butterflies' temperature niches, reaching up to 64% loss in 2100, even when assuming full dispersal within biogeographical realms[46]. This implies major range contractions and particular vulnerability of rare tropical species at higher elevations.

Drivers of butterfly range shifts

We compiled threat data linked to butterfly range shifts from 70 countries. For example, *Boloria aquilonaris* has lost much of its original habitat in Germany due to bog drainage (i.e., habitat loss and degradation)[47], while in Romania, habitat homogenisation and agricultural intensification caused severe range contraction for *Colias myrmidone*[48]. On the other hand, *Godartiana byses,* which prefers warmer habitats, has expanded from the states of Rio de Janeiro and Bahia to São Paulo in Brazil in response to climate warming[49]. In fact, global warming is leading many alpine butterflies to move uphill to track shifting isotherms and remain within suitable climatic conditions[50]. Biological invasions also explain shifts for some species. For instance, the introduction of *Pieris rapae* led to dramatic range contractions of *Pieris oleracea* in the United States[51].

We categorised these threats following the IUCN threat categories (see *literature search*). Overall, we identified nine primary threats that were directly or indirectly related to butterfly range shifts. *Climate change and severe weather* had the greatest impact, affecting 277 species out of 356 for which we had a reported threat in our data, while *energy production and mining* had the least reported impact (3 species; Figure 4A). Though not always supported by formal analyses, *climate change and severe weather* was linked to 163 species' range expansions, 131 species' range contractions, and to elevational range shifts for 61 species (Figure 4A). However, the relative importance of different threats varied across the three types of range shifts. While *human intrusions and disturbance* and *agriculture and aquaculture* were the dominant drivers associated with range contraction, both affecting 143 species, *climate change and severe weather* were the dominant driver linked to elevational range shifts, affecting 61 species. These elevational range shifts are particularly important as butterfly species richness, endemism, and phylogenetic diversity are highly clustered in mountain regions worldwide. Approximately two-thirds of all butterfly species are primarily mountain-dwelling species, but mountain climates are rapidly eroding in the face of climate change[46].

At the continental level, the distribution and intensity of threats differed across regions and among the three types of range shifts (Figure 4B). In most continents, *climate change and severe weather* were reported to have the highest impact, whereas *residential and* *commercial development*, as well as *invasive and other problematic species, genes and diseases* were the most prevalent threats in Oceania, and *human intrusions and disturbance* were dominant for South America (Figure 4B). *Climate change and severe weather* were consistently linked to horizontal range expansions in all continents, while several other threats were linked to horizontal contractions in different continents (Figure 4B). While there were one or two major threats in most continents, in Europe, several threats concurrently impacted butterfly range expansion and contraction (Figure 4B).

These findings highlight the diversity of direct and indirect human pressures shaping butterfly redistribution globally and underscore the need for region-specific conservation interventions. Species experiencing both horizontal range expansions and elevational range shifts may require increased habitat connectivity (i.e., the “direct” type of conservation management actions in the resist-accept-direct (RAD) framework)[52], while species contracting their ranges may benefit more from targeted habitat protection and restoration efforts (i.e., the “resist” type of actions in the RAD framework)[52,53,54]. Range expansions are often facilitated by rising temperatures, enabling cold-limited species to colonise higher latitudes or elevations. Conversely, range contractions are typically linked to land-use change, especially habitat loss, with species unable to persist in increasingly modified environments. The impact of a threat could also depend on change in the extent of occurrence or area of occupancy. For example, land-use change probably had the strongest effects on species range margins, where species are nearer the limits of their thermal tolerances[55].

Minimising drivers of range shifts to mitigate butterfly decline

Our data confirm pioneering studies on butterfly range shift, that butterflies tend to expand more than contract[6,9]. This is likely due to the phenotypic plasticity of butterflies, which allows them to survive in areas at the margins of supposed decline by adopting opportunistic strategies[56,57]. Generally, range expansion may not be problematic if species can move across the landscape and access available habitats to track environmental changes. However, range shift in butterflies can be restricted, if, for example, there is plasticity to respond within existing ranges[58], or expansion is constrained by foodplant availability[59]. However, consequences can be severe if habitat availability decreases, or becomes too scattered, or and/or isolated populations surrounded by dispersal barriers, such as on oceanic islands, sky islands or mountain tops[9,60]. Habitat heterogeneity is therefore crucial to provide refugia and buffer populations against abrupt losses[61,62].

Climate change mitigation remains essential and should be prioritised to minimise a climatic debt which expresses as lags in the biotic responses of butterfly populations to track the shifting isotherms. Even minor temperature increases may exceed physiological limits, alter seasonal phenology, or disrupt biotic interactions with host plants and mutualists[36,63,64]. For example, Scandinavian butterflies have expanded northwards with rising temperatures[35,65], whereas alpine butterfly species in the Alps are facing increasing “elevational squeeze” due to warming[66]. Limiting global warming will be crucial for maintaining the accessibility to thermally suitable habitats and avoiding range shift gaps[45]. Studies from Italy, Spain, and the UK show that butterflies retreat to shady areas on hot days, stressing the need for environmental heterogeneity under climate change[56,67,68] and a study in urban parks Brazil showed that fruit feeding butterflies occurrence is higher in parks with more shaded areas[69]. As exceeding the 2°C threshold outlined in the Paris Agreement temperature goal becomes increasingly probable[70], conservation strategies should also incorporate climate adaptation measures—such as protecting microrefugia[71], buffering habitat edges, and improving landscape connectivity —to strengthen resilience and help species move across the landscape or survive in their current locations where possible[54,72,73].

Equally important is the protection and restoration of habitat quality. Habitat modifications (e.g., *agriculture and aquaculture*, *residential and commercial development*, *human intrusions and disturbance*) were chiefly attributed to horizontal range contractions for butterflies (Figure 4), highlighting how vulnerable butterflies are to land-use change[39,74,75]. Habitat degradation decreases the availability of crucial host plants, nectar sources, and microclimates necessary for butterfly survival[76,77]. Strategic conservation should therefore focus on protecting intact and well-managed habitat patches, establishing habitat corridors, and restoring degraded areas to support population stability and movement[34,78,79]. Restoring habitat connectivity can enable butterfly recolonisation, boost biodiversity, and even recover ecosystem services[80]. Evidence shows that maximising the availability and accessibility of habitat patches, even small ones, enhances genetic diversity and supports metapopulation persistence when total habitat is sufficient[60,81].

Several other human-induced pressures can also impact butterfly range shifts, although they were less commonly reported. Urbanisation, roads, and buildings create dispersal barriers, making it challenging, even for mobile species, to move between habitat patches[16,82,83]. Urban forest remnants support fewer specialist butterfly species than rural forests in Tokyo[84], while invasive alien species can outcompete native butterfly populations[85]. Similarly, minimising pesticide and herbicide use is vital to improve habitat quality and prevent indirect declines in population sizes because efficient herbicide use in crop fields restricts the availability of larval foodplants in these fields as well as in adjacent fields[78,79]. Incorporating biodiversity conservation goals into infrastructure and land-use planning—such as through ecological corridors, design of stepping stones, and enhanced environmental impact assessments—can help sustain connectivity[53,81].

Finally, we must build ecological resilience to act as a long-term buffer against ecosystem or landscape instability[86]. Diverse, structurally complex ecosystems are better equipped to withstand environmental disturbances and maintain stable and genetically robust/healthy butterfly populations. It is important to conserve as many populations as possible to maintain or even increase genetic diversity[87,88]. By conserving biotic interactions, seasonal resource availability, and habitat diversity, conservationists can lower the risks of range contractions while facilitating range shifts for butterfly species facing multiple human pressures[79]. In the Brazilian Atlantic Forest, the spatial composition and configuration of the landscape was as important as climate conditions in explaining local butterfly diversity, with the primary threat to butterflies being the loss of natural forest remnants due to human activities[89].

Taken together, reducing the drivers of range shifts requires a multi-faceted approach—combining global climate efforts with local habitat protection, sustainable land management, and coordinated policy actions. Without addressing the pressures that cause biodiversity redistribution, even the best monitoring systems and conservation plans will struggle to prevent biodiversity loss in a rapidly changing world.

Future monitoring and conservation prospects

The combined effect of geographic and taxonomic biases likely creates a misleading picture of butterfly responses to environmental change[23]. Geographic and taxonomic biases significantly influence global biodiversity assessments and conservation strategies[90]. For example, the perceived dominance of reports on horizontal range expansions for butterfly species might be partly influenced by detection and reporting biases rather than by actual ecological trends. If horizontal range contractions and elevational range shifts are not adequately documented in tropical regions—where the impacts of climate change and land-use pressures are very severe—we would greatly underestimate the vulnerability of tropical butterflies[14,15,91,92].

