

A systematic review of assessing climate change risks on species and ecosystems: bibliometric overview, concepts, approaches, and trends

Hui Wu^a, Le Yu^{a,b,c,*}, Xiaoli Shen^d, Fangyuan Hua^e, Zhicong Zhao^{f,g}, Yixuan Li^h, Keping Ma^d

^a Department of Earth System Science, Ministry of Education Key Laboratory for Earth System Modeling, Institute for Global Change Studies, Tsinghua University, Beijing 100084, China

^b Ministry of Education Ecological Field Station for East Asian Migratory Birds, Beijing 100084, China

^c Tsinghua University (Department of Earth System Science)- Xi'an Institute of Surveying and Mapping Joint Research Center for Next-Generation Smart Mapping, Beijing 100084, China

^d State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China

^e Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 102213, China.

^f Institute for National Parks, Tsinghua University, Beijing, 100084, China

^g Department of Landscape Architecture, School of Architecture, Tsinghua University, Beijing, 100084, China

^h The University of Manchester, Manchester M13, The United Kingdom

* Corresponding author at: Department of Earth System Science, Ministry of Education Key Laboratory for Earth System Modeling, Institute for Global Change Studies, Tsinghua University, Beijing 100084, China. E-mail address: leyu@tsinghua.edu.cn (L. Yu)

Keywords: climate change, risk assessment, species, ecosystem, bibliometric analysis, vulnerability, model, early warning

Abstract

Non-technical summary. Climate change is significantly altering our planet, with greenhouse gas emissions and environmental changes bringing us closer to critical tipping points. These changes are impacting species and ecosystems worldwide, leading to the urgent need for understanding and mitigating climate change risks. In this study, we examined global research on assessing climate change risks to species and ecosystems. We found that interest in this field has grown rapidly, with researchers identifying key factors such as species' vulnerability, adaptability, and exposure to environmental changes. Our work highlights the importance of developing better tools to predict risks and create effective protect strategies.

Technical summary. The rising concentration of greenhouse gases, coupled with environmental changes such as albedo shifts, is accelerating the approach to critical climate tipping points. These changes have triggered significant biological responses on a global scale, underscoring the urgent need for robust climate change risk assessments for species and ecosystems. We conducted a systematic literature review using the Web of Science database. Our bibliometric analysis shows an exponential growth in publications since 2000, with over 200 papers published annually since 2019. Our bibliometric analysis reveals that the number of studies has exponentially increased since 2000, with over 200 papers published annually since

This is an Open Access article, distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives licence (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is unaltered and is properly cited. The written permission of Cambridge University Press must be obtained for commercial re-use or in order to create a derivative work.

2019. High-frequency keywords such as “impact,” “risk,” “vulnerability,” “response,” “adaptation,” and “prediction” were prevalent, highlighting the growing importance of assessing climate change risks. We then identified five universally accepted concepts for assessing the climate change risk on species and ecosystems: distribution, exposure, sensitivity, adaptivity, and vulnerability. We provided an overview of the principles, applications, advantages, and limitations of climate change risk modeling approaches like correlative approaches, mechanistic approaches, and hybrid approaches. Finally, we emphasize that the emerging trends of risk assessment of climate change, encompass leveraging the concept of telecoupling, harnessing the potential of geography, and developing early warning mechanisms.

Social Media summary

Climate change risks to biodiversity and ecosystem: Key insights, modeling approaches, and emerging strategies.

1. Introduction

Throughout the long history of the Earth’s movements, its climate has undergone constant change. However, the current anthropogenic “climate change” is distinct from natural climate variability caused by natural factors. Presently, greenhouse gas concentrations on Earth have reached their highest level in 2 million years and are continuing to rise. According to the World Meteorological Organization’s Global Climate Status 2022 (WMO, 2023), the global average temperature in 2022 was 1.15°C higher than the pre-industrial average (1850-1900), a rise that aligns with intermediate climate change scenarios predicting a continued upward trend. With current CO₂ emission trends, global temperatures are projected to rise by as much as 4.4 degrees Celsius by the end of the century, pushing the planet closer to an unmanageable tipping point for climate change. Presently, 3.5 billion people live in highly climate-vulnerable countries. Catastrophic consequences, including extreme weather events, mega-fires, ocean heatwaves, food crises, and biodiversity loss, can result from climate change (McDowell et al., 2018).

Life processes on Earth are intricately linked to environmental changes across multiple spatial and temporal scales (Davis & Shaw, 2001). The geographic distribution of any species depends on factors such as environmental tolerance, dispersal limits, and biological interactions with other species (Wunderling et al., 2022; Antão et al., 2022). The combined rate and magnitude of climate change have triggered global-scale biological responses. In the face of climate change, marine, freshwater, and terrestrial species often respond by shifting their locations to seek more suitable environmental conditions. Terrestrial species tend to shift to areas with lower temperatures and higher altitudes, while marine species move to deeper and colder waters. Additionally, species undergo changes in relative abundance, timing of activity, and microhabitat use across their ranges (Bates et al., 2014). Studies indicate that terrestrial species move on average 17 km poleward every decade, while marine species move about 72 km poleward every decade (Sorte et al., 2010; Chen et al., 2011; Poloczanska et al., 2013). However, some species’ response may lag behind climate change due to species-specific physiological, behavioral, ecological, and evolutionary responses or due to a lack of adequate

habitat connectivity and access to microhabitats and microclimates. It is crucial to recognize that species have limits to their ability to adapt to changing environments (Williams et al., 2008), and once these limits are exceeded, species are at risk of extinction.

Ecosystems play a vital role in supporting biological survival and development, offering both tangible material resources and intangible environmental conditions. The effects of changes in species distributions are not limited to a single system or dimension; instead, they involve feedbacks and linkages across multiple interacting spatial and temporal scales, extending to various ecosystems. Alterations in species diversity due to redistribution are likely to have indirect impacts on ecosystem conditions (Schmidt-Traub et al., 2021). According to predictions, vegetation in the Arctic will shift from being dominated by high-albedo lichens and mosses to low-albedo coniferous forests by 2050 (Pearson et al., 2013). The combined effects of earlier snowmelt and increased shrub density at high latitudes will reduce albedo, leading to increased net radiation and exacerbating warming in those regions (Chapin 3rd et al., 2005). Moreover, the combined impacts of warmer temperatures and drought will intensify plant stress, contributing to more severe pest outbreaks and tree mortality, further influencing ecosystems and their capacity to provide benefits to humans and other species.

Considering the far-reaching consequences of climate change on species and ecosystems, it becomes imperative to gain a comprehensive understanding of potential risks and develop effective strategies to mitigate its effects. Risk assessment serves as a systematic process of identifying, analyzing, and evaluating potential hazards and their associated impacts (IPCC, 2022). Traditional risk assessment methods were originally developed for specific hazards, such as chemical exposure, they were not explicitly designed to address the impacts of climate change (Rowland et al., 2011). Consequently, researchers have been dedicated to developing and refining climate-driven risk assessment methods. These methodologies integrate climate models, species distribution data, and ecological knowledge to predict future risks and assist in planning adaptation strategies. By utilizing climate-driven risk assessment, scientists and policymakers can better comprehend the potential consequences of climate change on biodiversity and ecosystems, thereby strengthening our capacity to respond effectively and protect vulnerable species and habitats.

The Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) protocol is designed to enhance the reproducibility of reviews and facilitate readers' understanding of the entire protocol followed during the literature review (Page et al., 2021). Following the PRISMA protocol, our study involved a systematic search in the Web of Science (WoS) core collection database. In the initial phase, we focused on identifying relevant records through two distinct searches: Topic 1: "species" AND "climate change" AND "risk"; Topic 2: "ecosystem" AND "climate change" AND "risk". Our search spanned from January 1, 2000, to December 31, 2022 (accessed on April 1, 2023). After retrieving pertinent publications, we refined the results to include only "Article" document types. This process yielded 7,570 articles for Topic 1 and 5,575 articles for Topic 2. The subsequent step involved a thorough screening process. We reviewed the titles and abstracts of each article to identify those addressing, describing, quantifying, or mapping climate change-related risks on species and ecosystems. Irrelevant literature was filtered out, and the 2,000 most relevant

articles for each of the two topics were used to conduct a bibliometric overview. In the final stage, we read the full text of each selected publication, extracting generally accepted concepts, approaches used to model risk, and emerging trends. The flowchart illustrating the literature screening and review process is shown in Fig. 1.

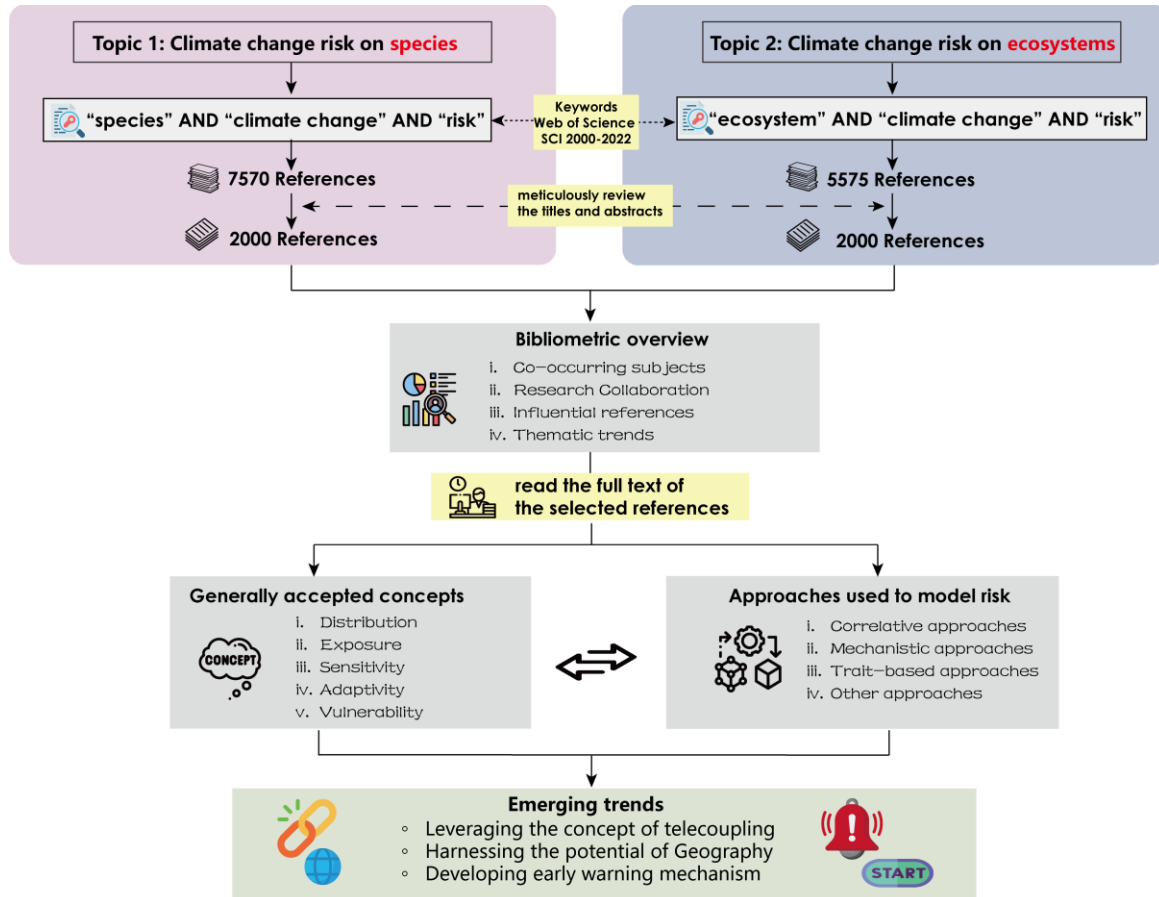


Fig. 1. Flowchart depicting the process of literature screening and review

2. Bibliometric overview of climate change risk assessment

Bibliometric analysis serves as an effective method for qualitatively and quantitatively analyzing a vast number of existing publications. CiteSpace, an open-source bibliometric software developed by Drexel University in 2004, stands as one of the most widely utilized tools for bibliometric analysis (Chen, 2006). By employing mathematical and statistical methods, CiteSpace analyzes data and offers knowledge map presentations.

