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10 Integrating demography, dispersal and interspecific interactions into bird distribution models

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12 **Author:**

13 Damaris Zurell

14 **Address:**

15 Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland,
16 Email: damaris.zurell@wsl.ch

17

18 **Abstract**

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

36 **Keywords:**

37

38 **Introduction**

39 Mitigating rapid biodiversity loss is one of the most vital challenges today. Even under most
40 conservative assumptions, we are currently experiencing biodiversity losses that are up to 100
41 times higher than the natural extinction rate (Ceballos, et al. 2015). And even worse, biodiversity
42 loss is predicted to further increase under climate change (Pereira, et al. 2010). The
43 consequences are difficult to gauge. Losing single species could have cascading effects on entire
44 ecosystems and could mean loss of important ecosystem functions and services (Cardinale, et al.
45 2012). For example, birds provide important services by transporting nutrients, by dispersing
46 seeds or by acting as disease control agents through scavenging.

47 Models have established as important tools in ecology that help testing hypotheses about
48 biodiversity functioning and that help making predictions of potential dynamics, for example
49 under climate change. Correlative species distribution models (SDMs) are by far the most widely
50 used modelling tool in biodiversity research as they are comparably easy to use and work with
51 relatively simple species occurrence data (Elith and Leathwick 2009, Guisan and Thuiller 2005,
52 Guisan and Zimmermann 2000). However, the value of SDMs in predicting climate change
53 induced biodiversity changes has been questioned for several reasons. For example, SDMs
54 implicitly assume the observed species-environment relationship to be at equilibrium and to
55 remain constant under future climate. They thus ignore any transient demographic and
56 dispersal dynamics, extinction debts, and changing interspecific interactions (Araújo and Guisan
57 2006, Zurell, et al. 2009, Zurell, et al. 2016a). Also, combining single-species SDMs to construct
58 site-specific species lists currently fails to correctly predict community assemblage, which may
59 in part relate to unaccounted interspecific interactions (Baselga and Araújo 2010, Guisan and
60 Rahbek 2011) as well as to scaling issues (Zurell, et al. 2016b). Consequently, we currently
61 observe two major research avenues aimed at (i) developing more dynamic and demographic
62 approaches to predict species response to environmental change but which hitherto focus on
63 single species only, and (ii) developing multi-species models that account for interspecific
64 interactions but which hitherto ignore either transient dynamics and demography or ignore
65 spatial dynamics.

66 In this review, I will summarise the current state of the art in these modelling approaches and
67 discuss necessary model developments to meet the challenges of understanding and predicting
68 biodiversity and specifically avian diversity under current and future climates. First, I will revisit
69 the theoretical background on the ecological niche concept and its relation to community
70 assembly, and give an overview on current demographic models and multi-species models. I will
71 discuss limitations of these approaches and promising future directions, especially in relation to
72 the complex life histories of birds. Because of the vast empirical knowledge on avian systems

73 and the high-quality data, birds offer unique possibilities of developing and refining more
74 realistic but also more generic models for predicting biodiversity dynamics under global change
75 (Engler, et al. THIS ISSUE).

76 **The ecological niche concept and community assembly**

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

86 Inferring the ecological niche of species from observational data is challenging because
87 biogeographic history, demographic processes and interspecific interactions also affect the
88 presence of a species. For example, the temperature extremes found within the geographic
89 range of a species may be less than what the species could physiologically tolerate and thus less
90 than what could be measured in a laboratory. Hutchinson distinguished the fundamental and the
91 realised niche of a species. The fundamental niche refers to all abiotic constraints that allow
92 positive population growth. Originally, the realised niche was formally described as those parts
93 of the fundamental niche to which the species is confined due to competitive exclusion and other
94 negative interactions (Hutchinson 1957). Refined niche theory acknowledges several more
95 processes including demographic and community processes that (i) constrain and thus shrink
96 the realised relative to the fundamental niche, including dispersal limitation and negative
97 interspecific interactions (Fig. 1a), and processes that (ii) expand the realised relative to the
98 fundamental niche, including source-sink dynamics, time-delayed extinctions and facilitation
99 (Fig. 1b) (Bruno, et al. 2003, Diez, et al. 2014, Holt, et al. 2005, Pulliam 2000, Schurr, et al. 2012).
100 Also, (genetic and behavioural) adaptation may lead to expanded niches under climate change
101 but, as pointed out above, most of the modelling approaches that I will discuss here focus on
102 contemporary demographic and community processes. Because of these dynamic processes, the
103 realised niche may vary across time and space (Holt 2009), and also across the life cycle of
104 species (Taboada, et al. 2013). For example, species may utilize different habitats and resources
105 for key events within their life cycle such as reproduction, overwintering and dispersal (Holt
106 2009, Jacob, et al. 2015, Naves, et al. 2003, Rotllan-Puig and Traveset 2016). This is most
107 prominent in migratory birds that move between distant regions on a seasonal basis, and for

108 which both seasonal niche-tracking and niche-switching have been reported (Eyres, et al. THIS
109 ISSUE, Gómez, et al. 2016, Laube, et al. 2015).