To close this gap and advance the field, we propose a three-fold framework: (i) expanding monitoring programs in underrepresented regions, (ii) integrating citizen science and local knowledge, and (iii) accounting for species range shifts in conservation planning.

Step I. Expanding monitoring in underrepresented regions

Existing monitoring programs for Europe and the United States help understand how butterflies respond to environmental changes (e.g.[93,94,95]). However, such systematic monitoring is missing from most parts of the world, especially in the Tropics, arid, and semi-arid regions[92,96], limiting our understanding of how tropical species may respond to global change drivers[97]. For one third of all species, not even a single occurrence record is currently available[46]. To address this gap, we urgently need to expand monitoring biodiversity programs in underrepresented regions[98]. This includes prioritising biodiversity hotspots and elevational gradients that are expected to be particularly sensitive to climate change and to act as sentinels of change.

Due to the lack of infrastructure, many tropical countries may struggle to allocate sufficient funding for long-term monitoring, underscoring the importance of international collaboration[28,33,99]. Thus, investment in capacity-building is essential: we need to invest both in the human resources to coordinate such efforts, and in knowledge-generation to generate a community of knowledge that can support a broader network of volunteers to be established. In places that are species-rich on the one hand, and lack historic efforts or investment on taxonomic knowledge, and citizen science engagement on the other hand, this remains a double-challenge. Active collaboration with regional researchers will also address the problem of parachute science by non-native researchers (i.e., inequity in research relationships between scientists from economically developed and developing countries)[100,101]. Historically, butterflies are one of the most iconic groups of insects studied by taxonomists and many museums and private collections preserve large numbers of vouchered specimens. Just like herbarium data, digitising butterfly museum collections (e.g. https://www.dissco.eu/) provides long-term records to improve mapping distributions over time, and few other groups besides plants offer such exceptional historical coverage[61,102].

Valuable biodiversity data also exists in local-language publications and museum or private collections, which are often isolated from global databases. Many key records—particularly from the Tropics—are published in non-English, non-indexed sources or remain unpublished, stored in natural history museums or university archives. These resources can aid in reconstructing historical range boundaries and bridging spatial and temporal gaps in species occurrence data. Adding such sources into biodiversity workflows would further improve the completeness of range change assessments.

We recommend: (I) identifying national or regional butterfly monitoring shortfalls using existing monitoring datasets to guide cost-effective investment; (II) establishing standardised protocols to harmonise data collection on butterfly distribution across countries and digitize museum and private collections; (III) integrating new technologies (e.g., camera traps, eDNA, AI-based image recognition) for cost-effective data collection in remote or logistically challenging landscapes; and (IV) ensuring long-term funding continuity through multi-agency partnerships, including UN biodiversity programmes, NGOs, and national governments.

Step II. Integrating citizen science data and local knowledge

With the increasing popularity of citizen science applications online (e.g., iNaturalist, Flora Incognita, eBird), we are witnessing a rapid surge in biodiversity data in recent years[103]. Yet, most citizen science records are taxonomically and geographically biased[104]. Despite increasing efforts and emerging methods to mitigate this problem, insect representation has not been improved, especially in the Tropics[28,105].

To improve this situation, community-led efforts are essential[28,106]. Opportunistic observations submitted by the public can greatly improve species range estimates[107,108], and semi-structured citizen science surveys provide important biodiversity monitoring information[109]. In Brazil, for instance, over 70% of threatened butterfly ranges improved through citizen science efforts[110,111]. In Bangladesh, 93% of butterfly occurrence records originated from Facebook photographs[112], revealing that one-third of Bangladeshi butterflies could go extinct under future climatic scenarios[14], while in the Philippines, citizen scientists documented many rare and elusive butterfly species[113]. Additionally, the growth of online citizen science platforms such as iNaturalist, Observation, Biodiversity Atlas India, and social media, has made it easier to collect, verify, and combine butterfly records at both the national and global extent[103]. Using these sources in biodiversity databases will be crucial for bridging ongoing monitoring gaps, especially in the Tropics[28]. These examples demonstrate a huge untapped potential, but also the need to explore alternative and complementary approaches for monitoring, such that would suit differing habitats, engage different public types, cultures and knowledge levels, and most importantly, lead to the desired outcomes of generating longer-term monitoring data. This could possibly be achieved through a combination of structured transect walks, time-bound counts (e.g. 15 min) and fruit baits for forest areas - but other approaches may need to be explored.

While citizen science tools can substantially improve data coverage, using these records to guide conservation planning requires both good design of citizen science programmes and robust data validation processes, where taxonomic expertise is essential[114,115]. To boost engagement, incentivising participation, especially for coordinators in developing countries, through recognition programmes or small grants, can be effective. Embedding citizen science in national biodiversity strategies can assist countries in tracking progress toward post-2020 Global Biodiversity Framework targets, including spatial planning, ecosystem monitoring, and biodiversity data mobilisation[116]. Finally, engaging communities in biodiversity monitoring—both at entry and specialised expert levels—can contribute to enhancing species knowledge and fostering nature experience, building scientific and conservation literacy through Learning-by-Doing[117]. Importantly, engaging in citizen science can promote environmental awareness, skills and social licence for both biodiversity science and conservation[118].

Step III. Accounting for species range shifts in conservation planning

Despite mounting evidence for species shifting their ranges in recent decades, current conservation frameworks, both regional and global, rarely include range dynamics, which limits their ability to protect biodiversity under changing climatic conditions. While protected areas have been established to insulate species from various direct threats[119], their effectiveness varies over time because the habitat suitability of a given species is constantly changing due to global change drivers, like climate change and biological invasions, which do not stop at the border of protected areas[119,120]. For example, 76% of insect species are inadequately represented within the current protected area system[121], while the situation is worse for the migratory butterfly species, with 85% being inadequately protected[122]. To address these limitations, conservation planning should incorporate real-time species range shift data[40,123]. Aligning national efforts with the Kunming-Montreal Global Biodiversity Framework will require systematically incorporating range shift data to inform spatial planning, monitoring, and progress reporting[124].

Existing assessments, such as the IUCN Red List, often depend on static species distribution maps, which may no longer represent the current or future distribution of suitable habitat. Most IUCN threatened insects are listed under criteria B or D2 (restricted range) rather than criterion A (population reduction), which can also account for declines in area or occupancy[125]. Developing and using dynamic range mapping solutions, based on observed data belonging to any available source (literature, museum and private collections, monitoring, citizen science platforms) and projected shifts, will help conservation efforts better identify at-risk populations and emerging threats.

Species undergoing range contractions and elevational range shifts require special attention, as they are often at elevated risk of extinction from habitat loss and thermal stress. In the temperate grassy woodlands of Australia, extensive agriculture and urbanisation have contributed to range contractions of several specialist species[126], emphasising the importance of maintaining environmental heterogeneity and sustainable thermal connectivity through the availability of elevational gradients. These species might need targeted measures, such as conserving climate refugia, restoring appropriate habitats, or, in some cases, assisted migration to suitable areas. Lastly, scenario-based forecasting using species distribution models can be a powerful tool for proactive conservation planning, especially so for data-poor species or for tracking species niche or assessing species vulnerability to global change[123,127]. Predicting where species are likely to move under future climate and land-use scenarios allows for early interventions, such as prioritising future conservation areas, restoring stepping-stone habitats, or establishing transboundary agreements for migratory or shifting species. Such models can also be used to identify potential reintroduction sites[128].

In summary, tackling the conservation implications of range shifts requires a move from reactive to adaptive strategies—ones that acknowledge uncertainty, incorporate predictive modelling, and embed species range dynamics into policy and practice.

Conclusion

Butterflies are a highly diverse and widely distributed group, contributing to many ecosystem services and serving as bioindicators and sentinels of change. We report that globally, the current detection rate for butterfly species range shifts affects one in ten species, often involving *climate change and extreme weather*, along with *agriculture and aquaculture* and *human intrusions and disturbance* as the most likely drivers of change. Despite our efforts building the largest dataset compiling reports of range shifts in butterflies, our understanding of how butterflies respond to global changes remains biased towards temperate species, with many species, especially in the Tropics, lacking data on range shifts. Expanding biodiversity monitoring, including citizen science approaches and accounting for range dynamics in conservation, will improve our understanding of butterfly responses to environmental change and help develop more adaptive, forward-looking conservation approaches. Without such global, coordinated efforts, including insects, we risk missing early warning signals of biodiversity collapse—especially in regions and taxa that are underrepresented in existing data repositories. Considering that many other taxa are experiencing similar shifts in their geographic range, our methods and recommendations are transferable to other taxonomic groups and scalable across terrestrial and marine realms to understand how biodiversity responds to global change drivers and thus work jointly towards effective conservation and restoration.