2.1 Co-occurring subjects

The number of studies on climate change risk on species and ecosystems has been exponentially increased since 2000 (Fig. 2a). Between 2000 and 2004, less than 25 papers are published in both fields,

whereas since 2013, more than 100 papers have been published each year, and the annual published papers has exceeded 200 since 2019. Fig. 2b presents the co-occurring subject categories network of topic 1, which comprises 59 nodes and 262 links. Notably, the top three categories in terms of research activity were as follows: Environmental Sciences & Ecology (1216, 0.14); Biodiversity & Conservation (551, 0.06); and Ecology (527, 0.58). The numbers in parentheses represent the number of articles and the centrality of the categories, respectively. Fig. 2c displays the co-occurring subject categories network of topic 2 consisting of 73 nodes and 198 links. In this case, the top three categories were as follows: Environmental Sciences (427, 0.54); Ecology (334, 0.24); and Biodiversity & Conservation (223, 0.06). Frequent co-occurrence among subject categories indicates that the field of study is inherently multidisciplinary and interdisciplinary.

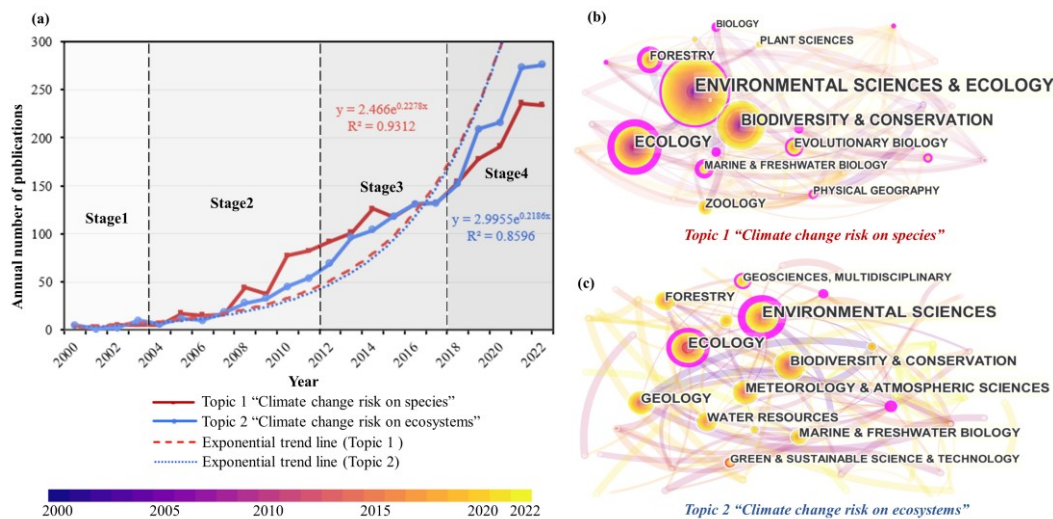


Fig. 2. Annual number of publications from 2000 to 2022, divided into four stages: Stage 1 (2000–2005), Stage 2 (2006–2010), Stage 3 (2011–2015), and Stage 4 (2016–2022), showing the growth trend in research on the topics (a); Co-occurring subject categories network of topic 1 “Climate change risk on species” (b); Co-occurring subject categories network of topic 2 “Climate change risk on ecosystems” (c).

2.2 Research collaboration

The number of publications in a given field represents the level of a country’s activity in that particular area, while the centrality values of nodes in the cooperation network signify the authority and leadership of countries within the field. The United States, the United Kingdom, and Australia are the top three countries in terms of the number of papers of topic 1, accounting for 42.27% of all research papers in this field (Fig. 3a). However, the centrality of these three countries is relatively lower, with values of 0.02, 0.13, and 0.18, respectively (Fig. 3b). The United States, China, and the United Kingdom are the top three countries in terms of the number of papers of topic 2, accounting for 40.69% of all research papers in this area (Fig. 3c). When considering centrality, France, Germany, and Finland take the lead, with centrality values of 0.21, 0.18, and 0.18, respectively (Fig. 3d). In both fields, it is evident that the top three countries in terms of the number of publications contribute to more than 40% of all publications, highlighting the significant disparity between

countries in research output within these fields. The large number of links between nodes in Fig. 3b and 3d further illustrates the extensive collaboration between countries across the globe.

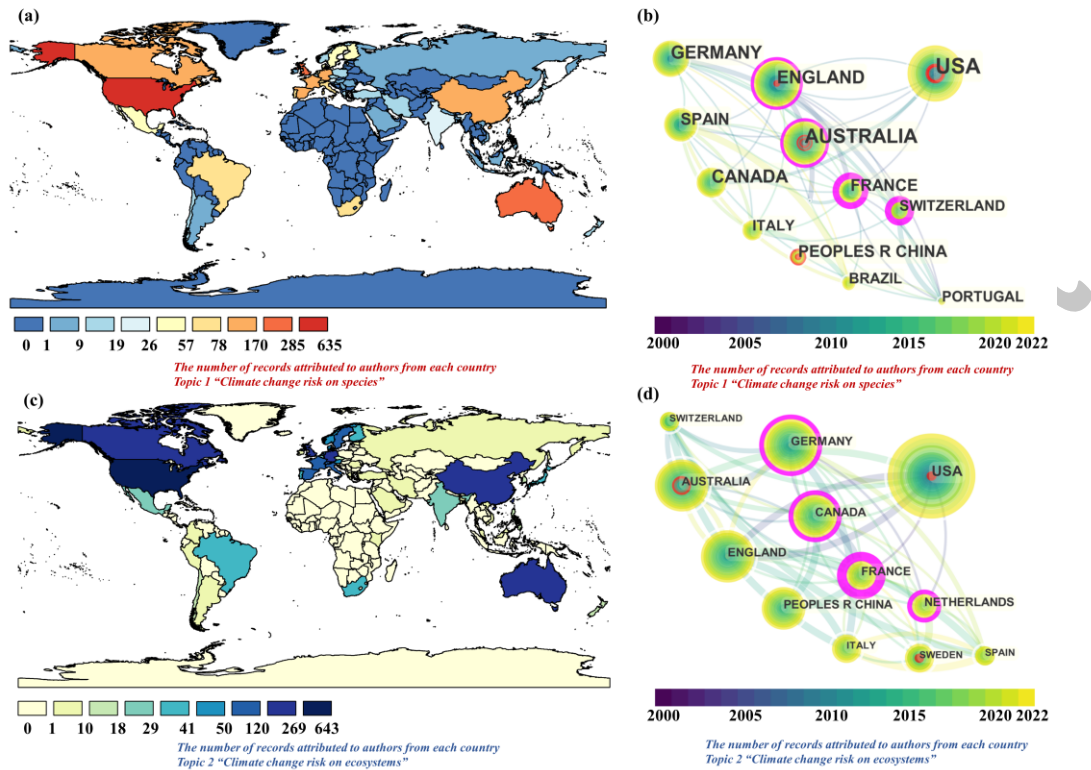


Fig. 3. The number of records attributed to authors from each country of topic 1 (a) and topic 2 (c). Country collaboration network of topic 1 (b) and topic 2 (d).

An institution co-authorship analysis was employed to unveil academic collaborations at the institutional (Fig. 4a-4b) and author levels (Fig. 4c-4d). In the field of topic 1, there were 193 institutions involved, resulting in 412 collaborations among them. The institutions with the highest research output included the Chinese Academy of Sciences (CAS), Consejo Superior de Investigaciones Científicas (CSIC), and the University of British Columbia (UBC). In the field of topic 2, the organizations with the largest research output in this field were the Chinese Academy of Sciences (CAS), the U.S. Geological Survey (USGS), and the U.S. Forest Service (USFS). The network of Topic 1 comprised 105 collaborations and 92 nodes, whereas the network of Topic 2 comprised 27 collaborations and 35 nodes. The centrality of many nodes in the network of topic 1 exceeded 0.10, particularly those associated with several authors who had the highest publication volumes. In contrast, the network of topic 2 exhibited a division into numerous isolated sub-networks, with no nodes having a betweenness centrality greater than 0.01. This suggests that authors in the field of topic 2 tended to collaborate in small teams, and there was limited collaboration between these teams.

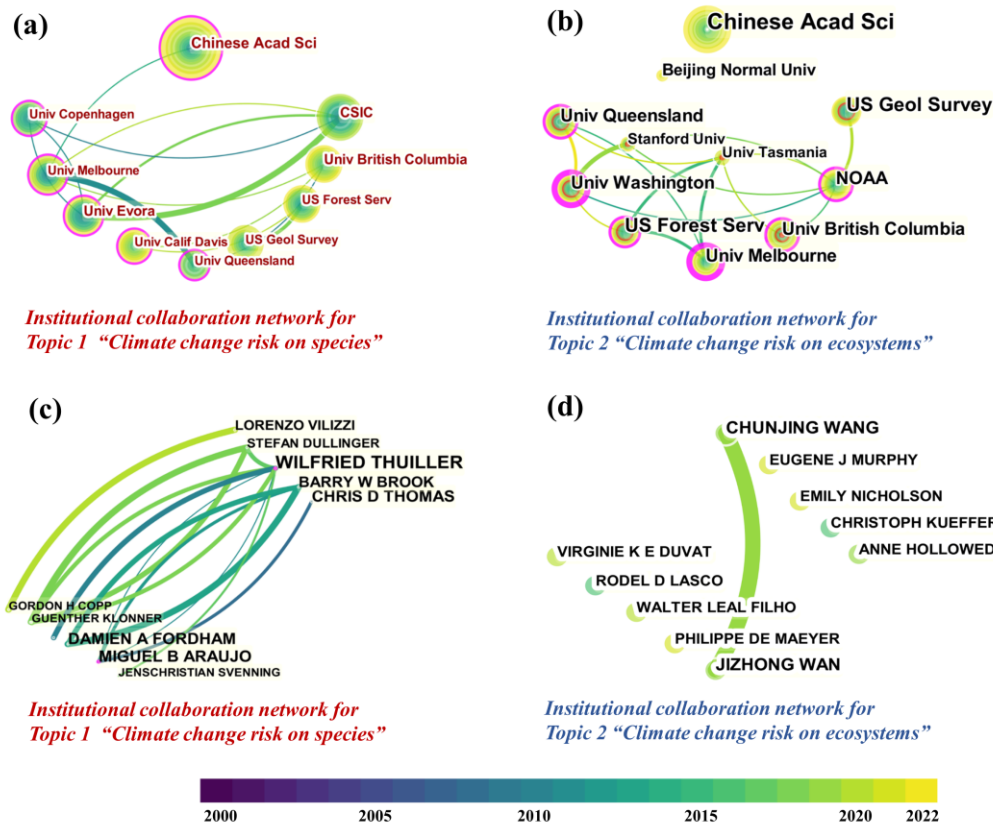


Fig. 4. Institutional collaboration network in the field of topic 1 (a) and topic 2 (b); Author collaboration network in the field of topic 1 (c) and topic 2 (d).

2.3 Influential references

Co-citation analysis allows us to gather valuable insights about the most frequently cited authors, references, and journals within a specific research area. The author co-citation network analysis in the field of topic 1 revealed a vast network comprising 2,344 nodes connected by 9,664 links, organized into 19 co-citation clusters. The author co-citation network analysis in the field of topic 2 comprised 2,226 nodes connected by 7,238 links, grouped into 19 co-citation clusters. Authors such as Parmesan C., Thomas C.D., and Thuiller W.C. featured prominently among the top 3 authors in both fields. Through an analysis of citation frequency, we identified 78,096 valid references of topic 1 and 102,697 valid references of topic 2. The three most cited articles in the field of topic 1 are as Urban (2015), Pecl et al. (2017), and Pacifici et al. (2015). Three most cited articles in the field of topic 2 are IPCC (2014), Pecl et al. (2017), and Seidl et al. (2017). Publications in the two fields are spread across 458 and 527 different journals, respectively (Fig. 5a and 5c). Journal co-citation analysis (Fig. 5b and 5d) show that the network of cited journals in the field of topic 1 comprises 1173 nodes organized into 71 co-citation clusters (modularity $Q = 0.538$, weighted average silhouette = 0.479). In contrast, the network of cited journals in the field of topic 2 consists of 1169 nodes organized into 81 co-citation clusters (modularity $Q = 0.7582$, weighted average silhouette = 0.6111).

