



Avian SDMs: current state, challenges, and opportunities

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Quantifying species distributions using species distribution models (SDMs) has emerged as a central method in modern biogeography. These empirical models link species occurrence data with spatial environmental information. Since their emergence in the 1990s, thousands of scientific papers have used SDMs to study organisms across the entire tree of life, with birds commanding considerable attention. Here, we review the current state of avian SDMs and point to challenges and future opportunities for specific applications, ranging from conservation biology, invasive species and predicting seabird distributions, to more general topics such as modeling avian diversity, niche evolution and seasonal distributions at a biogeographic scale. While SDMs have been criticized for being phenomenological in nature, and for their inability to explicitly account for a variety of processes affecting populations, we conclude that they remain a powerful tool to learn about past, current, and future species distributions – at least when their limitations and assumptions are recognized and addressed. We close our review by providing an outlook on prospects and synergies with other disciplines in which avian SDMs can play an important role.

Understanding the processes underlying the extent and limits of species distributions has fascinated scientists since the beginning of ecological research (Sclater 1858, Wallace 1876, Merriam 1894, Griggs 1914) and forms the heart of the field of biogeography (Gaston 2003). For over a century, biogeography has remained a largely descriptive discipline (Dahl 1921, Terborgh and Weske 1975, Root 1988), but it has now transformed into a much more dynamic field with modern technologies allowing for the collection and analysis of distributional and environmental information in previously unforeseeable ways. Moreover, interest in understanding the distribution of global biodiversity has increased due to pressing need to protect it against the multifaceted threats of climate change, habitat loss, and the appearance of invasive species. One of the main innovations spurring the modern development of biogeography has been the emergence of statistical models that link species occurrence data with spatial environmental information. These so-called species distribution models (SDMs; also known as environmental niche models, ENMs) combine information on species occurrences with relevant climatic and/or environmental predictor variables (Graham et al. 2004, Hijmans et al.

2005, Kriticos et al. 2012, He et al. 2015, Karger et al. 2016, Sullivan et al. 2016) to infer species–environment relationships, which are then used to predict species' distributions in space and time (Elith and Leathwick 2009, Maguire et al. 2015). Niche theory, traceable back to Grinnell (1917) and further developed by Hutchinson (1957), forms the conceptual basis of SDMs and allows for an interpretation of their results in the light of both methodological as well as biological uncertainties (Chase and Leibold 2003, Soberón and Peterson 2005, Soberón 2007, Godsoe 2010, Warren 2012).

Of the wide range of taxa for which SDMs have been applied, birds are among the most prominent groups. Birds are generally well-known (del Hoyo et al. 1992–2013, Newton 1998, 2003, 2007, Price 2009), and were the first taxonomic group used to identify biogeographic regions (Sclater 1858). Today, the biogeography and taxonomy of birds is well resolved, with high levels of phylogenetic and genomic coverage (Jetz et al. 2012, Zhang 2015, Jarvis 2016). Furthermore, their popularity with the general public has facilitated the development of digitally accessible databases containing observations made by birdwatchers in their local areas. eBird, for instance, an international observation platform run by the Cornell Lab for Ornithology (Sullivan et al. 2009, 2016), has so far generated 370 million records covering 98% of the world's bird species (following

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Clements et al. 2016). The availability of freely accessible bird occurrence data may help to explain why SDMs are frequently applied to model avian distributions in particular.

Nevertheless, SDMs have been criticized for a variety of reasons, ranging from critiques on their underlying theoretical concepts and the specific statistical modeling methods applied, to limitations and potential biases inherent to the use of species occurrence data, while taking into account the ecology of the organism to which an SDM is applied (see references in Fig. 1). Here, we argue that the high prevalence of avian occurrence data, together with the high taxonomic coverage and mobility of many birds, provides opportunities to address many of these criticisms (Fig. 1). Indeed, this may be a reason why birds are often used in a methodological context (Barbet-Massin et al. 2010, Zurell et al. 2016). Two factors make birds especially interesting to test hypotheses related to some of the key issues in contemporary distribution modeling, the first that birds are endotherms, and the second that they (often) show seasonal mobility (Fig. 1, Eyres et al. 2017, Methorst et al. 2017).

Endotherm distributions may be less directly linked to bioclimatic variables than ectotherm distributions (Huey 1991, Buckley et al. 2012, Huey et al. 2012, Soininen and Luoto 2014, but see Jankowski et al. 2013) – especially for lower temperature limits (Fig. 2A). For instance, the heavy supplemental feeding of birds in winter has facilitated expansion of the winter distribution of many species northwards (Newton 2003, Robb et al. 2008). These range shifts indicate that it is not physiological tolerance to cold climate, but rather the lack of sufficient resources needed to persist under such conditions, that ultimately causes range limitations for certain species. While the lower thermal

limit is fixed for ectotherms, as environmental temperature directly affects body temperature, endotherms have a high physiological capacity to buffer these circumstances (albeit at potentially high energetic costs, Porter and Gates 1969, Huey et al. 2012; Fig. 2A). The fact that resource availability will modify cold-limited range edges in endotherms, therefore, adds more uncertainty in climate-only SDMs for many birds.

Seasonal resource availability results in the varying seasonal distributions of many birds, and the effect of local climate on many species may therefore change throughout the year (Engler et al. 2014, Eyres et al. 2017; Fig. 2B). This variation is most apparent for long-distance migrants that breed in Arctic or temperate areas and overwinter in tropical or subtropical regions. For such species, the harsh winter conditions in their breeding areas do not directly affect them, and should therefore not be considered in the delimitation of niches (i.e. as a proximal predictor sensu Hutchinson 1957). However, local climate might affect other relevant characteristics of a breeding distribution (e.g. habitat, resources, or competing species) so that year-round climate can indirectly affect seasonal distributions in birds (i.e. as a distal predictor; Engler et al. 2014). Hence, the relevance of climatic predictors depends on the question. Given the unique combination of existing knowledge, data availability and variety of range dynamics in birds, avian SDMs provide us with great opportunities to learn more about past, current, and future species distributions – and how best to handle data and tools under different circumstances and study questions.

Here, we review the current state of the art of using SDMs and point to challenges and future opportunities in