Methods

We followed two primary steps to extract data on butterfly range shifts. First, we reviewed published literature. Recognising the bias in published literature, we invited 68 butterfly experts (co-authors) from 49 countries.

As many authors publish their research in non-English languages[38,129], we searched for published literature in 15 languages. For English-language studies, we used Web of Science and Google Scholar, and for non-English-language studies we used Google Scholar and local search systems (see supplementary methods).

We used a common template to extract information from both steps. We contacted IUCN SSC Butterfly and Moth Specialist group and Butterfly Conservation to compile a list of butterfly experts who have been doing field work for many years. When emailing the experts, we also requested them to share our study with their network so that we can reach the maximum number of people. Once each expert agreed, we asked them to share the same range-shift information, which we obtained from published studies, but based on their field surveys.

Once the data collection was done, we aggregated both the datasets from published studies and expert assessments to understand the global patterns of range shifts in butterflies. Finally, we used the most comprehensive and recent taxonomy of butterflies[30] to match range shift information and country-level distribution data.

Acknowledgements

We thank IUCN SSC Butterfly and Moth Specialist group and Butterfly Conservation for sharing the global list of butterfly experts who have been doing field work for many years.. We are grateful to all the volunteers and citizen scientists who collated butterfly distribution data across the world. We thank Orr Comay Eyal Simons for helping G.P. to calcualte the range shift for Israeli butterflies. U.A. was supported by a Forrest Research Foundation fellowship (2023/GR001415). A.B. gratefully acknowledges the support of the German Centre for Integrative Biodiversity Research (iDiv) and the sMon project funded by the German Research Foundation (DFG-FZT 118, 202548816). A.V.L.F. thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grant 304291/2020-0), and the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, grant 2021/03868-8). K.J. was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy—EXC 2037 'CLICCS—Climate, Climatic Change, and Society'—Project Number: 390683824, contribution to the Center for Earth System Research and Sustainability (CEN) of Universität Hamburg.

References

1. Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I. C., ... & Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, *355*(6332), eaai9214.

2. Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, *4*(8), 1044-1059.

3. Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145-148.

4. Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D. E., Coscieme, L., Golden, A. S., ... & Purvis, A. (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Science Advances*, *8*(45), eabm9982.

5. Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*(6045), 1024-1026.

6. Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., ... & Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, *2*(2), 121-124.

7. Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts–a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15-28.

8. Chan, W. P., Lenoir, J., Mai, G. S., Kuo, H. C., Chen, I. C., & Shen, S. F. (2024). Climate velocities and species tracking in global mountain regions. *Nature*, *629*(8010), 114-120.

9. Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., ... & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, *399*(6736), 579-583.

10. Vitasse, Y., Ursenbacher, S., Klein, G., Bohnenstengel, T., Chittaro, Y., Delestrade, A., ... & Lenoir, J. (2021). Phenological and elevational shifts of plants, animals and fungi under climate change in the European Alps. *Biological Reviews*, *96*(5), 1816-1835.

11. Filazzola, A., Matter, S. F., & Roland, J. (2020). Inclusion of trophic interactions increases the vulnerability of an alpine butterfly species to climate change. *Global Change Biology*, *26*(5), 2867-2877.

12. Braby, M. F., Bertelsmeier, C., Sanderson, C., & Thistleton, B. M. (2014). Spatial distribution and range expansion of the tawny Coster butterfly, *Acraea terpsicore* (Linnaeus, 1758)(Lepidoptera: Nymphalidae), in South-East Asia and Australia. *Insect Conservation and Diversity*, *7*(2), 132-143.

13. Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M., & Hargreaves, A. L. (2018). Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. *Global Ecology and Biogeography*, *27*(11), 1268-1276.

14. Chowdhury, S. (2023). Threatened species could be more vulnerable to climate change in tropical countries. *Science of the Total Environment*, *858*, 159989.

15. Colwell, R. K., & Feeley, K. J. (2025). Still little evidence of poleward range shifts in the tropics, but lowland biotic attrition may be underway. *Biotropica*, *57*(1), e13358.

16. Chowdhury, S., Braby, M. F., Fuller, R. A., & Zalucki, M. P. (2021). Coasting along to a wider range: niche conservatism in the recent range expansion of the Tawny Coster, *Acraea terpsicore* (Lepidoptera: Nymphalidae). *Diversity and Distributions*, *27*(3), 402-415.

17. Neff, F., Chittaro, Y., Korner-Nievergelt, F., Litsios, G., Martínez-Núñez, C., Rey, E., & Knop, E. (2025). Contrasting 50-Year trends of moth communities depending on elevation and species traits. *Ecology Letters*, *28*(8), e70195.

18. Kuussaari, M., Saccheri, I., Camara, M., & Hanski, I. (1998). Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos*, 384-392.

19. Betzholtz, P. E., Pettersson, L. B., Ryrholm, N., & Franzén, M. (2013). With that diet, you will go far: trait-based analysis reveals a link between rapid range expansion and a nitrogen-favoured diet. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1750), 20122305.

20. Soifer, L. G., Lockwood, J. L., Lembrechts, J. J., Antão, L. H., Klinges, D. H., Senior, R. A., ... & Scheffers, B. R. (2025). Extreme events drive rapid and dynamic range fluctuations. *Trends in Ecology & Evolution* (in press). https://doi.org/10.1016/j.tree.2025.06.009.

21. Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., De Ruffray, P., Vidal, C., ... & Gégout, J. C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, *479*(7374), 517-520.

22. Lenoir, J., & Svenning, J. C. (2015). Climate-related range shifts–a global multidimensional synthesis and new research directions. *Ecography*, *38*(1), 15-28.

23. Feeley, K. J., Stroud, J. T., & Perez, T. M. (2017). Most 'global'reviews of species' responses to climate change are not truly global. *Diversity and Distributions*, *23*(3), 231-234.

24. Taheri, S., Naimi, B., Rahbek, C., & Araújo, M. B. (2021). Improvements in reports of species redistribution under climate change are required. *Science Advances*, *7*(15), eabe1110.

25. Díaz, S., & Malhi, Y. (2022). Biodiversity: concepts, patterns, trends, and perspectives. *Annual Review of Environment and Resources*, *47*(1), 31-63.

26. Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences*, *118*(2), e2023989118.

27. Forister, M. L., Grames, E. M., Halsch, C. A., Burls, K. J., Carroll, C. F., Bell, K. L., ... & Riecke, T. V. (2023). Assessing risk for butterflies in the context of climate change, demographic uncertainty, and heterogeneous data sources. *Ecological Monographs*, *93*(3), e1584.

28. Chowdhury, S., Jahan, S. F., Akite, P., Benedetti, Y., Bonebrake, T. C., Freitas, A. V. L., ... & Kunte, K. (2025). Strategic conservation of tropical insects. EcoEvoRxiv. https://doi.org/10.32942/X2ZD1T .

29. Cooke, R., Outhwaite, C. L., Bladon, A. J., Millard, J., Rodger, J. G., Dong, Z., ... & Isaac, N. J. (2025). Integrating multiple evidence streams to understand insect biodiversity change. *Science*, *388*(6742), eadq2110.

30. Pinkert, S., Barve, V., Guralnick, R., & Jetz, W. (2022). Global geographical and latitudinal variation in butterfly species richness captured through a comprehensive country-level occurrence database. *Global Ecology and Biogeography*, *31*(5), 830-839.

31. Pöyry, J., Luoto, M., Heikkinen, R. K., Kuussaari, M., & Saarinen, K. (2009). Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, *15*(3), 732-743.

32. Kharouba, H. M., Lewthwaite, J. M., Guralnick, R., Kerr, J. T., & Vellend, M. (2019). Using insect natural history collections to study global change impacts: challenges and opportunities. *Philosophical Transactions of the Royal Society B*, *374*(1763), 20170405.

33. Freitas, A. V. L., P. E. Gueratto, J. Y. O. Carreira, G. M. Lourenço, L. T. Shirai, J. P. Santos, A. H. B. Rosa, G. B. Evora, R. R. Ramos & M. A. Marín. 2024. Fruit-Feeding butterfly assemblages: trends, changes, and the importance of monitoring schemes in Neotropical environments. pp 205–233. In: *Insect Decline and Conservation in the Neotropics*. León-Cortés, J. L. & Córdoba-Aguilar, A. (editors). Springer, Cham X + 311pp.

34. Bonebrake, T. C., Ponisio, L. C., Boggs, C. L., & Ehrlich, P. R. (2010). More than just indicators: a review of tropical butterfly ecology and conservation. *Biological Conservation*, *143*(8), 1831-1841.

35. Sunde, J., Franzén, M., Betzholtz, P. E., Francioli, Y., Pettersson, L. B., Pöyry, J., ... & Forsman, A. (2023). Century-long butterfly range expansions in northern Europe depend on climate, land use and species traits. *Communications Biology*, *6*(1), 601.