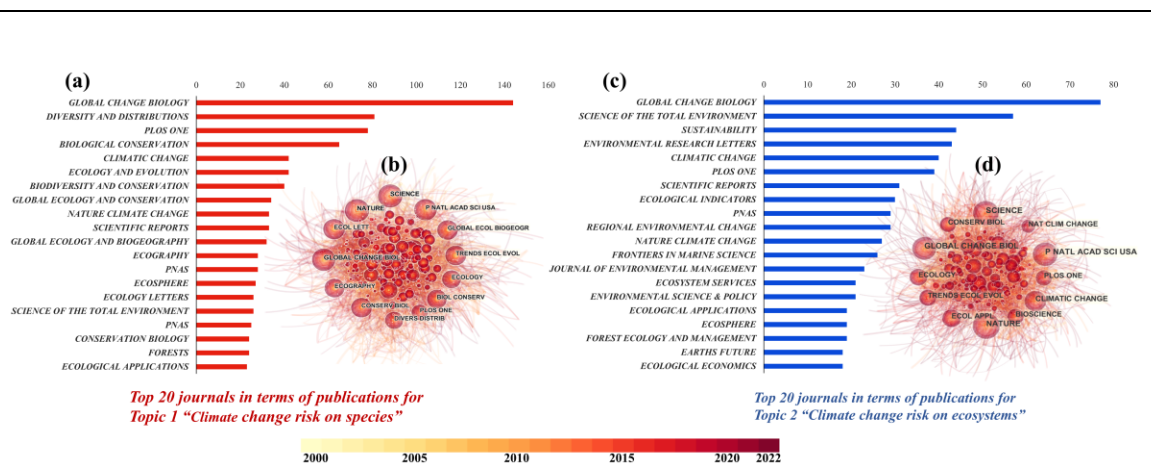


Fig. 5. Top 20 journals in term of publications in the field of “Climate change risk on species” (a) and the field of “Climate change risk on ecosystems” (c). Visualization of the journal co-citation network in the field of “Climate change risk on species” (b) and the field of “Climate change risk on ecosystems” (d).

2.4 Thematic trends

Keywords with high frequencies in a research area can effectively represent the hot topics of interest. In the field of topic 1, the top 10 keywords with the highest frequency are climate change, biodiversity, impact, extinction risk, conservation, distribution, model, risk, diversity, and response. In the field of topic 2, the top 10 keywords are climate change, impact, management, ecosystem service, biodiversity, risk, vulnerability, adaptation, conservation, and model. Table 1 presents the top 10 suddenly emerging keywords with high burst strength in the two fields. These observations illustrate that researchers are increasingly exploring novel topics such as climate change impacts, regional responses, and nature-based solutions. Among the high-frequency keywords in both fields, words such as impact, risk, vulnerability, resilience, response, adaptation, prediction, and management are prominent, signifying the growing importance of risk assessment and forewarning for the adaptation of species and ecosystems to climate change.

Table 1. The 10 keywords with strongest bursts in the field of topic 1 and topic 2

keywords	Topic 1 Climate change risk on species			Topic 2 Climate change risk on ecosystems			
	Strength	Begin	End	keywords	Strength	Begin	End
model	5.8275	2002	2007	climate change	11.0236	2000	2007
Europe	4.2486	2002	2010	risk	7.3376	2000	2008
bioclimate envelope	11.6689	2005	2012	ecosystem	4.7171	2006	2008
response	5.1215	2006	2008	global change	10.4325	2008	2014
migration	4.8972	2006	2015	plant	6.4747	2010	2013
niche model	4.7366	2008	2014	uncertainty	6.5312	2012	2017
envelope model	4.2059	2008	2012	California	6.4535	2013	2015
global change	4.769	2009	2017	future	5.0593	2013	2015
assisted colonization	6.6334	2010	2012	united states	4.8441	2014	2017
population model	4.8138	2011	2012	flood	4.6209	2014	2016

3. Generally accepted concepts to assess climate change risk

Assessing the climate change risk on species and ecosystem often involves the use of various ecological and conservation metrics. While no standardized unit of measurement exists explicitly for this purpose, researchers and conservationists commonly employ a combination of concepts to evaluate the impacts of climate change risk on species and ecosystems. These concepts provide valuable insights into different aspects of the ability of species and ecosystems to adapt and survive in the face of the changing climate risk (Fig.6, Table 2).

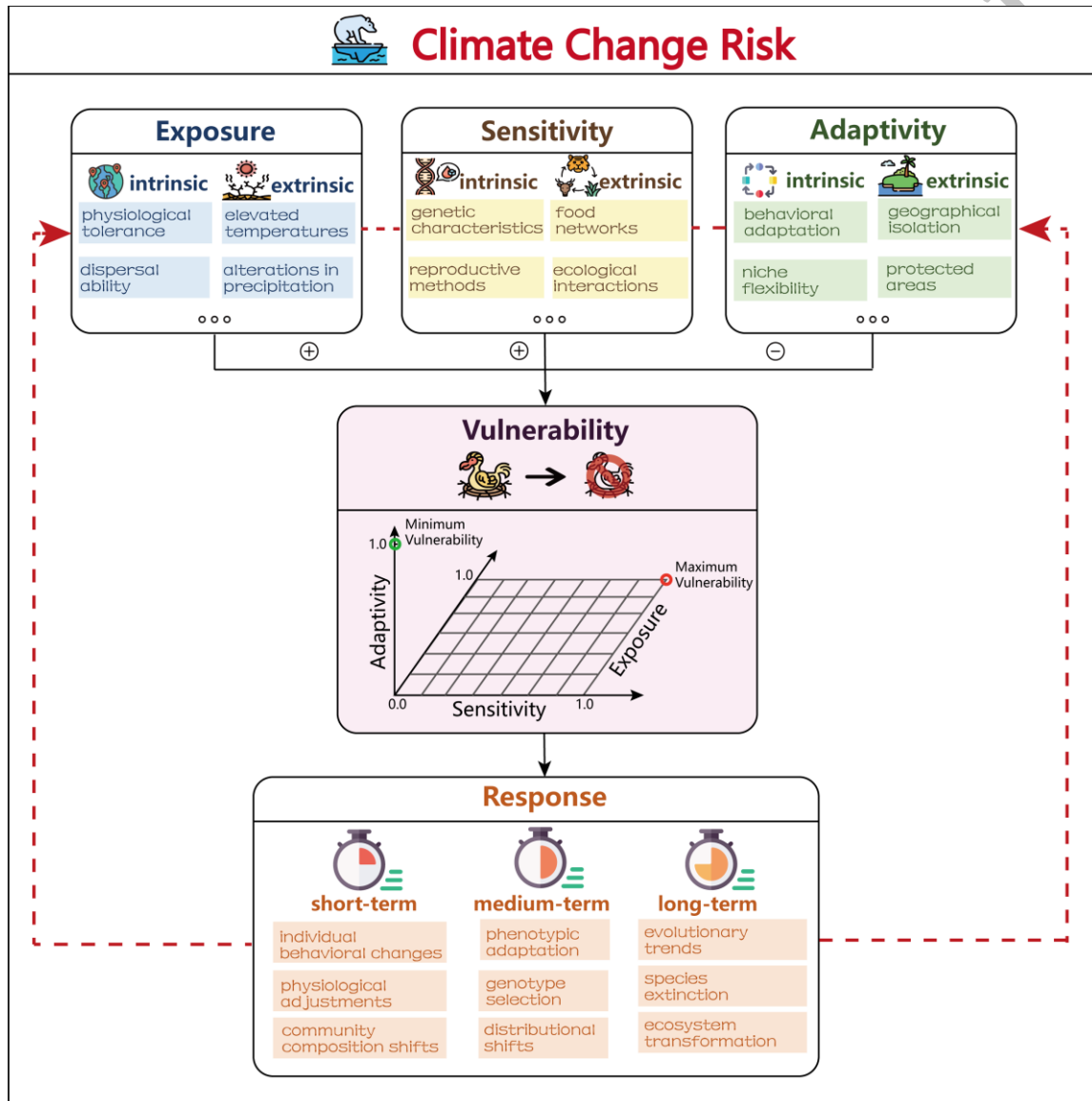


Fig. 6. Concepts used to assess climate change risk and their relations

1 **Table 2.** Examples of concepts in climate change risk assessments.

Types of concepts	Spatial scale	Temporal scale	Biological scale	Main findings	References
Exposure	local	future	ecosystem	There is substantial spatial heterogeneity in the exposure of ecosystem services to future climate changes on the Tibetan Plateau.	(Hua et al., 2021)
	regional	present	species, ecosystem	Chemical contaminant exposure can exacerbate the energetic challenges posed by climate change, leading to complex synergistic and antagonistic effects on organisms' fitness.	(Grunst et al., 2023)
	local	future	ecosystem	Mountain forests face high exposure to warming, which can trigger critical and potentially irreversible transitions in forest ecosystems, though topographic complexity can buffer some of these climate change impacts.	(Albrich et al., 2020)
Sensitivity	global	past	ecosystem	Ecologically sensitive regions, such as the Arctic tundra, tropical rainforest, and other key biomes, exhibit amplified responses to climate variability.	(Seddon et al., 2016)
	regional	past, future	species	Regional disparities in exposure to anthropogenic environmental changes, despite similar biotic sensitivity, may result in different extinction risks for plant species under future climate change scenarios.	(Song et al., 2021)
	global	present	species	Many terrestrial ectotherms have narrow physiological thermal-safety margins and must rely on thermoregulatory behavior to avoid overheating.	(Sunday et al., 2014)
Adaptation	local	present	species	Managed relocation is a critical strategy for mitigating climate change threats to the persistence of the endangered pygmy bluetongue lizard.	(Fordham et al., 2012)
	local	past	species	The uncertainty in selecting climate metrics significantly impacts projections of species distribution and the predicted benefits of adaptation actions.	(DeWeber & Wagner, 2018)
	local	future	species	Geographical adaptation to site conditions prevails over species-specific physiological traits in determining the vulnerability of Mediterranean rear-edge forests to climate change.	(Dorado-Liñán et al., 2019)
Vulnerability	local	future	species	Incorporating exposure, sensitivity, and adaptive capacity into spatial conservation prioritization significantly impacts the representation of species under climate change.	(Summers et al., 2012)
	local	past	ecosystem	Mozambican forest mangroves are highly vulnerable to climate change, particularly to sea level rise and tropical storms, highlighting the need for adaptive management at various spatial scales.	(Lee et al., 2018)
	global	past	ecosystem	Vulnerability of ecosystems to climate change is significantly moderated by habitat intactness, with larger, intact wilderness areas serving as crucial refugia.	(Eigenbrod et al., 2015)

This is an Open Access article, distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives licence (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is unaltered and is properly cited. The written permission of Cambridge University Press must be obtained for commercial re-use or in order to create a derivative work.

	local	past	species	Phenological responses of temperate and boreal trees to warming vary significantly depending on ambient spring temperatures, leaf habit, and geographic range.	(Montgomery et al., 2020)
Response	regional	future	ecosystem	Dynamics of Amazon dieback in response to climate change are robust, with uncertainty primarily driven by climate projections rather than ecosystem model parameters.	(Poulter et al., 2010)
	local	future	species	Climate change significantly impacts the regeneration potential of eucalypt species in South-Eastern Australia's temperate forests, leading to shifts in species distribution and potential declines in regeneration by 2050.	(Mok et al., 2012)

2 Note: The spatial scales are classified into three types: local, regional, and global. Temporal scales are divided into past, present, and future. Biological scales
3 include species and ecosystems.

Accepted Manuscript

3.1 Exposure

Climate change exposure pertains to the extent to which organisms and ecosystems are susceptible to climate change-related threats. These threats encompass intrinsic factors such as physiological tolerances and dispersal ability, as well as extrinsic factors like rising temperatures, shifts in precipitation patterns, changes in the frequency and intensity of meteorological events, including sea level rise, droughts, floods, and hurricanes (Cardillo et al., 2005; Brawn et al., 2017; Glazier & Gjoni 2024). For instance, higher temperatures influence both abiotic disturbances like fire, drought, wind, snow, and ice, and biotic disturbances such as insect infestations and pathogens. The complex interplay between these disturbances further compounds ecosystem disruptions (Seidl et al., 2017). The exposure of species and ecosystems to climate change varies significantly across different climate change scenarios. Under a global warming scenario of less than 2°C, it is anticipated that less than 2% of ecological assemblages will face sudden exposure events affecting over 20% of species worldwide. In contrast, if global warming reaches 4°C, 15% of assemblages will be at risk of sudden exposure (Trisos et al., 2020). Within the high emissions scenario, climate change exposure for ecological assemblages is expected to commence in tropical oceans by 2030 and subsequently expand to tropical forests and higher latitudes by 2050. Ureta et al. (2022) employed standardized Euclidean distances, considering current and future climate conditions at each grid point, which encompass annual temperature change, precipitation change, and historical records of hurricane intensity and fire occurrences, to forecast the risk of climate change exposure for species. Beyond alterations in the mean levels of climate factors, researchers are increasingly focusing on temporal shifts and structural impacts of these factors. Increased variability in winter snowmelt will intensify water shortages during the growing season and elevate the stochasticity of runoff (Wieder et al., 2022).

