



Rethinking ecological niches and geographic distributions in face of pervasive human influence in the Anthropocene

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ABSTRACT

Species are distributed in predictable ways in geographic spaces. The three principal factors that determine geographic distributions of species are biotic interactions (**B**), abiotic conditions (**A**), and dispersal ability or mobility (**M**). A species is expected to be present in areas that are accessible to it and that contain suitable sets of abiotic and biotic conditions for it to persist. A species' probability of presence can be quantified as a combination of responses to **B**, **A**, and **M** *via* ecological niche modeling (ENM; also frequently referred to as species distribution modeling or SDM). This analytical approach has been used broadly in ecology and biogeography, as well as in conservation planning and decision-making, but commonly in the context of 'natural' settings. However, it is increasingly recognized that human impacts, including changes in climate, land cover, and ecosystem function, greatly influence species' geographic ranges. In this light, historical distinctions between natural and anthropogenic factors have become blurred, and a coupled human–natural landscape is recognized as the new norm. Therefore, **B**, **A**, and **M** (BAM) factors need to be reconsidered to understand and quantify species' distributions in a world with a pervasive signature of human impacts. Here, we present a framework, termed human-influenced BAM (Hi-BAM, for distributional ecology that (i) conceptualizes human impacts in the form of six drivers, and (ii) synthesizes previous studies to show how each driver modifies the natural BAM and species' distributions. Given the importance and prevalence of human impacts on species distributions globally, we also discuss implications of this framework for ENM/SDM methods, and explore strategies by which to incorporate increasing human impacts in the methodology. Human impacts are redefining biogeographic patterns; as such, future studies should incorporate signals of human impacts integrally in modeling and forecasting species' distributions.

Key words: Anthropocene, climate change, ecological niche, evolution, invasive species, urbanization, geographic distribution.

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I. INTRODUCTION

Species have predictable distributional patterns in geographic spaces. The relationship between a species' geographic distribution and the environment has been a central question in ecology and biogeography, and many theoretical discussions of this relationship stem from the concept of ecological niche. Hutchinson's definition of fundamental niche has seen wide acceptance: in the hyper-volume space composed of environmental variables, 'a set of points, each one of which defines a possible set of environmental values permitting the species to live (Hutchinson, 1978, p. 160)' or 'to exist indefinitely' (Hutchinson, 1957, p. 416).

In recent decades, correlative approaches have been used to quantify relationships between species' occurrence and environmental conditions (e.g. climate, topography); this approach is termed ecological niche modeling (ENM) or species distribution modeling (SDM) (Franklin, 2010; Peterson *et al.*, 2011). A distinction can be made between the two terms in that ENM aims to estimate the species' ecological niche in environmental space, whereas SDM emphasizes the species' distribution in geographic space (Peterson & Soberón, 2012); in practice, the two terms refer to much the same set of analyses and are commonly used interchangeably in the literature. Recent advancements in primary biodiversity data digitization, environmental monitoring, and modeling algorithms and software have greatly promoted development of this field (Franklin, 2010). ENM/SDM has been applied broadly in biodiversity conservation, for invasive species management, estimating distributions of species of conservation concern, and aiding in rare species surveys (Peterson *et al.*, 2011; Guisan *et al.*, 2013).

The development and broad application of ENM/SDM was built on fundamental and theoretical work that underpins this field. Notably, the conceptualization of the BAM framework (Soberón & Peterson, 2005) and the critical

discussion of niche concepts and species' geographic distributions (Soberón, 2007; Soberón & Nakamura, 2009) have influenced the development and use of ENM/SDM. As species are distributed in predictable ways in geographic spaces, factors that determine these patterns can be classified into three categories: biotic interactions (**B**), abiotic conditions (**A**), and dispersal ability or mobility (**M**). In brief, a species is expected to be present in areas with suitable biotic interactions and abiotic conditions and that have been accessible to the species *via* dispersal over relevant time periods. As such, the probability of a species' presence can be quantified as a function of its mobility and its responses to and requirements of abiotic and biotic factors.

It is increasingly recognized that human impacts, including global warming, land cover change, and ecosystem changes, strongly affect species' geographic ranges (Ellis, 2015). Historical distinctions between natural and human-impacted areas have become blurred, and a coupled, human–natural landscape is recognized as the new norm. Therefore, the need to rethink the ecological basis of ENM/SDM becomes a crucial step to improve understanding and quantifying of species' distributions in a world with pervasive signatures of human impacts.

BAM provides a solid conceptual framework for studying species' ecological niches and geographic distributions, but is clearly cast in large part in natural settings and does not consider anthropogenic effects directly and integrally. In the context of the Anthropocene, characterized by increasing impacts from human activities (Steffen *et al.*, 2015; Steffen, Crutzen & McNeill, 2007), the three dimensions of BAM and the associated assumptions need to be re-evaluated to incorporate the effects of human impacts. Put another way, distributional estimates and forecasts in ENM/SDM are based on relationships between geographic distributions and environmental factors; these relationships can be altered profoundly by human activities, thus requiring reconsideration of the

underlying theory to account for human impacts appropriately.

Here, we present a revised synthesis of distributional ecology in a framework that conceptualizes factors related to human activities (anthropogenic factors) in six major categories (Table 1). We have organized this synthesis around the widely adopted BAM framework. We discuss how each anthropogenic driver directly or indirectly affects species' distributions by modifying the natural setup of **B**, **A**, and **M** and term this expanded framework human-influenced BAM (HiBAM; Fig. 1, Table 1). We discuss implications of such changes for ENM/SDM methods, and explore strategies by which to incorporate increasing human impacts in the methodology (Table 2).

II. OVERVIEW OF HUMAN IMPACTS ON BAM

The impacts of anthropogenic activities on the Earth's ecosystems and biodiversity have been discussed frequently in the literature and conceptualized as different groups of drivers (Salafsky *et al.*, 2008; Franklin *et al.*, 2016; Kelly *et al.*, 2020; Uchida *et al.*, 2021; Fenoglio *et al.*, 2021). Herein, we summarize human impacts in terms of six major groups of drivers based on a conceptual framework for understanding species' geographic distributions (Table 1).

(1) Human introduction of non-native species

Humans can affect species' distributions directly by intentionally or unintentionally introducing species outside of their native ranges, and these activities can break down biogeographic boundaries and redefine biodiversity patterns (Capinha *et al.*, 2015; Fricke & Svenning, 2020). Such introduction effects span the full taxonomic and functional spectrum, including animals, plants, viruses, bacteria, and fungi, and are noticeable at global scales; these effects will likely continue to increase with globalization (Seebens *et al.*, 2017).

Humans began introducing species intentionally in the form of domesticated animals and crop plants across global landscapes since the earliest times in recorded human history (Ahmad *et al.*, 2020). In modern times, effects of human introductions have been intensified by enhanced mobility (e.g. cars, trains, ships, aeroplanes), evidenced by the well-known 100 worst invasive species across the world (Lowe *et al.*, 2000). For example, the house rat (*Rattus rattus*), native to India, has been introduced unintentionally to all continents. The earliest known pandemics of plague (*Yersinia pestis*) were limited to Eurasia, but global-scale ship movements allowed the Third Pandemic of plague to reach ports worldwide (Frith, 2012). In many other cases, species introductions were intentional, for example as biological control (cane toad, *Rhinella marina*) (Shanmuganathan *et al.*, 2010) or food sources (giant African snail, *Lissachatina fulica*) (Thiengo *et al.*, 2007). Note that species introductions and

range expansion are not necessarily international or inter-continental, but can also be local or regional. For example, the geographic distribution of Eastern redcedar (*Juniperus virginiana*) has expanded to many grassland areas in the USA because of fire suppression and certain land management practices (Walker & Hoback, 2007).

Beside direct effects on species' geographic distributions, human-induced introductions of non-native species and alterations to the environment can also have indirect effects on species' geographic distributions by changing the status of biotic interactions (Young, 2014). A notable example is that successful establishment of invasive species after introduction can be attributed to release from predators or pathogens (i.e. altered biotic context) (Urban, Zarnetske & Skelly, 2013; Prior *et al.*, 2015). Additionally, establishment of invasive species can also lead to distributional changes of species that are native to the invaded site. Indeed, the presence of cane toad, a well-studied invasive species, is associated with a 40% combined decline of local species richness of reptiles, birds, and mammals in Australia (Jolly, Shine & Greenlees, 2015).

(2) Human-induced climate change

Anthropogenic activities are changing the Earth's climate at global scale, with pervasive direct effects on species' geographic distributions. Climate change is characterized by an increase in global mean temperature, which leads to range shifts poleward and to higher elevations for a wide variety of plants, vertebrates, and invertebrates (Hickling *et al.*, 2006; Lenoir *et al.*, 2008; Outhwaite, McCann & Newbold, 2022). Importantly, global warming is accompanied by more frequent extreme weather and climate events (Stott, 2016), such as floods, drought, and heatwaves, which are associated with large-scale die-off events (Welbergen *et al.*, 2008; Jones *et al.*, 2018; Hammond *et al.*, 2022). These extreme events play an important role in determining species' range boundaries (Smale & Wernberg, 2013; Osland, Day & Michot, 2020).

Further, broad-scale changes in plant species distributions due to climate change can modify abiotic conditions, which can subsequently affect geographic distributions of many other species. Indeed, warming effects in Arctic regions can be amplified by changes in albedo from forest cover loss (Swann *et al.*, 2010). In the Tropics, deforestation and fires are continuously decreasing the extent of rainforest in the Amazon Basin, with subsequent effects on regional climates (e.g. drier) (Staal *et al.*, 2020); by some estimates, at 25% deforestation, the eastern, central, and southern Amazon Basin could transition to non-forest ecosystems owing to regional drier climate, triggering major compositional and distributional changes of Amazonian biodiversity (Lovejoy & Nobre, 2018).

