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Dispersal and the transition to sympatry in vertebrates

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Under allopatric speciation models, a key step in the build-up of species richness is population dispersal leading to the co-occurrence of previously geographically isolated forms. Despite its central importance for community assembly, the extent to which the transition from spatial segregation (allopatry or parapatry) to coexistence (sympatry) is a predictable process, or alternatively one governed by chance and the vagaries of biogeographic history, remains poorly understood. Here, we use estimated divergence times and current patterns of geographical range overlap among sister species to explore the evolution of sympatry in vertebrates. We show that rates of transition to sympatry vary predictably according to ecology, being faster in marine or strongly dispersive terrestrial clades. This association with organism vagility is robust to the relative frequency of geographical speciation modes and consistent across taxonomic scales and metrics of dispersal ability. These findings reject neutral models of dispersal assembly based simply on evolutionary age and are not predicted by the main alternative view that range overlap is primarily constrained by biotic interactions. We conclude that species differences in dispersal limitation are fundamental in organizing the assembly of ecological communities and shaping broad-scale patterns of biodiversity over space and time.

1. Introduction

Most new species arise in geographical isolation (allopatry) and so a key step in the assembly of communities is the geographical expansion and overlap (sympatry) of these previously spatially isolated forms [1–4]. Niche assembly models predict that this build-up of sympatric diversity is a highly deterministic process [2,5]. In particular, by preventing the coexistence of ecologically similar species, competition for ecological resources is expected to generate non-random patterns in community structure, including the regular spacing of functional traits [5], the mutually exclusive occurrence of related species across geographical space [2] and slowdowns in the rate of community assembly over time [3]. It is sometimes postulated that dispersal is also a powerful force driving the predictable assembly of communities if the odds of range expansion, and thus the rate of species arrival, are heavily weighted by differences in organism vagility [6–8]. More often, however, the process of dispersal into a community has been viewed as a largely stochastic event with respect to species identity [9], with classic ‘dispersal assembly’ models assuming that the combination of lineages and traits assembling into communities is inherently unpredictable [10,11]. This ‘neutral-dispersal’ viewpoint has strikingly different implications for how local or regional biota assemble over time and yet, although extrinsic variation in the opportunity for dispersal may drive consistent patterns in range size or sympatric diversity [10,12–14], the role of intrinsic dispersal ability in regulating the geographical expansion of populations and their transition to sympatry is unclear, particularly over long macroevolutionary timescales [9,15].

The key problem is that the historical sequence of range expansion events leading to current patterns of sympatry cannot be directly followed through time. Thus, while many studies have examined how dispersal ability is related to current macroecological patterns (e.g. range size [7,14,15], range occupancy [16] and β -diversity [17]), most of these are based on a correlative approach that does not

explicitly address the underlying mechanisms. For instance, while a positive correlation between range size and vagility has been taken as evidence that dispersal ability drives rates of range expansion, the same statistical relationship is expected under a purely stochastic model if weak dispersers are subject to more rapid allopatric speciation [18–20], giving them less time to expand their distributions [15,21]. Testing the role of dispersal in limiting geographical range expansions, and the build-up of species within communities, thus requires a more mechanistic approach that explicitly deals with the dynamics of how sympatry between species arises over evolutionary time.

Here, we address the need for a historical framework by extending a recently developed phylogenetic model [22] to explore the transition to sympatry following speciation events in vertebrates (figure 1*a*). Using data on the geographical overlap and evolutionary divergence times between pairs of sister species (each other's closest relatives; figure 1*a*), we first compare the incidence of sympatry across major vertebrate clades encompassing a broad spectrum of dispersal potential: amphibians, primates, New World birds, reef fish and cetaceans (figure 1*b*). We then test the extent to which variation in the incidence of sympatry over time can be explained by a Deterministic Dispersal (DD) model in which transition rates to sympatry (σ) vary predictably according to intrinsic differences in organism vagility. We compare the fit of this deterministic model to a Stochastic Dispersal (SD) model in which differences in the probability of sympatry arise purely due to variation across species in the evolutionary time for dispersal (i.e. species age). Finally, we examine how the relative importance of these stochastic and deterministic processes may vary with scale, conducting our analysis across major vertebrate clades and separately within New World birds, the group for which phylogenetic data and robust indices of relative dispersal ability are most widely available (figure 1*b*).

Vertebrates provide the best template for these analyses because speciation generally involves a period of spatial separation [1,23,24]. Reproductive isolation may evolve in geographical isolation (allopatry) or in the presence of gene flow (parapatry), but in either case reproductively isolated vertebrate lineages arising from a single parent species tend to occur in sympatry only after undergoing a transition from spatial segregation to overlap [4,25,26]. However, robust assessments of these spatial dynamics must account for the possibility that some species have diverged in sympatry [1,23] and that, in regions with unstable environmental conditions (e.g. high latitudes [6]), sister species may have passed through multiple phases of sympatry and allopatry, such that currently allopatric species may in the past have had overlapping ranges [23,24,27]. To address this possibility, our likelihood framework allows us to robustly model and account for both potential variation in the relative frequency of allopatric (γ) and sympatric ($1 - \gamma$) speciation and for reverse transitions from sympatry back to allopatry (ε) (figure 1*a*).

