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Authors

Losin, Neil
Drury, Jonathan P
Peiman, Kathryn S
et al.

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The ecological and evolutionary stability of interspecific territoriality

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A singing male yellow-rumped warbler, a species that is interspecifically territorial in parts of its range with the congeneric black-throated green warbler.
251x325mm (300 x 300 DPI)

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60

1 **The ecological and evolutionary stability of interspecific territoriality**

2 Neil Losin¹, Jonathan P. Drury^{1,2}, Kathryn S. Peiman^{1,3}, Chaya Storch¹, Gregory F. Grether^{1*}

3
4 ¹Department of Ecology and Evolutionary Biology, 621 Charles E. Young Drive South,
5 University of California, Los Angeles, CA 90095-1606, USA

6 ²Current address: Institut de Biologie de l'ENS, 46 Rue d'Ulm, 75005 Paris, France

7 ³Current address: Department of Biology, Carleton University, Ottawa, Canada K1S 5B6

8 *Correspondence to: ggrether@ucla.edu, telephone (310-794-9769), fax (310-206-3987)

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12 displacement, convergence, niche conservatism, syntopy, phylogenetic, birds, Parulidae

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1
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3 **23 Abstract**
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5 24 Interspecific territoriality may play an important role in structuring ecological communities, but
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8 25 the causes of this widespread form of interference competition remain poorly understood. Here
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10 26 we investigate the phenotypic, ecological and phylogenetic correlates of interspecific
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12 27 territoriality in wood-warblers (Parulidae). Interspecifically territorial species have more recent
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15 28 common ancestors and are more similar phenotypically, and are more likely to hybridize, than
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17 29 sympatric, non-interspecifically territorial species. After phylogenetic corrections, however,
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20 30 similarity in plumage and territorial song are the only significant predictors of interspecific
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22 31 territoriality besides syntopy (fine-scale geographic overlap). Our results do not support the
23
24 32 longstanding hypothesis that interspecific territoriality occurs only under circumstances in which
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27 33 niche divergence is restricted, which combined with the high incidence of interspecific
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29 34 territoriality in wood-warblers (39% of species), suggests that this interspecific interaction is
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32 35 more stable, ecologically and evolutionarily, than commonly assumed.
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37 INTRODUCTION

38 Territoriality is a widespread behavioral tactic for partitioning space and defending food sources,
39 mates, and other resources (Maher & Lott 2000). Territorial signals, such as scent marks,
40 vocalizations, visual displays and distinctive colors, enable animals to identify potential rivals,
41 communicate about territory boundaries from a distance, and avoid unnecessary and costly fights
42 (Logue *et al.* 2010). When formerly allopatric species with similar territorial signals first come
43 into contact, interspecific territoriality, i.e., defense of space against individuals of other species,
44 can arise as a non-adaptive byproduct of intraspecific territoriality (Orians & Willson 1964;
45 Murray 1981). But territorial aggression is costly and thus selection is expected to favor
46 divergence in territorial signals and refinements in competitor recognition (i.e., divergent
47 agonistic character displacement) until interspecific territoriality is eliminated, unless the
48 benefits of excluding heterospecifics exceed the costs for at least one of the species (Orians &
49 Willson 1964; Grether *et al.* 2009).

50 Whether the conditions under which interspecific territoriality is evolutionarily stable are
51 common or rare is a longstanding, unresolved issue. Orians & Willson (1964) reasoned that
52 interspecific territoriality ought to persist only between species that compete for resources that
53 cannot be partitioned, because otherwise the species would be expected to diverge in ways that
54 reduce resource overlap (i.e., ecological character displacement), making interspecific territory
55 defense unprofitable. But interspecific territoriality itself is a mechanism of spatial habitat
56 partitioning that may pre-empt ecological character displacement and enable species with similar
57 ecological requirements to coexist (Robinson & Terborgh 1995; Grether *et al.* 2013).
58 Interspecific territoriality may also be adaptive when closely related species interfere with each
59 other reproductively, and are, in effect, competing for mates (Drury *et al.* 2015). If selection can

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3 60 maintain interspecific territoriality in cases of secondary contact between species that (still)
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5 61 recognize each other as competitors, it should also be possible for interspecific territoriality to
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8 62 evolve *de novo*, or be reinforced, through changes in competitor recognition functions or
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10 63 convergence in territorial signals (Cody 1973; Grether *et al.* 2009; Tobias & Seddon 2009; Drury
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13 64 *et al.* 2015; Reif *et al.* 2015).

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15 65 Murray (1981) argued that nearly all putative cases of adaptive interspecific territoriality
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17 66 could be better explained as misdirected intraspecific territoriality between species that rarely
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20 67 encounter each other, that only recently came into contact, or that coexist only in narrow contact
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22 68 zones, and variants of this hypothesis have been invoked to explain interspecific aggression in
23
24 69 numerous taxa (Grether *et al.* 2009; Peiman & Robinson 2010; Ord *et al.* 2011). The crux of
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26
27 70 Murray's (1981) argument is that species that overlap sufficiently in resource use for
28
29 71 interspecific territoriality to be adaptive would not be able to coexist. However, models of
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31 72 interspecific territoriality have shown that high levels of niche overlap are not required for
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34 73 interspecific territoriality to be adaptive (Cody 1973; Grether *et al.* 2009).

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36 74 The key ecological question, then, is whether interspecific territoriality mediates stable
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38 75 competitive interactions between species, potentially increasing species richness by allowing
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40 76 species with similar requirements to coexist (Robinson & Terborgh 1995), or instead is merely a
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43 77 temporary byproduct of recent secondary contact (Murray 1981). Here we take an empirical
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46 78 approach to the problem and ask which factors best predict interspecific territoriality in an avian
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48 79 clade with a well-resolved phylogeny.

