

The macroecological dynamics of species coexistence in birds

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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 (that is, 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.

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 maintained¹. 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 niches². 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 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 (that is, sympatry) between sister species²⁶. We assume that speciation typically generates species with non-overlapping distributions (that is, 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 (that is, divergence time) and thus the time available for colonization (‘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 traits³⁰. 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 ability²⁸ or living in more continuous

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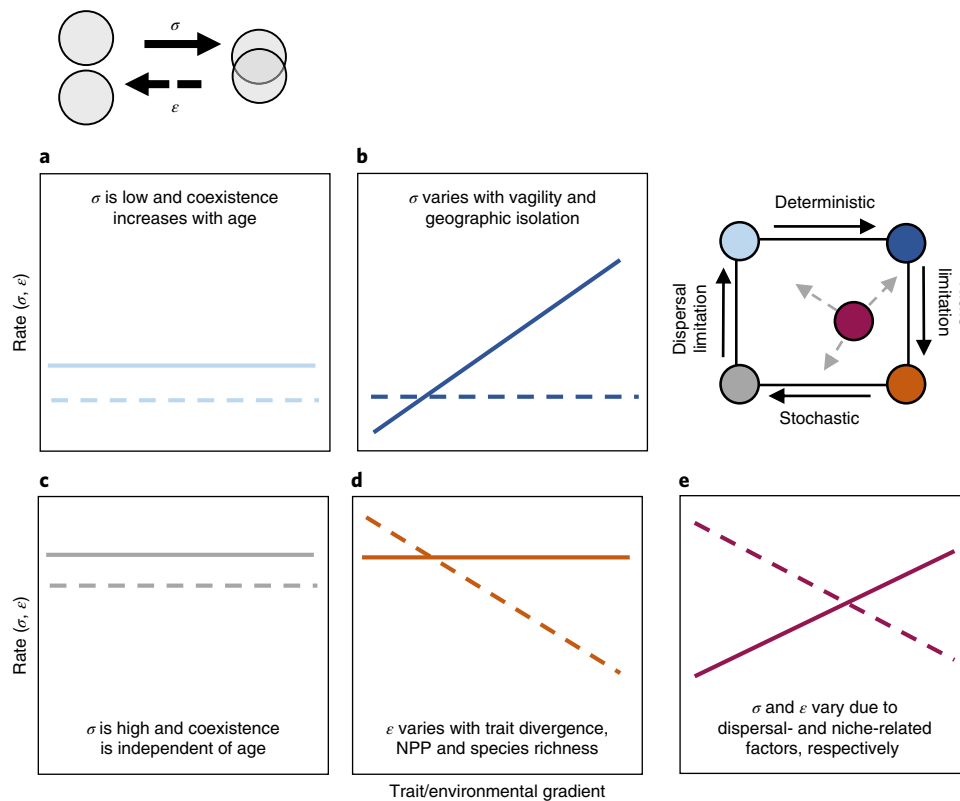


Fig. 1 | Models of species coexistence. Whether or not avian sister species coexist is governed by the rate at which lineages attain sympatry following speciation (σ , solid lines) and then return to a state of allopatry due to local extinction (ϵ , dashed lines). **a–e**, Different assembly models (neutral-dispersal, **a**; deterministic-dispersal, **b**; random-coexistence, **c**; niche-assembly, **d**; and dispersal- plus niche-assembly, **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 is approximately equal (**a**) or varies deterministically across species (**b**). Second, niche-assembly models lacking dispersal limitation (that is, 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.

habitats³¹ ('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 is expected to increase, with the abundance and diversity of available resources¹³ 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 bounds¹¹, although the existence of any such ecological limit remains debated^{5,12} ('bounded versus unbounded niche-assembly model'; Fig. 1d).

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, phylogenetic³⁴ and functional trait datasets (see Methods). Collectively, these enable fine-scale variation in phylogenetic age¹³, intrinsic dispersal ability (for example, the hand-wing index (HWI)—a measure of wing pointedness³⁵) and niche divergence (for example, 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 availability¹³), species richness and geographic connectivity (for example, 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 isolation²⁹. 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 of these sets of processes into a single synthetic framework ('dispersal- plus 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 modelled 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). The return transition rate in turn provides an estimate of the expected duration of coexistence (that is, $1/\epsilon$). 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