2. Material and methods

(a) Phylogenetic data and sister species

We obtained published molecular phylogenies for large well-defined clades of vertebrates (tree frogs [28], salamanders [29], cetaceans [30], primates [31] and reef fish [32,33]), favouring trees constructed using a relaxed-clock Bayesian method. For birds, we generated trees for nine predominantly New

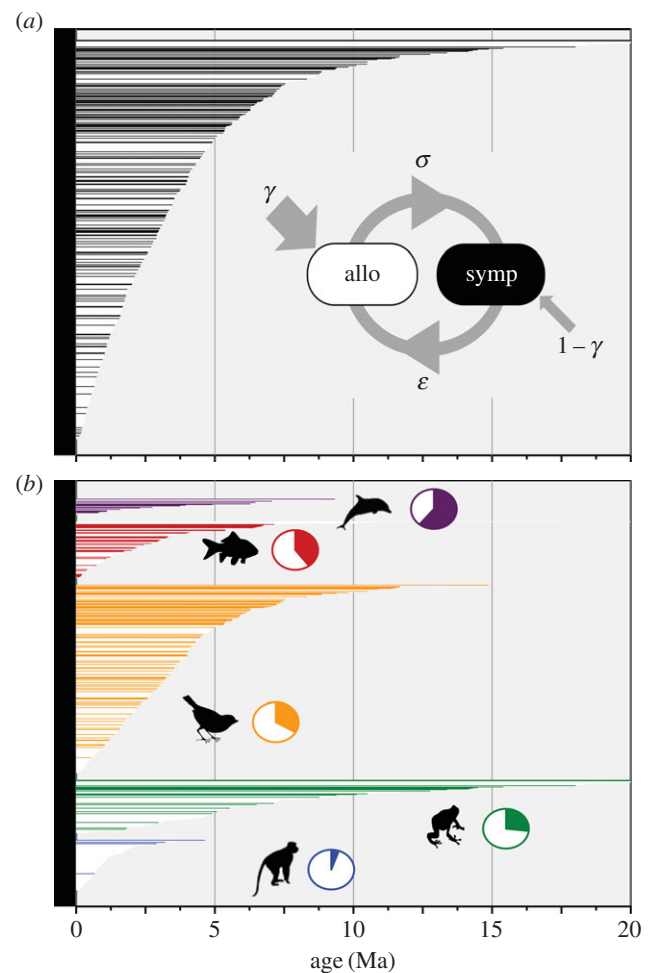


Figure 1. Evolutionary age and the incidence of sympatry (black in (a), colours in (b)) and allopatry (white) across vertebrate sister species. (a) Horizontal bars represent sister lineages ($n = 533$) ranked from bottom to top by increasing age (Ma). Inset provides a schematic summary of the evolutionary transition model and estimated parameters (γ = relative frequency of allopatric speciation, σ = rate of transition from allopatry to sympatry, ε = rate of transition from sympatry to allopatry). (b) The same data showing the incidence of sympatry and allopatry plotted separately for five focal groups.

World families (Passeriformes (Emberizidae, Icteridae, Parulidae, Thamnophilidae, Thraupidae, Troglodytidae and Turdidae), Piciformes (Ramphastidae) and Trogoniformes (Trogonidae)), with the addition of a recently published phylogeny for the ovenbirds (Furnariidae [34]). Trees were constructed in BEAST v. 1.5.4 [35] and dated using the well-established avian molecular clock [36] (see the electronic supplementary material, Appendix S1, for detailed phylogenetic procedures, and database S3 for sequence data and their sources).

From phylogenetic trees, we identified sister species pairs and their estimated divergence times, restricting our analysis to sister pairs from well-sampled genera ($\geq 70\%$ species sampling, median = 97% species sampling; electronic supplementary material, Appendix S1). Divergence times estimated from gene trees are expected to predate the time of population splitting because of ancestral polymorphisms. However, the magnitude of this effect is relatively small (0.2–0.3 Ma versus median pair age of 2.89 Ma [36]) and is not expected to vary with respect to dispersal. We excluded terrestrial sisters separated by marine barriers (i.e. species occurring on different landmasses or islands) because the factors limiting dispersal are likely to differ from those on land (e.g. salt water immersion for non-volant organisms). Our final dataset included 533 sister pairs from 33 families and eight taxonomic orders (electronic supplementary material, database S1).

