

Tempo and timing of ecological trait divergence in bird speciation

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Organismal traits may evolve either gradually or in rapid pulses, but the relative importance of these modes in the generation of species differences is unclear. Additionally, while pulsed evolution is frequently assumed to be associated with speciation events, few studies have explicitly examined how the tempo of trait divergence varies with respect to different geographical phases of speciation, starting with geographic isolation and ending, in many cases, with spatial overlap (sympatry). Here we address these issues by combining divergence time estimates, trait measurements and geographic range data for 952 avian sister species pairs worldwide to examine the tempo and timing of trait divergence in recent speciation events. We show that patterns of divergence in key ecological traits are not gradual, but instead seem to follow a pattern of relative stasis interspersed with evolutionary pulses of varying magnitude. We also find evidence that evolutionary pulses generally precede sympatry, and that greater trait disparity is associated with sympatry. These findings suggest that early pulses of trait divergence promote subsequent transitions to sympatry, rather than occurring after sympatry has been established. Incorporating models with evolutionary pulses of varying magnitude into speciation theory may explain why some species pairs achieve rapid sympatry whereas others undergo prolonged geographical exclusion.

Speciation in vertebrates may proceed over long and variable periods^{1–6}. From onset to completion, the process is often viewed as a cycle with three stages, beginning with geographic isolation (allopatry), followed by secondary contact initiated at range edges and finally prolonged spatial coexistence in overlapping geographical ranges (sympatry; see Fig. 1)^{1,5–7}. The process does not always proceed to the second or third stages, but the establishment of sympatry has been viewed by some as the only way to be certain that speciation is complete². In some forms of this model, here termed ‘geographic speciation’, sympatry can be delayed after secondary contact has been made, either by competitive interactions⁸ or incomplete reproductive isolation⁵. Thus sympatry may only occur when species traits are sufficiently divergent⁹, whereas recently diverged species with similar traits fail to overlap and instead exhibit abutting ranges (termed parapatry). However, although the pattern of increased trait divergence in sympatric versus non-sympatric sister lineages is widespread among animal taxa^{10,11}, the timing and geographical context of trait divergence is difficult to determine. In particular, trait divergence could arise primarily by the accumulation of differences either prior to sympatry¹² or after sympatry is established (for example, via character displacement)¹³.

The tempo and mode of ecological trait divergence during the geographic speciation cycle are also debated^{14,15}, with some studies describing divergence as slow or gradual throughout the process^{4,12}, while others describe abrupt, pulse-like changes occurring against a background of stasis¹⁶. Pulsed changes could occur either early, in allopatry or parapatry^{17,18}, or later, in sympatry^{9,13} (Fig. 1). Further, it is possible that ecological (local) adaptation in allopatry/parapatry, followed by subsequent species interactions in sympatry provide the context for multiple pulses of trait divergence over the course of geographic speciation cycles¹⁷.

Assessing the relative contributions of gradual versus pulse-and-stasis evolution to species differences involves challenges associated

with temporal scale¹⁹ and analytical approach¹⁴. On short timescales, microevolutionary studies indicate that stasis generally dominates²⁰, with abrupt pulses of divergence occasionally detected²¹. It is unclear whether these pulses ultimately contribute to species-level differences or simply represent brief departures of trait values from longer-term static, or gradually changing, means^{10,14,20,22}. Fossil time series, which allow analyses of complex mixtures of modes over timescales relevant to geographic speciation (10⁴ to 10⁷ years), show evidence for gradual change and stasis within lineages^{23,24}. Taxonomic issues and patchy geographic sampling of the fossil record, however, limit the extent to which the fossil record can be used to assess phenotypic divergence as a component of the geographic speciation cycle¹⁴.

These challenges have led to an increased use of phylogenetic approaches to assess the tempo and mode of phenotypic change associated with speciation. These methods generally use data from extant species to test for correlations between trait evolution and speciation²⁵ or to partition trait evolution between cladogenetic and anagenetic change²⁶. These approaches suggest that pulse-like speciation (cladogenetic) processes may contribute to trait divergence. However, such analyses are often conducted across large clades, potentially overlooking the role of extinction in generating observed patterns in extant diversity^{27–29}. Moreover, the assumption in most phylogenetic approaches that evolutionary pulses occur only at speciation¹⁵, which is modelled as a single instantaneous event^{30,31}, limits how much these approaches can tell us about the roles of pulsed and gradual evolution over the extended course of geographic speciation cycles.

Disentangling alternative divergence pathways at different stages of speciation is a key step to understand general patterns of trait evolution and to predict the fate of nascent species when changing environments redistribute geographic ranges^{2,18,32}. For example, minor trait divergence during the allopatric phase of speciation

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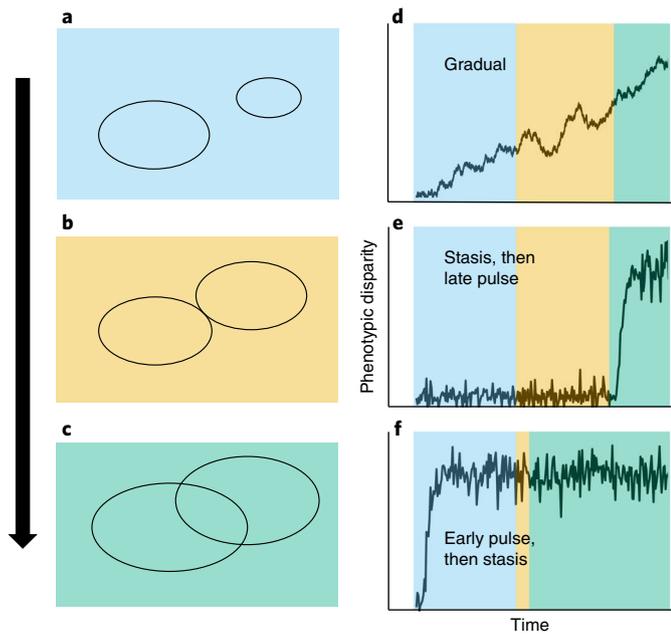


