Title: Predicting Bird Distributions Under Global Change

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ABSTRACT

Global change creates an urgent need to predict spatial responses of biota to support the conservation of sufficient habitat to maintain biodiversity. We present species distribution model theory and a synthesis of avian literature on approaches to collecting occurrence data, selecting explanatory variables and analytical processes currently in use to predict future distributions. We find that interpreting the validity of current predictive distributions is hindered by variation in spatio-temporal resolution of data sets that force hypothesis testing under the Grinnellian niche concept. Broadly, the capacity of species to shift their geographic ranges under land use and climate change is expected to be limited by both large scale (i.e., the physiological or fundamental niche) and small scale (i.e., the realized or tolerance niche) factors. We highlight the strengths and weaknesses of widely used explanatory variables and analytical approaches tailored to macrohabitat characteristics and the Grinnellian niche concept. This synthesis addresses if and how current approaches align with theory and makes recommendations for future directions to improve the accuracy of predictive distribution modelling.

KEY WORDS: species distribution model, environmental niche model, predictive distribution modeling, global change, climate change.

INTRODUCTION

Anthropogenic pressures on climate and land cover lead to altered ecosystems across, and have consequences for the geography of species distributions (Parmesan & Yohe, 2003). This creates an urgent need for understanding species spatial responses to global change and ensuring conservation of suitable habitat that supports population persistence and conserves biodiversity.

The accuracy of current predictive species distribution models, however, is limited due to variation in temporal and spatial resolution of datasets. The capacity of species to change their geographic ranges is limited by both large-scale factors (i.e., things that distinguish range-wide patterns like temperature and rainfall patterns - macrohabitat) and small-scale factors (i.e., things that drive responses by individuals like biotic interactions and resource availability - microhabitat). In this review, we explore the utility of predictive distribution modelling in guiding conservation action in birds. We focus on avian biodiversity because birds are excellent indicators of environmental change, may be more vulnerable to climate change than some other taxa (e.g., mammals), and they have the most widespread and in-depth databases on distributions (Morrison, 1986; Riddell et al., 2021). Insights from avian literature may also be generalizable to other taxa because birds display a wide variety of life history strategies, and citizen science initiatives and long-term research programs have yielded an abundance of predictive distribution literature (Şekercioğlu et al., 2019).

A multitude of factors can ultimately influence how species, populations and individuals respond to changing climate regimes. Individuals may lack flexibility in tracking relevant environmental cues to adjust the timing of life history events and to accommodate novel ecological circumstances. Alternatively, even when species are flexible in timing life history events, they may be unable to modulate behavior in response to environmental anomalies that affect recruitment. For example, advancing egg laying dates to match earlier spring warming temperatures may have negative consequences for nestling survival when the chances of cold snaps are decoupled from warming trends caused by climate change (Shipley et al., 2020). Predicting how species distributions could be altered (shift, contract or expand) with global change may be species-specific (Hallman & Robinson, 2020; Radosavljevic & Anderson, 2014),

but research into how particular axes of climate change affect species with different life history strategies, foraging guilds or habitat affinities provides promising insight that may apply to a wider number of unstudied species (e.g., changing rainfall regimes - Brawn et al., 2017; advances in spring phenology and breeding success - Sander et al., 2020).

A major gap in our understanding of how organisms may respond to changing environments lies in movement behavior. In birds, research on migration routes and resource tracking is well established in the Northern Hemisphere (Faaborg et al., 2010; Thorup et al., 2017), although much less information is available for species that undergo seasonal movements in the Southern Hemisphere. In the speciose Neotropics, >50% of bird species are known to be migratory, and an increase in knowledge of seasonal movements in remaining species could augment this estimate this by up to 15% (Jahn et al., 2020; Rappole, 1995). Complexity is added by varied seasonal movements that avian species undertake, including austral migrants (Jahn et al., 2004, 2013), elevational migrants (Barçante et al., 2017; Hsiung et al., 2018), partial migrants (Sekercioglu, 2010) and others with intratropical migration routes (e.g., Resplendent Quetzal - Papeş et al., 2012; Three-wattled Bellbird - Powell & Bjork, 1995) or extended daily foraging routines (e.g., Oilbirds - Holland et al., 2009). Migratory bird species have been shown to decline when the timing of annual life history events are mismatched with peaks in food availability (Møller et al., 2008; Sander et al., 2020). On the other hand, multiple species of Nearctic-Neotropical migrants are advancing dates of spring migration and breeding behavior in response to warming spring temperatures (Dunn & Møller, 2019; Pecl et al., 2017; Shipley et al., 2020), offering support to the idea of “evolutionary rescue” such that existing variation within annual programs may yield previously unknown adaptive potential (Helm et al., 2019). In this review, we use literature on predictive bird distribution modelling to inform future work

predicting the importance of dispersal limitation, biotic interactions and estimates of the fundamental niche to understand climate-driven distributional shifts in birds and other taxa.

With specific attention on global temperature increases caused by climate change, responses to shifting thermal environments will be varied and complex. Janzen's "seasonality hypothesis" suggests that tropical organisms should be particularly sensitive to anomalies in ambient conditions because their physiology is adapted to a relatively constant environment (Janzen, 1967). This idea has since received much empirical support (Sheldon et al., 2018), and highlighted the tropics for having a high concentration of thermal specialists that are vulnerable to climate change (Mora et al., 2013). Tropical ectotherms (i.e., arthropod prey) tend to live near the upper limits of their thermal optima and are therefore sensitive to even small temperature increases (Deutsch et al., 2008). Endotherms (like birds), on the other hand, have the capacity to tolerate ambient temperatures past their thermoneutral zone by raising metabolic activity to produce evaporative cooling, but this increases energy and water demands at temperature extremes (Gardner et al., 2011; Huey et al., 2012). Still, few studies have considered the potential effects on presumably more thermally flexible endotherms due to changes in a more thermally sensitive ectothermic prey base (Grady et al., 2019). An important consequence stemming from Janzen's hypothesis is that lowland tropical species could be particularly affected by novel conditions supplied by global change, resulting in broad-scale biotic attrition, except for populations immediately adjacent to montane regions, which would have some access to upslope thermal refugia (*sensu* Brodie et al., 2017; Colwell et al., 2008). At least some studies have shown that tropical birds are unlikely to experience acute thermal limits to their distributions (Londoño et al., 2015, 2017). While species may have a sufficient thermal margin to defend against climate warming (Pollock et al., 2021), they will likely experience added

thermoregulatory costs in response to shifting thermal regimes or movements (Londoño et al., 2017). As the effects of increased temperature on populations can interact with critical ecological and life-history parameters, temperature is expected to impact both current distributions and species' responses to changing thermal environments.

Our review aims to synthesize theory, methods, and data sources widely used to predict bird distributions under global change, and to highlight best-practices and opportunities for innovation and refinement. Understanding where species occur and why some areas are occupied but not others is essential for developing conservation and management plans. For most species, knowledge of their distribution is limited to areas that have been surveyed. However, predictive distribution modelling is important to identify areas for protection or management. Modelling wide-ranging, unevenly distributed, cryptic, or difficult to survey species all present problems for understanding factors driving occupancy. Understanding how behaviors and life history traits are linked to patterns of occupancy requires focused investigation but are nevertheless critical layers for informative distribution models. Here, we bring together the issues complicating predictive distribution modelling to offer a solutions-oriented approach to habitat conservation under global change.