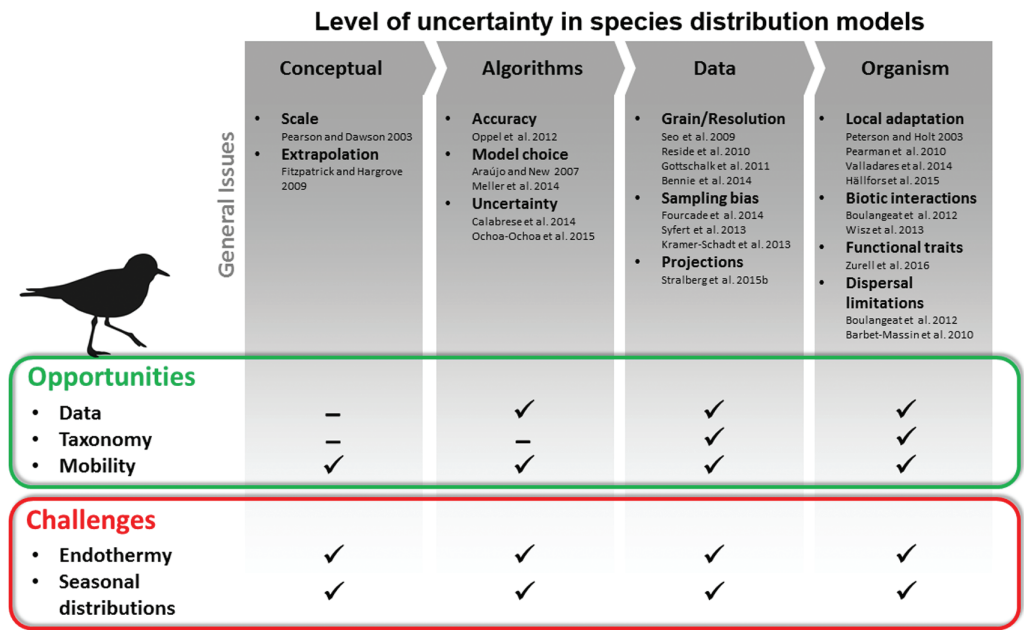


Figure 1. Schematic illustration of the general sources of uncertainty (with key references) affecting species distribution models (SDMs) at the conceptual level, as well as at the level of the algorithm, data, and the study organism. To this end, birds offer several opportunities and challenges at each of the different levels, offering either chances to improve SDM aspects in general, or areas where users need to pay special attention when running SDMs for their own purposes. The main opportunities lie in the good data and taxonomic coverage, as well as in the general high mobility of many species. Major challenges include the endothermy of birds and the seasonality of distributional patterns of many bird species (see text and Fig. 2 for details).

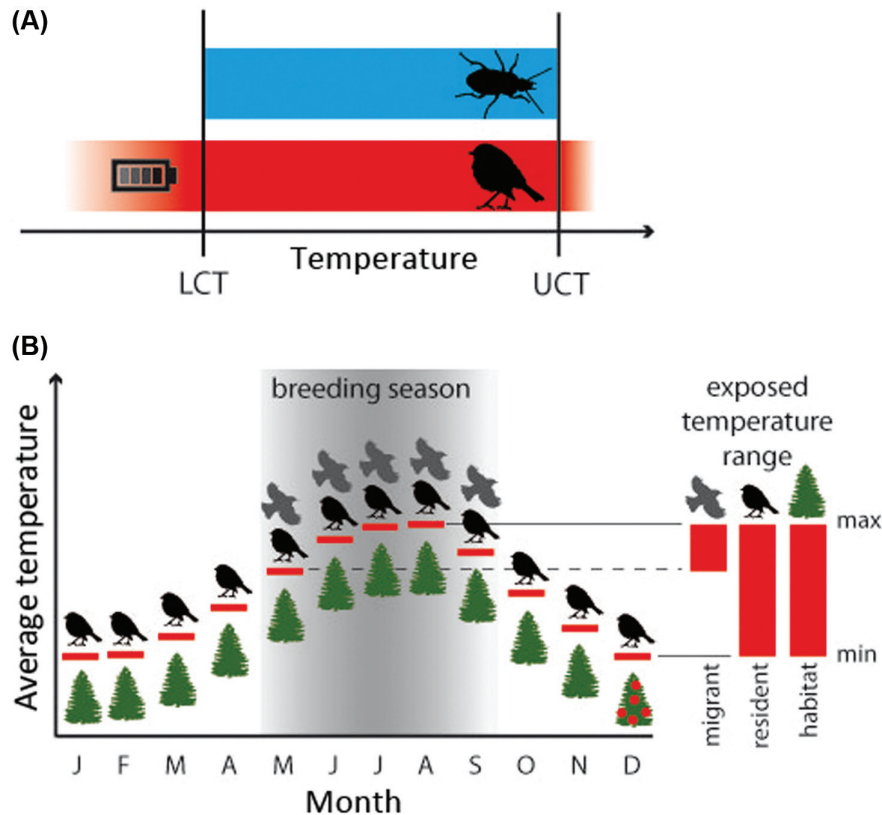


Figure 2. The two main challenges of modeling birds: (A) birds endothermy (red) can blur proximal thermal relationships as they occur in ectotherms (blue), especially at the lower critical temperature (LCT), where energy budgets (battery) can play a dominant role. On the other hand, upper critical temperatures (UCT) can be slightly regulated with transpiration and hence water availability. Note that this illustration focusses on the thermal performance from a physiological perspective (*sensu* Huey et al. 2012), while a multitude of behavioral adaptations allow for some additional plasticity in this relationship in both endo- and ectotherms; (B) the seasonality of range patterns in many birds requires proper thinking about variable selection, e.g. for studying breeding distributions (e.g. in temperate regions). While the exposed temperature range in migrants is smaller, pointing to the species' climatic niche – resident birds and general habitat patterns (such as vegetation) are affected by year-round climatic conditions.

modeling avian distributions. Our target audience is primarily represented by ornithologists interested in SDMs, but we also hope that researchers using SDMs for other species will find this review useful. We structured this review around individual research fields, starting with conservation and biological invasions, then highlighting the particular case of seabirds, and closing with the more general topics of modeling avian diversity, niche evolution and seasonal distributions at the biogeographic scale. After providing this concise overview of avian SDMs (which is accompanied by a detailed summary table; Table 1), we finalize our review by providing an outlook to future approaches and emerging synergies with other disciplines.

Assisting conservation

SDMs are frequently used for conservation purposes (Rodríguez et al. 2007). SDMs provide spatially explicit estimates of habitat suitability for target species, which are of great help for several conservation-related tasks, including: 1) the identification of priority areas or habitats for conservation; 2) the assessment of the potential impact of environmental changes; 3) the definition of ecological networks; and 4) the design of monitoring schemes.

Identifying priority areas or habitats for conservation

While at coarse continental scales, limits of bird distributions are relatively well known, more detailed, fine-grained information on range limits is lacking for many species (Lawler et al. 2011, Peterson et al. 2016). Many studies have used SDMs to identify critical areas for conservation, complement established reserve networks, consider data deficient species, or meet specific conservation targets (Seavy et al. 2012; see also Table 1 for more details and examples). An important extension of this approach is to independently assess the value of different habitats for important species-specific actions (e.g. for foraging or nesting; Brambilla and Saporetto 2014) or to benchmark established conservation concepts (such as the umbrella species concept, Fourcade et al. 2017). More explicitly, the increasing availability of fine-scale information has helped conservationists to evaluate species-specific human impacts (Braunisch et al. 2011, Coppes et al. 2017) or to identify (potential) nest sites (Kassara et al. 2011, Brambilla et al. 2013, Heuck et al. 2013). However, when such fine-scaled information is not available, downscaling information from coarser scales (such as from atlas data) could offer possible alternatives (but also poses new challenges; see Niamir et al. 2011, Bombi and D'Amen 2012, Keil et al. 2013, 2014 for

Table 1. Synopsis of the major topics commonly addressed by using avian SDMs, with general and specific applications and relative examples taken from published case studies.