Fig. 1 | The speciation cycle and phenotypic trait divergence. **a–c**, Bird speciation typically involves a sequence of geographical states, starting with an allopatric phase (**a**), followed by secondary contact initiated at range edges (**b**) and finally sympatry (**c**). **d–f**, Phenotypic divergence may take different pathways during this cycle: gradual models predict no pulse of divergence at any point in the cycle (**d**), whereas punctuated models involve stasis punctuated by pulses, which can follow the onset of coexistence (**e**) or precede it (**f**). Note that mutual exclusion in abutting (parapatric) ranges (as in **b**) is extended when traits are similar (**e**) and reduced when traits have already substantially diverged (**f**).

may be ephemeral if gene pools merge during secondary contact, whereas greater levels of divergence may lead to reproductive isolation and ultimately sympatry. This latter possibility could accentuate patterns of pulsed evolution in phylogenies and the fossil record, even when divergence itself is gradual^{18,32}. Framed by these uncertainties, our understanding of the rates and timing of trait divergence in vertebrate speciation remains highly incomplete, not least because the data required are often patchy for large samples of species. In particular, for most large taxonomic groups the information on ecological trait divergence and geographic distributions is not sufficiently resolved to explore divergence pathways in the context of geographical phases of speciation.

To address these issues, we examine phenotypic divergence, geographic relationships, and divergence times among 952 pairs of avian sister species. By restricting the analysis to sister species, we explicitly focus on ecological trait divergence associated with relatively recent speciation events, which reduces the impact of species extinction on our inferences relative to clade-wide approaches^{27,33}. For each pair of species, we estimated trait divergence and determined geographical relationships using a geospatial database of ~178 million species observation records^{34,35} and a set of standard range polygons. Combining detailed phenotypic, temporal and spatial information, we consider (1) whether pulse-and-stasis or gradual evolution predominate in ecological trait divergence over the extended duration of bird speciation, (2) whether divergence in ecological traits is associated with sympatry establishment and (3) how the estimated timing of divergence relates to the geographic phases of speciation.

Results

Using estimated divergence times for species pairs generated from phylogenetic trees^{36–38}, along with estimates of trait disparity for

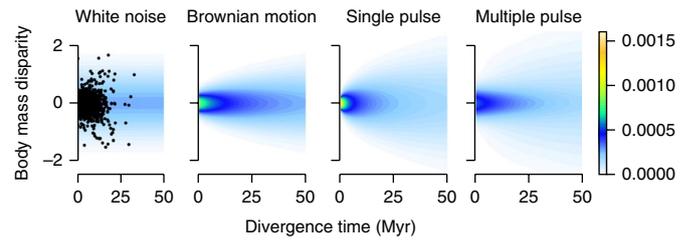


Fig. 2 | Tempo of body mass divergence for avian sister species.

Stochastic pulsed models provide better fits to patterns of body mass divergence and divergence time in avian sister species pairs ($n = 869$), with the best fit a single-pulse model (ΔAIC relative to the multiple-pulse model: 797). Colours denote probability density. The probability density for any time slice follows a normal distribution (most apparent in the white-noise model where the probability density distribution is independent of time). Relative probability density can be assessed within each time slice but not across time. For clarity, the empirical data points are plotted only on the white-noise model.

each pair of species, we fitted a set of evolutionary divergence models²² designed to span microevolutionary and macroevolutionary processes. We assessed relative support for four stochastic models: a Brownian motion ('gradual') divergence model, a 'single pulse' divergence model, a 'multiple pulse' divergence model and a time-independent ('white noise') divergence model. The first three models (gradual, single pulse, multiple pulse) incorporate an additional white noise component to represent bounded evolution processes at shorter timescales and to help to account for measurement error. In the single- and multiple-pulse models, the pulses are modelled as instantaneous jumps in trait values, which are representative of brief periods of high-rate directional evolution²² as expected in rapid evolution toward a new adaptive optimum³⁹ and not as saltational jumps. We interpret the single-pulse model as a pulse-and-stasis model, as the bounds of the bounded evolution component are narrow⁴⁰ (Supplementary Tables 1–4). For two important ecological traits—body mass and beak morphology (see Methods)—the single-pulse model has strong support relative to the other three models. Sensitivity analyses (Supplementary Tables 1–4) indicated that these results were robust to an alternate approach to phylogenetic reconstruction and divergence time estimation³⁸.

The difference in support between the single pulse and gradual models is consistent with phylogenetic studies that have found evidence for a contribution of speciation pulses in the accumulation of phenotypic diversity²⁶; difference in Akaike information criterion (ΔAIC) between the single-pulse and Brownian motion models is 899 for body mass, ΔAIC s between the single-pulse and Brownian motion models are 808, 920 and 967 for culmen length, beak depth and beak width, respectively (see Methods and Supplementary Tables 1–4). Our analyses suggest, however, that such pulses need not be completely coincident with speciation, that is, as reconstructed on phylogenetic trees as instantaneous events (nodes). Instead, such pulses may take place at some point in the course of a protracted geographic speciation process³⁰, as indicated by non-zero estimated waiting times to pulses.