PREDICTIVE DISTRIBUTION MODEL THEORY

The current dogma of species distribution modelling falls into two categories: 1) species distribution models (hereafter SDMs) that comprise presence records and abiotic data, and 2) ecological niche models (hereafter ENMs) that explicitly estimate the accessible environment (Soberón & Peterson, 2005). These approaches are meant to have high spatial accuracy but are not meant to inform on cause-and-effect species-habitat relationships (Merow et al., 2013).

Models can be based on different niche perspectives, which present unique frameworks for estimating drivers of occupancy across a species' range. The Grinnellian class of niche reflects abiotic drivers of site occupancy (Elton, 1927; Soberón, 2007; Wisz et al., 2013) and SDMs are mainly built under the Grinnellian niche concept (Figure 1; Saupe et al., 2012). Coarse-scale variables describing ecosystem characteristics are often the most relevant for predicting shifting distributions across large spatial extents. In comparison, the Eltonian class of niche includes estimates of biotic interactions and resource-consumer dynamics that are only quantifiable at local scales (Figure 1; Elton, 1927; Soberón, 2007). Finally, the Hutchinsonian class of niche reflects the functional role of a species, which is often estimated using functional traits and species' habitat requirements based on functional traits (Rosado et al., 2016), and projects the probability of site occupancy beyond study areas, including estimates of dispersal probabilities in ENMs (Figure 1). A species' ability to move beyond their current realized niche depends on the relative importance of abiotic factors, biotic interactions, and dispersal probability that operate at different spatial scales (Jankowski et al., 2013).

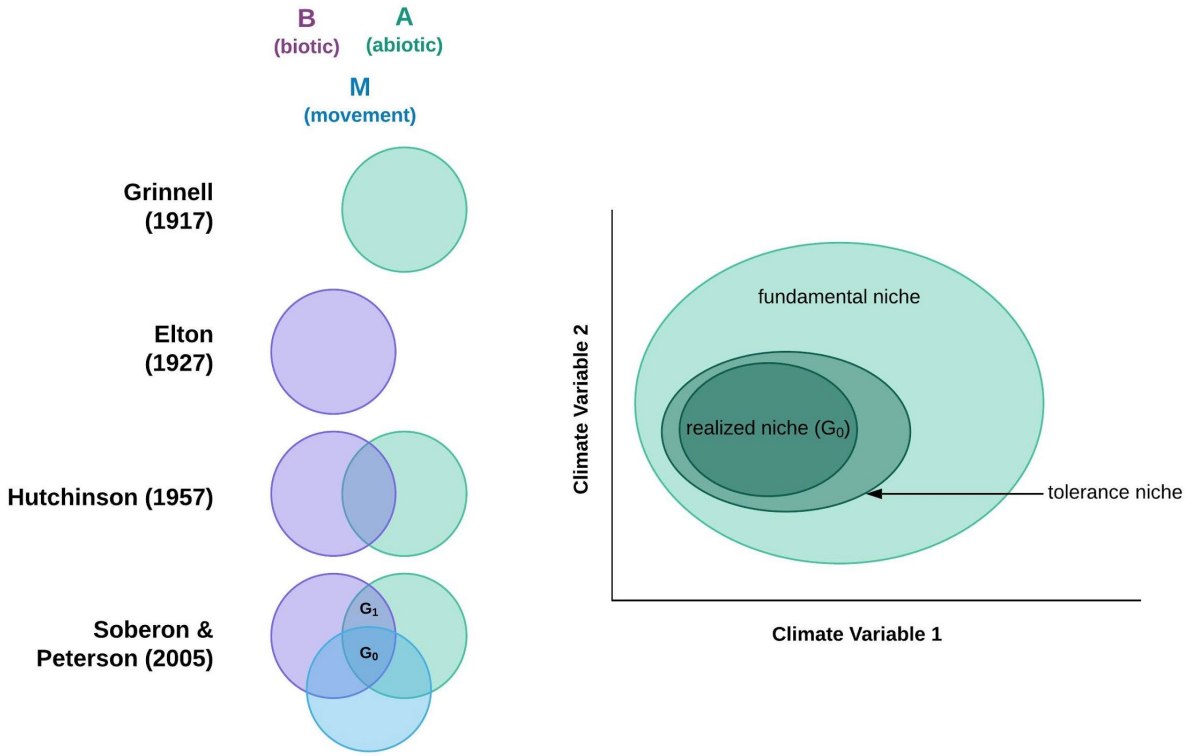

Figure 1. The "BAM" diagram. The relationship between "B" - biotic, "A" - abiotic, and "M" - movement (also thought of as "access" and defined by dispersal ability) with respect to the authors of various niche theories (left). The location of realized, tolerance, and fundamental niche along the intersection of two hypothetical climate variables (right). Sax et al. (2013) present an update to niche theory that considers three components of a species niche: 1) the "realized niche", i.e., conditions within the native range, 2) the "fundamental niche" - conditions, in which a species could thrive if it were introduced there, and 3) the "tolerance niche" - conditions, in which individuals could survive, but likely unable to maintain populations over the long-term. The fundamental niche is the set of appropriate abiotic conditions, and the realized niche is a smaller area where both abiotic and biotic environments are suitable. Theoretically not all of the realized niche could be accessible and so the potential range is yet smaller because it reflects only the area that is suitable and also accessible to the species. Occurrence is not

expected outside of the colored areas. The occupied area is represented by G_0, and G_1 reflects appropriate conditions that have not or cannot be accessed by the species (as described by Saupe et al., 2012).

Assessing occurrence or abundance along abiotic gradients is important for predicting future range shifts under global change, as this relates directly to species' and populations' responses to the environment. The gradual shifts in temperature and rainfall regimes can be expected to align with changes in species responses, reflecting the shifts in optimal ambient conditions and resulting in altered patterns of probability of occurrence or abundance. It is important to note that ENM products are only able to predict the probability of site occupancy within the range of abiotic conditions measured within current range boundaries, so will be limited where climate change introduces novel climates (e.g., Williams et al., 2007).

Spatial ecology theory dictates that species respond to continuous environmental gradients through gradual changes in abundance, as individuals experience shifting conditions moving toward or away from environmental optima over space (Austin, 2005, 2007). However, populations may also show thresholds in abiotic tolerances or in response to biotic factors that change their response shape (e.g., creating asymmetric or skewed response functions; e.g., Oksanen & Minchin, 2002). For example, the asymmetric abiotic stress (AASL) hypothesis predicts a steeper decrease in a species' probability of occurrence toward the more stressful end of a species' distribution, which has been supported in a number of vascular plant species (Dvorský et al., 2017). Other threshold-type effects can result in asymmetric responses shown across multiple species in communities (e.g., sharp ecotone boundaries, appearance of dominant predators or competitors; Jankowski et al., 2013). Identifying response shapes is of practical

interest to understand the impact of abiotic and biotic factors on occupancy. Comparisons across species distinguish commonalities and differences in responses to gradients and can point to key environmental variables driving patterns in community organization.

Heterogeneity within landscapes is important to consider in determining whether populations would be able to respond (in time and space) to changing conditions. Landscapes can vary in ways that affect both the phenology of resources (time) or availability of habitat (space); such variability can be tracked if conditions change at a pace that populations could respond to. Examples of this include species adapted to annually ephemeral or temporally patchy habitats such as wetlands and grasslands; species accustomed to such environments may have dispersal strategies that predispose them to better track climate (e.g., *Elaenia cristata* - Ritter et al., 2021). In other cases, habitat and resources are spatially patchily distributed, and the ability of species to respond to changing conditions may be more taxon-specific for those that rely on spatiotemporal heterogeneity that is naturally patchy. Examples of this include habitat specialists in naturally patchy habitats such as Amazonian white sand habitats (e.g., *Elaenia ruficeps* - Ritter et al., 2021).

