Shared patterns of spatial accumulation of lineages across terrestrial vertebrates

Nicholas M. A. Crouch

Abstract
Aim: Whether species co-occur with closely related taxa has long been thought to influence both the rate of species formation and maximum clade diversity. However, it is unclear whether these processes act concordantly across entire clades and between taxa with disparate dispersal and life history strategies. Quantifying these patterns will yield a better understanding of the factors regulating biodiversity. I investigate whether allopatry promotes lineage diversification leading to greater clade richness. I also test whether slowdowns in diversification and family richness are correlated with increased sympatry.

Location: Global.

Taxon: Birds, mammals, and amphibians.

Methods: Posterior distributions of speciation rate estimates were compared between different definitions of lineage allopatry. Temporal changes in speciation rate were compared against family diversity as well as the mean and maximum number of overlapping familial ranges.

Results: More diverse families accumulate more overlapping ranges, but this process is nonrandom with predominantly nonsister taxa overlapping. Sister species in allopatry have higher speciation rates, with rates generally suppressed when allopatry is defined using all confamilial taxa, suggesting that the effect changes over the course of a radiation. Slowdowns in diversification are uncorrelated with the maximum and mean number of regionally sympatric species, therefore appearing to be either an idiosyncratic feature of certain clades or at least not related to spatial packing of confamilial species.

Main conclusions: Allopatry of sister species is correlated with rapid diversification at 1–3 Ma timescales. At the family level, maximal clade diversity is achieved through increased sympatry of member species, that is, packing of related species within a single geographic area.

Keywords: allopatry, Amphibians, birds, diversification, mammals, slowdowns, sympatry
INTRODUCTION

Determining how species form, and why this rate varies in time and space, is essential for understanding taxonomic imbalance in the Tree of Life (Schluter, 2000). All speciation events have a geographic component describing whether new species form in the presence or absence of sister, or closely related, taxa (Barracloff & Vogler, 2000; Losos & Glor, 2003; Schenk & Steppan, 2018). Allopatric speciation has historically been considered to be the dominant process by which species may form as it involves physical interruption of gene flow (Barracloff & Vogler, 2000; Coyne & Orr, 2004; Huxley, 1942; Jordan, 1905; Mayr, 1963). The tendency for sister taxa to be separated by a physical barrier is sometimes referred to as “Jordan’s Rule” (Anacker & Strauss, 2014; Fitzpatrick & Turelli, 2006; Jordan, 1905). While sympatric speciation is increasingly considered to be important, and apparently possible even with ongoing gene flow (Bird et al., 2012; Bolnick & Fitzpatrick, 2007; Fitzpatrick & Turelli, 2006; Getz et al., 2016), such analyses are typically restricted to comparisons of sister taxa (Phillimore et al., 2008) and do not consider that clades can vary tremendously in their degree of sympatry with congeneric taxa (Kennedy et al., 2018). As allopatric distributions are thought to facilitate more rapid speciation, clades with opportunities to place a greater proportion of their constituent taxa in allopatry should experience more pronounced diversification, resulting in greater overall diversity. If this process occurs with little ecological differentiation between species, this may result in a “nonadaptive radiation” (Rundell & Price, 2009) where member species represent a series of allopatric replacements of their sisters (Rundell & Price, 2009). This can occur frequently in island systems, mediated through either dispersal, vicariance (as islands form and separate otherwise continuous populations, e.g., Cai et al., 2020), or a combination of both. A classic example is the genus Zosterops, white-eyes (Aves, Passeriformes, Zosteropidae), distributed primarily across islands in the southwest Pacific and Indian oceans. The proliferation of this genus has led to their being labeled an exemplar of a “great speciator” (Cai et al., 2020; Diamond et al., 1976; Moyle et al., 2009). Under this scenario, more depauperate clades should have proportionally more sympatric species. However, if clades are prone to ecological speciation, then an alternate hypothesis is that diversity should be negatively correlated with degree of allopatry as competitive displacement between species in sympatry generates greater diversity (Rundell & Price, 2009).