To estimate the timing of these divergence pulses, we used the rate parameter in the single-pulse model preferred in our analyses. For body mass, the expected waiting time to a pulse was ~670,000 years (95% confidence interval (CI) from likelihood profile: 275,000 years to 1.13 million years (Myr); see also Figs. 2 and 3, Supplementary Table 1). The expected waiting times to a pulse in beak morphology divergence in single-pulse models were ~440,000 years for culmen length (95% CI: 200,000 to 930,000 years), ~360,000 years for beak depth (95% CI: 100,000 to 720,000 years)

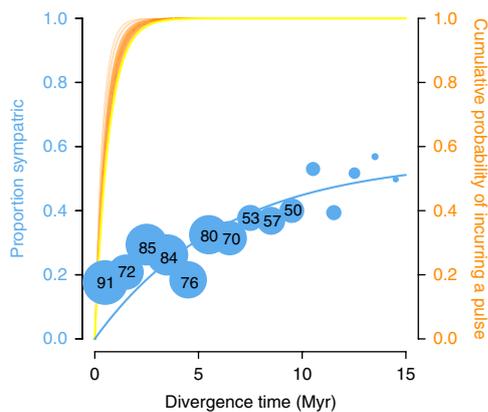


Fig. 3 | Timing of body mass divergence pulses and sympatry. Comparison of timescales suggests that mass divergence tends to precede sympatry among 952 avian sister species. Yellow and orange lines are cumulative probability distributions of incurring a pulse under the single-pulse model (yellow, estimated from maximum likelihood phylogenetic tree³⁶; orange, from 100 bootstrap trees). Circles are proportions of sympatric species pairs for million-year intervals of divergence time; circle sizes represent sample sizes, numbered where ≥ 50 . For visual comparison, an exponential decay model has been fitted to the proportion of sister pairs in sympatry (blue curve; assumes all sympatry is secondary). If we assume that rates of transition out of sympatry are low, the timing of divergence pulses is early compared with the generally delayed attainment of sympatry (that is, the yellow and orange curves are steeper than the blue curve).

and ~420,000 years for beak width (95% CI: 130,000 to 820,000 years; see Supplementary Tables 2–4).

To compare the accumulation of trait divergence with transitions from allopatry to sympatry, we calculated and visualized the cumulative distribution function (CDF) for undergoing a pulse of divergence over time (Fig. 3, see also Supplementary Fig. 1). The pulse magnitudes in the trait divergence models are variable (specifically they are drawn from a normal distribution with a mean of 0), such that we only expect large-magnitude pulses for a small fraction of species pairs. Most species pairs in this model accumulate modest trait divergence. Under this model, however, large-magnitude divergence is possible not only for older species pairs, but also for younger species pairs.

To compare our estimates of pulse timing and trait divergence accumulation with the progression to secondary contact (inclusive of both parapatry and sympatry) and sympatry, we obtained information on contact from a geospatial database of ~178 million species observation records^{34,35} and on sympatry from standard geographical range polygons⁴¹ (Fig. 4). Comparing the inferred timescales of trait divergence and sympatry suggests that pulses of trait divergence largely precede the establishment of sympatry (Fig. 3), which occur predominantly on the order of 10^6 years. This result is contingent on the assumption that transitions out of sympatry are infrequent⁷. The relative timescales of inferred trait divergence pulses and sympatry establishment (Fig. 3) suggest that many divergence pulses occur in the absence of sympatric interactions that could cause character displacement¹³. By contrast, we found that secondary contact occurs early and frequently enough among species pairs that the signature of initial allopatry is absent in our analyses of secondary contact and divergence time (Supplementary Fig. 3; Supplementary Section ‘Timing of secondary contact and sympatry’), leaving open the possibility that trait divergence often follows secondary contact, or that parapatric speciation (without an initial allopatric stage) occurs with regularity among birds (see below, Methods and Supplementary Information).

Pulses of ecological trait divergence theoretically reduce competition and reproductive interference among incipient species¹⁷, potentially overcoming constraints on sympatry establishment²⁷. The possibility that divergence by pulse-and-stasis evolution is widespread during speciation raises the question of whether divergence pulses are consequential for transitions through the geographic speciation process. Thus we tested whether variation in body mass and beak morphology predicted which species pairs are parapatric (with abutting distributions) or sympatric (with overlapping distributions). Focusing on all species pairs in secondary contact ($n=440$, see Methods), and accounting for the effects of divergence time, dispersal ability and latitude, we found evidence that sympatry is associated with greater divergence in ecological traits (Fig. 4, Supplementary Tables 8,9). In different analyses, either body mass divergence or aspects of beak morphology divergence had more support as predictors of sympatry (Supplementary Tables 8,9). Relationships between increased probability of sympatry and ecological trait divergence were present across sensitivity analyses accounting for a different approach to phylogenetic reconstruction and divergence time estimation (Supplementary Tables 12,13), and an alternate threshold for delineating sympatry versus parapatry (Supplementary Tables 14,15). These results are largely in agreement with previous studies showing that the transition from secondary contact to sympatry is associated with divergence in body mass and/or beak morphology^{11,12}.

The hand-wing index, a morphological proxy of dispersal ability^{12,43}, was also a consistent predictor of sympatry for species pairs in contact across analyses (Fig. 5, Supplementary Information). This effect could be observed if sympatric populations tend to be sinks supported by non-sympatric sources: species with elevated dispersal capacity may maintain sympatric sink populations whereas those with weak dispersal may fail to. Additionally, increased dispersal capacity may be associated with elevated founder population sizes or densities during colonization of the sister species’ range. These elevated founder population sizes may facilitate colonization within the ranges of sister species by surmounting the challenges of population establishment at low density or number^{44,45}.

