Reviews

Integrating demography, dispersal and interspecific interactions into bird distribution models

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Species' ranges are primarily limited by the physiological (abiotic) tolerance of the species, described by their fundamental niche. Additionally, demographic processes, dispersal, and interspecific interactions with other species are shaping species distributions, resulting in the realised niche. Understanding the complex interplay between these drivers is vital for making robust biodiversity predictions to novel environments. Correlative species distribution models have been widely used to predict biodiversity response but also remain criticised, as they are not able to properly disentangle the abiotic and biotic drivers shaping species' niches. Recent developments have thus focussed on 1) integrating demography and dispersal into species distribution models, and on 2) integrating interspecific interactions. Here, I review recent demographic and multi-species modelling approaches and discuss critical aspects of these models that remain underexplored in general and in respect to birds, for example, the complex life histories of birds and other animals as well as the scale dependence of interspecific interactions. I conclude by formulating modelling guidelines for integrating the abiotic and biotic processes that limit species' ranges, which will help to disentangle the complex roles of demography, dispersal and interspecific interactions in shaping species niches. Throughout, I pinpoint complexities of avian life cycles that are critical for consideration in the models and identify data requirements for operationalizing the different modelling steps.

Mitigating rapid biodiversity loss is one of the most vital challenges today. Even under most conservative assumptions, we are currently experiencing biodiversity losses that are up to 100 times higher than the natural extinction rate (Ceballos et al. 2015). And even worse, biodiversity loss is predicted to further increase under climate change (Pereira et al. 2010). The consequences are difficult to gauge. Losing single species could have cascading effects on entire ecosystems and could mean loss of important ecosystem functions and services (Cardinale et al. 2012). For example, birds provide important services by transporting nutrients, by dispersing seeds or by acting as disease control agents through scavenging.

Models have established as important tools in ecology that help testing hypotheses about biodiversity functioning and that help making predictions of potential dynamics, for example under climate change. Correlative species distribution models (SDMs) are by far the most widely used modelling tool in biodiversity research as they are comparably easy to use and work with relatively simple species occurrence data (Guisan and Zimmermann 2000, Elith and Leathwick 2009). However, the value of SDMs in predicting climate change induced biodiversity changes has been questioned for several reasons. For example, SDMs implicitly assume the observed species–environment relationship to be at equilibrium and to remain constant under future climate.

They thus ignore any transient demographic and dispersal dynamics, extinction debts, and changing interspecific interactions (Araújo and Guisan 2006, Zurell et al. 2009, 2016a). Also, combining single-species SDMs to construct site-specific species lists currently fails to correctly predict community assemblage, which may in part relate to unaccounted interspecific interactions (Baselga and Araújo 2010, Guisan and Rahbek 2011) as well as to scaling issues (Zurell et al. 2016b). Consequently, we currently observe two major research avenues aimed at 1) developing more dynamic and demographic approaches to predict species response to environmental change but which hitherto focus on single species only, and 2) developing multi-species models that account for interspecific interactions but which hitherto ignore either transient dynamics and demography or ignore spatial dynamics.

In this review, I will summarise the current state of the art in these modelling approaches and discuss necessary model developments to meet the challenges of understanding and predicting biodiversity and specifically avian diversity under current and future climates. First, I will revisit the theoretical background on the ecological niche concept and its relation to community assembly, and give an overview on current demographic models and multi-species models. I will discuss limitations of these approaches and promising future directions, especially in relation to the complex life histories of
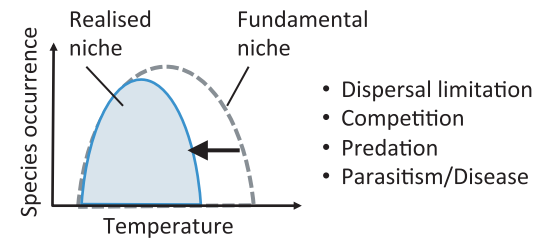
birds. Because of the vast empirical knowledge on avian systems and the high-quality data, birds offer unique possibilities of developing and refining more realistic but also more generic models for predicting biodiversity dynamics under global change (Engler et al. 2017).

The ecological niche concept and community assembly

Central to biodiversity research is the notion that life is not evenly distributed on Earth but species occur in distinct places and habitats. The geographic area where a species can be found is usually termed the species range. But what limits this range? We know that most species are fundamentally constrained by their physiological tolerance to environmental conditions and their resource requirements. For example, birds could be constrained by temperature due to its effect on thermoregulatory processes and on resource availability (Methorst et al. 2017). This relationship between species occurrence and environment is called the species niche and comprises all environmental conditions where the species can exist indefinitely exhibiting a positive net growth rate r (Hutchinson 1957).

