

# UC Merced

## Frontiers of Biogeography

### Title

The interface between Macroecology and Conservation: existing links and untapped opportunities

### Permalink

<https://escholarship.org/uc/item/6601q78t>

### Journal

Frontiers of Biogeography, 0(0)

### Authors

Santini, Luca  
Antão, Laura H.  
Jung, Martin  
et al.

### Publication Date

2021

### DOI







10.21425/F5FBG53025

### License

<https://creativecommons.org/licenses/by/4.0/> 4.0



## The interface between Macroecology and Conservation: existing links and untapped opportunities

Luca Santini<sup>1,2,3\*</sup> , Laura H. Antão<sup>4</sup> , Martin Jung<sup>5,6</sup> ,  
Ana Benítez-López<sup>7</sup> , Giovanni Rapacciuolo<sup>8</sup> ,  
Moreno Di Marco<sup>1</sup> , Faith A.M. Jones<sup>9,10</sup> , Jessica M. Haghkerdar<sup>9</sup>   
and Manuela González-Suárez<sup>11</sup> 

<sup>1</sup> Department of Biology and Biotechnologies “Charles Darwin”, Sapienza University of Rome, Rome, Italy; <sup>2</sup> National Research Council, Institute of Research on Terrestrial Ecosystems (CNR-IRET), Via Salaria km 29.300, 00015, Monterotondo, Rome, Italy, E-mail: luca.santini.eco@gmail.com; <sup>3</sup> Department of Environmental Science, Institute for Water and Wetland Research, Radboud University, P.O. Box 9010, NL-6500 GL, Nijmegen, The Netherlands; <sup>4</sup> Research Centre for Ecological Change, Organismal and Evolutionary Biology Research Programme, University of Helsinki, PO Box 65 Viikinkaari 1, 00014, Helsinki, Finland; <sup>5</sup> School of Life Sciences, University of Sussex, BN1 9QG, Brighton, UK; <sup>6</sup> Biodiversity, Ecology, and Conservation Research (BEC) Group, International Institute for Applied Systems Analysis (IIASA), Schlossplatz 1, A-2361, Laxenburg, Austria; <sup>7</sup> Integrative Ecology Group, Estación Biológica de Doñana (EBD-CSIC), Avda. Americo Vespucio 26, 41092 Sevilla, Spain; <sup>8</sup> NatureServe, Arlington, VA 22202, USA; <sup>9</sup> Centre for Biological Diversity and Scottish Oceans Institute, School of Biology, University of St Andrews, St Andrews, Fife KY16 9TH, UK; <sup>10</sup> Department of Forest and Conservation, Faculty of Forestry, University of British Columbia, Vancouver, V6T 1Z4, Canada; <sup>11</sup> Ecology and Evolutionary Biology, School of Biological Sciences, University of Reading, Reading, RG6 6EX, UK

\*Correspondence: Luca Santini, luca.santini.eco@gmail.com

### Abstract

Human activities are altering the structure of ecosystems, compromising the benefits they provide to nature and people. Effective conservation actions and management under ongoing global change rely on a better understanding of socio-ecological patterns and processes across broad spatiotemporal scales. Both macroecology and conservation science contribute to this improved understanding and, while they have different scopes, these disciplines have become increasingly interconnected over time. Here we describe examples of how macroecology has contributed to conservation science, and how conservation science can motivate further macroecological developments and applications. We identify challenges and untapped potential to further strengthen the links between these two disciplines. Major macroecological contributions include developing ecological theory, providing methodologies useful for biodiversity assessments and projections, making data more accessible and addressing knowledge gaps. These contributions have played a major role in the development of conservation science, and have supported outreach to policy makers, media, and the public. Nonetheless, a pure macroecological lens is limited to inform conservation decisions, particularly in local contexts, which frequently leads to the misuse of macroecological analyses for conservation applications, misunderstandings of research outputs, and skepticism among conservation practitioners and scientists. We propose possible solutions to overcome these challenges and strengthen links between macroecology and conservation science, including a stronger focus on ecological mechanisms and predictive approaches, and the creation of hybrid journals and meetings. Finally, we suggest new avenues for macroecological research that would further benefit conservation science.

### Highlights

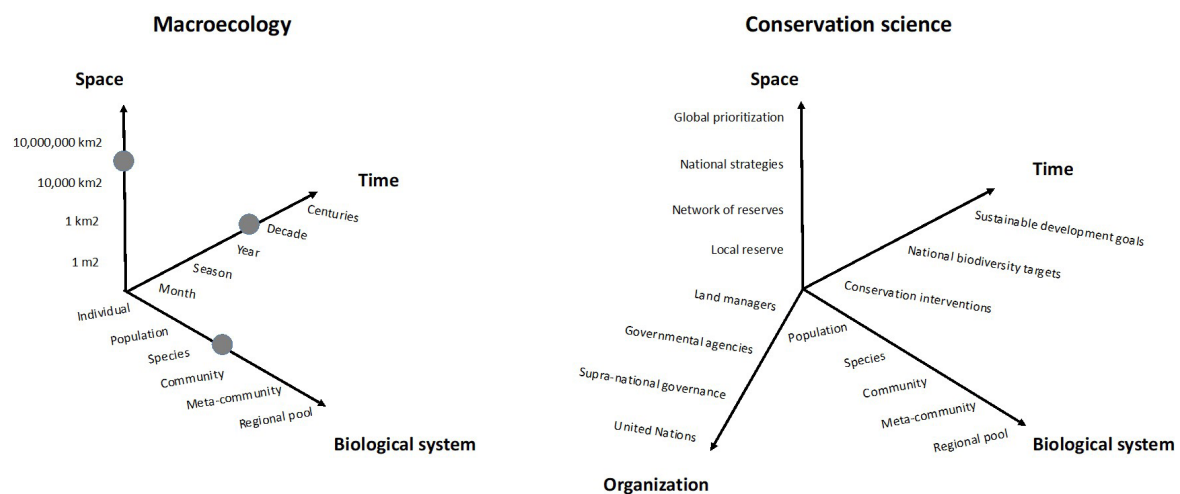
- Understanding broad-scale biological patterns and processes is crucial for effective conservation actions and management under ongoing global change.
- While Macroecology and Conservation science have different scopes, they have influenced - and benefitted from - each other over time.
- Macroecology has contributed to conservation by developing ecological theory and methodological approaches, making data more accessible, and addressing knowledge gaps.
- Macroecology has capitalized on data-gathering that was originally intended to support conservation initiatives, and gained an improved understanding of how natural patterns have been altered by recent human impact.
- Untapped opportunities remain that could foster additional interconnections and aid further development of both disciplines. We present possible solutions to improve connections and new avenues for macroecological research that can benefit conservation science.

**Keywords:** biodiversity assessments, biodiversity database, broad-scale biodiversity models, conservation practice, macroecological theory, media attention, public interest

## Macroecology and Conservation Science: diverging but complementary scopes

Macroecology and conservation science are both relatively young scientific disciplines arising from traditional ecology (Hintzen et al. 2019, McGill 2019). Although there can be overlap in academic research between them, the two disciplines often differ in their aims. Macroecology is the branch of ecology focused on broad-scale patterns, processes, and emergent properties of complex systems (Brown and Maurer 1989, Lawton 1999, Smith et al. 2008), where scale can be defined along three main axes: time, space, and taxonomy (Brown 1999, McGill 2019; Fig. 1). While typically characterized by a focus on broader scales and a top-down approach, the search for general principles

underlying the structure and functioning of life on earth that escape the specifics of individual systems can further distinguish macroecology from other disciplines, such as biogeography, meta-community or landscape ecology (Lawton 1999, Blackburn and Gaston 2002, Marquet 2002, Smith et al. 2008). Conservation science, conversely, is a mission-oriented discipline aimed at biodiversity conservation (Soulé 1985; Fig. 1). When first defined as a discipline it was considered a branch of ecology (i.e. conservation biology) but has become increasingly multidisciplinary over time, broadening into what is now collectively defined as conservation science (Box 1), which explicitly recognizes the role of humans in the conservation agenda by integrating disciplines such as economics, political science, and social sciences (Kareiva and Marvier 2012; we broadly



**Figure 1.** Scale in macroecology and conservation science, adapted from McGill (2019). The grey dots along the axes indicate the approximate values beyond which macroecology typically operates.

### Box 1 - GLOSSARY

**Macroecology** = Discipline aimed at delineating general principles able to explain patterns, processes and emergent properties of complex ecological systems at broad scales, where scale can be defined along three main axes: time, space and taxonomy.

**Conservation science** = Discipline concerned with all aspects of conservation, including e.g. biology, economics, policy, psychology, sociology, sustainable development, anthropology and ethics.

**Conservation biology** = Branch of conservation science dealing specifically with biological aspects, including e.g. genetics, population biology, ecosystems, and biodiversity.

**Conservation biogeography** = Subfield of conservation biology applying biogeographical principles, theories and analyses to address biodiversity conservation.

**Conservation research** = Research aimed at improving the theory underlying conservation science and exploring new approaches and methods for conservation practice.

**Conservation planning** = Quantitative approaches for the identification of conservation actions needed in order to meet a conservation goal.

**Conservation practice** = Implementation of conservation actions on the ground, which may include actual interventions on populations/habitats, interaction with policy makers and stakeholders, fundraising, education and communication with the public.

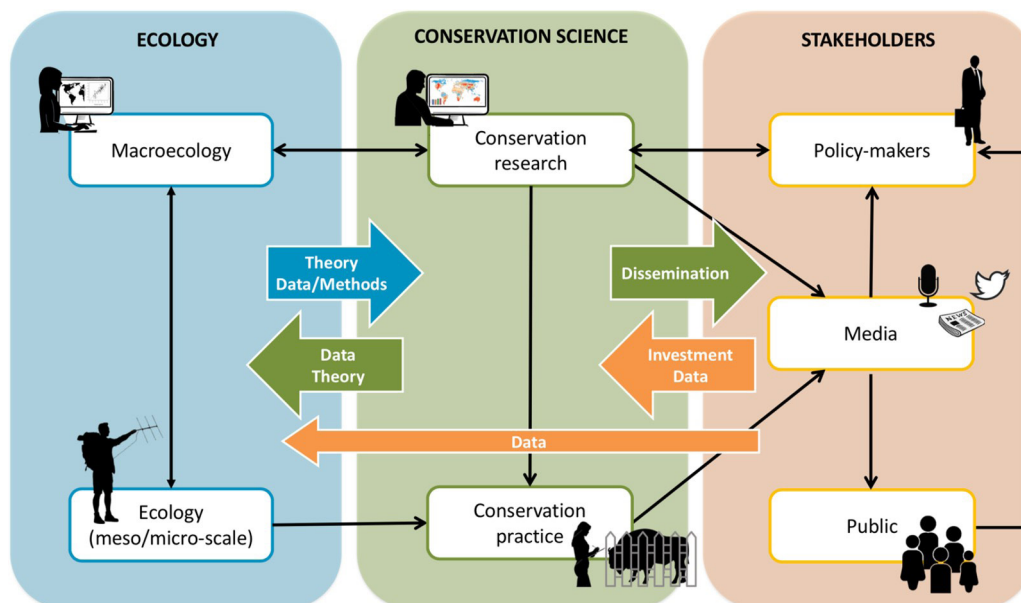
**Land manager** = Person in charge of managing and supervising the development lands, including areas dedicated to biodiversity conservation.

refer to conservation science throughout the paper, only referring to different conservation subfields where relevant). As a mission-driven discipline, conservation science has been subjected to many temporary and contrasting schools of thought (Mace 2014, Hintzen et al. 2019, Sandbrook et al. 2019). An important difference that characterizes the development of conservation science when compared to other ecological disciplines is that conservation scientists and practitioners are expected to provide recommendations and make decisions even when a solid theoretical or empirical underpinning is missing (Soulé 1985). Therefore, conservation science requires pragmatism and higher tolerance to uncertainty compared to other disciplines. Here we have adopted inclusive, operational definitions for conservation and macroecology (see Glossary – Box 1), but discipline boundaries are not strict, and we acknowledge that the research (and researchers) we discuss can potentially overlap other disciplines (e.g. meta-community ecology, biogeography, landscape ecology). As it commonly happens in science, different interpretations coexist, and achieving consensus in definitions goes beyond the scope of this work and is, arguably, not needed for the overall argument that further linking of top-down, broad-scale ecology with conservation can be useful.

Historically, much of conservation science has focused on specific populations or habitats. However, given the global nature and the synergistic effects of the multiple drivers of global change that characterize the Anthropocene, such as land-use, overexploitation and climate change (Barnosky et al. 2012, Halpern et al. 2019, IPBES 2019, Bowler et al. 2020), conservation

science has gradually adopted a broad-scale top-down perspective (Fig. 2). Today, conservation is an extremely diversified discipline that includes both researchers and practitioners working at scales that span from single populations and local habitats, up to global conservation efforts, such as those defined under the UN Convention on Biological Diversity. ‘Conservation biogeography’ has emerged as a hybrid field addressing conservation questions based on biogeographical principles (Whittaker et al. 2005). Broad-scale conservation analysed can be seen by some practitioners as purely academic exercises with little relevance for real-world applications (Prendergast et al. 1999). However adequate conservation planning in response to global-scale threats requires an understanding of the regional-scale context in which species are embedded (Knight et al. 2006, Pressey et al. 2013). Indeed, land managers and policy makers are already making conservation decisions within regional, national and international frameworks (e.g. Rewilding Europe and Natura 2000 in Europe, Evans 2012, Ceaşu et al. 2015) which largely exceed the average scale of traditional ecological studies (Estes et al. 2018, McGill 2019).

In 1989 James H. Brown argued that macroecology had much to offer to biodiversity conservation (Brown 1989), from predictions of extinctions due to habitat loss, to the identification of correlates of species extinction risk and drivers of species abundance and distribution. More than thirty years later, we argue that macroecology has indeed made substantial contributions and nowadays plays an important role in informing conservation science and, more indirectly,



**Figure 2.** Links between traditional ecology, macroecology, conservation research and practice, policy-makers and the public. We represent here the links discussed in the text, but acknowledge that many other links exist (e.g. between ecology and conservation) or are possible. We further note that this figure is an oversimplified representation of reality: disciplines are presented as distinct boxes, although we acknowledge that in reality science is fluid and boundaries between disciplines are often fuzzy, depending on the definitions used. We also acknowledge that many researchers today conduct research that crosses different disciplines’ boundaries.



conservation practice (Fig. 2), but that there remains untapped potential for further contributions. Here, we highlight some of the existing macroecological theoretical and methodological contributions to conservation science and provide insights into how links between the two disciplines can be further improved. We also show that conservation science has in turn contributed to contextualising the broad-scale patterns investigated by macroecology. On the other hand, the two disciplines are broad and diversified, and communication among respective researchers is often limited. This perspective article has three main goals: 1) to provide a broad overview of the interconnections between macroecology and conservation science, covering examples of how these disciplines contributed to their mutual development in terms of theory, data, methods, and outreach potential; 2) to discuss limitations in terms of scale, communications and mutual understanding; and 3) to outline opportunities for further interlinkages and synergies between the two disciplines. This perspective may help to foster further collaborations between macroecology and conservation, and hope to reach macroecology and conservation reaching researchers who could, but do not yet, conduct research at the interface of these two disciplines. While here we refer to groups of scientists belonging to distinct disciplines, we recognize that science today is highly interconnected, and many researchers do not exclusively fit in any of these distinct categories, and often conduct research across disciplines.