Finally, we inferred that contact between members of species pairs often occurs early (within the first 2 Myr) in the geographic speciation cycle (Supplementary Fig. 3), contrary to models of geographic speciation that specify that long periods of allopatry are necessary for speciation². This suggests a potentially wider role for parapatric speciation (speciation with no stage a in Fig. 1)⁴ than is often considered in bird speciation⁴⁶. In parapatric speciation, divergence pulses prior to sympatry would necessarily occur despite contact, and thus the potential for gene flow, between incipient species¹⁷. However, we also found that observed patterns of contact and divergence time among bird sister species could be explained by speciation models requiring some period of allopatry at the outset, but allowing for rapid rates of transition to secondary contact (speciation with reduced duration of stage a in Fig. 1; Supplementary Figs. 9,10, Supplementary Information). Stochastic modelling of species ranges indicated that an approximate minimum rate of transition to secondary contact of 0.3 transitions per million years is sufficient to explain the pattern of contact among sister pairs. That is, a 30% probability of a species pair coming into contact within a million years is sufficient to yield a combined set of divergence times for species pair contact approximating the empirical observations. Thus, trait divergence pulses may occur during periods of either allopatry or parapatry, with cases of both likely to be widespread. Our evidence for early contact during speciation suggests that selection (for example, local adaptation, immigrant inviability¹⁷ or other immigrant disadvantages and/or selection against intermediate phenotypes) frequently plays a role in driving or maintaining divergence in the early stages of speciation.

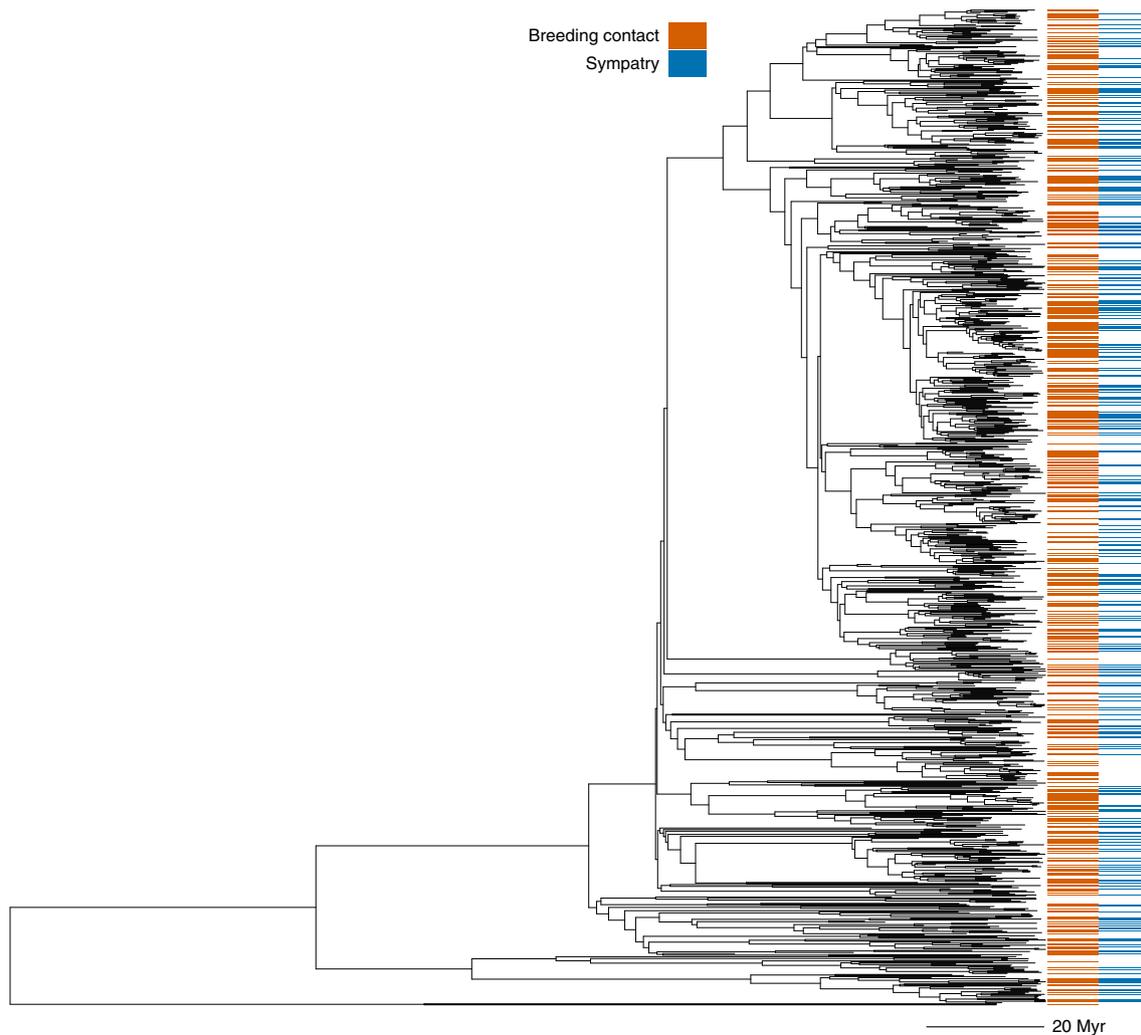


Fig. 4 | Phylogenetic patterns of contact and sympatry across avian sister species. Evolutionary and geographic range relationships among 952 pairs of sister species scored for breeding contact (orange) and sympatry (blue), showing that both are widespread in sister species across phylogeny. Pairs with breeding contact include both parapatric and sympatric species pairs. The tree is derived from the Burleigh tree³⁶ and has been pruned. Terminal branches are further pruned such that tips represent the most recent common ancestors of sister species pairs. There are 23 sister pairs that were scored as sympatric from range polygons, but for which no breeding contact records existed in the eBird dataset^{34,76}, probably reflecting a combination of sparse sampling in these sister species' ranges and limited syntopy despite broad geographic overlap.