Inferring the ecological niche of species from observational data is challenging because biogeographic history, demographic processes and interspecific interactions also affect the presence of a species. For example, the temperature extremes found within the geographic range of a species may be less than what the species could physiologically tolerate and thus less than what could be measured in a laboratory. Hutchinson distinguished the fundamental and the realised niche of a species. The fundamental niche refers to all abiotic constraints that allow positive population growth. Originally, the realised niche was formally described as those parts of the fundamental niche to which the species is confined due to competitive exclusion and other negative interactions (Hutchinson 1957). Refined niche theory acknowledges several more processes including demographic and community processes that 1) constrain and thus shrink the realised relative to the fundamental niche, including dispersal limitation and negative interspecific interactions (Fig. 1a), and processes that 2) expand the realised relative to the fundamental niche, including source-sink dynamics, time-delayed extinctions and facilitation (Fig. 1b) (Pulliam 2000, Bruno et al. 2003, Holt et al. 2005, Schurr et al. 2012, Diez et al. 2014). Also, (genetic and behavioural) adaptation may lead to expanded niches under climate change but, as pointed out above, most of the modelling approaches that I will discuss here focus on contemporary demographic and community processes. Because of these dynamic processes, the realised niche may vary across time and space (Holt 2009), and also across the life cycle of species (Taboada et al. 2013). For example, species may utilize different habitats and resources for key events within their life cycle such as reproduction, overwintering and dispersal (Naves et al. 2003, Holt 2009, Jacob et al. 2015, Rotllan-Puig and Traveset 2016). This is most prominent in migratory birds that move between distant regions on a seasonal basis, and for which both seasonal niche-tracking and niche-switching have been reported (Laube et al. 2015, Gómez et al. 2016, Eyres et al. 2017).
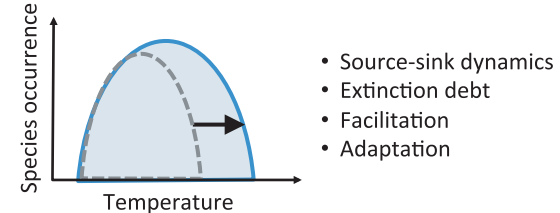

Figure 1. Schematic representation of biotic factors restricting or expanding the realised niche relative to the fundamental niche. Adapted from Bruno et al. (2003).

Community assembly theory is closely linked to the niche concept. Often, the metaphor of filters (Weiher and Keddy 1999) is used to describe how species from the regional species pool colonise and interact to form local communities (Fig. 2; Chase 2003, Leibold et al. 2004, HilleRisLambers et al. 2012). First, the dispersal filter refers to spatial and stochastic processes and determines whether a species can reach a specific geographic location depending on its dispersal capacity and chance events. Second, the environmental filter (or abiotic niche filter) selects those species that can establish and maintain positive population growth under the prevailing environmental conditions. Third, the biotic niche filter describes the processes of intra- and interspecific interactions that may affect a species' presence in a location. In reality, these filters do not simply act as one-directional sieves but complex feedbacks exist between species and filter levels, meaning that the species themselves can also affect the filter processes (HilleRisLambers et al. 2012). BAM (biotic, abiotic, movements) diagrams describe the same three processes affecting species' presence in a location, and more explicitly emphasise the interplay between these (Soberón and Nakamura 2009).

The concepts of limiting similarity and niche partitioning are important to understand long-term coexistence between species in local communities (MacArthur and Levins 1967). Contemporary coexistence theory formalises these ideas in a mechanistic framework that distinguishes between niche differences and differences in fitness (i.e. competitive dominance; Chesson 2000). Relative niche differences are important as they act as stabilising mechanisms (niche partitioning) whereas average fitness differences (inequalities) favour dominance and, in the absence of stabilising niche differences, lead to competitive exclusion (Fig. 2; Chesson 2000, Adler et al. 2007, Valladares et al. 2015). To make it more complicated, coexistence may also depend on the life cycle and the annual cycle of the interacting species. For example, stabilising mechanisms in plants have been shown to be strongest
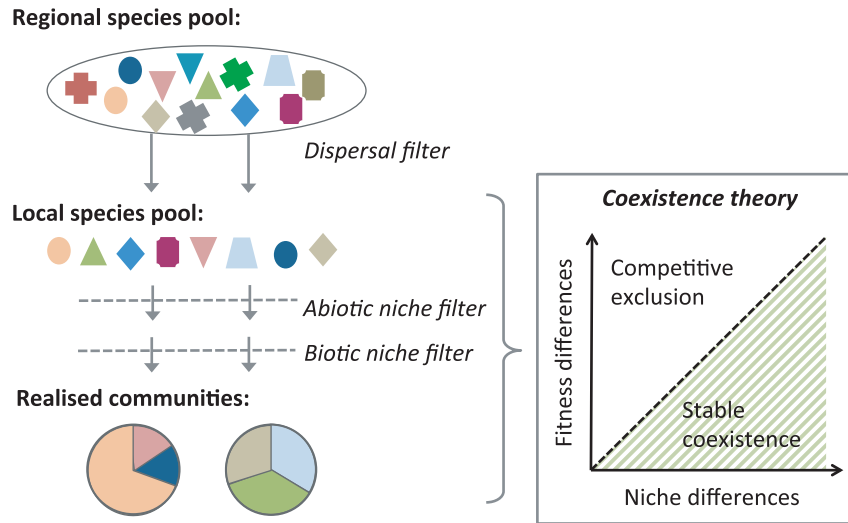
Figure 2. Schematic representation of the ecological filtering cascade and its relation to coexistence theory (HilleRisLambers et al. 2012). Species from the regional species have to pass different filters to establish within local communities. The dispersal filter selects species from the regional species pool that are able to colonise local sites depending on their dispersal ability and chance events. The abiotic niche filter and the biotic niche filter select those species that are able to maintain positive population growth under the given environmental conditions according to their physiology and resource requirements, and under given inter- and intraspecific interactions. Coexistence theory provides a framework for predicting the outcome of these niche filters (Chesson 2000). Species may differ in their abiotic niche requirements and in their competitive ability (ecological fitness). Large fitness differences between species will lead to competitive exclusion of the inferior competitor. These fitness differences can be overcome by niche differences and species can stably coexist whenever the niche differences are larger than the average fitness differences. Overall, relative niche and fitness differences will determine the presence and abundance of species in realised local communities.