(b) Geographical ranges and sympatry

Sister species were assigned as sympatric or allopatric based on current spatial overlap of species breeding distributions [37]. We quantified overlap using polygon range maps downloaded from the IUCN Red List assessment (<http://www.iucnredlist.org/technical-documents/spatial-data>) or kindly provided by C.D.L. Orme and I.P.F. Owens (birds) (electronic supplementary material, database S1) [38]. Marginal range overlap along narrow contact zones or owing to mapping error may not reflect true sympatry. For example, partially reproductively isolated species meeting in clinal hybrid zones are often mapped with narrowly overlapping ranges, but it would be incorrect to assume that they co-occur as independent populations because the hybrid zone is generally formed by a single interbreeding population [39]. Thus, here we only defined sympatry as non-trivial range overlap (more than 10% of the smaller species range). We do not distinguish between allopatric (geographically isolated) or parapatric (abutting) sisters, because for the purposes of our analysis these are equivalent in having non-overlapping distributions. Similarly, in montane regions, we treated species occurring on the same mountains but occupying distinct altitudinal ranges as non-overlapping, whether they were reported to be in narrow contact (parapatry) or disjunct (allopatry). Following previous studies (e.g. [25]), we used additional literature searches to corroborate geographical assignments, including evidence confirming that populations are sympatric during the breeding season. To test the robustness of our results to geographical assignments, we repeated our analysis using a more conservative threshold of 20% range overlap to define sympatry. Finally, in our analysis focused on birds, we accounted for potential latitudinal variation in rates of sympatry and dispersal by calculating the mean absolute latitude of species range centroids for each sister pair (i.e. $(|\text{Latitude Sister 1}| + |\text{Latitude Sister 2}|)/2$).

(c) Indices of dispersal ability

To quantify relative organism vagility across vertebrates, we searched the literature for estimates of species F_{ST} , an index of genetic differentiation among populations (0 = no differentiation, 1 = complete differentiation). Note that our measures of F_{ST} are calculated between populations of the same species, rather than between sister species. While F_{ST} does not directly measure gene flow [40], it is strongly correlated with broad-scale differences in dispersal ability [41] and provides a reliable index of relative vagility that is comparable across taxonomic groups [15,20,42]. We only used estimates based on comparable markers (microsatellites and/or allozymes) and measured over large spatial scales (i.e. more than 100 km; see the electronic supplementary material, Appendix S1). In total, we obtained F_{ST} values for 79 species (electronic supplementary material, database S2). To ensure that our results were robust to differences in study extent, we repeated all analyses for different subsets of the data (250–5000 km (main analysis), 400–2000 km and 100–5000 km; see the electronic supplementary material, Appendix S1 and table S2).

For analyses focused specifically on birds, we quantified relative vagility using wing shape as a biometric index of long-distance flight efficiency and dispersal ability. Previous empirical studies have shown that species with a higher wing aspect-ratio exhibit greater natal and migratory dispersal distances [43,44], less spatial population genetic differentiation [45] and are less prone to geographical isolation [18]. Thus, following Claramunt *et al.* [18], we used the hand–wing index (HWI) to quantify wing aspect-ratio, 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. We obtained

measurements from museum skins for 542 of the 550 species in our analysis, with an average of five individuals per species (we aimed for at least two from each sex). We used the average HWI of the mean sister species values ($\log_{10}$ transformed) or the value for the representative species if only one sister was available ($n = 8$).

As an alternative measure of dispersal, we used information in the literature to assign sister pairs to one of three dispersal syndromes (1 = weak, 2 = medium or 3 = strong) on the basis of three ecological and life-history traits: migratory tendency (1 = sedentary, 2 = short-distance migrants, 3 = long-distance migrants), degree of territoriality (1 = permanent year-round territoriality, 2 = seasonal or weak territoriality, 3 = non-territorial) and diet (1 = insectivore, 2 = omnivore, 3 = herbivore (i.e. fruit, seeds and nectar)). While these life-history traits are strongly correlated, each has been strongly linked to dispersal propensity, rates of gene flow and the likelihood of geographical isolation [19,45] (see the electronic supplementary material, Appendix S1, for further justification of traits, and database S1 for scores and data sources). In the case of diet, analyses were restricted to tropical birds (i.e. $|\text{Lat}| < 23.5^\circ$, $n = 225$) because some categories (e.g. insectivores) have dramatically different relationships with dispersal or migratory tendency in the temperate zone. Where sister species differed in dispersal syndrome (this occurred in less than 10% of pairs), we assigned the pair the higher of the sister species' scores, thus maintaining the ordinal scoring system.

(d) Modelling the transition to sympatry

We modelled the dynamics of sympatry across species as a constant rate Markov process [22]. This model allowed us to calculate the probability that a pair of species exists in its current geographical state (i.e. allopatry or sympatry) given the estimated time since divergence (t Ma) and the parameters governing the rate of transition from allopatry to sympatry (σ) and from sympatry back to allopatry (ε ; figure 1a). We used maximum likelihood (ML) to fit this model to our empirical data and estimate these parameters, implemented in the R package *msm* [46].