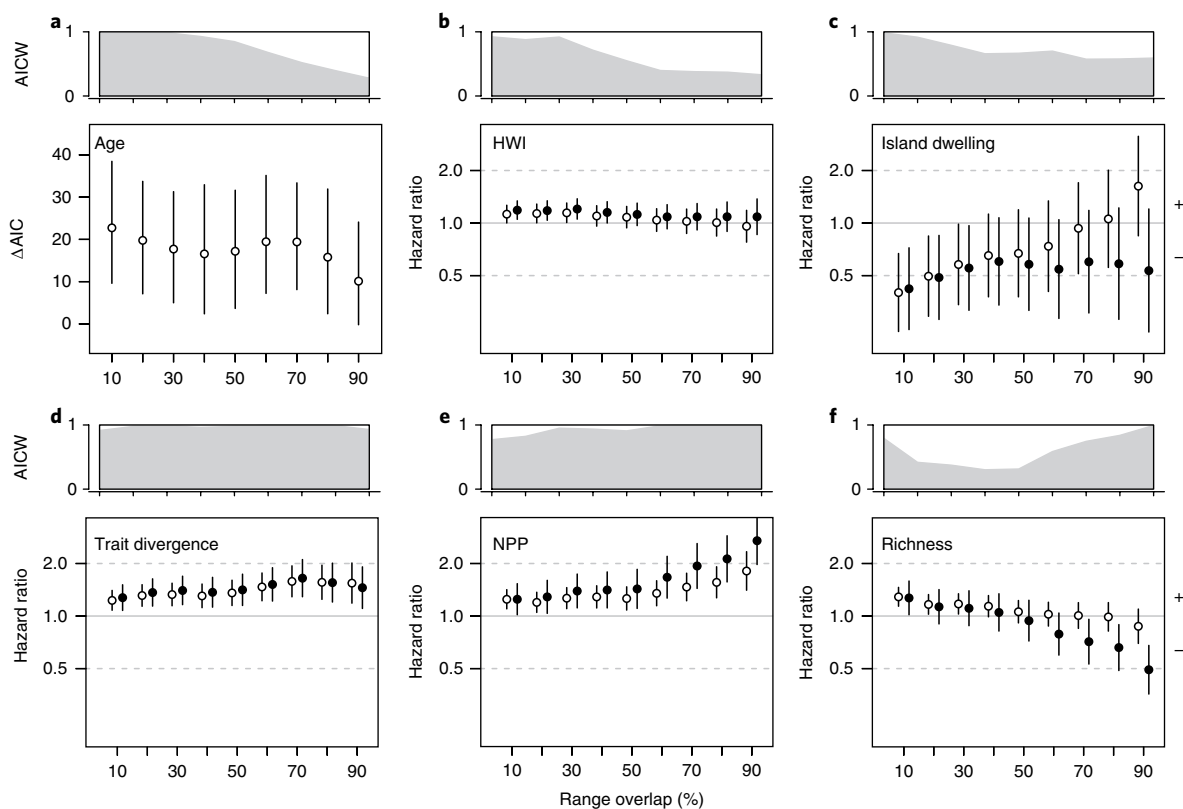


Fig. 2 | Historical, intrinsic and environmental predictors of sympatry in birds. a–f. The effect size for each variable, both in isolation (open circles) and for the full ‘dispersal- plus niche-assembly’ model (filled circles), including age (a), HWI (b), island dwelling (c), trait divergence (d), NPP (e) and species richness (f), is shown as a function of the percentage range overlap used to define coexistence ($n = 1,115$ pairs). Panels above each plot indicate support (AICW) for the inclusion of each variable in the full model. Effect sizes (and 95% CIs) show the hazard ratio, indicating the change in the transition rate to coexistence σ (b and c) or the duration of coexistence $1/\epsilon$ (d–f) for a unit change in the predictor. Hazard ratios greater than or less than 1 indicate positive and negative effects on coexistence, respectively. In a, a hazard ratio estimate is not available (see Methods). Support for the effect of age is plotted as the difference in AIC (Δ AIC) between a model excluding (random-coexistence model) and including (neutral-dispersal model) age, with higher values indicating greater support.

definitions of sympatry (10–90% overlap in 10% intervals), as well as models treating sympatry as a continuous rather than binary trait (see Methods).

Across all range overlap thresholds, we found that a neutral-dispersal model is strongly supported compared with a random-coexistence model (Figs. 2a and 3a, and Supplementary Table 1), with a maximum-likelihood estimate of $\sigma = 0.25$ ($>10\%$ range overlap, 95% confidence interval (CI): 0.21–0.32), equating to an average waiting time to sympatry following speciation of 3.92 million years (Myr) (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 Fig. 2 and Supplementary Table 2).