in early life stages (Chu and Adler 2015). In birds, it has been shown that competitive dominance and, thus, fitness differences may differ between seasons; for example, great tits are the dominant competitors for roost and nest sites whereas coexisting blue tits are the dominant competitors for insect larvae in the early breeding season (Fig. 4; Dhondt 2012). Such ontogenetic and seasonal shifts in coexistence mechanisms make it difficult to identify the true competitive mechanisms with current modelling approaches (Wittwer et al. 2015). Understanding the complex interplay between
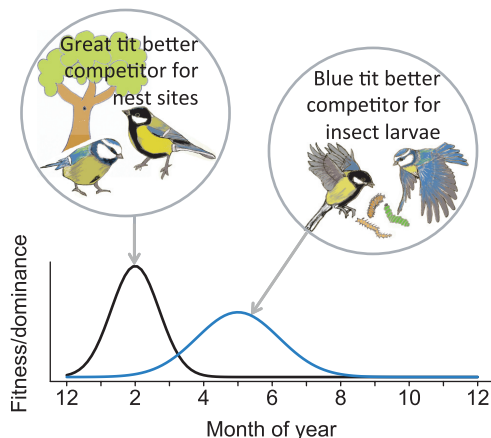

Figure 3. Proposed coexistence mechanism between great tits and blue tits. Coexistence could be maintained by seasonally shifting competitive dominance (fitness) with great tit being the dominant competitor for roost sites and nest sites, and blue tit being the dominant competitor for insect larvae during breeding period (Dhondt 2012, Wittwer et al. 2015). Illustrations by D. Zurell.
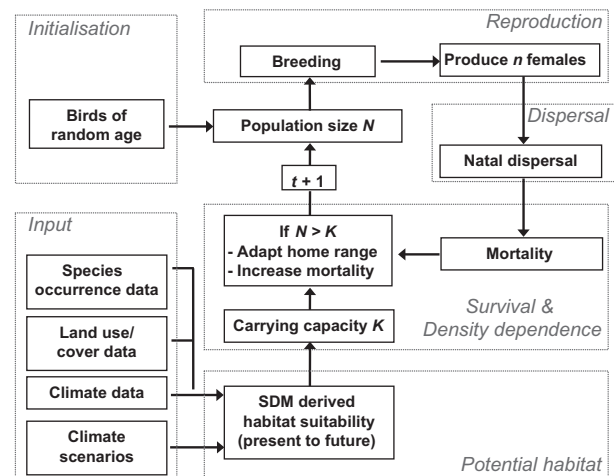

Figure 4. Simplified flow chart for hybrid model of Swiss black grouse population as described in Zurell et al. (2012). Species occurrence records and environmental data are used to parameterise the SDM. Then, the SDM is used to predict habitat suitability under current and future climate, which serves as input to the individual-based black grouse model (IBM). Initially, birds of random age are distributed in suitable cells. In each simulation year, female black grouse may breed and produce n juveniles that will disperse to new areas before the next breeding period. Dispersal distance is drawn from a negative exponential dispersal kernel, but individual birds can make adaptive settlement decisions to avoid unsuitable and overcrowded habitats and they also avoid traversing widely unsuitable area. All birds are subject to mortality. If population size exceeds local carrying capacity, which increases linearly with SDM derived habitat suitability above a minimum threshold, then individuals will disperse to less crowded habitats in the nearest neighbourhood or mortality is increased. Illustration adapted from Zurell (2011).

these processes and how they scale up to affect communities, however, is important because climate change will likely have non-trivial and possibly unprecedented effects on species range and community dynamics (Williams and Jackson 2007, Blois et al. 2013).

Current state of demographic and community models

The theoretical excursion above pinpoints many different factors and processes that potentially govern the presence of a species in a specific location. Many of these factors are not accounted for in traditional SDMs. This leads to two main problems in global change research. First, climate impact predictions by SDMs may be fallacious, for example because they do not consider any transient, time-delayed species responses (Zurell et al. 2009, 2016a). Hence, many authors urged to supplement (mainly single-species) SDMs with more mechanistic approaches (Araújo and Guisan 2006, Thuiller et al. 2008). However, as I will discuss below, not all of the suggested modelling approaches are able to overcome fundamental limitations of SDMs, for example the equilibrium assumption. This leads to the second great challenge that SDMs are not able to properly disentangle the realised from the fundamental niche (Araújo and Guisan 2006, Elith and Leathwick 2009, Schurr et al. 2012) because they do not explicitly consider any of the demographic and community processes presented in Fig. 1. For example, SDMs may estimate a smaller ecological niche than the species is actually able to occupy if the range or the niche of the species were not completely filled. This could happen because of dispersal limitation since the last glacial maximum (Sandel et al. 2011) or during invasion (Strubbe et al. 2013), or because the species is excluded from parts of its range due to interspecific competition (Laube et al. 2013) among others. Such bias in the fitted species–environment relationship would hamper both our understanding of what limits a species range and our ability to predict to novel environments.