If geographically structured ecological opportunity governs the propensity for lineages to speciate, then temporal changes in opportunity should be reflected in alterations to the speciation rate. A correlation between ecological opportunity and changing speciation rate is most frequently inferred when diversification slows towards the present, as commonly seen in molecular phylogenies (Phillimore & Price, 2008; Price, 2008; Pybus & Harvey, 2000; Rabosky & Lovette, 2008a, 2008b). Contemporary declines in speciation rate can be interpreted as a clade experiencing limits to diversity, with lineage proliferation slowing as there are fewer ecological roles for species to fill (Rabosky & Lovette, 2008a; Schluter, 2000; Walker & Valentine, 1984). Such slowdowns are commonly detected in molecular phylogenies by nodes being disproportionately shifted towards the root relative to the expectation under a pure-birth model of evolution (y statistic of Price, 2008; Pybus & Harvey, 2000; Weir, 2006), or by calculating the proportional difference in diversification rate between the first and second half of a clade’s phylogenetic history (µ, Pigot et al., 2010). Such metrics provide continuous approximations of clad dynamics, with likelihood-based approaches facilitating differentiation with, for example, continuous rate models (Etienne et al., 2016). Alternative likelihood-based approaches can also accommodate for additional statistical phenomena of phylogenies; for example, the “pull of the present” whereby the rate of diversification can appear to increase towards the tips of phylogenies due to these lineages having had less time to potentially go extinct (Nee et al., 1994; Stadler, 2011). Slowdowns in diversification might also occur if clades have a high degree of sympatry (Kennedy et al., 2018; Machac et al., 2013; Phillimore & Price, 2009; Weir, 2006). Alternatively, greater ecological constraint, such as through having extremes of morphology (Kennedy et al., 2020; Ricklefs, 2006), can cause the speciation rate to slow independent of geographic distribution, again resulting in deviations from the expected correlation between richness and allopatry. In fact, over-representation of depauperate clades relative to a homogeneous diversification process is common across vertebrate clades (Ricklefs, 2003, 2006, Supporting Information).

Clades may also deviate from the expected relationship with allopatry if they experience a burst of diversification independent of geographic distributions. The causes of these radiations can be myriad (Rundell & Price, 2009; Simões et al., 2016). For example, the exceptional diversification seen in Hawaiian crickets (Laupala) appears to be driven by selection on sexual traits (Mendelson & Shaw, 2005). As with the abundance of small clades, the major vertebrate lineages also show an over-abundance of particular diverse clades (Supporting Information).

Accurately quantifying the role of allopatry in driving lineage diversification requires phylogenetic data detailing the relationships between species. Although a phylogenetic framework permits more accurate definition of species states, some caution is required when examining macroevolutionary scales as taxonomic data are still required to construct phylogenies spanning entire clades (Chang et al., 2020) and deep nodes may be inaccurately defined as present-day distributions may not reflect historical ranges (Barracloff & Vogler, 2000; Liow et al., 2010; Phillimore et al., 2008). In the absence of additional information from the fossil record, such biases can affect, for example, inferences of the historical biogeography of clades (Meseguer et al., 2015). Nevertheless, increasing taxonomic coverage of phylogenetic data and refinement of spatial distributions of extant taxa has been illuminating, offering insight into numerous evolutionary processes (Pearse et al., 2019; Tucker et al., 2017; Webb et al., 2002). Additionally, the highlighted concerns can be accommodated by focusing on recently diverged species (Phillimore et al., 2008), where both geographic relationships and speciation
rates are more accurately estimated (Louca & Pennell, 2020, and references therein).