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 and 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 with

the mainland (Fig. 2c). These dispersal-related variables appear to mediate sympatry via their effects on geographic range expansion⁴¹. 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 Fig. 3).

The positive effect of intrinsic vagility on the attainment of sympatry has previously been identified²⁸, but the dynamics of sympatry on islands has remained unresolved⁴². On the one hand, it has been argued that geographic isolation should inhibit the attainment of sympatry because of reduced rates of island colonization, or because any small founding populations are more likely to suffer stochastic extinctions or introgression with residents³¹. On the other hand, coexistence may be promoted on islands because of a relaxation of biotic constraints, including the presence of fewer pathogens and competitors⁴². High levels of sympatry among some young island lineages, such as Darwin’s finches (Geospizinae), would appear to support the idea that relaxation of biotic constraints promotes coexistence. However, our analysis suggests that such cases are relatively rare, and that overall the attainment of sympatry is inhibited in insular systems compared with 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 competition²⁶, or other

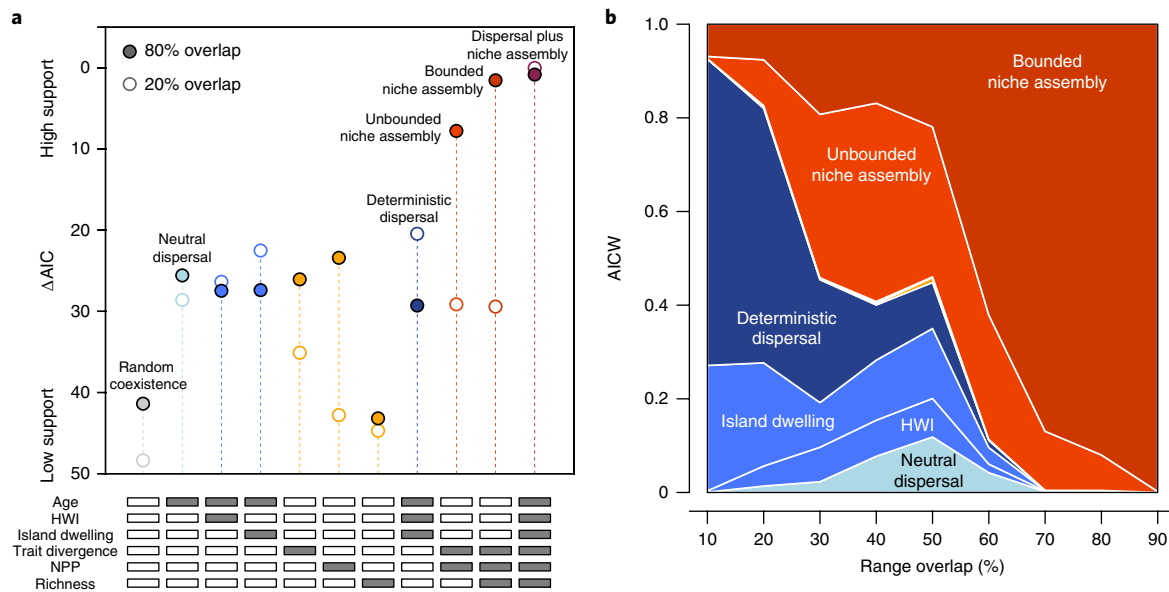


Fig. 3 | Relative support for different coexistence scenarios **a**, Support for each coexistence model (Δ AIC) is shown when sympatry among a global sample of avian sister species ($n=1,115$ pairs) is quantified using either a low (20%, open circle) or high (80%, filled circle) geographic range overlap threshold. **b**, Relative support (AICW) for dispersal- or niche-assembly scenarios as a function of geographic range overlap. In **a** and **b**, colours indicate dispersal-assembly (blue), niche-assembly (orange) or dispersal- plus 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 shown below **a**. In **b**, models with low support are not shown (see Supplementary Table 1 for model AIC values).

antagonistic interactions (for example, reproductive interference^{40,43} or shared natural enemies⁴²), 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 Fig. 2 and Supplementary Table 2), suggesting that competition is at least partially responsible for limiting sympatry.

In theory, similarity in species traits could promote coexistence by equalizing differences in fitness^{44,45}. However, our results demonstrate that phenotypic divergence is positively, rather than negatively, associated with coexistence, suggesting that the stabilizing 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 dimensions⁴⁶. Across birds, however, the effects of phenotypic divergence were primarily driven by a single axis, representing variation in beak and body size with additional trait axes having little or no discernible effect (Supplementary Fig. 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 scales¹³ and provides a compelling explanation for the strong global association between avian species richness and NPP⁴⁹. However, the precise mechanism linking productivity and coexistence remains unclear¹³. One possibility is that higher resource availability facilitates ecological niche divergence⁵⁰, 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 to 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 with a model lacking a negative effect of richness (Fig. 3b). 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}.