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50 80 The wood-warblers (Parulidae) represent a recent radiation with extensive post-speciation
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52 81 range overlap (Lovette & Hochachka 2006; Lovette *et al.* 2010). Unlike *Anolis* lizards and other
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55 82 taxa that show rapid niche differentiation (Glor *et al.* 2003), the wood-warblers exhibit
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3 83 phylogenetic niche conservatism and sympatric species often occupy very similar ecological
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5 84 niches (Lovette & Hochachka 2006). Despite early reports of fine-scale niche partitioning in
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8 85 wood-warblers (MacArthur 1958), this does not appear to be common; the species composition
9
10 86 of local communities varies considerably, and seasonal migration and low natal philopatry may
11
12 87 prevent foraging niches from evolving to match local species assemblages (Lovette &
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14 88 Hochachka 2006). The combination of high levels of sympatry and variable levels of niche
15
16 89 overlap make the wood-warblers a suitable group for testing alternative models of interspecific
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18 90 territoriality.

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22 91 Based on the hypothesis that interspecific territoriality evolves or persists under
23
24 92 ecological circumstances in which niche partitioning is constrained, Orians & Willson (1964)
25
26 93 predicted that it should primarily be found in birds that breed in structurally simple habitats, such
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28 94 as marshes or grasslands, or among species with highly specialized feeding niches, such as
29
30 95 nectarivory. To test these predictions, and the more general prediction that interspecific
31
32 96 territoriality is related to niche overlap, we gathered data from the literature on habitat
33
34 97 complexity, body size, bill length, and foraging guild, and we used the North American Breeding
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36 98 Bird Survey (Sauer et al. 2012) to measure the degree to which species are syntopic (i.e., occur
37
38 99 in the same habitats and localities; Rivas 1964). The hypothesis that interspecific territoriality
39
40 100 evolves in response to resource competition through convergence in territorial signals (Cody
41
42 101 1973) and the alternative hypothesis that interspecific territoriality is a non-adaptive byproduct of
43
44 102 overlap in territorial signals (Murray 1981) both predict that interspecifically territorial species
45
46 103 pairs should overlap more in territorial signals than non-interspecifically territorial species pairs,
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48 104 but only the convergence hypothesis predicts that this should remain so after controlling for
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50 105 phylogenetic relationships. To test these predictions, we measured species differences in male
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3 106 plumage coloration and territorial song. To test the hypothesis that reproductive interference
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5 107 promotes interspecific territoriality (Drury *et al.* 2015), we examined whether interspecific
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8 108 territoriality is associated with hybridization.
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10 109 Under all hypotheses above, interspecifically territorial species are predicted to be more
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12 110 closely related, on average, than sympatric non-interspecifically territorial species, because
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14 111 closely related species have had less time to diverge in traits that affect resource use, competitor
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16 112 recognition, and mate recognition. However, if interspecific territoriality evolves or persists
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18 113 because of resource competition, similarity in traits that affect resource exploitation (e.g., body
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20 114 size, bill length, foraging guild, habitat use) should be a better predictor of interspecific
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22 115 territoriality than phylogenetic distance (Orians & Willson 1964; Cody 1973). By contrast, if
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24 116 interspecific territoriality is a non-adaptive byproduct of overlap in territorial signals (Murray
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26 117 1981) or an adaptive response to reproductive interference (Drury *et al.* 2015), interspecifically
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28 118 territorial species pairs are predicted to be no more similar in such ecological traits than are non-
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30 119 interspecifically territorial species pairs, after controlling for phylogenetic relationships. Thus, by
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32 120 taking phylogenetic relationships into account, we address a longstanding debate about the
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34 121 adaptive significance of interspecific territoriality.
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40 122 To our knowledge, this is the first phylogenetically based analysis of the distribution of
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42 123 interspecific territoriality in any clade. We found that interspecific territoriality is quite common
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44 124 and does not just occur under restricted ecological circumstances. Moreover, this study provides
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46 125 the first phylogenetic evidence that similarity in territorial signals is linked to interspecific
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48 126 territoriality.
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55 128 **METHODS**
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6 130 **General approach**

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8 131 Even in North American birds, it cannot be assumed that all cases of interspecific territoriality
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10 132 have been reported. To make the best use of the information available, our approach was to
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12 133 compare known interspecifically territorial (IT) species pairs to other sympatric species pairs that
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14 134 can confidently be classified as non-interspecifically territorial (non-IT). Below we explain in
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16 135 detail how we made these determinations.
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22 137 **IT species pairs**

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24 138 We searched for reports of interspecific territorial aggression involving wood-warblers using the
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26 139 Birds of North America Online (BNA; Poole 2005), Web of Science, BIOSIS and Zoological
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28 140 Record databases (Thomson Reuters, New York, NY). We considered chases, attacks, aggressive
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30 141 displays and songs directed at heterospecifics to be interspecific territorial aggression, unless
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32 142 they occurred exclusively in the immediate vicinity of food or nests. We did not consider nest
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34 143 defense and dominance interactions in foraging aggregations to be territorial aggression. Some
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36 144 authors restrict the term interspecific territoriality to cases in which the species defend exclusive,
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38 145 non-overlapping territories. In this paper, we consider territorial aggression between species to
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40 146 be interspecific territoriality, whether it results in exclusive space use or not. Our threshold for
41
42 147 classifying a species pair as interspecifically territorial is that multiple occurrences of territorial
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44 148 aggression were reported in a single study. In many cases, additional supporting evidence is
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46 149 available from playback experiments, removal experiments, and territory mapping studies (see
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48 150 Table S1). However, because these additional types of evidence were not available for all species
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50 151 pairs, we did not use them as criteria for inclusion or exclusion.
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3 152 To evaluate whether it is likely that there are many unreported cases of interspecific
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6 153 territoriality in North American wood-warblers, we carried out a simple research effort analysis
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8 154 by tallying up the total number of published papers on each species. We searched Zoological
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10 155 Record using each species' current and previous scientific names and used logistic regression to
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12 156 assess whether the probability of a species being reported to be interspecifically territorial
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15 157 increases with the number of studies.
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19 20 159 **Non-IT species pairs**