Microclimate refugia allow animals to buffer themselves from acutely unfavorable conditions. One example of this is through behavioral thermoregulation. Ambient temperature is almost never constant in terrestrial environments—it varies by time, and by habitat, often at very small scales (Scheffers et al., 2014, 2017). Biologists have long understood that mobile animals exploit thermal heterogeneity to maintain optimal body temperature (Angilletta Jr & Angilletta, 2009; Angilletta et al., 2009; Cowles & Bogert, 1944; Porter et al., 1973; Stevenson, 1985). For cold-adapted species in a heating world, this can be achieved by shifting activity times to cooler periods of the year and day, and by moving to microhabitats that supply cooler microclimates.

This capacity to compensate for unfavorable ambient temperature by behavioral thermoregulation, known as the "Bogert Effect" (Huey et al., 2003), can at least partly mitigate the harmful effects of climate warming (Huey et al., 2012). However, behavioral thermoregulation is contingent on access to cooler areas and periods; animals already occurring in the most buffered environments have limited options for escape when conditions change. Furthermore, individuals could experience additional pressured from biotic interactions with species moving into their habitat to thermoregulate (Huey et al., 2012).

Dispersal limitation is one of three fundamental aspects of distribution theory (Figure 1). Understanding barriers to distributions caused by dispersal limitation has been of great interest, for example, in bird species unable to cross areas of unsuitable habitat, and has been studied both experimentally (e.g., Moore et al., 2008) and theoretically (e.g., Ribas et al., 2012, 2018). Selection pressures driving morphology, such as migratory compared to sedentary life histories, may also play a role in physically limiting dispersal distance (Capurucho et al., 2020; Claramunt et al., 2012; MacPherson et al., 2021; Sheard et al., 2020). Life history strategies also dictate the demographic trends in dispersal; for example, in many species it is the inexperienced young that disperse into new areas away from the territories of their parents (e.g., Florida Scrub Jay - Suh et al., 2020). Dispersal limitation is thus a complex and difficult-to-quantify aspect of predictive distribution modelling that is nevertheless fundamental for predicting the probability of range shifts with global change. Coupling studies of distribution modelling with quantifiable measures of dispersal capacity is an important next step toward making more informed predictions of species responses to changing environments (Travis et al., 2013; Urban et al., 2013).

Generally, when confronted with climate change, species change in one of three ways: 1) by going extinct, 2) surviving by shifting their geographic range, or 3) evolving in place.

Evidence from the fossil record suggests all three responses are common (Graham et al., 1996; Smith et al., 1995). The capacity to adapt or evolve *in situ* in response to climate change has been relatively understudied (Parmesan & Matthews, 2005). A recent meta-analysis of existing studies of phenological and morphological adaptations to climate change concluded that adaptation, while variable among taxa, will not likely work on a sufficient scale to mitigate the worst effects of ongoing climate change, whereas phenological adaptation (e.g., timing of reproduction or migration) may mitigate such effects, albeit imperfectly (Radchuk et al., 2019). The expectation that species with short generation times should be able to survive by evolving in place remains understudied. Advancing such research is hampered by the difficulty of conducting experiments on large numbers of species at sufficient time scales needed to develop a comprehensive framework (Holt et al., 2005; Pierson et al., 2015). Variability among taxa and short time scales signal that selection pressure has yet to be strong enough to produce measurable changes, though it appears that species shift their phenology faster where climate change velocity is faster (Poloczanska et al., 2013). Among abiotic drivers, mainly precipitation changes (but also temperature) seem to underlie adaptive responses to climate change (Caruso et al., 2017; Siepielski et al., 2017). Dramatic changes in climate over the remainder of this century are expected (Figure 2) with many species likely unable to survive in the areas they presently occupy (Ceballos et al., 2015; Sax et al., 2013). Ramping up efforts that prioritize long-term monitoring of populations will be important for informing predictions of the resiliency of species to climate change.