36. Gross, C. P., Kawahara, A. Y., & Daru, B. H. (2025). Climate and regional plant richness drive diet specialization in butterfly caterpillars. *BioRxiv*, 2025-01. https://doi.org/10.1101/2025.01.10.632438.

37. Oliveira, I. F., Azevedo, J., Werneck, F. P., da Silva, A. P., Cabral, J. S., & Baccaro, F. B. (2025). Mixed responses among closely related Neotropical butterflies under extreme climate and land cover changes. *Insect Conservation and Diversity*, *18*(3), 386-399.

38. Chowdhury, S., Gonzalez, K., Aytekin, M. Ç. K., Baek, S. Y., Bełcik, M., Bertolino, S., ... & Amano, T. (2022). Growth of non-English-language literature on biodiversity conservation. *Conservation Biology*, *36*(4), e13883.

39. Maes, D., & Van Dyck, H. (2001). Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario?. *Biological Conservation*, *99*(3), 263-276.

40. Maes, D., Van Calster, H., Herremans, M., & Van Dyck, H. (2022). Challenges and bottlenecks for butterfly conservation in a highly anthropogenic region: Europe's worst case scenario revisited. *Biological Conservation*, *274*, 109732.

41. Warren, M. S., Maes, D., van Swaay, C. A., Goffart, P., Van Dyck, H., Bourn, N. A., ... & Ellis, S. (2021). The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences*, *118*(2), e2002551117.

42. Wilson, R. J., Gutierrez, D., Gutierrez, J., & Monserrat, V. J. (2007). An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*, *13*(9), 1873-1887.

43. Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, *105*(18), 6668-6672.

44. Wright, S. J., Muller-Landau, H. C., & Schipper, J. A. N. (2009). The future of tropical species on a warmer planet. *Conservation Biology*, *23*(6), 1418-1426.

45. Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, *322*(5899), 258-261.

46. Pinkert, S., Farwig, N., Kawahara, A. Y., & Jetz, W. (2025). Global hotspots of butterfly diversity are threatened in a warming world. *Nature Ecology & Evolution*, *9*, 789-800.

47. Heinecke, C., Kastner, F., & Fresse, E. (2013). Die Großschmetterlinge (Makrolepidoptera) der Moore Oldenburgs (Deutschland, Niedersachsen)-Vorbereitung einer Langzeitstudie und Erste Ergebnisse. *DROSERA-Naturkundliche Mitteilungen aus Norddeutschland*, 2011(1/2), 81-97.

48. Szentirmai, I., Mesterházy, A., Varga, I., Schubert, Z., Sándor, L. C., Ábrahám, L., & Kőrösi, Á. (2014). Habitat use and population biology of the Danube Clouded Yellow butterfly *Colias myrmidone* (Lepidoptera: Pieridae) in Romania. *Journal of Insect Conservation*, *18*(3), 417-425.

49. Braga, L., Ramos, R. R., Aguiar, T. M. C., & Freitas, A. V. L. (2018). Distribution extension of *Godartiana byses* (Nymphalidae: Satyrinae) and first record for the state of São Paulo, Brazil. *The Journal of the Lepidopterists' Society*, *72*(2), 176-179.

50. Rödder, D., Schmitt, T., Gros, P., Ulrich, W., & Habel, J. C. (2021). Climate change drives mountain butterflies towards the summits. *Scientific Reports*, *11*(1), 14382.

51. Herlihy, M. V., Van Driesche, R. G., & Wagner, D. L. (2014). Persistence in Massachusetts of the veined white butterfly due to use of the invasive form of cuckoo flower. *Biological Invasions*, *16*(12), 2713-2724.

52. Lynch, A. J., Thompson, L. M., Beever, E. A., Cole, D. N., Engman, A. C., Hawkins Hoffman, C., ... & Wilkening, J. L. (2021). Managing for RADical ecosystem change: applying the Resist-Accept-Direct (RAD) framework. *Frontiers in Ecology and the Environment*, *19*(8), 461-469.

53. Horak, J., Šafářová, L., Trombik, J., & Menendez, R. (2022). Patterns and determinants of plant, butterfly and beetle diversity reveal optimal city grassland management and green urban planning. *Urban Forestry & Urban Greening*, *73*, 127609.

54. Thomas, C. D., Cunningham, C. A., Hulme, N. A., Bourn, N. A., Corrigan, E. C., Metherell, B. G., ... & Oates, M. (2025). A framework for species translocation: Prospects of returning the black-veined white butterfly to England. *Insect Conservation and Diversity*, 1-21 (in press). https://doi.org/10.1111/icad.12850.

55. Guo, F., Lenoir, J., & Bonebrake, T. C. (2018). Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications*, *9*(1), 1315.

56. Bruschini, C., Simbula, G., Benetello, F., Dell’Olmo, L., Lazzaro, L., Mugnai, M., ... & Dapporto, L. (2024). Micro-habitat shifts by butterflies foster conservation strategies to preserve pollinator diversity in a warming Mediterranean climate. *Ecological Indicators*, *166*, 112253.

57. Franzén, M., Francioli, Y., Askling, J., Kindvall, O., Johansson, V., & Forsman, A. (2022). Differences in phenology, daily timing of activity, and associations of temperature utilization with survival in three threatened butterflies. *Scientific Reports*, *12*(1), 7534.

58. Roy, D. B., Oliver, T. H., Botham, M. S., Beckmann, B., Brereton, T., Dennis, R. L., ... & Thomas, J. A. (2015). Similarities in butterfly emergence dates among populations suggest local adaptation to climate. *Global Change Biology*, *21*(9), 3313-3322.

59. Quinn, R. M., Caston, K. J., & Roy, D. B. (1998). Coincidence in the distributions of butterflies and their foodplants. *Ecography*, *21*(3), 279-288.

60. Multigner, L. F., Bras, A., DiLeo, M. F., & Saastamoinen, M. (2025). Relative Effects of Habitat Amount and Fragmentation Per Se on Genetic Diversity of the Glanville Fritillary Butterfly. *Molecular Ecology*, e70037.

61. Lewthwaite, J. M. M., Angert, A. L., Kembel, S. W., Goring, S. J., Davies, T. J., Mooers, A. Ø., ... & Kerr, J. T. (2018). Canadian butterfly climate debt is significant and correlated with range size. *Ecography*, *41*(12), 2005-2015.

62. Wilson, R. J., & Fox, R. (2021). Insect responses to global change offer signposts for biodiversity and conservation. *Ecological Entomology*, *46*(4), 699-717.

63. Roy, D. B., Rothery, P., Moss, D., Pollard, E., & Thomas, J. A. (2001). Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *Journal of Animal Ecology*, *70*(2), 201-217.

64. Hill, G. M., Kawahara, A. Y., Daniels, J. C., Bateman, C. C., & Scheffers, B. R. (2021). Climate change effects on animal ecology: butterflies and moths as a case study. *Biological Reviews*, *96*(5), 2113-2126.

65. Franzén, M., & Johannesson, M. (2007). Predicting extinction risk of butterflies and moths (Macrolepidoptera) from distribution patterns and species characteristics. *Journal of Insect Conservation*, *11*(4), 367-390.

66. Settele, J., Kudrna, O., Harpke, A., Kühn, I., Van Swaay, C., Verovnik, R., ... & Schweiger, O. (2008). *Climatic risk atlas of European butterflies*. Biorisk 1 (Special Issue). 710pp.

67. Colom, P., Traveset, A., Carreras, D., & Stefanescu, C. (2021). Spatio-temporal responses of butterflies to global warming on a Mediterranean island over two decades. *Ecological Entomology*, *46*(2), 262-272.

68. Hayes, M. P., Ashe-Jepson, E., Hitchcock, G. E., Clark, R., Hellon, J., Knock, R. I., ... & Turner, E. C. (2024). Heatwave predicts a shady future for insects: impacts of an extreme weather event on a chalk grassland in Bedfordshire, UK. *Journal of Insect Conservation*, *28*(5), 923-933.

69. Brown Jr, K. S., & Freitas, A. V. L. (2002). Butterfly communities of urban forest fragments in Campinas, São Paulo, Brazil: structure, instability, environmental correlates, and conservation. *Journal of Insect Conservation*, *6*(4), 217-231.

70. Cannon, A. J. (2025) Twelve months at 1.5 °C signals earlier than expected breach of Paris Agreement threshold. *Nature Climate Change*, *15*, 266–269.

71. Suggitt, A. J., Wheatley, C. J., Aucott, P., Beale, C. M., Fox, R., Hill, J. K., ... & Auffret, A. G. (2023). Linking climate warming and land conversion to species' range changes across Great Britain. *Nature Communications*, *14*(1), 6759.