Many different models exist that move beyond the static and single-species view of SDMs ranging from phenomenological to mechanistic approaches (Pereira et al. 2010, Dormann et al. 2012, Ehrlén and Morris 2015). In the following, I concentrate on models that focus on the niche concept, and can, in principle, be parameterised and calibrated from (broadly) field-measured data and do not require experimental knowledge (e.g. on physiology, Kearney and Porter 2004, Buckley 2008). After all, a main advantage of SDMs over most other approaches is that they can be readily applied to large numbers of species for which only limited data are available, and can thus provide a quick and purposeful screening of potential climate change impacts on biodiversity. Hence, on the one hand, we need models that are able to overcome fundamental limitations of SDMs, and on the other hand, we need models that are still comparably easy to apply to many different species.

It is important to note that the models discussed herein all make the fundamental assumption of niche conservatism and currently ignore any genetic and behavioural adaptations that could take place in response to climate and land use change. However, such adaptations have been observed to happen rapidly and in ecological time scale, for example

phenological changes in the timing of breeding and migration or changes in phenotypic plasticity among others (Nussey et al. 2005, Jonzén et al. 2006, Charmantier et al. 2008). Thus, although this review mainly focuses on how demographic, dispersal and community processes shape species' niches and their response to future environments, the integration of adaptive mechanisms is an important and ongoing research field and further model development is necessary in this direction (Urban et al. 2016), which I will briefly discuss at the end of this review.

Demographic models (of single species)

Over recent years, several demographic frameworks have been developed (or revived) for predicting (single) species niche and range dynamics more mechanistically (Franklin 2010, Pereira et al. 2010, Ehrlén and Morris 2015, Lurgi et al. 2015). Their main characteristic is that they do not only describe the abiotic constraints on the niche but also explicitly consider the fundamental demographic processes of birth, death and dispersal (or a subset of these processes). Several of these models still rely on SDMs and use SDM-derived habitat suitability to describe the niche and to constrain demography. Often, these kinds of models are referred to as hybrid SDMs (Thuiller et al. 2008). In the simplest case, habitat suitability maps predicted by SDMs are coupled with simple dispersal models that simulate colonisation of suitable area (Engler and Guisan 2009, Franklin 2010), and thus allow the identification of potential dispersal limitations under future climate change (Midgley et al. 2006, Normand et al. 2013).

More complex approaches supplement SDMs with population dynamic models that allow the estimation of population viability by explicitly modelling population growth. These hybrids are actually a rather diverse group that may differ widely in 1) the type of population dynamic model used, and 2) how exactly SDM derived habitat suitability and the population dynamic model are coupled. 1) The population dynamic model can be formulated as a classic meta-population model with colonisation and extinction of patches, as a demographic model based on logistic growth, on a matrix population model or on an individual-based model among others (Lurgi et al. 2015). 2) We can distinguish at least three different coupling types. Binary output from SDMs can be used to distinguish suitable from unsuitable areas and use these patch-matrix maps as underlying landscape for the population model (Akçakaya 2000, Wiegand et al. 2004, Cabral and Schurr 2010). In this case, demographic processes are simulated independent of the SDM but populations are restricted to those areas that the SDM predicted to be suitable. Alternatively, SDM derived habitat suitability can be used to scale the carrying capacity in the population model (Keith et al. 2008, Brotons et al. 2012, Zurell et al. 2012; also see Fig. 4) or to scale vital rates in the population models, for example survival (Dullinger et al. 2012) or recruitment (Albert et al. 2008).

A main conceptual problem of these hybrid models is that there is little theoretical and empirical support for the relationship between SDM derived habitat suitability and carrying capacity or vital rates (Thuiller et al. 2014, Ehrlén and Morris 2015). The shape of this relationship has

been assumed to be linear (Keith et al. 2008), linear above a presence–absence threshold (Zurell et al. 2012) or sigmoidal (Dullinger et al. 2012). The choice is not trivial as these relationships can result in largely different predictions (Zurell et al. 2016a). Furthermore, hybrids still make the fundamental assumption that the species is at equilibrium with its environment. If this assumption is not met, then separately fitting the SDM and the population model may actually lead to circularity problems. If, for example, a species is dispersal limited, then the SDM is implicitly accounting for this dispersal limitation in the niche estimate and the population model will account for it again, such that dispersal is actually accounted for twice (Gallien et al. 2010). Thus, simply coupling SDM output to population models does not allow disentangling the effects of demography and dispersal on the realised niche (Schurr et al. 2012). To overcome this limitation, Pagel and Schurr (2012) introduced a hierarchical Bayesian framework called dynamic range models (DRMs) that simultaneously estimate the parameters of a demographic and a dispersal model as well as the environmental response of demographic rates. DRMs thus avoid using SDMs but directly relate the intrinsic population growth rate of the population model to environmental variables and directly account for any dispersal effects, which allows disentangling abiotic and demographic components of the realised niche and should thus be advantageous over SDMs (Pagel and Schurr 2012, Schurr et al. 2012).

Using simulated data ('virtual ecologist approach', Zurell et al. 2010), we tested prediction accuracy of different SDM hybrids and DRMs under climate change and under different demographic and community processes (Zurell et al. 2016a). Surprisingly, although we found DRMs produced a better fit to current data, they often showed poorer predictions than some of the SDM hybrids under climate change scenarios. This was mainly attributable to available prior knowledge on process rates (e.g. dispersal) and the structural realism of the population dynamic model (i.e. correctly specified mechanisms and processes, Singer et al. 2016). Specifically, DRMs used the simple Ricker model (discrete version of logistic growth model) to represent population dynamics, ignoring any life-stage dependent responses to the environment, for example that fecundity depended on environment but survival did not. Thus, although DRMs are well grounded in ecological theory (cf. Fig. 1) and provide a major advance for disentangling different niche components (Schurr et al. 2012), it will need further model development into a more generic framework that allows taking into account complex life cycles and different environmental response of single life stages in order to make more robust predictions under climate change (Zurell et al. 2016a).

