Competition and hybridization drive interspecific territoriality in birds

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Costly interactions between species that arise as a by-product of ancestral similarities in communication signals are expected to persist only under specific evolutionary circumstances. Territorial aggression between species, for instance, is widely assumed to persist only when extrinsic barriers prevent niche divergence or selection in sympatry is too weak to overcome gene flow from allopatry. However, recent theoretical and comparative studies have challenged this view. Here we present a large-scale, phylogenetic analysis of the distribution and determinants of interspecific territoriality. We find that interspecific territoriality is widespread in birds and strongly associated with hybridization and resource overlap during the breeding season. Contrary to the view that territoriality only persists between species that rarely breed in the same areas or where niche divergence is constrained by habitat structure, we find that interspecific territoriality is positively associated with breeding habitat overlap and unrelated to habitat structure. Furthermore, our results provide compelling evidence that ancestral similarities in territorial signals are maintained and reinforced by selection when interspecific territoriality is adaptive. The territorial signals linked to interspecific territoriality in birds depend on the evolutionary age of interacting species, plumage at shallow (within-family) timescales, and song at deeper (between-family) timescales. Evidently, territorial interactions between species have persisted and shaped phenotypic diversity on a macroevolutionary timescale.

behavioral interference | interference competition | phylogenetic comparative methods | Passerines

Interspecific territoriality is among the most common forms of interference competition in animals (1–4), and has been shown to affect species range (5–8) and drive phenotypic evolution, particularly of traits involved in competitor recognition (9–14). Yet, interspecific territoriality itself remains poorly studied. While it is generally logical to infer that at least one individual benefits in common within-species interactions, this logic does not hold when the individuals are members of different species. The reason is that interspecific territoriality can arise simply as a by-product of intraspecific territoriality when species with similar territorial signals (e.g., song, coloration, scent marks) first come into secondary contact (15–17). Is interspecific territoriality merely a nuisance interaction that sometimes prevents species from coexisting? Or does it instead stabilize coexistence by conferring the same benefits that territoriality does within species? Based on its history of neglect in both ecology and evolutionary biology, one might infer the former, but research on this topic has surged in recent years, and the hypothesis that interspecific territoriality is usually adaptive is gaining traction (9, 18–21).

In theory, whether interspecific territoriality persists on an evolutionary timescale depends on several factors. If the species occupy distinctly different ecological niches, selection would ordinarily cause them to diverge in territorial signals and competitor recognition until interspecific territoriality is eliminated (22), an evolutionary process known as divergent agonistic character displacement (4, 9). Maladaptive interspecific territoriality could persist into the present, however, if secondary contact is too

recent for divergent agonistic character displacement to have occurred or selection has been too weak to overcome gene flow from allopatry (16, 17). Conversely, if the species occupy similar ecological niches and compete for common resources (e.g., food, nesting sites), interspecific territoriality could be maintained or evolve de novo through convergent agonistic character displacement, because partitioning space with competitors is adaptive (2, 9, 15, 23). The classic view is that adaptive interspecific territoriality should only persist when ecological character displacement is blocked by extrinsic barriers to niche divergence, such as structurally simple habitats (15). But interspecific territoriality itself causes spatial niche partitioning, which weakens selection for further niche divergence (24), and therefore could be an evolutionarily stable alternative to ecological character displacement (9). Interspecific mate competition arising from reproductive interference could also make interspecific territoriality adaptive if individuals that defend space against heterospecifics have higher reproductive success than those that do not (19, 25–27). The age of interacting lineages (i.e., time since the most recent common ancestor) also has an important bearing on the types of interspecific interactions likely to be observed (28). Maladaptive interspecific territoriality and adaptive interspecific territoriality maintained by interspecific mate competition should primarily be restricted to closely related species that are phenotypically similar owing to sharing a recent ancestor (29) (e.g., species belonging to

Significance

Historically, aggressive territorial interactions between members of different species have been dismissed as relatively rare occurrences and unimportant selective forces. We conducted the largest-ever comparative study of interspecific territorial behavior, amassing a dataset of all published observations of territorial aggression between species of North American perching birds. We found that interspecific territoriality is common, with individuals from nearly a third of all species defending territories against one or more other species. Contrary to the prevailing view, we also found abundant support for the hypothesis that interspecific territoriality is an adaptive response to resource competition and reproductive interference, not just a rare occurrence restricted to recently diverged lineages, and that interspecific territoriality constrains the evolutionary divergence of territorial signals.

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the same family). We would only expect to see interspecific territoriality between distantly related species if they compete for common limiting resources.

One way of tackling these questions is to take a comparative approach and ask which of the factors provided here helps explain why some species pairs are interspecifically territorial while others do not. Thus far, comparative studies of this sort have been relatively small in scale (18, 19, 28), and no previous studies have had sufficient phylogenetic depth to evaluate whether different types of interspecific territoriality prevail at different taxonomic or evolutionary time scales. We undertook the largest phylogenetic analysis of interspecific territoriality to date, amassing a database of 175 reports of interspecific territorial aggression in North American perching birds (Passeriformes). We focused on this taxon and geographic region primarily because of the rich literature on avian behavioral ecology and the availability of fine-scale biogeographical data (30). We searched all available sources and classified species pairs with multiple reported instances of territorial aggression as interspecifically territorial. We considered physical attacks, chases, agonistic displays, and territorial song directed at heterospecifics in the context of competition for space to be evidence of interspecific territorial aggression. Following previous authors, we did not consider aggression or dominance interactions observed solely in close proximity to food or nests to be evidence of territoriality (1, 18). To differentiate among the alternative explanations for interspecific territoriality listed here, we compiled data on the relevant predictor variables (*SI Appendix*, Table S1) and fit phylogenetic linear mixed models.