72. Thomas, J. A., Simcox, D. J., & Hovestadt, T. (2011). Evidence based conservation of butterflies. *Journal of Insect Conservation*, *15*(1), 241-258.

73. Riva, F., & Fahrig, L. (2022). The disproportionately high value of small patches for biodiversity conservation. *Conservation Letters*, *15*(3), e12881.

74. Schulze, C. H., Schneeweihs, S., & Fiedler, K. (2010). The potential of land-use systems for maintaining tropical forest butterfly diversity. In *Tropical Rainforests and Agroforests under Global Change: Ecological and Socio-economic Valuations* (pp. 73-96). Berlin, Heidelberg: Springer Berlin Heidelberg.

75. Habel, J. C., Teucher, M., Gros, P., Schmitt, T., & Ulrich, W. (2021). Land use and climate change affects butterfly diversity across northern Austria. *Landscape Ecology*, *36*(6), 1741-1754.

76. Konvicka, M., Benes, J., Cizek, O., Kopecek, F., Konvicka, O., & Vitaz, L. (2008). How too much care kills species: Grassland reserves, agri-environmental schemes and extinction of Colias myrmidone (Lepidoptera: Pieridae) from its former stronghold. Journal of insect Conservation, 12(5), 519-525.

77. Konvicka, M., Maradova, M., Benes, J., Fric, Z., & Kepka, P. (2003). Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Global Ecology and Biogeography*, *12*(5), 403-410.

78. New, T. R., Pyle, R. M., Thomas, J. A., Thomas, C. D., & Hammond, P. C. (1995). Butterfly conservation management. *Annual Review of Entomology*, *40*(1), 57-83.

79. Koh, L. P., & Sodhi, N. S. (2004). Importance of reserves, fragments, and parks for butterfly conservation in a tropical urban landscape. *Ecological Applications*, *14*(6), 1695-1708.

80. Sant'Anna, C. L. B., D. B. Ribeiro, L. C. Garcia & A. V. L. Freitas. 2014. Fruit-feeding butterfly communities are influenced by restoration age in tropical forests. *Restoration Ecology*, *22*(4): 480-485.

81. Riva, F., Haddad, N., Fahrig, L., & Banks-Leite, C. (2024). Principles for area-based biodiversity conservation. *Ecology Letters*, *27*(6), e14459.

82. León-Cortés, J. L., Córdoba-Aguilar, A., Rodríguez, P., & Rocha-Ortega, M. (2024). Habitat fragmentation and insect biodiversity change in Mexican landscapes. In *Insect Decline and Conservation in the Neotropics* (pp. 17-36). Cham: Springer International Publishing.

83. Merckx, T., & Van Dyck, H. (2019). Urbanization-driven homogenization is more pronounced and happens at wider spatial scales in nocturnal and mobile flying insects. *Global Ecology and Biogeography*, *28*(10), 1440-1455.

84. Soga, M., & Koike, S. (2012). Relative importance of quantity, quality and isolation of patches for butterfly diversity in fragmented urban forests. *Ecological Research*, *27*(2), 265-271.

85. Habel, J. C., Samways, M. J., & Schmitt, T. (2019). Mitigating the precipitous decline of terrestrial European insects: Requirements for a new strategy. *Biodiversity and Conservation*, *28*(6), 1343-1360.

86. Moore, J. W., & Schindler, D. E. (2022). Getting ahead of climate change for ecological adaptation and resilience. *Science*, *376*(6600), 1421-1426.

87. Hill, J. K., Hughes, C. L., Dytham, C., & Searle, J. B. (2006). Genetic diversity in butterflies: interactive effects of habitat fragmentation and climate-driven range expansion. *Biology Letters*, *2*(1), 152-154.

88. Minter, M., Dasmahapatra, K. K., Thomas, C. D., Morecroft, M. D., Tonhasca, A., Schmitt, T., ... & Hill, J. K. (2020). Past, current, and potential future distributions of unique genetic diversity in a cold-adapted mountain butterfly. *Ecology and Evolution*, *10*(20), 11155-11168.

89. Santos, J. P., T. Sobral-Souza, K. S. Brown Jr., M. H. Vancine, M. C. Ribeiro & A. V. L. Freitas. (2020). Effects of landscape modification on species richness patterns of fruit-feeding butterflies in Brazilian Atlantic Forest. *Diversity and Distributions*, *26*(2): 196-208.

90. Di Marco, M., Chapman, S., Althor, G., Kearney, S., Besancon, C., Butt, N., ... & Watson, J. E. (2017). Changing trends and persisting biases in three decades of conservation science. *Global Ecology and Conservation*, *10*, 32-42.

91. Molina-Martínez, A., León-Cortés, J. L., Regan, H. M., Lewis, O. T., Navarrete, D., Caballero, U., & Luis-Martínez, A. (2016). Changes in butterfly distributions and species assemblages on a Neotropical mountain range in response to global warming and anthropogenic land use. *Diversity and Distributions*, *22*(11), 1085-1098.

92. Boyle, M. J., Bonebrake, T. C., Dias da Silva, K., Dongmo, M. A., Machado França, F., Gregory, N., ... & Ashton, L. A. (2025). Causes and consequences of insect decline in tropical forests. *Nature Reviews Biodiversity*, 1-17.

93. van Swaay, C. A., Nowicki, P., Settele, J., & Van Strien, A. J. (2008). Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation*, *17*(14), 3455-3469.

94. Forister, M. L., Halsch, C. A., Nice, C. C., Fordyce, J. A., Dilts, T. E., Oliver, J. C., ... & Glassberg, J. (2021). Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West. *Science*, *371*(6533), 1042-1045.

95. Edwards, C. B., Zipkin, E. F., Henry, E. H., Haddad, N. M., Forister, M. L., Burls, K. J., ... & Schultz, C. B. (2025). Rapid butterfly declines across the United States during the 21st century. *Science*, *387*(6738), 1090-1094.

96. Lamarre, G. P. A., T. M. Fayle, S. T. Segar, B. C. Laird-Hopkins, A. Nakamura, D. Souto-Vilarós, S. Watanabe, and Y. Basset. 2020. Monitoring tropical insects in the 21st century. *Advances in Ecological Research*, *62*, 295–330.

97. Zografou, K., Knop, E., Sewall, B. J., Schweiger, O., De Moraes, C. M., Whitaker, M., & Kati, V. (2025). Butterfly body size shrinkage: the impact of ecological traits across varied environments. *bioRxiv*, 2025-02. http://dx.doi.org/10.1101/2025.02.06.636804.

98. van Swaay, C., Regan, E., Ling, M., Bozhinovska, E., Fernandez, M., Marini-Filho, O. J., ... & Underhill, L. (2015). Guidelines for standardised global butterfly monitoring. *Group on Earth Observations Biodiversity Observation Network*, Leipzig, Germany. GEO BON Technical Series, 1,

32.

99. Yau, E. Y. H., Jones, E. E., Tsang, T. P. N., Xing, S., Corlett, R. T., Roehrdanz, P., ... & Bonebrake, T. C. (2025). Spatial occurrence records and distributions of tropical Asian butterflies. *Scientific Data*, *12*(1), 1004.

100. Miller, J., White, T. B., & Christie, A. P. (2023). Parachute conservation: Investigating trends in international research. *Conservation Letters*, *16*(3), e12947.

101. Jarić, I., Diagne, C., & Chowdhury, S. (2025). Moving beyond continents for global and inclusive science. *Frontiers in Ecology and the Environment*, *23*(4), e2851.

102. Paterson, G., Albuquerque, S., Blagoderov, V., Brooks, S., Cafferty, S., Cane, E., ... & Wing, P. (2016). iCollections–Digitising the British and Irish Butterflies in the Natural History Museum, London. *Biodiversity Data Journal*, Sep (4), e9559.

103. Mason, B. M., Mesaglio, T, Heitmann, J. B., Chandler, M., Chowdhury, S., Gorta, S. B. Z., Grattarcola, F., Groom, Q., Hitchcock, C., Hoskins, L., Lowe, S. K., Marquis, M., Pernat, N., Shirey, V, Baasanmunkh, S, Callaghan, C. T. (2025). iNaturalist accelerates biodiversity research. *BioScience*, biaf104.

104. Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R., & Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports*, *7*(1), 9132.

105. Sheard, J. K., Adriaens, T., Bowler, D. E., Büermann, A., Callaghan, C. T., Camprasse, E. C., ... & Bonn, A. (2024). Emerging technologies in citizen science and potential for insect monitoring. *Philosophical Transactions of the Royal Society B*, *379*(1904), 20230106.

106. Martin, C. J., Twambaze, J. M., & Riva, F. (2025). A nature tourism and citizen science alliance. *BioScience*, *75*(5), 358-361.