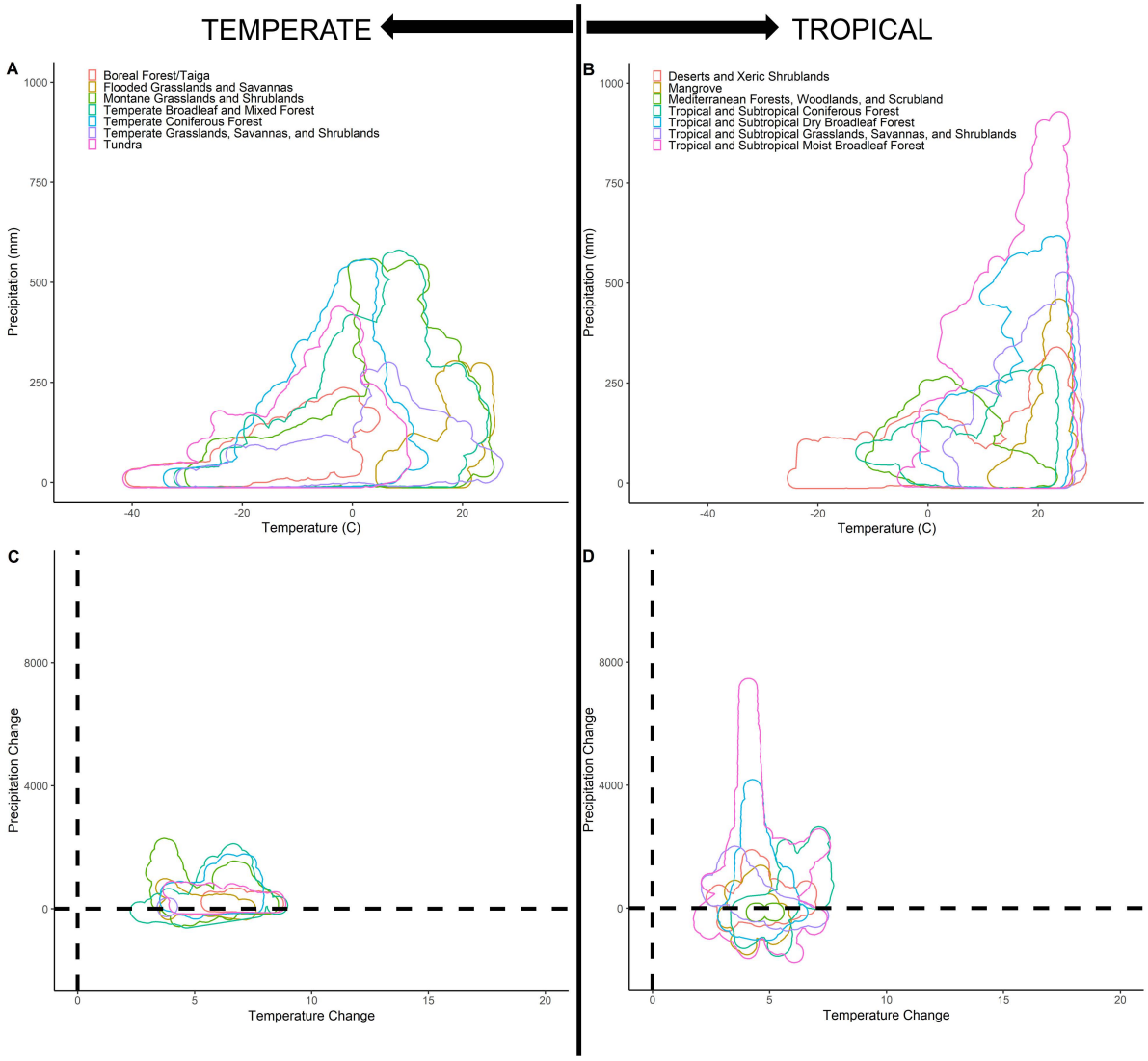

Figure 2. **Current climate and predicted change in climate of global terrestrial biomes**. Climographs of (A) temperate and (B) tropical and subtropical global terrestrial biomes. Projected changes in temperature and precipitation regimes for (C) temperate and (D) tropical and subtropical global terrestrial biomes. While some areas are predicted to have increased or decreased precipitation in the future, no areas are expected to have lower or stable temperatures. Temperature increases are predicted to be higher in temperate biomes, while changes in precipitation are greater for tropical biomes. Climographs built from The World Wildlife Fund terrestrial ecoregions (https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world) and current climate (2021-2040) from CanESM5 middle of the road scenario (SSP3-7.0)

accessed from Worldclim (https://www.worldclim.org/data/cmip6/cmip6climate.html). The projected change is modeled as the difference between current climate (2021-2040, described above) and future climate using the worst-case scenario (SSP4-6.0; 2081-2100) from CanESM5 global climate model data (Meinshausen et al., 2020). Species' presence, and thus biodiversity, is highly influenced by biome type, which shifts from one form to another according to temperature and rainfall regimes (Whittaker 1975). Projected changes in temperature and precipitation may cause global terrestrial biomes to shift in space, but spatial gains and losses by different biomes over time may not occur in synchrony with habitat needs to maintain biodiversity (Dorazio et al., 2015). R code for producing this figure can be found at https://github.com/mmacphe/Global_Change_Biomes.

Extinction risk (and conversely, population viability) centers on declining population and small population paradigms. Population declines are driven by deterministic (demographic, abiotic, and biotic) factors that cause reduction to small numbers (e.g., the Allee effect), and also by stochastic factors, which dominate the extinction dynamics of small populations (Caughley, 1994; Morris & Doak, 2002; Smith et al., 2021). The abiotic shifts in conditions due to climate change and the resulting shifts in species distributions play a role in both types of population dynamics. Shifting distributions can cause temporary or permanent reductions in habitat area (Thomas et al., 2006; van Rees & Reed, 2018), lowering carrying capacity and driving population declines at local or regional scales, or reducing connectivity and creating isolated subpopulations that are more susceptible to small-population dynamics (Anderson et al., 2009). The degree to which changing distributions result in commonly observed conservation impacts depends on a diversity of species traits including habitat preference and associations, phenotypic

266 plasticity, and current range and population size (Jiguet et al., 2007; Visser, 2008). Notably,
267 research based solely on changes in distributions tends to predict widespread extinctions due to
268 the aforementioned mechanisms, but plasticity, dispersal, and adaptation appear to have been key
269 for many species' resilience to past and current climate change (Moritz & Agudo, 2013). For
270 example, the Galapagos finches are a well-known example of phenotypic plasticity in bill
271 morphology in response to environmental change (Grant & Grant, 2020; Grant & Weiner, 2017;
272 Weiner, 1994).
273

274 OCCURRENCE DATA FOR PREDICTIVE DISTRIBUTION MODELLING

275 Occurrence data through time is the foundation for understanding species responses to global
276 change. To assess whether a change in distribution has occurred or will occur, researchers
277 require historical records to establish a baseline for comparison, followed by surveys at one or
278 more subsequent time points. Although birds are among the best studied animals, early baseline
279 inventories are still rare, and often consist of field notes (Reznick et al., 1994), which present
280 challenges particularly in reconstructing past abundances (Shaffer et al., 1998). Alternatively,
281 museum records are among the best sources of historical occurrence data, though they primarily
282 supply presence/absence data only (Shaffer et al., 1998).
283 In contrast to sparse information from the past, modern ornithologists benefit from
284 technological advances that offer unprecedented information on bird occurrence. As birds are
285 such mobile organisms, these include devices that can track individuals beyond specific field
286 research sites (satellite imagery - Borowicz et al., 2018; sophisticated automated biodiversity
287 data collection - Kitzes & Schricker, 2019; for birds within appropriate size ranges - McKinnon
288 & Love, 2018; and online citizen science efforts - Sullivan et al., 2009, 2014). They improve our

289 understanding of avian ecology by identifying previously unknown species-habitat relationships
290 (Jirinec et al., 2016), migratory routes (Jahn et al., 2016, 2021; Stanley et al., 2012, 2015),
291 foraging areas and behaviors (including accessing microhabitat refuges - Wolfson et al., 2020),
292 and wintering distributions (Renfrew et al., 2013). These advances facilitate discovery of species
293 responses to global change by revealing locations outside of direct observation. Aside from
294 emerging technologies, simpler bird monitoring approaches implemented in the past at large
295 scales have amassed rich longitudinal data (e.g., breeding bird surveys and regional atlases), and
296 band recoveries across the globe continue to supply information on bird population trends and
297 distributions (MacPherson et al., in prep).

298 A major challenge for predictive models is rarity or sparseness of point occurrence data.
299 Even with many potential sources of occurrence data, knowledge of bird distributions still varies
300 greatly by species, habitat, and geography. For example, rare, nocturnal, and/or secretive species
301 and those in remote areas are difficult to detect and model accurately (MacKenzie et al., 2005;
302 Stralberg et al., 2015). Rarity is a common characteristic of species in diverse tropical
303 communities and remains a major challenge for constructing species distribution and
304 environmental niche models for tropical species. Still, there are approaches to modelling rare
305 species, for example, using Bayesian network analysis (Hamilton et al., 2015) or "ensemble
306 small models" (ESMs; Breiner et al., 2015; see "Analytical Methods" section, below).

307 Decisions about which type of occurrence data is best for predicting distributions under
308 global change varies based on the trade-off between addressing processes affecting the core
309 distribution versus a more holistic understanding that includes unique responses at range
310 boundaries, during different life history activities, or between different sex and age classes.
311 Understanding of distributions could be improved by increasing the number of studies examining

range edges, and at finer temporal resolutions; “snapshots” in time do not provide a complete picture of spatial resource requirements for individuals or populations. Passive acoustic monitoring and long-term studies remain promising approaches for capturing relative abundance data to estimate population dynamics with respect to global change (Pérez-Granados et al., 2019; Pérez-Granados & Schuchmann, 2020; Sugai et al., 2020). Trait databases are gaining momentum as sources of functional diversity to test hypotheses under the Hutchinsonian niche concept (Gallagher et al., 2020; Leclerc et al., 2020; Matuoka et al., 2020). In particular, exploring how functional roles of species change across abiotic gradients can dramatically improve our understanding of abiotic tolerances to more accurately predict range dynamics. For example, bill size has been shown to be important for thermoregulation in birds (e.g., Danner & Greenberg, 2015) and a study of functional trait structure along a tropical elevational gradient in Malaysian Borneo linked larger bills in low elevation communities with thermal tolerance (Boyce et al., 2019). Current shortfalls in avian occurrence data (summarized by Lees et al., 2020) require an integrated approach to predicting bird distributions with global change. Although most efforts to collect occurrence data are from small spatial areas (e.g., from individual field research sites) and coarse resolutions (Table 1), even incomplete general natural history knowledge gained across spatial and temporal resolutions remains key to identifying important explanatory variables responsible for supporting site occupancy now and into the future.