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

124 The concepts of limiting similarity and niche partitioning are important to understand long-term
125 coexistence between species in local communities (MacArthur and Levins 1967). Contemporary
126 coexistence theory formalises these ideas in a mechanistic framework that distinguishes
127 between niche differences and differences in fitness (i.e., competitive dominance; Chesson
128 2000). Relative niche differences are important as they act as stabilising mechanisms (niche
129 partitioning) whereas average fitness differences (inequalities) favour dominance and, in the
130 absence of stabilising niche differences, lead to competitive exclusion (Fig. 2; Adler, et al. 2007,
131 Chesson 2000, Valladares, et al. 2015). To make it more complicated, coexistence may also
132 depend on the life cycle and the annual cycle of the interacting species. For example, stabilising
133 mechanisms in plants have been shown to be strongest in early life stages (Chu and Adler 2015).
134 In birds, it has been shown that competitive dominance and, thus, fitness differences may differ
135 between seasons; for example, great tits are the dominant competitors for roost and nest sites
136 whereas coexisting blue tits are the dominant competitors for insect larvae in the early breeding
137 season (Fig. 4; Dhondt 2012). Such ontogenetic and seasonal shifts in coexistence mechanisms
138 make it difficult to identify the true competitive mechanisms with current modelling approaches
139 (e.g., Wittwer, et al. 2015). Understanding the complex interplay between these processes and
140 how they scale up to affect communities, however, is important because climate change will
141 likely have non-trivial and possibly unprecedented effects on species range and community
142 dynamics (Blois, et al. 2013, Williams and Jackson 2007).

143 **Current state of demographic and community models**

144 The theoretical excursion above pinpoints many different factors and processes that potentially
145 govern the presence of a species in a specific location. Many of these factors are not accounted
146 for in traditional SDMs. This leads to two main problems in global change research. First, climate
147 impact predictions by SDMs may be fallacious, for example because they do not consider any
148 transient, time-delayed species responses (Zurell, et al. 2009, Zurell, et al. 2016a). Hence, many
149 authors urged to supplement (mainly single-species) SDMs with more mechanistic approaches
150 (Araújo and Guisan 2006, Guisan and Thuiller 2005, Thuiller, et al. 2008). However, as I will
151 discuss below, not all of the suggested modelling approaches are able to overcome fundamental
152 limitations of SDMs, for example the equilibrium assumption. This leads to the second great
153 challenge that SDMs are not able to properly disentangle the realised from the fundamental
154 niche (Araújo and Guisan 2006, Elith and Leathwick 2009, Schurr, et al. 2012) because they do
155 not explicitly consider any of the demographic and community processes presented in Figure 1.
156 For example, SDMs may estimate a smaller ecological niche than the species is actually able to
157 occupy if the range or the niche of the species were not completely filled. This could happen
158 because of dispersal limitation since the last glacial maximum (Sandel, et al. 2011) or during
159 invasion (Strubbe, et al. 2013), or because the species is excluded from parts of its range due to
160 interspecific competition (Laube, et al. 2013) among others. Such bias in the fitted species-
161 environment relationship would hamper both our understanding of what limits a species range
162 and our ability to predict to novel environments.

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

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

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

184 **Demographic models (of single species)**

185 Over recent years, several demographic frameworks have been developed (or revived) for
186 predicting (single) species niche and range dynamics more mechanistically (Ehrlén and Morris
187 2015, Franklin 2010, Lurgi, et al. 2015, Pereira, et al. 2010). Their main characteristic is that
188 they do not only describe the abiotic constraints on the niche but also explicitly consider the
189 fundamental demographic processes of birth, death and dispersal (or a subset of these
190 processes). Several of these models still rely on SDMs and use SDM-derived habitat suitability to
191 describe the niche and to constrain demography. Often, these kinds of models are referred to as
192 hybrid SDMs (Thuiller, et al. 2008). In the simplest case, habitat suitability maps predicted by
193 SDMs are coupled with simple dispersal models that simulate colonisation of suitable area
194 (Engler and Guisan 2009, Franklin 2010), and thus allow the identification of potential dispersal
195 limitations under future climate change (Midgley, et al. 2006, Normand, et al. 2013).