107. Basset, Y., Novotny, V., Miller, S. E., Weiblen, G. D., Missa, O., & Stewart, A. J. (2004). Conservation and biological monitoring of tropical forests: the role of parataxonomists. *Journal of Applied Ecology*, 163-174.

108. Sumner, S., Bevan, P., Hart, A. G., & Isaac, N. J. (2019). Mapping species distributions in 2 weeks using citizen science. *Insect Conservation and Diversity*, *12*(5), 382-388.

109. Kelling, S., Johnston, A., Bonn, A., Ruiz-Gutierrez, V., Bonney, R., Fink, D., Julliard, R., Hochachka, W.M., Fernandez, M., Kraemer, R. & Guralnick, R. (2019) Using semistructured surveys to improve citizen science data for monitoring biodiversity. *Bioscience*, *69*, 170-179.

110. Rosa, A. H., & Freitas, A. V. L. (2024). The role of citizens in conservation science: a case study with threatened Brazilian butterflies. *Journal of Insect Conservation*, 28(6), 1149-1160.

111. Rosa, A. H., Ribeiro, D. B., & Freitas, A. V. L. (2023). How data curation and new geographical records can change the conservation status of threatened Brazilian butterflies. *Journal of Insect Conservation*, 27(3), 403-414.

112. Chowdhury, S., Aich, U., Rokonuzzaman, M., Alam, S., Das, P., Siddika, A., ... & Callaghan, C. T. (2023). Increasing biodiversity knowledge through social media: A case study from tropical Bangladesh. *BioScience*, 73(6), 453-459.

113. Badon, J. A. T., Lahom-Cristobal, L., & Talavera, A. A. (2019). Philippine Lepidoptera butterflies and moths, inc. a new online resource for southeast Asian Lepidoptera. *News of the Lepidopterists' Society*, *61*, 178-179.

114. Hochkirch, A., Casino, A., Penev, L., Allen, D., Tilley, L., Georgiev, T., ... & Barov, B. (2022). *European red list of insect taxonomists*. Luxembourg: Publications Office of the European Union.

115. Pocock, M. J., Roy, H. E., Preston, C. D., & Roy, D. B. (2015). The Biological Records Centre: a pioneer of citizen science. *Biological Journal of the Linnean Society*, *115*(3), 475-493.

116. Danielsen, F., Ali, N., Andrianandrasana, H. T., Baquero, A., Basilius, U., de Araujo Lima Constantino, P., ... & Burgess, N. D. (2024). Involving citizens in monitoring the Kunming–Montreal global biodiversity framework. *Nature Sustainability*, *7*(12), 1730-1739.

117. Turrini, T., Dörler, D., Richter, A., Heigl, F. & Bonn, A. (2018) The threefold potential of environmental citizen science - Generating knowledge, creating learning opportunities and enabling civic participation. *Biological Conservation*, *225*, 176-186.

118. Kelly, R., Fleming, A., Pecl, G.T., Richter, A. & Bonn, A. (2019) Social license through citizen science: a tool for marine conservation. *Ecology and Society*, *24*(1), 16.

119. Maxwell, S. L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A. S., Stolton, S., ... & Watson, J. E. (2020). Area-based conservation in the twenty-first century. *Nature*, *586*(7828), 217-227.

120. Chowdhury, S., Jennions, M. D., Zalucki, M. P., Maron, M., Watson, J. E., & Fuller, R. A. (2023). Protected areas and the future of insect conservation. *Trends in Ecology & Evolution*, *38*(1), 85-95.

121. Chowdhury, S., Zalucki, M. P., Hanson, J. O., Tiatragul, S., Green, D., Watson, J. E., & Fuller, R. A. (2023). Three-quarters of insect species are insufficiently represented by protected areas. *One Earth*, *6*(2), 139-146.

122. Chowdhury, S., Cardillo, M., Chapman, J. W., Green, D., Norris, D. R., Riva, F., ... & Fuller, R. A. (2025). Protected area coverage of the full annual cycle of migratory butterflies. *Conservation Biology*, *39*(3), e14423.

123. Fordham, D. A., Akçakaya, H. R., Araújo, M. B., Keith, D. A., & Brook, B. W. (2013). Tools for integrating range change, extinction risk and climate change information into conservation management. *Ecography*, *36*(9), 956-964.

124. Convention on Biological Diversity (CBD). (2022). *Kunming–Montreal Global biodiversity framework*. Draft decision submitted by the President CBD/COP/15/L.25, 18 December 2022. https://www.cbd.int/conferences/2021-2022/cop-15/documents.

125. Edgar, G. J. (2025). IUCN Red List criteria fail to recognise most threatened and extinct species. *Biological Conservation*, *301*, 110880.

126. Braby, M. F. (1992). Distribution and range reduction in Victoria of the Eltham Copper Butterfly *Paralucia pyrodiscus lucida* Crosby. *The Victorian Naturalist*, *109*, 155-161.

127. Pottier, P., Kearney, M. R., Wu, N. C., Gunderson, A. R., Rej, J. E., Rivera-Villanueva, A. N., ... & Nakagawa, S. (2025). Vulnerability of amphibians to global warming. *Nature*, *639*, 954–961.

128. Maes, D., Ellis, S., Goffart, P., Cruickshanks, K. L., Van Swaay, C. A., Cors, R., ... & Bourn, N. A. (2019). The potential of species distribution modelling for reintroduction projects: the case study of the Chequered Skipper in England. *Journal of Insect Conservation*, *23*(2), 419-431.

129. Langdon, B. (2025). Tackling potential bias in global biodiversity indicators: The relevance of considering local data and non-English literature. *Journal of Applied Ecology* (in press). https://doi.org/10.1111/1365-2664.70125.

130. Wallingford, P. D., Morelli, T. L., Allen, J. M., Beaury, E. M., Blumenthal, D. M., Bradley, B. A., ... & Sorte, C. J. (2020). Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. *Nature Climate Change*, *10*(5), 398-405.

131. León-Cortés, J. L., Lennon, J. J., & Thomas, C. D. (2003). Ecological dynamics of extinct species in empty habitat networks. 1. The role of habitat pattern and quantity, stochasticity and dispersal. *Oikos*, *102*(3), 449-464.

List of table

Table 1. Types and definitions of range shifts considered in this study, including examples from butterfly species. We define *range shifts* as partial changes in species distributions across space or elevation, rather than complete shifts of entire populations from one location to another. Here, area of occupancy is defined as the area within its 'extent of occurrence' which is occupied by a taxon, excluding cases of vagrancy (IUCN, 2012).

Range shift type	Definition	Example
Range expansion	The process by which a species' range expands horizontally by colonising new locations and establishing viable populations beyond the margins of its original area of occupancy[130]. To be inclusive, we considered species new to a region as range-expanding species.	Between 2012 and 2019, *Acraea terpsicore*, native to the Indian subcontinent, expanded its geographic range at 135 km/year in Australia[16].
Range contraction	The process by which a species' range contracts horizontally by going locally extinct (i.e., extirpation) in parts of its original area of occupancy[130]. To be inclusive, we considered species that became extirpated from a region as range-contracting species.	Over the last 150 years, *Cupido minimus* has lost 40% of its habitat in the UK[131], leading to severe horizontal range contraction along the latitudinal gradient of the UK.
Elevational shift	The process by which a species' moves to higher or lower elevational areas (e.g., shifting its upper elevational limit, its optimum elevation or its lower elevational limit either upslope or downslope), compared to its original elevational range[5].	Between 1988 and 2011, *Vanessa cardui* experienced a range shift towards higher elevations at a rate of 83 m/year in Mexico, while *Danaus gilippus* shifted towards lower elevations at a rate of 32 m/year[91].