In order to achieve maximum diversity, lineages will likely have to pack species within a single geographic area. There is undoubt-edly variation; for example, species with larger ranges are more likely to overlap, but this broad trend has been long recognized in spatial patterns of diversity (MacArthur, 1969; Pigot et al., 2016). The processes that allow species, assuming speciation predominantly occurs in allopatry, to come back into secondary contact are distinct from those that drive species formation, despite being connected as part of an overall process of evolution (fig. 1 of Tobias et al., 2020). Secondary sympatry is generally facilitated by reducing competition between species (MacArthur, 1969, 1970; MacArthur & Levins, 1967) with this signature detectable through quantification of the relative timing of trait divergence and range overlap (Tobias et al., 2020, and references therein) as well as genomic data (Foote, 2018, and references therein). Therefore, dis-entangling allopatric speciation from the maintenance of allopatry likely requires integration of trait data which, although becoming increasingly common, is still lacking in coverage across major clades. Nevertheless, it may be possible to infer different evolutionary processes through different definitions of allopatry. For example, testing the effect of allopatry on speciation rates when defined using all confamilial taxa may also reflect the ability of species within families to coexist.

In this study, I evaluate whether lineages in allopatry and sympatry have differential speciation rates across three clades of terrestrial vertebrates of varying dispersal and life-history characteristics: birds, mammals, and amphibians. Within these clades, I leverage spatial and phylogenetic data for 200 families and over 23,000 species as well as multiple definitions of allopatry and sympathy. I test the hypothesis that lineages with a greater proportion of their species in allopatry should have higher speciation rates, resulting in greater overall diversity and increasing diversity through time, and that deviations from this relationship may be predicted by either elevated or reduced speciation rates.

2 | MATERIALS AND METHODS

2.1 | Spatial data and mapping of geographic states

Spatial data for avian taxa were provided by BirdLife International and NatureServe (2012), data on mammalian and amphibian taxa were downloaded from the International Union for Conservation of Nature (IUCN Red List, 2017). I updated 1674 synonymy differences between the species names in Jetz et al., (2012) and the data provided by BirdLife International and NatureServe (2012). There were an additional 177 species for which no geographic data were available, reflecting differential treatment of taxa as subspecies or full species. These taxa were excluded from these analyses.

In this work I primarily define sympathy as any overlap in the total geographic extent of taxa and allopatry as where those distributions are disjunct. This binary definition can be considered a crude manner of characterizing species’ ranges (Butlin et al., 2008); for example, sympathy can either be ‘mosaic’, where species’ ranges overlap but they predominantly subdivide habitats within the same geographic extent, or ‘pure’, where the species readily come into contact (Mallet et al., 2009). However, defining these terms in this way allows comparable statements to be made across clades with disparate life histories and dispersal abilities. Additionally, I compare species ranges within families because they are presumed or observed to have strong ecological similarities, and so I expect those taxa to be using broadly similar habitats. Seeking a more nuanced definition whereby some degree of overlap is permissible for two species to still be considered allopatic is hampered by the continuous degree to which ranges overlap, prohibiting an objective cutoff value. Other sources of data, such as point counts, may allow more detailed assessment of species distributions but are subject to taxonomic and spatial biases. Nevertheless, to test whether the results are sensitive to this manner of characterizing range overlap, I defined the geographic states of species allowing a 10% overlap in range size for a comparison to still be considered allopatric. In each case I compared the area of overlap to the range size of the smaller of the ranges being compared.

I took two approaches to defining allopatry at the species level. First, I followed fig. 2 of Weir and Price (2011) whereby nodes in a phylogeny are assigned a geographic state based on the ranges of the taxa descendant from that node (Figure 1A). For example, if the ranges of species descendant from a node overlap to any extent then that node is labeled ‘sympatric’; otherwise, the node is ‘allo-patric’. This process is performed iteratively over each node in the phylogeny for each family. I then assigned states to branches within the phylogeny based on the parent and daughter node state; that is, if both the parent and daughter node state are sympatric then that is the state assigned to the connecting branch. In instances where the parent and daughter nodes had different states, I labeled the branch as transitional between the respective states. Terminal phylogenetic branches, that is, those leading to species do not have a daughter node; therefore, I assigned these branches the same state as their parent node. This is a parsimonious approach based on the observable data. Incorporating phylogenetic data in model-based approaches can produce different results, particularly when branch lengths are long as there is a greater probability for range shifts to have occurred (Ree & Smith, 2008; Ronquist & Sanmartín, 2011; Sanmartín, 2014). The second method for quantifying the geographic state of phylogenetic branches refers only to terminal branches in a phylogeny (Figure 1B). Specifically, I quantified whether each species range overlapped with any other member of that family, regardless of the relationship between those taxa.

