

1 **Title:** The macroecological dynamics of species coexistence in birds

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3 **Authors:** Alex L. Pigot^{1,2}, Walter Jetz^{3,4}, Catherine Sheard⁵ and Joseph A. Tobias⁴

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5 **Affiliations:** ¹Centre for Biodiversity and Environment Research, Department of
6 Genetics, Evolution and Environment, University College London, London, United
7 Kingdom, ²Groningen Institute for Evolutionary Life Sciences, University of
8 Groningen, Box 11103, 9700 CC Groningen, The Netherlands. ³Department of
9 Ecology and Evolutionary Biology, Yale University, 165 Prospect Street, New
10 Haven, Connecticut 06520-8106, USA. ⁴Department of Life Sciences, Imperial
11 College London, Silwood Park, Ascot SL5 7PY, UK. ⁵School of Biology, University
12 of St Andrews, St Andrews KY16 9ST, UK.

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14 *Correspondence to: alex.pigot1@gmail.com

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21

22 **Abstract**

23 Ecological communities are assembled from the overlapping of species in
24 geographic space, but the mechanisms facilitating or limiting such overlaps are
25 difficult to resolve. Here we combine phylogenetic, morphological, and
26 environmental data to model how multiple processes regulate the origin and
27 maintenance of geographic range overlap across 1,115 pairs of avian sister
28 species globally. We show that coexistence cannot be adequately predicted by
29 either dispersal-assembly (i.e. biogeographic) models or niche-assembly models
30 alone. Instead, our results overwhelmingly support an integrated model with
31 different assembly processes dominating at different stages of coexistence. The
32 initial attainment of narrow geographic overlap is dictated by intrinsic dispersal
33 ability and the time available for dispersal, whereas wider coexistence is largely
34 dependent on niche availability, increasing with ecosystem productivity and
35 divergence in niche-related traits, and apparently declining as communities
36 become saturated with species. Furthermore, although coexistence of any
37 individual pair of species is highly stochastic, we find that integrating assembly
38 processes allows broad variation in the incidence and extent of coexistence to be
39 predicted with reasonable accuracy. Our findings demonstrate how phylogenetic
40 data coupled with environmental factors and functional traits can begin to clarify
41 the multi-layered processes shaping the distribution of biodiversity at large
42 spatial scales.

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44

45 Introduction

46 Ecological assemblages are formed from the overlapping of species in geographic
47 space. Explaining variation in the structure and richness of communities
48 therefore depends on understanding how complex patterns of geographic range
49 overlap are generated and maintained¹. Ultimately, species distributions are the
50 product of speciation, dispersal and extinction. Historical variation in these
51 biogeographic processes may therefore be a major driver of community
52 structure and broad-scale gradients in biodiversity²⁻⁶. In addition, these same
53 patterns are thought to be regulated by ecological interactions among species⁷⁻¹⁰.
54 Such niche-based assembly models have largely focused on the importance of
55 competition in constraining coexistence, and predict that patterns of geographic
56 overlap primarily reflect the degree of divergence in species ecological niches, as
57 well as limits to the number of species that can be packed within a habitat¹¹⁻¹³.
58 Although it is widely recognized that patterns of spatial overlap among species
59 probably reflect a mix of these different processes—both biogeographical and
60 ecological—it has been difficult to quantify their relative contributions because
61 most empirical tests of community assembly treat them in isolation and have
62 addressed patterns of coexistence over a limited range of spatial and temporal
63 scales¹⁴⁻¹⁷.

64 On the one hand, tests of niche-based assembly mechanisms rarely
65 explicitly consider the biogeographic processes underlying community
66 formation, or only do so to the extent that these provide a null expectation for
67 community structure^{18,19}. On the other hand, while dispersal-based
68 biogeographic models address this problem, they typically do so by ignoring
69 species ecological niches². Thus, even when purely dispersal- or niche-based
70 models can be rejected, this says little about the relative importance of, and
71 interaction between, these biogeographical and ecological processes. Most
72 progress in disentangling assembly models has come from studies focusing at
73 relatively fine spatial scales where the set of possible explanations for
74 community structure are generally more limited, and assemblages can be
75 experimentally manipulated^{10,20-22}. However, the relevance of these findings for
76 understanding major gradients in biodiversity remains unclear because they do
77 not consider the historical processes generating species diversity^{18,19,23} or how

78 the relative importance of dispersal- and niche-based factors may vary across
79 different spatial and temporal scales^{24,25}. Understanding the causes of large-scale
80 patterns in community structure and diversity therefore requires models
81 integrating both biogeographical and ecological processes into a single analytical
82 framework^{19,26,27}.