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22 160 Because most cases of interspecific territoriality involving wood-warblers are between two
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24 161 species of wood-warblers (see Table S1 in Supporting Information), including a taxonomically
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27 162 wider range of non-IT species pairs in the analysis would not be informative. We therefore
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29 163 limited all of our analyses to comparisons between sympatric species within this monophyletic
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31 164 group (Lovette *et al.* 2010). To ensure that only truly non-IT species pairs were included, we
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34 165 further restricted the analysis to species pairs that include one of the IT species and which occur
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36 166 in the area where interspecific territoriality was reported. The logic behind this criterion is that
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38 167 other cases of interspecific territoriality involving the same species in the same area would likely
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40 168 have been reported, but it would not be reasonable to assume that all cases of interspecific
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43 169 territoriality among wood-warblers in the same area (or elsewhere) have been reported. Based on
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46 170 these criteria, we identified 286 non-IT species pairs.
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48 171 To create the list of non-IT species pairs, we used the North American Breeding Bird
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50 172 Survey (BBS; Sauer *et al.* 2012). At each location where interspecific territoriality was reported,
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53 173 we found the 20 closest BBS routes that were run within ± 5 years of the conclusion of the study.
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55 174 Within these BBS routes and years, we restricted our search to routes on which both focal
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3 175 species were found and used up to three of the routes closest to the study location to generate a
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5 176 list of sympatric wood-warbler species.
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10 178 **Other data collected from the literature**
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13 179 We also used the BBS to measure the degree to which each species pair is syntopic
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15 180 (Rivas 1964) in the region where interspecific territoriality was reported. To measure the degree
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17 181 of syntopy, we found all BBS routes within a 250 km radius of the relevant study location(s).
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20 182 One BBS count route comprises 50 stops (a standardized 3-minute point count is performed at
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22 183 each stop). Within each route, we tallied the number of stops occupied by species 1, by species 2,
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24 184 and by both species. To obtain a regional measure of syntopy, we divided the observed number
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26 185 of stops where both species were found by the expected number of stops where both species
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28 186 would be found if their distributions were independent (e.g., if species 1 and 2 are found at
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30 187 proportions p and q , respectively, out of n possible stops, then the expected number of stops with
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32 188 both species is npq). This metric equals 0 if the species were never found together at the same
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34 189 stop, 1 if the species were found together as often as expected by chance, and >1 if the species
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36 190 were found together more often than expected by chance.
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41 191 Data on hybridization in parulids were obtained from McCarthy (2006) and we also
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43 192 searched for reports of hybridization since 2004 (we disregarded hybridization in captivity and
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45 193 anecdotal reports of hybridization in the wild that McCarthy (2006) classified as doubtful). We
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47 194 used the BNA habitat descriptions to assign each species a habitat complexity score on a three-
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49 195 point scale: 1, simple, such as tundra or grassland; 2, intermediate, such as chaparral or forest
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51 196 edge; and 3, complex, such as coniferous and deciduous forest. The main rationale for this
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53 197 habitat classification is that forests offer more opportunities for vertical stratification of niches,
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3 198 which has long been considered to be relevant for birds (MacArthur 1958; Orians & Willson
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5 199 1964). We based foraging guilds on de Graaf *et al.*'s (1985) classification of North American
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8 200 birds on three niche axes: food type, feeding substrate, and method of food collection. We
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10 201 measured foraging guild overlap for a given species pair as the number of axes on which the
11
12 202 species were classified in the same way, and we also categorized species pairs according to
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14 203 whether they overlapped on all three axes or not. We obtained mass and bill length (exposed
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16 204 culmen length) data from the BNA (Poole 2005), CRC handbook (Dunning 2008), and primary
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18 205 sources. When possible, we used only measurements of breeding season males from within the
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20 206 polygon delimited by the locations where interspecific territoriality was reported; if multiple
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22 207 sources were available, we calculated sample-size weighted averages.
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27 208 We calculated patristic distance (the total branch length separating two species in a
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29 209 phylogeny) between the species pairs included in our study using the `cophenetic.phylo` function
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31 210 in `ape` (Paradis *et al.* 2004) and Lovette *et al.*'s (2010) ultrametric molecular phylogeny of
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33 211 Parulidae, which is based on mitochondrial and nuclear sequence data.
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39 213 **Plumage and song data**

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41 214 To obtain a measure of species differences in plumage, we recruited volunteer observers to
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43 215 compare images of species pairs from field guides in a manner similar to other recent studies
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45 216 (Martin *et al.* 2015). Although human vision is an imperfect proxy for bird vision, human
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47 217 assessments of plumage differences have been shown to be highly correlated with differences
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49 218 calculated from reflectance spectra (Armenta *et al.* 2008; Seddon *et al.* 2010) and are now
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51 219 widely used in studies of avian coloration. We obtained digital scans of color illustrations of
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53 220 males of the species in our study from two field guides (Sibley 2000; Dunn & Alderfer 2006)
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3 221 and compiled the images into 21 sets with ~49 species comparisons per set using QuestionPro
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5 222 (<http://www.questionpro.com/>). Observers were presented with pairs of images from the same
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8 223 field guide and asked to rate the overall difference in plumage on a 0-4 scale (see Table S2). The
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10 224 presentation order of the image pairs was randomized for each person. At least five different
11
12 225 people completed each set (158 observers in total). For each species pair, we calculated the mean
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14 226 difference score across all observers within field guides and then across field guides. Observers
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16 227 were not informed about the objectives of the study.