We accounted for the possibility that some species may diverge in sympatry by including a parameter, γ , describing the probability that speciation occurred in allopatry (or sympatry, i.e. $1 - \gamma$; figure 1a) and evaluated a series of biogeographic scenarios of varying complexity. First, we assumed that all species pairs arise in allopatry ($\gamma = 1$, *Allo-one-way*), and then undergo an irreversible transition to sympatry with rate σ (i.e. we fix $\varepsilon = 0$). Second, we considered a two-way model (*Allo-two-way*) in which ε is also estimated as a free parameter, thus allowing reverse transitions back to allopatry (when $\varepsilon = 0$, this reduces to the *Allo-one-way* scenario). For completeness, we also fitted a *Symp-two-way* model in which all speciation occurs in sympatry (i.e. $\gamma = 0$). Finally, we estimated the relative frequency of speciation modes by fitting a *Mixed-two-way* model in which γ was allowed to vary from 0 to 1 in increments of 0.01. We used this likelihood profile to obtain estimates of σ under both the ML speciation scenario and for models across the 95% confidence interval set (i.e. within 1.92 log-likelihood units of the best model).

Our modelling framework assumes that the instantaneous probability of a sister pair transitioning between states is constant with species age and allows us to test whether these transition probabilities are equivalent, or instead vary, across sister species pairs. For each speciation scenario, we fitted a DD model in which σ was allowed to vary independently across vertebrate clades, comparing this to an SD model in which all species are governed by the same underlying σ . Relative model fit was assessed using Akaike information criterion (AIC) and posterior predictive simulations (electronic supplementary material, Appendix S1). We tested whether clade-specific estimates of σ (ln-transformed) were predicted by mean clade F_{ST} (arcsine transformed) using phylogenetic generalized least squares (PGLS) in the package *caper* [47]. Phylogenetic distances between clades were taken from

published estimates of divergence times in vertebrates (electronic supplementary material, Appendix S1 and Box S1).

To test the effects of dispersal in birds, we took the best-fitting speciation scenario for this clade (*Allo-one-way* and *Allo-two-way* model) and compared the fit of an SD model to a DD model, in which each dispersal trait was included as a continuous covariate on σ . We used the DD model to quantify the hazard ratio (i.e. the ratio of transition rates per unit change in the dispersal index). A significant relationship between dispersal and σ could arise if σ happens to be high in a few strongly dispersive clades. To control for this phylogenetic non-independence, we re-fitted all models including 'avian family' as an additional covariate on σ . Finally, to ensure that our results are not driven by covariation between dispersal ability and latitude, we repeated our analysis including the absolute latitude of each sister pair as a covariate on σ .

(e) Simulation tests

Estimates of divergence times, and the relative frequency of geographical states across vertebrate groups, could be influenced by taxonomic uncertainty. However, this seems unlikely to influence our conclusions because taxonomic revisions in vertebrates generally involve the elevation of allopatric subspecies to distinct species [24,39] and would thus tend to accentuate the existing pattern of young allopatric lineages in our data. In any case, we explicitly account for divergence times when modelling the temporal dynamics of sympatry, and simulations assuming different levels of cryptic diversity show that such dynamics are only weakly affected by differences in the sampling of recently diverged allopatric lineages (electronic supplementary material, Appendix S1 and figure S1).

To assess the robustness of our modelling framework and ability to distinguish different biogeographic scenarios (e.g. *Allo-one-way* versus *Allo-two-way*), we also performed extensive simulations under different combinations of σ ($\sigma = 0.01-10$), ε ($\varepsilon = 0.01-0.10$) and γ ($\gamma = 0-1$) and tested how this influenced the relationship between sympatry and species age (electronic supplementary material, Appendix S1). We then fitted our likelihood models to these simulated datasets to test whether estimates of σ were robust to the occurrence of sympatric speciation (i.e. $\gamma > 0$) and reversals to allopatry (i.e. $\varepsilon > 0$), both of which could provide alternative explanations for differences in observed levels of sympatry (electronic supplementary material, Appendix S1).

3. Results

(a) Taxonomic patterns of sympatry in vertebrates

Across our dataset, we found that 31% of vertebrate sister pairs are sympatric, with the remaining species occupying allopatric (or parapatric) distributions (figure 1a). As expected, the frequency of sympatry increased with time since divergence (figure 1a), the median age of sympatric species being almost twice as old (4.1 Ma) as allopatric species (2.2 Ma). However, we also found that different vertebrate clades are characterized by substantial differences in the incidence of sympatry in sister species, ranging from only 5% in primates to 61% in cetaceans (figure 1b).