Non-human primates are often considered flagship species in tropical forest ecosystems. Under the most pessimistic climate change scenario, it is estimated that 74% of primates inhabiting Neotropical forests may face exposure to a maximum upper temperature increase of up to 7°C. In contrast, primates residing in Madagascar's savannahs will experience less pronounced warming (Carvalho et al., 2019). Mammals that inhabit the same geographic ranges exhibit varying risks of climate change exposure due to differences in body size and movement patterns. Generally, larger species (>15 kg) and arboreal and semi-aquatic animals are at the highest risk. Even for sympatric species with relatively similar sensitivities, such as Disjunct plant genera, the risk of extinction differs considerably in response to various environmental exposures. The key climate change exposure factor for Disjunct plant genera in East Asia is the annual temperature range, while in the northeastern United States, it is annual precipitation (Song et al., 2021).

This is an Open Access article, distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives licence (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is unaltered and is properly cited. The written permission of Cambridge University Press must be obtained for commercial re-use or in order to create a derivative work.

3.2 Sensitivity

Sensitivity refers to the extent to which ecosystems and species respond to climate change. When assessing the impact of environmental changes on extinction risk, one of the primary sources of uncertainty is the potential variability in biological sensitivity (Song et al., 2021). This sensitivity encompasses a range of factors, including intrinsic elements such as genetic characteristics and reproductive methods, as well as extrinsic factors like food networks and ecological interactions.

Physiological characteristics that influence species and ecosystem sensitivity include traits such as temperature range tolerance, water acquisition, conservation and utilization efficiency, reproductive methods and strategies. For example, the generation length, defined in some studies as the average age of parents in the current generation, reflects the rate at which breeding individuals in a population are renewed. Species with longer generation lengths and lower reproduction rates have demonstrated a higher risk of extinction under climate change (Pacifi et al., 2017). In comparison to species with shorter generation lengths, those with longer generation lengths exhibit relatively smaller population responses to conservation measures, such as the establishment of protected areas and translocations (Leclerc et al., 2020a).

Ecological characteristics that influence species and ecosystem sensitivity include habitat features (niche breadth), position within food chains, and food networks (including primary diet, foraging niche, and foraging periods), life history features (species lifespan, body size, life history strategies, migration characteristics, etc.) (Sandin et al., 2014; Ureta et al., 2022). For mammals, habitat specialization and dietary specialization are vital factors for evaluating their sensitivity to climate change, as more specialized species are less likely to expand into new, suitable climate regions. Species with limited migration capabilities tend to be more sensitive to climate change. Ecosystems supported by unique species face higher risks of concurrent extinctions and critical loss of ecosystem functions due to disruptions in ecological interactions caused by climate change. In other words, such ecosystems exhibit lower ecological redundancy (similar combinations of ecological trait values) (Leclerc et al., 2020b).

Genetic characteristics influencing species and ecosystem sensitivity encompass genetic diversity, genetic adaptability, genetic drift, and so forth (Jezkova et al., 2011). For example, some fish populations with high genetic diversity may be more capable of adapting to changing water temperatures and quality. Certain species may already possess adaptive genetic traits for climate change conditions, including heat tolerance genes, increased drought resistance, or enhanced immune systems (Parmesan, 2006). Genetic drift refers to random changes in genetic characteristics within a population, which can lead to the emergence of new beneficial traits or the reduction of existing harmful traits. Wildlife populations with higher genetic drift are more likely to adapt to climate change across different geographical regions (Perry & Wu, 1960).

3.3 Adaptivity

Adaptivity is a term used to describe the capacity of species and ecosystems to respond to climate change. Various factors influence the adaptivity of species and ecosystems, including intrinsic factors like behavioral

adaptation and niche flexibility, as well as extrinsic factors such as geographical isolation and the presence of protected areas. Geographical isolation restricts opportunities for species to move to other landmasses, impacting their ability to adapt to climate change. For instance, isolated islands often offer fewer potential refuges, and if these islands have limited area and minimal elevational differences, the adaptability of species can be significantly compromised. Establishing protected areas is a recognized effective method for enhancing the adaptability of species and ecosystems to climate change. Protected areas can provide suitable habitats and increase habitat continuity, facilitating species migration from non-protected areas to protected ones (Ureta et al., 2022). Phylogenetic uniqueness measures the number of close relatives of each species and their phylogenetic distance (Jansson, 2009). Species pools with greater phylogenetic diversity possess higher evolutionary potential in the face of climate change, making them more likely to adapt and persist.

Physiological plasticity can potentially alleviate the impact of climate warming on organisms by reducing the thermal sensitivity of life processes and increasing physiological tolerance (Stillman et al., 2003; Seebacher et al., 2015). Species' behavioral avoidance can also protect organisms from the effects of climate change by minimizing exposure to high-cost or lethal temperatures (Sunday et al., 2014). Nevertheless, the roles of plasticity and species' behavioral avoidance in safeguarding species from extinction are still debated, as climate warming may surpass the adaptive capacity of plasticity or increase the costs associated with behavioral strategies (Sears et al., 2016). The current extinction rate of species also influences their adaptivity. According to the filtering hypothesis (Balmford, 1996), species with high extinction rates are more likely to withstand future climate change. This is because species that have evolved and survived in highly disturbed environments are more likely to persist in the face of new disturbances, such as climate change. However, species' adaptability is effective only within a certain range of climate change scenarios. In the best-case climate scenario (RCP2.6), plant genera with similar sensitivity in eastern Asia and eastern North America show distinct differences in vulnerability. However, under the most pessimistic scenario (RCP8.5), these differences vanish, and all genera become highly vulnerable. This suggests that severe climate change (RCP8.5) may override regional buffer capacities (Song et al., 2021).

3.4 Vulnerability

Vulnerability is the critical factor linking distribution, exposure, sensitivity, and adaptivity, offering a comprehensive assessment of species and ecosystems susceptibility to climate change. It also plays a key role in evaluating extinction risks (Bergstrom et al., 2021). The rate of species extinction on Earth is on the rise, with one out of every six species facing threats. Particularly noteworthy is that in South America, Australia, and New Zealand, the risk of species extinction is most pronounced (Malcolm et al., 2006; Warren et al., 2013; Foden et al., 2013; Urban, 2015). Islands and archipelagos, in particular, exhibit varying degrees of vulnerability to future climate change, with the Pacific region often displaying heightened vulnerability. In a comprehensive assessment by Thomas et al. (2004), which covered approximately 20% of the world's terrestrial surface, it was found that under the mid-range warming scenario in 2050, 15%-37% of species will be on the brink of extinction.

In the discourse on vulnerability and extinction risk, the concept of "extinction debt" is pivotal. Several studies (Devictor et al., 2012; Bertrand et al., 2016) suggest that the impact of climate change on local species richness is constrained and may paradoxically forecast an augmentation in species diversity, challenging conventional knowledge. For instance, in mountainous regions susceptible to climate warming, instances of plant extinctions are sporadic, even across a century-long time series of climate warming. In contrast, the overall richness of plant species at the local level has surged as species migrate to higher latitudes with climate warming (Tilman et al., 1994; Dullinger et al., 2012). This phenomenon is expounded by the concept of "extinction debt" (Rumpf et al., 2019), which posits that although habitat destruction or other detrimental factors may have initiated biodiversity decline, the actual extinction of species may be deferred into the future, owing to a time lag. Extinction debt implies that, notwithstanding efforts to mitigate habitat loss or other stressors, compromised biodiversity may still experience a gradual decline in the ensuing decades (Jackson Sax, 2010; Dullinger et al., 2012; Arno et al., 2020).

3.5 Response

Responses of species and ecosystems to environmental changes can be divided into short-term, medium-term, and long-term categories. In the short term, responses include individual behavioral changes, physiological adjustments, and shifts in community composition. Over the medium term, species may exhibit phenotypic adaptations, undergo genotype selection, and experience shifts in their geographic distribution. In the long term, environmental pressures can lead to evolutionary trends, species extinction, and overall ecosystem transformation (Moilanen et al., 2022). Importantly, there are feedback relationships between response and other components like exposure, sensitivity, and adaptation. For example, changes in a species' range reflect its ability to adapt to new climatic conditions, showcasing the profound influence of climate change on the survival and reproductive parameters of these species (Mahony et al., 2017; Zhou et al., 2023). However, changes in the distribution of species with particular behaviors, such as ecosystem engineers, can create feedback loops that influence their exposure to environmental changes (Cozzoli et al., 2021). A prominent feature of species redistribution driven by climate change is the rate and extent at which various species respond. This often leads to the disruption of pre-existing interactions and the formation of new ecological relationships concurrently. Such dynamics result in species either separating or engaging in novel interactions (Pecl et al., 2017). This disruption has significant consequences, affecting predatory, competitive, commensal, and parasitological relationships (Cahill et al., 2013). In European countries where agriculture plays a substantial role in the GDP, climate change projections (Civantos et al., 2012), anticipate a decrease in the distribution and abundance of vertebrates responsible for controlling crop pests.

4. Approaches for modeling climate change risk to species and ecosystems

When conducting assessment of climate change risk on species and ecosystems, it is imperative to collect a diverse set of environmental and biological parameters, as well as high-quality historical and real-time data. However, relying solely on these data is insufficient (Pettorelli et al., 2014). Scientific modeling is

essential to gain deeper insights into how organisms and ecosystems respond to climate change risks, serving as the cornerstone for evidence-based policy formulation and decision support (Chen et al., 2022; IPBES, 2016). Evaluating the vulnerability of species to climate change can be accomplished through various methods, including correlation-based approaches, mechanistic methods, hybrid approaches, criteria-based approaches, and other approaches (Fig.7).

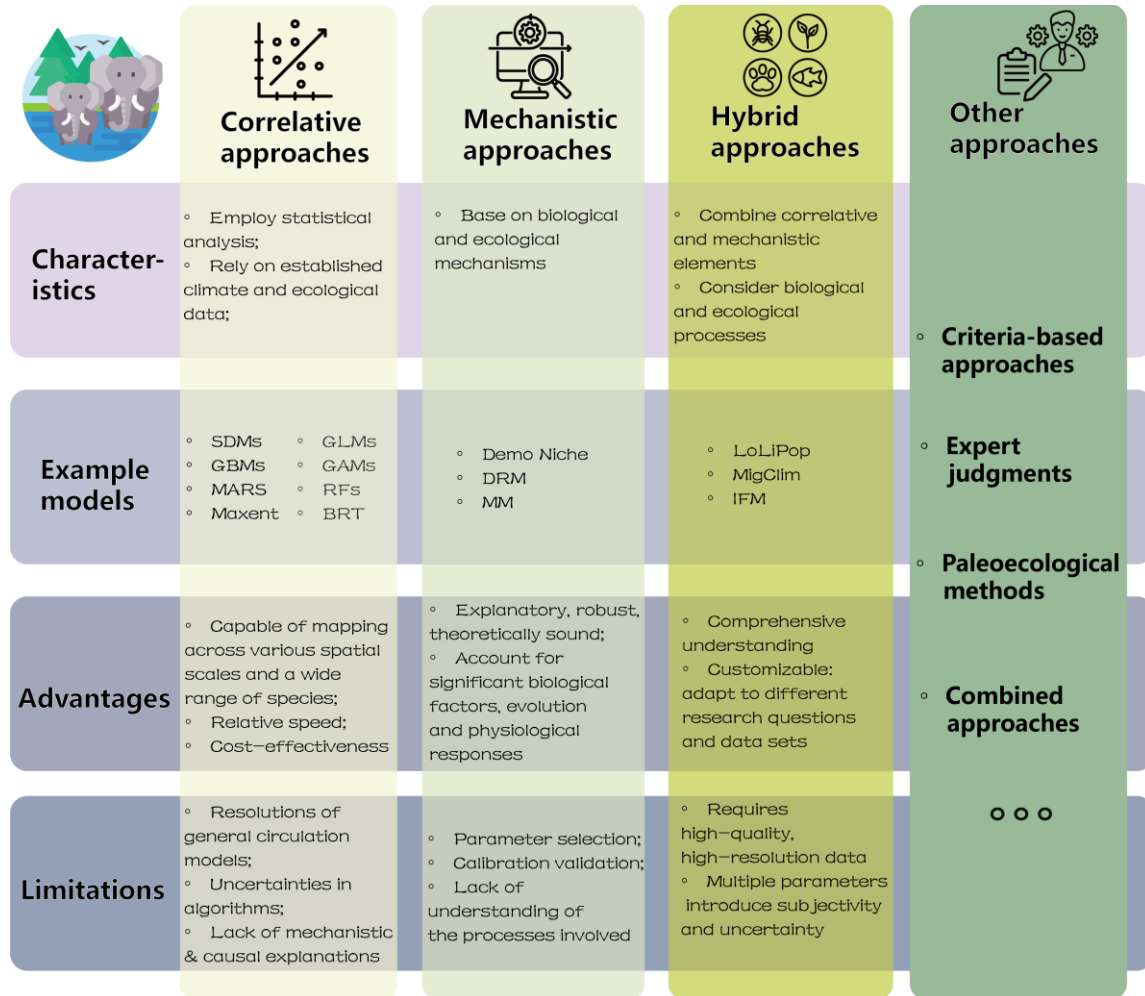


Fig. 7. Approaches for modeling climate change risk to species and ecosystems. The abbreviations of various modeling approaches represent: Species Distribution Models (SDMs), Generalized Linear Models (GLMs), Generalized Boosted Regression Models (GBMs), Generalized Additive Models (GAMs), Multiple Adaptive Regression Splines (MARS), Random Forests (RFs), Maximum Entropy (Maxent), Boosted Regression Trees (BRT), Demographic Niche Model (DemoNiche), Dynamic Range Models (DRM), Landscape and Life History Population Model (LoLiPop), Migration and Climate Model (MigClim), Incidence Function Models (IFM), and metabolism models (MM).