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20 228 We used two methods to quantify species differences in territorial song, one based on
21
22 229 human hearing and the other based on the spectrogram cross-correlation (SPCC) method (Clark
23
24 230 *et al.* 1987). Both methods have merits and are widely used in comparative studies of bird song.
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26
27 231 The SPCC method is not limited or biased by human perception but may fail to reveal song
28
29 232 pattern similarities that humans can detect (Bioacoustics Research Program 2011). We obtained
30
31 233 two song exemplars for each species recorded within the polygon delimited by the locations
32
33 234 where interspecific territoriality was reported (or as close to the polygon as possible) from xeno-
34
35 235 canto.org. We removed background noise (noise reduction = 22 dB, sensitivity = -7.97 dB,
36
37 236 frequency smoothing = 260 Hz, attack/decay time = 0.01 secs), cut out all parts of the recordings
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39 237 except for two bouts of singing, separated by a few seconds of silence, and then normalized the
40
41 238 edited song files using the default settings in Audacity (<http://web.audacityteam.org/>).

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45 239 For the human-based song comparison method, we compiled the songs into 37 sets with
46
47 240 ~20 species comparisons per set. Listeners were presented with a pair of songs and asked to rate
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49 241 the overall dissimilarity of the songs on a 0-4 scale (Table S2). The presentation order of the
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51 242 song comparisons was randomized for each person. At least five different people completed each
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3 243 set (278 listeners in total). For each species pair, we calculated the mean dissimilarity score
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5 244 across all listeners and then across song exemplars.
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8 245 To assess the repeatability of the mean plumage and song dissimilarity scores, we
9
10 246 calculated Spearman correlations between the means of different groups of observers that rated
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12 247 the same species pairs (a randomly selected subset of species pairs was repeated across sets
13
14 248 expressly for this purpose). Repeatability was high for both plumage ($\rho = 0.72$, $N = 21$) and song
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16 249 ($\rho = 0.80$, $N = 37$).
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20 250 The SPCC method involves sliding two spectrograms relative to each other and using the
21
22 251 maximum cross-correlation value as a measure of song similarity (Clark *et al.* 1987). We used
23
24 252 the default settings for SPCC (biased normalized spectrogram correlation, no filter) in RavenPro
25
26 253 v. 1.4 (Bioacoustics Research Program 2011). The mean SPCC for a given species pair across
27
28 254 song exemplars was used in data analyses.
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32 255 The SPCC song similarity and human-based song dissimilarity measures were
33
34 256 significantly correlated but not so strongly that they can be considered to be redundant measures
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36 257 ($r = -0.40$, $N = 305$ species pairs, $P < 0.0001$).
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40 41 259 **Statistical analyses**

42
43 260 The design of this study differs from most other species pair-based comparative studies in
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45 261 that not all pairwise combinations of species are relevant to include in the analysis. Statistical
46
47 262 methods for analyzing incomplete species pair matrices are still largely untested; we therefore
48
49 263 used two different methods and compared the results. Our first approach was to fit a standard
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51 264 multiple logistic regression (MLR) model and then use evolutionary simulations to compute
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53 265 phylogenetically corrected confidence intervals for the test statistics (for similar approaches, see
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3 266 Garland et al. 1993; Mahler et al. 2013; Drury et al. 2015). Specifically, we constructed a general
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5 267 linear model with interspecific territoriality as a binary outcome variable and the following
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8 268 species-pair predictor variables: body mass difference, bill length difference, plumage
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10 269 dissimilarity, foraging guild overlap (0 or 1), human song dissimilarity, SPCC song similarity,
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12 270 hybridization (0 or 1), and syntopy. We then simulated the evolution of traits representing the
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14
15 271 predictor variables along the phylogeny (see Appendix S1 and Table S3), calculated the relevant
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17 272 species-pair comparisons, recalculated the MLR model using the simulated data, and repeated
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20 273 these steps 5000 times to generate a null distribution for the z values of the model coefficients. If
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22 274 an observed z value lies outside the confidence limits of the corresponding null distribution, the
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24 275 model coefficient is considered to be statistically significant with a phylogenetic correction
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26
27 276 (Drury et al. 2015). We had directional predictions for each variable, and thus to obtain 1-tailed
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29 277 tests, we used 90% confidence intervals. We made phylogenetic corrections for species
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31 278 differences in body mass and bill length, foraging guild overlap, and the measures of plumage
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33 279 dissimilarity and song similarity/dissimilarity. Syntopy was included in the model as a covariate.
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36 280 As explained in Appendix S1, we used Brownian motion (BM) models to simulate the evolution
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38 281 of body mass and bill length and both BM and Ornstein-Uhlenbeck (OU) models to simulate the
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40 282 evolution of plumage and song. We report results for the full MLR model, with all predictor
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42 283 variables included, and a reduced MLR model. The reduced model was obtained by backward
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44
45 284 step-wise elimination; after AIC was minimized, we continued removing terms until any further
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48 285 model simplification increased AIC by >2 (Burnham & Anderson 2002).

49
50 286 Our second approach was to fit a phylogenetic linear mixed model (PLMM), which
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52 287 accounts for the effect of shared ancestry on trait divergence by fitting a phylogenetic variance-
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54 288 covariance matrix, constructed from the phylogeny, as a random effect (Hadfield & Nakagawa
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3 289 2010; Tobias et al. 2014a). This is a mathematically different approach than the evolutionary
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5 290 simulations described above and the comparative reliability (i.e., type I and type II error rates) of
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8 291 two approaches has yet to be established. We fitted a logistic PLMM in MCMCglmm (Hadfield
9
10 292 2010) to the same dataset as used in the MLR using the “categorical” model, with random effects
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12 293 specifying the phylogeny, the focal species and the species to which the focal species is
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14 294 compared, and an inverse gamma prior distribution. We included species in the ‘focal’ and
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16 295 ‘comparison’ categories an equal number of times where possible. To account for variation in the
17
18 296 time since divergence, we also included patristic distance in the model. Adding interactions
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20 297 between patristic distance and the other predictor variables did not improve the overall fit of the
21
22 298 model as measured by DIC. We ran each model for 20E6 iterations, discarding the first 1E6 runs
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24 299 as burn-in and sampling every 1E4 iterations, and assessed model convergence using graphic
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26 300 diagnostics.