In bird distribution modelling, several studies have used dynamic occupancy modelling to study recent range dynamics (Kéry et al. 2013, Butcher et al. 2014, Yackulic et al. 2015). Occupancy is described by colonisation and extinction processes (as in metapopulation models, Hanski 1998), which can be expressed as functions of environmental covariates (Kéry et al. 2013). These models have similarities to DRMs in that they are estimated in a hierarchical framework, allow disentangling the different factors determining range dynamics, and account for imperfect detection through an observer model (Guillera-Arroita 2017). Also, attempts have

been made to incorporate different life stages (Sutherland et al. 2014), and they have been successfully applied in climate impact analyses (Jones et al. 2016). In the future, their ability to adequately predict temporal dynamics following climate change should be compared to other range dynamic approaches (Zurell et al. 2016a).

Multi-species models

Results from our model comparison using simulated data (Zurell et al. 2016a) also showed that future predictions by single species models were especially poor under complex community dynamics. The importance of interspecific interactions is now widely acknowledged (Blois et al. 2013), and scientists have begun to develop ideas and model frameworks to account for these (Kissling et al. 2012, Wisz et al. 2013), aided by recent computational advances. Current multi-species frameworks can be distinguished into multivariate regression approaches based on static distribution data, the so-called joint species distribution models (JSDMs; Clark et al. 2014, Pollock et al. 2014, Warton et al. 2015, Ovaskainen et al. 2016b), and multivariate population models based on temporal abundance dynamics (Mutshinda et al. 2011, Wittwer et al. 2015).

Both model types aim at explaining the dependence between species, the joint probability of occurrence that is not accounted for by environmental variables alone (Clark et al. 2014). If the ranges of two species A and B overlap because they share similar environmental requirements, then the main question is whether they will occur independently of each other at a site or show some form of positive or negative association that is not explained by environment, meaning their probability of occurrence is higher or lower conditional on the presence of the other species (Fig. 5a). If both species are independent, then they could or could not co-occur simply by chance (Fig. 5b). If the species are not independent, then information of species B is necessary to predict the occurrence probability of species A. In the extremes, species A would only occur when B is present (Fig. 5c) or species A and B would always exclude each other (Fig. 5d).

To date, a few different JSDM algorithms have been implemented that differ in how the joint distribution is estimated (Warton et al. 2015). Unstructured covariance models estimate the occurrence probability of multiple species simultaneously and decompose species co-occurrence patterns into shared environmental response and residual patterns of co-occurrence (Ovaskainen et al. 2010, Pollock et al. 2014, Royan et al. 2016). As output, we obtain a covariance matrix of pairwise interactions. Latent variable models represent a computationally more efficient method based on unobserved (latent) variables that induce correlation between species (Letten et al. 2015, Warton et al. 2015, Ovaskainen et al. 2016a). These models do not estimate all pairwise residual correlations, but shrink the parameter space to a minimum number of latent variables that best describe the residual covariance between the species.

Unfortunately, although constituting a major advance in biodiversity modelling, it is not clear yet in how far JSDMs could fulfil our wish to model interspecific interactions. Specifically, the residual co-occurrence (joint distribution) may

(a) Joint probability

$$P(A \text{ and } B) = P(A|B) \cdot P(B)$$

(b) Species independent
$P(A|B) = P(A) = 0.5$

(c) Species always co-occur
$P(A|B) = 1$

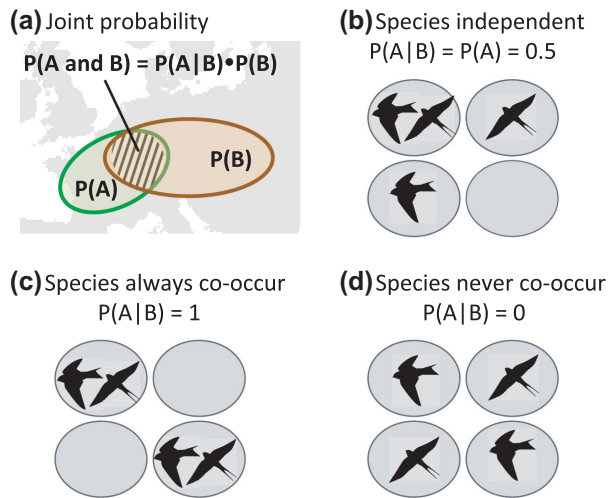**(d)** Species never co-occur
$P(A|B) = 0$

Figure 5. Schematic representation of joint probabilities of occurrence of two species A and B. (a) If species share parts of their environmental niche and their ranges overlap in space, then the joint probability P(A and B) expresses the probability that the two species will co-occur at any one site. (b–d) Show the potential co-occurrence patterns of two species, each with a prevalence of 0.5, that are (b) independent, meaning they could or could not co-occur simply by chance, and the extreme cases of species that are (c) always co-occurring and (d) mutually exclusive. (b–d) Adapted from M. McCarthy.