(3) Human-induced land cover change

Another global-scale effect of anthropogenic activities is land cover change (Foley *et al.*, 2005). It is estimated that three-

Table 1. Major human factors and examples of their impacts on species' geographic distributions. [D] and [ID] refer to the direct or indirect impact, respectively on biotic (B), abiotic (A) or dispersal ability (M) factors.

Human factors	Impacts on B, A, and M		
	Biotic interactions	Abiotic conditions	Dispersal ability
Human introduction of non-native species	[ID] Changes in community composition, thus changes in biotic interactions among native and non-native species, or among non-native species (Young, 2014; Capinha <i>et al.</i> , 2015)	[ID] Changes in abiotic conditions caused by a highly abundant invasive species (e.g. zebra mussel <i>Dreissena polymorpha</i> and water quality; Fahnenstiel <i>et al.</i> , 1995)	[D] Greatly increased accessible area at continental, regional, or local scale (Lowe <i>et al.</i> , 2000; Walker & Hoback, 2007)
Human-induced climate change	[ID] Changes in species' distributions that modify community composition and species interactions (Williams & Jackson, 2007)	[D] Novel climatic conditions, or novel combinations of conditions (Williams & Jackson, 2007)	[D & ID] Increased and decreased dispersal ability (Travis <i>et al.</i> , 2013)
Human-induced land cover change	[D & ID] Altered community composition and biotic interactions because of species' different responses to modified landscape (Fuller, 2000; Vitule <i>et al.</i> , 2012; Tsiafouli <i>et al.</i> , 2015; Sreekar <i>et al.</i> , 2017)	[D & ID] Changes in environmental conditions, such as land use and land cover (Song <i>et al.</i> , 2018), local climate (Phelan <i>et al.</i> , 2015), water attributes (Timpe & Kaplan, 2017), runoff, flood frequency, and siltation (Boulange <i>et al.</i> , 2021; Ma <i>et al.</i> , 2022), and fire regimes (Messina & Cochrane, 2007)	[D] Impeded (Merritt & Wohl, 2006; Shepard <i>et al.</i> , 2008) or enhanced (Brown <i>et al.</i> , 2006; Leuven <i>et al.</i> , 2009) dispersal
Human-induced pollution	[ID] Modified biotic interactions because of taxonomic differences in resistance to human pollution (Newman <i>et al.</i> , 1992; Bergmann <i>et al.</i> , 2017)	[D] Polluted air, land, and fresh and saltwater systems by toxic chemicals, light, and noise (Tyler Miller & Spoolman, 2015)	[D] Changed migration patterns (Masden <i>et al.</i> , 2009; Skarin <i>et al.</i> , 2015)
Humans as biotic agents (consumptive use)	[D] Changes in community composition and biotic interactions because of humans' selective use or species' different resilience to human consumptive use (Bennett <i>et al.</i> , 2002; Essington <i>et al.</i> , 2015)	[D] Changes in local and regional climatic conditions due to forest cover loss (Perugini <i>et al.</i> , 2017; Keenan & Kimmins, 1993; O'Brien, 1998)	[D] Habitat fragmentation, decreased habitat connectivity, and increased cost of dispersal (Fischer & Lindenmayer, 2007; Bonte <i>et al.</i> , 2012)
Humans as biotic agents (intrusions and disturbance)	[ID] Changes in community structure and thus biotic interactions due to differences in species-specific sensitivity to human disturbance (Blumstein <i>et al.</i> , 2005; Alexandrino <i>et al.</i> , 2016)	[ID] Above- and belowground environmental changes with extinction of keystone species (e.g. bison and wolf) (Knappp <i>et al.</i> , 1999; Frank, 2008) and bushmeat consumption (Brodie <i>et al.</i> , 2009)	[D] Spatial and temporal changes in animal movements (Filla <i>et al.</i> , 2017; Yang <i>et al.</i> , 2019)
Humans as selective and evolutionary drivers	[ID] Evolutionary changes in response to novel biotic interactors (e.g. hosts, competitors, predators) and evolved resistance to novel diseases (Strauss <i>et al.</i> , 2006)	[D] Altered soundscape and lightscape (Dumyahin & Pijanowski, 2011; Koen <i>et al.</i> , 2018)	[D] Increased accessible area of human-cultivated species (Flower <i>et al.</i> , 2021)
		[ID] Rapid evolution of tolerance to novel abiotic conditions (e.g. warm, cold, drought, water salinity, pollution) (Lee <i>et al.</i> , 2011; Turko <i>et al.</i> , 2016; Franks <i>et al.</i> , 2016; Coldsnow <i>et al.</i> , 2017; Ljungfeldt <i>et al.</i> , 2017; Tian <i>et al.</i> , 2022)	[ID] Rapid evolution of lower or higher dispersal (Cheptou <i>et al.</i> , 2008; Allford <i>et al.</i> , 2009; Hudson <i>et al.</i> , 2016; Ochocki & Miller, 2017)

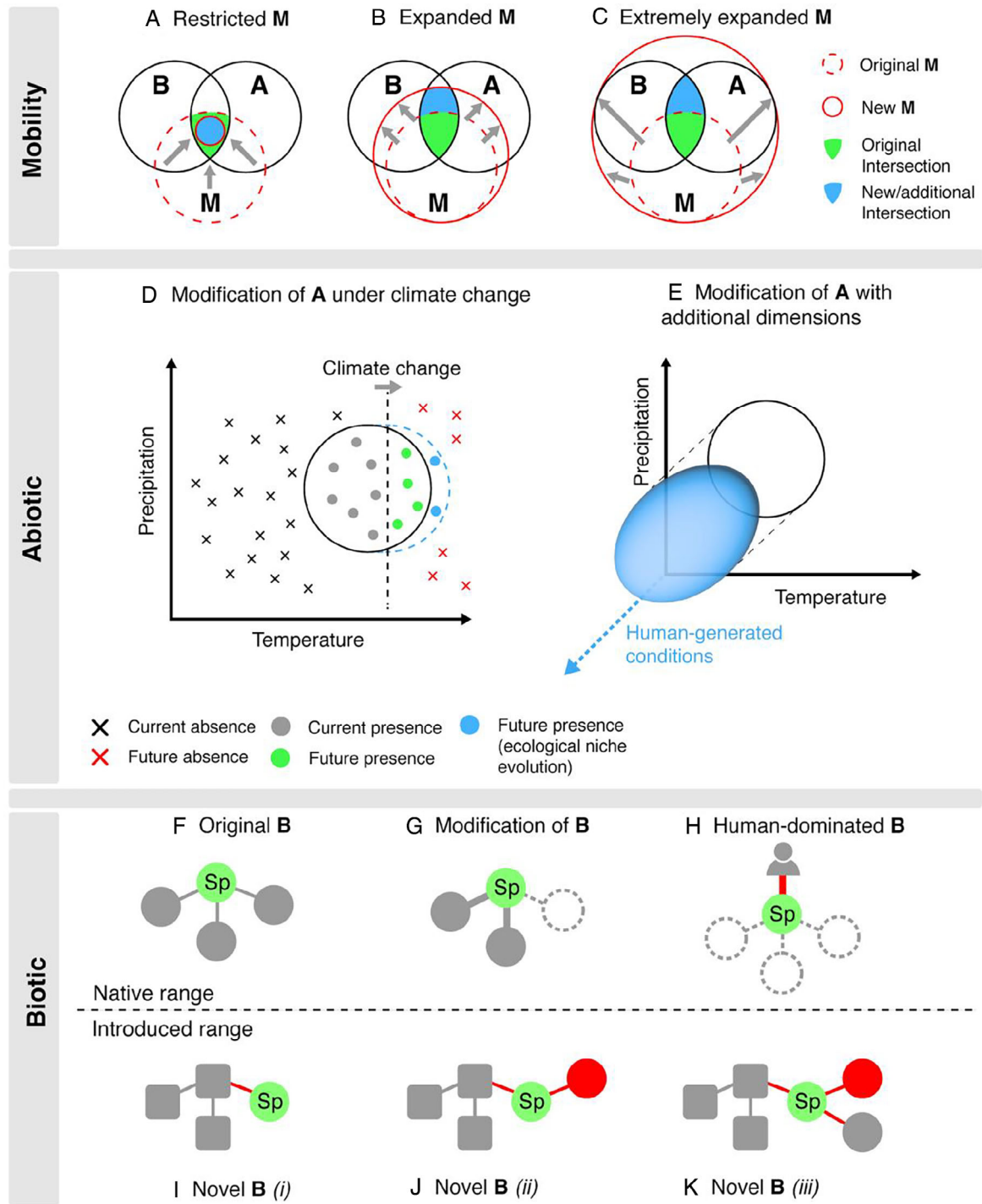


Fig. 1. Conceptual illustration of the effects of human-induced changes on biotic (**B**), abiotic (**A**) and mobility (**M**) factors that determine species' geographic distributions. Compared with natural settings, a species' dispersal ability (red circle) could be greatly reduced because of human-related restrictions (e.g. habitat fragmentation), thus becoming the most limiting factor for geographic distribution (**A**), or be greatly increased *via* human introduction (**B**, **C**), and thus no longer a limiting factor for geographic distribution (**C**). The original intersection of biotic, abiotic, and mobility factors is shown in green and the new or additional intersection is shown in blue. (**D**) The abiotic niche of a species in an environmental space (temperature and precipitation). The species is present in conditions (gray points) inside the abiotic niche (black circle). Human-driven climate change may create novel environmental conditions. Some novel conditions are inside the abiotic niche (green points) and may be occupied by the species, whereas some novel conditions are outside the abiotic niche (red crosses); the latter conditions may become suitable for a species in (Figure 1 legend continues on next page.)

quarters of global land area have been modified by humans in the past millennium, and one-third of global land area has been modified at least once in the past six decades (Luyssaert *et al.*, 2014; Arneith *et al.*, 2019; Winkler *et al.*, 2021). This massive scale of land cover change has caused habitat loss and degradation and biodiversity loss (Pimm & Raven, 2000; Foley *et al.*, 2005). Anthropogenic land use also leads to habitat fragmentation and decreased connectivity of species' populations (Fischer & Lindenmayer, 2007; Tucker *et al.*, 2018). The biotic factors within a species' geographic range, such as food sources and community composition, can also be modified by land cover change (Fuller, 2000; Tsiafouli *et al.*, 2015; Sreekar *et al.*, 2017).