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31 301 To visualize the relationships between interspecific territoriality, phylogenetic distance
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33 302 and the key predictor variables, we constructed heat map diagrams based on bivariate logistic
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35 303 regression models (see figure captions for further details).
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40 41 305 **RESULTS**

42
43 306 Of the 49 wood-warbler species that breed regularly in North America (American Ornithologists’
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45 307 Union Checklist <http://checklist.aou.org/>), 19 species have been reported to exhibit interspecific
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47 308 territoriality with one or more species of wood-warbler (excluding *Vermivora bachmanii* which
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49 309 may have been interspecifically territorial with *Setophaga discolor* but is probably extinct; Table
50
51 310 S1). Two of the 19 species have also been reported to be interspecifically territorial with
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53 311 *Empidonax minimus* and one has been reported to be interspecifically territorial with
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3 312 *Regulus satrapa* (Table S1). However, as explained above (*Non-IT species pairs* section), we did
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5 313 not include non-wood-warbler species (or species pairs) in our statistical analyses. While some
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7 314 cases of interspecific territoriality in wood-warblers may remain unreported, it seems unlikely
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9 315 that there are many unreported cases because the probability of species being reported to be
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11 316 interspecifically territorial does not increase significantly with the total number of published
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13 317 studies of the species (logistic regression estimate \pm se: 0.007 ± 0.005 , $P = 0.14$, $n = 49$ species).
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17 318 Most parulids (42 of 49 species) are found in habitats with high structural complexity,
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19 319 and there is no significant association between habitat complexity and interspecific territoriality
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21 320 (Table S4; Fisher's exact test, $P = 0.8$). IT species pairs do not overlap more in their foraging
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23 321 guild classifications than non-IT species pairs (range: 0-3; median: 2; Mann-Whitney test, $n_1 =$
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25 322 19, $n_2 = 286$, $P = 0.13$), nor are IT species pairs more likely to be members of the same foraging
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27 323 guild than are non-IT species pairs (10 of 19 IT species pairs versus 95 of 286 non-IT species
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29 324 pairs; Fisher's exact test, $P = 0.07$).
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34 325 On the average, IT species pairs are more closely related, more syntopic, more similar in
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36 326 all of the measured phenotypic characteristics, and also more likely to hybridize, than are non-IT
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38 327 species pairs (Table 1, Figures 1 and 2). Hybridization in the wild has been reported in 5 of 19 IT
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40 328 species pairs versus 23 of 286 non-IT species pairs (Fisher's exact test, $P = 0.02$). Extensive
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42 329 hybridization in the wild has been reported in 3 of 19 IT species pairs versus 0 of 286 non-IT
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44 330 species pairs (Fisher's exact test, $P < 0.0001$).
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48 331 In MLR analyses without a phylogenetic correction, body mass, plumage dissimilarity,
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50 332 song SPCC and syntopy emerged as significant predictors of interspecific territoriality (Table 2).
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52 333 Song SPCC and plumage dissimilarity remained significant predictors of interspecific
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54 334 territoriality after the OU phylogenetic correction but not after the BM phylogenetic correction
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3 335 (Tables 2 and S5). The PLMM results closely resemble the MLR-OU results (Tables 2, 3 and
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5 336 S5), although the *P*-value for song SPCC was marginal ($P = 0.05$). Body mass difference was not
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8 337 a significant predictor of interspecific territoriality in any of the phylogenetically corrected
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10 338 models (Tables 2, 3 and S5). Syntopy was a significant predictor of interspecific territoriality in
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12 339 all of the models, with or without a phylogenetic correction (Tables 2, 3 and S5).
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17 341 **DISCUSSION**

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20 342 Our literature survey revealed that 39% of wood-warblers that breed in North America are
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22 343 interspecifically territorial with one or more species in some part of their geographic range
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24 344 (Table S1). We found no evidence that interspecific territoriality is restricted to simple habitats
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26
27 345 or to species with highly specialized foraging niches. Most wood-warblers breed in complex
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29 346 habitats, such as coniferous and deciduous forests, and the incidence of interspecific territoriality
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31 347 is unrelated to habitat complexity (Table S4). All wood-warbler species are insectivorous, and
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34 348 insects are not a highly stratified food source. Thus, our results do not support Orians and
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36 349 Willson's (1964) predictions about the community ecological context of interspecific
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39 350 territoriality; we are not aware of any prior attempts to test these predictions. The high incidence
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41 351 of interspecific territoriality in wood-warblers and the lack of evidence that it only occurs in
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43 352 restricted ecological circumstances suggest that it is more stable, ecologically and evolutionarily,
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46 353 than many authors have assumed.

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48 354 Interspecifically territorial species tend to be phenotypically more similar to each other
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50 355 than non-interspecifically territorial species (Table 1), but our multivariate phylogenetic analyses
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52 356 showed that most of these phenotypic similarities can be explained by shared ancestry (Tables 2
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55 357 and 3). We did not find specific support for the prediction, based on the niche overlap hypothesis
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3 358 (Orians & Willson 1964), that ecological similarity is a better predictor of interspecific
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6 359 territoriality than phylogenetic distance. Nevertheless, it would be premature to conclude that
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8 360 interspecific territoriality is unrelated to resource competition. Wood-warblers exhibit
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10 361 phylogenetic niche conservatism (Lovette & Hochachka 2006), and thus phylogenetic distance
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12 362 may be a better index of overall ecological similarity (i.e., niche overlap) than the ecologically
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14 363 important traits included in our study (body mass, bill length, foraging guild). Perhaps many
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16 364 wood-warbler species are sufficiently ecologically similar for interspecific territoriality to be
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18 365 adaptive, but only species that encounter each other frequently have evolved to recognize each
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20 366 other as competitors. Consistent with this explanation, our syntopy metric was a highly
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22 367 significant predictor of interspecific territoriality (Tables 1-4). Syntopy itself can be viewed as a
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24 368 measure of ecological similarity (Lovette & Hochachka 2006), or more precisely in this case, as
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26 369 a measure of the degree to which species use the same breeding habitats. Thus, our finding that
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28 370 interspecific territoriality in wood-warblers occurs primarily between closely related species that
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30 371 are highly syntopic is consistent with the hypothesis that interspecific territoriality evolved (or
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32 372 persists) because of resource competition. By contrast, under the hypothesis that interspecific
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34 373 territoriality is maladaptive, it is only predicted to persist in narrow zones of contact between
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36 374 species (Murray 1981).