Table 1. Geospatial context of common occurrence data sources for birds and explanatory variables. Most occurrence data and explanatory variable data layers are of coarse spatial and temporal resolution, making them useful for testing hypotheses under the Grinellian class of

niche. Occurrence data sources with fine spatial and temporal resolution are not as common and require higher economic investment for acquiring location data (i.e., GPS tags) or physically tracking individual birds (i.e., radio-tracking) but could be important for testing hypotheses under the Eltonian class of niche. For a more detailed assessment of temporal categories for avian occurrence data see MacPherson et al. (in prep).

Geospatial data qualities	Examples of occurrence data sources	Examples of explanatory variables
Large spatial area, coarse spatial and/or temporal resolution	•Remote sensing assets (satellite imagery, aerial imagery etc.) •Automated radiotelemetry •Geolocators •eBird •Stable hydrogen isotopes •Genetic data	•Long-term averages in stable climates (e.g., WorldClim) •Land cover (e.g., MODIS, GlobCover, SPOT) •Phenology and vegetation indices (e.g., MODIS, Landsat) •Climate record (e.g., NCDC, ClimateNA, ClimateSA) •Atmospheric weather reanalyses (e.g., ERA, GPM, TRMM, NCEP)
Small spatial area, coarse spatial and/or temporal resolution	•Citizen science (e.g., Breeding Bird Surveys, Christmas Bird Counts) •Natural history collections •Field notes •Point count surveys •Passive acoustic monitoring •Long-term datasets •Bird banding data	
Large spatial area, fine spatial and/or temporal resolution	•GPS tags	•Digital elevation models (e.g., ASTER) •Vegetation indices (e.g., SPOT)
Small spatial area, fine spatial and/or temporal resolution	•VHF radio-tags	•Personal weather data loggers •Weather station data

SELECTING APPROPRIATE EXPLANATORY VARIABLES

Predicting distributions into the future relies on accurate assessments of current life history requirements. In this section, we synthesize the spatial and temporal resolution of explanatory variables commonly used to match distributions with habitat and resource needs. Producing sound predictive models requires suitable proxies for resource or habitat needs that are ecologically relevant (e.g., Burns et al., 2020; Randin et al., 2020). To scale up to entire distributions, there must be an underlying knowledge of a species' life history that effectively

links the lives of individuals to the explanatory variable (or proxy variable) associated with site occupancy. Predicting distributions into a future where the distributions of food webs will shift requires a breadth in knowledge of life history information to predict the probability of species ranges shifting individually or with their entire biotic community. This task is complicated by the potentially differing needs for each life history stage or demographic, which is often the case for birds (e.g., habitat requirements may differ between fledglings and adults). While the main considerations are the spatial and temporal resolutions of explanatory variables, biotic interactions can also play a critical role, and may need to be considered on a species-specific basis.

SPATIAL RESOLUTION OF EXPLANATORY VARIABLES

Selecting the correct spatial resolution of explanatory variables is key to producing the most accurate assessments of range shifts under global change. Passively remotely sensed spatial products (e.g., NDVI and BIOCLIM variables) can be proxies for features of the environment being used by individuals. Active remote sensing systems, for example light detection and ranging (LiDAR) has also been used to predict occupancy by light-demanding versus shade-tolerant plant species (Wüest et al., 2020). LiDAR can also offer direct measurements of structural features of habitat (e.g., vertical distribution of forest canopy elements and foliage density) useful in predicting species occupancy (e.g., Goetz et al., 2010). Remotely sensed variables are thought to reflect a contingency of resources assuming the data product conveys mutual information on a shared spatiotemporal scale with the amount of food resources (Riotte-Lambert & Matthiopoulos, 2020). There are some satisfying interpretations of the ecological relevance of these remotely sensed products (see Bridge et al., 2016 (EVI); Renfrew et al., 2013

372 (NDVI); Tøttrup et al., 2012 (drought)), although the typical purpose of using these large scale
373 variables is for spatial accuracy and not causal relationships, in that remotely sensed variables
374 generally serve as proxies for features of the environment used by individuals.

375 Nevertheless, many remotely sensed abiotic products do intend to reflect a direct habitat
376 resource or type. Habitat characteristics (i.e., land cover) are most often identified with remotely
377 sensed data, which depending on the sensor, can have a variety of resolutions. Medium-high
378 spatial resolutions (≤ 30m, e.g., Landsat, Sentinel) are useful to pair with more precise
379 occurrence data (e.g., GPS tags, point counts; Shirley et al., 2013), whereas low spatial
380 resolution (e.g., MODIS) can be useful for occurrence data such as geolocators or weather radar
381 (Heim et al., 2020). The temporal resolution of remotely sensed data is a limitation, especially
382 when modelling the dynamic nature of migratory birds and habitat changes (MacPherson et al.,
383 2018; Roslin et al., 2021). The limitations in remotely sensed spatio-temporal resolution should
384 not be a deterrent in SDMs, however, because the information gained is not possible with other
385 data sources (He et al., 2015; Randin et al., 2020). Still, applied interpretations when spatial
386 and/or temporal resolutions do not match should be made with caution.

387

388 TEMPORAL RESOLUTION OF EXPLANATORY VARIABLES

389 The temporal predictability of resources is important for predicting future distributions because
390 annual life history strategies are dependent upon correctly timing life cycle events with required
391 resources. For example, it is widely held that birds breeding at high latitudes must correctly time
392 the hatching of young with annual insect emergence to maximize fledging success, and early
393 arrival to breeding grounds may enhance reproductive success (Alerstam, 2011; Kokko et al.,
394 2006; Nilsson et al., 2013; Smith & Moore, 2005). Predictive distribution models are expected to

be the most accurate when species-habitat correlations are assessed using occurrence and environmental data gathered from the same time-period. However, the temporal resolution of occurrence data is much finer than that at which environmental data is typically collected; this can create a mismatch that limits the questions that can be answered using current approaches. The habitat requirements for fulfilling life history needs may vary depending upon the particular life history event (i.e., mate acquisition, rearing young, molting, migrating, etc.) and the species life history strategy. Life history strategies vary in birds from those that have evolved to rely on consistent resource availability (e.g., in the case of dietary or habitat specialists that cannot live outside of narrow environmental conditions), to periodic resource abundance (e.g., seasonal, annual, inter-annual weather patterns that drive migratory or irruptive population movements), or unreliable resource availability (e.g., in nomadic taxa), and it is important to match locality data in time to environmental data for accurate species-habitat assessment.