## Macroecology contributions to conservation science research

### *Developing theory*

Local studies provide insights into ecological mechanisms, but these are rarely generalizable across taxa and/or habitats, limiting predictive capacity (Currie 2019). Macroecology's search for emergent patterns has contributed to our understanding of generalizable ecological mechanisms (McGill and Nekola 2010, Marquet et al. 2014) leading to improved predictive capacity (Currie 2019). For example, the Metabolic Theory of Ecology, which explains how body size and temperature interact to determine metabolic rates (Gillooly et al. 2001, Brown et al. 2004), prompted much macroecological research relevant for conservation issues. Metabolic theory underlies the allometry of space use, which relates species population density with body mass and trophic levels (Brown and Maurer 1989, Jetz et al. 2004). Such relationships, in turn, determine the minimum area required to effectively conserve populations (Boyer and Jetz 2012), as well as the minimum geographic range area for the long-term persistence of species (Brown and Maurer 1987, Marquet and Taper 1998, Diniz-Filho et al. 2005, Carvajal-Quintero et al. 2017). Metabolic theory can also predict life history traits across trophic levels and body mass, which has been applied to inform the management of exploited populations, such as fisheries (Jennings and Blanchard 2004, Andersen et al.

2009, 2015, Gislason et al. 2010). Species abundance, geographic distribution and reproductive traits are key parameters that determine species extinction risk. Scaling relationships have been used to clarify how the intrinsic vulnerability of species to extinction varies with their size and other biological traits (Purvis et al. 2000, Cardillo et al. 2005a, Pearson et al. 2014, Böhm et al. 2016). Finally, the scaling of metabolic rate with body mass and its dependency on environmental temperature (Gillooly et al. 2001) underlies species tolerance and vulnerability to environmental change (Dillon et al. 2010, Araújo et al. 2013). Obviously, such relationships cannot be considered universally accurate as they describe broad biodiversity patterns, and improved estimates for conservation must be obtained for individual populations. For example, criticisms on the application of the metabolic theory to fisheries has exposed simplifications that may lead to flawed estimates (Valderrama and Fields 2017). However, such macroecological relationships allow to set prior expectations in the absence of more targeted studies.

The Unified Neutral Theory (Hubbell 2001), which emphasizes the importance of ecological drift and dispersal limitation to explain natural patterns, has also been widely used to derive predictions in conservation, for example regarding the number of species expected to go extinct (e.g. Hubbell et al. 2008). Several studies have shown that Neutral theory is capable of accurately predicting some informative parameters for conservation (e.g. extinction rates, invasion success), but not others, highlighting the role of neutral mechanisms in structuring communities, while also exposing the over-simplification of some assumptions (e.g. Gilbert et al. 2006, Daleo et al. 2009).

Macroecologists have long studied the relationship between the Grinnellian niche and species distribution (Maguire 1973, Colwell and Rangel 2009, Soberón and Nakamura 2009), leading to the development of methods for predicting species distributions that are now widely applied in conservation planning (e.g. Araújo et al. 2004), identifying undiscovered populations of rare species (e.g. Williams et al. 2009), and potential reintroduction areas (e.g. Martínez-Meyer et al. 2006). Such investigation also underlies many studies on the effects of global change on species distribution, providing essential risk assessments and scenario projections (Guisan and Thuiller 2005, Guisan et al. 2013; although their uncritical application has been criticized, e.g. Fourcade et al. 2018, Warren et al. 2020, Santini et al. 2021). For example, studies of geographic range contractions have shown that these rarely occur from margins to the centre, as originally hypothesized, with many highly threatened species now occupying a marginal area of their historical distributions (Channel and Lomolino 2000). More recent research further unveiled the interplay between climate change, anthropogenic threats and species traits in range contraction dynamics (Pacifi et al. 2020).

Macroecological research has also focused on community assembly rules (Münkemüller et al. 2020) and functional biogeography (Violle et al. 2014), and

these concepts have gradually started to be used for projections of biodiversity responses to environmental change, e.g. in terms of community filtering effects and changes in functional trait patterns (e.g. Dubuis et al. 2013, Blonder et al. 2015, Madani et al. 2018).

Macroecological principles are at the base of the Island Biogeography Theory (MacArthur and Wilson 1967), which underlies the concept of “rescue effect” (Brown and Kodric-Brown 1977) and has been pivotal for the development of conservation planning, specifically underlying the general principles of reserve design in terms of area, shape and isolation (Diamond et al. 1976). Subsequently, the SLOSS (Single Large or Several Small) debate has set the basis for landscape and conservation planning theory, exposing the trade-offs between population persistence, species richness and risk spread, as well as between single- and multi-species conservation plans (Ovaskainen 2002, Whittaker and Fernández-Palacios 2007, Le Roux et al. 2015). Whilst conceptually useful, the Island Biogeography Theory is not directly applicable to real case studies given the context-dependent nature of conservation problems, which normally require a more in-depth consideration of several factors (e.g. costs, risk of land to be converted, etc.; Margules and Pressey 2000).

Further fundamental contributions stem from emergent macroecological patterns like Species Abundance Distributions (SADs) and Species Area Relationships (SARs) (Rosenzweig 1995). Both SADs and SARs have been used to estimate long-term effects of habitat loss and fragmentation on species richness and abundance (Storch et al. 2012, Matthews and Whittaker 2015, Chisholm et al. 2018). For instance, SADs can inform conservation management and monitoring about the relative rarity of species in a community (McGill et al. 2007, Enquist et al. 2019), with changes in SADs acting as early-warning signals of disturbance processes such as biological invasions (Matthews and Whittaker 2015). Both SARs and SADs have been shown to be accurately predicted by the Maximum Entropy theory of ecology (Harte 2011), which relies on information on species richness, total abundance, and total metabolic rate of a community to predict several emergent patterns in macroecology. Further, the concept of “extinction debt” results from a delayed effect of habitat loss on species richness and abundance, derived as a direct consequence of habitat loss and fragmentation acting on broad spatio-temporal scales on entire biological communities. Although this concept was originally formulated as a species-level mechanism (Diamond 1972, Tilman et al. 1994), it has increasingly been treated as a disequilibrium of community level emergent properties following changes in the available area according to SARs (Halley et al. 2014). SARs have, however, been shown to overestimate extinction debts, and further development of this theory led to the conceptualization of the Endemic Area Relationships (EAR) as a more robust approach to estimate the number of extinctions expected at the equilibrium (Kinzig and Harte 2000).

The study of habitat fragmentation also benefit from a top-down approach, as conclusions drawn from individual patches do not scale up to landscape levels (Fahrig 2019). After decades of literature supporting the negative impacts of fragmentation on biodiversity, macroecological approaches have allowed disentangling the individual effects of habitat loss and fragmentation, suggesting that fragmentation per se may not yield negative effects on biodiversity, and only the amount of surrounding habitat matters - the Habitat Amount Hypothesis (Fahrig 2013). Results regarding this hypothesis are, however, mixed, and its implications are still currently debated (Saura 2020).

Macroecology has also developed frameworks to test hypotheses on biological invasions, delineating both generalized patterns of invasions (Blackburn and Duncan 2001a,b, Sax et al. 2002, Sax and Gaines 2008, Blackburn et al. 2017), as well as the profile of successful invasive species (e.g. Van Kleunen et al. 2010, Capellini et al. 2015, González-Suárez et al. 2015, Allen et al. 2017b). Species distribution models have been used to estimate drivers of invasion and the potential spread of invasive species (Bellard et al. 2016). Finally, broad-scale meta-analyses have allowed escaping from idiosyncrasies of single studies to synthesize the generalized secondary effects of defaunation on biological communities (e.g. Baum and Worm 2009, Gardner et al. 2019), with broad-scale simulations based on trait-based approaches further uncovering secondary effects of human impacts (Donoso et al. 2020, Enquist et al. 2020).

### *Improving data accessibility and filling knowledge gaps*

Evidence-based conservation depends on systematically assembled ecological data. Macroecologists (and other ecologists working at broad scales) have invested heavily in collating such data and, by doing so, have recently created a number of key publicly accessible databases of species occurrence (e.g. OBIS-SEAMAP, Halpin et al. 2006, BIEN, Maitner et al. 2018), abundance (e.g. PREDICTS, Hudson et al. 2014, BioTIME, Dornelas et al. 2018, TetraDENSITY, Santini et al. 2018, RivFishTIME, Comte et al. 2020), traits (e.g. PanTHERIA, Jones et al. 2009, TRY, Kattge et al. 2011, EltonTRAITS, Wilman et al. 2014, AmphibiO, Oliveira et al. 2017), and population demographics (e.g. COMPADRE, Salguero-Gomez et al. 2015, COMADRE, Salguero-Gómez et al. 2016). One of the key features is that these are standardised databases, allowing easier access to primary data otherwise hard to obtain and synthesise, and therefore offering the possibility to easily query spatio-temporal information on species occurrence, abundance and/or traits, which can readily inform biodiversity assessments and conservation plans (e.g. Edgar et al. 2016, Blowes et al. 2019, Enquist et al. 2019, Williams et al. 2019, Antão et al. 2020).

Crucially, such data compilation efforts have exposed spatial, temporal, and taxonomic biases and uncertainties in biodiversity knowledge (González-Suárez et al. 2012, Edgar et al. 2016, Meyer et al. 2016, Conde et al. 2019,

Dornelas et al. 2019) - the pervasive Eltonian, Linnean and Wallacean shortfalls. While these shortfalls remain an issue across ecology and conservation (Whittaker et al. 2005, Hortal et al. 2015), macroecological efforts have prompted research into statistical methods to address data gaps (Blackburn and Gaston 1998, Penone et al. 2014, Johnson et al. 2020), extract valuable information from opportunistically collected data (Isaac et al. 2014), and devise top-down approaches to guide future data collection (Rocchini et al. 2011, Stropp et al. 2016, Dornelas et al. 2019).

Furthermore, macroecology has unveiled statistical relationships that are often used in conservation to make inferences on poorly known areas or species. For instance, there are fairly comprehensive datasets for some traits (Wilman et al. 2014), while data for other traits (e.g. home range area, dispersal distance, reproductive traits) are only available for a relatively small number of species. Spatial and reproductive traits, however, provide key information for biodiversity conservation, including species minimum required area, colonisation potential and population resilience. Larger mammals, for example, live at lower population densities (Silva and Downing 1995), disperse longer distances (Whitmee and Orme 2012), tend to have slower reproductive rates and smaller reproductive outputs (Bielby et al. 2007), and require smaller populations for persistence (Hilbers et al. 2017). Conservation research has relied on such statistical relationships to estimate missing information relevant to conservation assessments or planning (Pacifci et al. 2013, Visconti et al. 2016, Santini et al. 2019, Bird et al. 2020). Because trait values span several orders of magnitude across taxa, inferred estimates facilitate the reduction of uncertainty for biodiversity conservation assessments, planning and projections, which would otherwise ignore key differences between species and would thus be even more taxonomically and geographically biased.

### *Providing tools for biodiversity assessments*

The quantification of biodiversity patterns and how they change in space and time are both a key goal of macroecology (McGill et al. 2015) and fundamental for conservation actions across scales. In an effort to standardize, quantify and monitor changes in biodiversity, macroecologists have started to propose the systematic use of biodiversity indicators (e.g. Pauly and Watson 2005, <https://www.bipindicators.net/>, Collen et al. 2009), and more recently of several Essential Biodiversity Variables that span from genetic diversity to ecosystem structure and function (Pereira et al. 2013, Kissling et al. 2018, Jetz et al. 2019, EBVs, <https://geobon.org/ebvs/what-are-ebvs/>). Such metrics can be used as indicators in biodiversity monitoring programs and ultimately inform policy-relevant scenarios.

Conservation science is increasingly integrating macroecological knowledge into global biodiversity assessments and projection of species extinction risks (Visconti et al. 2016, Carvajal-Quintero et al. 2017, Ceballos et al., 2017, Santini et al., 2019, Barbarossa et al. 2020). Global conservation

assessments and macroecological research are progressively considering different biodiversity dimensions, e.g. taxonomic, functional and phylogenetic diversity, and how these change spatially and temporally (i.e. beta-diversity) (Thuiller et al. 2015, Socolar et al. 2016, Brum et al. 2017, Pollock et al. 2017, Blowes et al. 2019, Rapacciuolo et al. 2019). Additionally, macroecological trait-based approaches and phylogenetic comparative methods have been adopted to predict which species are intrinsically more vulnerable to extinction (Purvis et al. 2000, Fisher and Owens 2004, Cardillo et al. 2005a) and may first go extinct in the future (Cooke et al. 2019b), as well as to predict the likely conservation status of poorly known species (Bland et al. 2015a), and even to design protected areas (Miatta et al. 2021).

Macroecologists have substantially contributed to develop species distribution modelling approaches (SDM; Guisan and Thuiller 2005), which have become a key tool for species conservation assessments (Guisan et al. 2013). SDMs have been used to quantify protected area coverage (Araújo et al. 2004), project species ranges shifts, contraction or expansion under alternative environmental and socioeconomic scenarios (Pearson and Dawson 2003, Thomas et al. 2004), and for informing conservation planning and prioritization (Kremen et al. 2008). The development of user-friendly tools for predicting species distributions (e.g. "Maxent", Phillips et al. 2004, "BIOMOD2", Thuiller et al. 2009, "sdm", Naimi & Araújo 2016, "wallace", Kass et al. 2018) has prompted much theoretical and applied research in conservation at different spatial scales. Further methodological advances have enabled accounting for species co-occurrence (potentially species interactions) on species' distributions (JSDMs, Pollock et al. 2014) and their responses to environmental change (Clark et al. 2014). More recently, joint dynamic SDMs (JSDMs, Thorson et al. 2016) and hierarchical modelling of species communities (Ovaskainen et al. 2017) have enabled integrating species distribution and/or abundance data, traits, phylogenetic relationships and environmental predictors to estimate community-wide change via both biotic and abiotic mechanisms. These methods have yet to be broadly applied to conservation, but have great potential for making more realistic predictions of community responses to global change (Rapacciuolo and Blois 2019), e.g. applying context-dependent JSJM (Tikhonov et al. 2017) along gradients of human disturbance.