Topic	General application	Examples	Specific issues	Examples
Conservation	Identification of priority areas for bird conservation	Guisan et al. 2013, Frick et al. 2014	Seabirds and marine environments	Lavers et al. 2014
			Identifying protected areas to meet specific targets	Naoe et al. 2015
			Identifying no-go areas to reduce human–wildlife conflicts in wind power planning	Reid et al. 2015
			Identifying specific habitats for certain species needs	Brambilla and Saporetto 2014
			Validating umbrella species to match conservation goals	Fourcade et al. 2017
	Evaluating or forecasting the effect of environmental changes	Green et al. 2008	Future effectiveness of protected areas over different spatial scales	Coetzee et al. 2009, Hole et al. 2009, 2011, Veloz et al. 2013, Virkkala et al. 2013, Brambilla et al. 2015
			Explicitly focussing on habitat change	Brambilla et al. 2010, Veloz et al. 2013
			Combined effects of climate and habitat changes	Chamberlain et al. 2013, Jongsomjit et al. 2013, Braunsch et al. 2014, Regos et al. 2015, 2016, Stralberg et al. 2015a, b
			Assessing changing wintering ranges	Tellería et al. 2016
			Integrating physiological limitations	Barbet-Massin et al. 2012, Methorst et al. 2017
			Impacts of climate change mitigation	Brambilla et al. 2016
			Predicting effects of climate change on ecological networks	Vos et al. 2008, Hole et al. 2009, Mazaris et al. 2013, Virkkala et al. 2013, Brambilla et al. 2017
			Including climate change adaptation strategies	Hole et al. 2011
			Determining areas for intensive searches or ecological studies	Tinoco et al. 2009, Fondazione Lombardia per l'Ambiente 2015, Bastos et al. 2016
			Coordinating avian influenza monitoring	Moriguchi et al. 2013
			Co-occurrence of interacting species	Brambilla et al. 2013
	Correlation of suitability with further population parameters	VanDerWal et al. 2009, Thuiller et al. 2014	Predicting abundance/ breeding density	Estrada and Arroyo 2012, Oliver et al. 2012, Barker et al. 2014a, Carrascal et al. 2015
			Territory size	Brambilla and Ficetola 2012
			Number of fledglings	Brambilla and Ficetola 2012
			Survival	Monnet et al. 2015
			Land use intensity	Fourcade et al. 2013
	Quantify extinction risk	Kissling 2013, Tracewski et al. 2016	Including changes in demography	Haché et al. 2016
			Including nest predation and food limitation	Harris et al. 2012
			Including wind farm construction	Bastos et al. 2016
			Range dynamics under climate change	Huntley et al. 2007, Reino et al. 2009, Graham et al. 2011
Invasive birds	Predictions of invasion risk	Muñoz and Real 2006, Nyári et al. 2006, Real et al. 2008, Strubbe and Matthysen 2009, Herrando et al. 2010, Stiels et al. 2011, Di Febbraro and Mori 2015, Fraser et al. 2015		

(Continued)

Table 1. Continued.

Topic	General application	Examples	Specific issues	Examples
Seabirds	Assessing niche conservatism	Strubbe et al. 2013, 2015b, Fernández and Hamilton 2015, Stiels et al. 2015	Anthropogenic drivers of invasion risk	Davis et al. 2014, Strubbe et al. 2015a
			Including dispersal limitations into invasion risk predictions	Hooten and Wikle 2008, Bled et al. 2011, Sullivan et al. 2012, Holloway et al. 2016
			Influence of propagule pressure on niche conservatism	Cardador et al. 2016
	Biotic interactions	–	Influence of intraspecific niche variation on niche conservatism	Strubbe et al. 2015a, Cardador et al. 2016
			Competitive impacts on native species	Strubbe et al. 2010, Batalha et al. 2013
			Facilitation between invasive species	Ancillotto et al. 2015
	Methodological studies	–	Impact of predictor variable selection on SDM behavior	Fernández et al. 2012, Strubbe and Matthysen 2014
	SDM use in marine environments	Wakefield et al. 2009, Huettmann et al. 2011, Robinson et al. 2011	Defining marine conservation areas and marine environmental planning	Arcos et al. 2012, McGowan et al. 2013, Humphries and Huettmann 2014, González Carman et al. 2016, Skov et al. 2016
	Methodological aspects	–	Understanding seabird ecology	Ludynia et al. 2013, Quillfeldt et al. 2013, 2015
			Identifying population estimates	Rayner et al. 2007
Avian diversity modeling	Predicting future impacts of marine environments	Rosenzweig et al. 2008	Impact of tracking device precision on seabird SDMs	Quillfeldt et al. 2017
			Transferability of predictions	Torres et al. 2015
			Sea surface temperature (SST) as a dominant predictor	Huettmann et al. 2011, Quillfeldt et al. 2015
	Stacking species distribution models	Ferrier and Guisan 2006	'Distance to nearest colony' as an important predictor	Quillfeldt et al. 2013, Mannocci et al. 2014
			Importance of frontal zones	Lieske et al. 2014, Skov et al. 2016
			Increasing of potential foraging habitat	Hazen et al. 2013
	Methodological aspects	–	Estimating breeding site loss	Russell et al. 2015, Cimino et al. 2016
			Increasing seabird-fishery conflicts	Krüger et al. 2017
			Predicting bird community composition to inform surveys	Feria and Peterson 2002
Niche evolution	Temporal change in species richness	–	Temporal change in species richness	Barbet-Massin et al. 2010, Schidelko et al. 2011, 2013, Levinsky et al. 2013, Distler et al. 2015
			Seasonal distribution patterns	Walther et al. 2011
			Differences between stacked SDMs and macroecological models	Guisan and Rahbek 2011, Calabrese et al. 2014, Distler et al. 2015, Zurell et al. 2016
	Single / Sister species comparisons	–	Comparison of different pooling strategies	Barker et al. 2014b
			Impact of restricted occurrence data	Barbet-Massin et al. 2010
			Implementing dispersal limitations	Schidelko et al. 2011, 2013, Barbet-Massin et al. 2012
			Using fine scale remote sensing data	Sheeren et al. 2014
Niche evolution	Single / Sister species comparisons	–	Comparing sister species along a faunal divide	Peterson et al. 1999

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Table 1. Continued.

Topic	General application	Examples	Specific issues	Examples
Seasonal niches	Comparison in higher taxonomic groups	–	Subspecies or species with hybrid zones or disjunct populations of a single species	Peterson and Holt 2003, Engler et al. 2013, Shipley et al. 2013
			Evolutionary history of species assemblages, species groups, and higher taxa	Peterson and Nyári 2007, Anciães and Peterson 2009, Pearman et al. 2014, Cooney et al. 2016
			Among-lineage history of migration routes	Ruegg et al. 2006
	Breeding vs wintering distributions	Martínez-Meyer et al. 2004, Papeş et al. 2011, Engler et al. 2014, Pérez-Moreno et al. 2016	Evolution of breeding vs wintering niches	Martínez-Meyer et al. 2004, Gómez et al. 2016
			Realized niches in migratory birds vs null model of residence	Laube et al. 2015
	Winter distributions	Lemoine and Böhning-Gaese 2003, Walther et al. 2004	Evolution of breeding vs wintering niches 'Niche following' and 'niche switching' Identifying wintering areas	Martínez-Meyer et al. 2004, Gómez et al. 2016 Joseph 1996, Joseph and Stockwell 2000 Tellería et al. 2014
	Sub-season variations	Cottee-Jones et al. 2015, Frey et al. 2016, Williams et al. 2017	Future predictions of wintering ranges	Barbet-Massin et al. 2009, Doswald et al. 2009, Hu et al. 2010
			Migration routes related to environmental factors	Klaassen et al. 2010
			Resident, nomadic, and irruptive species	Reside et al. 2010, Coppes et al. 2017, Eyres et al. 2017

overviews). Downscaling approaches in conjunction with SDMs have been used to guide local conservation actions in reptiles (Bombi et al. 2012). For birds, however, further studies are needed to capitalize on the comprehensive atlas data for birds.