Interplay between dispersal- and niche-assembly processes. Although limits to sympatry have variously been attributed to a number of distinct mechanisms²⁹, here we show that such single-factor explanations receive little empirical support compared with more complex scenarios involving multiple historical, intrinsic and environmental factors (Fig. 3a). Most importantly, models treat-

ing dispersal- and niche-related processes separately received little support compared with a fully integrated ‘dispersal- plus niche-assembly’ scenario (mean Akaike information criterion weight (AICW)=0.82; Fig. 3a and 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 vary 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 $\leq 20\%$, 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 $\geq 80\%$, AICW=100) (Fig. 3b and 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 communities²⁹. In particular, our results make two key predictions. First, for any given assemblage, the effects of niche differentiation in stabilizing 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 AICW values 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 with 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 $\geq 20\%$, coefficient of determination (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 Figs. 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 $\geq 20\%$, $R^2 = 0.73$; 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 anticipated²⁵ and reported in communities of rainforest trees⁵⁷. Our results suggest that this phenomenon may help explain why environmental models of species richness typically have such

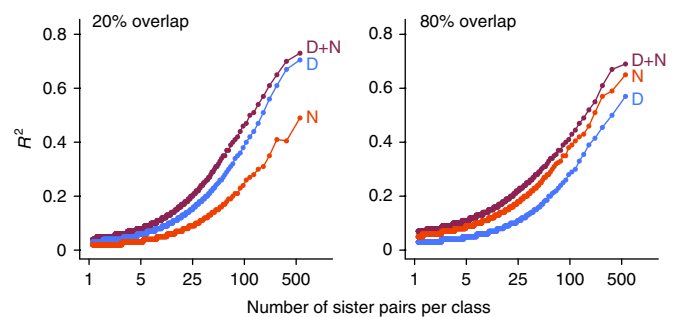


Fig. 4 | Scale dependency in the predictability of coexistence.

McFadden's⁷⁴ pseudo- R^2 of models predicting the frequency of sympatry (left, $\geq 20\%$ overlap; right, $\geq 80\%$ 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.

high explanatory power⁴⁹, despite the potentially idiosyncratic and historically contingent nature of individual species distributions⁵⁸.

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 unwind 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. ³⁹ (<http://birdtree.org>). We accounted 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 ($n = 6,670$), resulting in a mean of 2,152 sister species pairs per tree. Following our previous work¹³, we excluded sister pairs that (1) predominantly forage at sea ($n = 101$), (2) 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 (3) are extremely young (<0.75 Myr, $n = 191$) and thus where ongoing introgression and ancestral polymorphism is expected to confound reliable estimates of divergence times⁶⁰. Finally, we removed species pairs for which we were unable to obtain complete trait data ($n = 10$). In total, 3,352 species across the 100 trees were included in our analysis, with a mean of 1,115 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 rasterized (1 km resolution) expert-opinion maps of extent of occurrence (available to view at <http://mol.org>)⁶¹. We quantified range overlap between species according to the Szymkiewicz–Simpson coefficient ($\text{area}_{\text{overlap}} / \min(\text{area}_{\text{sister1}}, \text{area}_{\text{sister2}})$)¹³, and also incorporated information on species habitat and altitudinal preferences¹³ to ensure that coexisting species occupied

the same major habitat types and elevation zones. Following previous methods¹³, sister species occupying non-overlapping elevation zones (<20% proportional overlap) or utilizing different major habitat types (forest, shrubland, bare ground or 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: 110 km, equal to approximately 1° at the equator). We quantified the mean NPP ($\text{g C m}^{-2} \text{ yr}^{-1}$, 30' resolution)⁶² and richness of all 9,993 bird species (at the scale of 110 km 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 (that is, the union) while for sympatric pairs we calculated the mean values across those cells where both species were present (that is, 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)⁶³ 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^{36,64}. On average, we obtained measurements for 5.1 individuals per species (2 males and 2 females, where possible; see Supplementary Database 1 for specimen accession details and locality information for all birds measured).