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43 375 Evidence for widespread song convergence (or slowing of song divergence) has recently
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45 376 been found in sympatric lineages of ovenbirds and woodcreepers (Furnariidae), many of which
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47 377 may be interspecifically territorial (Tobias *et al.* 2014a). Similarly, a recent analysis of dawn
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49 378 choruses in the Amazon showed a pattern of temporal convergence in song among congeneric
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51 379 birds (Tobias *et al.* 2014b). To our knowledge, however, our study is the first to directly test for a
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53 380 relationship between similarity in territorial signals and interspecific territoriality. Two of the
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3 381 three phylogenetic statistical models that we employed indicate that interspecifically territorial
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5 382 species are convergent in song and plumage (Tables 2, 3). The disagreement between models
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8 383 was not between the MLR and PLMM approaches but instead between the MLR with a
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10 384 Brownian motion (BM) simulation of trait evolution and the other two models (Tables 2, 3). We
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12 385 are unable to determine whether our plumage and song data are fitted better by a BM or
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14 386 Ornstein-Uhlenbeck (OU) process (Appendix S1), but studies assessing the fit of models of trait
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16 387 evolution for plumage and song have generally found that OU models fit better than BM models
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18 388 (Seddon *et al.* 2013; Shultz & Burns 2013; Tobias *et al.* 2014a; Dale *et al.* 2015). Our results
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20 389 therefore offer at least tentative support for the hypothesis that interspecifically territorial species
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22 390 have converged in territorial signals (Cody 1973; Grether *et al.* 2009; Tobias *et al.* 2014a).

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27 391 Signal convergence could result from adaptation to a common visual or acoustic
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29 392 environment (Boncoraglio & Saino 2007), but all species pairs in our study are sympatric and we
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31 393 controlled for variation in syntopy. Thus, adaptation to the signaling environment is not a
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33 394 plausible explanation for our results. Another possible explanation is that convergence results
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35 395 from genetic introgression (Secondi *et al.* 2011). We did find higher rates of hybridization in IT
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37 396 species pairs than in non-IT species pairs (Table 1), but genetic introgression would also be
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39 397 expected to affect morphological traits, and we found no evidence for convergence in body mass
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41 398 or bill length in IT species pairs (Tables 2 and 3).

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46 399 Hybridization and other forms of reproductive interference can result in mate competition
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48 400 between species (Reitz & Trumble 2002). When males of different species compete for mates,
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50 401 interspecific territoriality can be adaptive even in the absence of resource overlap (Drury *et al.*
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52 402 2015). Although hybridization was not a significant predictor of interspecific territoriality in our
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54 403 multivariate models (Tables 2, 3), it may still be a contributing factor. Wood-warbler species
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3 404 with more similar territorial songs are more likely to hybridize (Willis *et al.* 2014). Three of the
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5 405 four wood-warbler species pairs that hybridize extensively in the wild (Willis *et al.* 2014) are
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8 406 interspecifically territorial, and two of those three IT species pairs are the most similar in song
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10 407 out of all 305 species pairs in our dataset (upper left points in Figure 2). Thus, territorial song,
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12 408 plumage, hybridization, interspecific territoriality and phylogenetic relatedness are closely
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15 409 entwined in wood-warblers – perhaps too much so to sort out causal relationships between these
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17 410 variables statistically.

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20 411 Interspecific territoriality, and indeed interference competition in general, is a complex
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22 412 and neglected subject (Grether *et al.* 2013). Our results suggest that interspecific territoriality is
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24 413 an important selective force acting over evolutionary timescales, rather than simply a transient or
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26 414 accidental byproduct of intraspecific territoriality. With a larger dataset, encompassing greater
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29 415 phylogenetic and ecological diversity, it may be possible to evaluate the relative influence of
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31 416 resource overlap and reproductive interference on the evolution of interspecific territoriality.
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584 **Table 1.** Summary of univariate comparisons between interspecifically territorial (IT) species
 585 pairs ($N = 19$) and non-interspecifically territorial (non-IT) species pairs ($N = 286$) of sympatric
 586 wood-warblers. Each variable was checked for deviations from normality and unequal variances
 587 (using F-tests) and transformed, if necessary, to meet t -test assumptions using the transformation
 588 shown in the table. In the case of body mass difference, no transformation eliminated the
 589 difference in variance between groups and thus the t -test for unequal variances was used
 590 (Satterthwaite's $df = 24.6$). For all other variables, a standard t -test was used and $df = 303$. One-
 591 tailed P -values are shown because the tested hypotheses make directional predictions. With a
 592 sequential Bonferroni correction for multiple tests (Holm 1979), across all seven P -values in the
 593 table, the criterion for statistical significance at $\alpha = 0.05$ is $P < 0.05$.