List of figures

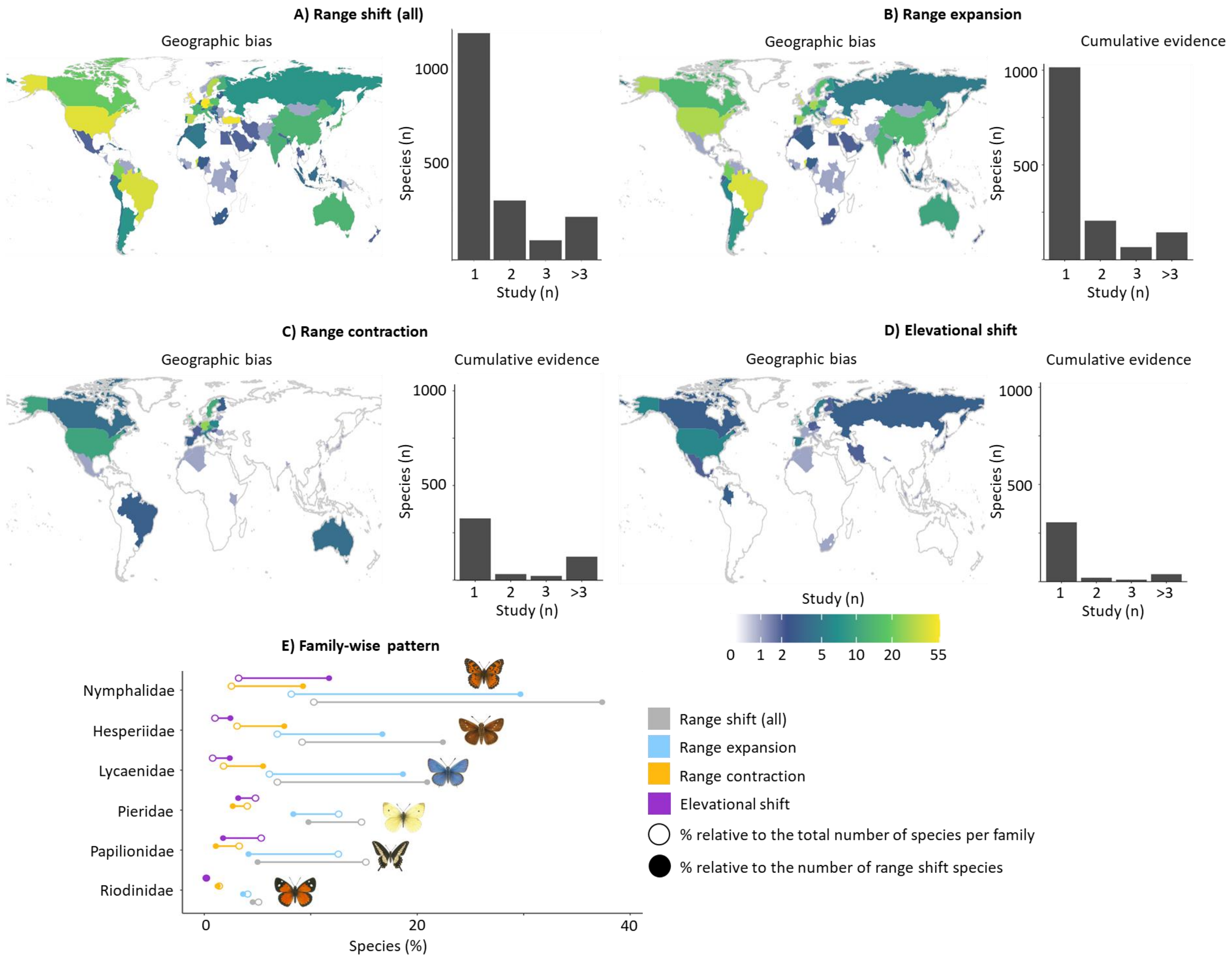
Figure 1. Global spatial patterns of 1758 butterfly range shifts in our data: geographic distribution and cumulative evidence (A-D) are shown, as well as family-wise distribution (E) in reporting butterfly range shifts. The colour legend (A-D), in log scale, shows the number of studies reporting range shifts for butterflies per country, where 0 means we did not obtain any range data from that country (shown in white). Histograms indicate the number of studies for which a given species had been reported to shift, with a clear bias towards single-study reports for a majority of butterfly species and a few cases of butterfly species being reported to shift from 2, 3 or more than 3 distinct studies. In (E), we calculated the '% relative to the total number of butterfly species' by comparing the number of range shifting species to the total number of documented butterfly species per family and the '% relative to the number of range shift species' by comparing the number of range shift species to the total number of range shift species in our data (n= 1758).

Figure 2. Proportion of shifting butterfly species relative to the total number of butterfly species known to occur within each country (Pinkert et al.[30], with 0% indicating we did not obtain any range shift data from that country (shown in white). High values in Europe reflect both genuine change and the much greater probability of detecting shifts given long-term programs; lower values in many tropical countries likely reflect data scarcity rather than biological stability.

Figure 3. Proportion of shifting butterfly species relative to the total number of range shift species, which were reported to have experienced shifts either in the focal country or elsewhere, with 0% indicating we did not obtain any range shift data of a species of that country (shown in white). High values in Europe reflect both genuine change and the much greater probability of detecting it given long-term programs; lower values in many tropical countries likely reflect data scarcity rather than biological stability.

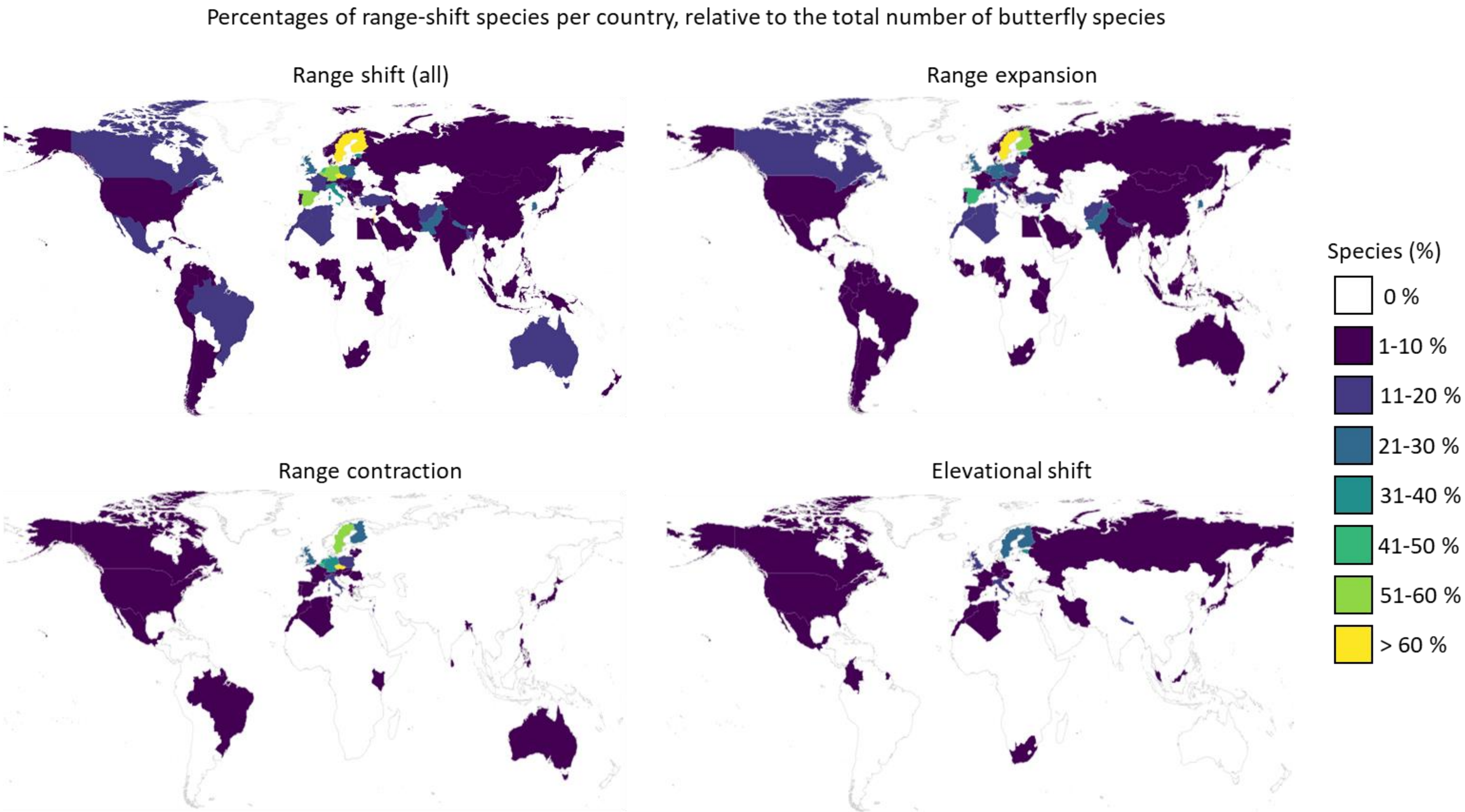
Figure 4. Distribution of threats attributed to butterfly species range shifts (compiled from published literature and experts). (A) Summary of the identified threats underlying butterfly species range shifts, where each bar shows the number of butterfly species for which range shifts were attributed to a given threat, and their distribution per continent (B). Here, 'threats by species' indicates the number of times the threat was reported in a given species-by-continent combination. Labels refer to *Climate* = climate change and severe weather, *Agriculture* = agriculture and aquaculture, *Intrusion* = human intrusions and disturbance, *Development* = residential and commercial development, *Transportation* = transportation and service corridors, *Modifications* = natural system modifications, *Invasive* = invasive and other problematic species, genes and diseases, *Resource use* = biological resource use, and *Energy* = energy production and mining.