indicate interspecific interactions but may also be caused by missing or sub-scale environmental covariates (Clark et al. 2014, Pollock et al. 2014, Harris 2015). Especially the latter is an important source of bias that is inherent in common species inventory data such as breeding bird atlases that are gridded to a certain resolution and may not necessarily reflect the spatial requirements of the many different species (Zurell et al. 2016b). It would be desirable to rigorously test under which circumstances JSDMs will reliably detect interspecific interactions, and how this is affected by complicating factors such as scale dependence. After all, interactions are spatially very localised processes between (small) numbers of individuals. For example, birds may compete locally for resources, for shelter and for nest sites (Dhondt 2012, Zurell et al. 2015). By contrast, the scale of data collection and analyses is often at plot or region scale, which may lead to information loss and distorted relationships (Clark et al. 2014). Additionally, it remains open, which interaction mechanisms could possibly be detected by JSDMs, at which scale, and which data types (co-occurrence or co-abundance) are required. A recent simulation study showed that co-occurrence patterns from predator–prey relationships could equal the co-occurrence patterns from either competitive or facilitative interactions (Araújo and Rozenfeld 2014). As the residual correlations estimated by JSDMs simply indicate whether co-occurrence is lower or higher than expected by chance given the environment, we can assume that current JSDM implementations will not allow unambiguous distinction of predator–prey (or consumer–resource) relationships and competitive or facilitative interactions, and will need further model development in this respect. Another challenge is that interspecific interactions are not constant in space and time (Callaway et al. 2002, Meier et al. 2011, He et al. 2013, Lawrence and

Barraclough 2016), and it has thus been proposed that non-stationarity in interaction coefficients should be considered in future research (Kissling et al. 2012, Wisz et al. 2013, Warton et al. 2015) but hitherto only one worked example using multi-species occupancy modelling exists (Rota et al. 2016).

A few examples on multivariate population models exist that use time series of multi-species co-occurrence or co-abundance to jointly estimate the relative importance of environmental stochasticity, environmental variables as well as intra- and interspecific interactions using Hierarchical Bayesian approaches (Mutshinda et al. 2009, 2011, Wittwer et al. 2015). Although hitherto confined to single communities, which ignores any spatial (meta-community) dynamics, these multivariate population models provide a promising way forward as they allow disentangling important components of coexistence theory, namely environmental dependence of demographic rates as well as intra- and interspecific density regulation.

Towards multi-species dynamic distribution models

What does all this imply for bird distribution modelling? Some examples exist that underline the merit of using dynamic distribution models for predicting avian species response to climate and land use change (Brotons et al. 2012, Zurell et al. 2012, Aben et al. 2016) and also for using multi-species modelling approaches (Royan et al. 2016) as large scale patterns of bird assemblages seem to be, at least partly, affected by interspecific interactions (Zurell et al. 2016b). Nevertheless, both demographic models and multi-species models still have many limitations and uncertainties, and the necessary step forward would be to develop an integrated modelling framework that is able to take into account all of the demographic, dispersal and interspecific processes acting on the niche (Fig. 1) (Urban et al. 2016). Operationalizing such a framework for specific avian systems, however, will not be an easy task and will require adequate screening methods and standard protocols to define the necessary model complexity and data requirements. At the same time, the large amount of high-quality data that is available on birds, also make birds a unique study system for improving on current modelling approaches that will also aid biodiversity modelling of other species groups. If we want to make robust predictions under global environmental change, it requires models that are structurally realistic and contain all (and only) relevant mechanisms that govern the dynamics in the specific system (Singer et al. 2016). Also, the additional effort of fitting complex mechanistic models needs to be well justified and targeted as both time and data requirements can be huge. If the system under study is highly stochastic and thus noisy, then simple SDMs may even outperform more complex models (Zurell et al. 2016a). In that sense, I see the different modelling frameworks discussed above as complimentary rather than opposing modelling strategies, each with its own strengths and weaknesses. Thereby, simpler models (containing less process detail and requiring less data) can serve as important screening methods helping to test hypotheses about niche determinants and, thus, helping to identify the necessary process detail (Fig. 6). At the same time, more complex models should only be favoured
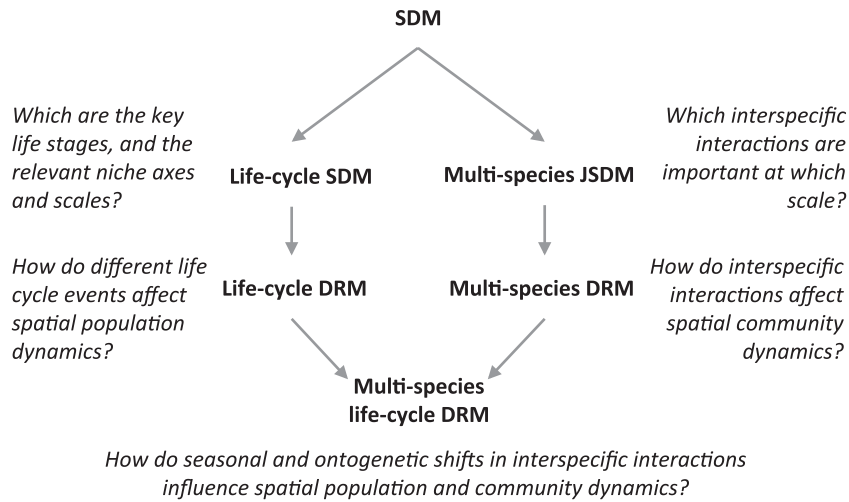
Figure 6. Proposed modelling cycle to move beyond simple SDMs to multi-species dynamic distribution models for avian assemblages. Each modelling step can help answering specific research questions and identifying necessary model complexity for subsequent modelling steps. (SDM: species distribution model; JSDM: joint species distribution model; DRM: dynamic range model).