SARs are commonly employed to assess the impact of land-use change and habitat loss globally (e.g. Chaudhary et al. 2015), and more recently have been combined with SDM modelling and conservation planning to assess the extent to which meeting global biodiversity targets would result in a reduction of species extinction risk globally (Hannah et al. 2020, Jung et al. 2021). Similarly, SADs have been recently used to identify global hotspots of rarity for plant species, and predict an increased risk of extinction in these regions due to high human pressures and expected climate change (Enquist et al. 2019).



Recently, BILBI (the Biogeographic Infrastructure for Large-scaled Biodiversity Indicators) has integrated advances in macroecological modelling, biodiversity informatics, remote sensing and high-performance computing to assess spatio-temporal changes in biodiversity at ~1km grid resolution across the terrestrial surface of the planet while reducing taxonomic biases (Hoskins et al. 2020). These approaches have already been used for protected area assessments (Ferrier et al. 2004), to quantify the contribution of wilderness areas to global biodiversity conservation (Di Marco et al. 2019a), and to forecast the risk of extinction of vascular plant biodiversity under climate and land-use change (Di Marco et al. 2019b).

Species distribution models and threat mapping products are widely used to delineate regional to global conservation plans. These broad-scale planning exercises can guide actions to meet global conservation targets (Pouzols et al. 2014, e.g. Venter et al. 2014) and provide an holistic view on how to account for numerous conservation priorities simultaneously. For example, O'Connor et al. (2021) revealed that large gains in biodiversity protection can be achieved with little additional conservation effort in Europe. By projecting species distribution in the future, Titley et al. (2021) identified globally important transboundary areas where international cooperation will be fundamental to mitigate the effects of climate change on biodiversity, and where physical barriers may be most detrimental to conservation. While the direct implementation of such plans in the real world are still limited, some have successfully been applied, by adjusting regional plans to local contexts in close collaboration with local stakeholders (e.g. the Cape region in South Africa and the Great Barrier Reef in Australia; Fernandes et al. 2005, Knight et al. 2006, Pressey et al. 2013).

### *Improving outreach actions*

Broad-scale macroecological biodiversity assessments regularly inform technical reports on the status and trends of biodiversity (Fig. 2; IPBES, GEOBON, Living Planet Report, State of Nature reports, Hof et al. 2015), which are then used for setting national and international targets for biodiversity conservation (e.g. Aichi targets, Tittensor et al. 2014). This, in turn, influences supranational (e.g. LIFE projects in Europe) and national allocation of funding for conservation actions in order to meet the agreed targets. For example, Natura 2000, the largest network of protected areas in the world, is a European strategy for biodiversity conservation that was established using a biogeographical approach (Evans 2012). Natura 2000 involves local conservation actions, land managers, conservation practitioners and researchers who are asked to periodically reassess species checklists, and limit or mitigate the environmental impacts of planned infrastructures (Evans 2012).

Global and regional macroecological analyses can be very powerful in raising public awareness

on biodiversity trends and conservation (Fig. 2; e.g. Cardinale et al. 2012, Ceballos et al. 2015, Urban 2015, Soroye et al. 2020), which is key to ensure biodiversity research and conservation are not relegated to a marginal role under economic uncertainty and priority fluctuations within limited budgets (Bakker et al. 2010, Sayer et al. 2012). Broad-scale conservation assessments are frequently in the top 100 of the most mentioned articles online according to the Altmetric score, an index designed to quantify media attention (e.g. <https://www.altmetric.com/top100>). This is fundamental because media attention can directly affect public interest, which may have strong influence on policy makers and the decisions they make. Media may be more likely to report on scientific research with broad implications across large areas or taxonomic groups than for single species (unless highly charismatic) or sites. Additionally, approaches focused on natural capital or ecosystem services that are inherently macroecological (across taxa and temporal and spatial scales) have indeed focused on quantifying tangible benefits of nature to people (Guerry et al. 2015), and serve the very practical purpose of raising awareness of the value of nature that goes beyond aesthetic, cultural or intrinsic values. The pressing need for efficient biodiversity assessment and conservation planning, and the importance of public awareness is highlighted by the fact that none of the set Aichi Biodiversity Targets for 2020 have been met for the second consecutive decade (Global Biodiversity Outlook 2020).

### *Conservation contributions to Macroecology*

Knowledge transfer between the two disciplines has not been unidirectional (Gaston & Blackburn 2003). First, public engagement and conservation monitoring activities have contributed to the development of macroecology (Fig. 2). Early broad-scale explorations of macroecological patterns were possible thanks to initiatives like the Audubon Christmas Bird Counts (e.g. Preston 1980, Bock and Ricklefs 1983). Several citizen science initiatives such as iNaturalist (<https://www.inaturalist.org/>; feeding directly into GBIF), eBird (ebird.org) or the UK and North American Breeding Bird Surveys currently provide large amounts of data for macroecological analyses (Brown and Williams 2019), as do more recent marine initiatives, such as the Reef Life Survey (Edgar & Stuart-Smith 2014). Provided sampling biases are properly accounted for (Isaac et al. 2014), these extensive datasets can provide crucial biodiversity information across spatial, temporal and taxonomic scales larger than most typical biodiversity data sources (Edgar et al. 2016, Chandler et al. 2017). Much macroecological science has also relied on data originally produced for conservation assessments; IUCN range maps, for example, have been widely used as proxies of species distribution to investigate macroecological patterns (Roll et al. 2017, Cooke et al. 2019a).

Second, the urgent conservation need to quantify and mitigate how multiple anthropogenic drivers threaten biodiversity across scales and realms



(Kerr et al. 2007, Halpern et al. 2019, IPBES 2019, Bowler et al. 2020) has proved to be a catalyst for macroecological innovation and stimulated macroecological research with real-world applications (Fig. 2). Numerous recent analyses relying on conservation science insights have unveiled the role of humans in shaping multiple current biodiversity change patterns. Such efforts have for example revealed a greater dependency on human pressure than life history and environmental drivers in explaining species range size (Murray and Dickman 2000, Di Marco and Santini 2015). Additionally, current geographic patterns of species richness (Torres-Romero and Olalla-Tárraga 2015, Sebastián-González et al. 2019), body mass distribution (Rapacciuolo et al. 2017, Santini et al. 2017), and functional and phylogenetic diversity (Faurby and Svenning 2015) are heavily influenced by humans. Similarly, broad-scale patterns of species movements (Tucker et al. 2018), population abundance (Benítez-López et al. 2019, Tucker et al. 2020, Santini and Isaac 2021) and ecological network structure (Fricke and Svenning 2020) appear distorted by human presence. Recent extinctions and invasions likely caused by human activities have also altered the number and distribution of biogeographic realms (Bernardo-Madrid et al. 2019). In the ocean, overfishing has historically greatly altered patterns of life history, biomass and community structure (Jennings and Blanchard 2004, Tittensor et al. 2009, Halpern et al. 2019). Most of the ocean area is currently experiencing increasing cumulative impacts (Halpern et al. 2019), with particular emphasis on climate change effects (Stuart-Smith et al. 2015, Antão et al. 2020). Ultimately, insights from conservation have led to an improved understanding of the drivers of macroecological patterns (Gaston and Blackburn 2003).

## Strengthening the link: challenges and opportunities

### Challenges

Despite numerous shared links, there still remain challenges in strengthening and developing further connections and synergies between macroecology and conservation science. First, there is a question of trade-off between generality and specificity. Macroecologists often focus on correlations and tolerate unexplained variance that may be less relevant at broad scales and/or when analysing many species, but becomes crucial at finer scales and for particular contexts (Lawton 1999). This can make macroecology somewhat detached from socio-ecological dynamics that managers face at the local scale (Gaston and Blackburn 1999, Kerr et al. 2007). However, such deviations from macroecological predictions are expected, and a crux of scientific research is to understand whether such exceptions are valuable to identify important additional drivers, uncover more complex mechanisms and eventually promote a deeper understanding of ecological systems (Marquet et al. 2014).

Macroecology generally operates at broad taxonomic, temporal or geographic scales which

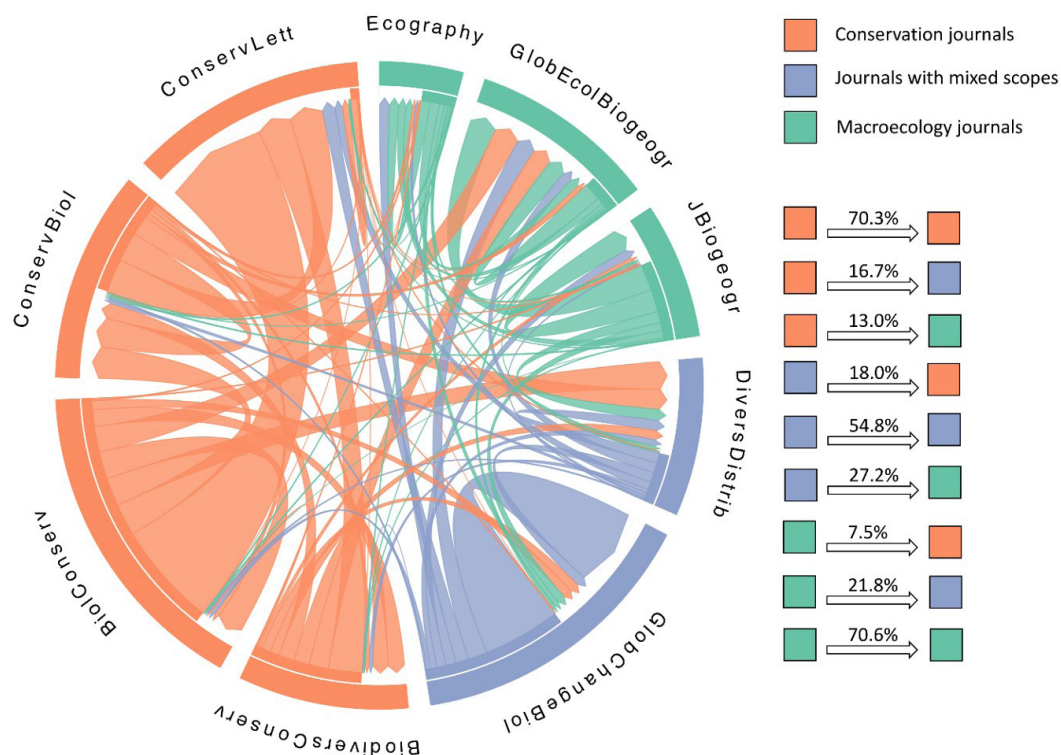
are relevant only for some aspects of conservation (Fig. 1). Scepticism and misunderstandings can arise when trying to interpret, extrapolate or apply results obtained at different scales and data resolutions. For example, conservation analyses performed across broad spatial scales or many species (e.g. Visconti et al. 2016, Hof et al. 2018) are generally too coarse or uncertain to inform the conservation of single species or individual sites. Yet, they can be used to develop plausible scenarios of biodiversity change in response to societal decisions (Leclère et al. 2020, Schipper et al. 2020), which in turn are useful to plan conservation actions and inform policy (Hannah et al. 2020, Jung et al. 2021, Soto-Navarro et al. 2020). Conversely, single species or population analyses provide specific information to guide management of the focal species or population, but are unsuitable for generalizing to other species or areas. The trade-off between generality and specificity is important to consider regarding the scale of interest. Ultimately, conservation decisions are scale-dependent (Hartley and Kunin 2003), with different scales addressing different goals and benefiting from different disciplines (Fig. 1). Global and regional assessments informed by macroecology may enable prioritizing among different potential actions, such as focusing conservation efforts on particular species or areas (Brooks et al. 2006, Venter et al. 2014, Pollock et al. 2017, Schipper et al. 2020), though conservation actions in practice will ultimately need to be implemented at national and local scales. While macroecological research cannot inform all aspects of conservation, it can provide a generalized and broad-scale context within which to consider conservation assessments and decisions that can then be tailored to individual species- or local-scale contexts (Fig. 2). An example are biodiversity hotspots (Myers et al. 2000), within which Conservation International has extensively invested in local conservation actions (<https://www.conservation.org/priorities/biodiversity-hotspots>).

One possible reason why macroecology may be unable to contribute more strongly to local conservation is that it has not yet succeeded in identifying the driving mechanisms of many observed ecological patterns (McGill and Nekola 2010, Currie 2019, McGill 2019). Statistical relationships can arise from multiple processes acting simultaneously, and multiple processes can lead to the same statistical pattern, which often results in several competing hypotheses. This makes the search for mechanisms particularly challenging in macroecology, and has led to calls for macroecological theories to be based on first principles (Marquet et al. 2014, 2015), although it has been argued that some mechanisms may have already been identified even if not recognized as such (McGill and Nekola 2010). An improved mechanistic understanding of macroecological patterns can increase our predictive capacity across scales, as well as transferability across space, time and taxa (Yates et al. 2018), and thus has the potential to make macroecological insights more applicable to local contexts (Connolly et al. 2017). On the other

hand, in the absence of a complete understanding of underlying mechanisms, observed correlations within a given domain can be used for predictions within the same domain (Currie 2019). Clearly, given the high frequency of non-informative correlations among variables in nature (Currie et al. 2020), an uncritical inference from large-scale statistical relationships can even be deleterious for conservation (e.g. Warren et al. 2014, 2020, Fourcade et al. 2018, Santini et al. 2021). While statistical relationships across species or large areas can hold varying degrees of uncertainty, when interpreted with caution, they are often preferable to expert-based approaches which, despite being fairly common in conservation, have proved to have low predictive capacity (Camerer and Johnson 1991, McCarthy et al. 2004).

A second challenge is that macroecologists and conservation scientists generally publish in different journals (Fig. 3) and attend separate meetings, which potentially limits reciprocal understanding and communication. This lack of communication can be further accentuated by the different scopes of the two disciplines (fundamental vs target-oriented research; Soulé 1985, Brown and Maurer 1989), influencing how science is performed and communicated. This dichotomy has recently led to important controversies on the interpretation of results on local biodiversity change, with conservation scientists focusing on

species decline, and macroecologists focusing on both negative and positive trends (Dornelas et al. 2014, Gonzalez et al. 2016, Vellend et al. 2017). These discussions are tightly linked to the focal spatial scale of change (local versus global), while highlighting the complexity of integrating such macroecological insights with key conservation actions, such as implementing protected areas, ecosystem restoration, or invasive species management (Primack et al. 2018). Conservation science may also require higher levels of pragmatism than macroecology. Rapid biodiversity loss calls for swift actions, which can mean making decisions even with high uncertainty and limited empirical knowledge (Soulé 1985). Macroecologists may instead present findings tentatively focusing on limitations and uncertainty without the pressure of needing a recommendation or decision (Rapacciuolo 2019). Conservation scientists may consequently perceive macroecology as too focused on the theoretical questions, without proposing practical solutions or addressing ongoing biodiversity change. Improved communication between the two disciplines could be achieved through more hybrid conferences (e.g. International Biogeography Society meetings) and journals (e.g. Diversity & Distributions, Global Change Biology), and through joint calls for grants fostering collaborations between macroecologists and conservation scientists. A recent analysis on the flow of



**Figure 3.** Flow of citations between journals whose scope is focused mainly either on macroecology or conservation, and hybrid journals between 2008 and 2017 (readapted from Fig. 2 in Benítez-López & Santini 2020). The outer circle width per journal indicates the total citations exchanged with other journals, whereas the inner circle indicates the proportion of outgoing citations. 135 papers were sampled in 2008 and all their citations were tracked for 10 years (further details on the data and methods in Benítez-López & Santini 2020). Journals are labeled using their official abbreviation.

citations among ecology journals (Benítez-López and Santini 2020) shows that conservation journals more frequently cite macroecology journals than vice versa, while hybrid journals tend to cite both conservation and macroecology journals more often than each group cites each other (Fig. 3). This suggests that hybrid journals potentially serve as key connectors between the two disciplines and provide a necessary forum for researchers working at their interface.