Results and Discussion

Interspecific Territoriality Is Widespread. In total, we identified 81 species pairs that engage in interspecific territoriality, involving a total of 104 species (32.3% of North American passerines; Fig. 1 and Dataset S1) (31), most of which ($n = 76$ species, or 73.1%) are interspecifically territorial with just one other species (range, 1 to 5 species; mean $\pm$ SD, 1.42 $\pm$ 0.83 species; $n = 104$). While most cases involve species from the same family ($n = 66$ species pairs, or 81.5%; 47 of which involve species from the same genus), a substantial number involve species from different families ($n = 15$ species pairs, or 18.5%). Interspecific territoriality was documented at from 1 to 8 locations per species pair (mean $\pm$ SD, 2.13 $\pm$ 1.77; $n = 81$) between 1914 and 2015. Field studies in which interspecific territoriality was documented ranged from 1 to 18 y in duration (mean $\pm$ SD, 4.06 $\pm$ 3.64 y; $n = 127$ studies), for a cumulative total of 516 study years.
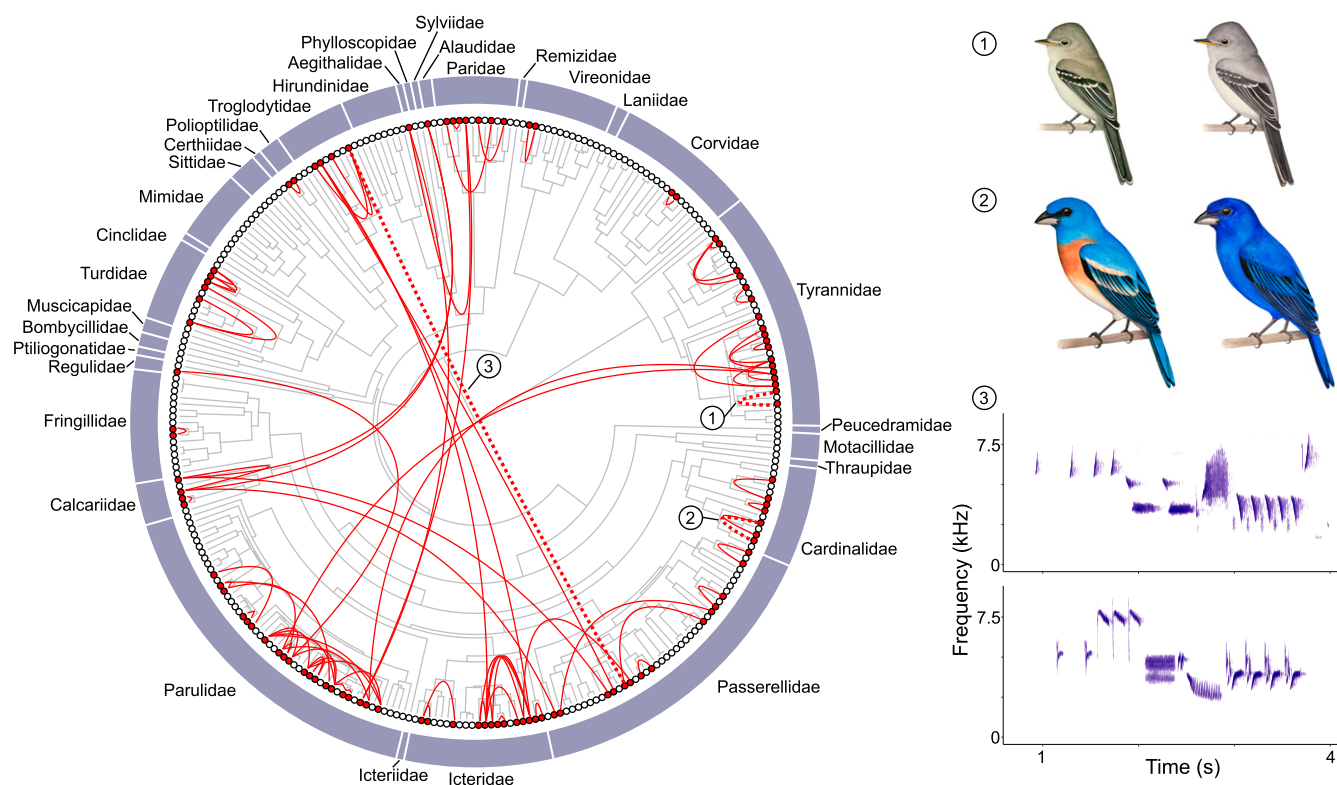
Interspecific Territoriality Is Not Simply a Maladaptive Consequence of Misidentification. Our results strongly implicate resource competition as a primary driver of interspecific territoriality (Fig. 2 and *SI Appendix*, Tables S2–S4). First, highly syntopic species, which overlap extensively in breeding habitat and therefore encounter each other frequently, are more likely to be interspecifically territorial than less syntopic species (Fig. 2 *A* and *D*). Second, species of similar mass (a common proxy for ecological similarity refs. 32 and 33) are more likely to engage in interspecific territoriality than species that differ more in mass (Fig. 2*B*). Third, species pairs in which both species nest in secondary tree cavities (i.e., cavities that they themselves do not excavate), which are often a limiting resource (34), are more likely to be interspecifically territorial than species that do not nest in tree cavities (Fig. 2*C*). Finally, in some cases, interspecific territoriality might be a response to nest predation rather than resource overlap. With nest-predating species removed from the analysis, foraging niche overlap joined the list of predictors of interspecific territoriality (*SI Appendix*, Table S5), further strengthening the evidence that interspecific territoriality is usually about resource competition.