We combined the nine log-transformed mean species trait values in a principal component (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 axes, and also the total Euclidian interspecies 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 coexistence⁶⁵. Because the beak has received particular attention as a key trait mediating competition for ecological resources^{65,66}, we re-ran our models using only beak-related traits (beak length, width and 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 HWI—a well-established proxy for flight ability in birds^{28,35}. HWI was calculated as

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

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 (that is, 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 before 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 process³⁶. 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)^{28,67–69}. 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 (Myr) and current geographical states of each sister pair (0 or 1), rates of σ and ϵ (sister pair⁻¹ Myr⁻¹) can be estimated using maximum likelihood³⁶. 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 (that is, 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 Fig. 1a). We compared this model with a 'random-coexistence model' lacking dispersal limitation by fixing σ at an arbitrarily large value ($\sigma=1,000$) and only estimating ϵ ($n=1$ parameter; Supplementary Fig. 1c). This is equivalent to assuming a waiting time to coexistence

following speciation (that is, $1/\sigma$) of only 1,000 years, which is essentially instantaneous compared with 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 (that is, $P = \sigma/(\sigma + \epsilon)$) and is identical across species pairs. Second, we fit 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 Fig. 1b).

A random-coexistence model fixing $\sigma=1,000$, 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 (that is, $1/\epsilon$) 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 ($n=2-4$ parameters; Supplementary Fig. 1d). Because we were particularly interested in isolating the effects of species richness on coexistence, we fit both a 'bounded niche-assembly model' and an 'unbounded niche-assembly model', which 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-plus niche-assembly model', integrating the effects of both dispersal limitation on σ and ecological niche availability on ϵ ($n=7$ parameters; Supplementary Fig. 1e). All models were fit in the R environment⁷⁰ using the *msm* package⁷¹. We assessed relative model fit on the basis of the Akaike information criterion (AIC)⁷². In addition to absolute AIC scores, we also calculated model 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-plus niche-assembly' model ($n=8$ parameters; Supplementary Fig. 3). We confirmed that σ is strongly positively associated with range size (Supplementary Fig. 3a). Having accounted for this effect, the independent contributions of organism vagility (Supplementary Fig. 3b) and island dwelling (Supplementary Fig. 3c) were largely removed, while the effects of niche-related variables remained unaltered (Supplementary Fig. 3d–f). Thus, while dispersal-related variables appear to mediate coexistence via their effects on geographic range expansions⁴¹, 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 Fig. 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 Fig. 7d–f). Second, we tested that the effects of time for dispersal (that is, 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 Fig. 2 and Supplementary Table 2)^{26,40}. We modelled this lag by fitting a series of breakpoint transition models in which the duration of coexistence (that is, $1/\epsilon$) 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 (that is, σ is small) and in which trait divergence also mediates coexistence were still strongly favoured (Supplementary Fig. 2 and Supplementary Table 2). These results support the notion that both time for dispersal and trait similarity impose important constraints on geographic range overlap, independent 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 colonization (Supplementary Fig. 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 generalized linear mixed model using the R package MCMCglmm⁷³. This statistical framework additionally allowed us to explore the effects of treating range overlap as either a binary or a continuous variable⁷³. Range overlap scores are zero-inflated, so we developed a two-part model including (1) all sister pairs ($n=1,115$) and treating sympatry as a binary variable (0 (overlap < 10%), 1 (overlap $\geq 10\%$)) and (2) those sister pairs with non-zero overlap scores ($n=514$) with sympatry modelled as a continuous variable. For case (2), proportional range overlap scores were logit-transformed, with overlap values of 1 set to 0.99 before 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 phylogenetic generalized linear mixed models were very similar to those based on

dynamic models (Supplementary Fig. 9 and 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 percentage range overlap threshold used to define coexistence (Supplementary Fig. 9 and Supplementary Table 5).

Assessing the predictability of sympatry across scales. For different combinations of variables and range overlap thresholds, we fit 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 1,000, 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's²⁴ pseudo- R^2 ,

$$R^2 = \frac{LL_{\text{full}}}{LL_{\text{null}}}$$

where LL_{null} and LL_{full} are the log-likelihoods of the intercept only and the full model, respectively.

Reporting Summary. Further information on experimental design is available in the Nature Research Reporting Summary linked to this article.

Code availability. The code is available in the Supplementary Data and via Figshare at <https://doi.org/10.6084/m9.figshare.6171185>.

Data availability. The data are available in the Supplementary Data and via Figshare at <https://doi.org/10.6084/m9.figshare.6171185>.

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Author contributions

A.L.P., W.J., C.S. and J.A.T. conceived the study. C.S., J.A.T. and W.J. contributed data. A.L.P. performed the analysis and wrote the first draft. All authors contributed to the writing of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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