The interface between macroecology and conservation: existing links and untapped opportunities

PERSPECTIVE

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

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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

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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

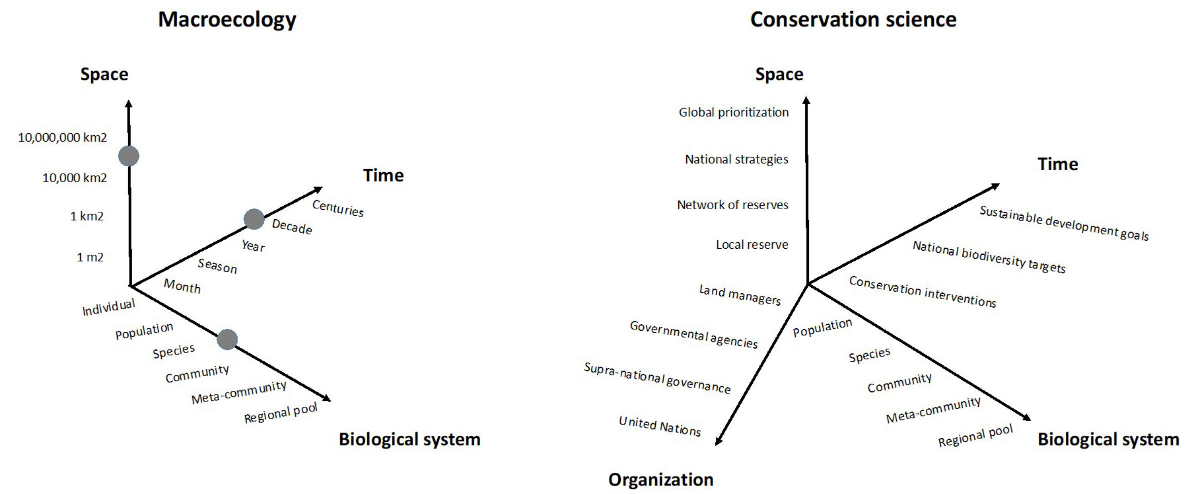

Figure. 1. Scale in macroecology and conservation science, adapted from McGill (2019). The grey dots along the axes indicate the approximate values beyond which macroecology typically operates.

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, Ceaușu 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,

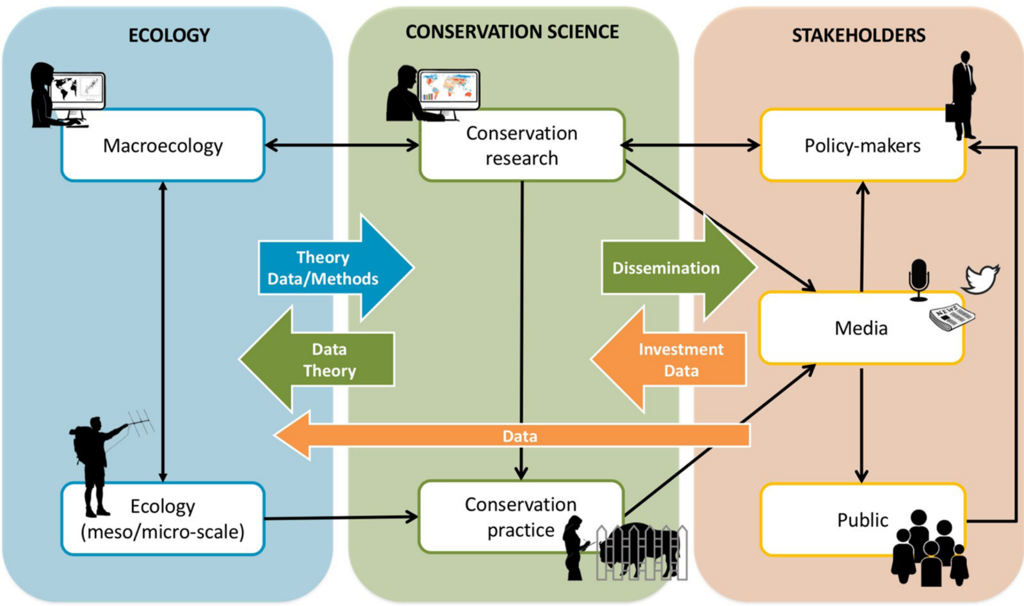

Figure. 2. Links between traditional ecology, macroecology, conservation research and practice, policy-makers and the public. We represent here the links discussed in the text, but acknowledge that many other links exist (e.g. between ecology and conservation) or are possible. We further note that this 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 acknoweldge 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 (Pacifici 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). SAR 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 (Pacifici 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 (JDSDMs, 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 JSDM (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 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

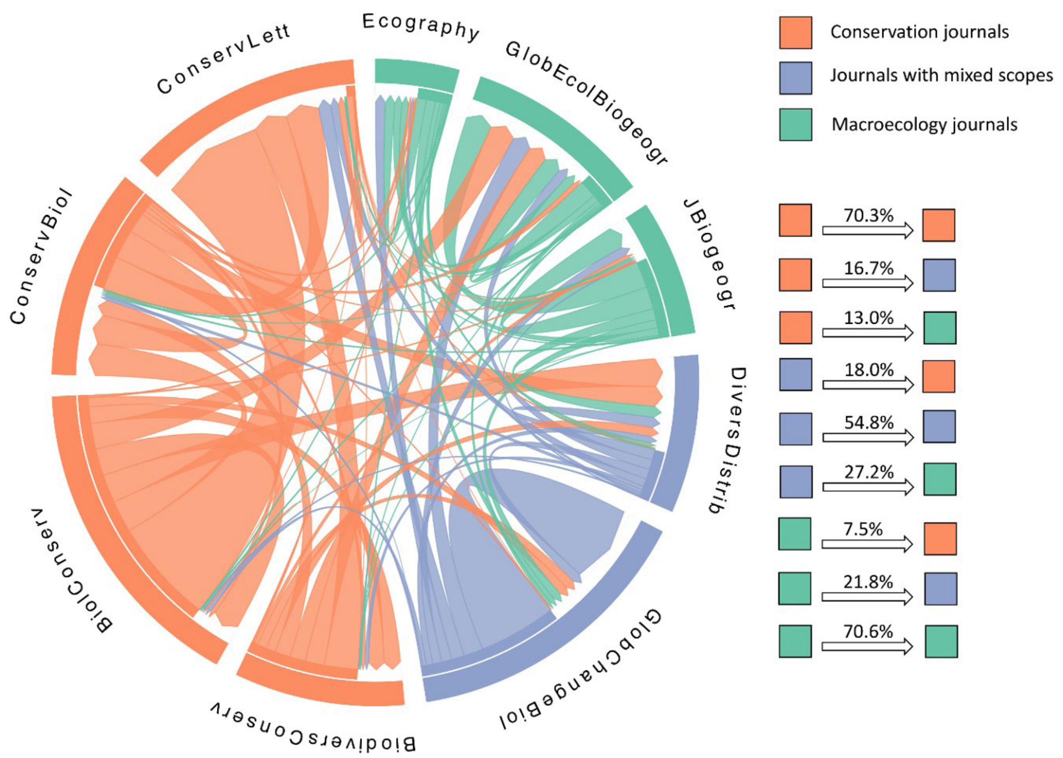

Figure. 3. Flow of citations between journals whose scope is focused mainly either on macroecology or conservation, and hybrid journals between 2008 and 2017 (readapted from Fig. 2 in Benítez-López & Santini 2020). The outer circle width per journal indicates the total citations exchanged with other 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.

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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.

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