We also found strong support for the hypothesis that interspecific territoriality is an adaptive response to interspecific mate competition (19, 25, 26). Hybridizing species were more likely to be interspecifically territorial than nonhybridizing species (Fig. 2*D*). The relationship between hybridization and interspecific territoriality exists even after controlling for phenotypic similarity and patristic distance, bolstering support for the hypothesis that reproductive interference, per se, promotes the evolutionary maintenance of interspecific territoriality. Moreover, a statistical interaction between syntopy and hybridization indicates that hybridizing species tend to be interspecifically territorial regardless of the degree of overlap in breeding habitat, while nonhybridizing species are much more likely to be interspecifically territorial if they are highly syntopic (Fig. 2*D* and *SI Appendix*, Tables S3 and S4). Therefore, hybridization is an important predictor of interspecific territoriality, even for species pairs with relatively low breeding habitat overlap. Together, these results suggest that interspecific territoriality in birds usually persists because of interspecific competition for mates, resources, or both, although nest predation might be a key factor in some cases (e.g., red-winged blackbirds and marsh wrens; Dataset S1).

Inter- versus Intrafamilial Interspecific Territorial Aggression. Passerine families generally represent distinct subclades (Fig. 1) of species that share a common suite of morphological, behavioral, and ecological characters that distinguish them from species in other families. We therefore carried out analyses to examine whether interspecific territoriality is predicted by different factors at the intra- and interfamily scales. With the analysis restricted to species in the same family (0.49 to 34.12 Ma; mean $\pm$ SD, 10.39 $\pm$ 4.76 Ma; $n = 712$; *SI Appendix*, Fig. S1), patristic distance and plumage dissimilarity emerged as predictors of interspecific territoriality; most cases of intrafamily, interspecific territoriality involve close relatives with similar plumage (Fig. 3 and *SI Appendix*, Tables S6 and S7A). If patristic distance and plumage dissimilarity were the only useful predictors, we could infer that interspecific territoriality among close relatives is a maladaptive by-product of similarity in territorial signals (16, 17). Instead, however, interspecific territoriality is also predicted by hybridization and several indicators of niche overlap and resource competition: high levels of syntopy, similar body sizes, the use of secondary tree cavities for nesting, and high overlap in foraging niche (Fig. 3*A* and *SI Appendix*, Table S7A). We also found an interaction between syntopy and hybridization qualitatively identical to the interaction found in our global analyses (*SI Appendix*, Fig. S2 and Tables S6 and S7A). Intrafamily, interspecific territoriality might often have arisen as a by-product of similarities between closely related species in plumage, but our results show that it is more likely to persist over evolutionary time when the species are actually in competition for resources other than space. It may be that interspecific territoriality is maintained by broad niche overlap in some cases, and by nest site competition, mate competition, or some combination of these factors in others.

In the case of interfamily species pairs (19.05 to 66.86 Ma; mean $\pm$ SD, 46.93 $\pm$ 18.60 Ma; $n = 906$; *SI Appendix*, Fig. S1), hybridization is not a factor because there are no interfamily hybrids and the only predictors of interspecific territoriality are song dissimilarity and syntopy (Fig. 3*C* and *SI Appendix*, Table S7B). Species that are more similar in territorial song and that overlap more in breeding habitat are more likely to be interspecifically territorial (Fig. 3*C*). Thus, once again, the results are in the direction predicted by the hypothesis that interspecific territoriality is an adaptive response to resource competition.

As an alternative approach, we split the species pairs according to their divergence times (<5 Ma, <10 Ma, >5 Ma, and >10 Ma; *SI Appendix*, Fig. S1). Among the youngest species pairs

Fig. 1. Interspecific territoriality is common and phylogenetically widespread among North American passerines, and occurs both within and between families. (*Left*) Phylogenetic network of interspecifically territorial species pairs in North American passerines (lines connect interspecifically territorial species). (*Top Right*) Two interspecifically territorial intrafamilial species pairs (1: dusky flycatcher [*Empidonax oberholseri*] and gray flycatcher [*Empidonax wrightii*]; 2: lazuli bunting [*Passerina amoena*] and indigo bunting [*Passerina cyanea*]). (*Bottom Right*) A spectrogram comparing songs of an interspecifically territorial interfamily species pair (3: song sparrow [*Melospiza melodica*] and Bewick's wren [*Thryomanes bewickii*]). Illustrations credit: Julie Johnson (artist).

(<5 Ma), patristic distance and syntopy are the only predictors of interspecific territoriality (*SI Appendix*, Table S8). Among the oldest species pairs (>10 Ma), syntopy and song similarity are the best predictors. In intermediate comparisons (>5 Ma or <10 Ma), interspecific territoriality is associated with plumage similarity, hybridization, and indices of resource competition (syntopy and mass; *SI Appendix*, Tables S8 and S9).

Conclusions

We found clear evidence that interspecific territoriality commonly arises between species as an adaptive response to competition. Within families, this competition can take the form of either resource competition or mate competition, whereas between families, interspecific territoriality arises largely in response to resource competition.