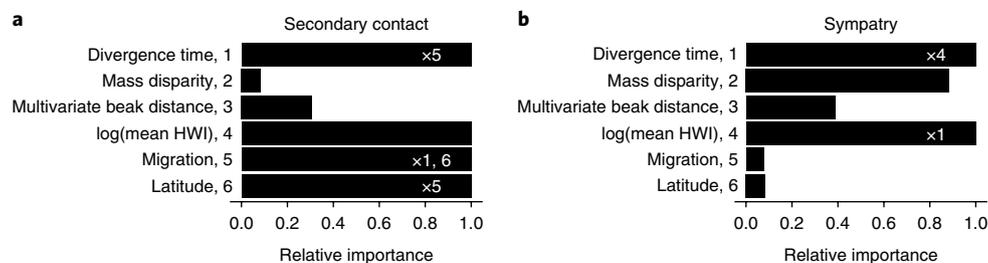


Fig. 5 | Factors associated with the establishment of secondary contact and sympatry in birds. **a, b**, Results of generalized linear models assessing the relative importance of predictors of breeding contact (**a**, $n = 849$ sister pairs) and sympatry (**b**, $n = 440$ sister pairs with breeding co-occurrence). Pairs with breeding contact include both parapatric and sympatric species pairs. Relative importance is estimated as the proportion of the summed model weights for all models with $\Delta AIC < 2$, and is indicative of the extent to which each variable is necessary to explain the variation. Pairwise interactions with relative importance greater than 0.6 are indicated by the numbers within the bar for each variable.

Discussion

A prevailing view on bird speciation is that ecological trait divergence sufficient to enable sympatry requires long periods of allopa-

try^{9,12}. Gradual evolution models, such as the random walk models, used in many phylogenetic comparative methods for continuous traits, are consistent with this prevailing view^{7,15}. However, gradual

divergence models inadequately account for strong divergence in young species pairs, unless they also incorporate brief bursts of faster gradual divergence^{48,49}, similar to pulses. Even the early burst model⁵⁰, used to represent the explosively rapid trait divergence dynamics in extant adaptive radiations²⁸, poorly accounts for highly divergent recent species pairs because it predicts comparatively slow evolutionary rates at the tips of phylogenetic trees. Thus, although widely used gradual models may adequately explain avian trait evolution at deeper macroevolutionary scales (as for comparing genera or families²⁸), our findings indicate that patterns of divergence among sister pairs are better captured by models incorporating pulsed divergence amid periods of stasis. In particular, the single pulse model we test here receives relatively strong support, and can help to explain the range of geographic speciation outcomes observed in nature, which includes many 'old' species pairs that are highly similar in ecological traits⁹ but also instances of abrupt ecological trait divergence in young species pairs^{10,17,51,52}.

The signal of trait divergence pulses during the geographic speciation cycle raises the question of how such pulses may take place. We suggest that pulses are likely to result from the intermittent discovery, by populations or lineages, of unoccupied adaptive peaks, as is expected in niche-filling models of diversification^{6,10}, or more generally from adaptive evolution on heterogeneous fitness landscapes^{14,53}. Unoccupied adaptive peaks may become occupied, via pulses of adaptive directional evolution, during or immediately following range expansion^{16,54}, for instance immediately following colonization of novel environments. Rapid phenotypic divergence may also result from local adaptation along environmental gradients, with or without gene flow⁵⁵. In such contexts, signals of pulsed divergence could plausibly arise from a combination of local (clinal) adaptation and the subsequent extinction of phenotypically intermediate populations^{16,18,56}. A key shared aspect of all these scenarios is that evolution on adaptive landscapes allows for pulse-and-stasis modes of divergence¹⁴. Our data may also be consistent with a role for character displacement⁵⁷ driving pulsed divergence in some instances. Comparing the timescales of trait divergence and sympatry establishment (Fig. 3), however, suggests that divergence pulses more frequently result from processes not requiring sympatry than processes that require sympatry.

Our finding that greater divergence in ecological traits is positively associated with the probability of sympatry accords well with what has been found previously in many other studies of vertebrates^{58,59}, including birds^{11,12}, using a variety of different methodological approaches. The focus of such studies is commonly character displacement^{11,58,60}, yet this association can also be explained by the spatial sorting of species ranges by competition^{12,61} or because these trait differences may be associated with stronger reproductive isolation^{5,62}. A previous study¹² found that the association of greater divergence in size and beak morphology of sympatric versus non-sympatric ovenbird species could be explained by a third factor, time since divergence, which they interpreted as evidence for spatial sorting of ecologically diverged lineages. Our results provide indirect support for this sorting hypothesis in a sample of species pairs that spans the diversity of birds, in that the timescale of ecological trait divergence under the single pulse model is faster than the relatively slow accumulation of sympatry in sister species pairs (Fig. 3)⁶². These findings suggest that pulses of trait divergence promote subsequent transitions to sympatry, rather than such pulses primarily occurring through character displacement after sympatry has been established. This interpretation is contingent on the assumption that the movement of species ranges over time results in low transition rates of sympatry to non-sympatry in sister pairs, i.e. that the curve in Fig. 3 is mostly representative of the initial achievement of secondary sympatry and not of an equilibrium between relatively even transition rates into and out of sympatry^{7,63}.