If misunderstandings are common within the research community, these are even more common between the research community, conservation practitioners and land managers (Prendergast et al. 1999, Cardillo and Meijaard 2012, Rapacciuolo 2019). Macroecology and broad-scale conservation studies often come with no or vague guidelines for conservation managers. This is again often due to the different goals and publication venues, but also to different backgrounds that hamper good reciprocal understanding. Researchers are often under pressure to publish high impact papers that emphasize scientific novelty instead of delineating guidelines and actions based on existing knowledge (Williams et al. 2020). Conservation practitioners may regard academic findings as of limited value and too theoretical for practical implementation (Prendergast et al. 1999, Cardillo and Meijaard 2012, Rapacciuolo 2019). Additionally, the objectives often diverge, with researchers frequently concerned with understanding the processes and identifying proactive actions aimed at anticipating further decline, while practitioners are commonly limited to immediate actions on already declining species (Cardillo and Meijaard 2012). Increased collaboration between macroecologists, conservation researchers and practitioners can help translate scientific findings and even reframe questions so they address conservation-related issues and ultimately provide clear guidelines for management. Conservation practitioners should also, whenever possible, consider proactive and predictive approaches to conservation planning (Cardillo and Meijaard 2012, Travers et al. 2019, Jézéquel et al. 2020).

### Opportunities

Sutherland and colleagues (2009) proposed a list of 100 questions worth exploring in biodiversity conservation. We outline several of those questions that can benefit from a macroecological approach. For example, conservation studies often focus on estimating biodiversity responses to isolated threats, with little consideration towards potential interaction effects among those threats. Yet, such interactions are highly prevalent and exhibit geographical patterns across the globe (Halpern et al. 2019, Bowler et al. 2020, Schipper et al. 2020). Macroecological approaches can help to understand these relationships. For example, land-use change and climate change can interact resulting in impact exacerbation or mitigation (Hof et al. 2018, Williams et al. 2019). Similarly, over-exploitation of wild species can be further exacerbated by habitat loss and fragmentation that increase human accessibility (Gallego-Zamorano et al. 2020, Romero-

Muñoz et al. 2020), or similarly by the combined effects of fishing and climate change (Halpern et al. 2019). Integrative assessments and models (such as GLOBIO) work in this direction, by modeling several anthropogenic pressures on ecosystems and combining them under different assumptions (Schipper et al. 2020).

As noted above, another promising avenue for macroecology is the shift from correlative to more mechanistic approaches that focus on causal relationships allowing to model several ecological dynamics simultaneously (Harfoot et al. 2014, Connolly et al. 2017). Data-driven approaches alone are in fact deemed insufficient to grasp the complexity of ecological systems, and a better integration of theory and data is often advocated (Marquet et al. 2014). Mechanistic models can contribute to this by assessing how well the predictions of theoretical models adhere to reality and their implications in complex systems, therefore suggesting hypotheses to be tested with data. However, diverse opinions exist in this regard, with other authors advocating for different approaches (see e.g. Currie 2019). Mechanistic approaches have been successfully used to explore the synergistic effects of habitat loss and fragmentation (Bartlett et al. 2016) or the occurrence of tipping points and non-linear dynamics in perturbed ecosystems (Newbold et al. 2016). These approaches also hold great potential to inform and improve conservation and management actions, which has been shown to be an under-researched area in conservation (Williams et al. 2020).

A future challenge for global conservation is developing a cost-efficient monitoring of biodiversity trends. Classical approaches to risk monitoring, e.g. the IUCN Red List, rely on expert-based assessments with periodical re-evaluations to update species conservation status. Given the high financial effort required for these tasks, we risk having assessments only for certain taxonomic groups, with those assessments becoming outdated as re-evaluations cannot be regularly conducted (Rondinini et al. 2014). An alternative approach, often proposed but not yet implemented, is to use comparative extinction risk modelling to disentangle the mechanisms that underpin higher extinction risk (Cardillo et al. 2005b, Bland et al. 2015b, Di Marco et al. 2015) or increase species vulnerability to threats such as road mortality or wildlife trade (González-Suárez et al. 2018, Scheffers et al. 2019). Once trained, these models could be used to predict species' risk using trait data and up-to-date information on human pressures. Periodically updating information on human pressures might help identify those species likely to experience changes in their risk status, and provide experts with a tool that can guide reassessment efforts strategically (Santini et al. 2019). Predictive models of extinction risk can also be combined with maps of land-use change to explore spatially-explicit future scenarios, helping to identify both high-risk and high-resilience areas (Powers and Jetz 2019).

The macroecological approach can also be extended to investigate problems that are not directly related



to species extinction risk, but are equally relevant for conservation science. For example, expansion of zoonotic diseases is becoming a global concern, which is exacerbated by habitat fragmentation, increasing contact between wildlife and humans, wildlife trade, and bushmeat consumption (Chomel et al. 2007). These issues offer fertile ground for in-depth macroecological explorations that can identify ecological drivers of risk and explore mitigation scenarios (Han et al. 2016, Stephens et al. 2016, Allen et al. 2017a), as well as identifying previously unknown major wildlife disease reservoirs (Pandit et al. 2018). Similarly, food production can have obvious impacts on biodiversity; therefore, predicting how climate change will alter the geography of food production has become a priority to plan mitigation measures (Hannah et al. 2013, Kehoe et al. 2017, Polaina et al. 2018). Broad-scale analyses can also consider how human welfare and migrations are related to climate change, and identify susceptible groups and areas (Bathiany et al. 2018, Xu et al. 2020), thus potentially anticipating impacts on biodiversity and reducing conflict probability. Conservation science is interconnected with multiple social and political aspects (Hintzen et al. 2019). For example, the conservation of species that lead to conflicts with humans (e.g. large carnivores) is not only dependent on habitat conditions or prey availability, but also on societal perception (Arbieu et al. 2019). In this context, macroecological models could be fine-tuned to incorporate additional information, such as human perceptions and values, and use the available information to make predictions in poorly known areas. Attempts in this direction have been made (Dressel et al. 2015), but can certainly be further improved.

A renowned problem in conservation is the “shifting baseline syndrome”, consisting in a gradual shift of the reference conditions as perceived by humans (Pauly 1995), which affects our ability to quantify the alteration of ecosystems by humans. Macroecology often focuses on the estimation of spatio-temporal ‘baselines’, attempting to disentangle the effect of humans on broad-scale diversity patterns to estimate the distribution of species or traits expected in the absence of humans (Jennings and Blanchard 2004, Faurby and Svenning 2015, Rapacciuolo et al. 2017, Santini et al. 2017, Lewandowska et al. 2020, Santini and Isaac 2021). This is a relatively new research avenue with much potential for contributing to conservation, for instance in the framing of restoration or rewilding actions.

Macroecology can further contribute to global conservation planning by highlighting synergies and trade-offs between global conservation targets (Blanchard et al. 2014, Di Marco et al. 2016). An illustrative example is provided by the Aichi Target 11, which states that at least 17% of terrestrial and 10% of marine areas should be protected (CBD 2010), “especially areas of particular importance for biodiversity and ecosystem services, [...], ecologically representative and well-connected systems of protected areas [...]”. When a limited amount of

area can be protected, acknowledging the trade-offs between different sub-objectives becomes critical. For example, biodiversity-rich areas do not necessarily correlate with areas of high carbon sequestration (Di Marco et al. 2018, Jung et al. 2021, Soto-Navarro et al. 2020), while ecological representativeness may differ from important biodiversity areas (McGowan et al. 2018), and lead to different plans than those that would maximize connectivity between protected areas (Santini et al. 2016). An improved understanding of the relationship between different facets of biodiversity and ecosystem services is therefore fundamental for informed conservation planning (Rodrigues and Brooks 2007, Rapacciuolo et al. 2019).

## Concluding remarks

Macroecology has already made substantial contributions to conservation science by offering a new broad-scale top-down perspective, harnessing insights from regional and global ecological processes (Currie 2019, McGill 2019). A full integration of the two disciplines is probably neither possible nor desirable, but further connectedness is possible and could be mutually beneficial. The interface between macroecology and conservation science is a particularly fruitful area of investigation, and there remains untapped potential for macroecology to guide conservation science, by linking cross-scale and cross-taxa patterns and dynamics, simultaneously evaluating multiple threats and species, and generating improved predictive models (Travers et al. 2019). Ultimately, a fundamental goal of conservation science is to be able to understand, forecast and act on biodiversity changes and its effects on human wellbeing. Conservation will benefit from using all tools available to effectively address biodiversity and environmental challenges. While macroecology might not provide answers to all these challenges, it is poised to gain an increasingly central role in guiding conservation actions and averting the ongoing biodiversity crisis.

## Acknowledgements

We thank M. Dornelas, F. Buschke, D. Currie, M. Cardillo, and other anonymous referees for constructive comments on previous versions of this manuscript. L.S. and M.D.M. acknowledge support from the MUR Rita Levi Montalcini programme, and L.A. acknowledges support from the Jane and Aatos Erkkö Foundation. A.B.L. was supported by a Juan de la Cierva-Incorporacion grant (IJCI-2017-31419) from the Spanish Ministry of Science, Innovation and Universities.

## Author Contributions

The team of authors includes researchers working on each or both disciplines. The ideas presented in this manuscript originated in two workshops held at the British Ecological Society Macroecology conferences in 2017 and 2018. LS and MGS have led the study and



coordinated the work of all co-authors, but this was truly a team effort. All authors have made substantial intellectual contributions along multiple discussions and all have contributed to the writing. The manuscript reflects their diversity of backgrounds, opinions and experiences.

## References

- Allen, T., Murray, K.A., Zambrana-Torrel, C., Morse, S.S., Rondinini, C., Di Marco, M., Breit, N., Olival, K.J. & Daszak, P. (2017a) Global hotspots and correlates of emerging zoonotic diseases. *Nature Communications*, 8, 1–10. <https://doi.org/10.1038/s41467-017-00923-8>
- Allen, W.L., Street, S.E. & Capellini, I. (2017b) Fast life history traits promote invasion success in amphibians and reptiles. *Ecology Letters*, 20, 222–230. <https://doi.org/10.1111/ele.12728>
- Andersen, K.H., Farnsworth, K.D., Pedersen, M., Gislason, H. & Beyer, J.E. (2009) How community ecology links natural mortality, growth, and production of fish populations. *ICES Journal of Marine Science*, 66, 1978–1984. <https://doi.org/10.1093/icesjms/fsp161>
- Antão, L.H., Bates, A.E., Blowes, S.A., Waldock, C., Supp, S.R., Magurran, A.E., Dornelas, M. & Schipper, A.M. (2020) Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nature Ecology and Evolution*, 4, 927–933. <https://doi.org/10.1038/s41559-020-1185-7>
- Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L. & Williams, P.H. (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Global Change Biology*, 10, 1618–1626. <https://doi.org/10.1111/j.1365-2486.2004.00828.x>
- Araújo, M.B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P.A., Valladares, F. & Chown, S.L. (2013) Heat freezes niche evolution. *Ecology Letters*, 16, 1206–1219. <https://doi.org/10.1111/ele.12155>
- Arbieu, U., Mehring, M., Bunnefeld, N., et al. (2019) Attitudes towards returning wolves (*Canis lupus*) in Germany: exposure, information sources and trust matter. *Biological Conservation*, 234, 202–210. <https://doi.org/10.1016/j.biocon.2019.03.027>
- Bakker, V.J., Baum, J.K., Brodie, J.F., Salomon, A.K., Dickson, B.G., Gibbs, H.K., Jensen, O.P. & Mcintyre, P.B. (2010) The changing landscape of conservation science funding in the United States. *Conservation Letters*, 3, 435–444. <https://doi.org/10.1111/j.1755-263X.2010.00125.x>
- Barbarossa, V., Schmitt, R.J.P., Huijbregts, M.A.J., Zarfl, C., King, H. & Schipper, A.M. (2020) Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. *Proceedings of the National Academy of Sciences USA*, 117, 3648–3655. <https://doi.org/10.1073/pnas.1912776117>
- Barnosky, A.D., Hadly, E.A., Bascompte, J., et al. (2012) Approaching a state shift in Earth's biosphere. *Nature*, 486, 52–58. <https://doi.org/10.1038/nature11018>
- Bartlett, L.J., Newbold, T., Purves, D.W., Tittensor, D.P. & Harfoot, M.B.J. (2016) Synergistic impacts of habitat loss and fragmentation on model ecosystems. *Proceedings of the Royal Society B*, 283, 20161027. <https://doi.org/10.1098/rspb.2016.1027>
- Bathiany, S., Dakos, V., Scheffer, M. & Lenton, T.M. (2018) Climate models predict increasing temperature variability in poor countries. *Science Advances*, 4, eaar5809. <https://doi.org/10.1126/sciadv.aar5809>
- Baum, J.K. & Worm, B. (2009) Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, 78, 699–714. <https://doi.org/10.1111/j.1365-2656.2009.01531.x>
- Bellard, C., Leroy, B., Thuiller, W., Rysman, J.F. & Courchamp, F. (2016) Major drivers of invasion risks throughout the world. *Ecosphere*, 7, e01241. <https://doi.org/10.1002/ecs2.1241>
- Benítez-López, A. & Santini, L. (2020) Game of Tenure: the role of “hidden” citations on researchers' ranking in Ecology. *Frontiers of Biogeography*, 12, e45195. <https://doi.org/10.21425/F5FBG45195>
- Benítez-López, A., Santini, L., Schipper, A.M., Busana, M. & Huijbregts, M.A.J. (2019) Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLoS Biology*, 17, e3000247. <https://doi.org/10.1371/journal.pbio.3000247>
- Bernardo-Madrid, R., Calatayud, J., González-Suárez, M., Rosvall, M., Lucas, P.M., Rueda, M., Antonelli, A. & Revilla, E. (2019) Human activity is altering the world's zoogeographical regions.