196 More complex approaches supplement SDMs with population dynamic models that allow the
197 estimation of population viability by explicitly modelling population growth. These hybrids are
198 actually a rather diverse group that may differ widely in (i) the type of population dynamic
199 model used, and (ii) how exactly SDM derived habitat suitability and the population dynamic
200 model are coupled. (i) The population dynamic model can be formulated as a classic meta-
201 population model with colonisation and extinction of patches, as a demographic model based on
202 logistic growth, on a matrix population model or on an individual-based model among others
203 (Lurgi, et al. 2015). (ii) We can distinguish at least three different coupling types. Binary output
204 from SDMs can be used to distinguish suitable from unsuitable areas and use these patch-matrix
205 maps as underlying landscape for the population model (Akçakaya 2000, Cabral 2009, Wiegand,
206 et al. 2004). In this case, demographic processes are simulated independent of the SDM but
207 populations are restricted to those areas that the SDM predicted to be suitable. Alternatively,
208 SDM derived habitat suitability can be used to scale the carrying capacity in the population
209 model (Brotóns, et al. 2012, Keith, et al. 2008, Zurell, et al. 2012; also see Fig. 4) or to scale vital
210 rates in the population models, for example survival (Dullinger, et al. 2012) or recruitment
211 (Albert, et al. 2008).

212 A main conceptual problem of these hybrid models is that there is little theoretical and empirical
213 support for the relationship between SDM derived habitat suitability and carrying capacity or
214 vital rates (Ehrlén and Morris 2015, Thuiller, et al. 2014). The shape of this relationship has
215 been assumed to be linear (Keith, et al. 2008), linear above a presence-absence threshold
216 (Zurell, et al. 2012) or sigmoidal (Dullinger, et al. 2012). The choice is not trivial as these
217 relationships can result in largely different predictions (Zurell, et al. 2016a). Furthermore,
218 hybrids still make the fundamental assumption that the species is at equilibrium with its
219 environment. If this assumption is not met, then separately fitting the SDM and the population
220 model may actually lead to circularity problems. If, for example, a species is dispersal limited,
221 then the SDM is implicitly accounting for this dispersal limitation in the niche estimate and the
222 population model will account for it again, such that dispersal is actually accounted for twice
223 (Gallien, et al. 2010). Thus, simply coupling SDM output to population models does not allow
224 disentangling the effects of demography and dispersal on the realised niche (Schurr, et al. 2012).
225 To overcome this limitation, Pagel and Schurr (2012) introduced a Hierarchical Bayesian
226 framework called dynamic range models (DRMs) that simultaneously estimate the parameters
227 of a demographic and a dispersal model as well as the environmental response of demographic
228 rates. DRMs thus avoid using SDMs but directly relate the intrinsic population growth rate of the
229 population model to environmental variables and directly account for any dispersal effects,
230 which allows disentangling abiotic and demographic components of the realised niche and
231 should thus be advantageous over SDMs (Pagel and Schurr 2012, Schurr, et al. 2012).

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

247 In bird distribution modelling, several studies have used dynamic occupancy modelling to study
248 recent range dynamics (Butcher, et al. 2014, Kéry, et al. 2013, Yackulic, et al. 2015). Occupancy is
249 described by colonisation and extinction processes (as in metapopulation models, Hanski,
250 1998), which can be expressed as functions of environmental covariates (Kéry, et al. 2013).
251 These models have similarities to DRMs in that they are estimated in a hierarchical framework,
252 allow disentangling the different factors determining range dynamics, and account for imperfect
253 detection through an observer model (Guillera-Arroita 2016). Also, attempts have been made to
254 incorporate different life stages (Sutherland, et al. 2014), and they have been successfully
255 applied in climate impact analyses (Jones, et al. 2016). In the future, their ability to adequately
256 predict temporal dynamics following climate change should be compared to other range
257 dynamic approaches (Zurell, et al. 2016a).

258 **Multi-species models**

259 Results from our model comparison using simulated data (Zurell, et al. 2016a) also showed that
260 future predictions by single species models were especially poor under complex community
261 dynamics. The importance of interspecific interactions is now widely acknowledged (Blois, et al.
262 2013), and scientists have begun to develop ideas and model frameworks to account for these
263 (Kissling, et al. 2012, Wisz, et al. 2013), aided by recent computational advances. Current multi-
264 species frameworks can be distinguished into multivariate regression approaches based on
265 static distribution data, the so-called joint species distribution models (JSMDs; Clark, et al. 2014,
266 Ovaskainen, et al. 2015, Pollock, et al. 2014, Warton, et al. 2015), and multivariate population
267 models based on temporal abundance dynamics (Mutshinda, et al. 2011, Wittwer, et al. 2015).