Our discovery that plumage and territorial song are associated with interspecific territoriality at different taxonomic and evolutionary time scales was not predicted by existing theory. A possible explanation is that song can evolve more rapidly than plumage (35) and can span larger phenotypic gaps between species. However, we did not find a pattern of plumage or song convergence in interspecifically territorial species pairs (*SI Appendix*, Tables S10–S12). We infer that most similarities between interspecifically territorial species are ancestral resemblances that have been maintained by selection. That is, the negative relationships we found between interspecific territoriality and species differences in plumage and song probably exist because ancestral similarities in territorial signals have been preserved by selection when interspecific territoriality is adaptive, and eroded through genetic drift and divergent character displacement processes otherwise. Nevertheless, a subset of interspecifically

territorial species pairs in our dataset could have converged in territorial signals to resemble each other more closely than their ancestors did without leaving a detectable signal of convergence at the clade level (36). Moreover, some species pairs might have evolved interspecific territoriality by converging in competitor recognition without converging in territorial signals. Indeed, several interspecific territorial species are rather dissimilar in plumage and territorial song (e.g., American robin and wood thrush). Exceptions in the other direction might be cases in which maladaptive interspecific aggression has been eliminated by divergence in competitor recognition based on preexisting species differences in plumage or song (e.g., Townsend's warbler and black-throated gray warbler).

We can definitively reject the hypothesis that adaptive interspecific territoriality is restricted to ecological scenarios in which niche divergence is constrained by structurally simple habitats, such as tundra and grassland (15) (*SI Appendix*, Tables S4 and S7). Although we did not test for other hypothesized constraints on niche divergence, such as fine-scale niche partitioning (15), our results thoroughly refute the view that avian interspecific territoriality is a rare and transient phenomenon (15–17).

Our results also refute the notion that interspecific territoriality is just a maladaptive by-product of intraspecific territoriality (16, 17). Certainly, in some cases, secondary contact might be too recent for the species to have evolved in response to each other, particularly if they rarely encounter each other during the breeding season. Our finding that hybridizing species tend to be interspecifically territorial regardless of the degree of overlap in breeding habitat could be viewed as evidence that some closely related species fall into that category, although competition for mates is another viable explanation for the persistence of

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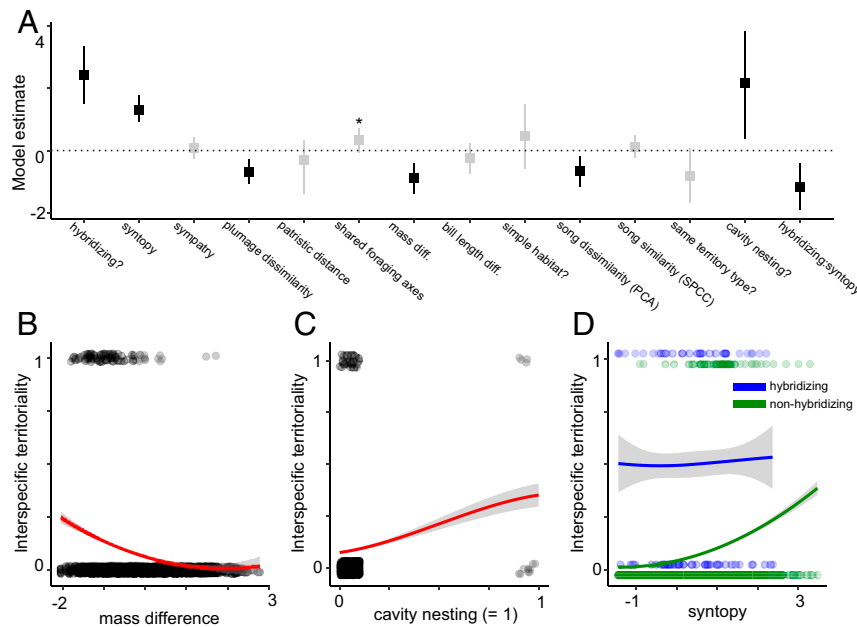
Fig. 2. Resource competition and reproductive interference predict interspecific territoriality in North American passerines. (*A*) Coefficient estimates from a logistic regression (phylogenetic generalized linear mixed model) of interspecific territoriality, from a best-fit model including interaction terms (*SI Appendix*, Table S4; *n* = 1,616 species pairs, of which 79 are interspecifically territorial). Points correspond to the median and error bars represent the 95% credibility interval from four combined MCMC chains. Black points indicate fixed effects with estimates whose 95% credibility intervals do not include 0. Plots in *B–D* show how the probability of species being interspecifically territorial varies with mass dissimilarity, secondary cavity nesting, syntopy, and hybridization. In *D*, hybridizing species pairs (blue) are more likely to be interspecifically territorial at all levels of syntopy, but nonhybridizing species pairs (green) are more likely to engage in interspecific territoriality when they overlap broadly in breeding habitat. When two nest-predating species were removed from the analysis, the proportion of shared foraging axes also emerged as a predictor of interspecific territoriality (*SI Appendix*, Table S5; indicated by an asterisk). In plots in *B–D*, the plotted lines are loess-smoothed model predictions, with shading representing the SE; the points are jittered to aid visualization.
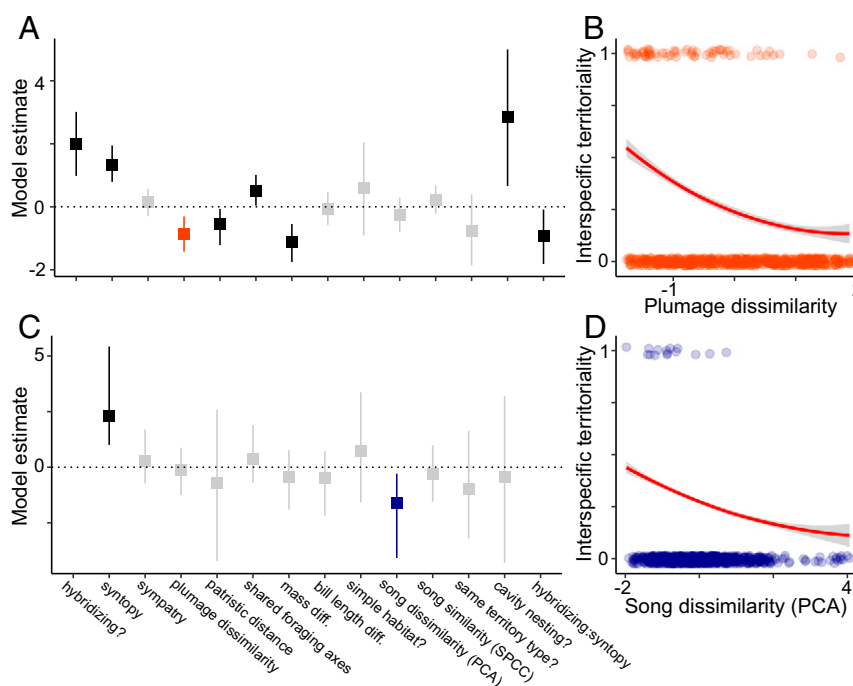
interspecific territorial aggression between species that do not compete ecologically (19, 25–27). In any case, our results clearly establish that the predominant pattern in North American passerines is that interspecific territoriality is positively associated with overlap in breeding habitat and other indices of resource competition.