(4) Human-induced pollution

The effects of anthropogenic activities extend beyond climate or land cover changes, to worldwide pollution of the air, land, and fresh and saltwater environments. Such pollutants include toxic chemicals, plastics, artificial light, and noise (Tyler Miller & Spoolman, 2015), among others. Those pollutants have led to spatial and temporal changes in animals' activity and geographic distributions (Overton *et al.*, 2022; La Sorte *et al.*, 2022). For example, one-third of the examined passerine species were found to have reduced abundance around noise-generating compressor stations (Bayne, Habib & Boutin, 2008). Consequently, a large body of literature is focused on selecting indicator species that are sensitive to environmental change (Siddig *et al.*, 2016), especially pollutants, such as lichens for air pollution and amphibians for water pollution.

Impacts of pollution on biodiversity are not only local, but also pronounced at continental scales. For example, it is estimated that one fifth of the land area in the USA is impacted by traffic noise (Forman, 2000), and noise pollution has become an important perturbation of breeding distributions of bird species in North America (Klingbeil *et al.*, 2020). Plastic pollution is known to pose threats to seabirds globally (Wilcox, Van Sebille & Hardesty, 2015). While pollution can restrict geographic distributions of many species (Finn, Grattarola & Pincheira-Donoso, 2023), different species will likely exhibit varying degrees of resilience to human pollution, thus leading to shifts in community composition and

changes in biotic interactions (Newman, Schreiber & Novakova, 1992; Bergmann *et al.*, 2017).

(5) Humans as biotic agents

Humans can also play a major and multifaceted role as a biotic agent in interspecific interactions that affect species' geographic distributions across space and time. Humans are consumers of many species, with effects that range from decreased abundance to local extirpation or global extinction (Faillettaz *et al.*, 2019; Ripple *et al.*, 2019). Humans also compete with other species for habitat and a variety of resources; for example, competition with carnivores for prey has affected carnivore range dynamics (Mech, 1995; Treves & Karanth, 2003). Humans can also play a positive role for some species. For example, conservation management actions can be critical for persistence of endangered species (Xu *et al.*, 2017); humans also act as efficient seed dispersers for crop species and many species considered as invasive (Ditmer *et al.*, 2021).

Besides having direct biotic effects, humans can also interact indirectly with other species through encroachment and disturbance (Salafsky *et al.*, 2008), affecting the spatial and temporal dynamics of species' geographic distributions. For example, disturbances can be caused by recreational activities on public lands, with many species avoiding such disturbance by shifting their spatial and temporal presence (Filla *et al.*, 2017; Yang *et al.*, 2019). This effect can cascade in food webs and modify the spatial and temporal presence of additional species (Muhly *et al.*, 2011; Ripple & Beschta, 2006); similar effects also have been noted in response to artificial nighttime lights in anthropogenic landscapes (Ditmer *et al.*, 2021).

(6) Humans as selective and evolutionary drivers

Anthropogenic effects on **B**, **A**, and **M** can be both extrinsic and intrinsic to a species. Extrinsically, human-induced changes can alter community composition, abiotic conditions, and the physical template for species' dispersal (Fig. 2). Intrinsically, humans can pose direct and indirect selection pressures on species, such as tolerance of novel abiotic conditions, capacity for interacting with novel species,

(Figure legend continued from previous page.)

the case of ecological niche evolution, such as the species becoming more heat tolerant (blue points). (E) In addition to the classic abiotic conditions, other human-generated factors are known to affect species' geographic distributions, which can increase the dimensionality when delineating the ecological niche (blue axis in E). (F–K) The biotic interactions (**B**) that determine a species' geographic distribution can also undergo various changes. Different species are represented by circles, their interactions are represented by solid lines (gray for natural connections and red for novel connections), and lost interactions are represented by dotted lines. (F) A biotic network of four species in a focal species' native range (species that interacted with the focal species in the native range are represented by gray circles). Because of human effects, the network could face changes in the strength (increased/decreased), quantity (more/fewer), and structure (simpler/more complex) of biotic interactions in the native range (G). In extreme cases, humans become the dominant factor in the network of biotic interactions (H). A focal species introduced outside the native range will face novel biotic interactions with the native species in the introduced range (gray squares) (I); it is possible for the focal species to interact with other introduced species (red circle) (J) or interact with species introduced from the focal species' native range (gray circle) (K) but in the context of the introduced range.

Table 2. Challenges for ecological niche modeling/species distribution modeling (ENM/SDM) in the context of human impacts and strategies to mitigate or address these challenges. BAM encompasses biotic interactions, abiotic conditions, and dispersal ability.

BAM factor	Challenges for ENM/SDM in the context of human impacts	Strategies to mitigate or address the challenges
A	Model extrapolation, although commonly associated with high uncertainty, is usually unavoidable and frequently can be involved in forecasting range dynamics because environments are changing rapidly with human activities.	<ul style="list-style-type: none"> (i) Quantify environmental novelty as a proxy to infer the uncertainty of predictions [see methodology in Elith <i>et al.</i> (2010) and Owens <i>et al.</i> (2013)]. (ii) Select model settings to enhance model spatial/temporal transferability through model tuning [see methodology in Muscarella <i>et al.</i> (2014) and Valavi <i>et al.</i> (2019)]. (iii) Incorporate biologically meaningful information in model fitting to enhance model extrapolation [see case studies in Calleja <i>et al.</i> (2020), Gamliel <i>et al.</i> (2020), and Feng <i>et al.</i> (2020)].
A	In addition to the commonly considered abiotic conditions (e.g. climate), the fundamental niche can be measured with environmental conditions that are driven by human activities, such as land use, chemical pollution or anthropogenic light and sound conditions that can limit (or facilitate) species' geographic distribution to varying degrees.	Incorporate appropriate human-related variables in model training and forecasting, with the consideration of focal species, spatial-temporal scale, and complexity of the response types [see use of human footprint for invasive species in Gallardo <i>et al.</i> (2015) and use of artificial night light and anthropogenic noise for birds in Wilson <i>et al.</i> (2021)].
A	Species' geographic distributions are experiencing a more rapid rate of change under accelerating human-induced environmental changes, thus we need a more dynamic view in modeling species' geographic distributions.	<ul style="list-style-type: none"> (i) Incorporate environmental data at fine spatio-temporal scales to capture the rapidly changing environments. See applications for bats (Hayes <i>et al.</i>, 2015) and birds (Runge <i>et al.</i>, 2015). (ii) Enhance the spatial and temporal match between species' occurrence data and environmental data. See example in Bateman <i>et al.</i> (2012).
M	Human-mediated dispersal and human-modified landscapes can greatly alter species' mobility, and thus their geographic distributions; therefore the view of natural dispersal capacity and natural barriers should be reconsidered in the context of human impacts.	Consider species' mobility in the context of human impacts when designing a model-training domain and conducting model projections.
B	The assumption of relatively static biotic interactions is more likely to be violated under scenarios of climate change, species range shifts, or human introductions.	Integrate human-induced dynamics of biotic interactions in modeling species' geographic distributions, such as using the presence, abundance, or suitability of relevant species as predictors (Kass <i>et al.</i> , 2020), modeling the co-occurrences of multiple species (Pollock <i>et al.</i> , 2014), and using traits to infer potential biotic interactions (Caron <i>et al.</i> , 2022).

and dispersal ability for maintaining existing or colonizing new sites (Otto, 2018) (Fig. 2). Rapid evolution directly or indirectly associated with human-induced changes has been documented in an increasing number of cases (Feder, 2010; Hoffmann & Sgrò, 2011; Diamond, 2017; Schilthuizen, 2019; Catullo *et al.*, 2019). Evidence is accumulating regarding the implications of climate change for rapid evolution of heat tolerance [e.g. water fleas (Geerts *et al.*, 2015); fishes (Ljungfeldt *et al.*, 2017); ants (Diamond *et al.*, 2017)] and cold tolerance [e.g. fishes (Barrett *et al.*, 2011); beetles (Tian *et al.*, 2022)].

Besides temperature, rapid evolution has also been documented in species' tolerances to drought, salinity, and pollution (Franks *et al.*, 2016; Turko *et al.*, 2016; Coldsnow *et al.*, 2017; Lee *et al.*, 2011). Landscape fragmentation caused by human activities not only affects distances that species are

able to disperse, but can also select for lower dispersal capacity (Cheptou *et al.*, 2008). On the other hand, selection for higher dispersal capacity is more frequent during biological invasions (Alford *et al.*, 2009; Hudson *et al.*, 2016; Ochocki & Miller, 2017). In communities modified by human activities, cases of evolutionary change have been documented in response to novel hosts (e.g. phytophagous insects shift onto exotic host plants), competitors (e.g. character displacement between native and introduced fish species), predators (e.g. morphological responses of native prey to introduced predators), as well as evolved resistance in response to novel diseases (reviewed in Strauss, Lau & Carroll, 2006).