83 Here we illustrate how the effects of dispersal- and niche-related
84 assembly processes can be disentangled by extending a dynamic model
85 describing the evolution of spatial overlap (i.e. sympatry) between sister
86 species²⁶. We assume that speciation typically generates species with non-
87 overlapping distributions (i.e. allopatry or parapatry)²⁸, and that the ensuing
88 dynamics of spatial overlap provide critical insights into the factors regulating
89 coexistence and the resulting broad-scale gradients in species richness^{19,29}. This
90 general framework underpins two alternative sets of models (Fig. 1). First, under
91 a 'Dispersal-assembly model', species overlap is constrained by the rate of
92 stochastic dispersal events, with the cumulative probability of sympatry
93 increasing with species age (i.e. divergence time) and thus the time available for
94 colonisation ('Neutral-dispersal model', Fig. 1a)²⁶. At the same time, stochastic
95 local extinctions may lead to species returning to a state of allopatry, potentially
96 decoupling the probability of sympatry from variation in species age. Dispersal-
97 assembly models are often equated with neutral dynamics but they may be
98 largely determined by species traits³⁰. In particular, the rate at which sympatry
99 is attained following speciation may vary across species depending on their
100 intrinsic vagility and geographic isolation, occurring more rapidly among species
101 with greater dispersal ability²⁸ or living in more continuous habitats³¹
102 ('Deterministic-dispersal model', Fig. 1b). Second, under a 'Niche-assembly
103 model', dispersal limitation is expected to be weak or absent and the probability
104 of sympatry should instead depend on rates of local extinction that vary
105 according to ecological niche availability. In particular, rates of local extinction
106 are expected to decrease, and thus the probability of coexistence increase, with
107 the abundance and diversity of available resources¹³ as well as the extent of
108 niche divergence between species^{26,32,33}. The main caveat is that, if ecological
109 niche space is limited, the probability of coexistence between sister species
110 should theoretically decline as sympatric diversity approaches these bounds¹¹,

111 although the existence any such ecological limit remains debated⁵⁻¹² ('Bounded
112 vs Unbounded niche-assembly model', Fig. 1d).

113

114 We apply this framework to a global dataset of avian sister species ($n = 1,115$
115 species pairs)¹³. Birds are an ideal system to test these scenarios because of the
116 availability of near-comprehensive geographic, phylogenetic³⁴ and functional
117 trait datasets (see Methods). Collectively, these enable fine-scale variation in
118 phylogenetic age¹³, intrinsic dispersal ability (e.g. the hand-wing index, a
119 measure of wing pointedness³⁵) and niche divergence (e.g. differences in beak
120 size^{36,37}) to be robustly quantified across multiple sister pairs from assemblages
121 with contrasting levels of net primary productivity (NPP, an index of resource
122 availability¹³), species richness and geographic connectivity (e.g. islands versus
123 the mainland). Here, we first evaluate the role of each of these dispersal- and
124 niche-related factors, which until now have largely been tested in isolation²⁹.
125 Then, by combining these factors into a series of models of increasing
126 complexity, we compare the relative support for a suite of coexistence scenarios
127 that variously treat dispersal- and niche-related processes as mutually exclusive
128 explanations, or that integrate both these sets of processes into a single synthetic
129 framework ('Dispersal+niche assembly model', Fig. 1e). Our aim is not simply to
130 accept or reject alternative hypotheses, but to establish the relative importance
131 of, and interplay between, biogeography and ecology in generating present-day
132 patterns of coexistence.

133 Results and Discussion

134 Neutral-assembly models

135 We modeled the dynamics of sympatry as a constant-rate Markov process which,
136 in its most basic form, contains two parameters that can be estimated through
137 maximum likelihood (see Methods)²⁶: the transition rate to sympatry (σ) and the
138 return transition rate to allopatry (ϵ). This latter parameter in turn provides an
139 estimate of the expected duration of coexistence (i.e. $1/\epsilon$). We start by
140 considering a Neutral-dispersal model in which all species are governed by equal
141 but low rates of σ and ϵ , and where the cumulative probability of coexistence

142 thus increases with species age (Fig. 1a)²⁶. This scenario can be compared to a
143 ‘Random coexistence model’, in which σ and ϵ are so high that the probability of
144 sympatry is independent of species age (Fig. 1c). Because the extent of sympatry
145 between species can vary from marginal to complete overlap, we explore the
146 effects of using different definitions of sympatry (10-90% overlap in 10%
147 intervals) as well as models treating sympatry as a continuous rather than a
148 binary trait (see Methods).

149 Across all range overlap thresholds, we found that a Neutral-dispersal
150 model is strongly supported compared to a Random coexistence model (Figs. 2a
151 and 3a, Supplementary Table 1), with the maximum likelihood estimate of $\sigma =$
152 0.25 (>10% range overlap, 95% CI: 0.21-0.32), equating to an average waiting
153 time to sympatry following speciation of 3.92 million years (95% CI: 3.14-4.80).
154 Thus, although it has been suggested that rapid range dynamics will erase the
155 historical effects of speciation^{38,39}, our results show that speciation has left a
156 persistent signature in current avian distributions. Evidence for a slow transition
157 rate to sympatry was maintained even after accounting for the potential
158 inhibitory effects of competition or incomplete reproductive isolation^{26,40},
159 supporting the notion that time for dispersal imposes an important constraint on
160 geographic range overlap (see Methods, Supplementary Figure 2, Supplementary
161 Table 2).

162

163 Deterministic-dispersal processes

164 Deterministic assembly models in which σ or ϵ vary as a function of dispersal- or
165 niche-related traits received significantly higher support than neutral models in
166 which sympatry dynamics are identical across species pairs (Fig. 3a,
167 Supplementary Table 1). In particular, species with more pointed wings—an
168 adaptation for long distance flight—attain sympatry more rapidly than less
169 dispersive species (Fig. 2b), while the transition to coexistence is delayed on
170 islands compared to the mainland (Fig. 2c). These dispersal-related variables
171 appear to mediate sympatry via their effects on geographic range expansion⁴¹. In
172 particular, although they remained significant predictors when considered
173 alongside niche-related variables, their independent contributions were largely

174 removed when accounting for variation in geographic range size (Supplementary
175 Figure 3).

176 The positive effects of intrinsic vagility on the attainment of sympatry has
177 previously been identified²⁸, but the dynamics of sympatry on islands has
178 remained unresolved⁴². On the one hand, it has been argued that geographic
179 isolation should inhibit the attainment of sympatry because of reduced rates of
180 island colonisation, or because any small founding populations are more likely to
181 suffer stochastic extinctions or introgression with residents³¹. On the other hand,
182 coexistence may be promoted on islands because of a relaxation of biotic
183 constraints, including the presence of fewer pathogens and competitors⁴². High
184 levels of sympatry among some young island lineages such as Darwin's finches
185 (Geospizinae) would appear to support this latter idea. However, our analysis
186 suggests that such cases are relatively rare, and that overall the attainment of
187 sympatry is inhibited in insular systems compared to more continuous mainland
188 habitats.

189

190 Niche-assembly processes

191 Both the extent of species trait divergence and ecosystem productivity were
192 negatively associated with ϵ , and thus positively associated with the duration of
193 sympatry (Figs. 2d-e and 3a). Such an effect of trait divergence is consistent with
194 previous studies suggesting that competition²⁶, or other antagonistic
195 interactions (e.g. reproductive interference^{40,43} or shared natural enemies⁴²), can
196 inhibit geographic overlap among young and ecologically similar species.
197 Importantly, the effect of trait divergence was maintained when including a
198 temporal lag in the attainment of sympatry expected due to either dispersal
199 limitation (Fig. 2d) or incomplete reproductive isolation (Supplementary Figure
200 2, Supplementary Table 2), suggesting that competition is at least partially
201 responsible for limiting sympatry.

202 In theory, similarity in species traits could promote coexistence by
203 equalising differences in fitness^{44,45}. However, our results demonstrate that
204 phenotypic divergence is positively, rather than negatively, associated with
205 coexistence, suggesting that the stabilising effects of niche differentiation
206 override any negative effects of differences in competitive ability. Experimental

207 evidence from plant communities indicates that coexistence may be promoted by
208 divergence across multiple niche dimensions⁴⁶. Across birds, however, the
209 effects of phenotypic divergence were primarily driven by a single axis,
210 representing variation in beak and body size with additional trait axes having
211 little or no discernible effect (Supplementary Figure 4). These different
212 conclusions may reflect the contrasting scale of our analysis, which focuses on
213 coexistence between only the most closely related and ecologically similar
214 species where divergence in size may be the most likely route to avoiding
215 competition^{47,48}. Because the strongest effects of phenotypic divergence were
216 obtained using body size, we focus on this metric throughout our analysis.

217 The positive effect of NPP on sympatry confirms the role of productivity
218 as a major driver of coexistence in birds at large spatial scales¹³ and provides a
219 compelling explanation for the strong global association between avian species
220 richness and NPP⁴⁹. However, the precise mechanism linking productivity and
221 coexistence remains unclear¹³. One possibility is that higher resource availability
222 facilitates ecological niche divergence⁵⁰, but our data provide limited support for
223 this hypothesis; the independent effect of productivity persisted even after
224 accounting for the extent of phenotypic divergence (Fig. 2e). This may be
225 because phenotypically similar species are partitioned along niche axes
226 overlooked by our analyses, such as foraging behaviour or microhabitat
227 preference. Alternatively, our results may support a niche packing model^{36,51} in
228 which high resource abundance promotes coexistence among phenotypically
229 similar species by reducing rates of local extinction^{17,52}. This model predicts that,
230 for a given level of trait divergence, coexistence is more likely in productive
231 environments, a pattern confirmed by our analysis.

232 Bounded models of species diversity predict that sympatry should
233 accumulate rapidly when diversity is low^{11,53,54}. As local richness increases and
234 niche space becomes filled, opportunities for invasion should decline, leaving
235 recently diverged lineages ‘stuck’ in a state of allopatry. Evidence that species
236 diversity is bounded remains controversial^{5,12} and our results initially also
237 appear to provide little support for this model; depending on the range overlap
238 threshold used to define sympatry, sister species coexistence is either unrelated
239 or weakly positively associated with total assemblage species richness (Fig. 2f).

240 However, in a multivariate model accounting for variation in ecosystem
241 productivity, the effect of species richness switched to become strongly negative,
242 suggesting that the continued build-up of widespread sympatry is inhibited in
243 assemblages containing a high standing diversity relative to their environmental
244 capacity (Fig. 2f). This Bounded niche-assembly model was strongly supported
245 compared to a model lacking a negative effect of richness (Fig. 3a). Although this
246 need not imply the existence of a hard upper limit to diversity^{17,55}, our results
247 provide key support for the hypothesis that broad-scale gradients in species
248 richness are strongly regulated by environmental constraints on coexistence^{12,49}
249 and cannot be explained by purely historical hypotheses focusing on differences
250 in the size or age of regional species pools^{5,56}.

251

252 The interplay between dispersal- and niche assembly processes

253 Although limits to sympatry have variously been attributed to a number of
254 distinct mechanisms²⁹, here we show that such single-factor explanations
255 receive little empirical support compared to more complex scenarios involving
256 multiple historical, intrinsic and environmental factors (Fig. 3e). Most
257 importantly, models treating dispersal- and niche-related processes separately
258 received little support compared to a fully integrated Dispersal+niche assembly
259 scenario (mean AICW = 0.82, Fig. 3a, Supplementary Table 1), highlighting how
260 global patterns of sympatry can only be understood on the basis of both
261 biogeographical and ecological factors.

262 One prediction of theoretical models integrating dispersal- and niche-
263 assembly processes is that the relative importance of niche availability should
264 increase as rates of dispersal decline^{15,21}. Our analysis supports this prediction,
265 by showing that the estimated effects of dispersal- and niche-related factors
266 varies predictably according to the geographic extent of sympatry (Figs. 2 and
267 3b). Specifically, while models representing metrics of dispersal limitation are
268 strongly supported when predicting the marginal overlap of species
269 distributions (overlap threshold $\leq 20\%$, AICW = 0.82), statistical support
270 switches overwhelmingly to models representing niche availability when
271 predicting whether species coexist more widely across their geographic range
272 (overlap threshold $\geq 80\%$, AICW = 100) (Figs. 3b, Supplementary Table 1). Thus,

273 while dispersal from adjacent allopatric source populations is critical in attaining
274 coexistence at the margins of species ranges, niche availability becomes
275 increasingly important in determining the extent of mutual range invasion.

276 An important implication of these results is that inferences based on any
277 single definition of sympatry are unlikely to provide a general explanation for
278 patterns of geographic range overlap. This may help explain the seemingly
279 conflicting findings of previous studies that have variously concluded a dominant
280 effect of either dispersal- or niche-based processes in structuring species
281 communities²⁹. In particular, our results make two key predictions. First, for any
282 given assemblage, the effects of niche differentiation in stabilising coexistence
283 should vary predictably between pairs of species according to their degree of
284 geographic range overlap. Second, the relative importance of niche-based
285 processes in maintaining diversity should vary across assemblages according to
286 the average geographic range overlap of the constituent species. To our
287 knowledge, these hypotheses have never been tested, but raise the prospect that
288 the processes maintaining coexistence locally may to a certain extent be
289 predictable on the basis of readily measured macroecological patterns.

290 While our analysis of AIC weights shows the relative support for different
291 coexistence scenarios (Fig. 3), this does not directly indicate the extent to which
292 patterns of coexistence are predictable on the basis of dispersal- and niche-
293 related factors or are instead dominated by stochastic dynamics. To address this,
294 we quantified the predictability of coexistence by comparing observed patterns
295 to those expected under each fitted model. Our results show that predictions of
296 whether any individual pair of species is sympatric have limited accuracy
297 regardless of the variables included in the model (overlap threshold $\geq 20\%$, $R^2 <$
298 0.1 , Fig. 4). This arises not because of poor model fit, but because most sister
299 pairs are similarly young, share similar traits, live in similar environments, and
300 are thus governed by similar dynamics (Supplementary Figures 5-6). In contrast,
301 when species pairs are sorted into classes according to these properties,
302 differences in the frequency of sympatry between classes can be predicted much
303 more effectively, with accuracy increasing with the number of species in each
304 class (overlap threshold $\geq 20\%$, $R^2 = 0.73$, Fig. 4).

305 These findings suggest that, while the probabilistic nature of dispersal
306 and local extinction events may appear to dominate at the scale of individual
307 sister pairs, when viewed across larger samples of species, the deterministic
308 effects of species traits and the environment lead to the emergence of more
309 predictable patterns. A similar shift from stochastic to deterministic dynamics
310 with increasing scale has previously been anticipated²⁵, and reported in
311 communities of rainforest trees⁵⁷. Our results suggest that this phenomenon may
312 help explain why environmental models of species richness typically have such
313 high explanatory power⁴⁹, despite the potentially idiosyncratic and historically
314 contingent nature of individual species distributions⁵⁸.

315

316

317 Conclusion

318 Our analysis of avian sister species takes a first step towards quantifying the
319 relative contributions of multiple assembly processes in generating patterns of
320 geographic range overlap at a global scale. The approach highlights the role of
321 numerous factors previously singled out as potential limits to sympatry by
322 showing that coexistence increases with the rate and time available for dispersal,
323 is further enhanced by ecosystem productivity and divergence in species traits
324 and is inhibited in insular environments or those containing large numbers of
325 species. We demonstrate that none of these factors in isolation can adequately
326 predict patterns of sympatry, which instead requires an integrated model
327 incorporating the combined effects of both dispersal- and niche-related
328 processes. While our findings thus reinforce the view that biodiversity is
329 structured by a complex tapestry of interwoven assembly processes, we have
330 shown that these interact in predictable ways to determine current patterns of
331 coexistence. Overall, our analysis demonstrates the power of combining
332 phylogenetic, environmental and phenotypic data to unweave these processes,
333 paving the way to a more mechanistic understanding of how broad-scale
334 gradients in species richness and community structure are generated and
335 maintained.

336

337 Methods

338 **Sister species geographic overlap**

339 We extracted avian sister pairs and their estimated divergence times (Myr) from
340 the time-calibrated phylogeny of ref³⁴ based on the backbone topology of ref⁶⁰
341 (<http://birdtree.org>). We account for uncertainty in both sister species
342 assignments and their divergence times by repeating our analysis across 100
343 trees drawn at random from the posterior distribution. All reported results are
344 the mean across the posterior distribution of trees. We pruned each tree to only
345 include species represented by genetic data ($n = 6670$), resulting in a mean of $n =$
346 2152 sister species pairs per tree. Following our previous work¹³, we excluded
347 sister pairs that i) predominantly forage at sea ($n = 101$), ii) belong to genera
348 poorly sampled in the tree (<70% species in the genus represented by genetic
349 data, $n = 724$) and thus where species are unlikely to represent true sisterhoods
350 and iii) are extremely young (<0.75 Myr, $n = 191$) and thus where ongoing
351 introgression and ancestral polymorphism is expected to confound reliable
352 estimates of divergence times⁶¹. Finally, we removed species pairs for which we
353 were unable to obtain complete trait data, $n = 10$. In total, $n = 3352$ species
354 across the $n = 100$ trees were included in our analysis, with a mean of $n = 1115$
355 sister pairs per tree.

356 We quantified coexistence on the basis of the native breeding
357 distributions and broad-scale habitat occupancy of species. For each sister pair,
358 we estimated the area of distributional overlap from rasterised (1 km resolution)
359 expert opinion maps of extent of occurrence (available to view at
360 <http://mol.org>)⁶². We quantified range overlap between species according to the
361 Szymkiewicz-Simpson coefficient [$\text{Area}_{\text{Overlap}} / \min(\text{Area}_{\text{Sister1}}, \text{Area}_{\text{Sister2}})$]¹³, and
362 also incorporated information on species habitat and altitudinal preferences¹³ to
363 ensure that coexisting species occupied the same major habitat types and
364 elevation zones. Following previous methods¹³, sister species occupying non-
365 overlapping elevation zones (<20% proportional overlap) or utilising different
366 major habitat types (forest, shrubland, bare ground, wetland) were assigned as
367 not coexisting ($n = 97$).

368 **Predictors of species coexistence**

369 To calculate extrinsic predictors of sympatry (NPP, species richness and island
370 dwelling) we extracted species polygon ranges onto an equal area grid
371 (resolution of 110km, equal to approximately 1 degree at the equator). We
372 quantified the mean NPP (gCM^{-2} , 30' resolution)⁶³ and richness of all 9993 bird
373 species (at the scale of 110km grid cells) across the geographic distribution of
374 each sister pair. For allopatric sister pairs, we calculated the mean value across
375 the combined geographic range of both species (i.e. the union) while for
376 sympatric pairs we calculated the mean values across those cells where both
377 species were present (i.e. the intersection). Sister pairs were assigned as 'island
378 dwelling' if the majority of either species range was found on islands.

379 To quantify dispersal ability and niche similarity, we compiled a database
380 of phenotypic traits for all sister species based on estimates of mean species
381 body mass (g)⁶⁴ and eight linear traits (beak length [measured both as culmen
382 from beak tip to skull, and beak tip to nares], beak width and depth [at anterior
383 nares], tarsus length, wing length [carpal joint to wing tip], first secondary length
384 [carpal joint to tip of first secondary], and tail length). We measured these eight
385 traits from museum skins and live birds in the field; see ref³⁶ for detailed
386 methods. Traits were selected based on their well-established association with
387 flight ability, habitat and resource use, thus representing the key dimensions of
388 the avian niche^{36,65}. On average, we obtained measurements for 5.1 individuals
389 per species (2 males and 2 females, where possible); see Database S1 for
390 specimen accession details and locality information for all birds measured.

391 We combined the nine log-transformed mean species trait values in a
392 principal components (PC) analysis. The first synthetic axis represents an overall
393 index of size (PC1), with the remaining axes quantifying variation in shape
394 (Supplementary Table 3). We retained the first four PC axes which collectively
395 account for >95% of the variance in species trait values (Supplementary Table
396 3). For each sister pair, we quantified the distance (log-transformed) between
397 species along individual PC axis, and also the total Euclidian inter-species
398 distance along all axes combined. Total Euclidian distance is primarily driven by
399 the first few PC axes, which account for the majority of trait variance. We
400 therefore also calculated the total Euclidian distance after scaling each axis to

401 unit variance to test a model in which multiple trait dimensions contribute
402 equally to explaining coexistence⁴⁶. Because the beak has received particular
403 attention as a key trait mediating competition for ecological resources^{66,67}, we re-
404 ran our models using only beak-related traits (beak length, width, depth) as
405 inputs into our PC analysis (Supplementary Table 4) to examine the specific
406 effects of beak divergence on coexistence.

407 We modelled the effects of intrinsic vagility using the hand-wing index
408 (HWI), a well-established proxy for flight ability in birds^{28,35}. HWI was calculated
409 as

$$HWI = \frac{100 \times \text{Kipp's distance}}{\text{wing chord}}$$

410 where wing chord is the distance from the carpal joint (wrist) to the tip of the
411 longest primary, and Kipp's distance is the distance between the tips of the
412 longest primary feather and the first secondary feather, both measured on the
413 closed wing (i.e. wing length minus first secondary length). Kipp's distances for
414 flightless species of the genus *Apteryx* could not be measured because they lack
415 visible wings or wing-feathers, and so these species were assigned the minimum
416 HWI observed across the dataset. In our analysis, we used the average HWI of
417 each sister pair (log-transformed). In all cases, predictor variables were scaled to
418 unit variance prior to analysis to enable effects sizes to be compared.

419 **Modelling coexistence dynamics**

420 We modelled the dynamics of species coexistence over time as a constant-rate
421 Markov process²⁶. In this model, we assumed that speciation occurs in allopatry
422 (or parapatry) so that at the time of population divergence sister species have
423 non-overlapping spatial distributions (state = 0). In birds, this assumption is
424 justified because previous empirical studies have shown that sympatric
425 speciation is extremely rare (<5% of speciation events)^{28,68-70}. Following
426 speciation, species pairs transition to a state of sympatry (state = 1) at rate σ
427 and, having attained sympatry, return to a state of allopatry at rate ϵ . Given the
428 observed ages (millions of years, Myr) and current geographical states of each

429 sister pair (0 or 1), rates of σ and ϵ (per sister pair/Myr) can be estimated using
430 maximum likelihood²⁶. Rather than assume a single range overlap threshold to
431 define sympatry, we repeated our analysis assuming different thresholds,
432 exploring values from 10-90% in 10% increments.

433 We tested how variables associated with the strength of dispersal
434 limitation influence the attainment of sympatry in two stages. First, we tested for
435 an effect of time for dispersal (i.e. species age), by fitting a 'Neutral-dispersal
436 model' in which both σ and ϵ were treated as free parameters that were
437 estimated from the data ($n = 2$ parameters, Supplementary Figure 1a). We
438 compared this model to a 'Random-coexistence model' lacking dispersal
439 limitation, by fixing σ at an arbitrarily large value ($\sigma = 1000$) and only estimating
440 ϵ ($n = 1$ parameter, Supplementary Figure 1c). This is equivalent to assuming a
441 waiting time to coexistence following speciation (i.e. $1/\sigma$) of only 1000 years,
442 which is essentially instantaneous compared to the average age of the sister
443 species in our dataset (median = 5.15 Myr). According to this Random-
444 coexistence model, the probability of coexistence (P) is simply defined by the
445 relative rates of σ and ϵ [i.e. $P = \sigma/(\sigma + \epsilon)$] and is identical across species pairs.
446 Second, we fitted a set of 'Deterministic-dispersal models' in which we estimated
447 the log-linear effects of species dispersal ability (HWI) and island dwelling on σ ,
448 both individually ($n = 3$ parameters) and together ($n = 4$ parameters)
449 (Supplementary Figure 1b).

450 A Random-coexistence model fixing $\sigma = 1000$, provides a null expectation
451 for testing the effects of dispersal limitation, but also provides the foundation for
452 'Niche-assembly models' testing how the duration of coexistence following
453 secondary contact (i.e. $1/\epsilon$) varies according to environmental or ecological
454 traits. Thus, we tested the effects of NPP, trait divergence and species richness on
455 coexistence by including each of these terms as a covariate on ϵ , either
456 individually or together ($n = 2$ to 4 parameters, Supplementary Figure 1d).
457 Because we were particularly interested in isolating the effects of species
458 richness on coexistence we fitted both a 'Bounded niche-assembly model' and an
459 'Unbounded niche-assembly model', that included all niche-related parameters
460 ($n = 4$ parameters) or excluded species richness ($n = 3$ parameters) respectively.
461 Finally, we combined all predictor variables into a single 'Dispersal+niche

462 assembly model' integrating the effects of both dispersal limitation on σ and
463 ecological niche availability on ϵ (Supplementary Figure 1e, $n = 7$ parameters).
464 All models were fitted in the R environment⁷¹ using the *msm* package⁷². We
465 assessed relative model fit on the basis of the Akaike Information Criterion
466 (AIC)⁷³. In addition to absolute AIC scores, we also calculated model AIC weight
467 (AICW), which quantifies the relative probability that each model is correct given
468 the set of models being compared.

469 Dispersal-related variables are specifically expected to promote
470 coexistence by facilitating geographic range expansions. To explore this
471 possibility, we included the maximum range size of each sister pair as an
472 additional predictor of σ in our Dispersal+niche assembly model ($n = 8$
473 parameters) (Supplementary Figure 3). We confirmed that σ is strongly
474 positively associated with range size (Supplementary Figure 3a). Having
475 accounted for this effect, the independent contributions of organism vagility
476 (Supplementary Figure 3b) and island dwelling (Supplementary Figure 3c) were
477 largely removed, while the effects of niche-related variables remained unaltered
478 (Supplementary Figure 3d-f). Thus, while dispersal-related variables appear to
479 mediate coexistence via their effects on geographic range expansions⁴¹, our
480 results suggest that niche-related variables facilitate coexistence independently
481 of any effect on range size.

482

483 **Sensitivity analyses**

484 We conducted additional analyses to ensure that our results were robust to
485 model assumptions. First, rather than using the individual species age estimates
486 from each tree (Supplementary Figure 7a-c) we repeated our analysis using the
487 mean age for each sister pair across the posterior distribution of trees, obtaining
488 very similar results (Supplementary Figure 7d-f). Second, we tested that the
489 effects of time for dispersal (i.e. species age) and trait divergence were robust to
490 the inclusion of a temporal lag in the establishment of sympatry ($n = 8$
491 parameters), as expected if incomplete reproductive isolation initially inhibits
492 coexistence following speciation (Supplementary Figure 2, Supplementary Table
493 2)^{26,40}. We modelled this lag by fitting a series of breakpoint transition models in
494 which the duration of coexistence (i.e. $1/\epsilon$) was initially low (or high) following

495 speciation but could then increase (or decrease) after a given period of time had
496 elapsed. Model support was evaluated for different breakpoint values from 1 to 6
497 Myr post speciation in 0.5 Myr intervals. Although we found evidence that the
498 duration of coexistence increases with time since speciation, models with a slow
499 attainment of secondary contact (i.e. σ is small) and in which trait divergence
500 also mediates coexistence were still strongly favoured (Supplementary Figure 2,
501 Supplementary Table 2). These results support the notion that both time for
502 dispersal and trait similarity impose important constraints on geographic range
503 overlap independently of any inhibitory effect of incomplete reproductive
504 isolation.

505 Third, although the models presented focus on how niche-related
506 variables (trait divergence, NPP and species richness) influence ϵ and thus the
507 duration of coexistence, we found that our conclusions were also robust to the
508 alternative assumption that these variables instead influence σ , which can be
509 interpreted as the rate of successful colonisation (Supplementary Figure 8).
510 Fourth, to ensure the significant relationships we detected were not driven by
511 the phylogenetic non-independence of sister species pairs, we examined the
512 effects of each predictor in a phylogenetic generalised linear mixed model
513 (PGLMM) using the R package MCMCglmm⁷⁴. This statistical framework
514 additionally allowed us to explore the effects of treating range overlap as either a
515 binary or a continuous variable⁷⁴. Range overlap scores are zero-inflated and so
516 we developed a two-part model including i) all sister pairs ($n = 1115$) and
517 treating sympatry as a binary variable (0 [overlap < 10%], 1 [overlap \geq 10%]) and
518 ii) those sister pairs with non-zero overlap scores ($n = 514$) with sympatry
519 modelled as a continuous variable. For the latter, proportional range overlap
520 scores were logit-transformed, with overlap values of 1 set to 0.99 prior to
521 transformation. We ran each model for 2.5 million iterations with a burn-in of
522 10,000 iterations and a thinning interval of 25,000 iterations.

523 Because phylogenetic heritability (H^2) in the incidence ($H^2 = 0.22$ 95% CI
524 [0.04, 0.50]) or extent ($H^2 = 0.05$ 95% CI [0, 0.30]) of sympatry is low, results
525 obtained using PGLMMs were very similar to those based on dynamic models
526 (Supplementary Figure 9, Supplementary Table 5). In particular, this analysis
527 confirmed the directional effect and significance of each predictor variable and

528 recovered a similar shift in the identity of core predictors—from dispersal-
529 related to niche-related variables—with the % range overlap threshold used to
530 define coexistence (Supplementary Figure 9, Supplementary Table 5).

531

532 **Assessing predictability of sympatry across scales**

533 For different combinations of variables and range overlap thresholds, we fitted
534 an individual-level logistic-regression predicting sister species sympatry or
535 allopatry (0,1). We then divided our dataset of sister pairs into n quantiles
536 according to their predicted probabilities of sympatry, examining values of n
537 from 2 to 1000 corresponding to class sizes of ~ 500 to ~ 1 sister pairs
538 respectively. Finally, we fit a group-level logistic-regression predicting the
539 frequency of sympatry across classes and calculated McFadden's⁵⁹ Pseudo- R^2 ,

$$R^2 = \frac{LLFull}{LLNull}$$

540 where $LLNull$ and $LLFull$ are the log-likelihoods of the intercept only and full
541 model respectively.

542

543

544 **Data Availability**

545 The data analysed here is available in the Supplementary Data and
546 10.6084/m9.figshare.6171185

547

548 **Code Availability**

549 The code used in this analysis is available in the Supplementary Data and
550 10.6084/m9.figshare.6171185

551

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560

561 **Author contributions**

562 ALP, WJ, CS and JAT conceived the study; CS, JAT and WJ contributed data; ALP
563 performed the analysis and wrote the first draft. All authors contributed to the
564 writing of the manuscript.

565

566 **Declaration of competing interests**

567 The authors declare no competing interests.

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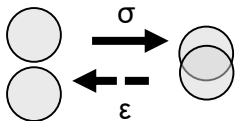
743

744 **Figure 1. Models of species coexistence.** Whether avian sister species coexist
745 is governed by the rate at which lineages attain sympatry following speciation (σ ,
746 solid lines), and then return to a state of allopatry due to local extinction (ϵ ,
747 dashed lines). Different assembly models (a-e) make different predictions
748 regarding the absolute rates of these dynamics, and their relationship with
749 species traits or environmental contexts (lines are for illustration only). First,
750 dispersal limitation may lead to a slow transition to sympatry at a rate that (a) is
751 approximately equal or (b) varies deterministically across species. Second,
752 niche-assembly models lacking dispersal limitation (i.e. σ is high), predict that
753 the return rate to allopatry is modulated by ecological factors that may either be
754 equivalent (c) or differ predictably across species (d). Finally, transition rates to
755 and from coexistence may vary across species according to both dispersal- and
756 niche-related factors (e). Together these models define a two-dimensional space,
757 quantifying both the degree of stochasticity and the relative contribution of
758 dispersal- and niche-based processes in limiting coexistence. NPP is net primary
759 productivity (see Methods).
760

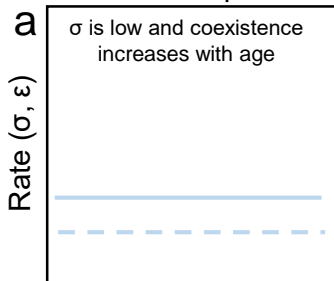
761 **Figure 2. Historical, intrinsic and environmental predictors of sympatry in**
762 **birds.** The effect size for each variable, both in isolation (open circles) and for
763 the full Dispersal+niche assembly model (filled circles, including; age, HWI,
764 island dwelling, trait divergence, NPP and species richness), is shown as a
765 function of the % range overlap used to define coexistence ($n = 1,115$ pairs).
766 Panels above each plot indicate support (AIC weight, AICW) for the inclusion of
767 each variable in the full model. Effect sizes (and 95% CI) show the hazard ratio,
768 indicating the change in the transition rate to coexistence σ (b, c) or the duration
769 of coexistence $1/\varepsilon$ (d-f) for a unit change in the predictor. Hazard ratios greater
770 or less than 1 indicate positive and negative effects on coexistence, respectively.
771 In (a) a hazard ratio estimate is not available for 'age' (see Methods). Support for
772 the effect of age is plotted as the difference in AIC between a model excluding
773 (Random-coexistence model) and including (Neutral-dispersal model) age, with
774 higher values indicating greater support. HWI (hand-wing index) is a measure of
775 wing shape related to dispersal ability (see Methods).
776
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780

781 **Figure 3. Relative support for different coexistence scenarios** (a) Support for
782 each coexistence model (ΔAIC) is shown when sympatry among a global sample
783 of avian sister species ($n = 1,115$ pairs) is quantified using either a low (20%,
784 open circle) or high (80%, filled circle) geographic range overlap threshold. (b)
785 the relative support (AIC weight) for Dispersal- or Niche-assembly scenarios as a
786 function of geographic range overlap. In (a, b) colours indicate Dispersal-
787 assembly (blue), Niche-assembly (orange) or Dispersal+niche assembly
788 (magenta) models, with darker shading within each group of models indicating
789 more complex multi-predictor scenarios. The variables included in each model
790 are highlighted under (a). In (b) models with low support are not shown (see
791 Supplementary Table 1 for model AIC values).

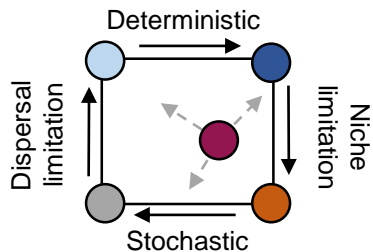
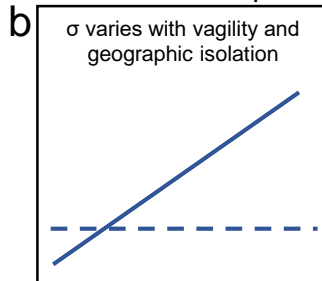
792 **Figure 4. Scale-dependency in the predictability (R^2) of coexistence.**
793 McFadden's⁵⁹ Pseudo- R^2 of models predicting the frequency of sympatry (left,
794 $\geq 20\%$ overlap; right, $\geq 80\%$ overlap) across classes of varying size (1 to 500
795 sister pairs) when including Dispersal- (D), Niche- (N) or both Dispersal- and
796 Niche-assembly (D+N) processes.
797



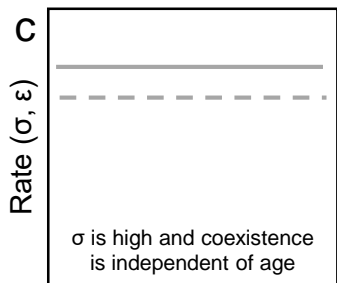
Neutral dispersal



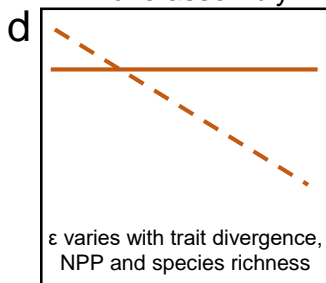
Deterministic dispersal



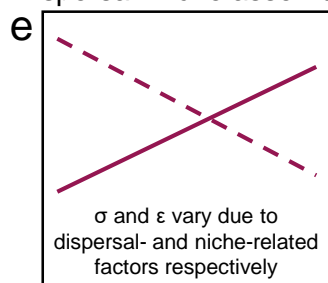
Random coexistence



Niche assembly



Dispersal+niche assembly



Trait/environmental gradient