The temporal resolutions for widely used climate data varies, with trade-offs between temporal and spatial resolution in addition to the state of products limiting the types of distribution questions that can be informed by them (Table 1). Here, we demonstrate this point by explaining temperature and rainfall data sources because these are the two most widely used and generally important environmental factors in species distribution modelling (Bradie & Leung, 2017). The finest spatial and temporal resolution of environmental data is typically from weather station data from the nearest station to the research site (e.g., from https://www.wunderground.com/history) or by collecting weather data alongside occurrence data using data loggers available from various manufacturers (e.g., Meter, Truebner). The ERA5-Land dataset provides fine scale (hourly) temperature and precipitation data, but at a 9 km spatial resolution from January 1981 to present

418 (https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land?tab=overview). National
419 Centers for Environmental Prediction (NCEP) provides global temperature and precipitation data
420 (four-times daily) data at a 0.25 x 0.25 degree grid resolution from 1948-present
421 (https://psl.noaa.gov/data/gridded/data.ncep.reanalysis.surface.html). WorldClim is a commonly
422 used source of environmental data and the current version (2.1) provides global monthly values
423 of min and max temperature, and precipitation averaged from 1970-2000 (Fick & Hijmans,
424 2017). Historical monthly min and max temperature, and total precipitation data used for
425 hindcasting are averaged by decade from 1960-2018 (Fick & Hijmans, 2017; Harris et al., 2014).
426 BioClim data are 19 quarterly estimates derived from WorldClim monthly temperature and
427 rainfall values that are thought to be more biologically meaningful than raw temperature or
428 rainfall data (Busby, 1991). Bioclimatic variables have been averaged for the years 1970-2000 to
429 generate monthly estimates (Fick & Hijmans, 2017). Despite being powerful tools for assessing
430 macroclimate associations, caution should be used when using the most accessible climate
431 products to assess the probability of future range locations.

432 To build robust predictive models, it is necessary to match the spatial and temporal
433 resolution of the occurrence data with that of the habitat characteristics. The temporal resolution
434 of remotely sensed data is a limitation, especially when modelling the dynamic nature of
435 migratory birds where dynamic seasonal habitat changes drive short-term habitat quality (e.g.,
436 seasonally flooded mudflat habitat for migrating shorebirds; Twedt, 2013). Google Earth Engine
437 (a java script based platform where one can write their own code to integrate many satellite
438 products and independently calculate indices such as NDVI) is a flexible tool that can facilitate
439 identifying the correct temporal resolution of land cover data to robustly test explanatory power
440 of land cover variables. Examples of data sets in Google Earth Engine include vegetation indices

(Landsat, ~2 weeks temporal resolution), products for creating land cover classifications (SPOT, ~1 month), and land cover datasets (e.g., GlobCover, Cropland Data Layers, National Land Cover Database; Table 1).

BIOTIC FACTORS

Modeling future range shifts in response to global change rarely considers biotic factors. This omission is the main reason why an assumption of SDMs - that the species is at equilibrium with their environment - is rarely, if ever, met (Pearson & Dawson, 2003). If this assumption were true, a species' realized and fundamental niche would completely overlap as long as the species could access all available suitable niche space (Figure 1). Consideration of biotic factors has the potential to significantly enrich the field of predictive distribution modelling with more accurate forecasts, and here we synthesize leading research contributing to this end at both the intraspecific and interspecific level.

There remains a gap in statistical approaches that account for biotic interactions in forecasting species distributions. It is thought that biotic interactions vary along abiotic gradients such that biotic interactions can either enhance or reduce predicted ranges (Louthan et al., 2015). However, because capturing this information requires both high spatial and high temporal accuracy across all abiotic scenarios within the realized niche, there are few examples to draw from. One promising approach to including biotic interactions in predictive spatial modelling is the development of causal models that estimate the influence of interspecific competition using co-occurrence data (e.g., Staniczenko et al., 2017). The scope and strength of biotic factors may be correlated with abiotic pressures (Louthan et al., 2015), and may differ depending upon which range edge is being considered. For example, much work has been done in the bird literature to

464 improve our understanding of species-habitat relationships through the study of hybrid zones,
465 which typically occupy only one part of a species range (e.g., Taylor et al., 2014). Quantification
466 of biotic factors, like the ones described here, requires targeted species-specific research to test
467 hypotheses within the Eltonian and Hutchinsonian classes of niche. This research is mainly done
468 within small spatial extents and without consideration of temporal or spatial resolution (e.g., co-
469 occurrence records from different time periods or datasets with different spatial resolutions -
470 Atauchi et al., 2018; Palacio & Girini, 2018; see also König et al., 2021), but some research has
471 been done at large spatial extents and coarse resolutions (e.g., Acorn Woodpecker occurrence
472 with Colombian Oaks in the Northern Andes - Freeman & Mason, 2015).

473 Modelling future range shifts in response to global change must consider the role of
474 intraspecific biotic factors that shape current distributions. Intraspecific competition can drive
475 density-dependent range shifts in migratory species such that interannual selection of wintering
476 locations are dependent on group size and food availability (Corre et al., 2020). Dispersal
477 limitation can contribute to inadequacies in recruitment to new or population sink sites, limiting
478 population recovery or range shifts despite available habitat (Palma et al., 2020). The ability to
479 update behaviors when circumstances change (behavioral flexibility) may be key for driving
480 range shifts or expansions under global change (Blaisdell et al., 2020). Further, bird species
481 capable of behavioral innovation (a.k.a. plasticity) often have lower risk of extinction, as they are
482 better able to adapt to changing ecosystems and habitat destruction (Ducatez et al., 2020; Reed et
483 al., 1999). Additionally, metapopulation dynamics can affect the introgression of adaptive traits
484 such that maladaptive traits restrict range shifts under global change (e.g., Garcia-R & Matzke,
485 2021; Lavretsky et al., 2020). Each of these examples are implicitly expected to vary across

abiotic gradients, highlighting the importance of assessing the probability of site occupancy beyond the core of a species distribution.

Perhaps more difficult is estimating the strength of interspecific biotic factors in shaping distributions because this requires a breadth of natural history knowledge beyond that of the species in question. However, interspecific biotic factors are thought to have strong influences on the probability of site occupancy. Species may be excluded through predator/prey dynamics where patches of habitat occupied by a species' predator may be less likely to be occupied by the species being studied (Léandri-Breton & Bêty, 2020). Interspecific competition can also exclude species and is often assessed using co-occurrence data (Elsen et al., 2017; Freeman et al., 2016, 2019; Jankowski et al., 2010). Commensalisms, where one organism benefits from the presence of another organism and the other unaffected, can also facilitate site occupancy (Aitken & Martin, 2007). Including data on the presence of predators, competitors, and commensalisms in SDMs can be a useful addition to improving models (Jankowski et al., 2013). Alternatively, the spatial overlap with other taxa may have little influence if the focal species exhibits behavioral avoidance (e.g., via interference competition - Jaeger, 1970; or predator-prey dynamics - Lukas et al., 2021) or the spatio-temporal scope of data are not aligned.

The utility of SDMs to guide predictions of distributions under global change will certainly be limited by the spatio-temporal resolution of environmental variables. Even when researchers are mindful when selecting environmental data suited to answer questions about their occurrence data (i.e., using ecologically relevant environmental and climate data across biologically relevant space and timescales), a challenge remains in combining and contrasting the Grinnellian class of niche (e.g., climate variables) against other niche classes that require finer temporal and spatial data (e.g., density of interacting species). This problem can further

complicate predictive models if site occupancy is dependent on time-lags, as is the case in some migratory species (Bridge et al., 2016), and is explored further in the following "Analytical Methods" section.

ANALYTICAL METHODS

Predictive models of species distributions can be divided into correlative versus mechanistic approaches (Figure 3). Correlative models elucidate relationships between species occurrence and spatially explicit explanatory variables and can be viewed as hypothesis generating tools. Data to parameterize correlative models are more readily available, making them the dominant source of predictive distribution models. Mechanistic models are hypothesis-testing tools that incorporate physiological tolerance to predict where species will be capable of persisting within their physiological limits (Guisan & Zimmermann, 2000).