Note that the various responses to anthropogenic changes rest on the underlying genetics of a species. Besides direct human impacts on a species' genetic makeup (e.g. domestication;

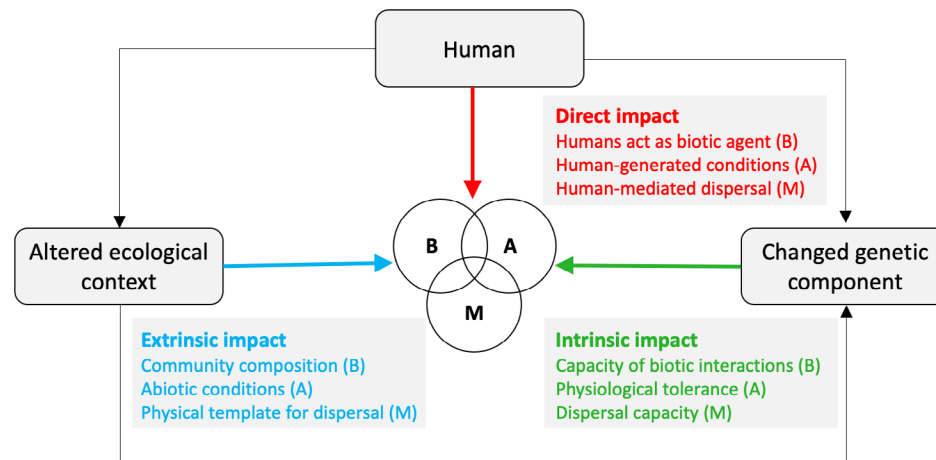


Fig. 2. Conceptual illustration of human impacts on biotic (**B**), abiotic (**A**) and mobility (**M**) factors. Humans can directly affect all parts of the BAM framework and species' geographic distributions *via* acting as a biotic agent, by human-generated environmental conditions, and by human-mediated dispersal. Human impacts can also lead to extrinsic and intrinsic changes to BAM. Extrinsicly, human-induced changes can alter community composition, abiotic conditions, and the physical template for species' dispersal. Intrinsically, humans can also impose direct and indirect selection pressures on species, such as tolerance of novel abiotic conditions, capacity for interacting with novel species, and necessary dispersal ability for maintaining existing or colonizing new sites.

Young, 2016), 'hidden' pathways affecting genetics of a species, either intentional, incidental, or accidental, can have implications for changes in BAM and geographic distribution of a species. For example, human-mediated introductions represent a pathway that can modify gene flow among populations, thus affecting adaptation of populations in the introduced range (Storfer, 1999; Barbour, Potts & Vaillancourt, 2003). Introduction of transgenic DNA through escaped genetically modified salmon (Smith *et al.*, 2010) and pollen from transgenic crops (Warwick *et al.*, 2003) can have consequences for the species' wild populations or their relatives. Reductions in population size leading to bottlenecks and enhanced drift (Willi, Griffin & Van Buskirk, 2013) can alter trajectories of population responses to human impacts (Kayanne *et al.*, 2022). Lastly, pronounced cases of natural resources exploitation can lead to selection (e.g. reduced body size, earlier sexual maturity, reduced antler size, increased timidity) that would likely affect each BAM component (Andersen, Marty & Arlinghaus, 2018; Allendorf & Hard, 2009).

(7) The socioeconomic context

Importantly, the impact of the six major anthropogenic drivers on species' geographic distributions can vary with socioeconomic conditions, including cultural, demographic, economic, political, and institutional (Kelly *et al.*, 2020; Uchida *et al.*, 2021). For example, introduction of non-native species is closely associated with economic activities, especially international trade (Chapman *et al.*, 2017; Hulme, 2021), and the issue of invasive species can be mediated by human culture and policies (Robbins, 2004; Reino *et al.*, 2017). The spatial distribution of environmental impacts, such as air pollution, greenhouse gas emissions,

and deforestation, depends strongly on human density, economic status, and environmental policies (Bradshaw, Giam & Sodhi, 2010; Feng *et al.*, 2021).

III. IMPLICATIONS AND CHALLENGES OF HUMAN IMPACTS FOR ENM/SDM

(1) Human activities can directly and indirectly affect B, A, and M

In this section, we conceptualize human impacts on species' geographic distribution in the context of the BAM framework (Fig. 1). First, **M** could expand or contract with human activities (Fig. 1A–C), leading to new configurations of **B**, **A**, and **M** factors. In extreme cases, when **M** is very limited, the species' geographic distribution will be equivalent to **M**, whereas **B** and **A** will not be limiting factors (Fig. 1A); when **M** is extremely broad, the species could occur at any site with suitable **A** and **B** factors (Fig. 1C). Compared with the classic setup of the BAM diagram where **B**, **A**, and **M** all intersect each other, the extremely limited or expanded **M** constitutes simpler scenarios that may reduce the complexity of model considerations and thus potentially enhance model performance.

Owing to climate change and various other anthropogenic global changes, novel combinations of environmental conditions are emerging across geographic space. Some of these novel conditions are within the species' abiotic niche, and can potentially be occupied by the species; other novel conditions may be beyond a species' tolerance (Fig. 1D). Besides the non-analogue conditions relative to present (e.g. extreme temperature and precipitation), conditions generated by human activities such as chemical pollution [e.g. pesticides

(Simonich & Hites, 1995); plastics (Du *et al.*, 2022)] and built environments [e.g. dams (Zhang & Gu, 2023); roads (Grilo *et al.*, 2021)] are also emerging as important factors in determining species' distributions (Fig. 1E). Such conditions (e.g. pollution, artificial light, noise) may have not existed before, or played only weak roles compared with natural conditions (e.g. climate). These novel conditions could be treated as additional dimensions in Hutchinson's hyper-volume niche space (Hutchinson, 1957).

Similarly, those new considerations of **A** can lead to new configurations of **B**, **A**, and **M** factors. The emergence of suitable novel conditions (and novel combinations of conditions) can lead to an expanded **A**. Loss of previously existing suitable conditions (or combinations of conditions) can restrict **A**. Changes in physiological tolerances of species to abiotic conditions expand or restrict **A**. Many human-generated factors (e.g. pollution, noise) can reduce the geographic distributions of many species, thus one may expect many species to show a restricted **A** (Finn *et al.*, 2023). Some species are 'winners', with stable or expanded **A**, especially those with traits that facilitate coping with, or rapid evolutionary adaptation to, human-generated factors (Sih, Ferrari & Harris, 2011). For example, plant species with tolerance to anthropogenic pollution are associated with colonization of metal-polluted habitats (Meyer *et al.*, 2016), and bird species that vocalize at higher frequencies are known to inhabit noisy urban areas (Hu & Cardoso, 2009).

The natural settings of biotic interactions also face various changes as a result of human activities. For example, if natural biotic interactions are visualized as a network (Fig. 1F) where nodes represent species and width of connectors between nodes (i.e. edges) represents strength of interactions, the numbers of edges could decrease owing to species extinction; the strength of interactions could change as well (Fig. 1G). Humans can also become a major or the only interacting node for a focal species due to the extinction of other species (Fig. 1H; here termed the human-dominant network hypothesis). In the scenario of an introduced species, the novel species could be exposed to the biotic network of the introduced range (Fig. 1I). In cases of multiple introductions, species from the same or different origins may form entirely novel biotic networks in the introduced range (Fig. 1J, K).

The various types of biotic interactions can be grouped based on their effects on the focal species. For example, competition has negative effects on the interacting species, mutualism has positive effects, and commensalism effects are positive for one and neutral for the other species. In theory, biotic interactions could be integrated in a unified modeling framework, which will inform the changes (expanded or restricted) to **B** under human impacts (Fig. 1F–K), although many challenges exist as regards observing, measuring, and modeling these interactions in practice (Catchen *et al.*, 2023; Strydom *et al.*, 2021).

Note that human-induced changes in **B**, **A**, and **M** may have interactive effects. Human introductions of species could directly increase the area accessible to species (**M**), and thus could lead to expanded accessibility to novel

abiotic and biotic conditions. Changes in community composition (**B**) may occur because species can respond differently to environmental changes (**A**); changes to spatial configuration of environmental conditions on a landscape can affect the dispersal (**M**) cost of species as well. Changes to **B** caused by humans could lead to changes to **M** (e.g. decreased **M** due to loss of pollinators or seed dispersers of plant species). Changes in **B** over a large spatial extent can trigger changes in **A** (e.g. deforestation-induced regional climate change in the Amazon Basin).

(2) The effects of human drivers can vary over spatial and temporal scales

The temporal and spatial context of a research question requires careful consideration of possible anthropogenic effects on predictor variables and species' records, and the implications of these effects on ENM/SDM. Humans have used and altered natural landscapes for millennia, and the intensity of human impacts has increased particularly since 1950, which is known as the start of the 'great acceleration' (Steffen *et al.*, 2015, 2007). For example, in Europe, the expansion of human populations during the Neolithic has been linked to gradual continental forest fragmentation and deforestation (Roberts *et al.*, 2018). While deforestation rates vary temporally and spatially, in the last few decades the intensification of land use has increased the area of young forest stands globally from 11.3% in 1900 to 33.6% of forest area in 2015 (McDowell *et al.*, 2020). Substantial, accelerated forest cover loss was reported in the last decade in the Brazilian Amazon Basin (Trancoso, 2021).

Human impacts on the geographic ranges of species likely began tens of thousands of years ago. A global analysis of mammal distributions found that global, regional, and local extinctions by humans over the last 130,000 years have substantially altered mammal diversity patterns (Faurby & Svenning, 2015). In more recent times, beginning in the 18th century, some North American ungulates and carnivores experienced over 50% contraction of historical ranges; others shifted their ranges, and a few species, such as raccoon (*Procyon lotor*) and coyote (*Canis latrans*), experienced range expansions (Laliberte & Ripple, 2004). In the last 50 years, extinction risk has increased for about 23% of carnivores and ungulates worldwide (Di Marco *et al.*, 2014). More generally, human pressures (e.g. human population growth and density) are strong predictors of geographic ranges of 92% of terrestrial mammals (Di Marco & Santini, 2015).