4.1 Correlative approaches

Correlation-based methods rely on established climate and ecological data, encompassing factors like

species distribution, temperature, and rainfall (Kong et al., 2021). These methods employ statistical analysis to assess species and ecosystems' vulnerability. These predictions involve comparing current and future climate data to identify regions where species survival and ecosystem stability may be at risk. Traditional Species Distribution Models (SDMs) are often categorized as correlation-based methods, as they primarily examine the correlations between species distribution and environmental variables (Summers et al., 2012; Song et al., 2021). In their description of the current distribution model of Ethiopian Arabica coffee, Moat et al. (2019) utilized the comprehensive SDM, employing six modeling techniques: Generalized Linear Models (GLMs), Generalized Boosted Regression Models (GBMs), Generalized Additive Models (GAMs), Multiple Adaptive Regression Splines (MARS), Random Forest (RFs), and Maximum Entropy (Maxent). Tagliari et al. (2021) employed four statistical algorithms to model the bioclimatic niche and distribution of seven studied baobab species: GLMs, GAMs, RFs, and Maxent. Curd et al. (2023) employed landscape metrics in species distribution modeling to characterize the internal structure and variations within species distribution areas, using four algorithms: GLMs, GAMs, RFs, and boosted regression trees (BRT). Parametric models like GLM and GBM, along with non-parametric models like GAM and MARS, are well-known for their robustness and are standard regression models. In contrast, classification tree models such as RF, BRT and Probability distribution models like Maxent, belonging to machine learning methods, are more complex algorithms.

Relevant models are capable of mapping across various spatial scales and a wide range of species. However, they do come with certain limitations and uncertainties, primarily originating from climate data, algorithms, and biological assumptions (Pearson et al., 2006; Guisan & Rahbek, 2011). Uncertainties in climate data can be attributed to general circulation models and their resolutions. Different parameters and model structures can yield diverse outcomes when simulating future climate systems (Wiens et al., 2009; Bagchi et al., 2013). Furthermore, climate data is typically less detailed compared to other data used in correlation models, such as environmental and biological data, often proving inadequate for modeling rare species or those with smaller geographical ranges (Guisan & Thuiller, 2005). Uncertainties in algorithms arise from variations in model performance and simulation outcomes resulting from the choice of different correlation methods and predictor variables. Some studies have mitigated these uncertainties by producing ensemble predictions, which involve averaging probabilities and confidence intervals from various models (Carvalho et al., 2011). Uncertainties related to biological assumptions hinge on the presumption that the relationship between species and their environmental conditions will persist in the future (Harrison et al., 2006). As in reality, the ecological niche of some species is influenced not only by their optimal climate but also by non-biological, biological, geographic, historical, and anthropogenic factors (Guisan & Thuiller, 2005). As future climate conditions evolve, species may select different and more suitable ecological niches than their current ones. Despite criticism that correlation models lack mechanistic and causal explanations and have limited capabilities when assessing species with sparse distribution points and small geographical ranges, they have been widely used in regional and global analyses due to their relative speed and cost-effectiveness.

4.2 Mechanistic approaches

The mechanistic approach is grounded in a comprehensive understanding of biological and ecological mechanisms, which are employed to analyze species' physiological, ecological, and behavioral responses to climate change. This approach encompasses species' life history traits, physiological ecological processes, and adaptability, which typically necessitate a more substantial body of biological and experimental data. Mechanistic models such as Demographic Niche Model (DemoNiche), Landscape and Life History Population Model (LoLiPop), Migration and Climate Model (MigClim) build upon correlation models like SDMs by incorporating mechanistic components such as diffusion or population dynamics. On the other hand, process-based dynamic range models (DRM), incidence function models (IFM), and age-structured metapopulation models do not rely on traditional SDMs; they directly infer the dynamics of environment-population quantity from data, thereby delving deeper into the mechanisms governing biological processes (Zurell et al., 2016). Riddell et al. (2018) integrate experimental physiological and behavioral traits into species distribution models to predict extinction risk based on individuals' ability to maintain energy balance under scenarios with and without plasticity.

Mechanistic models are widely regarded as more explanatory, robust, and theoretically sound (Kearney & Porter, 2009). Unlike correlation models, which can only simulate the ecological niches that species have already occupied, mechanistic models may provide a better representation of the fundamental ecological niches of species, even those that are not currently reflected in their distribution (Monahan, 2009; Kearney & Porter, 2009). Mechanistic models can also explicitly account for significant biological factors, including evolution and physiological responses. However, the limitations and uncertainties of mechanistic models primarily arise from the lack of understanding of the processes involved and the challenges associated with parameter selection, calibration, and validation during the modeling process. Mechanistic models rely on detailed data obtained from laboratory or field experiments, such as reproductive rates and physiological tolerances (Deutsch et al., 2008; Jenouvrier, 2009; Radchuk et al., 2013), and many species lack this data, rendering mechanistic models less widely applicable and often confined to a few rare or endangered species (Hunter et al., 2010). Similar to correlation models, mechanistic models typically do not account for interactions between species.

4.3 Hybrid approaches

Hybrid approaches integrate both correlative and mechanistic elements, offering a comprehensive framework for understanding species' responses to climate change by considering not only statistical relationships between variables but also biological and ecological processes (Cozzoli et al. 2021). Example models, such as LoLiPop, MigClim, and Incidence Function Models (IFM), capture the complex interactions between environmental factors and species traits. Intrinsic Traits encompass a species' body size (Jones et al., 2009), dietary breadth (IUCN, 2022), dispersal distance, generation length, litter size (Tacutu et al., 2013), annual reproductive rate (Jones et al., 2009) and activity pattern (Wilman et al., 2014). Spatial Traits relate

to a species' distribution range and encompass the highest temperature within the species' range, the lowest temperature, temperature seasonality, precipitation seasonality, and altitudinal range.

The key advantage of hybrid approaches lies in their flexibility and adaptability. They offer comprehensive insights into species vulnerability while being customizable to suit different research questions and datasets. However, these approaches often require high-quality, high-resolution data, and the process of selecting and calibrating multiple parameters can introduce subjectivity and uncertainty (Hunter et al., 2010). Hybrid models rely on detailed data obtained from laboratory or field experiments, such as reproductive rates and physiological tolerances (Deutsch et al., 2008; Radchuk et al., 2013).

4.4 Other approaches

In addition to the relevant models, mechanistic models, and trait-based methods mentioned earlier, there are several other methods for assessing climate change risks on species and ecosystems. These include criteria-based approaches, expert judgments, the paleoecological method, and combined approaches.

Criteria-based approaches typically utilize the categories and standards established by the International Union for Conservation of Nature (IUCN) Red List (Maclean & Wilson, 2011; Visconti et al., 2015) to categorize species into different threat categories based on the risks posed by climate change. These standardized methods are applicable to a wide range of global species (IUCN, 2022) and consider multiple aspects of how climate change risks impact species and ecosystems. Pearson et al. (2014) employed a simulation approach based on general life history types and found that most variables critical for predicting extinction risk are already incorporated into the IUCN Red List criteria for species conservation assessments, suggesting that the current assessment criteria may be more effective at identifying vulnerable species and ecosystems in the context of climate change than previously thought.

Expert judgments based on their knowledge and experience are sometimes used to assess climate change risk on species and ecosystems, especially in situations with limited data. Camac et al. (2021) employed structured expert judgment to predict species and community responses to global change.

Paleoecological methods can be leveraged to understand how species have responded to past climate fluctuations, providing insights into predicting potential responses of species in the future. Clark et al. (2018) analyzed 594 published paleoecological records to reveal changes in the composition and structure of terrestrial vegetation since the last glacial period and predict the extent of ecosystem transformations under future emission scenarios. Pineda-Munoz et al. (2021) investigated whether human-induced changes in species' geographic ranges have altered their climate niches using fossil records.

Combined approaches integrate above approaches based on related mechanisms (Ureta et al., 2022). Pearson et al. (2014) combined ecological niche models (ENMs) with population demographic models to develop the generic life history method (GLH), which represents a species' extinction risk as the probability of zero abundance by 2100, rather than the proportion of species extinctions resulting from bioclimatic envelope contractions.

5. Emerging trends of risk assessment of climate change

Exploring the intricate interactions, feedback loops, and spillover effects among climate change, biodiversity, and ecosystems is of paramount importance in various global future scenarios. Given the inherent uncertainty in climate change predictions and the dynamic and complex responses of species and ecosystems, the following directions warrant further in-depth exploration:

5.1 *Leveraging the concept of telecoupling*

As a global phenomenon, the impacts of climate change on species and ecosystems in one region can reverberate across borders, affecting ecosystems and species in distant regions through various pathways such as species competition, transboundary migration, and the interconnectedness of ecosystem service supply chains. This intricate global interplay finds elucidation through the telecoupling concept, which delineates the complex interconnections among global changes, environmental impacts, and social feedbacks across different regions worldwide. Within the telecoupling framework, each system comprises agents, causes, and effects, with connections forged through the exchange of information, material, energy, people, capital, and organisms (Liu et al., 2013).

For instance, climate change may disrupt patterns of species migration, prompting some species to relocate towards northern or higher-altitude areas in response to warming climates (Hulina et al., 2017). Such migrations can introduce new species to destination areas, altering local ecosystems and potentially precipitating local species extinction or ecosystem collapse. The telecoupling framework facilitates comprehension of the ramifications of these migrations on destination-area ecosystems and their repercussions on ecosystems in the source areas (López-Hoffman et al., 2017; Schröter et al., 2018). Furthermore, the impacts of climate change on ecosystem services can propagate through extensive supply chains, reshaping interdependencies among disparate ecosystems. The telecoupling concept aids in discerning how climate change influences the supply and demand of ecosystem services in diverse regions, while also evaluating the overarching stability of global ecosystem services (Hulina et al., 2017). Given that the impacts of climate change often transcend national boundaries, locally oriented conservation endeavors may yield adverse spillover effects, imperiling the sustainability of remote regions (Liu, 2014). Thus, the telecoupling concept underscores the imperative of transnational ecosystem management and cooperation, entailing facets such as resource sharing, information exchange, and policy coordination.

5.2 *Empirical Research on Climate Change Risks*

Despite established theoretical frameworks, there is a pressing need for large-scale experimental efforts to rigorously test hypotheses and explore factorial experimental designs. Such studies should investigate the physiological, behavioral, and ecological responses of various species under changing climatic conditions. Recent literature underscores the importance of integrating empirical approaches with existing models to provide a comprehensive understanding of climate change-mediated responses. For instance, Glazier & Gjoni

(2024) emphasize that metabolism, a key driver of biological processes, is influenced by numerous intrinsic and extrinsic factors, including body size and environmental conditions. This need for empirical research becomes particularly evident when considering species distribution. While it is commonly believed that species will migrate to higher elevations and latitudes as temperatures rise, Tagliari et al. (2021) reveal that mean annual temperature is not the only limiting factor in determining species distribution. Instead, species may adapt their ranges in response to a variety of climate variables. For example, in tropical regions, many species are expected to move toward the equator to avoid the impacts of seasonal temperature fluctuations. This highlights the critical role of empirical studies in uncovering adaptive strategies and understanding the nuanced responses of species to climate change.