(b) Reliability of estimated transition rates and biogeographic scenarios

Simulations showed that different biogeographic scenarios (*Allo-one-way*, *Allo-two-way*, *Symp-two-way* and *Mixed-two-way* models) each leave distinct signatures in how the probability of sympatry varies with species age (electronic supplementary

Table 1. Stochastic and deterministic models of the transition to sympatry in vertebrates. Biogeographic scenario indicates the geographical speciation mode (allopatric: *Allo-two-way* and *Allo-one-way*; sympatric: *Symp-two-way* or estimated: *Mixed-two-way*) and whether transitions to sympatry were irreversible (*Allo-one-way*) or not (*Allo-two-way*, *Symp-two-way*, *Mixed-two-way*). npar indicates the number of estimated parameters; AIC, Akaike information criterion.

biogeographic scenario	SD		DD	
	npar	AIC	npar	AIC
<i>Allo-two-way</i>	2	590.95	10	552.47
<i>Mixed-two-way</i>	3	582.35	15	560.87
<i>Allo-one-way</i>	1	611.12	5	583.77
<i>Symp-two-way</i>	2	619.94	10	598.19

material, figures S2). In particular, while γ controls the initial probability of sympatry, the shape of the age-sympatry relationship is independently determined by both σ and ε . Specifically, while σ determines how rapidly sympatry initially increases with species age, the relative value of ε determines the level at which sympatry eventually asymptotes (i.e. $\sigma/(\sigma + \varepsilon)$; electronic supplementary material, figure S2). Because of these independent effects, our simulations confirm that σ can be reliably estimated under a broad range of conditions and that these estimates are robust to the occurrence of both sympatric speciation and reverse transitions to allopatry (electronic supplementary material, figures S3).

(c) Dispersal and the transition to sympatry in vertebrates

When we applied our modelling framework across all vertebrates, we found that a model in which each vertebrate clade is characterized by a distinct transition rate to sympatry (DD) fits significantly better ($\Delta\text{AIC} = 38.5$) than one assuming equal rates (SD, table 1; electronic supplementary material, table S1). A scenario whereby allopatric speciation is the universal route through which species diverge fits best, specifically when allowing for reverse transitions to allopatry (*Allo-two-way*), and with sympatry arising at a rate that varies markedly across groups (table 1). Simulations using the ML parameter estimates showed that this DD *Allo-two-way* model predicts the present incidence of sympatry observed across vertebrate groups with a high degree of accuracy (electronic supplementary material, Appendix S1 and figure S4). Differences in the incidence of sympatry across clades would be expected due to variation in species age but our results show that this alone is unable to predict the observed patterns (electronic supplementary material, figure S4).

According to the DD *Allo-two-way* model, we estimate that σ is slowest in primates ($\sigma = 0.05$) and amphibians ($\sigma = 0.06$), intermediate in birds ($\sigma = 0.14$) and fastest in reef fish ($\sigma \gg 10$) and cetaceans ($\sigma = 1.61$) (electronic supplementary material, table S1). These differences in rates translate into dramatic differences in how the probability of sympatry accumulates with time since speciation in each group (figure 2a). For instance, our model predicts that after 5 Ma of divergence, only 21–23% of primate and amphibian sister pairs will have attained sympatry compared with 46% of