- Ecology Letters, 22:, 1297–1305. <https://doi.org/10.1111/ele.13321>
- Bielby, J., Mace, G.M., Bininda-Emonds, O.R.P., Cardillo, M., Gittleman, J.L., Jones, K.E., Orme, C.D.L. & Purvis, A. (2007) The fast-slow continuum in mammalian life history: an empirical reevaluation. *The American Naturalist*, 169, 748–757. <https://doi.org/10.1086/516847>
- Bird, J.P., Martin, R., Akçakaya, H.R., Gilroy, J., Burfield, I.J., Garnett, S., Symes, A., Taylor, J., Şekercioğlu, Ç.H. & Butchart, S.H.M. (2020) Generation lengths of the world's birds and their implications for extinction risk. *Conservation Biology*, 34, 1252–1261. <https://doi.org/10.1086/516847>
- Blackburn, T. & Gaston, K.J. (1998) Some Methodological Issues in Macroecology. *American Naturalist*, 151, 68–83. <https://doi.org/10.1086/286103>
- Blackburn, T.M. & Duncan, R.P. (2001a) Determinants of establishment success in introduced birds. *Nature*, 414, 195–197. <https://doi.org/10.1038/35102557>
- Blackburn, T.M. & Duncan, R.P. (2001b) Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *Journal of Biogeography*, 28, 927–939. <https://doi.org/10.1046/j.1365-2699.2001.00597.x>
- Blackburn, T.M. & Gaston, K.J. (2002) Macroecology is distinct from biogeography. *Nature*, 418, 723–723. <https://doi.org/10.1038/418723b>
- Blackburn, T.M., Scrivens, S.L., Heinrich, S. & Cassey, P. (2017) Patterns of selectivity in introductions of mammal species worldwide. *NeoBiota*, 33, 33–51. <http://doi.org/10.3897/neobiota.33.10471>
- Blanchard, J.L., Andersen, K.H., Scott, F., Hintzen, N.T., Piet, G. & Jennings, S. (2014) Evaluating targets and trade-offs among fisheries and conservation objectives using a multispecies size spectrum model. *Journal of Applied Ecology*, 51, 612–622. <https://doi.org/10.1111/1365-2664.12238>
- Bland, L.M., Collen, B., Orme, C.D.L. & Bielby, J. (2015a) Predicting the conservation status of data-deficient species. *Conservation Biology*, 29, 250–259. <https://doi.org/10.1111/cobi.12372>
- Bland, L.M., Orme, C.D.L., Bielby, J., Collen, B., Nicholson, E. & McCarthy, M.A. (2015b) Cost-effective assessment of extinction risk with limited information. *Journal of Applied Ecology*, 52, 861–870. <https://doi.org/10.1111/1365-2664.12459>
- Blonder, B., Nogués-Bravo, D., Borregaard, M.K., et al. (2015) Linking environmental filtering and disequilibrium to biogeography with a community climate framework. *Ecology*, 96, 972–985. <https://doi.org/10.1890/14-0589.1>
- Blowes, S.A., Supp, S.R., Antão, L.H., et al. (2019) The geography of biodiversity change in marine and terrestrial assemblages. *Science*, 366, 339–345. <https://doi.org/10.1126/science.aaw1620>
- Bock, C.E. & Ricklefs, R.E. (1983) Range size and local abundance of some North American songbirds: a positive correlation. *American Naturalist*, 122, 295–299. <https://doi.org/10.1086/284136>
- Böhm, M., Williams, R., Bramhall, H.R., Mcmillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J. & Collen, B. (2016) Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. *Global Ecology and Biogeography*, 25, 391–405. <https://doi.org/10.1111/geb.12419>
- Bowler, D.E., Bjorkman, A.D., Dornelas, M., et al. (2020) Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. *People and Nature*, 2, 380–394. <https://doi.org/10.1002/pan3.10071>
- Boyer, A.G. & Jetz, W. (2012) Conservation biology. In: *Metabolic ecology: a scaling approach* (ed. by R.M Sibly, J.H. Brown and A. Kodric-Brown), pp. 271–279. Wiley-Blackwell.
- Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D. & Rodrigues, A.S.L. (2006) Global biodiversity conservation priorities. *Science*, 313, 58–61. <http://doi.org/10.1126/science.1127609>
- Brown, E.D. & Williams, B.K. (2019) The potential for citizen science to produce reliable and useful information in ecology. *Conservation Biology*, 33, 561–569. <http://doi.org/10.1111/cobi.13223>
- Brown, J.H. (1989) Applications: human ecology and conservation biology. In: *Macroecology* (ed.

- by J.H. Brown), pp. 204–224. The University of Chicago Press.
- Brown, J.H. (1999) Macroecology: progress and prospect. *Oikos*, 87, 3–14. <https://doi.org/10.2307/3546991>
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789. <https://doi.org/10.1890/03-9000>
- Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, 58, 445–449. <https://doi.org/10.2307/1935620>
- Brown, J.H. & Maurer, B.A. (1987) Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. *American Naturalist*, 130, 1–17. <https://doi.org/10.1086/284694>
- Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, 243, 1145–1150. <http://doi.org/10.1126/science.243.4895.1145>
- Brum, F.T., Graham, C.H., Costa, G.C., Hedges, S.B., Penone, C., Radeloff, V.C., Rondinini, C., Loyola, R. & Davidson, A.D. (2017) Global priorities for conservation across multiple dimensions of mammalian diversity. *Proceedings of the National Academy of Sciences USA*, 114, 7641–7646. <http://doi.org/10.1073/pnas.1706461114>
- Camerer, C. & Johnson, E. (1991) The process-performance paradox in expert judgment: how can experts know so much and predict so badly? In: *Toward a general theory of expertise: prospects and limits* (ed. by K.A. Ericsson and J. Smith), pp. 195–217. Cambridge University Press.
- Capellini, I., Baker, J., Allen, W.L., Street, S.E. & Venditti, C. (2015) The role of life history traits in mammalian invasion success. *Ecology Letters*, 18, 1099–1107. <https://doi.org/10.1111/ele.12493>
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L. & Purvis, A. (2005a) Multiple causes of high extinction risk in large mammal species. *Science*, 309, 1239–1241. <https://doi.org/10.1126/science.1116030>
- Cardillo, M. & Meijaard, E. (2012) Are comparative studies of extinction risk useful for conservation? *Trends in Ecology and Evolution*, 27, 167–171. <https://doi.org/10.1016/j.tree.2011.09.013>
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., et al. (2012) Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67. <https://doi.org/10.1038/nature11148>
- Carvajal-Quintero, J.D., Januchowski-Hartley, S.R., Maldonado-Ocampo, J.A., Jézéquel, C., Delgado, J. & Tedesco, P.A. (2017) Damming fragments species' ranges and heightens extinction risk. *Conservation Letters*, 10, 708–716. <https://doi.org/10.1111/conl.12336>
- CBD (2010) Strategic plan for biodiversity 2011–2020. Montreal.
- Ceaușu, S., Hofmann, M., Navarro, L.M., Carver, S., Verburg, P.H. & Pereira, H.M. (2015) Mapping opportunities and challenges for rewilding in Europe. *Conservation Biology*, 29, 1017–1027. <http://doi.org/10.1111/cobi.12533>
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M. & Palmer, T.M. (2015) Accelerated modern human – induced species losses: entering the sixth mass extinction. *Science Advances*, 1, 1–5. <http://doi.org/10.1126/sciadv.1400253>
- Ceballos, G., Ehrlich, P.R. & Dirzo, R. (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences USA*, 114, E6089–E6096. <https://doi.org/10.1073/pnas.1704949114>
- Chandler, M., See, L., Copas, K., et al. (2017) Contribution of citizen science towards international biodiversity monitoring. *Biological Conservation*, 213, 280–294. <https://doi.org/10.1016/j.biocon.2016.09.004>
- Channel, R. & Lomolino, M.V. (2000) Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography*, 27, 169–179. <http://doi.org/10.1046/j.1365-2699.2000.00382.x>
- Chaudhary, A., Verones, F., De Baan, L. & Hellweg, S. (2015) Quantifying land use impacts on biodiversity: combining species-area models and vulnerability indicators. *Environmental Science and Technology*, 49, 9987–9995. <https://doi.org/10.1021/acs.est.5b02507>
- Chisholm, R.A., Lim, F., Yeoh, Y.S., Seah, W.W., Condit, R. & Rosindell, J. (2018) Species–



- area relationships and biodiversity loss in fragmented landscapes. *Ecology Letters*, 21, 804–813. <https://doi.org/10.1111/ele.12943>
- Chomel, B.B., Belotto, A. & Meslin, F.X. (2007) Wildlife, exotic pets, and emerging zoonoses. *Emerging Infectious Diseases*, 13, 6–11. <http://doi.org/10.3201/eid1301.060480>
- Clark, J.S., Gelfand, A.E., Woodall, C.W. & Zhu, K. (2014) More than the sum of the parts: forest climate response from joint species distribution models. *Ecological Applications*, 24, 990–999. <https://doi.org/10.1890/13-1015.1>
- Collen, B., Loh, J., Whitmee, S., McRae, L., Amin, R. & Baillie, J.E.M. (2009) Monitoring change in vertebrate abundance: the living planet index. *Conservation Biology*, 23, 317–327. <https://doi.org/10.1111/j.1523-1739.2008.01117.x>
- Colwell, R.K. & Rangel, T.F. (2009) Hutchinson's duality: the once and future niche. *Proceedings of the National Academy of Sciences USA*, 106, 19651–19658. <https://doi.org/10.1073/pnas.0901650106>
- Comte, L., Carvajal-Quintero, J., Tedesco, P.A., et al. (2020) RivFishTIME: a global database of fish time-series to study global change ecology in riverine systems. *Global Ecology and Biogeography*, 30, 38–50. <https://doi.org/10.1111/geb.13210>
- Conde, D.A., Staerk, J., Colchero, F., et al. (2019) Data gaps and opportunities for comparative and conservation biology. *Proceedings of the National Academy of Sciences USA*, 201816367. <https://doi.org/10.1073/pnas.1816367116>
- Connolly, S.R., Keith, S.A., Colwell, R.K. & Rahbek, C. (2017) Process, mechanism, and modeling in macroecology. *Trends in Ecology and Evolution*, 32, 835–844. <http://doi.org/10.1016/j.tree.2017.08.011>
- Cooke, R.S.C., Bates, A.E. & Eigenbrod, F. (2019a) Global trade-offs of functional redundancy and functional dispersion for birds and mammals. *Global Ecology and Biogeography*, 28, 484–495. <http://doi.org/10.1111/geb.12869>
- Cooke, R.S.C., Eigenbrod, F. & Bates, A.E. (2019b) Projected losses of global mammal and bird ecological strategies. *Nature Communications*, 10, 2279. <https://doi.org/10.1038/s41467-019-10284-z>
- Currie, D.J. (2019) Where Newton might have taken ecology. *Global Ecology and Biogeography*, 28, 18–27. <https://doi.org/10.1111/geb.12842>
- Currie, D.J., Pétrin, C. & Boucher-Lalonde, V. (2020) How perilous are broad-scale correlations with environmental variables? *Frontiers of Biogeography*, 12, e44842. <https://doi.org/10.21425/F5FBG44842>
- Daleo, P., Alberti, J. & Iribarne, O. (2009) Biological invasions and the neutral theory. *Diversity and Distributions*, 15, 547–553. <https://doi.org/10.1111/j.1472-4642.2009.00576.x>
- Di Marco, M., Butchart, S.H.M., Visconti, P., Buchanan, G.M., Ficetola, G.F. & Rondinini, C. (2016) Synergies and trade-offs in achieving global biodiversity targets. *Conservation Biology*, 30, 189–195. <https://doi.org/10.1111/cobi.12559>
- Di Marco, M., Collen, B., Rondinini, C. & Mace, G. (2015) Historical drivers of extinction risk: using past evidence to direct future monitoring. *Proceedings of the Royal Society B*, 282, 20150928. <https://doi.org/10.1098/rspb.2015.0928>
- Di Marco, M., Ferrier, S., Harwood, T.D., Hoskins, A.J. & Watson, J.E.M. (2019a) Wilderness areas halve the extinction risk of terrestrial biodiversity. *Nature*, 573, 582–585. <http://doi.org/10.1038/s41586-019-1567-7>
- Di Marco, M., Harwood, T.D., Hoskins, A.J., Ware, C., Hill, S.L. & Ferrier, S. (2019b) Projecting impacts of global climate and land-use scenarios on plant biodiversity using compositional-turnover modelling. *Global Change Biology*, 25, 2763–2778. <https://doi.org/10.1111/gcb.14663>
- Di Marco, M. & Santini, L. (2015) Human pressures predict species' geographic range size better than biological traits. *Global Change Biology*, 21, 2169–2178. <https://doi.org/10.1111/gcb.12834>
- Di Marco, M., Watson, J.E.M., Currie, D.J., Possingham, H.P. & Venter, O. (2018) The extent and predictability of the biodiversity–carbon correlation. *Ecology Letters*, 21, 365–375. <https://doi.org/10.1111/ele.12903>
- Diamond, J., Terborgh, J., Whitcomb, R.F., Lynch, J.F., Opler, P.A., Robbins, C.S., Simberloff, D.S. & Abele, L.G. (1976) Island biogeography and conservation: strategy and limitations.