In combination, our results may help to resolve the long-standing question of why only some nascent species survive over evolutionary time. One of the major threats to young lineages is fusion through swamping gene flow upon contact². We have demonstrated that this risk is widespread among nascent bird species because the lag time to secondary contact is generally short (Supplementary Figs. 3 and 6–8), supporting the view that gene flow routinely becomes possible early in the speciation process. In particular, species pairs with minimally divergent phenotypes may incur increased hybridization rates or increased hybrid fitness relative to more diverged pairs, potentially leading to the extinction of one member of the species pair. Importantly, though, our findings also suggest that species pairs undergoing major early pulses of ecological trait divergence are more likely to rapidly transition to sympatry, escaping both fusion and mutual exclusion, and possibly extending their lifespan as independent lineages^{56,64–66}. Elevated rates of extinction in less-divergent young lineages may increase the signature of large early pulses in datasets compiled from extant species, such as that presented here. Thus, differential extinction coupled with pulses of early trait divergence may play a critical role in explaining broad-scale patterns in the longevity, macroevolutionary diversity, and geographical distribution of species.

Methods

Sister pairs. We selected all ($n = 2,076$) pairs of avian sister species (that is, each other's closest relatives) from the maximum likelihood topology of a previously reported avian supermatrix phylogenetic analysis³⁶ (hereafter 'Burleigh tree'), which contains 6,714 of the ~10,500 bird species in the world. The inclusion of pairs of non-sister lineages would not invalidate our analyses, but for the purposes of interpretation we excluded pairs that may not represent true sister species because one taxon may have a closer relative. Specifically, we excluded 763 pairs belonging to genera with <75% species-level sampling, and another 62 pairs that were deemed unlikely to be true sister species based on either molecular evidence from other studies or taxonomic problems. For most analyses, we further removed 299 species pairs for which we could not adequately score the presence or absence of contact (Supplementary Dataset 6). Different analyses used different subsets of sister pairs, depending on data availability and quality (see Supplementary Datasets 1–6). In using the sister pair dataset to make inferences about the speciation process, we leveraged the broad variation in divergence times and stages of the geographic speciation cycle represented among sister pairs, including pairs that are in the early stages of divergence.

Divergence times. Divergence time estimates were obtained from an ultrametric tree inferred from the Burleigh tree³⁶ using penalized likelihood analysis implemented in r8s^{37,67}. The r8s analysis used 20 fossil calibrations and constrained the root of the tree to a maximum age of 110 Myr ago. However, applying a maximum age constraint to the root node had little effect on estimates of sister pair divergence times (Supplementary Fig. 5). A list of the fossil calibrations (Supplementary Dataset 7, see also ref.⁶⁸) and a command block for the r8s analyses are available in the Supplementary Information. We performed sensitivity analyses using alternate sets of divergence time estimates, both from bootstrap analysis of the Burleigh tree, and from an independent phylogenetic and dating analysis³⁸ (see Supplementary Information).

Ecological trait measurements. *Body mass.* Divergence in body size may be a strong contributor to ecological divergence, potentially reducing interspecific competition^{10,69} or reproductive interference⁵. We compiled data on body mass (a proxy for body size) for species pairs from updated global datasets^{70–72}. When multiple body mass values were reported, we took the mean; when male and female body masses were reported separately, we calculated an average of the two sex-specific means. We estimated body mass disparity as the difference between species in natural log of mean body mass. This estimate is a unitless measurement representing proportional change in body mass².

Beak morphology. Species with similar body mass may partition niches according to diet. Thus, to quantify differences in foraging ecology among sister species, we collected three beak measurements (culmen length, beak depth, beak width) associated with food item selection and manipulation^{73,74}. Culmen length was measured as the distance from the distal part of the nostril to the beak tip. Beak depth and beak width were both measured at the distal edge of the nostril. All beak measurements were made on wild birds or museum specimens using calipers, to the nearest 0.1 mm ($n \geq 4$ individuals sampled per species, ≥ 2 males and ≥ 2 females, where possible; see Supplementary Information for further details about the beak morphology dataset). For evolutionary mode analyses, we estimated

proportional differences between species' phenotypes by taking the difference of the natural log of the mean body mass of each species²². To calculate multivariate species differences, we first fit separate phylogenetic generalized linear regressions of the log species means of each of the beak measurements on species log mean body mass (with Ornstein-Uhlenbeck errors⁷⁵; see Supplementary section 5 'Predictors of contact and sympatry'). We then calculated the Mahalanobis distance between the three beak measurement residuals from the phylogenetic generalized linear regressions for each species pair to estimate multivariate divergence in beak morphology.

Dispersal. Highly vagile taxa with greater dispersal capacities should undergo faster range expansions, potentially leading to earlier secondary contact in nascent species⁴³. This can be associated with faster transition rates to sympatry⁶³, but when secondary contact is very early, it may also slow or reverse the speciation process by promoting gene flow, leading to merged gene pools rather than continued divergence². Because of the importance of dispersal in geographic speciation models, we assessed how dispersal capacity influences transitions from allopatry to secondary contact, and from secondary contact to sympatry, respectively. As it is difficult to measure dispersal capacity directly, we instead used the hand-wing index (HWI), an index of wing shape related to the aspect ratio of the wing⁴³ and a proxy for flight performance and dispersal capacity in birds^{42,43,63,76}. Using measurements (to the nearest 0.5 mm) taken from wild birds and museum specimens, we calculated this index as

$$HWI = 100 \times \frac{WL - SL}{WL}$$

where WL (wing length) is the length of the closed wing from carpal joint to wing tip, and SL (secondary length) is the distance from the carpal joint to the tip of the first secondary feather. As a secondary index of dispersal, we also used range maps⁴¹ to assess migratory behaviour. If either member of a pair was illustrated as migratory to any degree, the species pair was scored as migratory.