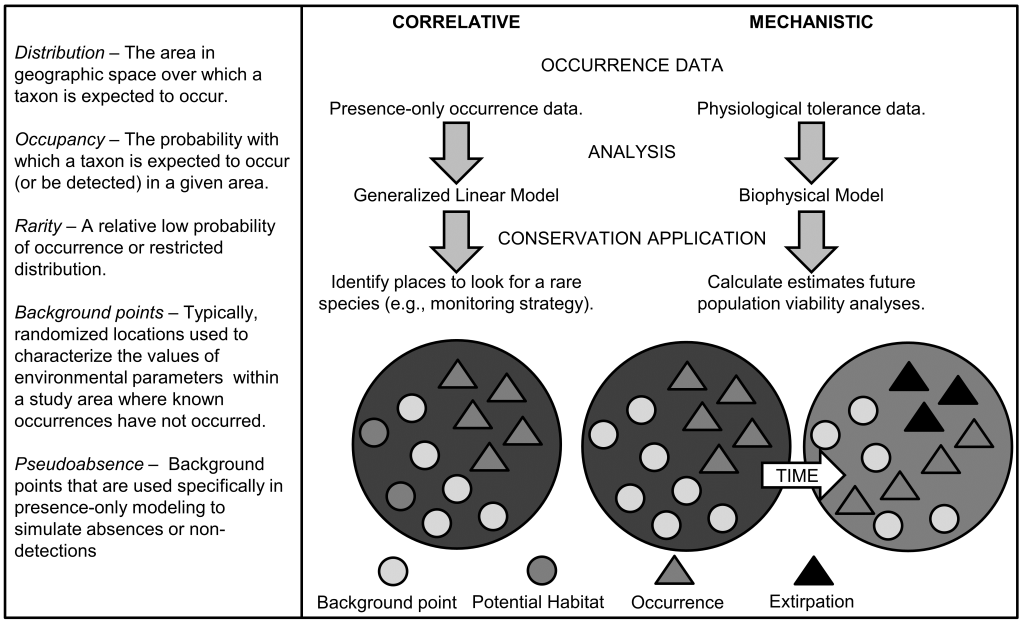

Figure 3. Analytical processes for species distribution models. Left: important terms used in describing distribution model data. Right: Parallel workflows for example correlative versus mechanistic predictive modelling.

Descriptions of range characteristics that are the outcome of correlative SDMs can help us better understand species and their sensitivities to global change. MAXENT is one of the most popular SDM approaches, widely used for its ability to use presence-only datasets where true absence or non-detection data are typically hard to find (Elith & Leathwick, 2007; Merow et al., 2013). MAXENT has been useful for modelling distributions of rare or cryptic species due to its apparent high performance with small or incomplete datasets (Aubry et al., 2017; Pearson et al., 2007; Phillips et al., 2006; Wisz et al., 2008; but see also Marini et al., 2009). Boosted regression trees (BRTs) are one of many machine learning techniques well-suited to modelling complex ecological data because they can handle different types of predictor variables, fit complex nonlinear relationships, accommodate missing data and automatically handle interaction effects between predictors (Elith et al., 2008; Graham et al., 2008). BRTs have been used to predict bird distributions using occurrence data for waterfowl (Barker et al., 2014), shorebirds (Dalgarno et al., 2017), seabirds (Oppel et al., 2012), and owls (Domahidi et al., 2019). Hierarchical Bayesian models can integrate various data types (e.g., presence-absence, presence-only, count data) to create reliable spatio-temporal distribution models (Hefley & Hooten, 2015). Using continuous spatial predictor variables such as land cover, the abundance and distribution of species can be predicted over a continuous latent surface (Chakraborty et al., 2010), which has been useful with waterfowl aerial survey data (Herbert et al., 2018, 2021). Generalized linear models (GLMs) and generalized additive models (GAMs) can be employed to understand distributions across multiple environmental conditions and also conceptualize patterns in distributions of abundances across environmental gradients (Augustin et al., 1996; Smith & Edwards, 2021). GAMs can be used to estimate species' response curves with smoothing functions, which offer more flexibility

548 to capture complex shapes not possible with GLMs (e.g., Maggini et al., 2011). One drawback to
549 GAMs, however, is that evaluation of response shapes (e.g., optima, skewness) is done through
550 visual inspection rather than statistically. Huisman-Olff-Fresco (HOF) models are used to predict
551 occupancy along abiotic gradients and are particularly useful in evaluating alternative shapes of
552 species responses to gradients, for example, if changes in abundance do not exhibit the widely
553 assumed symmetric Gaussian functions, but instead show asymmetric, threshold-like changes in
554 occupancy over space. HOF response curves can be used to highlight distinct distribution
555 patterns such as species replacements, allowing inference of potential biotic interactions that are
556 otherwise difficult to measure (Jansen & Oksanen, 2013). The choice of predictive SDM
557 technique and quality of SDM product are based predominantly on the type of occurrence data
558 available and secondarily on spatiotemporal matching of explanatory variables.

559 Mechanistic approaches to SDMs model physico-chemical processes that drive species'
560 presence. More specifically, biophysical models predict areas where physico-chemical processes
561 meet life history needs (Kearney, 2006; Michael Kearney & Porter, 2009). For example, a
562 biophysical model for the endangered Night Parrot (*Pezoporus occidentalis*) shows how air
563 temperature increases of 3 °C would lead to lethal levels of dehydration (Kearney et al., 2016).
564 Bayesian networks (BNs) are another type of mechanistic model that go beyond species-habitat
565 correlations by also considering processes that influence occupancy across space and time (i.e.,
566 site access and selection - Jones, 2001). Originally employed to model human judgement (Pearl,
567 1985), BNs have only recently been adapted for predictive SDMs (MacPherson et al., 2018;
568 Staniczenko et al., 2017). Mechanistic models are informed by causal relationships based on
569 empirical research or expert knowledge, the latter of which are referred to as belief networks
570 (Drew & Collazo, 2014; MacPherson et al., 2018). Mechanistic models enable the identification

of the most important variables driving distribution patterns through mapping the fundamental niche, which is helpful to inform conservation and management decisions when circumstances change.

Conservation plans rely on SDMs for future species distributions, despite the small, but growing, body of literature on ways to incorporate climate change into conservation planning (Jones & Cheung, 2015; Loyola et al., 2013; Nakao et al., 2013; Terribile et al., 2012). Using correlative predictive models is likely to overestimate range shifts and extinction risk due to the violations of common assumptions in correlative distribution modeling. For example, SDMs tend to violate the assumption that the individual species is currently at equilibrium within its environment (Early & Sax, 2014; Sax et al., 2013) and do not take into account species interactions (Pearson & Dawson, 2003). Despite these criticisms, SDMs remain the "best" widely accessible approach currently in use for identifying potential future habitat-area (Tingley et al., 2014).