- Science, 193, 1027–1032. <https://doi.org/10.1126/science.193.4257.1027>
- Diamond, J.M. (1972) Biogeographic kinetics: estimation of relaxation times for avifaunas of Southwest Pacific Islands. *Proceedings of the National Academy of Sciences USA*, 69, 3199–3203. <https://doi.org/10.1073/pnas.69.11.3199>
- Dillon, M.E., Wang, G. & Huey, R.B. (2010) Global metabolic impacts of recent climate warming. *Nature*, 467, 704–706. <https://doi.org/10.1038/nature09407>
- Diniz-Filho, J.A.F., Carvalho, P., Bini, L.M. & Tôrres, N.M. (2005) Macroecology, geographic range size-body size relationship and minimum viable population analysis for new world carnivora. *Acta Oecologica*, 27, 25–30. <https://doi.org/10.1016/j.actao.2004.08.006>
- Donoso, I., Sorensen, M.C., Blendinger, P.G., Kissling, W.D., Neuschulz, E.L., Mueller, T. & Schleuning, M. (2020) Downsizing of animal communities triggers stronger functional than structural decay in seed-dispersal networks. *Nature Communications*, 11, 1–8. <http://doi.org/10.1038/s41467-020-15438-y>
- Dornelas, M., Antão, L.H., Moyes, F., et al. (2018) BioTIME: a database of biodiversity time series for the Anthropocene. *Global Ecology and Biogeography*, 27, 760–786. <https://doi.org/10.1111/geb.12729>
- Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. & Magurran, A.E. (2014) Assemblage time series reveal biodiversity change but not systematic loss. *Science*, 344, 296–299. <http://doi.org/10.1126/science.1248484>
- Dornelas, M., Madin, E.M.P., Bunce, M., et al. (2019) Towards a macroscope: leveraging technology to transform the breadth, scale and resolution of macroecological data. *Global Ecology and Biogeography*, 28, 1937–1948. <https://doi.org/10.1111/geb.13025>
- Dressel, S., Sandström, C. & Ericsson, G. (2015) A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976–2012. *Conservation Biology*, 29, 565–574. <http://doi.org/10.1111/cobi.12420>
- Dubuis, A., Rossier, L., Pottier, J., Pellissier, L., Vittoz, P. & Guisan, A. (2013) Predicting current and future spatial community patterns of plant functional traits. *Ecography*, 36, 1158–1168. <https://doi.org/10.1111/j.1600-0587.2013.00237.x>
- Edgar, G.J., Bates, A.E., Bird, T.J., Jones, A.H., Kininmonth, S., Stuart-Smith, R.D. & Webb, T.J. (2016) New approaches to marine conservation through the scaling up of ecological data. *Annual Review of Marine Science*, 8, 435–461. <https://doi.org/10.1146/annurev-marine-122414-033921>
- Edgar, G.J. & Stuart-Smith, R.D. (2014) Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data*, 1, 140007. <https://doi.org/10.1038/sdata.2014.7>
- Enquist, B.J., Abraham, A.J., Harfoot, M.B.J., Malhi, Y. & Doughty, C.E. (2020) The megabiota are disproportionately important for biosphere functioning. *Nature Communications*, 11, 1–11. <https://doi.org/10.1038/s41467-020-14369-y>
- Enquist, B.J., Feng, X., Boyle, B., et al. (2019) The commonness of rarity: global and future distribution of rarity across land plants. *Science Advances*, 5, eaaz0414. <https://doi.org/10.1126/sciadv.aaz0414>
- Estes, L., Elsen, P.R., Treuer, T., Ahmed, L., Caylor, K., Chang, J., Choi, J.J. & Ellis, E.C. (2018) The spatial and temporal domains of modern ecology. *Nature Ecology and Evolution*, 2, 819. <https://doi.org/10.1038/s41559-018-0524-4>
- Evans, D. (2012) Building the European Union's Natura 2000 network. *Nature Conservation*, 1, 11–26. <https://doi.org/10.3897/natureconservation.1.1808>
- Fahrig, L. (2019) Habitat fragmentation: a long and tangled tale. *Global Ecology and Biogeography*, 28, 33–41. <https://doi.org/10.1111/geb.12839>
- Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography*, 40, 1649–1663. <http://doi.org/10.1111/JBI.12130>
- Faurby, S. & Svenning, J.C. (2015) Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Diversity and Distributions*, 21, 1155–1166. <https://doi.org/10.1111/ddi.12369>
- Fernandes, L., Day, J., Lewis, A., et al. (2005) Establishing representative no-take areas in the great barrier reef: large-scale

- implementation of theory on marine protected areas. *Conservation Biology*, 19, 1733–1744. <https://doi.org/10.1111/j.1523-1739.2005.00302.x>
- Ferrier, S., Powell, G.V.N., Richardson, K.S., Manion, G., Overton, J.M., Allnutt, F., Cameron, S.E., Mantle, K., Burgess, N.D. & Daniel, P. (2004) Mapping more of terrestrial biodiversity for global conservation assessment. *BioScience*, 54, 1101–1109. [https://doi.org/10.1641/0006-3568\(2004\)054\[1101:MMOTBF\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[1101:MMOTBF]2.0.CO;2)
- Fisher, D.O. & Owens, I.P.F. (2004) The comparative method in conservation biology. *Trends in Ecology and Evolution*, 19, 391–398. <http://doi.org/10.1016/j.tree.2004.05.004>
- Fourcade, Y., Besnard, A.G. & Secondi, J. (2018) Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography*, 27, 245–256. <https://doi.org/10.1111/geb.12684>
- Fricke, E.C. & Svenning, J.C. (2020) Accelerating homogenization of the global plant–frugivore meta-network. *Nature*, 585, 74–78. <https://doi.org/10.1038/s41586-020-2640-y>
- Gallego-Zamorano, J., Benítez-López, A., Santini, L., Hilbers, J.P., Huijbregts, M.A.J. & Schipper, A.M. (2020) Combined effects of land use and hunting on distributions of tropical mammals. *Conservation Biology*, 34, 1271–1280. <https://doi.org/10.1111/cobi.13459>
- Gardner, C.J., Bicknell, J.E., Baldwin-Cantello, W., Struebig, M.J. & Davies, Z.G. (2019) Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. *Nature Communications*, 10, 1–7. <https://doi.org/10.1038/s41467-019-12539-1>
- Gaston, K.J. & Blackburn, T.M. (1999) A critique for macroecology. *Oikos*, 84, 353–368.
- Gaston, K.J. & Blackburn, T.M. (2003) Macroecology and conservation biology. In: *Macroecology: concepts and consequences* (ed. by Blackburn, T.M., & Gaston, K.J.), pp. 345–367. Blackwell Publishing, Oxford.
- Gilbert, B., Laurance, W.F., Leigh Jr, E.G. & Nascimento, H.E.M. (2006) Can neutral theory predict the responses of Amazonian tree communities to forest fragmentation? *The American Naturalist*, 168, 304–317. <http://doi.org/10.1086/506969>
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001) Effects of size and temperature on metabolic rate. *Science*, 293, 2248–2251. <http://doi.org/10.1126/science.1061967>
- Gislason, H., Daan, N., Rice, J.C. & Pope, J.G. (2010) Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries*, 11, 149–158. <https://doi.org/10.1111/j.1467-2979.2009.00350.x>
- González-Suárez, M., Bacher, S. & Jeschke, J.M. (2015) Intraspecific trait variation is correlated with establishment success of alien mammals. *American Naturalist*, 185, 737–746. <https://doi.org/10.1086/681105>
- González-Suárez, M., Lucas, P.M. & Revilla, E. (2012) Biases in comparative analyses of extinction risk: mind the gap. *Journal of Animal Ecology*, 81, 1211–1222. <https://doi.org/10.1111/j.1365-2656.2012.01999.x>
- González-Suárez, M., Zanchetta Ferreira, F. & Grilo, C. (2018) Spatial and species-level predictions of road mortality risk using trait data. *Global Ecology and Biogeography*, 27, 1093–1105. <https://doi.org/10.1111/geb.12769>
- Gonzalez, A., Cardinale, B.J., Allington, G.R.H., Byrnes, J., Endsley, K.A., Brown, D.G., Hooper, D.U., Isbell, F., O'Connor, M.I. & Loreau, M. (2016) Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. *Ecology*, 97, 1949–1960. <https://doi.org/10.1890/15-1759.1>
- Guerry, A.D., Polasky, S., Lubchenco, J., et al. (2015) Natural capital and ecosystem services informing decisions: from promise to practice. *Proceedings of the National Academy of Sciences USA*, 112, 7348–7355. <https://doi.org/10.1073/pnas.1503751112>
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Guisan, A., Tingley, R., Baumgartner, J.B., et al. (2013) Predicting species distributions for conservation decisions. *Ecology Letters*, 16, 1424–1435. <https://doi.org/10.1111/ele.12189>
- Halley, J.M., Sgardeli, V. & Triantis, K.A. (2014) Extinction debt and the species-area relationship: a neutral perspective. *Global*

- Ecology and Biogeography, 23, 113–123. <https://doi.org/10.1111/geb.12098>
- Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F., O'Hara, C., Scarborough, C. & Selkoe, K.A. (2019) Recent pace of change in human impact on the world's ocean. *Scientific Reports*, 9, 11609. <https://doi.org/10.1038/s41598-019-47201-9>
- Halpin, P.N., Read, A.J., Best, B.D., Hyrenbach, K.D., Fujioka, E., Coyne, M.S., Crowder, L.B., Freeman, S.A. & Spoerri, C. (2006) OBIS-SEAMAP: developing a biogeographic research data commons for the ecological studies of marine mammals, seabirds, and sea turtles. *Marine Ecology Progress Series*, 316, 239–246. <http://doi.org/10.3354/meps316239>
- Han, B.A., Kramer, A.M. & Drake, J.M. (2016) Global patterns of zoonotic disease in mammals. *Trends in Parasitology*, 32, 565–577. <http://doi.org/10.1016/j.pt.2016.04.007>
- Hannah, L., Roehrdanz, P.R., Ikegami, M., Shepard, A. V., Shaw, M.R., Tabor, G., Zhi, L., Marquet, P.A. & Hijmans, R.J. (2013) Climate change, wine, and conservation. *Proceedings of the National Academy of Sciences USA*, 110, 6907–6912. <http://doi.org/10.1073/pnas.1210127110>
- Hannah, L., Roehrdanz, P.R., Marquet, P.A., et al. (2020) 30% land conservation and climate action reduces tropical extinction risk by more than 50%. *Ecography*, 43, 943–953. <https://doi.org/10.1111/ecog.05166>
- Harfoot, M.B.J., Newbold, T., Tittensor, D.P., et al. (2014) Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. *PLoS Biology*, 12. <https://doi.org/10.1371/journal.pbio.1001841>
- Harte, J. (2011) *Maximum entropy and ecology: a theory of abundance, distribution, and energetics*, Oxford University Press, New York.
- Hartley, S. & Kunin, W.E. (2003) Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology*, 17, 1559–1570. <https://doi.org/10.1111/j.1523-1739.2003.00015.x>
- Hilbers, J.P., Santini, L., Visconti, P., Schipper, A.M., Pinto, C., Rondinini, C. & Huijbregts, M.A.J. (2017) Setting population targets for mammals using body mass as a predictor of population persistence. *Conservation Biology*, 31, 385–393. <http://doi.org/10.1111/cobi.12846>
- Hintzen, R.E., Papadopoulou, M., Mounce, R., Banks-Leite, C., Holt, R.D., Mills, M., Knight, A., Leroi, A.M. & Rosindell, J. (2019) Relationship between conservation biology and ecology shown through machine reading. *Conservation Biology*, 34, 721–732. <https://doi.org/10.1111/cobi.13435>
- Hof, C., Dehling, D.M., Bonn, A., et al. (2015) Macroecology meets IPBES. *Frontiers of Biogeography*, 7, 155–167. <http://doi.org/10.21425/F57428888>
- Hof, C., Voskamp, A., Biber, M.F., Böhning-Gaese, K., Engelhardt, E.K., Niamir, A., Willis, S.G. & Hickler, T. (2018) Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity. *Proceedings of the National Academy of Sciences USA*, 115, 13294–13299. <https://doi.org/10.1073/pnas.1807745115>
- Hortal, J., De Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015) Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 46, 523–549. <https://doi.org/10.1146/annurev-ecolsys-112414-054400>
- Hoskins, A.J., Harwood, T.D., Ware, C., Williams, K.J., Perry, J.J., Ota, N., Croft, J.R., Yeates, D.K., Jetz, W., Golebiewski, M., Purvis, A., Robertson, T. & Ferrier, S. (2020) BILBI: supporting global biodiversity assessment through high-resolution macroecological modelling. *Environmental Modelling & Software*, 132, 104806. <https://doi.org/10.1016/j.envsoft.2020.104806>
- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Hubbell, S.P., He, F., Condit, R., Borda-de-Água, L., Kellner, J. & Ter Steege, H. (2008) How many tree species are there in the Amazon and how many of them will go extinct? *Proceedings of the National Academy of Sciences USA*, 105, 11498–11504. <https://doi.org/10.1073/pnas.0801915105>
- Hudson, L.N., Newbold, T., Contu, S., et al. (2014) The PREDICTS database: a global database of how local terrestrial biodiversity responds



- to human impacts. *Ecology and Evolution*, 4, 4701–4735. <https://doi.org/10.1002/ece3.1303>
- IPBES (2019): Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (ed. by S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A. Pfaff, S. Polasky, A. Purvis, J. Razzaque, B. Reyers, R. Roy Chowdhury, Y. J. Shin, I. J. Visseren-Hamakers, K. J. Willis, and C. N. Zayas). IPBES secretariat, Bonn, Germany. 56 pp. <https://doi.org/10.5281/zenodo.3553579>
- Isaac, N.J.B., van Strien, A.J., August, T.A., de Zeeuw, M.P. & Roy, D.B. (2014) Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, 5, 1052–1060. <https://doi.org/10.1111/2041-210X.12254>
- Jennings, S. & Blanchard, J.L. (2004) Fish abundance with no fishing: predictions based on macroecological theory. *Journal of Animal Ecology*, 73, 632–642. <https://doi.org/10.1111/j.0021-8790.2004.00839.x>
- Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. (2004) The scaling of animal space use. *Science*, 306, 266–268. <https://doi.org/10.1126/science.1102138>
- Jetz, W., McGeoch, M.A., Guralnick, R., et al. (2019) Essential biodiversity variables for mapping and monitoring species populations. *Nature Ecology and Evolution*, 3, 539–551. <https://doi.org/10.1038/s41559-019-0826-1>
- Jézéquel, C., Tedesco, P.A., Darwall, et al. (2020) Freshwater fish diversity hotspots for conservation priorities in the Amazon Basin. *Conservation Biology*, 34, 956–965. <http://doi.org/10.1111/cobi.13466>
- Johnson, T.F., Isaac, N.J.B., Paviolo, A. & González-Suárez, M. (2020) Handling missing values in trait data. *Global Ecology and Biogeography*, 5, 51–62. <https://doi.org/10.1111/geb.13185>
- Jones, K.E., Bielby, J., Cardillo, M., et al. (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, 90, 2648. <https://doi.org/10.1890/08-1494.1>
- Jung, M., Arnell, A., de Lamo, X., et al. (2021) Areas of global importance for terrestrial biodiversity, carbon, and water. *Nature Ecology and Evolution*. <https://doi.org/10.1038/s41559-021-01528-7>
- Kareiva, P. & Marvier, M. (2012) What is Conservation Science? *BioScience*, 62, 962–969. <http://doi.org/10.1525/bio.2012.62.11.5>
- Kass, J.M., Vilela, B., Aiello-Lammens, M.E., Muscarella, R., Merow, C. & Anderson, R.P. (2018) Wallace: a flexible platform for reproducible modeling of species niches and distributions built for community expansion. *Methods in Ecology and Evolution*, 9, 1151–1156. <https://doi.org/10.1111/2041-210X.12945>
- Kattge, J., Diaz, S., Lavorel, S., et al. (2011) TRY—a global database of plant traits. *Global Change Biology*, 17, 2905–2935. <https://doi.org/10.1111/j.1365-2486.2011.02451.x>
- Kehoe, L., Romero-Muñoz, A., Polaina, E., Estes, L., Kreft, H. & Kueemmerle, T. (2017) Biodiversity at risk under future cropland expansion and intensification. *Nature Ecology and Evolution*, 1, 1129. <https://doi.org/10.1038/s41559-017-0234-3>
- Kerr, J.T., Kharouba, H.M. & Currie, D.J. (2007) The macroecological contribution to global change solutions. *Science*, 316, 1581–1584. <http://doi.org/10.1126/science.1133267>
- Kinzig, A.P. & Harte, J. (2000) Implications of endemic-area relationships for estimates of species extinctions. *Ecology*, 81, 3305–3311. [https://doi.org/10.1890/0012-9658\(2000\)081\[3305:IOEARF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[3305:IOEARF]2.0.CO;2)
- Kissling, W.D., Ahumada, J.A., Bowser, A., et al. (2018) Building essential biodiversity variables (EBVs) of species distribution and abundance at a global scale. *Biological Reviews*, 93, 600–625. <https://doi.org/10.1111/brv.12359>
- Van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13, 235–245. <http://doi.org/10.1111/j.1461-0248.2009.01418.x>
- Knight, A.T., Driver, A., Cowling, et al. (2006) Designing systematic conservation assessments that promote effective implementation: best practice from South Africa. *Conservation*