I also used two definitions for geographical co-occurrence at the family level, which uses all constituent species’ ranges concurrently. First, I quantified the degree of sympathy in a family following Weir (2006), whereby the score a family receives is the maximum number of overlaps between all of the ranges of all taxa within a family
Figure 1 Summary of the different approaches to quantifying geographic states used in this study. In all panels rectangles represent species’ ranges. (A) Definition following Weir and Price (2011), whereby a node is defined as sympatric or allopatric depending on whether any of the descendant taxa have overlapping ranges. For example, node 1 is sympatric because species g overlaps with a range from species a–f, and node 2 because species d overlaps with one of species a–c. A transition from allopatry to sympatry is not shown here but is present in the empirical data. (B) Terminal branches are labeled as allopatric or sympatric depending on whether the species overlaps with any other species range. Therefore, species e is labeled as sympatric despite being allopatric with its sister species f. (C) Degree of sympathy defined by overlapping ranges, which can be (i) where the degree of sympathy of a clade is defined as the maximum number of overlapping ranges (following Weir, 2006), four in this example. (ii) Take the mean of the number of overlapping ranges (Kennedy et al., 2018), two in this example.

I compared the degree of sympathy for families defined using all constituent species ranges (maximum and mean number of overlapping ranges, Figure 1C) against two aspects of family evolutionary history: temporal change in speciation rate and overall species richness. I quantified whether clades show deviation from constant diversification using two metrics: the γ statistic (Pybus & Harvey, 2000) calculated using the R package ‘ape’ (Paradis & Schliep, 2018), and the ρ statistic (Pigot et al., 2010), ρ is calculated by comparing the diversification history in the first (r₁) and second (r₂) half of the phylogenetic data (ρ = (r₂ − r₁)/(r₁ + r₂), Pigot et al., 2010), where r = (log[n₂] − log[n₁])/t (Magallon & Sanderson, 2001). The ρ statistic accommodates for the fact that γ artificially scales with clade size when diversification rates vary through time (McPeek, 2008; Pigot et al., 2010). For both metrics, negative values indicate clades showing decelerating diversification rates, and positive values increasing rates. I defined family richness as the number of described species according to the taxonomic data provided by the authors of the respective studies. I also calculated the correlation between maximum and mean number of overlapping ranges against γ and ρ statistic.
values when the number of overlapping ranges had been corrected for family richness—more speciose families may have a greater number of overlapping ranges by chance—by dividing $\gamma$ and $\rho$ scores by the number of species in the family. If $\gamma$ and/or $\rho$ correlated with family size, then testing for a relationship between these variables and the number of overlapping ranges would potentially suffer from collinearity.

I compared family richness, $\gamma$, and $\rho$ values against the relative age of allopatric nodes (mean age of allopatric nodes—mean age of sympatric nodes) within each family. It is likely that sympatric nodes will be comparatively older than allopatric nodes as their geographic state is defined using all their descendant taxa. Deviation from this relationship may be correlated with clade diversification dynamics. For example, a positive correlation between the age of sympatric nodes and either $\gamma$ or $\rho$ statistic values would be evidence of sympathy slowing clade diversification over time.