The effects of anthropogenic activities also vary with spatial scale (grain and extent) and may extend across scales (i.e. teleconnections; Heffernan *et al.*, 2014). Locally, removal of forest cover creates hotter and drier microclimatic conditions (Keenan & Kimmins, 1993); at regional scales, the thermal environment is further modified by the interaction between climate change and forest cover loss (Nowakowski *et al.*, 2017). Additionally, local microclimate conditions can be influenced by human land use in the landscape matrix; for example, proximity to urban centres can increase winter

temperature of forest fragments (Latimer & Zuckerberg, 2017). Urbanization can also impact energetic expenditures of species as they alter their activity patterns (e.g. increased nocturnal activity, larger foraging areas), resulting in higher energetic costs (Wang, Smith & Wilmers, 2017). More generally, species' responses to urbanization are dependent on traits such as mobility and habitat preference: plants with high dispersal ability and narrow habitat preferences respond positively to urbanization, while birds and butterflies with similar traits (high mobility, specialists) respond negatively to urbanization (Concepción *et al.*, 2015).

When urbanization has positive effects on some species, such as red fox (*Vulpes vulpes*), coyote, Eurasian badger (*Meles meles*), and raccoon (Bateman & Fleming, 2012), it can contribute to landscape-scale diversity of mammal communities (Parsons *et al.*, 2018). At a global extent, humans are changing diversity patterns and community composition (Young, 2014) by transporting species, thus rendering environmental gradients (climatic, topographic) ineffective as dispersal barriers, besides altering species' dispersal limitations. For example, plant communities in mountain regions in Europe, North America, and South America share a few dozen species as a result of long-distance dispersal of Eurasian plant species by humans (Seipel *et al.*, 2012).

The spatial and temporal variability of human impacts adds more complexity to estimating species' potential distributions. Recent contractions in species' ranges due to intensification of human activities may introduce incorrect model assumptions regarding species' climatic suitability (Martínez-Freiría *et al.*, 2016). In a study evaluating climate change implications on mammal distributions, models calibrated with contemporary (1965–present) occurrence records of North American mammals forecasted narrower future potential distributions compared to models trained on historical records dating back to the 1900s (Faurby & Araújo, 2018).

(3) Rethinking fundamental and realized niche concepts in the context of human impacts

Ecological niche theory distinguishes two states of the niche: fundamental and realized. Some reconsideration of the two terms is needed in the context of human impacts. The fundamental niche is defined in a hyper-volume within which environmental conditions permit a species to persist indefinitely (Hutchinson, 1957). In this context, the environment is interpreted as abiotic conditions (or scenopoetic or non-interactive variables; Hutchinson, 1978) that are not modified by a species (in contrast to biotic or interactive conditions; Peterson *et al.*, 2011). In addition to the abiotic conditions commonly analysed, such as climate and elevation, the fundamental niche can be measured or quantified with environmental conditions that are driven or generated by human activities (Fig. 1E), such as land use, chemical pollution, or anthropogenic light and sound conditions. Species have different tolerances with respect to these conditions, and therefore these conditions exert different degrees of limitation on the species' geographic distribution. Similar

to classic, abiotic (scenopoetic) conditions, human-related abiotic conditions are generally not modified by species. Therefore, given the prevalence and magnitude of human impacts across the globe, human-related abiotic conditions should be included as additional dimensions (axes) of the environment when measuring the hyper-volume of the fundamental niche (Fig. 1E).

The realized niche (i.e. the modification of the fundamental ecological niche by considerations of biotic interactions and movement) can also be dramatically impacted by human-induced changes in biotic interactions and dispersal abilities. Species' realized niches can expand with increased dispersal ability, or when relieved from natural enemies, or when the overall effect of biotic interactions favors a focal species' population growth; likewise, the realized niche can contract in opposite situations. In an extreme scenario of realized niche expansion, realized niches could be potentially larger than the fundamental niche because of two human-induced mechanisms. First, humans can create favorable abiotic conditions within an area naturally unsuitable for a species' long-term persistence. Examples could be individuals living in zoos, botanical gardens, or nurseries that are outside a species' range (Sax, Early & Bellemare, 2013). Besides these controlled or constrained examples, there are also cases from more 'natural' settings. Multiple European bat species were observed wintering in urban environments north of their historical wintering range, likely because of the structural and thermal habitat provided by cities (Sachanowicz *et al.*, 2019; Vlaschenko *et al.*, 2023), and introduced bivalves overcame cold temperature limitations by inhabiting thermal plumes associated with a power plant (Simard *et al.*, 2012; Laine, 2006). From the perspective of geographical range, these species could be considered as being present in locations with unsuitable conditions (i.e. outside the fundamental niche) when measured at a coarse spatial resolution (e.g. mean temperature across 100 km²); although one may argue that conditions of the microhabitat at fine spatial scale can still exist within a species' fundamental niche.

The other human-induced mechanism through which a species' realized niche could be larger than its fundamental niche is resource subsidy for species to overcome limiting abiotic conditions and thus persist in naturally unsuitable conditions. These human subsidies can drastically increase the abundance of some species (e.g. 7–8 times for coyote, cat, and red fox; reviewed in Newsome *et al.*, 2015). Abundance changes can occur within or outside a species' geographic range. For example, human subsidies have enabled establishment of red fox populations north of the climate-imposed distribution limit (Elmhagen *et al.*, 2017); this may likely be a case where the realized niche is larger than the fundamental niche, although the latter is more commonly inferred than measured. The human interference with a species' realized niche is analogous to cases in which facilitation between species in natural settings expands the realized niche of a species beyond the fundamental niche (Soberón & Arroyo-Peña, 2017; Bruno, Stachowicz & Bertness, 2003). Such cases may constitute exceptions to the

common assertion that the realized niche is a subset of the fundamental niche (Hutchinson, 1957), although, to our knowledge, this possibility has not been systematically evaluated in the literature (Soberón & Arroyo-Peña, 2017).

(4) Assessing the assumptions of ENM/SDM in the context of human impacts

ENM/SDM builds upon several assumptions (Zurell *et al.*, 2020) that need to be considered before applying this modeling approach to various research questions. As humans are changing environments and species' geographic distributions, it is worth assessing whether the assumptions will hold in this anthropogenic context, and whether cases of violation of assumptions are frequent.

Equilibrium status assumes that a species is present at all suitable locations and absent at all unsuitable locations (Araújo & Pearson, 2005). However, the equilibrium status of species' geographic distribution is rarely evaluated (Foster, Kharouba & Smith, 2022); given the dynamics of abiotic conditions, dispersal limitations, and biotic interactions, the geographic distributions of many species likely deviate from equilibrium to some degree (i.e. non-equilibrium) (Peterson *et al.*, 2011). From a more practical perspective, a dispersal-based approach has been proposed and broadly used in the ENM/SDM literature: instead of considering all locations (e.g. the whole world or a continent), a study area (or modeling domain) is defined based on species' dispersal ability in a spatial and temporal context, so that species' distribution data (presences and absences) can better fit the equilibrium assumption in this study area. For example, dispersal distance (Feng & Papeş, 2015) or natural barriers (Cooper & Soberón, 2018) have been used to define a study area, as opposed to political boundaries or worldwide maps. However, species' natural dispersal ability can be greatly increased with human introductions. In extreme cases in which a species can potentially reach (or 'explore') anywhere through human transportation, approaches based on natural dispersal will violate the assumption of equilibrium. Human activities can also restrict or impede species' dispersal *via* built environments and infrastructure (e.g. transportation systems). Therefore, refined dispersal ability and artificial dispersal barriers (e.g. Taylor, Papeş & Long, 2018) have to be considered in ENM/SDM to fit better the assumption of equilibrium (see Section IV.4 for solutions). Note that equilibrium status discussed above is commonly considered in geographic space and is different from environmental equilibrium, which refers to occupying all suitable abiotic conditions in the environmental space (Foster *et al.*, 2022). A species could reach environmental equilibrium without reaching geographic equilibrium (see example in Foster *et al.*, 2022), because one point in environmental space can be represented by multiple locations in geographic space (Soberón & Nakamura, 2009); as such, environmental equilibrium could be more applicable for making inferences of the ecological niche, which is considered a goal of ENM compared to SDM (Peterson & Soberón, 2012).

In applications of correlative ENM/SDM, biotic interactions are usually not quantified directly, and are generally assumed to be uniform or at least weak across the geographic distribution (or the modeling domain) of a species. This idea likely lies on the macroecological assumption that biotic interactions are more important determinants of species' distributions at fine spatial scales than at coarse spatial scales [termed the Eltonian Noise Hypothesis (Pearson & Dawson, 2003; Peterson *et al.*, 2011)], besides the difficulty of quantifying biotic interactions adequately. Overlooking biotic interactions is unsatisfactory, and has led to ambiguity in the interpretation of the modeling goal: neither fundamental niche nor realized niche, but something in between (Soberón & Nakamura, 2009). Nevertheless, the assumption of constant biotic interactions may still largely hold if the model is only applied to the study area or the modeling domain where the species distribution data were collected. This assumption is more likely to be violated when the model is transferred across space and/or time, because the network of biotic interactions can face dramatic, or even unpredictable, changes compared with the natural setting of the native area (Fig. 1). Biotic interactions can no longer be assumed to be constant because novel communities can be formed under scenarios of climate change, species range shifts, or human introductions, thus the identities of the species that would interact with a focal species, as well as the strength of these interactions, are expected to deviate from the natural settings.