- Biology, 20, 739–750. <https://doi.org/10.1111/j.1523-1739.2006.00452.x>
- Kremen, C., Cameron, A., Moilanen, A., et al. (2008) Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science*, 320, 222–226. <http://doi.org/10.1126/science.1155193>
- Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, 84, 177–192. <https://doi.org/10.2307/3546712>
- Leclère, D., Obersteiner, M., Barrett, M., et al. (2020) Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, 58, 551–556. <https://doi.org/10.1038/s41586-020-2705-y>
- Lewandowska, A.M., Jonkers, L., Auel, H., Freund, J.A., Hagen, W., Kucera, M. & Hillebrand, H. (2020) Scale dependence of temporal biodiversity change in modern and fossil marine plankton. *Global Ecology and Biogeography*, 29, 1008–1019. <https://doi.org/10.1111/geb.13078>
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*, Princeton University Press, Princeton, New Jersey.
- Mace, G.M. (2014) Whose conservation? *Science*, 345, 1558–1560. <http://doi.org/10.1126/science.1254704>
- Madani, N., Kimball, J.S., Ballantyne, A.P., et al. (2018) Future global productivity will be affected by plant trait response to climate. *Scientific Reports*, 8, 1–10. <https://doi.org/10.1038/s41598-018-21172-9>
- Maguire, B. (1973) Niche response structure and the analytical potentials of its relationship to the habitat. *The American Naturalist*, 107, 213–246. <https://doi.org/10.1086/282827>
- Maitner, B.S., Boyle, B., Casler, N., et al. (2018) The bien r package: a tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods in Ecology and Evolution*, 9, 373–379. <https://doi.org/10.1111/2041-210X.12861>
- Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, 405, 243–253. <https://doi.org/10.1038/35012251>
- Marquet, P.A. (2002) The search for general principles in ecology. *Nature*, 418, 723–723. <https://doi.org/10.1038/418723c>
- Marquet, P.A. & Taper, M.L. (1998) On size and area: patterns of mammalian body size extremes across landmasses. *Evolutionary Ecology*, 12, 127–139. <https://doi.org/10.1023/A:1006567227154>
- Marquet, P.A., Allen, A.P., Brown, J.H., et al. (2014) On theory in ecology. *BioScience*, 64, 701–710. <https://doi.org/10.1093/biosci/biu098>
- Marquet, P.A., Allen, A.P., Brown, J.H., et al. (2015) On the importance of first principles in ecological theory development. *BioScience*, 65, 342–343. <https://doi.org/10.1093/biosci/biv015>
- Martínez-Meyer, E., Peterson, A.T., Servín, J.I. & Kiff, L.F. (2006) Ecological niche modelling and prioritizing areas for species reintroductions. *Oryx*, 40, 411–418. <https://doi.org/10.1017/S0030605306001360>
- Matthews, T.J. & Whittaker, R.J. (2015) On the species abundance distribution in applied ecology and biodiversity management. *Journal of Applied Ecology*, 52, 443–454. <https://doi.org/10.1111/1365-2664.12380>
- McCarthy, M.A., Keith, D., Tietjen, J., et al. (2004) Comparing predictions of extinction risk using models and subjective judgement. *Acta Oecologica*, 26, 67–74. <https://doi.org/10.1016/j.actao.2004.01.008>
- McGill, B. (2019) The what, how and why of doing macroecology. *Global Ecology and Biogeography*, 28, 6–17. <https://doi.org/10.1111/geb.12855>
- McGill, B.J., Etienne, R.S., Gray, J.S., et al. (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, 10, 995–1015. <https://doi.org/10.1111/j.1461-0248.2007.01094.x>
- McGill, B.J., Dornelas, M., Gotelli, N.J. & Magurran, A.E. (2015) Fifteen forms of biodiversity trend in the anthropocene. *Trends in Ecology and Evolution*, 30, 104–113. <https://doi.org/10.1016/j.tree.2014.11.006>
- McGill, B.J. & Nekola, J.C. (2010) Mechanisms in macroecology: AWOL or purloined letter? Towards a pragmatic view of mechanism. *Oikos*, 119, 591–603. <https://doi.org/10.1111/j.1600-0706.2009.17771.x>
- McGowan, J., Smith, R.J., Di Marco, M., Clarke, R.H. & Possingham, H.P. (2018) An Evaluation of Marine Important Bird and Biodiversity Areas in the Context of Spatial Conservation Prioritization. *Conservation Letters*, 11, e12399. <https://doi.org/10.1111/conl.12399>

- Meyer, C., Weigelt, P. & Kreft, H. (2016) Multidimensional biases, gaps and uncertainties in global plant occurrence information. *Ecology Letters*, 19, 992–1006. <https://doi.org/10.1111/ele.12624>
- Miatta, M., Bates, A.E. & Snelgrove, P.V.R. (2021) Incorporating biological traits into conservation strategies. *Annual Review of Marine Science*, 13. <https://doi.org/10.1146/annurev-marine-032320-094121>
- Münkemüller, T., Gallien, L., Pollock, L.J., et al. (2020) Dos and don'ts when inferring assembly rules from diversity patterns. *Global Ecology and Biogeography*, 29, 1212–1229. <https://doi.org/10.1111/geb.13098>
- Murray, B.R. & Dickman, C.R. (2000) Relationships between body size and geographical range size among Australian mammals: has human impact distorted macroecological patterns? *Ecography*, 23, 92–100. <https://doi.org/10.1111/j.1600-0587.2000.tb00264.x>
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858. <https://doi.org/10.1038/35002501>
- Naimi, B. & Araújo, M.B. (2016) sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography*, 39, 368–375. <https://doi.org/10.1111/ecog.01881>
- Newbold, T., Hudson, L.N., Arnell, A.P., et al. (2016) Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science*, 353, 288–291. <https://doi.org/10.1126/science.aaf2201>
- O'Connor, L.M., Pollock, L.J., Renaud, J., Verhagen, W., Verburg, P.H., Lavorel, S., Maiorano, L. & Thuiller, W. (2021) Balancing conservation priorities for nature and for people in Europe. *Science*, 372, 856–860. <https://doi.org/10.1126/science.abc4896>
- Oliveira, B.F., São-Pedro, V.A., Santos-Barrera, G., Penone, C. & Costa, G.C. (2017) AmphiBIO, a global database for amphibian ecological traits. *Scientific Data*, 4, 170123.
- Ovaskainen, O. (2002) Long-term persistence of species and the SLOSS problem. *Journal of Theoretical Biology*, 218, 419–433. <https://doi.org/10.1006/jtbi.2002.3089>
- Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T. & Abrego, N. (2017) How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, 20, 561–576. <https://doi.org/10.1111/ele.12757>
- Pacifici, M., Rondinini, C., Rhodes, J.R., Burbidge, A.A., Cristiano, A., Watson, J.E.M., Woinarski, J.C.Z. & Di Marco, M. (2020) Global correlates of range contractions and expansions in terrestrial mammals. *Nature Communications*, 11, 2840. <https://doi.org/10.1038/s41467-020-16684-w>
- Pacifici, M., Santini, L., Di Marco, M., Baisero, D., Francucci, L., Grottolo Marasini, G., Visconti, P. & Rondinini, C. (2013) Generation length for mammals. *Nature Conservation*, 5, 87–94. <https://doi.org/10.3897/natureconservation.5.5734>
- Pandit, P.S., Doyle, M.M., Smart, K.M., Young, C.C.W., Drape, G.W. & Johnson, C.K. (2018) Predicting wildlife reservoirs and global vulnerability to zoonotic Flaviviruses. *Nature Communications*, 9, 5425. <https://doi.org/10.1038/s41467-018-07896-2>
- Pauly, D. (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution*, 10, 430. [http://doi.org/10.1016/s0169-5347\(00\)89171-5](http://doi.org/10.1016/s0169-5347(00)89171-5)
- Pauly, D. & Watson, R. (2005) Background and interpretation of the “Marine Trophic Index” as a measure of biodiversity. *Philosophical Transactions of the Royal Society B*, 360, 415–423. <http://doi.org/10.1098/rstb.2004.1597>
- Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12, 361–371. <https://doi.org/10.1046/j.1466-822X.2003.00042.x>
- Pearson, R.G., Stanton, J.C., Shoemaker, K.T., et al. (2014) Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, 4, 217–221. <https://doi.org/10.1038/nclimate2113>
- Penone, C., Davidson, A.D., Shoemaker, K.T., Di Marco, M., Rondinini, C., Brooks, T.M., Young, B.E., Graham, C.H. & Costa, G.C. (2014) Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution*, 5, 961–970. <https://doi.org/10.1111/2041-210X.12232>

- Pereira, H.M., Ferrier, S., Walters, M., et al. (2013) Essential biodiversity variables. *Science*, 339, 277–278. <https://doi.org/10.1126/science.1229931>
- Phillips, S.J., Dudík, M. & Schapire, R.E. (2004) A maximum entropy approach to species distribution modeling. In: *Proceedings of the 21<sup>st</sup> International Conference on Machine Learning*, p. 655–662.
- Polaina, E., González-Suárez, M., Kuemmerle, T., Kehoe, L. & Revilla, E. (2018) From tropical shelters to temperate defaunation: the relationship between agricultural transition stage and the distribution of threatened mammals. *Global Ecology and Biogeography*, 27, 647–657. <https://doi.org/10.1111/geb.12725>
- Pollock, L.J., Thuiller, W. & Jetz, W. (2017) Large conservation gains possible for global biodiversity facets. *Nature*, 546, 141. <https://doi.org/10.1038/nature22368>
- Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., Vesik, P.A. & McCarthy, M.A. (2014) Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, 5, 397–406. <https://doi.org/10.1111/2041-210X.12180>
- Pouzols, F.M., Toivonen, T., Di Minin, E., Kukkala, A.S., Kullberg, P., Kuusterä, J., Lehtomäki, J., Tenkanen, H., Verburg, P.H. & Moilanen, A. (2014) Global protected area expansion is compromised by projected land-use and parochialism. *Nature*, 516, 383–386. <https://doi.org/10.1038/nature14032>
- Powers, R.P. & Jetz, W. (2019) Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nature Climate Change*, 9, 323. <https://doi.org/10.1038/s41558-019-0406-z>
- Prendergast, J.R., Quinn, R.M. & Lawton, J.H. (1999) The gaps between theory and practice in selecting nature reserves. *Conservation Biology*, 13, 484–492. <https://doi.org/10.1046/j.1523-1739.1999.97428>
- Pressey, R.L., Mills, M., Weeks, R. & Day, J.C. (2013) The plan of the day: managing the dynamic transition from regional conservation designs to local conservation actions. *Biological Conservation*, 166, 155–169. <https://doi.org/10.1016/j.biocon.2013.06.025>
- Preston, F.W. (1980) Noncanonical distributions of commonness and rarity. *Ecology*, 61, 88–97. <https://doi.org/10.2307/1937159>
- Primack, R.B., Miller-Rushing, A.J., Corlett, R.T., Devictor, V., Johns, D.M., Loyola, R., Maas, B., Pakeman, R.J. & Pejchar, L. (2018) Biodiversity gains? The debate on changes in local- vs global-scale species richness. *Biological Conservation*, 219, A1. <https://doi.org/10.1016/j.biocon.2017.12.023>
- Purvis, A., Agapow, P.M., Gittleman, J.L. & Mace, G.M. (2000) Nonrandom extinction and the loss of evolutionary history. *Science*, 288, 328–330. <https://doi.org/10.1126/science.288.5464.328>
- Rapacciuolo, G. (2019) Strengthening the contribution of macroecological models to conservation practice. *Global Ecology and Biogeography*, 28, 54–60. <https://doi.org/10.1111/geb.12848>
- Rapacciuolo, G. & Blois, J. (2019) Understanding ecological change across large spatial, temporal and taxonomic scales: integrating data and methods in light of theory. *Ecography*, 42, 1247–1266. <https://doi.org/10.1111/ecog.04616>
- Rapacciuolo, G., Graham, C.H., Marin, J., Behm, J.E., Costa, G.C., Hedges, S.B., Helmus, M.R., Radeloff, V.C., Young, B.E. & Brooks, T.M. (2019) Species diversity as a surrogate for conservation of phylogenetic and functional diversity in terrestrial vertebrates across the Americas. *Nature Ecology and Evolution*, 3, 53–61. <https://doi.org/10.1038/s41559-018-0744-7>
- Rapacciuolo, G., Marin, J., Costa, G.C., Helmus, M.R., Behm, J.E., Brooks, T.M., Hedges, S.B., Radeloff, V.C., Young, B.E. & Graham, C.H. (2017) The signature of human pressure history on the biogeography of body mass in tetrapods. *Global Ecology and Biogeography*, 26, 1022–1034. <https://doi.org/10.1111/geb.12612>
- Rocchini, D., Hortal, J., Lengyel, S., Lobo, J.M., Jiménez-Valverde, A., Ricotta, C., Bacaro, G. & Chiarucci, A. (2011) Accounting for uncertainty when mapping species distributions: The need for maps of ignorance. *Progress in Physical Geography*, 35, 211–226. <https://doi.org/10.1177/0309133311399491>
- Rodrigues, A.S.L. & Brooks, T.M. (2007) Shortcuts for biodiversity conservation planning: the



- effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics*, 38, 713–737. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095737>
- Roll, U., Feldman, A., Novosolov, M., et al. (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology and Evolution*, 1, 1677–1682. <https://doi.org/10.1038/s41559-017-0332-2>
- Romero-Muñoz, A., Benítez-López, A., Zurell, D., et al. (2020) Increasing synergistic effects of habitat destruction and hunting on mammals over three decades in the Gran Chaco. *Ecography*, 43, 954–966. <https://doi.org/10.1111/ecog.05053>
- Rondinini, C., Di Marco, M., Visconti, P., Butchart, S.H.M. & Boitani, L. (2014) Update or outdate: long-term viability of the IUCN Red List. *Conservation Letters*, 7, 126–130. <https://doi.org/10.1111/conl.12040>
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press.
- Le Roux, D.S., Ikin, K., Lindenmayer, D.B., Manning, A.D. & Gibbons, P. (2015) Single large or several small? Applying biogeographic principles to tree-level conservation and biodiversity offsets. *Biological Conservation*, 191, 558–566. <https://doi.org/10.1016/j.biocon.2015.08.011>
- Salguero-Gómez, R., Jones, O.R., Archer, C.R., et al. (2016) COMADRE: a global data base of animal demography. *Journal of Animal Ecology*, 85, 371–384. <https://doi.org/10.1111/1365-2656.12482>
- Salguero-Gomez, R., Jones, O.R., Archer, C.R., et al. (2015) The COMPADRE plant matrix database: an open online repository for plant demography. *Journal of Ecology*, 103, 202–218. <https://doi.org/10.1111/1365-2745.12334>
- Sandbrook, C., Fisher, J.A., Holmes, G., Luque-Lora, R. & Keane, A. (2019) The global conservation movement is diverse but not divided. *Nature Sustainability*, 2, 316–323. <https://doi.org/10.1038/s41893-019-0267-5>
- Santini, L., Benítez-López, A., Maiorano, L., Cengic, M. & Huijbregts, M.A.J. (2021) Assessing the reliability of species distribution projections in climate change research. *Diversity and Distributions*, 27, 1035–1050. <https://doi.org/10.1111/ddi.13252>
- Santini, L., Butchart, S.H.M., Rondinini, C., Benítez-López, A., Hilbers, J.P., Schipper, A.M., Cengic, M., Tobias, J.A. & Huijbregts, M.A.J. (2019) Applying habitat and population-density models to land-cover time series to inform IUCN Red List assessments. *Conservation Biology*, 33, 1084–1093. <https://doi.org/10.1111/cobi.13279>
- Santini, L., González-Suárez, M., Rondinini, C. & Di Marco, M. (2017) Shifting baseline in macroecology? Unravelling the influence of human impact on mammalian body mass. *Diversity and Distributions*, 23, 640–649. <https://doi.org/10.1111/ddi.12555>
- Santini, L. & Isaac, N.J.B. (2021) Rapid Anthropocene realignment of allometric scaling rules. *Ecology Letters*, 24, 1318–1327. <https://doi.org/10.1111/ele.13743>
- Santini, L., Isaac, N.J.B. & Ficetola, G.F. (2018) TetraDENSITY: a database of population density estimates in terrestrial vertebrates. *Global Ecology and Biogeography*, 27, 787–791. <https://doi.org/10.1111/geb.12756>
- Santini, L., Saura, S. & Rondinini, C. (2016) Connectivity of the global network of protected areas. *Diversity and Distributions*, 22, 199–211. <https://doi.org/10.1111/ddi.12390>
- Saura, S. (2020) The Habitat Amount Hypothesis implies negative effects of habitat fragmentation on species richness and occurrence. *Journal of Biogeography*, 48, 11–22. <https://doi.org/10.1111/jbi.13958>
- Sax, D.F. & Gaines, S.D. (2008) Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences USA*, 105, 11490–11497. <https://doi.org/10.1073/pnas.0802290105>
- Sax, D.F., Gaines, S.D. & Brown, J.H. (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *The American Naturalist*, 160, 766–783. <https://doi.org/10.1086/343877>
- Sayer, J.A., Endamana, D., Ruiz-Perez, M., Boedhihartono, A.K., Nzooh, Z., Eyebe, A., Awono, A. & Usongo, L. (2012) Global financial crisis impacts forest conservation in Cameroon. *International Forestry Review*, 14, 90–98. <https://doi.org/10.1505/146554812799973172>

- Scheffers, B.R., Oliveira, B.F., Lamb, I. & Edwards, D.P. (2019) Global wildlife trade across the tree of life. *Science*, 366, 71–76. <https://doi.org/10.1126/science.aav5327>
- Schipper, A.M., Hilbers, J.P., Meijer, J.R., et al. (2020) Projecting terrestrial biodiversity intactness with GLOBIO 4. *Global Change Biology*, 26, 760–771. <https://doi.org/10.1111/gcb.14848>
- Sebastián-González, E., Barbosa, J.M., Pérez-García, J.M., et al. (2019) Scavenging in the Anthropocene: human impact drives vertebrate scavenger species richness at a global scale. *Global Change Biology*, 25, 3005–3017. <https://doi.org/10.1111/gcb.14708>
- Silva, M. & Downing, J.A. (1995) The allometric scaling of density and body mass: a non-linear relationship for terrestrial mammals. *American Naturalist*, 145, 704–727. <https://doi.org/10.1086/285764>
- Smith, F.A., Lyons, S.K., Ernest, S.K.M. & Brown, J.H. (2008) Macroecology: more than the division of food and space among species on continents. *Progress in Physical Geography*, 32, 115–138. <https://doi.org/10.1177/0309133308094425>
- Soberón, J. & Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences USA*, 106, 19644–19650. <https://doi.org/10.1073/pnas.0901637106>
- Socolar, J.B., Gilroy, J.J., Kunin, W.E. & Edwards, D.P. (2016) How Should beta-diversity inform biodiversity conservation? *Trends in Ecology and Evolution*, 31, 67–80. <https://doi.org/10.1016/j.tree.2015.11.005>
- Soroye, P., Newbold, T. & Kerr, J. (2020) Climate change contributes to widespread declines among bumble bees across continents. *Science*, 367, 685–688. <https://doi.org/10.1126/science.aax8591>
- Soto-Navarro, C., Ravilious, C., Arnell, A., et al. (2020) Mapping co-benefits for carbon storage and biodiversity to inform conservation policy and action. *Philosophical Transactions of the Royal Society B*, 375, 20190128. <https://doi.org/10.1098/rstb.2019.0128>
- Soulé, M.E. (1985) What is Conservation Biology? *BioScience*, 35, 727–734. <https://doi.org/10.2307/1310054>
- Stephens, P.R., Altizer, S., Smith, K.F., et al. (2016) The macroecology of infectious diseases: a new perspective on global-scale drivers of pathogen distributions and impacts. *Ecology Letters*, 19, 1159–1171. <https://doi.org/10.1111/ele.12644>
- Storch, D., Keil, P. & Jetz, W. (2012) Universal species-area and endemics-area relationships at continental scales. *Nature*, 488, 78–81. <https://doi.org/10.1038/nature11226>
- Stropp, J., Ladle, R.J., Ana, A.C., Hortal, J., Gaffuri, J., H. Temperley, W., Olav Skøien, J. & Mayaux, P. (2016) Mapping ignorance: 300 years of collecting flowering plants in Africa. *Global Ecology and Biogeography*, 25, 1085–1096. <https://doi.org/10.1111/geb.12468>
- Stuart-Smith, R.D., Edgar, G.J., Barrett, N.S., Kininmonth, S.J. & Bates, A.E. (2015) Thermal biases and vulnerability to warming in the world's marine fauna. *Nature*, 528, 88–92. <https://doi.org/10.1038/nature16144>
- Sutherland, W.J., Adams, W.M., Aronson, R.B., et al. (2009) One hundred questions of importance to the conservation of global biological diversity. *Conservation Biology*, 23, 557–567. <https://doi.org/10.1111/j.1523-1739.2009.01212.x>
- Thomas, C.D., Cameron, A., Green, R.E., et al. (2004) Extinction risk from climate change. *Nature*, 427, 145–148. <https://doi.org/10.1038/nature02121>
- Thorson, J.T., Ianello, J.N., Larsen, E.A., Ries, L., Scheuerell, M.D., Szuwalski, C. & Zipkin, E.F. (2016) Joint dynamic species distribution models: a tool for community ordination and spatio-temporal monitoring. *Global Ecology and Biogeography*, 25, 1144–1158. <https://doi.org/10.1111/geb.12464>
- Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD—a platform for ensemble forecasting of species distributions. *Ecography*, 32, 369–373. <https://doi.org/10.1111/j.1600-0587.2008.05742.x>
- Thuiller, W., Maiorano, L., Mazel, F., Guilhaumon, F., Ficetola, G.F., Lavergne, S., Renaud, J., Roquet, C. & Mouillot, D. (2015) Conserving the functional and phylogenetic trees of life of European tetrapods. *Philosophical Transactions of the Royal Society B*, 370, 20140005. <https://doi.org/10.1098/rstb.2014.0005>

- Tikhonov, G., Abrego, N., Dunson, D. & Ovaskainen, O. (2017) Using joint species distribution models for evaluating how species-to-species associations depend on the environmental context. *Methods in Ecology and Evolution*, 8, 443–452. <https://doi.org/10.1111/2041-210X.12723>
- Tilman, D., May, R.M., Lehman, C.L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature*, 371, 65–66. <https://doi.org/10.1038/371065a0>
- Titley, M.A., Butchart, S.H.M., Jones, V.R., Whittingham, M.J. & Willis, S.G. (2021) Global inequities and political borders challenge nature conservation under climate change. *Proceedings of the National Academy of Sciences USA*, 118, e2011204118. <https://doi.org/10.1073/pnas.2011204118>
- Tittensor, D.P., Walpole, M., Hill, S.L.L., et al. (2014) A mid-term analysis of progress towards international biodiversity targets. *Science*, 346, 241–244. <https://doi.org/10.1126/science.1257484>
- Tittensor, D.P., Worm, B. & Myers, R.A. (2009) Macroecological changes in exploited marine systems. In: *Marine Macroecology* (ed. by J.D. Witman), pp. 310–337. University of Chicago Press.
- Torres-Romero, E.J. & Olalla-Tárraga, M.A. (2015) Untangling human and environmental effects on geographical gradients of mammal species richness: a global and regional evaluation. *Journal of Animal Ecology*, 84, 851–860. <https://doi.org/10.1111/1365-2656.12313>
- Travers, H., Selinske, M., Nuno, A., Serban, A., Mancini, F., Barychka, T., Bush, E., Rasolofson, R.A., Watson, J.E.M. & Milner-Gulland, E.J. (2019) A manifesto for predictive conservation. *Biological Conservation*, 237, 12–18. <https://doi.org/10.1016/j.biocon.2019.05.059>
- Tucker, M., Santini, L., Carbone, C. & Mueller, T. (2020) Mammal population densities at a global scale are higher in human-modified areas. *Ecography*, 44, 1–13. <https://doi.org/10.1111/ecog.05126>
- Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., et al. (2018) Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science*, 359, 466–469. <https://doi.org/10.1126/science.aam9712>
- Urban, M.C. (2015) Accelerating extinction risk from climate change. *Science*, 348, 571–573.
- Valderrama, D. & Fields, K.H. (2017) Flawed evidence supporting the Metabolic Theory of Ecology may undermine goals of ecosystem-based fishery management: the case of invasive Indo-Pacific lionfish in the western Atlantic. *ICES Journal of Marine Science*, 74, 1256–1267. <https://doi.org/10.1093/icesjms/fsw223>
- Vellend, M., Dornelas, M., Baeten, L., et al. (2017) Estimates of local biodiversity change over time stand up to scrutiny. *Ecology*, 98, 583–590. <https://doi.org/10.1002/ecy.1660>
- Venter, O., Fuller, R.A., Segan, D.B., et al. (2014) Targeting global protected area expansion for imperiled biodiversity. *PLoS Biology*, 12, e1001891. <https://doi.org/10.1371/journal.pbio.1001891>
- Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J. & Kattge, J. (2014) The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences USA*, 111, 13690–13696. <https://doi.org/10.1073/pnas.1415442111>
- Visconti, P., Bakkenes, M., Baisero, D., et al. (2016) Projecting global biodiversity indicators under future development scenarios. *Conservation Letters*, 9, 5–13. <https://doi.org/10.1111/conl.12159>
- Warren, D.L., Cardillo, M., Rosauer, D.F. & Bolnick, D.I. (2014) Mistaking geography for biology: inferring processes from species distributions. *Trends in Ecology and Evolution*, 29, 572–580. <https://doi.org/10.1016/j.tree.2014.08.003>
- Warren, D.L., Matzke, N.J. & Iglesias, T.L. (2020) Evaluating presence-only species distribution models with discrimination accuracy is uninformative for many applications. *Journal of Biogeography*, 47, 167–180. <https://doi.org/10.1111/jbi.13705>
- Whitmee, S. & Orme, C.D.L. (2012) Predicting dispersal distance in mammals: a trait-based approach. *Journal of Animal Ecology*, 82, 211–221. <https://doi.org/10.1111/j.1365-2656.2012.02030.x>
- Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. (2005) Conservation biogeography: assessment and prospect. *Diversity and Distributions*,



- 11, 3–23. <https://doi.org/10.1111/j.1366-9516.2005.00143.x>
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*, 2<sup>nd</sup> edn. Oxford University Press, Oxford.
- Williams, D.R., Balmford, A. & Wilcove, D.S. (2020) The past and future role of conservation science in saving biodiversity. *Conservation Letters*, e12720. <https://doi.org/10.1111/conl.12720>
- Williams, J.J., Bates, A.E. & Newbold, T. (2019) Human-dominated land uses favour species affiliated with more extreme climates, especially in the tropics. *Ecography*, 43, 391–405. <https://doi.org/10.1111/ecog.04806>
- Williams, J.N., Seo, C., Thorne, J., Nelson, J.K., Erwin, S., O'Brien, J.M. & Schwartz, M.W. (2009) Using species distribution models to predict new occurrences for rare plants. *Diversity and Distributions*, 15, 565–576. <https://doi.org/10.1111/j.1472-4642.2009.00567.x>
- Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M. & Jetz, W. (2014) EltonTraits 1.0: species-level foraging attributes of the world's birds and mammals. *Ecology*, 95, 2027. <https://doi.org/10.1890/13-1917.1>
- Xu, C., Kohler, T.A., Lenton, T.M., Svenning, J.C. & Scheffer, M. (2020) Future of the human climate niche. *Proceedings of the National Academy of Sciences USA*, 117, 11350–11355. <https://doi.org/10.1073/pnas.1910114117>
- Yates, K.L., Bouchet, P.J., Caley, M.J., et al. (2018) Outstanding challenges in the transferability of ecological models. *Trends in Ecology and Evolution*, 33, 790–802. <https://doi.org/10.1016/j.tree.2018.08.001>
- Submitted: 4 May 2021,  
First decision: 15 June 2021,  
Accepted: 11 July 2021
- Edited by Janet Franklin