Our analyses treat interspecific territoriality as a dichotomous variable, but in reality, interspecific aggression varies both within and among species pairs. For instance, Bewick's wrens and house wrens defend nonoverlapping territories at many locations (see references in Dataset S1), but one study found extensive territory overlap and little interspecific aggression (37), which suggests that interspecific territoriality is facultative in this species pair. Unfortunately, although North American birds are well-studied relative to many animal taxa, published behavioral observations are too sparse to quantify fine-scale variation in the strength or frequency of interspecific territoriality for all species pairs, which would be necessary in a comparative study such as ours. Future studies focused on understanding why interspecific territoriality is facultative in the wrens and other species pairs could be quite valuable. Another shortcoming of the existing literature, and consequently of our study, is that information on asymmetries in aggression and dominance between species is not consistently available. Such asymmetries can have important ecological consequences (38, 39), and may affect how species evolve in response to each other (13, 14, 40). Species also vary considerably in the specificity of aggression toward heterospecifics: some species are notoriously indiscriminate (41). The effect of such asymmetries on the evolution of interspecific territoriality remains an open question for further study.

On a methodological note, sympatry (coarse-scale geographic overlap) is much more commonly used as a proxy for species interactions (42) than syntopy (fine-scale geographic overlap), as

sympatry can be measured from species range maps while syntopy requires much more fine-grained spatial data (*Methods*). In principle, however, syntopy is a better index of niche overlap and interspecific encounter rates than sympatry, and our analyses bear that out, at least for interspecific territoriality (syntopy was predictive of interspecific territoriality in every model that we fit while sympatry never was). Syntopy would probably be a better metric than sympatry for predicting other types of species interactions as well, and is likely to be a viable option, as fine-grained spatial data are becoming increasingly available for many taxonomic groups.

While abundant evidence suggests that competition between species is important at local spatial scales and shallow timescales, investigators have only recently begun to model the evolutionary impacts of species interactions using analytical tools that combine ecological data with information on the shared evolutionary history of interacting species (43, 44). Previously, studies conducted at deep timescales largely focused on resource competition between species (45–47). Yet a large body of research conducted at shallower timescales demonstrates that behavioral interference, such as interspecific aggression and reproductive interference, also influences trait evolution and range dynamics (4, 48). Our work demonstrates that behavioral interference can impact patterns that emerge at deep timescales and fundamentally alter the trajectory of trait diversification in an evolving clade. Overall, given the key role that aggressive and reproductive interference can play in ecological and evolutionary outcomes in dynamic assemblages (4), our results suggest that accounting for behavioral interactions between species (e.g., in models of range shifts resulting from climate change) is paramount for adequately capturing the ecological and evolutionary dynamics of animal communities.

Fig. 3. Different factors mediate interspecific territoriality between species of the same family. (*A* and *B*) and different families (*C* and *D*). (*A*) Coefficient estimates from a logistic regression phylogenetic linear mixed model of interspecific territoriality, restricted to members of the same family (*SI Appendix*, Table S7A; n = 710 species pairs, of which 64 are interspecifically territorial). (*B*) In intrafamilial comparisons, interspecific territoriality is more likely between species with similar plumage. (*C*) Coefficient estimates from a logistic regression phylogenetic linear mixed model of interspecific territoriality, restricted to members of different families (*SI Appendix*, Table S7B; n = 906 species pairs, of which 15 are interspecifically territorial). (*D*) In interfamilial comparisons, interspecific territoriality is more likely between species with similar songs. In plots in *A* and *C*, points correspond to the median and error bars represent the 95% credibility interval from four combined MCMC chains. Black points (and points with color) indicate fixed effects with estimates whose 95% credibility intervals do not include 0. In plots in *B* and *D*, the plotted lines are loess-smoothed model predictions, with shading representing the SE, and the points are jittered vertically to aid visualization.