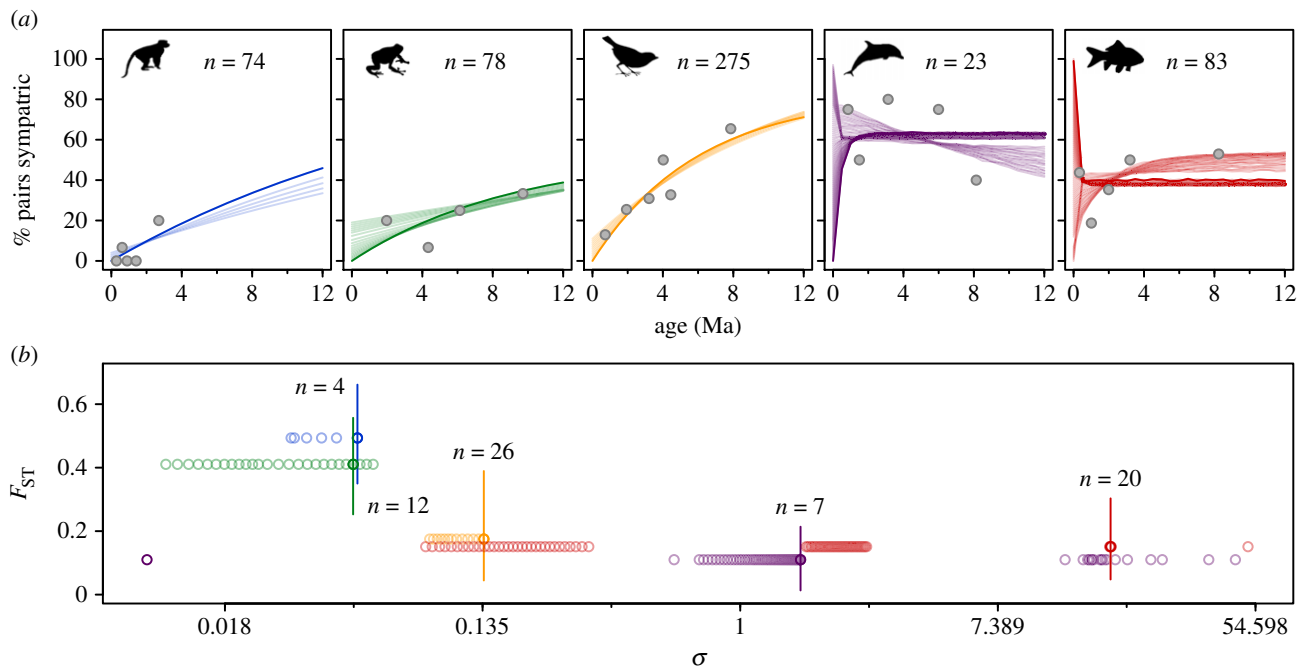


Figure 2. (a) The percentage of sympatric sister pairs as a function of time since divergence predicted under the *Allo-two-way* (ML estimates, dark shading) and *Mixed-two-way* (light shading, 95% confidence set) models. Grey circles (for illustration only) denote observed values within age quantiles. (b) The relationship between mean group F_{ST} (higher values indicate reduced dispersal) and the transition rate to sympatry (σ) (ln-transformed). Coloured bars indicate the ML value of σ and spread of F_{ST} estimates for each vertebrate group (95% quantile). Coloured circles correspond to the range of estimates of σ shown in (a). n = number of sister pairs in (a), and numbers of species with F_{ST} data in (b).

birds, closely matching the incidence of sympatry observed across age quantiles (figure 2a). By contrast, in reef fish and cetaceans, we estimate rapid transitions between geographical states (i.e. high σ and ε), so that the probability of sympatry is largely independent of age and is instead simply determined by the relative rates of σ and ε (figure 2a).

When we modelled each vertebrate clade separately, we found that among terrestrial clades the *Allo-one-way* and *Allo-two-way* models have an almost equal fit and that estimates of σ are similar regardless of whether we account for reverse transitions to allopatry or not (electronic supplementary material, table S1). Thus, while there is evidence that some currently allopatric pairs may formerly have had overlapping ranges (under the *Allo-two-way* model, we estimate $\varepsilon > 0$), this appears to occur relatively infrequently and the inclusion of this additional parameter does not significantly increase the likelihood of the data (electronic supplementary material, table S1). Our models therefore show that the low levels of sympatry observed among terrestrial sister species can only be explained by a slow transition rate to sympatry (electronic supplementary material, table S1). By contrast, for marine groups (reef fish and cetaceans), we found that even opposing speciation scenarios (i.e. $\gamma = 1$ or 0) have an almost equal likelihood, leading to greater uncertainty in estimates of σ (figure 2b; electronic supplementary material, table S1 and figure S5). To account for this uncertainty when testing the relationship between σ and F_{ST} , we fitted our PGLS model using the values of σ from across the 95% confidence set of *Mixed-two-way* models fit to each clade (figure 2b; see the electronic supplementary material, Appendix S1). Our phylogenetic comparative analysis shows a significant negative association between σ and F_{ST} , indicating that sympatry is attained more rapidly in groups characterized by low levels of within-species genetic differentiation, indicative of large dispersal distances (figure 2b;

slope = -8.61 , $p = 0.034$, $r^2 = 0.82$ (results are the median estimates from across 1000 models sampled from the 95% CI set)). We find that regardless of the geographical context of speciation, patterns of sympatry in the ocean require a model with rapid transitions between geographical states (figure 2; electronic supplementary material, table S1). As a result, the negative relationship between σ and F_{ST} is robust to variation in speciation scenarios (electronic supplementary material, table S2). Furthermore, all these results remained qualitatively unchanged regardless of the spatial scale over which F_{ST} was measured and when we repeated our analysis defining sympatry as more than 20% range overlap (electronic supplementary material, tables S1 and S2).

(d) Dispersal and the transition to sympatry in birds

We found substantial variation in the frequency of sympatry across avian clades, with sympatry among sisters being rare in some families (e.g. Furnariidae 22.4%), intermediate in others (e.g. Icteridae 41.2%) or even widespread (e.g. Thraupidae 50%). Our results support a DD model in which σ is strongly accelerated in bird species with a high HWI, indicative of greater flight performance (hazard ratio = 5.45 (95% CI 1.41 : 21.06), $p < 0.05$, $\Delta AIC = 4.09$; electronic supplementary material, table S3; figure 3a). According to this model, the mean waiting time to sympatry (i.e. $1/\sigma$) is more than four times shorter among the strongest (4.1 Ma) compared with the weakest (19 Ma) fliers. This association between vagility and σ was also present when using ecological or life-history traits (figure 3b; electronic supplementary material, table S3): σ was faster in long-distance migrants than in sedentary species ($\Delta AIC = 8.86$; figure 3b; electronic supplementary material, table S3), for species in which territoriality is weak or absent compared with those defending fixed territories year-round ($\Delta AIC = 17.23$; figure 3b; electronic supplementary material,