Assessing the potential impact of environmental changes

Forecasting the potential effects of environmental changes on species populations has been one of the central applications of SDMs for avian and non-avian species (Brotons 2014). Typical approaches to conservation include forecasting range shifts according to climate change and the efficiency of the current networks of protected areas, from local (Veloz et al. 2013) to continental scales (Hole et al. 2011, Table 1). Other studies have assessed the impacts of habitat change (Brambilla et al. 2010) – also involving climate change (Chamberlain et al. 2013) on populations. Moreover, recent SDM applications assessed possible threats to biodiversity posed by mitigation actions against climate change (Wetzel et al. 2012 for mammals; Brambilla et al. 2016 for birds), an essential, yet often neglected topic (Turner et al. 2010). Such studies have already contributed to the identification of the main sites for species conservation in a changing world, but should be further refined, for example by integrating species-specific physiological constraints (Methorst et al. 2017) to make SDMs even more valuable tools for conservation planning.

Defining ecological networks

Networks of protected areas are an essential conservation tool in human-altered landscapes (Opdam et al. 2006). Yet, only a few studies have used SDMs to delineate suitable corridors for birds, whereas this has been done/performed more frequently for several other taxa (Rödder et al. 2016). However, as their distribution can be strongly affected by landscape structure (Clergeau and Burel 1997), birds have been used to explore patterns of connectivity at medium to broad scales (Amos et al. 2014). Although the need to preserve functional habitat networks to allow species to persist as climate changes is acknowledged, only a few studies have associated habitat networks based on avian SDMs with projected variations in distribution and connectivity at fine spatial scales (Virkkala et al. 2013). Given the increased awareness of the need to preserve connectivity in a human-altered landscape under climate change (Verboom et al. 2010), we call for more research on this topic with a focus on fine spatial scales.

Designing monitoring schemes

A classic application of SDMs is to identify areas where field surveys should be performed (Raxworthy et al. 2003). Case studies in an ornithological context are rare, but SDMs have been applied to coordinate an avian influenza monitoring program in Japan (Moriguchi et al. 2013). Tinoco et al. (2009) used an SDM to predict the potential distribution for

the endangered violet-throated metaltail *Metallura baroni*, based on limited occurrence data. They used this model to guide field surveys for the species, and indeed found a positive relationship between species occurrence and suitability values calculated by the model, which thus represented a useful tool to guide explorations. Further applications could be 1) to identify representative regions for monitoring species trend/occurrence over time in a given part of their range or 2) in areas with varying habitat suitability, 3) to refine potential ranges according to co-occurrence patterns, and 4) to identify monitoring sites subject to different extinction probabilities due to global change or other human impacts (Table 1).

Other applications

In recent years, a growing number of studies have tried to relate environmental suitability estimated by SDMs to population parameters relevant for conservation (Thuiller et al. 2014). Results are still inconsistent across studies (Bean et al. 2014, Unglaub et al. 2015), but there is an increasing number of examples in birds, where environmental suitability derived from SDMs correlates with other population parameters such as breeding density, territory size, or survival (Table 1). More research is needed on whether the observed correlations can be generalized and identified as causative across birds and whether dynamic distribution models (i.e. SDMs that incorporate other population parameters, Zurell 2017) may improve such predictions.

Further, SDMs have been used to quantify species' extinction risk by estimating changing habitat availability (Tracewski et al. 2016) – partly by taking into account additional information on demography, nest predation, and food limitation (Harris et al. 2012, Kissling 2013, Haché et al. 2016). In conjunction with long-term ecological research and monitoring studies, such approaches hold strong potential to assess impacts of many aspects of anthropogenic environmental change or in the context of environmental planning (Bastos et al. 2016). To this end, data from long-term monitoring projects have been shown to provide useful information for predicting trends in bird distributions using SDMs, representing an important supplement to atlas data (Brotons et al. 2007).

Finally, despite the frequent use of SDMs in the conservation biology literature, there are only a few examples showing how SDMs have affected the decision-making process or environmental planning (Guisan et al. 2013, McShea 2014, Meineri et al. 2015). This scarce practical implementation of the recommendations provided by SDM studies has been attributed to a lack of communication between scientists and stakeholders (Addison et al. 2013), even though some attempts to change this situation have been made (Guillera-Aroita et al. 2015, Rödder et al. 2016). As far as we are aware, no ornithological work has yet been carried out in this direction. Nevertheless, we think that birds will motivate new work in that direction, thanks to the important role birds play in conservation management and planning.

Assessing invasive birds

Invasive alien species pose severe threats to biodiversity and ecosystem functioning (McGeoch et al. 2010, Simberloff et al. 2013), and birds have been assessed in this regard (Strubbe et al. 2011, Baker et al. 2014, Martin-Albarracin et al. 2015). Their introductions can also be considered as 'unplanned' or 'imperfect' experiments that can be used to test eco-evolutionary hypotheses (Sax et al. 2007). To investigate how and to what extent SDMs have been used in avian invasion biology, we carried out a literature search (see Supplementary material Appendix 1 and Table 1 for details on search procedures and the papers identified). Given the vast amount of data available on bird introductions (Blackburn et al. 2009), it is surprising to see that our literature review uncovered only 27 papers applying SDMs to study avian invasions dealing with less than 10% of the 420 species that have established non-native populations worldwide (Dyer et al. 2017). Moreover, studied species come from only 11 families, with Anatidae (15 species), Phasianidae (6), Estrildidae (5) and Psittacidae (4) being the most prevalent – the very taxa from which a higher than expected number of invasive bird species derive (Blackburn et al. 2009). Aside from bird introductions to islands (which constitute the majority of all bird introductions), historical introductions to continental land masses mainly concern the Nearctic and Palearctic ecozones. However, SDMs have been applied only to a limited set of high-profile, well-known avian invaders introduced to continental Europe and North America. In general, invasive birds have not been extensively studied using SDMs; probably because the impacts associated with invasive birds are minor compared to other taxa (Evans et al. 2016). Indeed, the species for which multiple SDM studies have been performed were invaders with well-known impacts on biodiversity and agriculture, such as Estrildids and Psittacids. Only two publications explicitly discussed competitive impacts from avian invaders by using SDMs, and these studies concluded that those effects are likely to be (relatively) minor (Strubbe et al. 2010, Batalha et al. 2013). Most conservation-related publications have focused on predicting the future range expansion of already established invasive birds. Compared to native species, range shift predictions for invasive birds can show greater sensitivity to model assumptions, possibly because invasive birds are not (yet) in equilibrium with the environment and tend to have smaller initial distributions (Holloway et al. 2016).