Ensemble modeling strategies, in which the predictions of multiple approaches are combined or used simultaneously, are often suggested to better encompass the range of uncertainty in prediction (Araújo & New, 2007). This method accounts for the fact that model choice is often the greatest source of quantifiable uncertainty in species distribution modeling, and reduces sources of bias from the use of a single algorithm (Dormann et al., 2008; Jarnevich et al., 2017). Implementing ensembles of five or more of the algorithms and approaches described above has been greatly facilitated by software packages like BIOMOD (Thuiller et al., 2009) and VisTrails SAHM (Morisette et al., 2013), which bring methods together into a single analytical environment. Ensembles can be used to assess a range of potential projected outcomes, forming a "bounding box" or "consensus" across algorithm predictions (Araújo & New, 2007).

Analysis with model ensembles typically involves scaling and averaging model outputs and, often weighting these by some measurement of model performance such as "area under the curve" score.

The ongoing "big data revolution" in many fields including ornithology (La Sorte et al., 2018) has increased use of artificial intelligence for data handling and analysis (Xia et al., 2020), especially in correlative distribution modeling. Machine learning algorithms like MAXENT (Merow et al., 2013), random forests (Mi et al., 2017), neural networks (e.g., Manel et al., 1999), deep learning (Benkendorf & Hawkins, 2020) and boosted regression trees (Elith et al., 2006) are now commonly applied SDMs, and are valued for prediction and interpolation. They are excellent tools for insight into potential future shifts under global change (Elith, 2017).

DISCUSSION

Predicting where species will live in a warmer future is a central goal of modern ecology. This effort has recast the basic research question of what limits distribution of species – why a species lives *here* but not *there* – as an applied question. Species are already on the move in response to recent decades of warming (and, depending on the region, predicted trends of reduced or increased rainfall; Figure 2), supporting long-held theory that climate limits species' geographic ranges (Tingley et al., 2009). However, the match between species' distributions and climatic conditions is often weak; species vary considerably in their observed responses to recent climate change. These observations indicate that we are still in the early stages of ecological forecasting. In this research review, we have highlighted the theory underpinning how climate is related to species' distributions and focused especially on the types of data sources and analytic approaches

that are useful for predictive modeling of species' geographic responses to ongoing climate change.

Here we briefly highlight three motivating questions to guide future research; the answers to these questions are particularly likely to generate useful insights.

1. Is dispersal a rate-limiting step in range expansions?

The proximate driver of range shifts is dispersal; ranges expand when individuals move beyond the existing range limit. Dispersal constraints are thus one obvious explanation for cases where species' observed range shifts are failing to track changing climate. Birds have incredible capacities for dispersal (e.g., Slager, 2020), making it tempting to gloss over a possible role for dispersal constraints in avian range shifts, including unexplored topics such as site fidelity. However, tropical species often show extreme limitations on dispersal, suggesting that longer-distance range shifts (e.g., across latitudes) may be slow, particularly when landscapes are patchy, or when species show high specialization to their associated habitats. In the temperate zone, even some long-distance migrants may show incredible site fidelity to breeding (and wintering) territories (Winger et al., 2019), which suggests the possibility that rapid range shifts may be difficult to achieve. Lastly, dispersal may be possible but may introduce a new trade-off with other components of the annual life cycle, such as migration. For example, the ability of boreal breeding birds to take advantage of newly available forest habitat in the Arctic may be constrained by a trade-off with ever-increasing migration distances.

2. Are species particularly rare at their range limits?

638 Ecological theory assumes that species are most abundant at the center or core of their range and
639 become progressively rarer towards their range limits (the "abundant-center hypothesis; Brown,
640 1984). However, empirical patterns of abundance often fail to fit these expectations. Whether the
641 abundant-center hypothesis generally holds or not is now a matter of debate (e.g., Dallas et al.,
642 2020), and the answer may have consequences for rates of species' range shifts. For example,
643 low abundances at range edges could lead to slower rates of range shifts than if abundance
644 distributions are more uniform across a core-to-limit transect through a species' geographic
645 range. This could be due to simple numeric effects – range shifts are easier when there are more
646 individuals at the range edge to start with – or to genetic effects. That is, low abundances (and
647 hence lower genetic diversity) could reduce local rates of adaptation at range edges, with gene
648 flow from the abundant range center swamping any effect of local adaptation at the range edge
649 that would facilitate range expansion when conditions change (Haldane, 1956; but see Kottler et
650 al., 2021). Studies on invasive species have the potential to improve our understanding of the
651 mechanisms that promote expansion from original range boundaries (e.g., the tolerance niche of
652 the Asian Openbill Bird - Lei & Liu, 2021; and climate matching in the European Bee-eater -
653 Stiels et al., 2021).
654
655 *3. How does land use change interact with climate change?*
656 Like most of the range shift literature, we have focused in this review on predicting species'
657 responses to changes in climate per se. But species are shifting (or failing to shift) their ranges in
658 landscapes that, more often than not, are dominated by human activities. Studies that
659 simultaneously incorporate both land use and climate change as drivers of distributional change
660 are few in number but hold great promise for several reasons. First, land use change is an

obvious driver of species' distributions; many species simply do not persist in landscapes with extreme levels of human control. Second, appropriate habitat for most species in human-dominated landscapes consists of habitat patches of varying sizes with varying levels of connectivity (e.g., Neilan et al., 2019). This fact elevates the role of dispersal in determining whether patches (and, scaled-up to a larger geographic scale, regions) are occupied by a given species. Third, habitat change directly affects local-scale climate. Fragmented forests, for example, average substantially warmer and drier than primary forests (Kapos, 1989), and "urban heat islands" alter local temperatures that are known to affect bird distributions (in migrants - Bonnet-Lebrun et al., 2020; and residents - Latimer & Zuckerberg, 2021). Hence, land use change can act as a multiplier of temperature effects on species.

The consequences of climate change for species are potentially severe, with widespread predictions of extinctions. Some evidence suggests these dire predictions may be coming true. For example, warming temperatures have led to local extinctions in mountaintop communities in southeastern Peru as species shift their geographic ranges to track climate, a potential harbinger of the possible extinction of high elevation tropical species (Feeley et al., 2012; Freeman et al., 2018; Rehm & Feeley, 2016). Yet species may be more resilient than models assume; for example, genetic data indicate that many species were able to persist through dramatic climate fluctuations in the Pleistocene (Bocalini et al., 2021; Song et al., 2020; Wogan et al., 2020).

CONCLUSION

Humans have already made Earth hotter than it has been since before the Pleistocene (~ 2 million years ago). This rapid change in Earth's climate has set species on the move and led to a plethora

of scientific research aimed at predicting where species will live in the coming decades as warming continues. These predictions, though frequently made, are seldom tested. Without this crucial step of model validation, it is impossible to assess the usefulness of predictive models. Here, we have presented theory and highlighted a range of data sources and analytical approaches that can be used to predict species' geographic responses to climate change. Ever-greater computational power, combined with increasingly large datasets of species occurrence and landscape covariates, permit the use of greater complexity in models. However, more complex does not necessarily equate to better. The litmus test for any predictive model is how well it predicts reality. To this end, we advocate for an increasing focus on collecting empirical data that matches the spatio-temporal resolution of occurrence data with environmental variables, tests hypotheses beyond the Grinnellian class of niche, and directly evaluates model predictions (e.g., using mechanistic SDMs or resurveys). For example, the long-term predictions from models whose predictions are not met over the short-term are unlikely to be helpful. Determining species' resiliency will depend on accurate estimates of the fundamental niche including which attributes make some species more vulnerable than others, which abiotic gradients are the most important to consider for the promotion of population persistence, and including biotic interactions in predictive, validated models. The ongoing pursuit of meaningful predictive distribution models under land use and climate change will be of great utility.

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