The macroecology and evolution of avian competence for *Borrelia burgdorferi*

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Running head: Avian competence for *Bb*sl

Keywords: machine learning; boosted regression tree; birds; transmission; tick-borne disease; Lyme borreliosis; phylogenetics

Abstract

Most efforts to predict novel reservoirs of emerging infectious diseases rely upon information about the infection status of host species rather than their competence, the ability to transmit pathogens to new susceptible hosts or vectors. Although competence can be difficult to quantify, tick-borne pathogens can provide a useful model system, as larval ticks can become infected only when feeding on a competent host during their first bloodmeal. For tick-borne diseases, competence has been best studied for *Borrelia burgdorferi* sensu lato (*Bb*sl), the pathogen that causes Lyme borreliosis, an increasing public health priority across the northern hemisphere. Major reservoirs include several small mammal species, but birds may play an underrecognized role in human risk of acquiring this tick-borne pathogen, given their ability to disperse infected ticks across large spatial scales. Here, we provide a global synthesis of the ecological and evolutionary factors that determine the ability of bird species to infect larval ticks with *Bb*sl. We find strong phylogenetic patterns in competence, which clusters in thrushes and has evolved multiple times across birds. With boosted regression trees, we distinguish competent birds with 76% accuracy and show competent species are more likely to fledge early, have low baseline corticosterone, breed at high latitudes, and have more diverse migratory movements into their breeding range. We use these trait profiles to predict over 100 likely but unsampled *Bb*sl-competent birds, including novel concentrations of avian reservoirs in the Neotropics and pelagic zones. