Title: The macroecological dynamics of species coexistence in birds

Authors: Alex L. Pigot[1,2], Walter Jetz[3,4], Catherine Sheard[5] and Joseph A. Tobias[4]

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

*Correspondence to: alex.pigot1@gmail.com

Keywords: community assembly, competition, dispersal, ecological niche, speciation, diversity gradients.

Number of words (3498)
Abstract (200)

Abstract

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

Introduction

Ecological assemblages are formed from the overlapping of species in geographic space. Explaining variation in the structure and richness of communities therefore depends on understanding how complex patterns of geographic range overlap are generated and maintained[1]. Ultimately, species distributions are the product of speciation, dispersal and extinction. Historical variation in these biogeographic processes may therefore be a major driver of community structure and broad-scale gradients in biodiversity[2-6]. In addition, these same patterns are thought to be regulated by ecological interactions among species[7-10]. Such niche-based assembly models have largely focused on the importance of competition in constraining coexistence, and predict that patterns of geographic overlap primarily reflect the degree of divergence in species ecological niches, as well as limits to the number of species that can be packed within a habitat[11-13]. Although it is widely recognized that patterns of spatial overlap among species probably reflect a mix of these different processes—both biogeographical and ecological—it has been difficult to quantify their relative contributions because most empirical tests of community assembly treat them in isolation and have addressed patterns of coexistence over a limited range of spatial and temporal scales[14-17].

On the one hand, tests of niche-based assembly mechanisms rarely explicitly consider the biogeographic processes underlying community formation, or only do so to the extent that these provide a null expectation for community structure[18,19]. On the other hand, while dispersal-based biogeographic models address this problem, they typically do so by ignoring species ecological niches[2]. Thus, even when purely dispersal- or niche-based models can be rejected, this says little about the relative importance of, and interaction between, these biogeographical and ecological processes. Most progress in disentangling assembly models has come from studies focusing at relatively fine spatial scales where the set of possible explanations for community structure are generally more limited, and assemblages can be experimentally manipulated[10,20-22]. However, the relevance of these findings for understanding major gradients in biodiversity remains unclear because they do not consider the historical processes generating species diversity[18,19,23] or how the relative importance of dispersal- and niche-based factors may vary across different spatial and temporal scales[24,25]. Understanding the causes of large-scale patterns in community structure and diversity therefore requires models integrating both biogeographical and ecological processes into a single analytical framework[19,26,27].

Here we illustrate how the effects of dispersal- and niche-related assembly processes can be disentangled by extending a dynamic model describing the evolution of spatial overlap (i.e. sympatry) between sister species[26]. We assume that speciation typically generates species with non-overlapping distributions (i.e. allopatry or parapatry)[28], and that the ensuing dynamics of spatial overlap provide critical insights into the factors regulating coexistence and the resulting broad-scale gradients in species richness[19,29]. This general framework underpins two alternative sets of models (Fig. 1). First, under a 'Dispersal-assembly model', species overlap is constrained by the rate of stochastic dispersal events, with the cumulative probability of sympatry increasing with species age (i.e. divergence time) and thus the time available for colonisation ('Neutral-dispersal model', Fig. 1a)[26]. At the same time, stochastic local extinctions may lead to species returning to a state of allopatry, potentially decoupling the probability of sympatry from variation in species age. Dispersal-assembly models are often equated with neutral dynamics but they may be largely determined by species traits[30]. In particular, the rate at which sympatry is attained following speciation may vary across species depending on their intrinsic vagility and geographic isolation, occurring more rapidly among species with greater dispersal ability[28] or living in more continuous habitats[31] ('Deterministic-dispersal model', Fig. 1b). Second, under a 'Niche-assembly model', dispersal limitation is expected to be weak or absent and the probability of sympatry should instead depend on rates of local extinction that vary according to ecological niche availability. In particular, rates of local extinction are expected to decrease, and thus the probability of coexistence increase, with the abundance and diversity of available resources[13] as well as the extent of niche divergence between species[26,32,33]. The main caveat is that, if ecological niche space is limited, the probability of coexistence between sister species should theoretically decline as sympatric diversity approaches these bounds[11], although the existence of any such ecological limit remains debated[5-12] ('Bounded vs Unbounded niche-assembly model', Fig. 1d).

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

We apply this framework to a global dataset of avian sister species (*n* = 1,115 species pairs)[13]. Birds are an ideal system to test these scenarios because of the availability of near-comprehensive geographic, phylogenetic[34] and functional trait datasets (see Methods). Collectively, these enable fine-scale variation in phylogenetic age[13], intrinsic dispersal ability (e.g. the hand-wing index, a measure of wing pointedness[35]) and niche divergence (e.g. differences in beak size[36,37]) to be robustly quantified across multiple sister pairs from assemblages with contrasting levels of net primary productivity (NPP, an index of resource availability[13]), species richness and geographic connectivity (e.g. islands versus the mainland). Here, we first evaluate the role of each of these dispersal- and niche-related factors, which until now have largely been tested in isolation[29]. Then, by combining these factors into a series of models of increasing complexity, we compare the relative support for a suite of coexistence scenarios that variously treat dispersal- and niche-related processes as mutually exclusive explanations, or that integrate both these sets of processes into a single synthetic framework (‘Dispersal+niche assembly model’, Fig. 1e). Our aim is not simply to accept or reject alternative hypotheses, but to establish the relative importance of, and interplay between, biogeography and ecology in generating present-day patterns of coexistence.

Results and Discussion

Neutral-assembly models

We modeled the dynamics of sympatry as a constant-rate Markov process which, in its most basic form, contains two parameters that can be estimated through maximum likelihood (see Methods)[26]: the transition rate to sympatry (σ) and the return transition rate to allopatry (ε). This latter parameter in turn provides an estimate of the expected duration of coexistence (i.e. $1/\varepsilon$). We start by considering a Neutral-dispersal model in which all species are governed by equal but low rates of σ and ε, and where the cumulative probability of coexistence thus increases with species age (Fig. 1a)[26]. This scenario can be compared to a 'Random coexistence model', in which σ and ε are so high that the probability of sympatry is independent of species age (Fig. 1c). Because the extent of sympatry between species can vary from marginal to complete overlap, we explore the effects of using different definitions of sympatry (10-90% overlap in 10% intervals) as well as models treating sympatry as a continuous rather than a binary trait (see Methods).

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

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

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

Deterministic-dispersal processes

Deterministic assembly models in which σ or ε vary as a function of dispersal- or niche-related traits received significantly higher support than neutral models in which sympatry dynamics are identical across species pairs (Fig. 3a, Supplementary Table 1). In particular, species with more pointed wings—an adaptation for long distance flight—attain sympatry more rapidly than less dispersive species (Fig. 2b), while the transition to coexistence is delayed on islands compared to the mainland (Fig. 2c). These dispersal-related variables appear to mediate sympatry via their effects on geographic range expansion[41]. In particular, although they remained significant predictors when considered alongside niche-related variables, their independent contributions were largely removed when accounting for variation in geographic range size (Supplementary Figure 3).

The positive effects of intrinsic vagility on the attainment of sympatry has previously been identified[28], but the dynamics of sympatry on islands has remained unresolved[42]. On the one hand, it has been argued that geographic isolation should inhibit the attainment of sympatry because of reduced rates of island colonisation, or because any small founding populations are more likely to suffer stochastic extinctions or introgression with residents[31]. On the other hand, coexistence may be promoted on islands because of a relaxation of biotic constraints, including the presence of fewer pathogens and competitors[42]. High levels of sympatry among some young island lineages such as Darwin's finches (Geospizinae) would appear to support this latter idea. However, our analysis suggests that such cases are relatively rare, and that overall the attainment of sympatry is inhibited in insular systems compared to more continuous mainland habitats.

Niche-assembly processes

Both the extent of species trait divergence and ecosystem productivity were negatively associated with ε, and thus positively associated with the duration of sympatry (Figs. 2d-e and 3a). Such an effect of trait divergence is consistent with previous studies suggesting that competition[26], or other antagonistic interactions (e.g. reproductive interference[40,43] or shared natural enemies[42]), can inhibit geographic overlap among young and ecologically similar species. Importantly, the effect of trait divergence was maintained when including a temporal lag in the attainment of sympatry expected due to either dispersal limitation (Fig. 2d) or incomplete reproductive isolation (Supplementary Figure 2, Supplementary Table 2), suggesting that competition is at least partially responsible for limiting sympatry.

In theory, similarity in species traits could promote coexistence by equalising differences in fitness[44,45]. However, our results demonstrate that phenotypic divergence is positively, rather than negatively, associated with coexistence, suggesting that the stabilising effects of niche differentiation override any negative effects of differences in competitive ability. Experimental evidence from plant communities indicates that coexistence may be promoted by divergence across multiple niche dimensions[46]. Across birds, however, the effects of phenotypic divergence were primary driven by a single axis, representing variation in beak and body size with additional trait axes having little or no discernible effect (Supplementary Figure 4). These different conclusions may reflect the contrasting scale of our analysis, which focuses on coexistence between only the most closely related and ecologically similar species where divergence in size may be the most likely route to avoiding competition[47,48]. Because the strongest effects of phenotypic divergence were obtained using body size, we focus on this metric throughout our analysis.

The positive effect of NPP on sympatry confirms the role of productivity as a major driver of coexistence in birds at large spatial scales[13] and provides a compelling explanation for the strong global association between avian species richness and NPP[49]. However, the precise mechanism linking productivity and coexistence remains unclear[13]. One possibility is that higher resource availability facilitates ecological niche divergence[50], but our data provide limited support for this hypothesis; the independent effect of productivity persisted even after accounting for the extent of phenotypic divergence (Fig. 2e). This may be because phenotypically similar species are partitioned along niche axes overlooked by our analyses, such as foraging behaviour or microhabitat preference. Alternatively, our results may support a niche packing model[36,51] in which high resource abundance promotes coexistence among phenotypically similar species by reducing rates of local extinction[17,52]. This model predicts that, for a given level of trait divergence, coexistence is more likely in productive environments, a pattern confirmed by our analysis.

Bounded models of species diversity predict that sympatry should accumulate rapidly when diversity is low[11,53,54]. As local richness increases and niche space becomes filled, opportunities for invasion should decline, leaving recently diverged lineages 'stuck' in a state of allopatry. Evidence that species diversity is bounded remains controversial[5,12] and our results initially also appear to provide little support for this model; depending on the range overlap threshold used to define sympatry, sister species coexistence is either unrelated or weakly positively associated with total assemblage species richness (Fig. 2f). However, in a multivariate model accounting for variation in ecosystem productivity, the effect of species richness switched to become strongly negative, suggesting that the continued build-up of widespread sympatry is inhibited in assemblages containing a high standing diversity relative to their environmental capacity (Fig. 2f). This Bounded niche-assembly model was strongly supported compared to a model lacking a negative effect of richness (Fig. 3a). Although this need not imply the existence of a hard upper limit to diversity[17,55], our results provide key support for the hypothesis that broad-scale gradients in species richness are strongly regulated by environmental constraints on coexistence[12,49] and cannot be explained by purely historical hypotheses focusing on differences in the size or age of regional species pools[5,56].

The interplay between dispersal- and niche assembly processes

Although limits to sympatry have variously been attributed to a number of distinct mechanisms[29], here we show that such single-factor explanations receive little empirical support compared to more complex scenarios involving multiple historical, intrinsic and environmental factors (Fig. 3e). Most importantly, models treating dispersal- and niche-related processes separately received little support compared to a fully integrated Dispersal+niche assembly scenario (mean AICW = 0.82, Fig. 3a, Supplementary Table 1), highlighting how global patterns of sympatry can only be understood on the basis of both biogeographical and ecological factors.

One prediction of theoretical models integrating dispersal- and niche-assembly processes is that the relative importance of niche availability should increase as rates of dispersal decline[15,21]. Our analysis supports this prediction, by showing that the estimated effects of dispersal- and niche-related factors varies predictably according to the geographic extent of sympatry (Figs. 2 and 3b). Specifically, while models representing metrics of dispersal limitation are strongly supported when predicting the marginal overlap of species distributions (overlap threshold ≤ 20%, AICW = 0.82), statistical support switches overwhelmingly to models representing niche availability when predicting whether species coexist more widely across their geographic range (overlap threshold ≥ 80%, AICW = 100) (Figs. 3b, Supplementary Table 1). Thus, while dispersal from adjacent allopatric source populations is critical in attaining coexistence at the margins of species ranges, niche availability becomes increasingly important in determining the extent of mutual range invasion.

An important implication of these results is that inferences based on any single definition of sympatry are unlikely to provide a general explanation for patterns of geographic range overlap. This may help explain the seemingly conflicting findings of previous studies that have variously concluded a dominant effect of either dispersal- or niche-based processes in structuring species communities[29]. In particular, our results make two key predictions. First, for any given assemblage, the effects of niche differentiation in stabilising coexistence should vary predictably between pairs of species according to their degree of geographic range overlap. Second, the relative importance of niche-based processes in maintaining diversity should vary across assemblages according to the average geographic range overlap of the constituent species. To our knowledge, these hypotheses have never been tested, but raise the prospect that the processes maintaining coexistence locally may to a certain extent be predictable on the basis of readily measured macroecological patterns.

While our analysis of AIC weights shows the relative support for different coexistence scenarios (Fig. 3), this does not directly indicate the extent to which patterns of coexistence are predictable on the basis of dispersal- and niche-related factors or are instead dominated by stochastic dynamics. To address this, we quantified the predictability of coexistence by comparing observed patterns to those expected under each fitted model. Our results show that predictions of whether any individual pair of species is sympatric have limited accuracy regardless of the variables included in the model (overlap threshold ≥ 20%, $R^2 <$

0.1, Fig. 4). This arises not because of poor model fit, but because most sister pairs are similarly young, share similar traits, live in similar environments, and are thus governed by similar dynamics (Supplementary Figures 5-6). In contrast, when species pairs are sorted into classes according to these properties, differences in the frequency of sympatry between classes can be predicted much more effectively, with accuracy increasing with the number of species in each class (overlap threshold ≥ 20%, $R^2 = 0.73$, Fig. 4).

These findings suggest that, while the probabilistic nature of dispersal and local extinction events may appear to dominate at the scale of individual sister pairs, when viewed across larger samples of species, the deterministic effects of species traits and the environment lead to the emergence of more predictable patterns. A similar shift from stochastic to deterministic dynamics with increasing scale has previously been anticipated[25], and reported in communities of rainforest trees[57]. Our results suggest that this phenomenon may help explain why environmental models of species richness typically have such high explanatory power[49], despite the potentially idiosyncratic and historically contingent nature of individual species distributions[58].

Figure 4. **Scale-dependency in the predictability (R^2) of coexistence**. McFadden's[59] Pseudo-R^2 of models predicting the frequency of sympatry (left, ≥20% overlap; right, ≥80% overlap) across classes of varying size (1 to 500 sister pairs) when including Dispersal- (D), Niche- (N) or both Dispersal- and Niche-assembly (D+N) processes.

Conclusion

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

Methods

Sister species geographic overlap

We extracted avian sister pairs and their estimated divergence times (Myr) from the time-calibrated phylogeny of ref[34] based on the backbone topology of ref[60] (http://birdtree.org). We account for uncertainty in both sister species assignments and their divergence times by repeating our analysis across 100 trees drawn at random from the posterior distribution. All reported results are the mean across the posterior distribution of trees. We pruned each tree to only include species represented by genetic data (n = 6670), resulting in a mean of n = 2152 sister species pairs per tree. Following our previous work[13], we excluded sister pairs that i) predominantly forage at sea (n = 101), ii) belong to genera poorly sampled in the tree (<70% species in the genus represented by genetic data, n = 724) and thus where species are unlikely to represent true sisterhoods and iii) are extremely young (<0.75 Myr, n = 191) and thus where ongoing introgression and ancestral polymorphism is expected to confound reliable estimates of divergence times[61]. Finally, we removed species pairs for which we were unable to obtain complete trait data, n = 10. In total, n = 3352 species across the n = 100 trees were included in our analysis, with a mean of n = 1115 sister pairs per tree.

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

Predictors of species coexistence

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

To quantify dispersal ability and niche similarity, we compiled a database of phenotypic traits for all sister species based on estimates of mean species body mass (g)[64] and eight linear traits (beak length [measured both as culmen from beak tip to skull, and beak tip to nares], beak width and depth [at anterior nares], tarsus length, wing length [carpal joint to wing tip], first secondary length [carpal joint to tip of first secondary], and tail length). We measured these eight traits from museum skins and live birds in the field; see ref[36] for detailed methods. Traits were selected based on their well-established association with flight ability, habitat and resource use, thus representing the key dimensions of the avian niche[36,65]. On average, we obtained measurements for 5.1 individuals per species

(2 males and 2 females, where possible); see Database S1 for specimen accession details and locality information for all birds measured.

We combined the nine log-transformed mean species trait values in a principal components (PC) analysis. The first synthetic axis represents an overall index of size (PC1), with the remaining axes quantifying variation in shape (Supplementary Table 3). We retained the first four PC axes which collectively account for >95% of the variance in species trait values (Supplementary Table 3). For each sister pair, we quantified the distance (log-transformed) between species along individual PC axis, and also the total Euclidian inter-species distance along all axes combined. Total Euclidian distance is primarily driven by the first few PC axes, which account for the majority of trait variance. We therefore also calculated the total Euclidian distance after scaling each axis to unit variance to test a model in which multiple trait dimensions contribute equally to explaining coexistence[46]. Because the beak has received particular attention as a key trait mediating competition for ecological resources[66,67], we re-ran our models using only beak-related traits (beak length, width, depth) as inputs into our PC analysis (Supplementary Table 4) to examine the specific effects of beak divergence on coexistence.

We modelled the effects of intrinsic vagility using the hand-wing index (HWI), a well-established proxy for flight ability in birds[28,35]. HWI was calculated as

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

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

Modelling coexistence dynamics

We modelled the dynamics of species coexistence over time as a constant-rate Markov process[26]. In this model, we assumed that speciation occurs in allopatry (or parapatry) so that at the time of population divergence sister species have non-overlapping spatial distributions (state = 0). In birds, this assumption is justified because previous empirical studies have shown that sympatric speciation is extremely rare (<5% of speciation events)[28,68-70]. Following speciation, species pairs transition to a state of sympatry (state = 1) at rate σ and, having attained sympatry, return to a state of allopatry at rate ε. Given the observed ages (millions of years, Myr) and current geographical states of each sister pair (0 or 1), rates of σ and ε (per sister pair/Myr) can be estimated using maximum likelihood[26]. Rather than assume a single range overlap threshold to define sympatry, we repeated our analysis assuming different thresholds, exploring values from 10-90% in 10% increments.

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

A Random-coexistence model fixing σ = 1000, provides a null expectation for testing the effects of dispersal limitation, but also provides the foundation for 'Niche-assembly models' testing how the duration of coexistence following secondary contact (i.e. 1/ε) varies according to environmental or ecological traits. Thus, we tested the effects of NPP, trait divergence and species richness on coexistence by including each of these terms as a covariate on ε, either individually or together (n = 2 to 4 parameters, Supplementary Figure 1d). Because we were particularly interested in isolating the effects of species richness on coexistence we fitted both a 'Bounded niche-assembly model' and an 'Unbounded niche-assembly model', that included all niche-related parameters (n = 4 parameters) or excluded species richness (n = 3 parameters) respectively. Finally, we combined all predictor variables into a single 'Dispersal+niche assembly model' integrating the effects of both dispersal limitation on σ and ecological niche availability on ε (Supplementary Figure 1e, n = 7 parameters). All models were fitted in the R environment[71] using the msm package[72]. We assessed relative model fit on the basis of the Akaike Information Criterion (AIC)[73]. In addition to absolute AIC scores, we also calculated model AIC weight (AICW), which quantifies the relative probability that each model is correct given the set of models being compared.

Dispersal-related variables are specifically expected to promote coexistence by facilitating geographic range expansions. To explore this possibility, we included the maximum range size of each sister pair as an additional predictor of σ in our Dispersal+niche assembly model (n = 8 parameters) (Supplementary Figure 3). We confirmed that σ is strongly positively associated with range size (Supplementary Figure 3a). Having accounted for this effect, the independent contributions of organism vagility (Supplementary Figure 3b) and island dwelling (Supplementary Figure 3c) were largely removed, while the effects of niche-related variables remained unaltered (Supplementary Figure 3d-f). Thus, while dispersal-related variables appear to mediate coexistence via their effects on geographic range expansions[41], our results suggest that niche-related variables facilitate coexistence independently of any effect on range size.

Sensitivity analyses

We conducted additional analyses to ensure that our results were robust to model assumptions. First, rather than using the individual species age estimates from each tree (Supplementary Figure 7a-c) we repeated our analysis using the mean age for each sister pair across the posterior distribution of trees, obtaining very similar results (Supplementary Figure 7d-f). Second, we tested that the effects of time for dispersal (i.e. species age) and trait divergence were robust to the inclusion of a temporal lag in the establishment of sympatry (n = 8 parameters), as expected if incomplete reproductive isolation initially inhibits coexistence following speciation (Supplementary Figure 2, Supplementary Table 2)[26,40]. We modelled this lag by fitting a series of breakpoint transition models in which the duration of coexistence (i.e. $1/\varepsilon$) was initially low (or high) following speciation but could then increase (or decrease) after a given period of time had elapsed. Model support was evaluated for different breakpoint values from 1 to 6 Myr post speciation in 0.5 Myr intervals. Although we found evidence that the duration of coexistence increases with time since speciation, models with a slow attainment of secondary contact (i.e. σ is small) and in which trait divergence also mediates coexistence were still strongly favoured (Supplementary Figure 2, Supplementary Table 2). These results support the notion that both time for dispersal and trait similarity impose important constraints on geographic range overlap independently of any inhibitory effect of incomplete reproductive isolation.

Third, although the models presented focus on how niche-related variables (trait divergence, NPP and species richness) influence ε and thus the duration of coexistence, we found that our conclusions were also robust to the alternative assumption that these variables instead influence σ, which can be interpreted as the rate of successful colonisation (Supplementary Figure 8). Fourth, to ensure the significant relationships we detected were not driven by the phylogenetic non-independence of sister species pairs, we examined the effects of each predictor in a phylogenetic generalised linear mixed model (PGLMM) using the R package MCMCglmm[74]. This statistical framework additionally allowed us to explore the effects of treating range overlap as either a binary or a continuous variable[74]. Range overlap scores are zero-inflated and so we developed a two-part model including i) all sister pairs (n = 1115) and treating sympatry as a binary variable (0 [overlap < 10%], 1 [overlap≥ 10%) and ii) those sister pairs with non-zero overlap scores (n = 514) with sympatry modelled as a continuous variable. For the latter, proportional range overlap scores were logit-transformed, with overlap values of 1 set to 0.99 prior to transformation. We ran each model for 2.5 million iterations with a burn-in of 10,000 iterations and a thinning interval of 25,000 iterations.

Because phylogenetic heritability (H^2) in the incidence (H^2 = 0.22 95% CI [0.04, 0.50]) or extent (H^2 = 0.05 95% CI [0, 0.30]) of sympatry is low, results obtained using PGLMMs were very similar to those based on dynamic models (Supplementary Figure 9, Supplementary Table 5). In particular, this analysis confirmed the directional effect and significance of each predictor variable and recovered a similar shift in the identity of core predictors—from dispersal-related to niche-related variables—with the % range overlap threshold used to define coexistence (Supplementary Figure 9, Supplementary Table 5).

Assessing predictability of sympatry across scales

For different combinations of variables and range overlap thresholds, we fitted an individual-level logistic-regression predicting sister species sympatry or allopatry (0,1). We then divided our dataset of sister pairs into n quantiles according to their predicted probabilities of sympatry, examining values of n from 2 to 1000 corresponding to class sizes of ~500 to ~1 sister pairs respectively. Finally, we fit a group-level logistic-regression predicting the frequency of sympatry across classes and calculated McFadden's[59] Pseudo-R^2,

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

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

Data Availability

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

Code Availability

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

Acknowledgements

We are grateful to Chris Cooney, Chris Trisos and members of the Jetz Lab for their feedback and helpful discussion, and to three anonymous reviewers whose comments greatly improved the manuscript. This research was funded by the Netherlands Organisation for Scientific Research VENI grant 863.13.003 (to ALP), NASA Biodiversity Grant NNX11AP72G and NSF grants NSF DBI 1262600, DBI 0960550, and DEB 1026764 (to WJ), Oxford Clarendon Fund and US-UK Fulbright Commission (to CS), John Fell Fund and NERC grant NE/I028068/1 (to JAT).

Author contributions

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

Declaration of competing interests

The authors declare no competing interests.

References

1 Ricklefs, R. E. Disintegration of the ecological community. *Am Nat* **172**, 741-750 (2008).

2 Hubbell, S. P. *The unified neutral theory of biodiversity and biogeography*. 375 (Princeton University Press, 2001).

3 Wiens, J. J. The niche, biogeography and species interactions. *Philos T R Soc B* **366**, 2336-2350 (2011).

4 MacArthur, J. W. & Wilson, E. O. *The theory of island biogeography*. 203 (Princeton University Press, 1967).

5 Harmon, L. J. & Harrison, S. Species diversity is dynamic and unbounded at local and continental scales. *The American Naturalist* **185**, 584-593 (2015).

6 Leprieur, F. *et al.* Plate tectonics drive tropical reef biodiversity dynamics. *Nat Commun* **7**, 11461, https://doi.org/10.1038/ncomms11461 (2016).

7 MacArthur, R. H. *Geographical Ecology: patterns in the distributions of species*. 269 (Harper and Row, 1972).

8 Diamond, J. M. in *Ecology and Evolution of Communities* (eds M. L. Cody & J. M. Diamond) (Harvard University Press, 1975).

9 Chase, J. M. & Leibold, M. A. *Ecological niches: linking classical and contemporary approaches*. (University of Chicago Press, 2003).

10 Levine, J. M. & HilleRisLambers, J. The importance of niches for the maintenance of species diversity. *Nature* **461**, 254-257 (2009).

11 Price, T. D. *et al.* Niche filling slows the diversification of Himalayan songbirds. *Nature* **509**, 222-225 (2014).

12 Rabosky, D. L. & Hurlbert, A. Species richness at continental scales is dominated by ecological limits. *Am Nat* **185**, 572-583 (2015).

13 Pigot, A. L., Tobias, J. A. & Jetz, W. Energetic constraints on species coexistence in birds. *Plos Biol* **14**, e1002407 (2016).

14 Vellend, M. *The theory of ecological communities*. 248 (Princeton University Press, 2016).

15 Gravel, D., Canham, C. D., Beaudet, M. & Messier, C. Reconciling niche and neutrality: the continuum hypothesis. *Ecol Lett* **9**, 399-409 (2006).

16 Leibold, M. A. *et al.* The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* **7**, 601-613 (2004).

17 Tilman, D. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *P Natl Acad Sci USA* **101**, 10854-10861 (2004).

18 Pigot, A. L. & Etienne, R. S. A new dynamic null model for phylogenetic community structure. *Ecol Lett* **18**, 153-163 (2015).

19 Mittelbach, G. & Schemske, D. W. Ecological and evolutionary perspectives on community assembly. *Trends Ecol Evol* **30**, 241-247 (2015).

20 Boulangeat, I., Gravel, D. & Thuiller, W. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecol Lett* **15**, 584-593 (2012).

21 Tilman, D. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**, 81–92 (1997).

22 Gilbert, B. & Lechowicz, M. J. Neutrality, niches, and dispersal in a temperate forest understory. *P Natl Acad Sci USA* **101**, 7651-7656 (2004).

23 Warren, D. L., Cardillo, M., Rosauer, D. F. & Bolnick, D. I. Mistaking geography for biology: inferring processes from species distributions. *Trends Ecol Evol* **29**, 572-580 (2014).

24 McGill, B. J. Matters of Scale. *Science* **328**, 575-576 (2010).

25 Chase, J. M. Spatial scale resolves the niche versus neutral theory debate. *J Veg Sci* **25**, 319-322 (2014).

26 Pigot, A. L. & Tobias, J. A. Species interactions constrain geographic range expansion over evolutionary time. *Ecol Lett* **16**, 330-338 (2013).

27 Weber, M. G., Wagner, C. E., Best, R. J., Harmon, L. J. & Matthews, B. Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution. *Trends Ecol Evol* **32**, 291-304 (2017).

28 Pigot, A. L. & Tobias, J. A. Dispersal and the transition to sympatry in vertebrates. *P Roy Soc B-Biol Sci* **282** (2015).

29 Weber, M. G. & Strauss, S. Y. Coexistence in Close Relatives: Beyond Competition and Reproductive Isolation in Sister Taxa. *Annual Review of Ecology, Evolution and Systematics* **47**, 359-381 (2016).

30 Lowe, W. H. & McPeek, M. A. Is dispersal neutral? *Trends Ecol Evol* **29**, 444-450 (2014).

31 Mayr, E. Bird Speciation in Tropics. *J Ecol* **57**, 1-17 (1969).

32 Davies, T. J., Meiri, S., Barraclough, T. G. & Gittleman, J. L. Species co-existence and character divergence across carnivores. *Ecol Lett* **10**, 146-152 (2007).

33 Anacker, B. L. & Strauss, S. Y. The geography and ecology of plant speciation: range overlap and niche divergence in sister species. *P Roy Soc B-Biol Sci* **281** (2014).

34 Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444-448 (2012).

35 Claramunt, S., Derryberry, E. P., Remsen, J. V. & Brumfield, R. T. High dispersal ability inhibits speciation in a continental radiation of passerine birds. *P Roy Soc B-Biol Sci* **279**, 1567-1574 (2012).

36 Pigot, A. L., Trisos, C. & Tobias, J. A. Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *P Roy Soc B-Biol Sci* **283** (2016).

37 Grant, P. R. & Grant, B. R. Evolution of character displacement in Darwin's finches. *Science* **313**, 224-226 (2006).

38 Losos, J. B. & Glor, R. E. Phylogenetic comparative methods and the geography of speciation. *Trends Ecol Evol* **18**, 220-227 (2003).

39 Fitzpatrick, B. M. & Turelli, M. The geography of mammalian speciation: mixed signals from phylogenies and range maps. *Evolution* **60**, 601-615 (2006).

40 Weir, J. T. & Price, T. D. Limits to speciation inferred from times to secondary sympatry and ages of hybridizing species along a latitudinal gradient. *Amer. Nat.* **177**, 462-469 (2011).

41 Kennedy, J. D. *et al.* The influence of wing morphology upon the dispersal, geographical distributions and diversification of the Corvides (Aves; Passeriformes). *P Roy Soc B-Biol Sci* **283**, 20161922 (2016).

42 Ricklefs, R. E. Host-pathogen coevolution, secondary sympatry and species diversification. *Philos T R Soc B* **365**, 1139-1147 (2010).

43 Cooney, C. R., Tobias, J. A., Weir, J. T., Botero, C. A. & Seddon, N. Sexual selection, speciation, and constraints on geographical range overlap in birds. *Ecol Lett* **20**, 863-871 (2017).

44 Mayfield, M. M. & Levine, J. M. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol Lett* **13**, 1085-1093 (2010).

45 Chesson, P. Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* **31**, 343-366 (2000).

46 Kraft, N. J. B., Godoy, O. & Levine, J. M. Plant functional traits and the multidimensional nature of species coexistence. *P Natl Acad Sci USA* **112**, 797-802 (2015).

47 Brown, W. L. & Wilson, E. O. Character Displacement. *Syst Zool* **5**, 49-64 (1956).

48 Hutchinson, G. E. Homage to Santa-Rosalia or why are there so many kinds of animals? *Am Nat* **93**, 145-159 (1959).

49 Currie, D. J. *et al.* Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol Lett* **7**, 1121-1134 (2004).

50 Pfennig, D. W. & Pfennig, K. S. Character displacement and the origins of diversity. *Am Nat* **176**, S26-S44 (2010).

51 Macarthur, R. & Macarthur, J. W. On bird species diversity. *Ecology* **42**, 594-598 (1961).

52 Hurlbert, A. H. & Jetz, W. More than "More Individuals": The Nonequivalence of Area and Energy in the Scaling of Species Richness. *Am Nat* **176**, E50-E65 (2010).

53 Rosenzweig, M. L. in *The Ecology and Evolution of Communities* (eds M. Cody & J. M. Diamond) (Harvard University Press, 1975).

54 Rabosky, D. L. & Glor, R. E. Equilibrium speciation dynamics in a model adaptive radiation of island lizards. *P Natl Acad Sci USA* **107**, 22178-22183 (2010).

55 Cornell, H. V. Is regional species diversity bounded or unbounded? *Biological Reviews* (2012).

56 Jetz, W. & Fine, P. V. A. Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *Plos Biol* **10.** https://doi.org/10.1371/journal.pbio.1001292(2012).

57 Garzon-Lopez, C. X., Jansen, P. A., Bohlman, S. A., Ordonez, A. & Olff, H. Effects of sampling scale on patterns of habitat association in tropical trees. *J Veg Sci* **25**, 349–362 (2014).

58 Lawton, J. H. Are there general laws in ecology? *Oikos* **84**, 177-192 (1999).

59 McFadden, D. in *Frontiers in econometrics* (ed P. Zarembka) 104-142 (Academic Press, 1974).

60 Hackett, S. J. *et al.* A phylogenomic study of birds reveals their evolutionary history. *Science* **320**, 1763-1768 (2008).

61 Weir, J. T. & Schluter, D. Calibrating the avian molecular clock. *Mol Ecol* **17**, 2321-2328 (2008).

62 Jetz, W., Wilcove, D. S. & Dobson, A. P. Projected impacts of climate and land-use change on the global diversity of birds. *Plos Biol* **5**, 1211-1219. https://doi.org/10.1371/journal.pbio.0050157 (2007).

63 Cramer, W. *et al.* Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biol* **5**, 1-15 (1999).

64 Wilman, W., Belmaker, J., Simpson, J., de la Rosa, C. & Rivadeneira, M. M. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* **95**, 2027–2027 (2014).

65 Miles, D. B. & Ricklefs, R. E. The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology* **65**, 1629-1640 (1984).

66 Grant, P. R. *The ecology and evolution of Darwin's finches*. (Princeton University Press, 1999).

67 Schoener, T. W. Large-billed insectivorous birds: a precipitous diversity gradient. *Condor* **73**, 154-&, doi:Doi 10.2307/1365836 (1971).

68 Mayr, E. *Systematics and the origin of species*. (Columbia University Press, 1942).

69 Coyne, J. A. & Price, T. D. Little evidence for sympatric speciation in island birds. *Evolution* **54**, 2166-2171 (2000).

70 Phillimore, A. B. *et al.* Sympatric speciation in birds is rare: insights from range data and simulations. *Am Nat* **171**, 646-657 (2008).

71 R: A Language and Environment for Statistical Computing (Vienna Available at: http://cran.r-project.org/. 2015).

72 Jackson, C. H. Multi-state models for panel data: The msm package for R. *J Stat Softw* **38**, 1-28 (2011).

73 Burnham, K. P. & Anderson, D. R. Multimodel Inference. *Sociological Methods and Research* **33**, 261-304 (2004).

74 Hadfield, J. D. & Nakagawa, S. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J Evolution Biol* **23**, 494-508 (2010).

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

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

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

Figure 4. Scale-dependency in the predictability (R^2) of coexistence. McFadden's[59] Pseudo-R^2 of models predicting the frequency of sympatry (left, ≥20% overlap; right, ≥80% overlap) across classes of varying size (1 to 500 sister pairs) when including Dispersal- (D), Niche- (N) or both Dispersal- and Niche-assembly (D+N) processes.