Another intensive research focus has been on eco-evolutionary hypotheses underlying invasion success. Niche conservatism is a particularly well-tested hypothesis in this regard, with one-third of papers uncovered by our literature search tackling this topic (Supplementary material Appendix 1). The general picture that emerges from these studies is that differences between native and invasive climate niches are prevalent, but they mainly arise through a partial occupation of native niche conditions in the invasive range. Cases of niche expansion have been reported, too, and studies on ring-necked parakeets *Psittacula krameri* suggested that species with prior-adaption to human-dominated habitats in the native range, intra-specific niche differences

and differential propagule pressure may expand their niche into climates not occupied across their native ranges (Jackson et al. 2015, Strubbe et al. 2015a, Cardador et al. 2016). One other study (Ancillotto et al. 2015) suggested that interspecific interaction with previously established ring-necked parakeets may have facilitated niche expansion of invasive Alexandrine parakeets *P. eupatria* in Europe. More research on a larger number of species across multiple habitats is needed to confirm the generality of these findings.

Modeling seabirds at sea

Compared to terrestrial habitats, SDMs have been generally under-utilized in marine environments (Robinson et al. 2011). Within marine communities, SDMs were mainly applied to fish and marine mammals, and in the context of conservation planning (Dambach and Rödder 2011). Thus, the development of seabird SDMs is recent and strongly depends on data availability. In contrast to the data-rich avian occurrence information in terrestrial areas, the collection of marine species distribution data has been difficult. One of the first efforts to build a prediction model for seabird distribution came from the Canadian Atlantic (Huettmann and Diamond 2001), where comprehensive data set of seabird observations offshore was collected (Hyrenbach et al. 2012). Today, 16 yr after these first seabird SDMs, our knowledge of seabird distributions at sea has increased immensely, through extensive data collection from tracking devices that started with the satellite tracking of wandering albatrosses *Diomedea exulans* (Jouventin and Weimerskirch 1990) and Adélie penguins *Pygoscelis adeliae* (Davis and Miller 1992). Online databases such as OBIS-SEAMAP (<<http://seamap.env.duke.edu>>; Halpin et al. 2009) or the Seabird Tracking Database (<<http://seabirdtracking.org/>>) now contain millions of data points for over a hundred different seabird species. By now, miniaturized tracking devices can be applied to birds as small as Leach's storm-petrels *Oceanodroma leucorhoa* (i.e. around 40 g, Pollet et al. 2014), while larger devices can record bird behavior and environmental variables such as water temperature at different depths in diving seabirds at high temporal and spatial resolution (Masello et al. 2010). All these data have great potential for use in SDM approaches, e.g. to define conservation areas (González Carman et al. 2016) and to improve our understanding of seabird ecology (Quillfeldt et al. 2015).

Seabirds on land – colony and nesting sites

For highly mobile and seasonal organisms such as seabirds, the different requirements of the species in the annual cycle (e.g. for foraging, reproducing or nesting; Mackey and Lindenmayer 2001) need to be taken into account. In seabirds, foraging and nesting occur in distinct habitats, and models often focused on either the foraging (marine) or the breeding (terrestrial) distribution. The breeding success and consequently the distribution of breeding colonies depends on a range of parameters including those more important at the nest, e.g. air temperature and rain, and those determining food availability in the surrounding marine environment (Cimino et al. 2016). For example, an analysis of

seabirds breeding on British coasts based on air and sea surface temperatures and precipitation calculated that 65% of seabird species are likely to lose breeding sites (25–100%) by 2100, and more northerly species are especially vulnerable (Russell et al. 2015). On a smaller scale, predictive habitat modeling has been used to aid in population estimates of burrowing seabirds in difficult terrain, such as on steep islands. Rayner et al. (2007) tested a model for breeding Cook's petrels *Pterodroma cookii*, based on altitude, slope, and distance from ridgelines, and recovered a better predictive fit compared with two more commonly used area-based models.

SDMs of seabird distributions at sea

Seabirds typically spend most of their time away from the breeding colonies, foraging at sea. Outside the breeding season they may be away from land for many months, and marine SDMs need to be redefined to match the environmental conditions that are important for marine predators. Seabirds are an ecologically heterogeneous group of birds, comprising highly mobile pelagic birds such as petrels and albatrosses (Procellariiformes), as well as birds with much more constrained breeding season foraging ranges (e.g. many alcids, cormorants, and penguins). According to their movements, the spatial scale will need to be large for pelagic, surface-feeding birds, while environmental conditions in deeper water layers or parameters such as bottom topography may play a greater role for diving seabirds. In addition, an appropriate temporal scale also needs to be applied. Seabirds may be highly aggregated over short time-scales, but more uniformly distributed in relation to environmental gradients over longer time-scales (Robinson et al. 2011). However, a disadvantage of longer-term averages is that they may not represent conditions important for particular seasonal events.

The optimal scale for an SDM also depends on the data sources and data quality, as well as the research question. For example, high-resolution tracking data have been used to compare sex differences in habitat relationships of penguins (Ludynia et al. 2013) or to assess the marine distribution of black-browed albatrosses *Thalassarche melanophrys* in areas important for fisheries (González Carman et al. 2016), whereas boat-based surveys and seabird tracking data have been used to identify foraging hotspot areas off the Mediterranean Iberian coast (Arcos et al. 2012) and California (McGowan et al. 2013). However, especially for small species, technical issues prevent tracking devices from recording high-resolution occurrence data. Nevertheless, a first attempt to compare SDM outputs using data from different tracking devices show that uncertainties from different spatial resolutions are rather low compared to other sources of uncertainty such as different SDM algorithms (Quillfeldt et al. 2017).

Large-scale analyses are now also possible using publicly available data, e.g. occurrence data from online databases such as the Ocean Biogeographic Information System (OBIS: <www.iobis.org>) or the Global Biodiversity Information Facility (GBIF: <www.gbif.org>). A recent example of such large-scale analyses are circumpolar predictive models of 27 seabird species north of the Arctic circle (Huettmann et al. 2011) and their overlap with human activities

(Humphries and Huettmann 2014). However, large-scale analyses need to consider that seabirds with several populations in different ocean basins may be subject to local adaptations, and the transferability of the model extrapolations needs to be evaluated (Torres et al. 2015), hence confirming findings from terrestrial systems (Pearman et al. 2010, Valladares et al. 2014).

Sea surface temperature (SST) is the most frequently used environmental parameter in seabird SDMs. SST is a main forcing variable in marine ecosystems because phytoplankton and bacteria, which provide the base of the food web, are sensitive to temperature changes and have a critical impact on the functioning of the entire pelagic system. Furthermore, certain SST values are also often associated with water masses rich in nutrients. These favorable conditions can cascade up the whole food web to seabirds, which occupy the higher trophic levels in marine ecosystems. SST is therefore a proxy indirectly related to prey abundance or availability, and it is the most important predictor of distribution for seabirds in Arctic (Huettmann et al. 2011) and Antarctic waters (Quillfeldt et al. 2015).