2.4 | Speciation rate estimation

For all three phylogenetic sets, I calculated lineage-specific speciation rates using Bayesian analysis of macroevolutionary mixtures (BAMM, Rabosky, 2013, 2014; Rabosky et al., 2014, 2017). I performed these analyses on the full species-level phylogeny for each clade (birds $n = 9993$, mammals $n = 5805$, amphibians $n = 7239$), regardless of whether all species could be included in the subsequent analyses. Analyzing the complete phylogeny without clade-specific sampling fractions removes potential biases, such as artificially creating diversification rate shifts in the clades where they are used (Stadler, 2013). Nevertheless, accurate branch length estimation remains critical; here, I used TACT to minimize this potential source of error. For all analyses I recorded MCMC and event data every 5000 generations, specified a prior on the number of rate shifts of 50, and allowed rate shifts to occur on all branches. I ran the bird analysis for 75 million generations and the mammal and amphibian analyses for 50 million generations. Effective sample sizes for model parameters are provided in Table S1.

2.5 | Speciation rate comparisons

Comparisons of speciation rates between sympatric and allopatric lineages are constrained to terminal branches as rate estimates for extant species are not obscured by unknown extinction rates (Harvey et al., 1994; Louca & Pennell, 2020; Nee et al., 1992). Specifically, I quantified whether there were any significant differences between allopatric and sympatric terminal branches using structured rate permutations on phylogenies (STRAPP; Rabosky & Huang, 2016). STRAPP samples rate estimates from the posterior distribution of BAMM analyses (here 1000 samples) and performs phylogenetically corrected correlation tests with a specified trait (lineage allopatry). I performed STRAPP analyses for two different definitions of allopatry: when allopatry is defined using sister taxa (Figure 1A, Weir & Price, 2011), and allopatry defined using all confamilial taxa (Figure 1B). I analysed all families within each major clade concurrently (birds $n = 9527$, mammals $n = 4833$, and amphibians $n = 2593$) using the traitdependentBAMM function in the R package ‘BAMMtools’ (Rabosky, Grundler, et al., 2014), specifying the Mann-Whitney $U$ statistic for the correlation method, as the trait is binary. Each value in the posterior distribution of the $U$ statistic is compared against a null value, generated by permuting the rate values at each step. Visualizing the difference between these values indicates whether the trait impacts lineage diversification, with values exceeding zero indicating a positive association between the trait (allopatry) and speciation rate (Rabosky & Huang, 2016).

3 | RESULTS

The proportion of terminal branches defined as allopatric differed substantially between the two species-level approaches. Quantifying branches following Weir and Price (2011, here Figure 1A) produced broadly similar results across all three vertebrate clades (birds 52% mammal 57%, amphibians 68%). When I defined allopatry using all confamilial taxa (Figure 1B) the proportion of allopatric species was dramatically lower, but still roughly equivalent (birds 3%, mammals 4%, amphibians 6%). This difference derives from the high probability of overlapping with at least one other range when all confamilial taxa were considered. At the family level, $\gamma$ and $\rho$ were moderately correlated across all three clades (birds: Pearson’s $r = 0.66$, mammals $r = 0.56$, amphibians $r = 0.64$). Family richness was uncorrelated with both $\gamma$ (birds: Pearson’s $r = 0.18$, mammals $r = 0.02$, amphibians $r = -0.32$) and $\rho$ (birds $r = 0.21$, mammals $r = 0.14$, amphibians $r = -0.03$). As expected, the average ages of sympatric nodes were older than allopatric nodes (Figure S4), but I found only weak correlations between the relative age of allopatric nodes and family richness, $\gamma$, and $\rho$ (Figure S5).

Family diversity was correlated with both the maximum and mean number of overlapping ranges across all three vertebrate clades when analysed concurrently ($r = 0.41$ and 0.25, respectively), as well as within individual clades (Figure 2). Mean and maximum values were highly correlated with each other ($r = 0.85$ birds, 0.85 for mammals, and 0.80 for amphibians). I found no significant correlations between the mean or maximum number of overlapping clades and family $\gamma$ or $\rho$ statistic values in any of the three clades (Figure 2). Nor did I find a correlation between $\gamma$ or $\rho$ statistic values and range scores when the latter were scaled by family richness (Supporting Information). Therefore, slowdowns in diversification appear to be restricted to specific clades.