5.3 Harnessing the potential of Geography

Geography studies have a critical role to play in addressing challenges such as climate change, biodiversity loss, and the provision of essential ecosystem services. The advent of remote sensing technologies, geographic information systems, and the emergence of machine learning have revolutionized risk assessment of climate change on species and ecosystems (White et al., 2017; Zamora-Gutierrez et al., 2021). Integrated mapping and modeling have proven to be invaluable tools for monitoring and assessing species and ecological changes on a large spatial scale (Yu et al., 2022). By incorporating these technologies into risk assessments, we can attain a comprehensive understanding of ecosystem dynamics and enhance the accuracy of predictions and warnings (Du et al., 2023; Ni et al., 2023). Incorporating species distribution models into comprehensive assessment models and establishing connections between species redistribution due to climate change and ecosystem integrity through large-scale multi-generational experiments are critical for a deeper understanding of the adaptive responses of organisms and ecosystems to environmental changes, presenting a central challenge (Peel et al., 2017; Cabral et al., 2023).

Harnessing the potential of geography also involves integrating the outcomes of climate change risk assessments on species and ecosystems into the design of new nature reserves and the formulation of conservation strategies. As the latest framework developed under the Convention on Biological Diversity (CBD), the Kunming-Montreal Global Biodiversity Framework was advanced by China during its presidency in 2022 (Shen et al., 2023). To achieve these ambitious objectives, it is necessary to integrate climate change considerations into biodiversity and ecosystem conservation and restoration efforts. Researches have demonstrated that the inclusion of various aspects of vulnerability significantly influences spatial conservation priorities (Thuiller et al., 2005; Carvalho et al., 2010; Crossman et al., 2012). For example, incorporating the adaptability of species and ecosystems when determining priority conservation areas can enhance the representation of a wide range of species. However, prioritizing vulnerable species may reduce the overall representation of priority conservation areas for other species (Summers et al., 2012). Hence, in making decisions regarding conservation planning aimed at reducing the vulnerability of species and ecosystems to climate change, it is essential to fully acknowledge the sensitivity of spatial conservation priorities to different vulnerability components. In addition to identifying priority areas for climate change

adaptation, there should be a focus on promoting sustainable land management and fostering international cooperation.

5.4 Developing early warning mechanism

Sudden changes in the structure, function, and composition of ecosystems occurring with little to no warning can have irreversible and far-reaching consequences for biodiversity and human societies (Newton et al., 2021). Pressures from global climate change manifest in the form of chronic ‘presses’ and/or acute ‘pulses,’ leading to ecosystem collapses. Responses to climate change pressures on ecosystems can be categorized into four collapse profiles: abrupt, smooth, stepped, and fluctuating. Predicting which species and ecosystems are most susceptible to the effects of climate warming is crucial for guiding conservation strategies to minimize species extinctions and ecosystem collapses (van Heerwaarden & Sgrò, 2021). Concerning climate change risk warnings for ecosystems, polar regions, semi-arid areas, and small islands are widely acknowledged as the habitats most susceptible to influence. Regarding climate change risk warnings for species, forecasts (Clusella-Trullas et al., 2011; Kellermann et al., 2012; Sunday et al., 2012) indicate that tropical/mid-latitude species face the highest risks because they already reside near their upper critical thermal limits.

However, complex systems often yield unforeseen outcomes and thresholds. Assessing trends before and after climate change at the species and ecosystem levels typically requires decades of continuous data, and acquiring long-term datasets for species and biological systems can be challenging. Fossil records offer valuable insights into how species and ecosystems have responded to climate change (Finnegan et al., 2015). Nevertheless, understanding their recent ongoing responses necessitates the collection of various environmental and biological parameters, real-time data streams, and high-quality near-real-time data (Pettorelli et al., 2014). With ongoing advancements in atmospheric science, ecology, and computer science, it is imperative to enhance climate change warning methods and tools and integrate this information into decision support frameworks for species and ecosystems. The above-mentioned early warning efforts also require substantial policy, financial support, and international collaboration to establish the necessary monitoring plans to record and respond to climate change. Even with these efforts, nature’s response will remain dynamic, and the mechanisms by which species and ecosystems respond to climate change may not be fully understood or predictable now and in the future. This uncertainty calls for flexible, dynamic management to swiftly adapt to changing conditions within limited timeframes, seize opportunities, and mitigate adverse impacts.

6. Conclusions

Climate change, reaching an unprecedented magnitude in millennia, poses profound risks to global biodiversity and demands comprehensive research efforts. This study provides a novel bibliometric analysis of the research landscape on “Risk assessment for species and ecosystems responding to climate change” from 2000 to 2022, identifying key themes, trends, and collaborations. The novelty of our work lies in

integrating various approaches to access species and ecosystem risks, such as correlative approaches, mechanistic approaches, trait-based approaches, and criteria-based models, offering a comprehensive view of their strengths and limitations. Our findings emphasize the critical need for developing more accurate risk assessment tools, particularly those that consider abrupt, unpredictable changes in ecosystems and their potential for irreversible impacts on both biodiversity and human societies. By identifying five universally accepted concepts—distribution, exposure, sensitivity, adaptivity, and vulnerability—our research provides a solid foundation for future studies and practical applications in risk management and early warning systems. Moreover, our work highlights emerging trends, including the telecoupling concept and the application of geographical data for more precise predictions, which could significantly expand the utility and applicability of climate change risk assessments.

Financial Support, Conflict of Interest and Research Transparency and Reproducibility

Acknowledgements

The authors would like to thank the editors and anonymous reviewers for their constructive comments and suggestions for improvement.

Author Contributions

Hui Wu: Conceptualization, Methodology, Software, Visualization, Writing-Original draft preparation. Le Yu: Conceptualization, Supervision, Writing - Review & Editing. Xiaoli Shen: Conceptualization, Writing - Review & Editing. Fangyuan Hua: Writing - Review & Editing. Zhicong Zhao: Writing - Review & Editing. Yixuan Li: Writing - Review & Editing. Keping Ma: Writing - Review & Editing.

Funding Statement

This research was funded by the National Key R&D Program of China (2022YFE0209400, 2024YFF1307600), National Natural Science Foundation of China (42401314), the China Postdoctoral Science Foundation (2023M741885), the Tsinghua University Initiative Scientific Research Program (20223080017), the National Key Scientific and Technological Infrastructure project “Earth System Science Numerical Simulator Facility” (EarthLab), and the Investigation Research Program between Ecological Environment and Human Health in Wuyi Mountain (20242120035)

Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Research Transparency and Reproducibility

Data will be made available on request.

References

- Albrich, K., Rammer, W., & Seidl, R. (2020). Climate change causes critical transitions and irreversible alterations of mountain forests. *Global Change Biology*, *26*(7), 4013–27.
- Antão, L. H., Weigel, B., Strona, G., Hällfors, M., Kaarlejärvi, E., Dallas, T., Csergő, A. M., MacLean, H. J., Saccheri, I. J., Rolshausen, G., Pearce-Higgins, J. W., & Laine, A. L. (2022). Climate change reshuffles northern species within their niches. *Nature Climate Change*, *12*(6), 587–592.
- Arnth, A., Shin, Y. J., Leadley, P., Rondinini, C., Bukvareva, E., Kolb, M., Midgley, G. F., Oberdorff, T., Palomo, M. G., & Saito, O. (2020). Post-2020 biodiversity targets need to embrace climate change. *Proceedings of the National Academy of Sciences*, *117*(49), 30882–30891.
- Bagchi, R., Crosby, M., Huntley, B., Hole, D. G., Butchart, S. H. M., Collingham, Y., Kalra, M., Rajkumar, J., Rahmani, A., Pandey, M., Gurung, H., Trai, L.T., Quang, N. V., & Willis, S.G., 2013. Evaluating the effectiveness of conservation site networks under climate change: accounting for uncertainty. *Global Change Biology*, *19*, 1236–48.
- Balmford, A. (1996). Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends in Ecology and Evolution*, *11*, 193–196.
- Bates, A. E., Pecl, G. T., Frusher, S., Hobday, A. J., Wernberg, T., Smale, D. A., Sunday, J. M., Hill, N. A., Dulvy, N. K., Colwell, R. K., Holbrook, N. J., Fulton, E. A., Slaughter, E. L., & Watson, R. A. (2014). Defining and observing stages of climate-mediated range shifts in marine systems. *Global Environmental Change*, *26*, 27–38.
- Bergstrom, D. M., Wienecke, B. C., van den Hoff, J., Hughes, L., Lindenmayer, D. B., Ainsworth, T. D., Baker, C. M., Bland, L., Bowman, D. M. J. S., Brooks, S. T., Canadell, J. G., Constable, A. J., DellaSala, D. A., Mackey, B., Manica, A., Possingham, H. P., Schroeter, S., Terauds, A., & Shaw, J. D. (2021). Combating ecosystem collapse from the tropics to the Antarctic. *Global Change Biology*, *27*(9), 1692–1703.
- Bertrand, R., Riofrio-Dillon, G., Lenoir, J., Drapier, J., De Ruffray, P., Gégout, J. C., & Loreau, M. (2016). Ecological constraints increase the climatic debt in forests. *Nature Communications*, *7*, 12643.
- Brawn, J., Benson, T., Stager, M., Sly, D., & Tarwater, N.E.C. (2017). Impacts of changing rainfall regime on the demography of tropical birds. *Nature Climate Change*, *7*, 133–136.
- Cabral, J. S., Mendoza, A., Pinto, A., Oberpriller, J., Mimet, A., Kieslinger, J., Antão, L. H., & Zurell, D. (2023). The road to integrate climate change projections with regional land-use- biodiversity models. *People and Nature*, *00*, 1–26.
- Cahill, A. E., Aiello-Lammens, M. E., Fisher-Reid, M. C., Hua, X., Karanewsky, C. J., Ryu, H. Y., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., Warsi, O., & Wiens, J. J. (2013). How does climate change cause

extinction? *Proceedings of the Royal Society of London*, 280, 20121890.

- Camac, J. S., Umbers, K. D. L., Morgan, J. W., Geange, S. R., Hanea, A., Slatyer, R. A., McDougall, K. L., Venn, S. E., Vesk, P. A., Hoffmann, A. A., & Nicotra, A. B. (2021). Predicting species and community responses to global change using structured expert judgement: An Australian mountain ecosystems case study. *Global Change Biology*, 27(18), 4420–4434.
- Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O. R. P., Sechrest, W., Orme, C. D. L., & Purvis, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science*, 309(5738), 1239–1241.
- Carvalho, S. B., Brito, J. C., Crespo, E. J., & Possingham, H. P. (2010). From climate change predictions to actions—Conserving vulnerable animal groups in hotspots at a regional scale. *Global Change Biology*, 16(12), 3257–3270.
- Carvalho, J. S., Graham, B., Rebelo, H., Bocksberger, G., Meyer, C. F. J., Wich, S., & Kühl, H. S. (2019). A global risk assessment of primates under climate and land use/cover scenarios. *Global Change Biology*, 25(9), 3163–3178.
- Carvalho, S. B., Brito, J. C., Crespo, E. G., Watts, M. E., & Possingham, H. P. (2011). Conservation planning under climate change: Toward accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time. *Biological Conservation*, 144(7), 2020–2030.
- Chapin III, F. S., Sturm, M., Serreze, M. C., McFadden, J. P., Key, J. R., Lloyd, A. H., McGuire, A. D., Rupp, T. S., Lynch, A. H., Schimel, J. P., Beringer, J., Chapman, W. L., Epstein, H. E., Hinzman, L. D., Jia, G., Ping, C. L., Tape, K. D., Thompson, C. D. C., Walker, D. A., & Welker, J. M. (2005). Role of land-surface changes in Arctic summer warming. *Science*, 310(5748), 657–660.
- Chen, C. (2006). CiteSpace II: detecting and visualizing emerging trends and transient patterns in scientific literature. *Journal of the American Society for Information Science*, 57, 359–377.
- 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, 1024–1026.
- Chen, Y., Jiang, Z., Fan, P., Ericson, P. G. P., Song, G., Luo, X., Lei, F., & Qu, Y. (2022). The combination of genomic offset and niche modelling provides insights into climate change-driven vulnerability. *Nature Communications*, 13(1), 1–15.
- Civantos, E., Thuiller, W., Maiorano, L., Guisan, A., & Araújo, M. B. (2012). Potential impacts of climate change on ecosystem services in Europe: The case of pest control by vertebrates. *Bioscience*, 62, 658–666.
- Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., Brewer, S., Bush, M. B., Chase, B. M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M. E., Gosling, W. D., Haberle, S., Hotchkiss, S. C., Huntley, B., Ivory, S. J., Kershaw, A. P., Kim, S.-H., Latorre, C., Leydet, M., Lézine, A.-M., Liu, K.-B., Liu, Y., Lozhkin, A. V., McGlone, M. S., Marchant, R. A., Momohara, A., Moreno, P. I., Müller, S., Otto-Bliesner, B. L., Shen, C., Stevenson, J., Takahara, H., Tarasov, P. E., Tipton, J., Vincens, A., Weng, C., Xu, Q., Zheng, Z., & Jackson, S. T. (2018). Past and future global

transformation of terrestrial ecosystems under climate change. *Science*, 923, 920–923.