over simpler models if their explanatory value is higher than that of simpler models or if the research question requires using more complex models. Here, I suggest five basic modelling steps for developing and operationalizing multi-species dynamic distribution models for avian assemblages. The single steps each have high value for answering specific questions (Fig. 6). Before modelling, we should always contemplate whether more complex modelling approaches are necessary to answer the question at hand or to describe the particular study system, whether the data for such modelling are available and whether the efforts of data compilation and model estimation are well justified and balanced against the benefits.

Life-cycle SDM

Model development
Birds have complex life cycles that should be accounted for in both correlative and mechanistic models as different life stages may differ strongly in their niche requirements. For example, juvenile birds often require different food resources than adults (e.g. smaller, or more protein-rich; Newton 1998). Also, birds may have different spatial and habitat requirements depending on life stage, for example for breeding, foraging, finding shelter or overwintering. Many birds are at least partially migratory and thus experience environmental conditions in different geographic areas with potentially important implications for survival and overall fitness (Hewson et al. 2016). I suggest developing standard workflows for identifying key life stages of birds in the models, for example using traits, and for identifying the relevant niche axes and scales. Simple life-stage specific SDMs (Taboada et al. 2013) can be overlaid to distinguish, for example, source habitats, which contribute both to survival and reproduction, from sink habitats, which do not support reproduction but may nevertheless allow survival or are even important refuges during winter or other stressful times (Naves et al. 2003), or to distinguish habitats that promote dispersal (Rotllan-Puig and Traveset 2016). Following the hypothesis that source populations should be more stable

over time than sink populations, accurate life-cycle SDMs should be better at explaining population stability over time than conventional SDMs (Oliver et al. 2012).

Data requirements
Analogously to conventional SDMs, life-cycle SDMs require simple species occurrence data (e.g. presence-only, presence/absence, or abundance data). Above that, more detailed information on species' ecology and life cycle are needed, which are often available through trait information in literature (e.g. foraging habitat, breeding habitat, nesting substrate; Zurell et al. 2016b). For evaluation of life-cycle SDMs, abundance time series for different places would be valuable, to assess whether population stability is better explained by these life-cycle SDMs than by simple SDMs.

Life-cycle DRM

Model development
Demographic models allow simulation of transient population dynamics to specific environmental stressors and estimation of population viability. As discussed earlier, DRM-like approaches provide a promising tool for disentangling environmental and demographic components of the niche (Pagel and Schurr 2012, Schurr et al. 2012). However, applying them to birds will necessitate developing more generic DRM approaches that are able to take into account complex life cycles (Zurell et al. 2016a), for example by means of matrix population models. For efficient parameterisation (Hartig et al. 2011, 2012), it is important to gather as much prior information on relevant processes and potential parameter domains as possible. This will require definition of critical life stages (the knowledge of which is often available empirically) and their relevant niche axes (for example by screening through life-cycle SDMs), but also a more mechanistic understanding of dispersal. Furthermore, migratory birds, in particular long-distance migrants, are especially challenging for predicting population viability as their fitness is determined by factors experienced in both their breeding and wintering grounds, as well as en route

between the two. Ideally, full annual cycle models should be developed but will require a lot of additional knowledge to identify those factors that are limiting to population viability (Marra et al. 2015).

Data requirements

Life-cycle DRMs will require species occurrence data, but also data that carry information on species' demography. This could be a number of abundance time series that mirror the outcome of demographic processes or could be demographic rates measured at different places (Zurell et al. 2016a). Additionally, information on dispersal will be advantageous to limit the plausible parameter range. Such prior information can be obtained, for example, by analyses of ring data (Paradis et al. 1998) or telemetry data (Weston et al. 2013). Using efficient numerical optimisers, all these different data sources can be combined within a single parameterisation process, for example – but not exclusively – using Bayesian methods (Hartig et al. 2011, 2012).

Multi-species JSDM

Model development

JSDMs have the potential of becoming important screening tools helping to elucidate patterns of potential inter-specific interactions in community assemblages. However, for this we need to better understand how JSDMs' ability to identify and quantify different interaction mechanisms from co-occurrence and co-abundance data is affected by species' characteristics and species' prevalence, by species detection probability, and by scale among others. For example, interspecific interactions are believed to become less important at large spatial scales (Eltonian noise hypothesis) but this scale dependence may differ largely between species (McGill 2010). Also, at increasing spatial scale the residual correlation between species in the models may become increasingly distorted and less informative of interspecific interactions because of shared environmental response or niche partitioning at the sub-scale (Clark et al. 2014). Furthermore, for large numbers of species, interpretability of JSDMs may be hampered, and we thus need to develop adequate methods for dimension reduction (Kissling et al. 2012). Whereas the latent variable models (Warton et al. 2015) provide a computational form of dimension reduction, I see great potential for developing more trait-based approaches, as traits carry information on important niche and fitness differences that drive interspecific interactions (HilleRisLambers et al. 2012), and may also help to remove implausible (trophic) interactions (Morales-Castilla et al. 2015).