Commonly, the calibrated model is projected to another landscape and/or time where the environmental conditions could be outside the range of the calibration data and thus lead to model extrapolations. Model extrapolations are not supported by data, but rather rely on model assumptions (Gelman & Hill, 2006) and thus are potentially highly inaccurate. It is worrisome that model extrapolation can be common when forecasting species' distributions because of rapidly changing environments (Williams & Jackson, 2007). Therefore, assumptions used in model extrapolation should be re-evaluated.

One major assumption is that the relationships obtained from training occurrences and abiotic predictors will still hold when the model is projected to novel abiotic values (Jiménez-Valverde *et al.*, 2009). Therefore, the reliability of model predictions depends on two circumstances: (i) the training data are representative of the fundamental niche; and (ii) the fundamental niche does not change (i.e. is conserved) over relevant timescales (Peterson, Soberón & Sanchez-Cordero, 1999). The first circumstance can easily be violated as a species rarely occupies its potential distribution fully owing to biotic and dispersal limitations (with the exception of humans or species introduced by humans globally), so the occupied environmental conditions rarely fully represent its fundamental niche; another insuperable reality is that not all combinations of environmental conditions are represented in the geographic space at a given time (Soberón & Peterson, 2005), so a species can never occupy non-existent environmental conditions. Even when the first circumstance is met, the assumption of a 'static' relationship can be violated if changes occur to the fundamental niche. The assumption of niche conservatism is supported by a large volume of evidence (Peterson, 2011), although

exceptions of rapid evolution are also accumulating (Salamin *et al.*, 2010). Rapid evolution of the fundamental niche could occur frequently in the future, given the emergence of novel environmental conditions and faster pace of human-induced environmental changes. Therefore, enhanced model extrapolation is needed for more reliable model predictions (see solutions in Section IV.1).

(5) The need for a more dynamic view of species' geographic distributions

Under natural rates of environmental change, barring major stochastic events, a species' geographic distribution could be viewed as (or assumed to be) relatively stable over timescales of decades. This stability is commonly summarized as current or extant range maps (e.g. extant geographic range of *Dasybus novemcinctus* compiled by IUCN; Loughry, McDonough & Abba, 2014). This stable nature of geographic distributions allows some flexibility of temporal mismatch between occurrences and environmental data, or congruence at a coarse temporal extent. For example, many applications of ENM/SDM conduct model training with occurrences across a range of years and the mean environmental conditions across the same temporal extent. In other words, the model is built on the idea of a 'static' geographic distribution under current conditions, and is used to predict a relatively static geographic distribution under future environmental conditions (i.e. from static to static), or relatively more dynamic distributions when dispersal or other factors are considered (i.e. from static to dynamic). This approach can be advantageous for correlative modeling, without worrying too much about inaccuracies caused by temporal mismatch between occurrences and the environment. However, this advantage is lost or weakened when a species' geographic range is experiencing rapid changes on shorter timescales and/or the environment is changing rapidly, which can affect the inference of the association between species' distribution and suitable environmental conditions. For example, a species with low dispersal capacity could fail to track the shift in locations with suitable environments, in which case the modeling approach that uses multi-decadal cumulative or mean data will more likely be affected by the temporal mismatch between species' occurrence and suitable environments. Therefore, in the Anthropocene, a species' geographic distribution needs to be viewed in a more dynamic manner, and new modeling approaches (e.g. from dynamic to dynamic) will be needed to account for changes in species' ranges and the environment on fine temporal scales.

IV. WAYS TO IMPROVE ENM/SDM IN PRACTICE IN THE CONTEXT OF HUMAN IMPACTS

We outline five major challenges for ENM/SDM in the context of human impacts and propose strategies to mitigate or address the challenges (Table 2).

(1) Enhance model extrapolation under novel environmental conditions

Model extrapolation represents a significant challenge in correlative modeling (Yates *et al.*, 2018). Statistical textbooks generally recommend avoiding model extrapolation owing to potential inaccuracies in model predictions. However, model extrapolation is likely unavoidable for many biological and ecological studies and, with the various risks acknowledged, can provide meaningful predictions in guiding natural resource management and biodiversity conservation under global change (ecological forecasting syndrome; Chen, Liang & Feng, 2023), which is among the most frequent uses of ENM/SDM.

Current modeling algorithms have different 'behaviors' towards model extrapolation. 'Fishbowl models' (e.g. minimum-volume ellipsoid; Van Aelst & Rousseeuw, 2009) tend to assume a regular 'shape' or boundary of the niche (Loyola, 2012), beyond which the environmental conditions are unsuitable for a species. These algorithms simply predict zero probability of presence beyond the conditions of training presences. Several regression algorithms are able to extrapolate by extending the response curve following the slope obtained from training data, ultimately extending a fitted model towards infinity along the axes of predictors (Qiao *et al.*, 2019). However, this type of extrapolation relies on assumptions about the underlying relationship (e.g. unimodal curve; Anderson, 2013), and predictions may be acceptable when environmental conditions are similar to that of the training data; however, errors associated with extrapolation increase as one moves further beyond the training data (Fitzpatrick *et al.*, 2018).

Several machine learning algorithms extrapolate beyond the training data by 'clamping', which uses the boundary prediction to substitute the predictions beyond the training data (Qiao *et al.*, 2019). This type of behavior could be considered as an intermediate option compared with the previous two (Anderson, 2013), and in certain cases may yield less-extreme predictions (as opposed to, for example, zero probabilities predicted by fishbowl models or high probabilities predicted by a regression model with a monotonically increasing extrapolation curve). However, clamping can also be sensitive to the boundary conditions (Anderson, 2013). For example, in extreme cases in which the boundary condition is predicted to be highly suitable or highly unsuitable, one can derive overestimation or underestimation, respectively, of a species' potential distribution under novel environmental conditions.

New approaches have been proposed in the literature to improve model extrapolation. The main philosophy is to incorporate biologically meaningful information in model fitting, thus overcoming the limitation of the correlative approaches. Such biologically meaningful information (e.g. biological responses to climate) is expected to extrapolate better in novel environmental conditions compared with a correlation-inferred relationship. First, this external information could be about the shape of the fundamental niche,

which can be assumed to be regular (e.g. an ellipsoid) as opposed to irregular shapes (e.g. patterns learned from data by machine learning algorithms). The shape of the fundamental niche, although seemingly a simple piece of information, can serve as a strong framework in guiding model extrapolation (Jiménez *et al.*, 2019). Second, this shape assumption can be fine-tuned to define the structure of a response curve that determines quantitatively the probability of presence as a response to environmental conditions. For example, the response curve can be conceived as a plateau model with three connected segments: uphill, horizontal, and downhill (Brewer *et al.*, 2016), which fits well with the idea of an optimal range of conditions for a species and reduced suitability away from the optimal ones.

Further, external information, such as experiments or expert opinions, can be used to adjust the parameter estimations of the conceptual models to improve their biological connotation. For example, physiological limits may be used to inform model extrapolation regarding conditions beyond which the probability of presence is at a minimum (Brewer *et al.*, 2016). Similarly, laboratory experiments characterizing species' responses to limiting factors can be used to guide the slope of the response curve under extrapolative conditions (Feng *et al.*, 2020). Importantly, successful implementation of these approaches relies on the availability of biologically meaningful information and well-defined links or assumptions between this information and species' geographic distributions. For example, temperature measured in the laboratory could be used to define the shape of an ecological niche or describe a response curve quantitatively. To use such information in a real landscape, a corresponding abiotic variable from a real landscape is needed to represent the laboratory temperature. The establishment of such a link is difficult, because laboratory experiments are usually conducted under controlled (e.g. constant) conditions over limited time periods (e.g. days) whereas environmental conditions used in ENM/SDM can vary in complex patterns and commonly represent the integration of responses to conditions over longer time periods (e.g. months to years) (Feng *et al.*, 2020; Feng & Papeş, 2017). In a broader sense, biological information could be extended to include knowledge about related species. Building upon the theory of phylogenetic niche conservatism (e.g. closely related species with similar ecological niches; Peterson *et al.*, 2011), studies have shown improved model performance across space (Castaño-Quintero *et al.*, 2020) and time (Guillory & Brown, 2021), by including information about related species (Smith *et al.*, 2019).

In addition, when no external information is available to facilitate model forecasting, model extrapolation could be enhanced through specialized model tuning (Muscarella *et al.*, 2014). Typically, model tuning is used to select optimal settings based on model evaluation indices. The evaluation indices can be calculated with independent testing data, but more commonly a subset of species' occurrence data withheld from model training is used to calculate indices (Peterson *et al.*, 2011). A common practice for the latter

approach is to separate the training occurrences into multiple subsets randomly and to use one subset in rotation for model testing, in replicate runs (cross-validation). In contrast to random subsetting, new methods are proposed to separate the occurrences spatially or temporally, to evaluate models under a transfer scenario where testing data and training data have partial or no overlap in environmental space (Roberts *et al.*, 2017). Therefore, this transfer can involve both model interpolation and extrapolation. The difference in data separation methods can lead to different interpretations of model performance. If a model performs well with spatial/temporal subsetting, it can be assumed to have better transferability, giving the researcher higher confidence in the model's performance in a real transfer scenario. In theory, data can also be separated in environmental space, which would enhance the confidence of model extrapolation (Valavi *et al.*, 2019), although the ways in which partitioning is done in environmental space will have complicated consequences (Roberts *et al.*, 2017).