268 Both model types aim at explaining the dependence between species, the joint probability of
269 occurrence that is not accounted for by environmental variables alone (Clark, et al. 2014). If the
270 ranges of two species A and B overlap because they share similar environmental requirements,
271 then the main question is whether they will occur independently of each other at a site or show
272 some form of positive or negative association that is not explained by environment, meaning
273 their probability of occurrence is higher or lower conditional on the presence of the other
274 species (Fig. 5a). If both species are independent, then they could or could not co-occur simply
275 by chance (Fig. 5b). If the species are not independent, then information of species B is
276 necessary to predict the occurrence probability of species A. In the extremes, species A would
277 only occur when B is present (Fig. 5c) or species A and B would always exclude each other (Fig.
278 5d).

279 To date, a few different JSMD algorithms have been implemented that differ in how the joint
280 distribution is estimated (Warton, et al. 2015). Unstructured covariance models estimate the
281 occurrence probability of multiple species simultaneously and decompose species co-occurrence

282 patterns into shared environmental response and residual patterns of co-occurrence
283 (Ovaskainen, et al. 2010, Pollock, et al. 2014, Royan, et al. 2016). As output, we obtain a
284 covariance matrix of pairwise interactions. Latent variable models represent a computationally
285 more efficient method based on unobserved (latent) variables that induce correlation between
286 species (Letten, et al. 2015, Ovaskainen, et al. 2016, Warton, et al. 2015). These models do not
287 estimate all pairwise residual correlations, but shrink the parameter space to a minimum
288 number of latent variables that best describe the residual covariance between the species.

289 Unfortunately, although constituting a major advance in biodiversity modelling, it is not clear yet
290 in how far JSMDs could fulfil our wish to model interspecific interactions. Specifically, the
291 residual co-occurrence (joint distribution) may indicate interspecific interactions but may also
292 be caused by missing or sub-scale environmental covariates (Clark, et al. 2014, Harris 2015,
293 Pollock, et al. 2014). Especially the latter is an important source of bias that is inherent in
294 common species inventory data such as breeding bird atlases that are gridded to a certain
295 resolution and may not necessarily reflect the spatial requirements of the many different species
296 (Zurell, et al. 2016b). It would be desirable to rigorously test under which circumstances JSMDs
297 will reliably detect interspecific interactions, and how this is affected by complicating factors
298 such as scale dependence. After all, interactions are spatially very localised processes between
299 (small) numbers of individuals. For example, birds may compete locally for resources, for shelter
300 and for nest sites (Dhondt 2012, Zurell, et al. 2015). By contrast, the scale of data collection and
301 analyses is often at plot or region scale, which may lead to information loss and distorted
302 relationships (Clark, et al. 2014). Additionally, it remains open, which interaction mechanisms
303 could possibly be detected by JSMDs, at which scale, and which data types (co-occurrence or co-
304 abundance) are required. A recent simulation study showed that co-occurrence patterns from
305 predator-prey relationships could equal the co-occurrence patterns from either competitive or
306 facilitative interactions (Araújo and Rozenfeld 2014). As the residual correlations estimated by
307 JSMDs simply indicate whether co-occurrence is lower or higher than expected by chance given
308 the environment, we can assume that current JSMD implementations will not allow
309 unambiguous distinction of predator-prey (or consumer-resource) relationships and
310 competitive or facilitative interactions, and will need further model development in this respect.
311 Another challenge is that interspecific interactions are not constant in space and time (Callaway,
312 et al. 2002, He, et al. 2013, Lawrence and Barraclough 2016, Meier, et al. 2011), and it has thus
313 been proposed that non-stationarity in interaction coefficients should be considered in future
314 research (Kissling, et al. 2012, Warton, et al. 2015, Wisz, et al. 2013) but hitherto only one
315 worked example using multi-species occupancy modelling exists (Rota, et al. 2016).

316 A few examples on multivariate population models exist that use time series of multi-species co-
317 occurrence or co-abundance to jointly estimate the relative importance of environmental

318 stochasticity, environmental variables as well as intra- and interspecific interactions using
319 Hierarchical Bayesian approaches (Mutshinda, et al. 2009, Mutshinda, et al. 2011, Wittwer, et al.
320 2015). Although hitherto confined to single communities, which ignores any spatial (meta-
321 community) dynamics, these multivariate population models provide a promising way forward
322 as they allow disentangling important components of coexistence theory, namely environmental
323 dependence of demographic rates as well as intra- and interspecific density regulation.