Other commonly used environmental parameters include salinity, surface chlorophyll concentration or the standard deviation of SST as a proxy for oceanic fronts (i.e. water mass boundaries such as the Polar Front of the Southern Ocean). However, some seabird distribution models have been developed without considering any physical or biological properties of the sea water, but have instead focused on the underlying topography, such as bathymetry, shelf break distance or sea bank presence (Lieske et al. 2014). Also, during the breeding season, the distance to the nearest colony or coast often explains a large part of the distribution (Quillfeldt et al. 2013, Mannonci et al. 2014) and should be added as a further predictive variable.

Most species distribution models in marine environments have used static variables or long-term oceanographic averages (Quillfeldt et al. 2013). Such marine variables with a global coverage have been assembled in the Bio-ORACLE data set (Tyberghein et al. 2012) as well as in the MARSPEC data set (Sbrocco and Barber 2013) at spatial resolutions of 5 arcmin and 0.5 arcmin respectively. However, when fine-resolution dynamic predictor variables from high-resolution hydrodynamic models or remote sensing (Blondeau-Patisier et al. 2014) are available together with sufficiently detailed information on species abundance, the dynamic coupling between the seabird distribution and the natural variability of their habitat can be modeled in (near) real-time. For example, dynamic species distribution models for red-throated divers *Gavia stellata* in the outer Thames estuary, United Kingdom, confirmed their tight association with frontal zones (Skov et al. 2016).

Finally, one aim of predicting species distributions is to project them into the future. Climate change and human impacts such as fishing and eutrophication influence the dynamics and interactions of marine populations and species. An SST rise of 1–6°C by 2100 has been predicted by climate change scenarios (Rosenzweig et al. 2008) and its impact could expand e.g. potential foraging habitat, although other factors such as changing wind regimes or changing conditions at breeding sites also need to be incorporated (Hazen et al. 2013, Cimino et al. 2016). The recent

addition of future layers to the Bio-ORACLE data set (Jueterbock et al. 2013) now makes data for the end of the 21st and the 22nd centuries more accessible to researchers (Krüger et al. 2017).

Avian diversity modeling

Quantification and analysis of biodiversity are among the most important issues in ecology (Gotelli and Colwell 2001), and SDMs have been widely used in this regard. Examples range from predicting community composition (Vallecillo et al. 2016), to identifying biodiversity hotspots (García 2006), and explaining current, historical, and future species richness patterns (Ihlow et al. 2012, Levinsky et al. 2013, Costa et al. 2014). Given our broad ecological and distributional knowledge in ornithology, birds are eminently suitable to address methodological and conceptual challenges in estimating species richness and provide a solid data basis for the development and application of such methods (Sutherland et al. 2016).

Stacked SDMs

The usual procedure in modeling species richness is a two-step process: in step one, single-species SDMs are constructed, whereas in step two, their raw or binary predictions are stacked (S-SDMs, Ferrier and Guisan 2006). An early application of an avian S-SDM was conducted by Feria and Peterson (2002). They found congruence between field inventory data and modeled predictions, which pointed to the capability of S-SDMs to predict species richness correctly and opened up new opportunities for conservation measures (Feria and Peterson 2002). Also, S-SDMs offer ways to analyze seasonal distribution patterns (Walther et al. 2011), which led to a better understanding of population declines of migratory birds. S-SDMs have also been used to estimate current, historical and future species richness in birds: in African and Austral-Asian estrildid finches (Estrildidae), a general spatial stability of diversity patterns through time could be revealed (Schidelko et al. 2011, 2013).

Differences between S-SDMs and MEMs

Another way to estimate species richness is the application of macroecological models (MEMs). In contrast to S-SDMs, MEMs estimate species richness directly, based on theoretical expectations or from controlling factors like available energy, environmental heterogeneity, disturbance or history (Guisan and Rahbek 2011, Distler et al. 2015). Methodologically, MEMs are typically based on a curve-fitting correlative approach or predictive simulations (Hawkins et al. 2003, Gotelli et al. 2009). In a study of North American breeding birds, current and future species richness was estimated via S-SDMs and MEMs (Distler et al. 2015). Both methods provided similar patterns of species richness in comparison to historical observation data. Despite the general high predictability, the local processes causing geographical variation in species richness patterns remain unclear (Distler et al. 2015). Zurell et al. (2016) evaluated the ecological factors affecting model performance of MEMs and S-SDMs. By

modeling Swiss breeding birds, the authors found that different functional groups affect model predictions and suggested that species- or group-specific environmental predictor sets should be incorporated to improve species richness models (Zurell et al. 2016). Within such groups, species richness patterns can be accurately predicted, for example as shown for Canadian waterfowl assemblages (Barker et al. 2014b).

Criticism and suggestions for solutions

Despite their frequent application, S-SDMs have been criticized, primarily because they have a high risk of overestimating species richness at species-poor locations and underestimating species richness at species-diverse sites (Calabrese et al. 2014, Zurell et al. 2016). These limitations are thought to be due to three factors: S-SDMs 1) often predict areas to be climatically suitable that are out of reach for some species; 2) ignore constraints of the carrying capacity that cap maximum species numbers of a given location; and 3) do not include biotic interactions (Guisan and Rahbek 2011). These factors, which affect all SDMs, accumulate in S-SDMs, resulting in unreliable predictions of species richness (Hortal and Lobo 2006, Pineda and Lobo 2009). Consequently, Guisan and Rahbek (2011) suggest a modeling framework that integrates S-SDMs and MEMs together with filters for dispersal and ecological assembly rules. In contrast, Calabrese et al. (2014) attribute overprediction to incorrect stacking methods. When this bias was removed, S-SDMs and MEMs performed similarly (Calabrese et al. 2014).

Avian niche evolution

The evolution of species' ecological niches intersects ecological, biogeographic and evolutionary research (Wiens 2011). One of the main paradigms in evolutionary studies, niche conservatism, states that there is a tendency of species to retain their fundamental niche over time (Ricklefs and Latham 1992, Webb et al. 2002, Wiens and Graham 2005). More specifically, phylogenetic niche conservatism assumes species to be ecologically more similar to each other than can be expected based on their phylogenetic relationships (Losos 2008a). There has been a contentious debate on whether niche conservatism should be considered mainly as a pattern (Losos 2008a, see also Losos 2008b, 2011) or a process (Wiens and Graham 2005, Wiens 2008, Pyron et al. 2015). While we do not aim to repeat this debate, we underline the opportunities that studies on niche evolution offer for our understanding of fundamental evolutionary patterns and processes (Wiens et al. 2010), and call for caution concerning different definitions as well as practical pitfalls (Münkemüller et al. 2015).

Studies on niche dynamics have been conducted at different time scales, ranging from decades to centuries (e.g. in species invasions) to tens of millions of years (e.g. in ancestral niche reconstruction; Peterson 2011). Studies on niche conservatism based on introduced species and the comparison of native with invasive ranges (Peterson and Viglais 2001, Peterson 2003 for reviews; Stiels et al. 2011, 2015, Strubbe et al. 2013 for avian examples) are extensively

dealt with in the section 'Assessing invasive birds'. In this section, we focus on processes that require longer evolutionary timescales, from intraspecific phylogeography to speciation and clade phylogenies. In addition, we focus on SDM studies as an essential part of the methodological toolbox that provides insights into the dynamics of ecological niches (Pearman et al. 2008). Nonetheless, other methods are also suited for these analyses (see Hawkins et al. 2006, La Sorte and Jetz 2010, Khaliq et al. 2015 and Cooney et al. 2016 for examples).