Geographical phases of speciation. Secondary contact. We examined evidence for contact in species pairs using ~178 million bird species observation records stored in the eBird observational record database^{34,35}. We downloaded the eBird Basic Dataset (EBD_relOct-2013, from <http://ebird.org>). For a given species pair, contact was defined by evidence for the co-occurrence of both species on the same day at the same reported locality. Evidence that such co-occurrence takes place was interpreted as evidence for contact between species ranges. We wrote a Perl script that, for all sister species pairs, identified all instances when both species were listed at the exact same latitude and longitude on the same day. However, the spatial extent of eBird checklists varies when it is reported (Supplementary Fig. 4), such that some apparent co-occurrence records might come from checklists made for large areas or long transects. Furthermore, some co-occurrence records may result from human-aided introductions to areas extrinsic to native ranges or from ambiguity in different taxonomic treatments. To address these issues, we compared our contact scoring with what would result from contact scoring from range maps⁴¹ and examined eBird records where there was any discrepancy (see additional details in Supplementary Information 'General supplementary methods'). These data quality checks resulted in the re-scoring of 15 species pairs (from having contact to having no contact) and the exclusion of an additional 29 species pairs from the analysis where contact could not be scored with confidence (Supplementary Dataset 6).

Because contact can take place outside of the breeding range in cases where either member of a species pair is migratory, we scored breeding contact for such species pairs specifically by examining whether co-occurrence took place in the breeding range and breeding season, using breeding range maps⁴¹ and breeding phenology descriptions⁷⁰, respectively. To qualify as evidence of breeding contact, species co-occurrences in species pairs with any migratory behaviour had to be reported on the same day and in the same locality during the known breeding seasons of both species⁷⁰ and within the known breeding range of at least one of the two species⁴¹. For species pairs without known migratory behaviour, we assumed evidence of contact was indicative of breeding contact (see also Supplementary Information).

Because co-occurrence is unlikely to be reported for species with very few observations, we excluded sister pairs where at least one species had fewer than 10 eBird reported sightings. Our contact scores probably underestimate the true extent of contact among species pairs, as even after this filtering process, the minimum number of observations strongly predicts the probability of species pair contact in our dataset (GLM with the log of the minimum observations as sole predictor: coefficient estimate = $3.8 \times 10^{-4} \pm 8.5 \times 10^{-5}$ s.e.m.; Supplementary Table 5). Consequently, we conducted sensitivity analyses adopting an alternate minimum threshold, 20 or 50 instead of 10, for observations (Supplementary Table 5 and Supplementary Fig. 8). We also checked observational evidence for contact, discounting co-occurrence cases likely to be attributable to anthropogenic introductions, and excluding cases potentially based on misidentifications or taxonomic confusion (see included and excluded species pairs in Supplementary Datasets 1,6).

Sympatry. To examine the transition from contact to broad range overlap (sympatry), we calculated per cent breeding range overlap from geographic range polygons⁴¹ with a custom R script, using the R libraries *rgdal*, *rgeos*, *maptools* and

raster. A small subset of species pairs (17 of 440) could not be scored using our automated routine, and their range overlap was estimated visually. Species pairs with a range overlap >20% of the smaller range^{63,77,78} were scored as sympatric, while those with contact but with ≤20% range overlap were scored as parapatric (having abutting ranges)⁶³. This range overlap threshold may seem high based on the definition of parapatry as the circumstance where ranges abut but are separate⁷⁹. Range maps are coarse-grained, however, such that ranges that do not substantially overlap in reality appear to have overlap in range maps. As this 20% threshold, like any threshold, was somewhat arbitrary, we performed additional analyses using an overlap of >10% scored as sympatric (Supplementary Tables 14,15).

Analyses. Tempo of ecological trait divergence. To examine the tempo and timing of trait divergence, we evaluated the relative support for four divergence models across the set of species pairs for which body mass or beak morphology data were available ($n = 869$ species pairs for body mass, $n = 945$ species pairs for beak morphology). For all four traits, we defined disparities as the between-species difference in the log mean²². We fit one model of time-independent bounded evolution, as well as three different models that comprise a bounded evolution component on shorter timescales and one of three additional components for longer timescales²². These longer-timescale components are a gradual evolution model (Brownian motion) and two forms of pulsed divergence: a single-pulse model where a single instantaneous displacement occurs following a waiting time sampled from an exponential distribution and a multiple-pulse model where the expected number of displacements for a given divergence time is determined by a Poisson process. We examined relative support for these models using AIC from likelihood calculations performed in R. We calculated confidence intervals for the Poisson rate parameter λ , the inverse of which is taken as the expected waiting time to a pulse, using likelihood profiling. To generate likelihood profiles, we calculated the likelihood of single pulse models with a series of fixed λ values at increments of 0.01, over an interval containing the maximum likelihood parameter estimate. We assume the log likelihood ratio is chi-square distributed, and define the 95% confidence interval for λ as the interval for which the likelihood is within 1.92 units of the maximum likelihood model. To visualize the cumulative probability of incurring a pulse for Fig. 3, we used the equation for the cumulative distribution function for an exponential distribution, $1 - e^{-\lambda t}$.

Secondary contact and sympatry. We examined the probability of contact versus non-contact, and parapatry versus sympatry, using GLM with binomial error distributions, implemented in R⁸⁰. In analyses of contact and breeding contact for sister pairs, we began by predicting the probability of contact, with divergence time as the only predictor (Supplementary Figs. 3a,b and 7). We subsequently performed a model generation and selection routine (using the genetic algorithm of R package *glmulti*⁸¹; see Supplementary Information) to examine which among a set of phenotypic measures best predict contact or sympatry while accounting for the effects of three variables that may influence the timing of transitions from allopatry to sympatry: divergence time¹², latitude⁵ and dispersal ability⁶³. The predictors of primary interest were between-species disparity in two traits implicated in ecological and reproductive isolation: body mass⁸² and beak morphology⁸³. We incorporated disparity in beak morphology (i) as the Mahalanobis distance between species residuals from phylogenetic linear regressions of beak measurements on body mass (see above), or (ii) by including each of the three residuals (from phylogenetic linear regressions of culmen length, beak width and beak depth on body mass) as predictors. We used disparities in mean body mass and beak morphology as predictors in these analyses instead of sex-specific disparities as (i) many individuals in these datasets are not sexed, (ii) overall sexual size dimorphism is minor, and (iii) species interactions involve both males and females, such that the mean of these measurements is likely to be relevant.