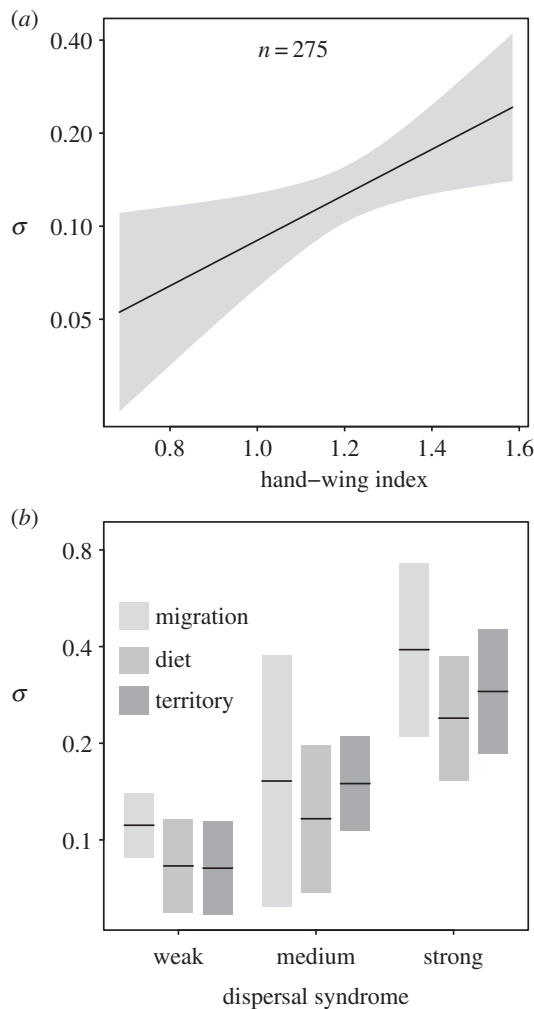


Figure 3. The relationship between dispersal and the transition rate to sympatry (σ) in birds ($n = 275$) according to (a) the HWI and (b) ecological dispersal syndromes. Black lines show ML rate estimates and grey shading the 95% CI.

table S3), and among tropical species adapted to tracking patchy resources (e.g. fruit, seeds and nectar) compared with those specialized on more stable, uniformly distributed resources (e.g. arthropods) ($\Delta\text{AIC} = 10.12$; figure 3b; electronic supplementary material, table S3). With the exception of diet, all effects remained significant even after accounting for potential differences in σ across avian families (electronic supplementary material, table S3). Our data confirm a positive relationship between σ and latitude (hazard ratio = 1.02 (95% CI 1.002 : 1.04), $p < 0.05$, $\Delta\text{AIC} = 2.35$), and we estimate that the average waiting time to sympatry is almost twice as long in the tropics (9 Ma, $|\text{Lat}| < 23.5^\circ$) compared with the temperate zone (4.9 Ma). Importantly, the associations we detected between dispersal and σ remained significant when we included latitude as an additional covariate in our models (electronic supplementary material, table S3). Finally, these results remained qualitatively unchanged when using different definitions of sympatry (more than 10% or more than 20% range overlap) and when accounting for reverse transitions to allopatry (i.e. $\varepsilon > 0$; electronic supplementary material, table S4).

4. Discussion

Our analyses reveal that the dramatic differences across vertebrates in the dynamics of sympatry following speciation

cannot be explained simply by differences in species age and thus evolutionary time for dispersal, but instead are predictable on the basis of intrinsic differences in dispersal ability. Transition rates to sympatry are fastest in highly mobile marine organisms (reef fish and cetaceans) and slowest in non-volant terrestrial taxa (amphibians and primates). Birds, with their power of flight, are intermediate between these extremes of dispersal limitation and accordingly transition to sympatry at an intermediate rate. It is possible that focusing on such dramatically different clades overemphasizes the importance of intrinsic dispersal constraints, and that such effects are likely to decline at increasingly fine taxonomic scales due to reduced contrast, or greater ecological equivalency, among species [11]. However, when we focused exclusively on birds, we found that transition rates to sympatry remained highly predictable, varying deterministically in accordance with differences in dispersal potential. Our analyses show that rates of sympatry were consistently higher in species with greater vagility or flight performance, as indicated by three separate traits: migratory behaviour, non-territoriality and the HWI. Together, these results suggest that dispersal limitation is a key deterministic mechanism regulating geographical range expansion and thus the tempo and sequence of how sympatry between species arises over time.