324 **Towards multi-species dynamic distribution models**

325 What does all this imply for bird distribution modelling? Some examples exist that underline the
326 merit of using dynamic distribution models for predicting avian species response to climate and
327 land use change (Aben, et al. 2016, Brotons, et al. 2012, Zurell, et al. 2012) and also for using
328 multi-species modelling approaches (Royan, et al. 2016) as large scale patterns of bird
329 assemblages seem to be, at least partly, affected by interspecific interactions (Zurell, et al.
330 2016b). Nevertheless, both demographic models and multi-species models still have many
331 limitations and uncertainties, and the necessary step forward would be to develop an integrated
332 modelling framework that is able to take into account all of the demographic, dispersal and
333 interspecific processes acting on the niche (Fig. 1) (Urban, et al. 2016). Operationalizing such a
334 framework for specific avian systems, however, will not be an easy task and will require
335 adequate screening methods and standard protocols to define the necessary model complexity
336 and data requirements. At the same time, the large amount of high-quality data that is available
337 on birds, also make birds a unique study system for improving on current modelling approaches
338 that will also aid biodiversity modelling of other species groups. If we want to make robust
339 predictions under global environmental change, it requires models that are structurally realistic
340 and contain all (and only) relevant mechanisms that govern the dynamics in the specific system
341 (Singer, et al. 2016). Also, the additional effort of fitting complex mechanistic models needs to be
342 well justified and targeted as both time and data requirements can be huge. If the system under
343 study is highly stochastic and thus noisy, then simple SDMs may even outperform more complex
344 models (Zurell et al., 2016a). In that sense, I see the different modelling frameworks discussed
345 above as complimentary rather than opposing modelling strategies, each with its own strengths
346 and weaknesses. Thereby, simpler models (containing less process detail and requiring less
347 data) can serve as important screening methods helping to test hypotheses about niche
348 determinants and, thus, helping to identify the necessary process detail (Fig. 6). At the same
349 time, more complex models should only be favoured over simpler models if their explanatory
350 value is higher than that of simpler models or if the research question requires using more
351 complex models. Here, I suggest five basic modelling steps for developing and operationalizing
352 multi-species dynamic distribution models for avian assemblages. The single steps each have
353 high value for answering specific questions (Fig. 6). Before modelling, we should always

354 contemplate whether more complex modelling approaches are necessary to answer the question
355 at hand or to describe the particular study system, whether the data for such modelling are
356 available and whether the efforts of data compilation and model estimation are well justified
357 and balanced against the benefits.

358 1) Life-cycle SDM

359 *Model development:* Birds have complex life cycles that should be accounted for in both
360 correlative and mechanistic models as different life stages may differ strongly in their niche
361 requirements. For example, juvenile birds often require different food resources than adults (e.g.
362 smaller, or more protein-rich; Newton 1998). Also, birds may have different spatial and habitat
363 requirements depending on life stage, for example for breeding, foraging, finding shelter or
364 overwintering. Many birds are at least partially migratory and thus experience environmental
365 conditions in different geographic areas with potentially important implications for survival and
366 overall fitness (Hewson, et al. 2016). I suggest developing standard workflows for identifying
367 key life stages of birds in the models, for example using traits, and for identifying the relevant
368 niche axes and scales. Simple life-stage specific SDMs (Taboada, et al. 2013) can be overlaid to
369 distinguish, for example, source habitats, which contribute both to survival and reproduction,
370 from sink habitats, which do not support reproduction but may nevertheless allow survival or
371 are even important refuges during winter or other stressful times (Naves, et al. 2003), or to
372 distinguish habitats that promote dispersal (Rotllan-Puig and Traveset 2016). Following the
373 hypothesis that source populations should be more stable over time than sink populations,
374 accurate life-cycle SDMs should be better at explaining population stability over time than
375 conventional SDMs (Oliver, et al. 2012).