Materials and Methods

Interspecifically Territorial Species Pairs. We searched exhaustively for reports of interspecific territoriality involving passerines that breed in the United States and Canada, starting with the Birds of North America (BNA) species accounts (49). We attempted to verify observations in the BNA by consulting the cited literature or contacting BNA authors. We also searched Web of Science, Zoological Record, Current Contents, BIOSIS (Thomson Reuters, New York, NY), Google Scholar (https://scholar.google.com), and Proquest (https://search.proquest.com/) for information on aggression and territoriality in North American passerines. We conducted the initial literature search by species, using all current and past scientific names and English common names found in the BNA or Avibase (50). When we found evidence of interspecific territoriality, we searched for other papers in which both species were mentioned. As explained in greater detail in the Introduction, we classified species as interspecific territoriality if we found multiple reported instances of territorial aggression between them. Interspecific territoriality might be facultative or geographically variable in some species pairs, but the currently available data are too sparse to classify most species pairs in those ways.

Noninterspecifically Territorial Species Pairs. To obtain a comparison group of noninterspecifically territorial species, we used the North American Breeding Bird Survey (BBS) 10-stop dataset (30) to determine which potentially interacting species of birds were present at the locations and during the periods of the studies in which interspecific territoriality was documented. Following ref. 18, we assumed that researchers studying interspecific territoriality would have reported interspecific aggression between their study species and other species present at the same study sites, had they observed it.

At each study site, we found the 20 closest BBS routes that were run within ±5 y of the end of the study (or the first 10 y of the BBS, if the study was completed before 1966). Within those routes and years, we selected up to three routes where both focal species were observed and created a list of "potential interactor" species for the site. We considered potential interactor species to include those in the focal species' family or any family documented to be interspecifically territorial with a species in the focal

species' family. The final list of noninterspecifically territorial species pairs consists of all species pairs that include a focal species (i.e., a species that was observed engaging in interspecific territoriality) and a species on the list of potential interactors for the same study sites.

Sympatry Measurements. We estimated the degree of sympatry (breeding range overlap) for each species pair, using data from three different sources, and combined them into a single estimate. First, we obtained digital species range maps (i.e., shapefiles) from BirdLife International (51) and estimated sympatry as the area of breeding range overlap divided by the breeding range area of the species with the smaller breeding range (i.e., the Szymkiewicz-Simpson coefficient). All 1,618 species pairs in our dataset should have nonzero sympatry estimates because they were found on the same BBS routes. However, the range maps of eight species pairs did not overlap and nine species pairs included a species that was not recognized by BirdLife International (all of the species are currently recognized by the American Ornithological Society). Therefore, we also obtained Szymkiewicz-Simpson estimates of sympatry from the BBS and eBird (52) datasets. We downloaded BBS 10-stop data for the United States and Canada in April 2018 (30) and, using an R script, cycled through the species pairs and routes, counting the number of runs with both species and dividing this by the number of runs with the species observed on the fewest routes. We used the mean of this ratio across routes as the sympatry estimate. We downloaded data for the United States and Canada from eBird.org in April 2018. We considered an eBird observation to be in the zone of sympatry if it was made within the length of one BBS route (39,428 m) from an observation of the other species in the same year and during the peak breeding months of both species (see *Other Data Collected from the Literature*). We cycled through the species pairs and years, counting the number of observations in sympatry and dividing by the number of observations of the species found on the fewest BBS routes (i.e., the species with the smaller range), after removing observations made outside the peak breeding season and reducing observations within 70 m of each other in the same year to a single observation (to minimize the influence of cases in which individual rare birds were

recorded by multiple eBird users; ref. 52). We then averaged the values across years to obtain the sympatry estimate. The three sympatry estimates were strongly positively correlated (BBS vs. Birdlife, $r = 0.77$; eBird vs. Birdlife, $r = 0.62$; eBird vs. BBS, $r = 0.79$; all $P < 0.0001$). We combined them into a single estimate by first scaling them using z-transformations (mean = 0; SD = 1), calculating the mean of these rescaled values, and then rescaling the mean values to the original scale and range of the nonzero Birdlife sympatry estimates.

Syntopy Measurements. Although range-wide sympatry is often used as a proxy for the potential for species interactions, fine-scale co-occurrence (syntopy) is likely a much more meaningful predictor of the potential for species interactions (18). To obtain regional measures of syntopy for each species pair, we used the BBS 50-stop data (30), identifying BBS routes where both species were observed within 250 km of the site where interspecific territoriality was reported. On each such route, we divided the number of stops where both species were observed by the number of stops where either species was observed and used the mean across all shared routes as the estimate of syntopy. This method worked for 1,581 species pairs. For the remaining 37 species pairs, we obtained continental estimates of syntopy and used linear regression to replace the missing regional syntopy estimates with rescaled continental syntopy estimates. As described here, our species pair list is based on the species found on the three BBS routes nearest the sites where interspecific territoriality was reported within the time frame (± 5 y) of the corresponding studies, using the BBS 10-stop data, which are available for the duration of the BBS (1966 to present). However, our regional syntopy estimates required the full-resolution BBS 50-stop data, which generally are not available before 1997. Thirty-seven of the 1,618 species pairs were not found on a BBS route within 250 km of the corresponding interspecific territoriality study sites in the 50-stop data, and consequently could not be assigned a regional syntopy value. Our solution was to obtain continental syntopy estimates for every species pair and to replace the missing regional estimates with predicted values based on the continental estimates. We obtained continental syntopy estimates from the 50-stop data by dropping the 250-km restriction, but this still left six species pairs without syntopy estimates (i.e., these species were not found together on the same BBS routes after 1996). Therefore, we also obtained syntopy estimates using data from eBird.org, while retaining our BBS-based operational definitions of syntopy (402 m, the nominal search radius at a BBS stop) and sympatry (39,428 m, the length of a BBS route). As with the sympatry estimates, we filtered the eBird data to include only the peak breeding months (see *Other Data Collected from the Literature*) and to remove redundant observations. We then divided the number of observations in syntopy by the total number of observations of either species in sympatry in each year, and averaged the values across years to obtain syntopy estimates for each species pair. We replaced 31 missing regional BBS syntopy estimates with predicted values from the regression of log(BBS regional syntopy+0.01) on log(BBS continental syntopy+0.01) (adjusted $R^2 = 0.66$; $P < 0.001$). The remaining 6 missing regional syntopy estimates were replaced with predicted values from the regression of log(BBS regional syntopy+0.01) on eBird syntopy (adj. $R^2 = 0.37$; $P < 0.001$). It was not possible to estimate syntopy for two interspecifically species pairs (Woodhouse's scrub-jay/California scrub-jay and black-tailed gnatcatcher/California gnatcatcher), so these pairs were removed from all analyses.