Species pairs and intraspecific niche evolution

Theory predicts that in the case of niche conservatism, an SDM based on one species from a pair of sister species should be able to predict the distribution of the sister taxon. The study by Peterson et al. (1999) was one of the first to test this hypothesis in birds and found a clear prevalence of ecological niche conservatism along a faunal divide in Mexico. Other studies testing the niche conservatism hypothesis were based on single pairs of sister species with hybrid zones (Engler et al. 2013), subspecies (Peterson and Holt 2003), or disjunct populations of the same species (Shipley et al. 2013). In the case of young species or lineages, whose origin dates back to the Pleistocene, it is particularly promising to apply paleodistribution models (Nogués-Bravo 2009), as reliable climate data are available for this time frame. For example, it is possible to test whether past potential distributions correspond to the contemporary distribution of phylogroups (Peterson and Nyári 2007). In a recent example, Peterson and Anamza (2017) hindcasted SDMs to test the ring species concept in the greenish warbler *Phylloscopus trochiloides*. Their SDM hindcast provided further evidence for multiple, isolated refugia around the ring during and since the Late Pleistocene, leading to the conclusion that this warbler should no longer be considered as a ring species as both genomic and geographic evidence coincide in indicating that its differentiation took place in allopatry.

Multi-species phylogenies

In contrast to single-species assessments, studies on avian niche evolution based on multi-species approaches typically consider much longer timescales, e.g. when studying genera or families that frequently diversified over millions of years. Phylogenetic comparative methods (Felsenstein 1985, Webb et al. 2002) are typically (although not exclusively) used for a direct integration of niche models into phylogeographic studies (Chan et al. 2011, Alvarado-Serrano and Knowles 2014). In an early avian study, Rice et al. (2003) used SDMs to reconstruct the niche evolution in *Aphelocoma* jays and found strong deviation from niche conservatism; however, these results were contradicted by McCormack et al. (2009). On the basis of tests against explicit null models and measurements of niche overlap in multivariate space (Warren et al. 2009), McCormack et al. (2009) rejected such a pattern of niche divergence, which contradicts models of ecological speciation assumed to be prevalent in this group.

Further studies testing different aspects of niche conservatism found mixed signals in several avian lineages (Table 2).

Table 2. Summary of studies investigating avian niche conservatism on large temporal scales using SDMs and phylogenies.

Reference	Niche conservatism	Study group	Remarks
Anciães and Peterson 2009	mostly yes	family Pipridae	sister species mostly similar
Cooney et al. 2016	no	7657 bird species	linked to species diversification
Gómez et al. 2016	yes and no	family Parulidae	seasonal niche evolution
Laube et al. 2015	no	genus <i>Sylvia</i>	seasonal niche evolution
Martínez-Meyer et al. 2004	yes and no	genus <i>Passerina</i>	seasonal niche evolution
McCormack et al. 2009	yes	genus <i>Aphelocoma</i>	with null models (Rice et al. 2003)
Miller et al. 2013	yes	family Meliphagidae	different results for precipitation vs temperature
Nyári and Reddy 2013	yes and no	genus <i>Pomatorhinus</i>	differences among clades, areas, age of clades
Pearman et al. 2014	no	European breeding birds	climatic niches less conservative than trophic niches
Peterson and Nyári 2007	yes	<i>Schiffornis turdinus</i> complex	intraspecific pattern among phylogroups
Peterson and Holt 2003	yes and no	Mexican bird species and subspecies	climatic and vegetation data
Peterson et al. 1999	yes	Mexican birds	sister species along faunal divide
Rice et al. 2003	no	genus <i>Aphelocoma</i>	without null models (McCormack et al. 2009)

For instance, Nyári and Reddy (2013) revealed patterns of niche filling and convergent evolution among different lineages of the babbler genus *Pomatorhinus* for different climatic variables. Furthermore, apart from some interesting exceptions, niches in manakins (Pipridae) are conservative in terms of ecological landscape and climate (Anciães and Peterson 2009). Miller et al. (2013) studied niche conservatism in Australian honeyeaters (Meliphagidae) and showed an expansion of some lineages into drier environments. Moreover, the climatic niche of European breeding birds is less conservative than their trophic niche (Pearman et al. 2014). In conclusion, avian niche evolution is by no means a straightforward process, and the high overall variability of different outcomes in recent studies (Table 2) calls for systematic assessments on larger taxonomic and geographic extents, where SDMs will play a crucial role.

Seasonal niches in time and space

Considerations on ecological niches are more complex in organisms with seasonal distributions, which may require a seasonal niche concept (Martínez-Meyer et al. 2004, Nakazawa et al. 2004, Engler et al. 2014). Realized niches indeed can strongly differ through time in migratory birds that inhabit different areas during their annual cycle (Berthold 2001). Nomadic and irruptive species can reveal an even more complex pattern (Reside et al. 2010,

Cottee-Jones et al. 2015, Eyres et al. 2017). Typical migratory birds show a breeding and a non-breeding (wintering) distribution. Due to their high mobility, migratory birds can either follow their climatic niche from one season to another (so-called ‘niche followers’ or ‘niche trackers’) or they experience different climatic conditions (i.e. ‘niche switchers’; Joseph 1996, Joseph and Stockwell 2000, Martínez-Meyer et al. 2004, Williams et al. 2017). Yet, the differentiation between ‘niche following’ or ‘niche switching’ species is not attributed to migration per se but surely has implications for the evolution of migration (Nakazawa et al. 2004). Still, SDM studies focusing on migratory species are rare, and results do not point to a clear pattern of tracking or switching climatic niches (Table 3). Modeling approaches were also used to identify little-known wintering areas (Walther et al. 2004), to address the constraints of migration (Toews 2017), or to evaluate the effects of climate change on migratory birds (Lemoine and Böhning-Gaese 2003, Doswald et al. 2009). Seasonal niches also have implications for more application-oriented research on habitat use and conservation (see ‘Assisting conservation’; Osborne et al. 2001, Osborne and Suárez-Seoane 2008, Suárez-Seoane et al. 2008). A subtle case of niche switching is represented by species that change habitat and/or breeding site within the same season, mostly from one brood to the subsequent one(s) (Brambilla and Rubolini 2009). Such a switch may occur on local or regional scales (Powell and Frasch 2000, Gilroy et al. 2010, Brambilla and Pedrini 2011), to large

Table 3. Seasonal aspects of occupied climatic niches (‘switching’ and ‘following’) in migratory birds.