Data requirements

It has not been tested yet under which circumstances these models will perform more accurately with species co-abundance data compared to co-occurrence data but we may hypothesise that co-abundance data carry more information and could thus ease inference. For either data, one should pay attention to scaling issues inherent in the sampling. For example, bird atlas data obtained from point counts may ensure greater spatial overlap between the different species than data from transect counts although this certainly depends on the spatial requirements of the species as well as on the length of the transects and radii around sample points. Additionally, trait data on trophic and habitat niche could help to remove implausible interaction links between species. Trait data describing, for example, spatial requirements such as home range size and territorial behaviour may help to account for the scale dependence of interspecific interactions.

Multi-species DRM

Model development

A critical step forward in biodiversity modelling would be the development of multi-species demographic models, which combine the ideas of DRMs (Pagel and Schurr 2012) and of multivariate population models (Wittwer et al. 2015). Such multi-species DRMs will simultaneously estimate the environmental response of demographic rates and dispersal of multiple species as well as the interaction links and strengths between species, and will thus help disentangling the biotic components of the niche (Fig. 1). Within the model framework, interaction coefficients could follow (discrete versions of) the Lotka–Volterra competition equations that allow the estimation of asymmetric interactions (Chesson 2000). These models will allow evaluating how environment and interspecific interactions limit population growth and spread of single species, and how these factors interact to form complex meta-community dynamics. Needless to say that such models would require rigorous testing to guide application. Also, they will benefit from any prior knowledge on potential species interactions to reduce computational efforts, and can thus gain from screening by simpler JSDMs.

Data requirements

Multi-species DRMs will require species co-occurrence (or co-abundance) data, and a number of co-abundance time series. The latter could be supplemented or possibly substituted by demographic data of a number of different places, but with the constraint that (at least some of) the measured demographic rates of multiple species need to stem from the same place and time. Additionally, information on dispersal is advantageous (cf. life-cycle DRMs).

Multi-species life-cycle DRM

Model development

The last step for predictive multi-species demographic models would be the integration of life cycles into the multi-species DRMs described above. Such a framework will not only allow assessing the sensitivity of different life stages to environmental stressors but will also allow evaluating how seasonal and ontogenetic shifts in interspecific interactions influence population and community dynamics in space and time. It could thus help elucidating such complex shifts in competitive dominance as illustrated by the blue tit and great tit example of Fig. 3. For operationalizing this framework, all knowledge gained from the previous screening and modelling steps regarding the represented complexity of the species' life cycle and the potential interspecific interactions will be highly valuable.

Data requirements

These models are undoubtedly the most data hungry and require the full set of data discussed above including species co-occurrence data, a number of co-abundance time series and/or multi-species demographic data (potentially from multiple seasons), dispersal information, and trait data. Thus, we will probably be able to develop such models for a limited number of species groups. By taking an inverse modelling approach such as Bayesian computation or other numerical parameterisation frameworks (Hartig et al. 2011, 2012), model parameters can also be found with limited prior information. However, higher quality and quantity of data and prior information will speed up the computational process and it will also limit the problem of equifinality (meaning that different parameter settings could yield the same patterns).

Summary

For improved biodiversity scenarios, there is an urgent need to develop and validate more mechanistic approaches that are well founded in ecological theory and incorporate multi-species interactions, demography and dispersal in order to improve predictions of future communities (Blois et al. 2013, Urban et al. 2016). The multi-species dynamic distribution models described herein provide the means for disentangling the complex roles of life-stage dependent demography, dispersal and biotic interactions in shaping species' niches. However, developing and operationalizing such a framework will require quite a large amount of data, which are not currently available for many species. For birds, the data may not be perfect for all localities or for all families, but the quantity and quality of data, and the empirical knowledge on avian life cycles is still among the best for animals. From a modelling perspective, birds thus offer a unique possibility to close the gap between our complex empirical understanding and the way species distributions are currently modelled in global change context. The integrated modelling framework described herein will require bringing together advanced modelling strategies with the vast empirical knowledge and diverse data sources on avian diversity. This will aid our understanding of how small-scale phenomena such as species interactions and local demography and behaviour scale up to affect complex range and community dynamics. The different steps of the integrated modelling framework will help testing hypotheses about prevailing environmental constraints and potential demographic and community processes and, thus, may help identifying the necessary process detail. These modelling protocols will not only be relevant for birds but also for other animals and even plants because consideration of the behavioural complexity in avian diversity at each step of the model development should make the models extremely flexible and generic.

Additionally, when applying these models, we need to keep in mind that they still make the fundamental assumption of niche conservatism, which will be violated if the species adapted genetically or behaviourally to novel environmental conditions. If such adaptations have been observed in the system under study (Nussey et al. 2005, Jonzén et al. 2006, Charmantier et al. 2008), then the approaches described herein will likely be inappropriate unless adaptive mechanisms are accounted for explicitly or the sensitivity of predictions against different assumptions of niche evolution is tested. Approaches exist for predicting behaviour bottom up, for example for predicting optimal life histories of migratory birds (McNamara et al. 1998) that could potentially be integrated with such multi-species demographic models. For successful integration, however, still more empirical knowledge is needed to understand how complex behaviours such as timing of migration and reproduction evolve in birds and, thus, how fast they may adapt under global environmental change as these factors may ultimately limit the predictive capacity of distribution models.

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