Intraspecific Territoriality. We used the BNA species accounts as our primary source for classifying the type of territoriality exhibited by a species, and consulted the primary literature as needed to clarify ambiguous cases. The territory type categories that we recognized, and their correspondence to Nice's (53) classic categories (type A, B, C, etc.), are nonterritorial, including species in which males defend the area immediately around females (i.e., mate defense without territoriality); mating territory, lekking species (type C);, nesting territory, colonial breeding species (type D); mating and nesting territory, defense centered around the nest, but of an area larger than the nest site, most foraging occurs elsewhere (type B); and multipurpose breeding territory, used for mating, nesting, and feeding, and includes general site-specific dominance without clearly defined territory boundaries (type A).

All but four of the 197 species in this dataset have intraspecific territories. Most species (82.7%) have multipurpose breeding territories, but mating and nesting territories are also common (10.7%). Only one species has mating territories, and nesting territories are also uncommon in this clade (4.1%). We tested whether sympatric species that defend the same type of territory are likelier to be interspecifically territorial.

Plumage Dissimilarity. We recruited volunteers to quantify the pairwise dissimilarity of the plumages of the species pairs in our study by creating online comparison sets in which volunteers scored the magnitude of difference (i.e., dissimilarity) between illustrations of the two species. We compiled scanned images of males from two field guides (54, 55) into different comparison sets with 35 to 40 species comparisons per set, using Survey Gizmo (https://www.surveygizmo.com/). For each species comparison, participants were presented with a pair of images of males from the same field guide and asked to rate the overall dissimilarity of the plumage of the two images using a 0 to 4 scale. The order of the comparisons was randomized for each participant, and other precautions were taken to avoid systematic biases. Each set of images was scored by an average of 9.1 people (range, 6 to 61). For each species pair, we calculated the mean difference score across all available rankings, and this served as our index of plumage dissimilarity. This project did not meet the criteria for requiring institutional review board approval, since humans are not the subject of our research, but rather, volunteer participants in data collection.

To distribute the comparison sets, we advertised them through social networking platforms and through University of California, Los Angeles, classrooms. We included a test for color blindness and removed the responses of participants who failed the test. We also tested for effects of the order of the pairs of images in the set, the field guide from which the images came, and the identity of the set in which the pair of images appeared. To quantify these influences, in each set, we included the same species pair from the same field guide as the first and last questions; for a different species pair, pairs of images from both field guides within a comparison set; and a pair of images from one of the other sets. In each case, we found that respondents provided similar scores, regardless of position in the comparison set (Spearman correlation between score when presented first vs. last, $\rho = 0.91$; N = 76), the illustration source ($\rho = 0.77$; N = 76), and the identity of the comparison set ($\rho = 0.87$; N = 76).

Song Similarity and Dissimilarity. We selected high-quality sound files from xeno-canto.org or the Macaulay library for each species in our dataset (Dataset S2), within or as close as possible to the region where interspecific territorial behavior was observed (for interspecific territoriality species) and with as little background noise as possible. Based on descriptions in the BNA, species were classified as having small (fewer than 4 song types per individual) or large (4 or more song types) repertoires. For species with small repertoires, two sound files were collected; for species with large repertoires, four sound files were collected. Sound files were selected to match descriptions in the BNA of the species' territorial vocalizations.

For each sound file, one song was selected, edited, and converted into a 16-bit WAV file. A "song" is defined as a vocalization that includes tonal elements, exceeds 0.5 s in duration, and is preceded and followed by intervals greater than 1 s (56), unless otherwise specified in the BNA, such as if a bout of calls is used for territorial displays instead of songs (e.g., corvids use calls instead of songs for territorial displays). We edited each song by reducing noise in Audacity version 2.1.3 (https://www.audacityteam.org/), using starting values of noise reduction = 12, sensitivity = 6, and frequency smoothing = 0, setting sampling to 44,100 Hz. After all sound files were edited, they were normalized together to a peak amplitude of -1 dB.

The start and stop times of each note within the file were manually detected with the R package warbleR (57). Notes separated by less than 10 ms were treated as one note (56). Acoustic parameters were extracted using functions in warbleR, and additional parameters were calculated as in ref. 56. We then averaged the acoustic parameters across song files for each species and conducted a principal component analysis on these averaged parameters. We then calculated the Euclidean distance between all principal component axes as a measure of song dissimilarity between species.

Finally, we used the warbleR package to conduct spectral cross-correlation analysis (58) of all song files. This method compares time slices of two song files and returns the maximum correlation between the frequency-time structures of the files. We performed this analysis on all song files for each species pair, and then averaged the maximum cross-correlations as a measure of song similarity between species.

Song dissimilarity (principal component analysis) and song similarity (spectral cross-correlation) were only moderately negatively correlated (Spearman's $\rho = -0.40$; $P < 0.001$), indicating that they each contain nonredundant information about pairwise song similarity.