Variable	Transform	IT pairs		Non-IT pairs		t	P
		Mean	SE	Mean	SE		
Body mass difference	$\sqrt{}$	1.10	0.11	1.50	0.04	3.34	0.001
Bill length difference	$\sqrt{}$	0.78	0.09	1.04	0.03	2.31	0.01
Plumage dissimilarity		3.51	0.18	4.06	0.03	3.78	0.0001
Song dissimilarity		3.57	0.17	3.79	0.04	1.33	0.09
SPCC song similarity	$\sqrt{}$	0.38	0.02	0.29	0.01	-3.62	0.0002
Syntopy	$\log(x+0.01)$	0.32	0.16	-0.11	0.04	-2.55	0.006
Patristic distance		55.9	7.6	98.6	1.8	5.93	<0.0001

Table 2. Analysis of predictors of interspecific territoriality, using multiple logistic regression (MLR) with a phylogenetic correction. Model 1 includes all available predictor variables, besides patristic distance. Model 2 resulted from using stepwise elimination. Continuous predictor variables were transformed as shown in Table 1 and then converted to z -scores. Confidence intervals of the z statistic based on phylogenetic simulations are shown for Brownian motion (BM) and Ornstein-Uhlenbeck (OU) evolutionary models. Estimates that differ significantly from zero after phylogenetic correction are indicated in bold.

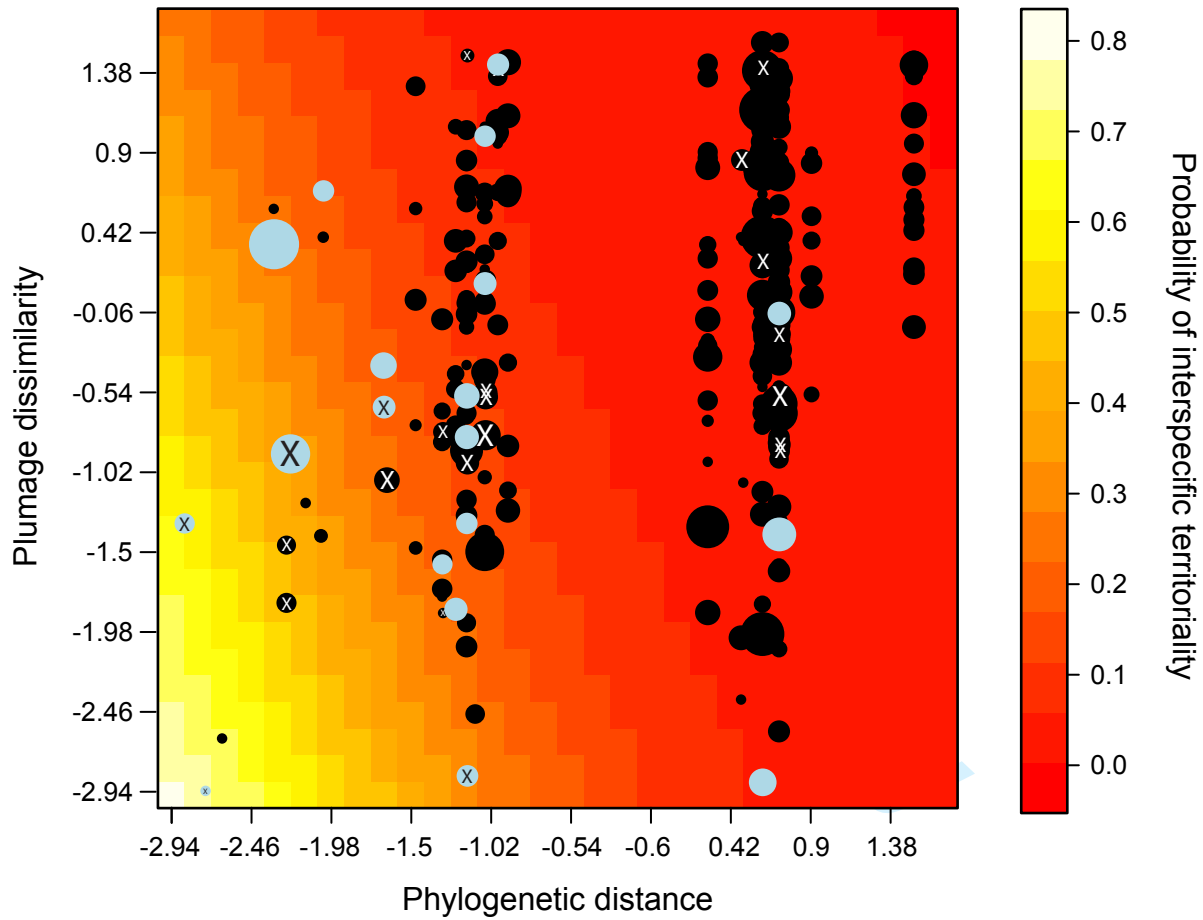
Model	Variable	Estimate	SE	z	Uncorrected P	BM 90% CI of z $\sigma^2=0.016$	OU 90% CI of z $\sigma^2=0.016, \alpha=0.079$
1	Body mass difference	-1.39	0.82	-1.70	0.09	-2.56, 0.67	-2.88, 0.29
AIC	Bill length difference	-0.38	0.34	-1.14	0.25	-2.58, 0.72	-2.84, 0.35
114.8	Plumage dissimilarity	-0.83	0.27	-3.04	0.002	-3.21, 0.05	-2.10, 1.15
	Foraging guild overlap	0.71	0.56	1.27	0.20	-0.82, 2.48	-0.53, 2.81
	Hybridization	1.06	0.74	1.44	0.15	-0.01, 2.05	-0.84, 1.71
	SPCC song similarity	1.20	0.46	2.60	0.009	-0.21, 2.84	-1.26, 1.99
	Human song dissimilarity	0.17	0.29	0.58	0.56	-3.24, 0.01	-2.13, 1.18
	Syntopy	0.95	0.34	2.78	0.005		
2	Body mass difference	-1.68	0.76	-2.22	0.026	-2.73, 0.47	-2.99, 0.19
AIC:	Plumage dissimilarity	-0.94	0.27	-3.45	0.0006	-3.49, 0.38	-2.11, 1.12
111.6	SPCC song similarity	1.14	0.42	2.70	0.007	0.31, 3.02	-1.19 1.98
	Syntopy	0.95	0.33	2.92	0.003		

Table 3. Analysis of predictors of interspecific territoriality, using logistic phylogenetic linear mixed model (PLMM).