The vertebrate groups we studied span the full range of dispersal potential, from marine organisms that can travel vast distances during transoceanic migrations (cetaceans) or as larvae carried on the current (reef fish) [15,42], to weakly dispersing amphibians and primates where sister species are often separated by extremely narrow geographical barriers (e.g. rivers [48]). In marine groups, we find that range dynamics are rapid relative to the time scale of speciation, implying that dispersal is unlikely to limit species distributions. This finding may help to explain why previous studies have shown mixed or weak evidence for a relationship between geographical range size, evolutionary age and dispersal potential in the oceans [15,49]. By contrast, we found that the probability of sympatry in terrestrial vertebrates increases only slowly with time since divergence and that clade-wide differences in species age are therefore an important contributor to variation in the incidence of sympatry. Thus, our results not only demonstrate that dispersal is a highly deterministic force driving predictable patterns of sympatry across clades, but also highlight the critical importance of evolutionary time in explaining the build-up of sympatric diversity in terrestrial systems.

Across birds and most other terrestrial organisms, traits associated with low dispersal are concentrated in the tropics, where more stable environmental conditions and stronger geographical or environmental barriers are expected to slow the pace of range dynamics compared with high latitudes [19]. Overall, our results are consistent with those of previous studies suggesting that rates of sympatry increase with latitude [25,26]. However, even after accounting for this geographical variation, we find that species with contrasting ecologies are characterized by substantial differences in the transition rate to sympatry. These transitions are slowest in highly sedentary bird species, feeding on relatively stable resources (i.e. tropical insectivores) that remain on fixed territories year-round and that lack biomechanical adaptations for sustained flight (i.e. have rounded wings) [18,19,45], with the opposite set of traits accelerating the transition to sympatry.

Thus, dispersal limitation appears to mediate range dynamics regardless of taxonomic scale or geographical context.

The pervasive association we find between vagility and the transition to sympatry is not predicted by conventional explanations for limits to coexistence, including niche assembly models focused on interspecific competition [3,22,50], or those highlighting the role of reproductive interference [25], and shared natural enemies (e.g. pathogens [51]). Rather, these hypotheses are not specific regarding the association between rates of sympatry and differences in dispersal ability, and instead predict that rates of sympatry increase with time since speciation as constraints on range overlap weaken [22,50]—the opposite patterns to those we detect in vertebrates. We do not conclude that biotic interactions play no role in limiting the geographical overlap of closely related species. On the contrary, widespread evidence of this effect has been reported in previous studies, including apparent delays in sympatry caused by interspecific competition across ecological gradients [3,25,51] and within a single avian radiation (Furnariidae) [22]. However, our results across a much broader taxonomic sample of birds and other vertebrates suggest that the signature of biotic constraints on coexistence is swamped by other factors over longer timescales and that the overall tempo of range expansions leading to sympatry are primarily dictated by differences in dispersal limitation.

The spread of populations observed following recent environmental change [6,8] or the introduction of species to novel regions [52] is often rapid relative to the rates of species diversification, perhaps implying that dispersal constraints would be unlikely to limit range expansion over the macroevolutionary timescales studied here [15,49]. The patterns revealed in our sample of marine taxa are potentially consistent with this view, with transitions between sympatry and allopatry occurring so rapidly as to erase any signal of the geographical context of speciation [27]. By contrast, we show that differences in intrinsic dispersal potential provide the best explanation for the failure of many terrestrial vertebrate species to attain sympatry even millions of years after speciation. This makes sense because barriers to dispersal in terrestrial systems have extremely protracted effects that vary according to dispersal limitation, for example when rivers, mountain ranges or narrow regions of unsuitable climate and vegetation cause longstanding disjunctions in the geographical ranges of sister

species in lineages with low dispersal ability, but not those with high dispersal ability [19,45,48].

The idea that dispersal simply accelerates geographical range expansion, and hence range overlap, seems plausible enough, yet the underlying process may be more nuanced. For example, if increased dispersal ability leads to greater propagule pressure—in this case, a larger number of individuals invading the geographical range of their sister lineage—then this may increase the opportunity for evolutionary divergence in ecological or reproductive traits by processes such as character displacement [53]. Theoretically, this could accelerate divergence in ecological niches or mating signals, thus relaxing ecological competition, strengthening reproductive isolation and ultimately facilitating early range invasions in dispersive sister species. From this perspective, the roles of biotic interaction and dispersal limitation are not independent, as evolutionary processes may reduce the extent to which competition and interbreeding place constraints on range overlap in dispersive taxa.

Dispersal has long been viewed as an integral component of community assembly, but the concept commonly adopted is akin to Simpson's classic 'sweepstakes' model [54], in which invasion is a lottery and species have an equal chance of holding a winning ticket [9–12,55]. Thus, 'dispersal assembly' models generally assume that rates of biogeographic dispersal are equivalent across species (i.e. neutral) [10–12], and any evidence of predictable structure in communities is automatically attributed to biotic interactions [2,56,57]. Our results are contrary to these assumptions and suggest instead that dispersal limitation is the key deterministic mechanism regulating the tempo and sequence of how sympatry between species arises over time. A corollary of this conclusion is that contemporary patterns of species co-occurrence may be consistent with stochasticity and yet mask high levels of non-neutrality in the history of assembly. We propose that biases in dispersal may drive many of the predictable differences in structure observed across ecological communities.

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