- Clusella-Trullas, S., Blackburn, T.M., & Chown, S.L. (2011). Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *American Naturalist*, 177, 738–751.
- Cozzoli, F., Shokri, M., da Conceição, T. G., Herman, P. M., Hu, Z., Soissons, L. M., Van Dalen, J., Ysebaert, T., & Bouma, T. J. (2021). Modelling spatial and temporal patterns in bioturbator effects on sediment resuspension: A biophysical metabolic approach. *Science of The Total Environment*, 792, 148215.
- Crossman, N.D., Bryan, B.A., & Summers, D.M. (2012). Identifying priority areas for reducing species vulnerability to climate change. *Diversity and Distributions*, 18, 60–72.
- Curd, A., Chevalier, M., Vasquez, M., Boyé, A., Firth, L. B., Marzloff, M. P., Bricheno, L. M., Burrows, M. T., Bush, L. E., Cordier, C., Davies, A. J., Green, J. A. M., Hawkins, S. J., Lima, F. P., Meneghesso, C., Mieszowska, N., Seabra, R., & Dubois, S. F. (2023). Applying landscape metrics to species distribution model predictions to characterize internal range structure and associated changes. *Global Change Biology*, 29(3), 631–647.
- Davis, M.B., & Shaw, R.G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, 292, 673–679.
- 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, 6668–6672.
- Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D. B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I., & Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, 2, 121–124.
- DeWeber, J. T., & Wagner, T. (2018). Probabilistic measures of climate change vulnerability, adaptation action benefits, and related uncertainty from maximum temperature metric selection. *Global Change Biology*, 24(6), 2735–48.
- Dorado-Liñán, I., Piovesan, G., Martínez-Sancho, E., Gea-Izquierdo, G., Zang, C., Cañellas, I., Castagneri, D., Di Filippo, A., Gutiérrez, E., Ewald, J., Fernández-de-Uña, L., Hornstein, D., Jantsch, M. C., Levanič, T., Mellert, K. H., Vacchiano, G., Zlatanov, T., & Menzel, A. (2019). Geographical adaptation prevails over species-specific determinism in trees' vulnerability to climate change at Mediterranean rear-edge forests. *Global Change Biology*, 25(4), 1296–1314.
- Du, Z., Yu, L., Chen, X., Li, X., Peng, D., Zheng, S., Hao, P., Yang, J., Guo, H., & Gong, P. (2023). An Operational Assessment Framework for Near Real-time Cropland Dynamics: Toward Sustainable Cropland Use in Mid-Spine Belt of Beautiful China. *Journal of Remote Sensing*, 3, 0065.
- Dullinger, S., Gattlinger, A., Thuiller, W., Moser, D., Zimmermann, N. E., Guisan, A., Willner, W., Plutzer, C., Leitner, M., Mang, T., Caccianiga, M., Dimböck, T., Ertl, S., Fischer, A., Lenoir, J., Svenning, J.-C., Psomas, A., Schmatz, D. R., Silc, U., Vittoz, P., & Hülber, K. (2012). Extinction debt of high-mountain

-
- plants under twenty-first-century climate change. *Nature Climate Change*, 2, 619–622.
- Eigenbrod, F., Gonzalez, P., Dash, J., & Steyl, I. (2015). Vulnerability of ecosystems to climate change moderated by habitat intactness. *Global Change Biology*, 21(1), 275–286.
- Finnegan, S., Anderson, S. C., Harnik, P. G., Simpson, C., Tittensor, D. P., Byrnes, J. E., Finkel, Z. V., Lindberg, D. R., Liow, L. H., Lockwood, R., Lotze, H. K., McClain, C. R., McGuire, J. L., O'Dea, A., & Pandolfi, J. M. (2015). Paleontological baselines for evaluating extinction risk in the modern oceans. *Science*, 348, 567–570.
- Foden, W. B., Butchart, S. H. M., Stuart, S. N., Vié, J.-C., Akçakaya, H. R., Angulo, A., DeVantier, L., Gutsche, A., Turak, E., Cao, L., Donner, S. D., Katariya, V., Bernard, R., Holland, R. A., Hughes, A. F., O'Hanlon, S. E., Garnett, S. T., Şekerciöğlü, Ç. H., & Mace, G. M. (2013). Identifying the World's Most Climate Change Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals. *PLOS ONE* 8, e65427.
- Fordham, D. A., Watts, M. J., Delean, S., Brook, B. W., Heard, L. M. B., & Bull, C. M. (2012). Managed relocation as an adaptation strategy for mitigating climate change threats to the persistence of an endangered lizard. *Global Change Biology*, 18(9), 2743–55.
- Glazier, D. S., & Gjoni, V. (2024). Interactive effects of intrinsic and extrinsic factors on metabolic rate. *Philosophical Transactions of the Royal Society B*, 379(1896), 20220489.
- Grunst, M. L., Grunst, A. S., Grémillet, D., & Fort, J. (2023). Combined threats of climate change and contaminant exposure through the lens of bioenergetics. *Global Change Biology*, 29, 5139–68.
- Guisan, A., & Rahbek, C. (2011). SESAM - a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *Journal of Biogeography*, 38, 1433–1444.
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993–1009.
- Harrison, P. A., Berry, P. M., Butt, N., & New, M. (2006). Modelling climate change impacts on species' distributions at the European scale: Implications for conservation policy. *Environmental Science & Policy*, 9(2), 116–128.
- Hua, T., Zhao, W., Cherubini, F., Hu, X., & Pereira, P. (2021). Sensitivity and future exposure of ecosystem services to climate change on the Tibetan Plateau of China. *Landscape Ecology*, 36(12), 3451–3471.
- Hulina, J., Bocetti, C., Campa, H., III, Hull, V., Yang, W., & Liu, J. (2017). Telecoupling framework for research on migratory species in the Anthropocene. *Elementa: Science of the Anthropocene*, 5, 5.
- Hunter, C. M., Caswell, H., Runge, M. C., Regehr, E. V., Amstrup, S. C., & Stirling, I. (2010). Climate change threatens polar bear populations: A stochastic demographic analysis. *Ecology*, 91(10), 2883–2897.
- IPBES. (2016). Summary for policymakers of the methodological assessment of scenarios and models of biodiversity and ecosystem services of the Intergovernmental Science Policy Platform on Biodiversity and Ecosystem Services.
- IPCC. (2014). Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to

the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

- IPCC. (2022). *Climate Change 2022: Impacts, Adaptation and Vulnerability*. Cambridge: Cambridge University Press.
- Jackson, S.T., & Sax, D.F. (2010). Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in Ecology and Evolution*, *25*, 153–160.
- Jansson, R. (2009). Extinction risks from climate change: Macroecological and historical insights. *F1000 Biology Reports*, *1*, 44.
- Jenouvrier, S., Caswell, H., Barbraud, C., Holland, M., Strøve, J., & Weimerskirch, H. (2009). Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(6), 1844–1847.
- Jezkova, T., Olah-Hemmings, V., & Riddle, B. R. (2011). Niche shifting in response to warming climate after the last glacial maximum: Inference from genetic data and niche assessments in the chisel-toothed kangaroo rat (*Dipodomys microps*). *Global Change Biology*, *17*(11), 3486–3502.
- Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., Safi, K., Sechrest, W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib, M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., Teacher, A., Bininda-Emonds, O. R. P., Gittleman, J. L., Mace, G. M., & Purvis, A. (2009). PanTHERIA: A species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, *90*(9), 2648.
- Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*(4), 334–350.
- Kellermann, V., Overgaard, J., Hoffmann, A. A., Fløjgaard, C., Svenning, J. C., & Loeschcke, V. (2012). Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(40), 16228–16233.
- Kong, L., Xu, W., Xiao, Y., Pimm, S. L., Shi, H., & Ouyang, Z. (2021). Spatial models of giant pandas under current and future conditions reveal extinction risks. *Nature Ecology and Evolution*, *5*(9), 1309–1316.
- Leclerc, C., Courchamp, F., & Bellard, C. (2020). Future climate change vulnerability of endemic island mammals. *Nature Communications*, *11*(1), 1–9.
- Leclerc, C., Villéger, S., Marino, C., & Bellard, C. (2020). Global changes threaten functional and taxonomic diversity of insular species worldwide. *Diversity and Distributions*, *26*(4), 402–414.
- Lee, C. K. F., Duncan, C., Owen, H. J. F., & Pettorelli, N. (2018). A new framework to assess relative ecosystem vulnerability to climate change. *Conservation Letters*, *11*(2), e12372.
- Liu, J. (2014). Forest sustainability in China and implications for a telecoupled world. *Asia & the Pacific Policy Studies*, *1* (1), 230–250.
- Liu, J., Hull, V., Batistella, M., DeFries, R., Dietz, T., Fu, F., Hertel, T. W., Izaurralde, R. C., Lambin, E. F., Li, S., Martinelli, L. A., McConnell, W. J., Moran, E. F., Naylor, R., Ouyang, Z., Polenske, K. R.,

-
- Reenberg, A., Rocha, G. de M., Simmons, C. S., Verburg, P. H., Vitousek, P. M., Zhang, F., & Zhu, C. (2013). Framing sustainability in a telecoupled world. *Ecology & Society*, *18*(2), 26.
- López-Hoffman, L., Diffendorfer, J., Wiederholt, R., Bagstad, K. J., Thogmartin, W. E., McCracken, G., Medellín, R. L., Russell, A., & Semmens, D. J. (2017). Operationalizing the telecoupling framework for migratory species using the spatial subsidies approach to examine ecosystem services provided by Mexican free-tailed bats. *Ecology & Society*, *22*(4), 23.
- Maclean, I. M. D., & Wilson, R. J. (2011). Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(30), 12337–12342.
- Mahony, C. R., Cannon, A. J., Wang, T., & Aitken, S. N. (2017). A closer look at novel climates: New methods and insights at continental to landscape scales. *Global Change Biology*, *23*(9), 3934–3955.
- Malcolm, J. R., Liu, C., Neilson, R. P., Hansen, L., & Hannah, L. (2006). Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology*, *20*(2), 538–548.
- McDowell, N., Allen, C. D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., Christoffersen, B., Davies, S., Doughty, C., Duque, A., Espirito-Santo, F., Fisher, R., Fontes, C. G., Galbraith, D., Goodsman, D., Grossiord, C., Hartmann, H., Holm, J., Johnson, D. J., Kassim, A. R., Keller, M., Koven, C., Kueppers, L., Kumagai, T., Malhi, Y., McMahon, S. M., Mencuccini, M., Meir, P., Moorcroft, P., Muller-Landau, H. C., Phillips, O. L., Powell, T., Sierra, C. A., Sperry, J., Warren, J., Xu, C., & Xu, X. (2018). Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytologist*, *219*(3), 851–869.
- Moat, J., Gole, T.W., & Davis, A.P. (2019). Least concern to endangered: Applying climate change projections profoundly influences the extinction risk assessment for wild Arabica coffee. *Global Change Biology*, *25*(2), 390–403.
- Moilanen, A., Lehtinen, P., Kohonen, I., Jalkanen, J., Virtanen, E. A., & Kujala, H. (2022). Novel methods for spatial prioritization with applications in conservation, land use planning and ecological impact avoidance. *Methods in Ecology and Evolution*, *13*(5), 1062–1072.
- Mok, H. F., Arndt, S. K., & Nitschke, C. R. (2012). Modelling the potential impact of climate variability and change on species regeneration potential in the temperate forests of South-Eastern Australia. *Global Change Biology*, *18*(3), 1053–72.
- Monahan, W.B. (2009). A mechanistic niche model for measuring species' distributional responses to seasonal temperature gradients. *PLoS One* *4*, e7921.
- Montgomery, R. A., Rice, K. E., Stefanski, A., Rich, R. L., & Reich, P. B. (2020). Phenological responses of temperate and boreal trees to warming depend on ambient spring temperatures, leaf habit, and geographic range. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(19), 10397–405.
- Newton, A. C., Britton, R., Davies, K., Diaz, A., Franklin, D. J., Herbert, R. J. H., Hill, R. A., Hodder, K., Jones, G., Korstjens, A. H., Lamb, A., Olley, J., Pinder, A. C., Roberts, C. G., & Stafford, R. (2021).