1054 **Figure 1**



1055

Figure 2



Percentages of range-shift species per country, relative to the total number of butterfly species
Range shift (all)
Range expansion
Range contraction
Elevational shift
Species (%)
0 %
1-10 %
11-20 %
21-30 %
31-40 %
41-50 %
51-60 %
> 60 %

Figure 3

Percentages of range-changed species per country, relative to the total number of range-shift species

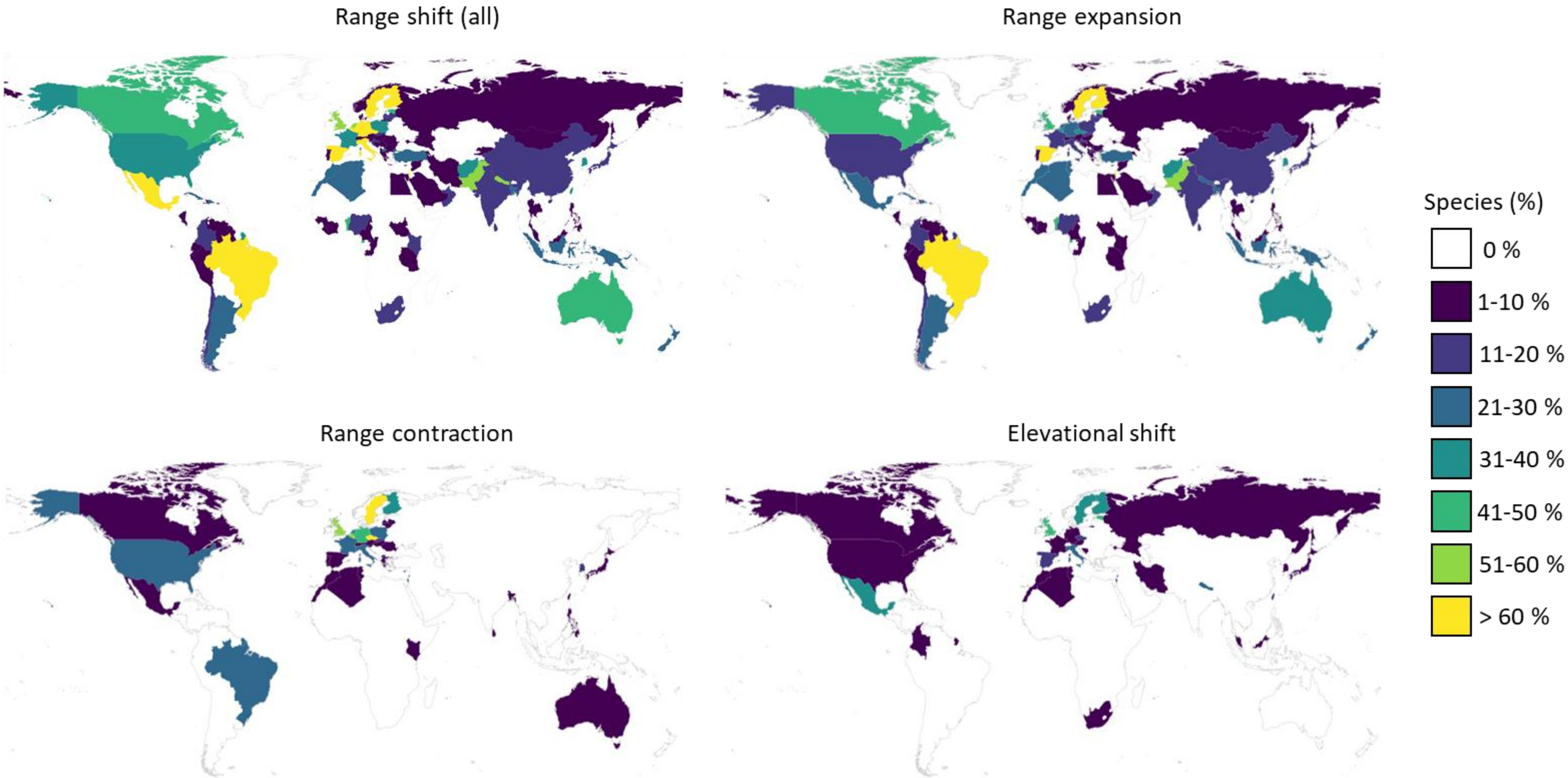
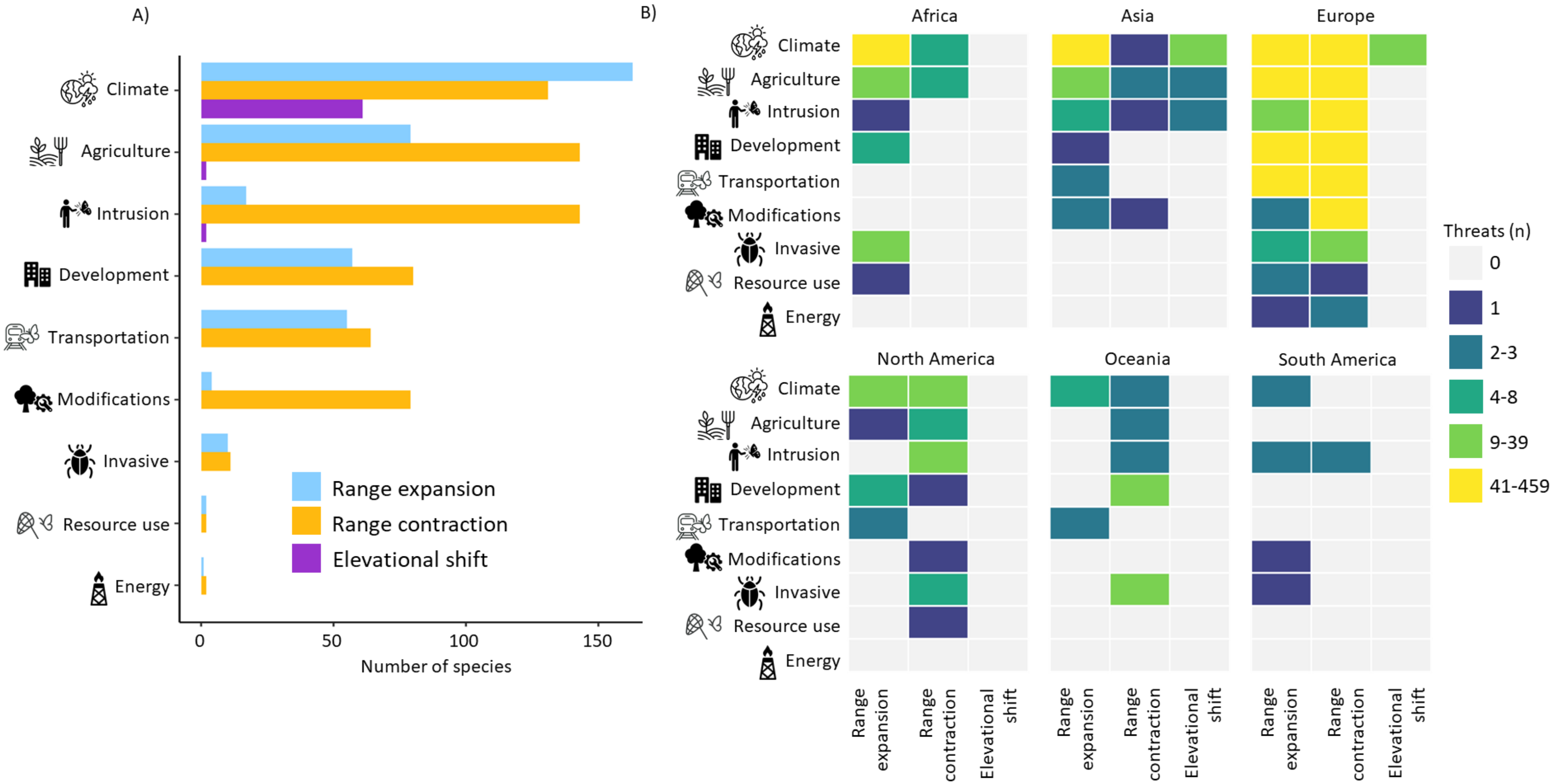


Figure 4



A)
Climate
Agriculture
Intrusion
Development
Transportation
Modifications
Invasive
Resource use
Energy
0
50
100
150
Number of species
Range expansion
Range contraction
Elevational shift
B)
Africa
Asia
Europe
North America
Oceania
South America
Range expansion
Range contraction
Elevational shift
Threats (n)
0
1
2-3
4-8
9-39
41-459