I predicted that family richness should be positively correlated with the proportion of allopatric taxa. Contrary to this, I found no correlation between the proportion of allopatric terminal branches and family richness when allopatry was defined using sister species and, more strikingly, a negative correlation when allopatry was defined using all confamilial taxa (Figure 3). The negative relationship is clear, although families that have no allopatric taxa cover almost
the full range of diversity seen across the clades. I also predicted that deviation from a relationship could be explained by variation in clade diversification dynamics; however, I found no correlation between family diversity and mean family speciation rate or clade diversification dynamics (Figure 4) regardless of whether the families with no allopatric branches were excluded or included. Birds had a weak positive relationship between family diversity and speciation rate ($r = 0.35$), but there was significant noise in the relationship. The proportion of allopatric branches in each family was uncorrelated with mean speciation rate, $\gamma$, and $\rho$ (Supporting Information). I did find a weak positive correlation between the proportion of evolutionary time (in millions of years) spent in allopatry and family
I found a contrasting effect of allopatry on speciation rates of terminal branches. When defined using sister species all three vertebrate clades showed a significant positive distribution of centered U-statistics, indicating a higher speciation rate in allopatry (Figure 5). Quantifying allopatry using confamilial taxa resulted in significant negative skews to the posterior distribution of centered U-statistics for mammals and amphibians (Figure 5), indicating species in allopatry have suppressed speciation rates. Conversely, birds showed a positive distribution, indicating higher rates in allopatry. These avian taxa defined as allopatric using all confamilial taxa showed a significant bias towards island-dwelling—75% of these species are found exclusively on islands, including 25 Zosterops species (n = 263, island data from Sheard et al., 2020).

Allowing a threshold of a 10% range overlap for a relationship to still be considered allopatric did not affect the results. This was due to the small number of species that changed their geographic state. When allopatry was defined following Figure 1A the proportion of allopatric species for mammals and amphibians was unchanged. For birds the value was slightly lower (51% opposed to 52% originally), but this was due to the lower sample size for this analysis (n = 5010), with 11 species changing geographic state. When allopatry was defined using all confamilial species, the number of allopatric species rose slightly for birds and mammals (4% and 5%, respectively), with amphibians unchanged. Due to these minimal changes in state association, there was no change in the overserved relationships between proportion of family allopatry and diversity, and speciation rate estimates (Figures S7 and S8).

4 | DISCUSSION

I predicted that family richness should be positively correlated with the proportion of the constituent taxa existing in allopatry and that strong positive and negative deviations from this relationship may be explained by exceptionally high speciation rates or slowdowns in speciation rate, respectively. I found that family diversity is positively correlated with the number of overlapping ranges (Figure 2), but these overlaps are not predominantly between sister species (Figure 3). Therefore, even though I do find elevated speciation rates for allopatric sister species (Figure 5), maximum diversity within clades may be achieved through greater spatial packing of species in a single geographic area. Family diversity was also uncorrelated with mean family speciation rate or metrics describing clade diversification dynamics (γ and p). Both γ and p statistic values were themselves independent of both the maximum and mean number of overlapping ranges within families. Species richness of families with no allopatric members when defined at the family level span nearly the full range of richness values; therefore, I suggest that the diversity of these families is dictated solely by factors outside of those examined here. For example, for avian species, factors such as morphology have been suggested to govern limits to diversity (Kennedy et al., 2020; Ricklefs, 2006).
A potential factor for not identifying the hypothesized relationships is an inability to include all predictive variables. In particular, spatial variation in “carrying capacity”—the total number of species that can be supported in a region—may also limit diversity. Accurate quantification of “carrying capacity” is considerably challenging; while spatial gradients in diversity can be readily documented, quantifying whether regions are saturated, or at equilibrium (Hutchinson, 1957; Walker & Valentine, 1984) is more ambiguous, and likely involves consideration of more than just the available resources (Storch & Okie, 2019). Therefore, while this work offers perspective on certain theory across broad macroevolutionary scales, interpretation of results, as well as consideration of future directions, must also involve consideration of these limitations.