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

383 2) Life-cycle DRM

384 *Model development:* Demographic models allow simulation of transient population dynamics to
385 specific environmental stressors and estimation of population viability. As discussed earlier,
386 DRM-like approaches provide a promising tool for disentangling environmental and
387 demographic components of the niche (Pagel and Schurr 2012, Schurr, et al. 2012). However,
388 applying them to birds will necessitate developing more generic DRM approaches that are able

389 to take into account complex life cycles (Zurell, et al. 2016a), for example by means of matrix
390 population models. For efficient parameterisation (Hartig, et al. 2011, Hartig, et al. 2012), it is
391 important to gather as much prior information on relevant processes and potential parameter
392 domains as possible. This will require definition of critical life stages (the knowledge of which is
393 often available empirically) and their relevant niche axes (for example by screening through life-
394 cycle SDMs), but also a more mechanistic understanding of dispersal. Furthermore, migratory
395 birds, in particular long-distance migrants, are especially challenging for predicting population
396 viability as their fitness is determined by factors experienced in both their breeding and
397 wintering grounds, as well as en route between the two. Ideally, full annual cycle models should
398 be developed but will require a lot of additional knowledge to identify those factors that are
399 limiting to population viability (Marra, et al. 2015).

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

409 3) Multi-species JSDM

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

425 interactions (HilleRisLambers, et al. 2012), and may also help to remove implausible (trophic)
426 interactions (Morales-Castilla, et al. 2015).

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

438 4) Multi-species DRM

439 *Model development:* A critical step forward in biodiversity modelling would be the development
440 of multi-species demographic models, which combine the ideas of DRMs (Pagel and Schurr
441 2012) and of multivariate population models (Wittwer, et al. 2015). Such multi-species DRMs
442 will simultaneously estimate the environmental response of demographic rates and dispersal of
443 multiple species as well as the interaction links and strengths between species, and will thus
444 help disentangling the biotic components of the niche (Fig. 1). Within the model framework,
445 interaction coefficients could follow (discrete versions of) the Lotka-Volterra competition
446 equations that allow the estimation of asymmetric interactions (Chesson 2000). These models
447 will allow evaluating how environment and interspecific interactions limit population growth
448 and spread of single species, and how these factors interact to form complex meta-community
449 dynamics. Needless to say that such models would require rigorous testing to guide application.
450 Also, they will benefit from any prior knowledge on potential species interactions to reduce
451 computational efforts, and can thus gain from screening by simpler JSDMs.

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

457 **5) Multi-species life-cycle DRM**

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

467 *Data requirements:* These models are undoubtedly the most data hungry and require the full set
468 of data discussed above including species co-occurrence data, a number of co-abundance time
469 series and/or multi-species demographic data (potentially from multiple seasons), dispersal
470 information, and trait data. Thus, we will probably be able to develop such models for a limited
471 number of species groups. By taking an inverse modelling approach such as Bayesian
472 computation or other numerical parameterisation frameworks (Hartig, et al. 2011, Hartig, et al.
473 2012), model parameters can also be found with limited prior information. However, higher
474 quality and quantity of data and prior information will speed up the computational process and
475 it will also limit the problem of equifinality (meaning that different parameter settings could
476 yield the same patterns).

477 **Summary**

478 For improved biodiversity scenarios, there is an urgent need to develop and validate more
479 mechanistic approaches that are well founded in ecological theory and incorporate multi-species
480 interactions, demography and dispersal in order to improve predictions of future communities
481 (Blois, et al. 2013, Urban, et al. 2016). The multi-species dynamic distribution models described
482 herein provide the means for disentangling the complex roles of life-stage dependent
483 demography, dispersal and biotic interactions in shaping species' niches. However, developing
484 and operationalizing such a framework will require quite a large amount of data, which are not
485 currently available for many species. For birds, the data may not be perfect for all localities or
486 for all families, but the quantity and quality of data, and the empirical knowledge on avian life
487 cycles is still among the best for animals. From a modelling perspective, birds thus offer a
488 unique possibility to close the gap between our complex empirical understanding and the way
489 species distributions are currently modelled in global change context. The integrated modelling
490 framework described herein will require bringing together advanced modelling strategies with
491 the vast empirical knowledge and diverse data sources on avian diversity. This will aid our

492 understanding of how small-scale phenomena such as species interactions and local
493 demography and behaviour scale up to affect complex range and community dynamics. The
494 different steps of the integrated modelling framework will help testing hypotheses about
495 prevailing environmental constraints and potential demographic and community processes and,
496 thus, may help identifying the necessary process detail. These modelling protocols will not only
497 be relevant for birds but also for other animals and even plants because consideration of the
498 behavioural complexity in avian diversity at each step of the model development should make
499 the models extremely flexible and generic.