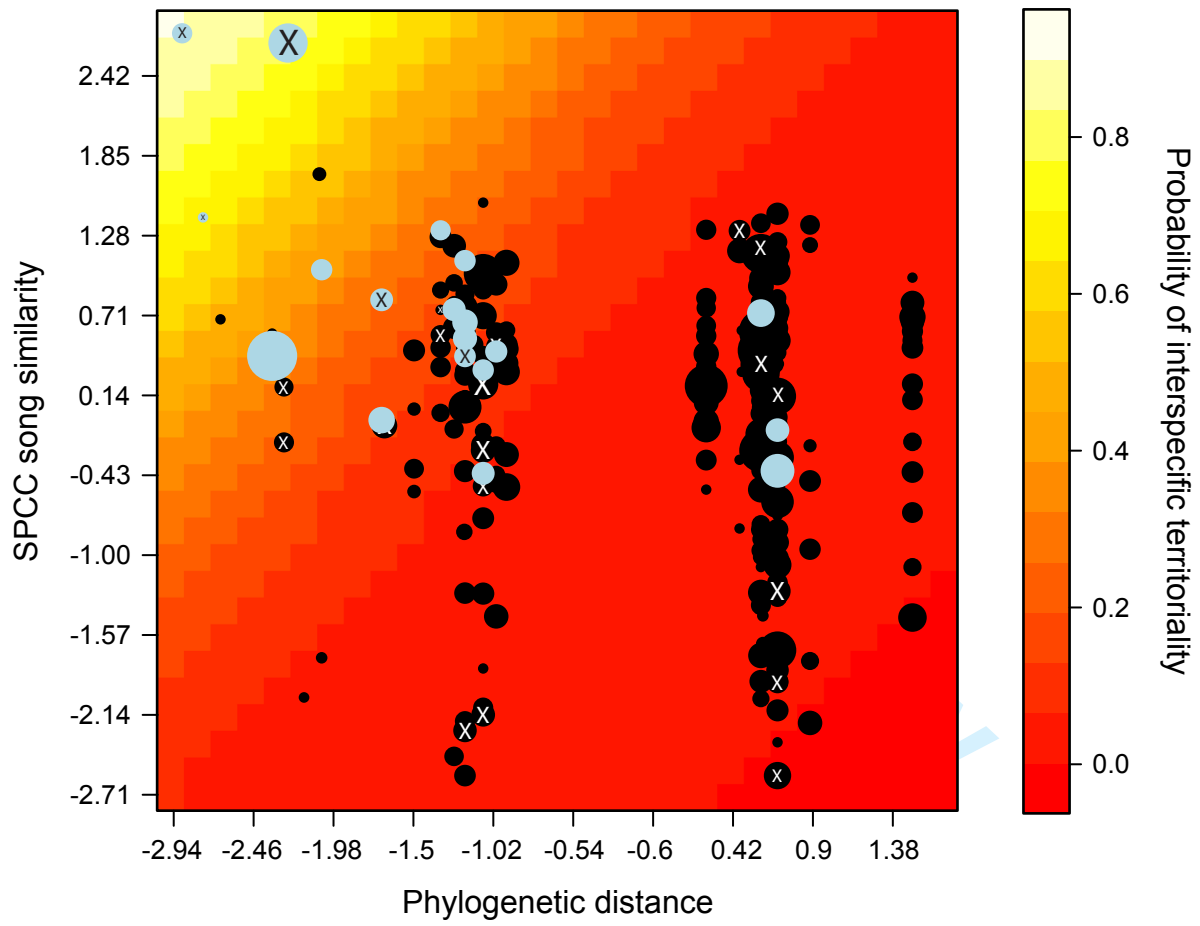
Variable	posterior mean	95% CI (lower)	95% CI (upper)	effective n	P_{MCMC}
Intercept	-2184.94	-4037.18	-693.14	1900	0.0011
Body mass difference	-256.79	-704	150.74	2249	0.15
Bill length difference	-53.29	-346.77	225.23	2286	0.71
Plumage dissimilarity	-302.37	-677.5	-35.71	1900	0.0095
Foraging guild overlap	366.99	-158.26	948.01	1900	0.12
Hybridization	-156.56	-1079.86	553.38	2065	0.72
Syntopy	462.97	131.94	938.54	1900	<0.0005
SPCC song similarity	319.75	-47.43	751.51	1900	0.051
Human song dissimilarity	130.35	-120.98	458.93	1895	0.31
Patristic distance	-438.37	-880.18	-46.65	1900	0.004

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5 Figure 1. Plumage dissimilarity between sympatric wood-warbler species pairs plotted against
6 phylogenetic (patristic) distance. Light blue circles identify interspecifically territorial species
7 pairs ($N = 19$); black circles identify non-interspecifically territorial species pairs ($N = 286$). The
8 size of the circles is proportional to $\log(\text{syntopy} + 0.5)$. Species pairs that have been reported to
9 hybridize are marked with an X. The background color shows the predicted probability of
10 interspecific territoriality, based on a MLR model with plumage dissimilarity and patristic
11 distance as predictors (plumage dissimilarity: estimate \pm SE = -0.48 ± 0.26 , $z = -1.88$, $P = 0.060$;
12 patristic distance: estimate \pm SE = -1.16 ± 0.29 , $z = -3.95$, $P < 0.0001$; residual $df = 302$).
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14 Phylogenetic distances are clustered due to periods of rapid cladogenesis during the
15 diversification of wood-warblers (Lovette & Hochachka 2006).
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33 Figure 2. Song similarity between sympatric wood-warbler species pairs plotted against
34 phylogenetic (patristic) distance. For color and symbol key, see Figure 1. Predicted values were
35 based on a MLR model with song similarity and patristic distance as predictor variables (song
36 similarity: estimate \pm SE = 0.88 ± 0.39 , $z = 2.28$, $P = 0.023$; patristic distance: estimate \pm SE = -
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