Allopatry is thought to promote speciation through immediate removal of gene flow between separated populations (Barraclough & Vogler, 2000; Coyne & Orr, 2004; Huxley, 1942; Mayr, 1963). I find contrasting support for this assertion between the different definitions of allopatry and across the three major vertebrate clades. When allopatry is defined using sister taxa I find species across all three clades to have higher speciation rates (Figure 5). Therefore, it can be concluded that geographical separation promotes more rapid cessation of gene-flow and the formation of new species (Barraclough & Vogler, 2000; Coyne & Orr, 2004; Huxley, 1942; Mayr, 1963).
Quantifying allopatry using the distributions of all confamilial taxa shows suppressed speciation rates for mammals and amphibians, with birds still maintaining an elevated rate (Figure 5). For mammals and amphibians I suggest two interpretations. First, this result may imply that ecological competition between confamilial taxa drives lineage diversification, rather than ecological opportunity. This process can be considered equivalent to divergent natural selection or ‘ecological speciation’ (Dobzhansky, 1951; Mayr, 1942; Schluter, 2000), whereby disruptive selection produces a bimodal distribution of trait values that, through reinforcement, may ultimately lead to reproductive isolation (Bird et al., 2012; Débarre, 2012; Dieckmann & Doebeli, 1999; Schluter, 2000; Turelli et al., 2001). This process can also be referred to as ‘competitive speciation’ (Schluter, 2000). Alternatively, this result shows that diversity is limited by the ability of species to co-exist (Gause, 1934; Hutchinson, 1961). It may be that these clades differentiate on other ecological axes, such as morphology, to enable greater diversity to accumulate within the same area (i.e., they have higher sympatric carrying-capacity compared to more depauperate clades). Differentiation in ecomorphological traits to allow secondary sympatry is slow (i.e., millions of years, Weir & Price, 2011), which suggests that time is the principal limiter of diversity in sympathy (Price, 2010). However, given the long-standing appreciation that clade richness can deviate from that predicted from time alone (Magallon & Sanderson, 2001), this answer is likely incomplete. It seems most likely that an analysis incorporating trait data as well as species distributions, across the macroevolutionary scale examined here, will be best suited to differentiate between species formation in allopatry and the processes that maintain allopatry (Tobias et al., 2020).

The two greatest obstacles to a study such as this are accurate reconstruction of the relationships between species and accommodating for temporal fluctuations in species’ spatial extent. It is truly a global effort of researchers to generate sequence data for extant biodiversity, yet the magnitude of this diversity (~23,000 species in the three clades included here) means gaps invariably remain. I have attempted to mitigate the effects of species sampling by placing those taxa lacking molecular data in the backbone phylogeny using the most up-to-date methods, which provide increased accuracy with estimating diversification rates (Chang et al., 2020). Therefore, while I can be relatively confident in the estimation of rates, continued production of sequence data will likely have a greater impact on resolving the relationships between species, and thus assignment of geographic states. However, it is less clear how to incorporate temporal variation in species’ distributions. Lability of range sizes is well documented for extant taxa as well as in the fossil record (Barraclough & Vogler, 2000; Foote et al., 2008; Liow et al., 2010; Liow & Stenseth, 2007; Losos & Glor, 2003). The magnitude of this problem is also potentially high. The average age of nodes subtending two extant species exceeds extreme Pleistocene climatic fluctuations (birds mean = 2.93 Myr, n = 3362, mammals mean = 1.95 Myr, n = 1950, amphibians mean = 2.74 Myr, n = 2384), meaning it is reasonable to expect that, at the most extreme, species ranges have changed more than a dozen times since they diverged from their sister. Despite these concerns, I find a consistent pattern across disparate clades, and even within individual clades. Therefore, even though one must be mindful of such concerns, it appears possible to distinguish biological signal through any introduced noise.