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

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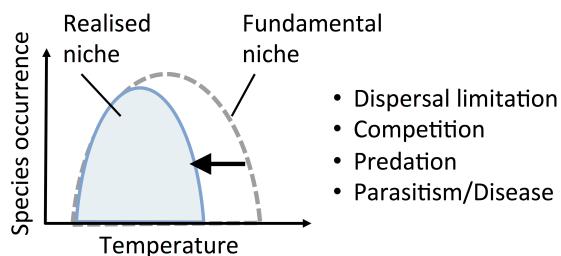
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749 **Figures**

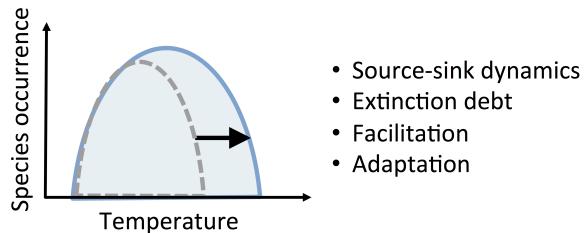
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(a) Biotic factors restricting the realised niche



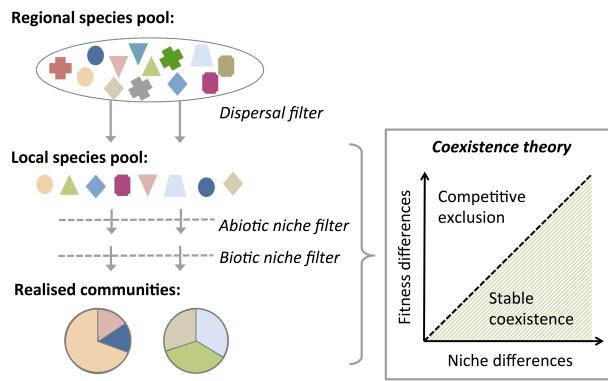
(b) Biotic factors expanding the realised niche



752

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

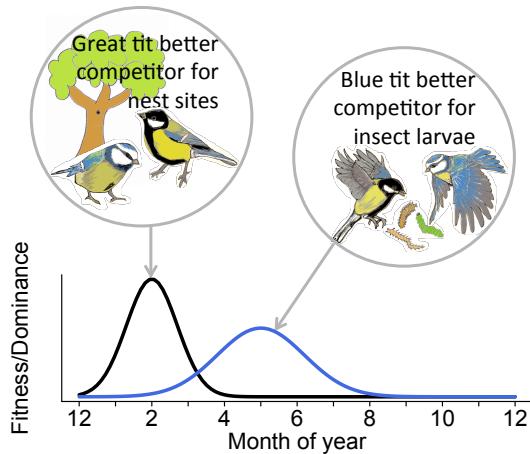
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756

757 Figure 2. Schematic representation of the ecological filtering cascade and its relation to
 758 coexistence theory (HilleRisLambers, et al. 2012). Species from the regional species have to pass
 759 different filters to establish within local communities. The dispersal filter selects species from
 760 the regional species pool that are able to colonise local sites depending on their dispersal ability
 761 and chance events. The abiotic niche filter and the biotic niche filter select those species that are
 762 able to maintain positive population growth under the given environmental conditions
 763 according to their physiology and resource requirements, and under given inter- and
 764 intraspecific interactions. Coexistence theory provides a framework for predicting the outcome
 765 of these niche filters (Chesson 2000). Species may differ in their abiotic niche requirements and
 766 in their competitive ability (ecological fitness). Large fitness differences between species will
 767 lead to competitive exclusion of the inferior competitor. These fitness differences can be
 768 overcome by niche differences and species can stably coexist whenever the niche differences are
 769 larger than the average fitness differences. Overall, relative niche and fitness differences will
 770 determine the presence and abundance of species in realised local communities.