Other Data Collected from the Literature. We obtained species mean mass values from refs. 59 and 60, using midsex means, where data for both sexes were available. In the case of geographically variable species, we selected mean mass values closest to the locations where interspecific territoriality

was documented. We obtained species mean male bill lengths from refs. 49, 61, and 62. Since bill lengths are measured in multiple ways, we used linear regressions based on the subset of species with multiple types of measurements to convert the mean bill lengths of all species to the "exposed culmen" measurement scale (exposed culmen vs. skull-to-tip, adjusted $R^2 = 0.99$ [$P < 0.001$; $df = 144$]; exposed culmen vs. nares-to-tip, adjusted $R^2 = 0.99$ [$P < 0.001$; $df = 59$]).

We obtained data on peak breeding months and whether species nest in cavities from the BNA. We used de Graaf's (63) method for classifying foraging guilds on three axes (food type, foraging substrate, and foraging technique) and calculated the proportion of overlap across the axes for each species pair as an index of foraging niche overlap. Following ref. 18, we used the BNA habitat descriptions to assign each species a habitat complexity score on a three-point scale: 1, simple (e.g., tundra, grassland); 2, intermediate (e.g., chaparral, forest edge); and 3, complex (forest). The rationale for this habitat classification is that forests offer more opportunities for vertical stratification of niches, which has long been considered to be relevant for avian territoriality (15, 64).

We determined whether species pairs in our dataset hybridize from ref. 65 and by searching the literature for hybridization reports since 2000. We disregarded hybridization in captivity and doubtful, unsubstantiated reports of hybridization in the wild (65).

Phylogeny. We obtained a time-calibrated phylogeny of the species in our study from birdtree.org (66, 67), downloading a posterior distribution of 1,000 trees and obtaining the maximum-clade credibility tree in TreeAnnotator v1.8.4 (68). We added three species to the phylogeny for three cases in which lineages from the birdtree.org phylogeny were split into two unique species that both breed in North America [*Troglodytes troglodytes* split into *T. pacificus* and *T. hiemalis* (69); *Aphelocoma californica*, split into *A. californica* and *A. woodhouseii* (70); and *Amphispiza belli* split into *Artemisiospiza belli* and *A. nevadensis* (71)]. We then calculated patristic distance (the branch length separating two species in the phylogeny; i.e., two times the amount of time separating each species from their common ancestor) between species from this phylogeny, using the R package ape (72).

Statistical Analyses. Our dataset is structured similarly to an interaction network, with interspecific territoriality providing links between species (Fig. 1), analogous to networks of plants and their pollinators or other similar multitrophic interaction networks (73–76). As with several previous evolutionary analyses of networks (75, 76), we used phylogenetic linear mixed models (PLMMs) (77, 78) adapted for analyses of species interaction (20, 42), since our dataset is pairwise in nature (i.e., the data are species comparisons, rather than tip values). We fit PLMMs with interspecific territoriality as a categorical response variable to identify predictors of interspecific territoriality using the R package MCMCglmm (79). As described previously (18, 20), we included the species identifiers and the phylogeny as random effects, specifying the nodes in the phylogeny representing the most recent common ancestor of the species in a pair. These models were originally adapted from animal models used in quantitative genetics to estimate heritability of traits (78), and, similar to other phylogenetic regressions (80), statistically account for the phylogenetic nonindependence of

model residuals. The influence of the phylogeny can be estimated from the random effect component of the PLMM, the phylogenetic intraclass correlation coefficient is identical to the λ parameter (often referred to as phylogenetic signal) estimated from phylogenetic generalized least squares models (81). We used an uninformative, inverse Wishart distribution as a prior distribution for the random effects, and fixed the residual variance at 1. For the fixed effects, we used a flat prior (82). To fit the model, we ran an MCMC chain for at least 2×10^6 generations, recording model results every 10^3 generations and ignoring the first 2×10^4 generations as burn-in (in some cases, 10^7 generations were required to achieve convergence). We fit each model four times and merged the four chains after verifying convergence using Gelman-Rubin diagnostics in the R-package coda (83, 84). We also visually inspected trace plots for each model to verify model convergence. To facilitate parameter exploration and standardize regression coefficients, we transformed several continuous predictor variables (*SI Appendix*, Table S2) and rescaled all continuous fixed effects using *z*-transformations.

Testing for Evolutionary Convergence in Territorial Signals. To test for territorial signal convergence among interspecific territoriality species pairs, we fit PLMMs with song or plumage dissimilarity as the dependent variable (42). We reasoned that if convergence has occurred as an adaptive response to resource and mate competition, interspecific territoriality species that compete more intensely for resources (or mates) should be more similar in territorial signals than interspecific territoriality species experiencing relatively lower amounts of competition. That is, the magnitude of convergence should scale with the magnitude of competition in interspecific territoriality species pairs. Noninterspecific territoriality species pairs, in contrast, should not exhibit any particular relationship between signal dissimilarity and resource competition. With plumage dissimilarity as the dependent variable, we restricted the analysis to confamilial species pairs and tested for interactions between interspecific territoriality and our indices of reproductive interference and resource overlap. In addition, to test for convergence in plumage caused by interspecific competition for resources other than mates and secondary cavity nest sites, we removed hybridizing and cavity nesting species pairs and repeated this analysis. With song dissimilarity as the dependent variable, we restricted the analysis to interfamily species pairs and tested for interactions between interspecific territoriality and resource overlap indices (there are no interfamily hybrids or interfamily interspecific territoriality species pairs that both nest in cavities in our dataset).

Data & Code Availability. All data and code are available at https://github.com/jonathanpdrury/intersp_territoriality_in_passerines.

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