Operationalising the concept of ecosystem collapse for conservation practice. *Biological Conservation*, 264, 109366.

- Ni, H., Yu, L., Gong, P., Li, X., & Zhao, J. (2023). Urban renewal mapping: A case study in Beijing from 2000 to 2020. *Journal of Remote Sensing*, 3, 0072.
- Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E. M., Butchart, S. H. M., Kovacs, K. M., Scheffers, B. R., Hole, D. G., Martin, T. G., Akçakaya, H. R., Corlett, R. T., Huntley, B., Bickford, D., Carr, J. A., Hoffmann, A. A., Midgley, G. F., Pearce-Kelly, P., Pearson, R. G., Williams, S. E., Willis, S. G., Young, B., & Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, 5(3), 215–225.
- Pacifici, M., Visconti, P., Butchart, S. H. M., Watson, J. E. M., Cassola, F. M., & Rondinini, C. (2017). Species' traits influenced their response to recent climate change. *Nature Climate Change*, 7(3), 205–208.
- Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., Shamseer, L., Tetzlaff, J. M., Akl, E. A., Brennan, S. E., Chou, R., Glanville, J., Grimshaw, J. M., Hróbjartsson, A., Lalu, M. M., Li, T., Loder, E. W., Mayo-Wilson, E., McDonald, S., McGuinness, L. A., Stewart, L. A., Thomas, J., Tricco, A. C., Welch, V. A., Whiting, P., & Moher, D. (2021). The PRISMA 2020 statement: An updated guideline for reporting systematic reviews. *International Journal of Surgery*, 88, 105906.
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637–669.
- Pearson, R. G., Phillips, S. J., Loranty, M. M., Beck, P. S. A., Damoulas, T., Knight, S. J., & Goetz, S. J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change. *Nature Climate Change*, 3(7), 673–677.
- Pearson, R. G., Stanton, J. C., Shoemaker, K. T., Aiello-Lammens, M. E., Ersts, P. J., Horning, N., Fordham, D. A., Raxworthy, C. J., Ryu, H. Y., McNeese, J., & Akçakaya, H. R. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, 4(3), 217–221.
- Pearson, R. G., Thuiller, W., Araújo, M. B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T. P., & Lees, D. C. (2006). Model-based uncertainty in species range prediction. *Journal of Biogeography*, 33(10), 1704–1711.
- Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., Lenoir, J., Linnetved, H. I., Martin, V. Y., McCormack, P. C., McDonald, J., Mitchell, N. J., Mustonen, T., Pandolfi, J. M., Pettorelli, N., Popova, E., Robinson, S. A., Scheffers, B. R., Shaw, J. D., Sorte, C. J. B., Strugnell, J. M., Sunday, J. M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E., & Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355(6332), eaai9214.
- Perry, T.O., & Wu, W.C. (1960). Genetic variation in the winter chilling requirement for date of dormancy break for *Acer rubrum*. *Ecology*, 41, 790–794.

-
- Pettorelli, N., Laurance, W. F., O'Brien, T. G., Wegmann, M., Nagendra, H., & Turner, W. (2014). Satellite remote sensing for applied ecologists: Opportunities and challenges. *Journal of Applied Ecology*, *51*(4), 839–848.
- Pineda-Munoz, S., Wang, Y., Lyons, S. K., Tóth, A. B., & McGuire, J. L. (2021). Mammal species occupy different climates following the expansion of human impacts. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(2), e1922859118.
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., Brander, K., Bruno, J. F., Buckley, L. B., Burrows, M. T., Duarte, C. M., Halpern, B. S., Holding, J., Kappel, C. V., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Schwing, F., Thompson, S. A., & Richardson, A. J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*(10), 919–925.
- Poulter, B., Hattermann, F., Hawkins, E., Zaehle, S., Sitch, S., Restrepo-Coupe, N., Heyder, U., & Cramer, W. (2010). Robust dynamics of Amazon dieback to climate change with perturbed ecosystem model parameters. *Global Change Biology*, *16*(9), 2476–2495.
- Radchuk, V., Turlure, C., & Schtickzelle, N. (2013). Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, *82*, 275–285.
- Riddell, E. A., Odom, J. P., Damm, J. D., & Sears, M. W. (2018). Plasticity reveals hidden resistance to extinction under climate change in the global hotspot of salamander diversity. *Science Advances*, *4*(7), 1–10.
- Rowland, E.L., Davison, J.E., & Graumlich, L.J. (2011). Approaches to evaluating climate change impacts on species: a guide to initiating the adaptation planning process. *Journal of Environmental Management*, *47*, 322–337.
- Rumpf, S. B., Hülber, K., Wessely, J., Willner, W., Moser, D., Gattringer, A., Klöner, G., Zimmermann, N. E., & Dullinger, S. (2019). Extinction debts and colonization credits of non-forest plants in the European Alps. *Nature Communications*, *10*(1), 4293.
- Sandin, L., Schmidt-Kloiber, A., Svenning, J.-C., Jeppesen, E., & Friberg, N. (2014). A trait-based approach to assess climate change sensitivity of freshwater invertebrates across Swedish ecoregions. *Current Zoology*, *60*(2), 221–232.
- Schmidt-Traub, G., Locke, H., Gao, J., Ouyang, Z., Adams, J., Li, L., Sala, E., Shaw, M. R., Troëng, S., Xu, J., Zhu, C., Zou, C., Ma, T., & Wei, F. (2021). Integrating climate, biodiversity, and sustainable land-use strategies: Innovations from China. *National Science Review*, *8*(7), nwaal39.
- Schröter, M., Koellner, T., Alkemade, R., Amhold, S., Bagstad, K. J., Erb, K.-H., Frank, K., Kastner, T., Kissinger, M., Liu, J., López-Hoffman, L., Maes, J., Marques, A., Martín-López, B., Meyer, C., Schulp, C. J. E., Thober, J., Wolff, S., & Bonn, A. (2018). Interregional flows of ecosystem services: Concepts, typology, and four cases. *Ecosystem Services*, *31*, 231–241.
- Sears, M. W., Angilletta, M. J., Jr., Schuler, M. S., Borchert, J., Dilliplane, K. F., Stegman, M., Rusch, T. W., & Mitchell, W. A. (2016). Configuration of the thermal landscape determines thermoregulatory

performance of ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, 113(38), 10595–10600.

- Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, 531(7593), 229–32.
- Seebacher, F., White, C.R., & Franklin, C.E. (2015). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change*, 5(1), 61–66.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, 7(6), 395–402.
- Shen, X., Liu, M., Hanson, J. O., Wang, J., Locke, H., Watson, J. E. M., Ellis, E. C., Li, S., & Ma, K. (2023). Countries' differentiated responsibilities to fulfill area-based conservation targets of the Kunming-Montreal Global Biodiversity Framework. *One Earth*, 6(5), 548–559.
- Song, H., Ordonez, A., Svenning, J. C., Qian, Yin, X., Mao, L., Deng T., & Zhang, J. (2021). Regional disparity in extinction risk: Comparison of disjunct plant genera between eastern Asia and eastern North America. *Global Change Biology*, 27(9), 1904–1914.
- Sorte, J. B., Williams, S. L., & Carlton, J. T. (2010). Marine range shifts and species introductions: Comparative spread rates and community impacts. *Global Ecology and Biogeography*, 19(3), 303–316. <https://doi.org/10.1111/j.1466-8238.2009.00519.x>
- Stillman, J. H. (2003). Acclimation capacity underlies susceptibility to climate change. *Science*, 301(5629), 65–65.
- Summers, D. M., Bryan, B. A., Crossman, N. D., & Meyer, W. S. (2012). Species vulnerability to climate change: Impacts on spatial conservation priorities and species representation. *Global Change Biology*, 18(7), 2335–2348.
- Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences of the United States of America*, 111(15), 5610–5615.
- Sunday, J.M., Bates, A.E., & Dulvy, N.K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2, 686–690.
- Tagliari, M. M., Danthu, P., Leong Pock Tsy, J.-M., Cornu, C., Lenoir, J., Carvalho-Rocha, V., & Vieilledent, G. (2021). Not all species will migrate poleward as the climate warms: The case of the seven baobab species in Madagascar. *Global Change Biology*, 27(23), 6071–6085.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427(6970), 145–148.

-
- Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(23), 8245–8250.
- Tilman, D., May, R. M., Lehman, C. L., & Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature*, *371*(6492), 65–66.
- Trisos, C.H., Merow, C., & Pigot, A.L. (2020). The projected timing of abrupt ecological disruption from climate change. *Nature*, *580*(7804), 496–501.
- Urban, M.C. (2015). Accelerating extinction risk from climate change. *Science*, *348*, 6234.
- Ureta, C., Ramírez-Barrón, M., Sánchez-García, E. A., Cuervo-Robayo, A. P., Munguía-Carrara, M., Mendoza-Ponce, A., Gay, C., & Sánchez-Cordero, V. (2022). Species, taxonomic, and functional group diversities of terrestrial mammals at risk under climate change and land-use/cover change scenarios in Mexico. *Global Change Biology*, *28*(23), 6992–7008.
- van Heerwaarden, B., & Sgrò, C. M. (2021). Male fertility thermal limits predict vulnerability to climate warming. *Nature Communications*, *12*(1), 2214.
- Visconti, P., Bakkenes, M., Baisero, D., Brooks, T., Butchart, S. H. M., Joppa, L., Alkemade, R., Di Marco, M., Santini, L., Hoffmann, M., Maiorano, L., Pressey, R. L., Arponen, A., Boitani, L., Reside, A. E., van Vuuren, D. P., & Rondinini, C. (2015). Projecting global biodiversity indicators under future development scenarios. *Conservation Letters*, *9*(1), 5–13.
- Warren, R., VanDerWal, J., Price, J., Welbergen, J. A., Atkinson, I., Ramirez-Villegas, J., Osborn, T. J., Jarvis, A., Shoo, L. P., Williams, S. E., & Lowe, J. (2013). Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change*, *3*(7), 678–682.
- White, K. S., Gregovich, D. P., & Levi, T. (2018). Projecting the future of an alpine ungulate under climate change scenarios. *Global Change Biology*, *24*(3), 1136–1149.
- Wieder, W. R., Kennedy, D., Lehner, F., Musselman, K. N., Rodgers, K. B., Rosenbloom, N., Simpson, I. R., & Yamaguchi, R. (2022). Pervasive alterations to snow-dominated ecosystem functions under climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(30), e2205556119.
- Wiens, J. A., Stralberg, D., Jongsomjit, D., Howell, C. A., & Snyder, M. A. (2009). Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(Supplement 2), 19729–19736.
- Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLOS Biology*, *6*(12), e325.
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of 277 the world's birds and mammals. *Ecology*, *95*(7), 2027.
- World Meteorological Organisation (WMO). (2023). State of the Global Climate 2022.
- Wunderling, N., Staal, A., Sakschewski, B., Hirota, M., Tuinenburg, O. A., Donges, J. F., Barbosa, H. M. J., & Winkelmann, R. (2022). Recurrent droughts increase risk of cascading tipping events by outpacing

adaptive capacities in the Amazon rainforest. *Proceedings of the National Academy of Sciences of the United States of America*, 119(32), e2200081119.

Yu, L., Du, Z., Dong, R., Zheng, J., Tu, Y., Chen, X., Hao, P., Zhong, B., Peng, D., Zhao, J., Li, X., Yang, J., Fu, H., Yang, G., & Gong, P. (2022). FROM-GLC Plus: Towards near real-time and multi-resolution land cover mapping. *GIScience and Remote Sensing*, 59(1), 1026–1047.

Zamora-Gutierrez, V., Rivera-Villanueva, A. N., Martínez Balvanera, S., Castro-Castro, A., & Aguirre-Gutiérrez, J. (2021). Vulnerability of bat–plant pollination interactions due to environmental change. *Global Change Biology*, 27(14), 3367–3382.

Zhou, Z., Steiner, N., Fivash, G. S., Cozzoli, F., Blok, D. B., van IJzerloo, L., van Dalen, J., Ysebaert, T., Walles, B., & Bouma, T. J. (2023). Temporal dynamics of heatwaves are key drivers of sediment mixing by bioturbators. *Limnology and Oceanography*, 68(5), 1105–1116.

Zurell, D., Thuiller, W., Pagel, J., Cabral, J. S., Münkemüller, T., Gravel, D., Dullinger, S., Normand, S., Schiffrers, K. H., Moore, K. A., & Zimmermann, N. E. (2016). Benchmarking novel approaches for modelling species range dynamics. *Global Change Biology*, 22(8), 2651–2664.

Accepted Manuscript