As a minimum, if extrapolation is unavoidable, environmental novelty needs to be quantified as a proxy to infer the uncertainty of predictions. Previous studies have suggested that model accuracy decays with environmental novelty (Fitzpatrick *et al.*, 2018; Qiao *et al.*, 2019). Essentially, the environmental novelty can be viewed as dissimilarity between environmental conditions of training data and the conditions on which the model is to be projected. Such dissimilarity can be calculated as distances to the reference data set (Elith, Kearney & Phillips, 2010) or in refined ecological settings (the relative novelty of a set of conditions in the context of the reference data cloud; Owens *et al.*, 2013).

(2) Incorporate anthropogenic-related predictors in the modeling process

It is increasingly important to account for human-related factors that are crucial in determining species' geographic distributions. For example, Gallardo, Zieritz & Aldridge (2015) trained models with five anthropogenic variables as proxies of the human footprint, and found that such variables explained a substantial amount (23% on average) of invasive species' distributions. Other anthropogenic variables that are less commonly used in models (e.g. artificial light, sound, pollution) may have affected species distributions at large spatial extents (Escobar, Awan & Qiao, 2015). For example, artificial light at night and air pollution are known to negatively affect bird migrations (Overton *et al.*, 2022; La Sorte *et al.*, 2022). The improved nocturnal visibility caused by coastal development can affect the timing and distribution of foraging opportunities for shorebirds (Dwyer *et al.*, 2013).

To incorporate anthropogenic factors into ENM/SDM applications, the data must meet some conditions from a practical perspective. In the simplest manner, the data format needs to be compatible with that of other commonly used climatic layers (e.g. gridded data at the same spatial resolution as the non-anthropogenic data layers). The spatial extent of anthropogenic factors should cover the geographic

range of the species or the spatial extent of sampling that characterizes the species' distribution. A larger spatial extent (e.g. global or continental) of anthropogenic factors can guarantee broader applications in ENM/SDM studies. The temporal dimension of anthropogenic factors can be important as well, because many human activities are highly variable, and in some cases are under accelerating change (Steffen *et al.*, 2015). Therefore, high temporal resolution of the anthropogenic variables is preferred to capture the dynamics of certain anthropogenic factors; however, to achieve temporal matching, species' occurrences would need to be recorded with a temporal resolution similar to that of the anthropogenic factors.

We have compiled a list of anthropogenic variables that show potential for ENM/SDM studies (Table 3). Most of these data are available at global extents with at least moderate spatial resolution (e.g. 1 km), and thus can be combined with other commonly used abiotic layers (e.g. climate). Future projections of a subset of those data are available. Some of these data layers represent a general index of human impact, such as human footprint, calculated as functions of multiple other human-related factors. By contrast, other layers represent different dimensions of human societies more directly, such as human population density, human migration, and gross domestic product (GDP). The list also covers major anthropogenic changes of the environment, such as global air, light and noise pollution, pesticide usage, and nitrogen and phosphorus fertilizer applications. Lastly, we also included global data representing major modifications of the Earth's surface: cropland maps, transportation infrastructures, and dams. Such anthropogenic variables can be used directly or modified further, for example by calculating the percentage of cropland or the distance to highways.

From an application perspective, including additional predictors in a model can potentially increase model complexity. In simple scenarios in which human effects are positive or negative for a species' distribution (Bennett *et al.*, 2002; Gallardo *et al.*, 2015), anthropogenic predictors would be added as simple terms (e.g. linear) to the existing predictors. On the other hand, when anthropogenic factors have variable effects (Toews, Juanes & Burton, 2017, 2018) or potentially interact with other predictors, the model would need to include sufficiently complex response types in the fitting process.

The use of anthropogenic factors in ENM/SDM is not restricted to model training: they can be applied in model forecasting, similar to forecasts of potential distributions under various climate change scenarios. In particular, future land-use and land-cover projections through 2100 (with extensions to 2300) are available from the Land-Use Harmonization project that were generated under the Shared Socioeconomic Pathways greenhouse gas scenarios of the World Climate Research Program Coupled Model Intercomparison Project (CMIP6) (Hurtt *et al.*, 2020; Rocha, Vale & Lima-Ribeiro, 2021). This data set covers 12 land-use and land-cover classes, including natural vegetation, agriculture, and urban areas. The future projections of climate, land

use, and land cover are typically built on socioeconomic scenarios (e.g. human population growth and economic development) and are available for various political units or finer spatial resolutions (e.g. Hauer & CIESIN, 2021; Gao, 2020; Shaykheeva *et al.*, 2016).

(3) Incorporate environmental data at fine spatio-temporal scale to capture anthropogenic changes

Climatic conditions are known to play major roles in determining species' geographic distributions at large spatial extents (Pearson & Dawson, 2003). Thus, it is common practice to include climatic variables in ENM/SDM, and most applications in the literature rely on multi-decadal mean conditions, such as the 1970–2000 means in *Worldclim* v.2.1 (Fick & Hijmans, 2017) or 1979–2013 means for *CHELSA* v.1.2 (Karger *et al.*, 2018), likely due to the convenience of their global coverage and 'plug and play' data format.

However, recent rapid environmental changes, within the last 1–2 decades, may not be captured by the commonly used decadal data and thus may misrepresent relationships between species' current geographic distributions and the environments. Rapid climate changes are characterized not only by mean conditions, but also by the frequency and intensity of extreme events, such as droughts and heatwaves (Mann & Gleick, 2015; Jones *et al.*, 2018). Those changes in climatic conditions are prominent in influencing species' geographic distributions: global warming leads to gradual distribution shifts, and extreme events can affect population dynamics rapidly and are known to be influential in determining limits of species' geographic ranges (Smale & Wernberg, 2013; Osland *et al.*, 2020). Human-induced climatic effects could be global or regional, or at landscape scales, such as city heat island effects (Phelan *et al.*, 2015), with important implications for species' ecology and distribution (Hamblin *et al.*, 2017; Battles & Kolbe, 2019). Therefore, environmental data at fine spatio-temporal scales are needed to capture the environmental changes caused by human activities.

Ideally, the environmental data should be matched temporally with species' occurrences to obtain time-specific environmental values associated with species' occurrences. The precision of temporal matching can be increased from considering only year, to month, to exact matching of the day, to be precise in matching relevant environmental conditions to occurrences. The time-specific approach was found to quantify better species' responses to temporal variation in environmental conditions (Gschweng *et al.*, 2012; Williams, Willemoes & Thorup, 2017; Smeraldo *et al.*, 2018; Ingenloff & Peterson, 2021). When precise temporal matching is not possible, an alternative approach is to calculate mean conditions across moving temporal windows, as opposed to using static, multi-decadal mean conditions. In addition, species' occurrences also need to be matched with environmental data at high spatial resolution so that variation in environmental conditions is not blurred by coarse spatial resolution of data. Note that this is not meant to match a

Table 3. A list of spatial data sets of human impacts. All data sets have global coverage (spatial extent). A data set may be relevant to biotic interactions (**B**), abiotic conditions (**A**), and dispersal ability (**M**). The spatial resolution of an angular measurement (e.g. 30 arc-second) is also transformed into a spatial distance in the metric system at the equator (e.g. 1 km). NA, not applicable.

Data set	Spatial resolution	Temporal resolution	Temporal extent	Future projection	Speculated relevance to B, A, and M	Reference
Global human footprint	30 arc-second (ca. 1 km)	9 year	1995–2004		B, A, M	WCS & CIFESIN (2005)
Global cropland maps	0.9 arc-second (ca. 30 m)	4 year	2000–2003; 2004–2007; 2008–2011; 2012–2015; 2016–2019		B, A, M	Potapov <i>et al.</i> (2022)
Human population density	30 arc-second (ca. 1 km)	10 year	2000–2100	✓	B, A, M	Gao (2020)
Global human food waste	30 arc-second (ca. 1 km)	1 year	2000		B, A, M	Oro <i>et al.</i> (2013)
Global human settlement layer	100 m 1 km	5 year	1975–2030	✓	B, A	Pesaresi & Politis (2023)
Global gridded gross domestic product (GDP)	1 degree (ca. 110 km)	1 year	1990; 1995; 2000; 2005		B, A	Nordhaus & Chen (2016)
Global gridded annual land-use transitions	0.5 degree (ca. 55 km)	1 year	1500–2100	✓	B, A	Hurt <i>et al.</i> (2011)
Global land projection	30 arc-second (ca. 1 km)	5 year	2015–2100	✓	B, A	Chen <i>et al.</i> (2022)
Global pesticide grids	5 arc-min (ca. 10 km)	1 year	2015; 2020; 2025	✓	B, A	Maggi <i>et al.</i> (2020)
Global human migration grids	30 arc-second (ca. 1 km)	10 year	1970–1980; 1980–1990; 1990–2000		B, M	de Sberinin <i>et al.</i> (2015)
The global dam database	NA (vector point)	1 year	2011		A, M	Lehner <i>et al.</i> (2011)
Global dam tracker	NA (vector polygon)	1 year	1900–2017		A, M	Zhang & Gu (2023)
Global roads open access data set	NA (vector line)	30 year	1980–2010		A, M	CIESIN & ITOS (2013)
OpenStreetMap (e.g. seaports and railway)	NA (vector point)	Hourly–monthly	Up to present		A, M	OpenStreetMap (2022a); OpenStreetMap (2022b)
Global roads inventory project	5 arc-minutes (ca. 10 km)	18 year	1997–2015		A, M	Meijer <i>et al.</i> (2018)
Global roads density						
Global air pollution	0.01 degree (ca. 1.1 km)	1 year	1998–2021		A	van Donkelaar <i>et al.</i> (2021)
Global artificial night lights	30 arc-second (ca. 1 km)	1 year	2015		A	Falchi <i>et al.</i> (2016)
Global noise pollution	NA (vector line)	1 year	2016		A	Martinelli (2017)
Global 1-km downscaled urban land extent	30 arc-second (ca. 1 km)	10 year	2000–2100	✓	A	Gao & Pesaresi (2021)
Global urban heat island data set	NA (vector polygon)	1 year	2013		A	CIESIN (2016)
Global high resolution daily extreme urban heat exposure	NA (vector polygon)	1 year	1983–2016		A	Tuholske <i>et al.</i> (2021)
The anthropogenic biomes of the world	5 arc-min (ca. 10 km)	1 year	2000		A	Ellis <i>et al.</i> (2014)
Global nitrogen fertilizer application	0.5 degree (ca. 55 km)	7 year	1994–2001		A	Potter <i>et al.</i> (2012a)
Global phosphorus fertilizer application	0.5 degree (ca. 55 km)	7 year	1994–2001		A	Potter <i>et al.</i> (2012b)
Accessibility to cities	30 arc-second (ca. 1 km)	1 year	2015		M	Weiss <i>et al.</i> (2018)

precise location with its environment at that precise moment, because such data are not available for most species across their ranges, and data are commonly aggregated to slightly coarse spatial resolutions. Another caveat is that, when matching species' presence data with the environmental conditions, such presence data are assumed to represent the long-term persistence of a species, as opposed to short-term presence in unsuitable or marginal conditions (e.g. occasional observations outside a known range or a sink population that goes extinct).