Reference	Niche comparison	Study species	Remarks
Gómez et al. 2016	following and switching	wood warblers (Parulidae)	migrants rather track niches, residents rather switch niches
Joseph and Stockwell 2000	following	<i>Myiarchus swainsoni</i>	stopover sites considered
Klaassen et al. 2010	switching	<i>Circus aeruginosus</i>	stopover sites considered
Laube et al. 2015	switching	<i>Sylvia</i> warblers	also land cover considered
Marini et al. 2010	following	<i>Amazona pretrei</i>	tropical study area
Marini et al. 2013	switching	<i>Alecturus tricolor</i>	apparently not migratory, little known species
Martínez-Meyer et al. 2004	following and switching	<i>Passerina</i> buntings	conserved wintering niches
Nakazawa et al. 2004	following, switching, mixed	21 Nearctic-Neotropical migrants	majority: niche following
Papeş et al. 2011	(presumed) following	<i>Procnias tricarunculatus</i>	tropical study area
Pérez-Moreno et al. 2016	following, switching, mixed	13 Nearctic-Neotropical migrants	intra-seasonal changes considered
Williams et al. 2017	switching	<i>Cuculus canorus</i>	temporally explicit SDMs, presence data from satellite tracking

(e.g. continental) scales (Rohwer et al. 2009). SDMs may greatly help defining the spatial and temporal variation of habitat suitability for those species, but until now their use has been limited to a few cases (Brambilla et al. 2012, Sardà-Palomera et al. 2012). However, new frameworks that incorporate such diverging species–environment relationships in time and space (e.g. multi-state SDMs; Frans et al. 2017) may facilitate future studies. Ignoring these issues could in turn induce an underestimation of areas needed for effective conservation (Runge et al. 2016) or an over-prediction of ranges in general (Reside et al. 2010). A careful selection of presence records is hence pivotal to limit such risks (Chamberlain et al. 2013). Future prospects for integrative studies on avian seasonal niches include a more in-depth look at different migratory strategies (Eyres et al. 2017), a consideration of flyways and the extension to further avian groups and less well-studied migration systems.

Outlook

SDMs have greatly changed the way we study biodiversity, enhancing our understanding from broad biogeographic patterns to local applications alike. In this review, we summarized the current state of SDM applications in ornithology and pointed to general, as well as specific, challenges related to avian systems. So, what is the way forward?

From our point of view as avian ecologists, we need further developments of SDM techniques concerning conservation issues. In particular, we need more studies that link SDM predictions with demography and with temporal changes in habitat suitability and species distribution. Additionally, we need to better understand the conservation implications of dispersal and biotic interactions, and how to account for both in SDMs (Heikkinen et al. 2007). Finally, we need better evaluations of current and future conflicts with other human activities – even though first attempts in this direction have been made (Harris et al. 2012). A holistic perspective of species' dispersal abilities and the effects of biotic interactions on species distributions would also enhance general and applied studies concerning climate and habitat change, particularly when planning conservation strategies for target species (see Jeschke and Strayer 2008 and Wiens et al. 2009 for overviews).

In addition, the combination of avian SDMs with other data sources offers new opportunities to enhance SDM predictions in birds at various spatial and temporal scales. For instance, Campos-Cerquiera and Aide (2016) showed the prospects of using an autonomous bioacoustic monitoring scheme with automated species identification to inform range predictions in the rare elfin woods warbler *Setophaga angelae*. After removing false-positives in such a data set (Campos-Cerquiera and Aide 2016), bioacoustic monitoring can deliver very accurate presence–absence information that could also be used for SDM approaches in rare, cryptic, nocturnal or otherwise hard to find bird species. Also, the identification of individuals in species with a complex song (Petrusková et al. 2015) might allow study of species–environment relationships in SDMs at the individual level

to e.g. link individual performance to predicted population- or species-level habitat suitability.

While it has been proposed that niche conservatism is prevalent along short to moderate time scales (Peterson 2011), a comparison of evidence for avian (climatic) niche conservatism over different time scales reveal ambiguous patterns. Fortunately, methodological toolboxes are now available and filled with algorithms to study eco-evolutionary processes including the reconstruction of ancestral niches (Evans et al. 2009, Revell 2012, Garamszegi 2014 and references therein). At the same time, highly-resolved phylogenetic and genomic data are available for an increasing number of avian taxa (Jetz et al. 2012, Jarvis 2016), and birds might even be the first well-known class of animals for which a comprehensive phylogeny will be available in the near future (Zhang 2015). The quantification of ecological niches has benefited from new methodological approaches (Broennimann et al. 2012, Blonder et al. 2014, but see Qiao et al. 2016), which cope with the multivariate parameters typical for underlying environmental data. Future studies using novel tools and further refined data of past environments will greatly help to gain a holistic understanding of avian niche evolution and its related pattern and processes.

Finally, genetic data offers another promising source of information that could be included into SDMs (Fordham et al. 2014, Gontelli and Stanton-Geddes 2015). This integration began with phylogenetic studies on niche evolution (summarized in Chan et al. 2011, Alvarado-Serrano and Knowles 2014; see section above and Eyres et al. 2017 for an overview in birds), but the use of finer-scale genetic information together with SDMs is a much more recent innovation (Fordham et al. 2014). Using information generated from genetic markers systems such as microsatellites or single nucleotide polymorphisms can add relevant insights into population structure and refine SDMs below the species level (Gonzalez et al. 2011). Due to local adaptation, species–environment relationships may change among genetic groups, and data pooling at the species level may consequently lead to an overestimation of potential distribution (Oney et al. 2013). This source of uncertainty can be crucial when assessing climate change impacts (Valladares et al. 2014, Gontelli and Stanton-Geddes 2015). The majority of studies with birds as focal species use SDMs alongside fine-scale genetic information to supplement hypotheses on the recent evolutionary history of the species (McKay et al. 2010, Qu et al. 2012, Pavlova et al. 2013, Barrientos et al. 2014, Congrains et al. 2016). Genetic information is also used to study the impact of global change on species' standing genetic variation (Ralston and Kirchman 2013, Habel et al. 2014, Walsh et al. 2015) and functional connectivity (Manthey and Moyle 2015). With the emergence of genome sequencing and its broad applications in avian systems (see Kraus and Wink 2015, Toews et al. 2016 for recent reviews), new insights will be gained into the adaptive variation of single genes or groups of genes on a multitude of avian systems in the near future – including non-model organisms. Thus, instead of quantifying species–environment relationships, SDM may contribute towards a better understanding of genotype–environment

relationships of differentially expressed genes at a genomic, transcriptomic or even epigenomic level (Manthey and Moyle 2015, Mason and Taylor 2015).

Considering their current and potential new uses, SDMs will likely remain an important tool in the ornithologists' toolbox in the future. As shown throughout our review, birds fulfill many prerequisites to work on remaining open questions in biogeography, ecology, and evolution, given their excellent data coverage and high level of what we already know about birds (Fig. 1). Most importantly, conservation applications will benefit from steadily increasing resolution in occurrence records and environmental predictors spanning across the earth to meet the challenges birds face in the Anthropocene. This development is particularly true for invasive birds, where studies so far have focused only on a handful of these species. Again, given the excellent knowledge about birds, studying additional invasive species will likely gain further insights into the processes facilitating (avian) invasion success. The pioneering role birds have can also be used to improve studies in marine systems, to conduct optimized species richness predictions or to enhance our perspective on how we approach the niche as such – pointing towards a more dynamic consideration of this entity. Therefore, we hope for many more ground-breaking avian SDMs yet to come.

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Supplementary material (Appendix JAV-01248 at <www.avianbiology.org/appendix/jav-01248>). Appendix 1.