Temporal variation in speciation rates is a pervasive pattern across the Tree of Life. In particular, declining rates towards the present are thought to reflect clades experiencing ecological limits in response to increasing diversity. Previous research found that clades exhibit more pronounced slowdowns with a greater maximum diversity in a single geographic location (Weir, 2006), or in families with a greater overall number of co-occurring lineages (Kennedy et al., 2018). In both cases here, I found no relationship (Figure 2), with this result consistent between the two approaches to quantifying diversification histories (γ and ρ). This difference is most likely attributable to
differences in sampling rate, as I aimed for wide taxonomic coverage to capture a greater amount of variation across the three vertebrate clades. Weir (2006) looked at 17 clades (predominantly genera) of lowland Neotropical birds and Kennedy et al., (2018) examined speciose passerine families, as these clades could be expected to experience greater limits to diversity (as discussed above). I also found no correlation when correcting for asymmetry in family richness. This step was not performed by Weir (2006) or Kennedy et al., (2018), with the latter reporting no correlation between the mean number of regionally sympatric species and family richness, unlike the weak positive correlation found here, or between \( \gamma \) and richness, as found here. Given these differences, and that diversification slowdowns are also shown to be independent of clade sympathy in other studies (Phillimore & Price, 2009), I suggest that the relationship between slowdowns and geographic co-occurrence is a particular phenomenon of certain clades (possibly those with reduced dispersal capabilities as the strongest correlation was recovered with amphibians, \(-0.40\), or with strong competitive exclusion, Price, 2010), and not a broad taxonomic trend. Further investigation of this relationship will necessitate the introduction of extinct species in a phylogenetic framework to more accurately differentiate slowdowns in speciation rate from other possibilities; notably, increasing extinction rate (Rabosky & Lovette, 2008b). Additionally, future work may consider different spatial scales. As mentioned above, continental definitions of allopatry and sympathy may not manifest at local scales if, for example, species exploit unique parts of the environment (Mallet et al., 2009). If resources are more limited within specific geographic regions, then slowdowns in diversification may be area-specific, and not detectable at continental scales as examined here.

These results suggest the effect of allopatry on lineage diversification and accumulation of species changes over the course of a radiation. Higher speciation rates in allopatry defined with sister species shows that the cessation of gene flow does promote more rapid speciation. At a broader (and presumably older) timescale maximal family diversity occurs through greater spatial packing of species; demonstrated though suppressed speciation rates in allopatry (except birds) in conjunction with an inverse relationship between the proportion of allopatric lineages and family richness. Quantification of allopatry at different scales and through multiple definitions across three clades of terrestrial vertebrates therefore facilitates construction of generalized hypotheses regarding the role of allopatry in driving lineage diversification and accumulation.

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**DATA AVAILABILITY STATEMENT**

The spatial data used in this study can be downloaded from the IUCN website: [https://www.iucnredlist.org/resources/spatial-data-download](https://www.iucnredlist.org/resources/spatial-data-download). The raw phylogenetic data files were downloaded from the following sources: for birds the data are provided via http://birdtree.org/., for mammals the data are available on Dryad ([https://datadryad.org/stash/dataset/doi:10.5061/dryad.tb03d03](https://datadryad.org/stash/dataset/doi:10.5061/dryad.tb03d03)), and for amphibians the data (as well as for the other clades) can be downloaded from [http://vertlife.org/data/](http://vertlife.org/data/). A markdown document detailing how all analyses were performed is provided in the Supporting Information. The specific phylogenetic data (with re-analysis of placing species using taxonomic data), custom R scripts, and results generated from this study are available on Dryad ([https://doi.org/10.5061/dryad.79cnph7f](https://doi.org/10.5061/dryad.79cnph7f)).

**ORCID**

Nicholas M. A. Crouch [https://orcid.org/0000-0002-3504-8245](https://orcid.org/0000-0002-3504-8245)

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Nick Crouch is broadly interested in macroevolutionary radiations; how aspects of species’ ecology may facilitate diversification and, in turn, be affected by increasing diversity. He is also interested in how these processes affect the formations of different ecological communities.

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