To account for differences among sister species pairs in dispersal ability, we also included the average log HWI (ref. ⁴³) and migratory status of the sister pair as predictors. We further included divergence time and midpoint latitude (average of the two median observational latitudes for each species from eBird³⁵). Our model generation routine permitted all pairwise interactions between predictors to enter the model, under the constraint that all models were marginal. We report support for all predictors entering the set of contact models with $\Delta AIC < 2$ (Supplementary Tables 6,7). All continuous variables were scaled and centred, such that estimated slope magnitudes for individual variables are meaningful in relation to one another.

For GLM examining the probability of sympatry versus parapatry, we first limited the sister species dataset to those pairs with breeding contact. This restriction focuses the analysis on taxa that have the opportunity to interact to some degree in the breeding season⁸⁴. The response variable in GLM is the geographic configuration: parapatric (in contact but without substantial range overlap) versus sympatric (having substantial range overlap: > 20% of the smaller range in the analyses presented in the main text). We again used a genetic algorithm (see Supplementary Information) to generate model variants and performed model selection using the R package *glmulti*⁸¹.

To assess the sensitivity of our results to uncertainty in phylogenetic inference and divergence time estimates, we repeated all GLM analyses using mean

divergence times for our species pairs from 100 samples of the pseudo-posterior distribution of trees from an alternative Bayesian species-level phylogenetic analysis³⁸ (hereafter, the 'Jetz tree'; Supplementary Tables 9–12). For analyses examining the probability of contact (and breeding contact) with divergence time, we performed additional sensitivity analyses using divergence time estimates from 100 bootstraps of the Burleigh tree and for each of the 10,000 pseudo-posterior samples from the Jetz tree (Supplementary Fig. 7).

Simulations of range dynamics. To aid in the interpretation of our GLM predicting local co-occurrence, we performed stochastic range dynamic simulations⁶³. We used these simulations to place an approximate lower bound on the rate of secondary contact establishment from an initially allopatric configuration. To perform this estimation, we simulated the establishment of secondary contact using a simple model⁶³, in which sister pairs can be in one of two states: in contact and not in contact. We simulated transitions into and out of contact over a set of possible rates from 0.1 to 0.8 per million years, in which the forward rate (rate of transition from isolation to contact, σ) is always greater than or equal to the reverse rate (rate of transition out of contact, ϵ). The forward and reverse rates are constant⁶³, and the variation in rates among species arises only from stochasticity. Reverse rates were simulated at 0.005, 0.01, 0.05, 0.1, 0.2 and 0.5 times each of the forward rates. We present the maximum intercept calculated across all reverse rates (ϵ) for each simulated forward rate (σ) (Supplementary Figs. 5,12). To calculate the approximate percentage of species pairs coming into secondary contact by given points in time following divergence (100,000 years, 1 Myr), we simulated range dynamics with $\sigma=0.3$ and $\epsilon=0.15$ (corresponding to the minimal σ that yielded intercept >0.434 , and the value of ϵ that yielded the highest intercept for $\sigma=0.3$).

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

Code availability. Computer code for analyses not found in the Supplementary Information can be obtained from the authors upon request.

Data availability. We provide the datasets used to perform the analyses in this manuscript in a Microsoft Excel file (.xlsx) in the Supplementary Information.

Received: 28 April 2017; Accepted: 2 May 2018;

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Acknowledgements

We are grateful to numerous data collectors who contributed to eBird, GenBank and the CRC bird body mass dataset (see Supplementary Information). We also thank N. Alioravainen, E. Braun, S. Jones, R. Kimball, D. Ksepka, M. Neate-Clegg, A. Pigot, A. Ragsdale and G. Zhelezov for data collection and technical assistance. This work was supported by the National Science Foundation (DEB-1208428 to J.G.B.), the Natural Environment Research Council (NE/I028068/1 to J.A.T.) and the Oxford Clarendon Fund and US–UK Fulbright Commission (to C.S.).

Author contributions

J.G.B. and J.P.M. conceived the study; J.G.B., J.P.M. and J.A.T. designed the conceptual framework and analyses; J.G.B. performed dating analyses and assembled phylogenetic occurrence and body mass information; J.A.T. and C.S. provided morphometric data; J.P.M. integrated datasets, and designed and performed statistical analyses with significant input from J.G.B., J.A.T. and C.S.; J.P.M. and C.S. produced figures and tables; J.P.M. wrote the manuscript, with significant input from all authors.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41559-018-0570-y>.

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Data collection

Custom Perl code was written to extract co-occurrence records from eBird data, and is available by request from the senior author (gburleigh@ufl.edu).

Data analysis

Analyses were performed in R versions 3.2 - 3.3, utilizing a number of specialized libraries (ape v. 4.1, phylolm v. 2.5, phytools v. 0.6-20, geiger v.2.0.6, lme4 v. 1.1-13, glmulti v. 1.0.7, rgdal v. 1.2-8, rgeos v. 0.3-23, maptools, raster v. 2.5-8, sp v. 1.2-5, maxLik v. 1.3-4). Fossil calibration of the phylogenetic tree was performed using r8s (but is not novel to this manuscript).

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Sample size	No a priori calculations were made to determine adequate sample size. We describe in detail in the Methods section how we arrived at sample sizes.
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