The feasibility of the high spatio-temporal matching approach depends critically on data availability. Among environmental data that are publicly available, data sets with high spatial (e.g. <1 km) and temporal resolution (e.g. daily) are relatively rare, particularly at global or continental extents and moderate temporal extents (e.g. from 2000 to present). Existing data sets are characterized by trade-offs between resolution and extent and between space and time. For example, the *CHELSA* climatic data set has daily temperature at 30-arc-second resolution (~800 m) at global extent, but is based on 20-year averages (as opposed to every day across the 20 years). *PRISM*, another climatic data set, has daily and monthly data on temperature at yearly scale from 1981 to present, but is only available for the extent of the USA. Note that such climatic data (e.g. temperature, precipitation) are not actual measurements in each cell of the grid; instead, the cell values are conditions inferred through spatial interpolation from weather station measurements, thus containing some uncertainties. Compared with the traditional weather station and interpolated climate data, remote-sensing satellites can provide good alternatives for environments at relatively high spatial (e.g. 500 m) and temporal resolution (daily) at global extent, with the limitation that most data are only available for the last 2–3 decades.

(4) Consider anthropogenic factors in the design of model training domains

The spatial extent across which correlative models are to be trained is a key determinant of the quality of many such models (Barve *et al.*, 2011), because that area determines the environmental variability of pseudo-absences or background data from which the (relative) probabilities of presences are calculated by the models (Phillips *et al.*, 2009). Until this realization (Anderson & Raza, 2010; Giovanelli *et al.*, 2010; Barve *et al.*, 2011), training areas for models were chosen for convenience, and too often without justification (Feng *et al.*, 2019). The BAM conceptual framework for distributional ecology (Soberón & Peterson, 2005) points to the area that has been accessible to the species over relevant time periods (termed **M**) as the appropriate area over which correlative models should be calibrated (Barve *et al.*, 2011), as it represents the set of sites where the species has likely been present, and has had the opportunity to establish populations or not, depending in large part on the suitability of the conditions manifested there.

However, even with these realizations, the current practice in distributional ecology is to make proxy assumptions about

the extent and characteristics of **M**. Perhaps most commonly, researchers use a distance buffer around the known occurrence points as an approximation of species' dispersal 'reach' (Feng & Papeş, 2015); others delineate areas guided by biogeographic knowledge of the species, or use ecoregions or biotic regions (Cooper & Soberón, 2018). These proxies are generally unsatisfactory because they assume equal rates of diffusion in all directions, or depend on other species' range boundaries being a relevant indicator of dispersal potential for a particular species. These assumptions can be further challenged by anthropogenic changes of the natural landscape that subsequently affect species' dispersal ability. For example, highways can limit species' dispersal; on the contrary, roads can serve as dispersal corridors for some species, either naturally or facilitated by humans (Tikka, Högmander & Koski, 2001; Brown *et al.*, 2006; Rauschert, Mortensen & Bloser, 2017).

A recent publication, however, offered an intriguing and more satisfactory path forward in this aspect of modeling methodology. Machado-Stredel, Cobos & Peterson (2021) created a simulation environment that included niche aspects (*via* an initial, simple assumption about the shape and size of the niche of the species in question), dispersal ability, and environmental characteristics of sites through time. Being explicitly designed for estimating **M**, this simulation platform allows the user to create 'hard' dispersal barriers (e.g. a road or a fence), and could be modified to take current climate change processes into account. The simulated **M** will critically depend on timespan of interest and dispersal parameters (e.g. dispersal kernel and dispersal events) (Machado-Stredel *et al.*, 2021). Careful consideration of how anthropogenic factors would affect a particular species could guide development of simulations of **M** that would explicitly quantify human effects, thus avoiding the assumption-based approaches currently in use by many researchers.

(5) Incorporate human-induced dynamics of biotic interactions in modeling species' geographic distributions

Incorporating biotic factors in ENM/SDM relies on the assumption that their roles in shaping species' geographic distribution at large spatial scale are comparable to those of abiotic factors, although this point is often debated in the literature (Soberón & Nakamura, 2009; de Araújo, Marcondes-Machado & Costa, 2014; Fraterrigo, Wagner & Warren, 2014). The difficulty in assessing the role of biotic factors partly lies on the complexities with which biotic relationships could vary across space and through time [e.g. pollination (Burkle & Alarcón, 2011); herbivory (Ruttenberg *et al.*, 2019)] and multi-species interactions that can be determining a focal species' distribution. Nevertheless, substantial changes in biotic communities potentially induced by anthropogenic activities warrant more formal consideration of biotic factors.

A common practice is to use the presence, abundance, or suitability of relevant species, together with other abiotic

variables, as predictors in correlative models. Examples include use of distribution of prey species as predictors of the suitability of predator species (Gherghel, Brischoux & Papeş, 2018), pollinators as predictors of plant species (Giannini *et al.*, 2013), or host species presence as predictors of presence of parasites or viruses (Giannini *et al.*, 2013). Inclusion of species as predictors requires prior knowledge of species' interactions, and relies on the assumption that the species included can facilitate or limit a focal species' range. The effectiveness of this approach could depend on multiple factors, such as strength of the assumed biotic relationship at the focal spatial scale (Soberón & Nakamura, 2009) and the spatial variation of the biotic relationship (Early & Keith, 2019). Another limitation is the assumed unidirectional interaction, e.g. the species used as predictor is treated as a fixed variable that is not influenced by the distribution of the focal species (Pollock *et al.*, 2014).

Another approach is to model multiple species' distributions simultaneously with a joint species distribution model (Pollock *et al.*, 2014). This correlative approach tries to quantify co-occurrences of multiple species, with biotic interactions inferred from the residuals, after accounting for abiotic factors. The major advantage here is the ability to partition out the contribution of abiotic factors, leaving the residuals to account for other ecological or evolutionary processes, including biotic interactions. On the other hand, the causal relationship of species' interactions is not explicitly modeled, which is similar to correlative approaches, thus it can be difficult to interpret the estimated species association (Zurell, Pollock & Thuiller, 2018), which could be scale-dependent (König *et al.*, 2021).

Compared with correlative quantification of biotic interactions, the trait-based approach can be promising in quickly inferring biotic interactions (e.g. trophic interactions) when empirical data are not available, with the potential advantage of higher transferability across space and time (Caron *et al.*, 2022). Information on biotic interactions can also be organized and synthesized with a network modeling approach to make refined quantifications and predictions of biotic interactions across space and time (Strydom *et al.*, 2021; Marjakangas *et al.*, 2022). Further, the rapidly growing databases of functional traits and species interactions, such as *Mangal* (Poisot *et al.*, 2016) and *GloBi* (Poelen, Simons & Mungall, 2014), can make this modeling approach more broadly applicable to studying the role of biotic interactions in species' geographic distribution across scales.

From a macroecology perspective, the biotic networks are likely becoming simpler over time, at least globally, because of biotic homogenization (Rahel, 2000; Clavel, Julliard & Devictor, 2011; Magurran *et al.*, 2015) and mass extinctions (Ceballos *et al.*, 2015) caused by anthropogenic factors. As total numbers of species decrease with extinction, within the remaining species, a subset becomes abundant and widespread (e.g. generalist species, invasive species), creating a simplified biotic network at global scales. Studies have found weaker predator–prey interactions in urban areas compared

with those in rural environments (Early & Keith, 2019). Quantification of biotic interactions, understanding their role in species geographic distributions, and their inclusion in ENM/SDM could thus become easier tasks, owing to the misfortune of biotic interactions simplified by human factors.

V. CONCLUSIONS

- (1) Human factors have profoundly affected and are still increasingly affecting species' geographic distributions, directly or indirectly, *via* various biological, ecological, and evolutionary processes at a global scale.
- (2) The three main factors that determine geographic patterns of species, i.e. biotic interactions (**B**), abiotic conditions (**A**), and dispersal ability (**M**) (also known as the BAM diagram), need to be reconsidered to understand and quantify species' distributions in a world with a pervasive signature of human impacts.
- (3) Existing assumptions and theories of species' geographic distributions are challenged by human factors. As such, a more dynamic view of species' geographic distributions is needed in the BAM diagram: novel biotic interactions and environmental conditions as well as species' adaptation, and restricted or expanded dispersal capacities and modified landscape connectivities.
- (4) Future studies should incorporate anthropogenic factors and consider their impacts in **B**, **A**, and **M** (Human-influenced BAM or Hi-BAM) in modeling and forecasting species' distributions.

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