771

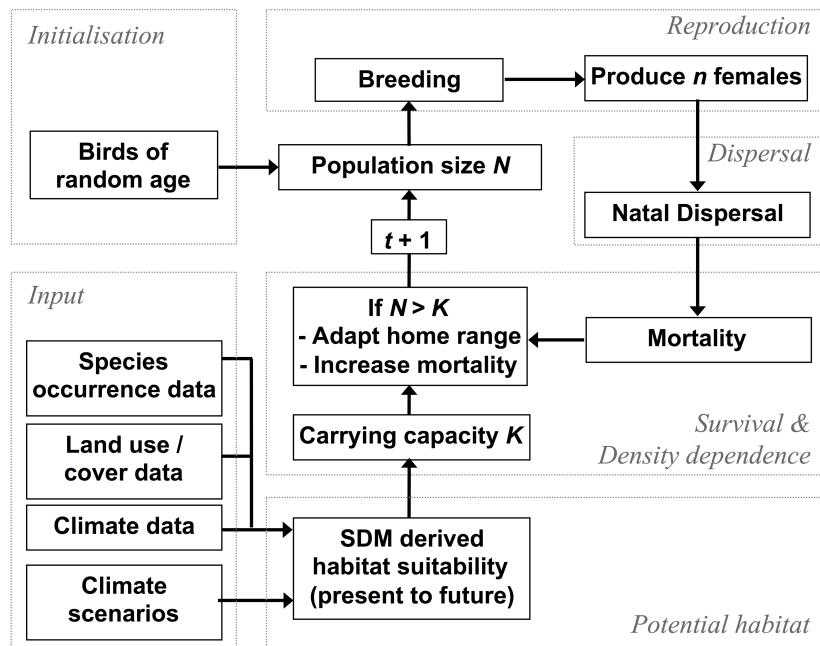


772

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

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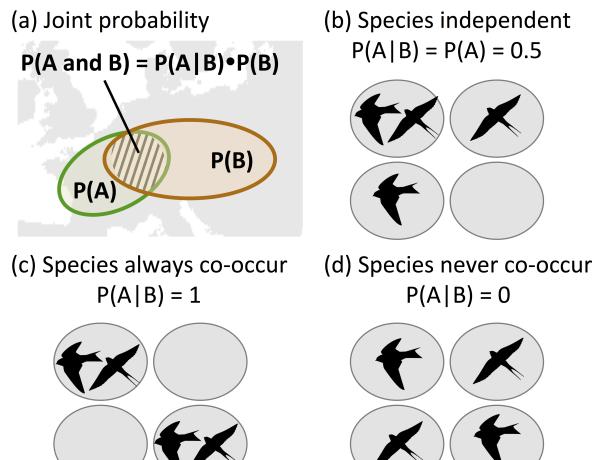


780

781 Figure 4. Simplified flow chart for hybrid model of Swiss black grouse population as described in
 782 Zurell, et al. (2012). Species occurrence records and environmental data are used to
 783 parameterise the SDM. Then, the SDM is used to predict habitat suitability under current and
 784 future climate, which serves as input to the individual-based black grouse model (IBM). Initially,
 785 birds of random age are distributed in suitable cells. In each simulation year, female black
 786 grouse may breed and produce n juveniles that will disperse to new areas before the next
 787 breeding period. Dispersal distance is drawn from a negative exponential dispersal kernel, but
 788 individual birds can make adaptive settlement decisions to avoid unsuitable and overcrowded
 789 habitats and they also avoid traversing widely unsuitable area. All birds are subject to mortality.
 790 If population size exceeds local carrying capacity, which increases linearly with SDM derived
 791 habitat suitability above a minimum threshold, then individuals will disperse to less crowded
 792 habitats in the nearest neighbourhood or mortality is increased. Illustration adapted from Zurell
 793 (2011).

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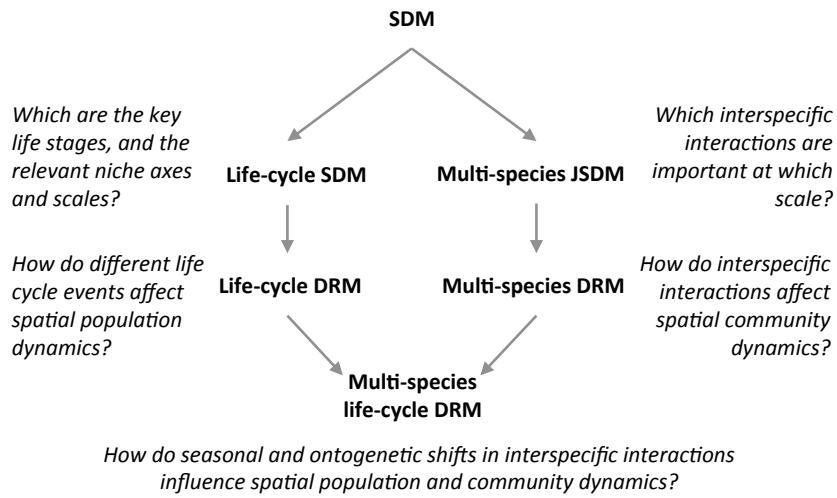
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796

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

804



805

806 Figure 6. Proposed modelling cycle to move beyond simple SDMs to multi-species dynamic
 807 distribution models for avian assemblages. Each modelling step can help answering specific
 808 research questions and identifying necessary model complexity for subsequent modelling steps.
 809 (SDM: species distribution model; JSDM: joint species distribution model; DRM: dynamic range
 810 model)

811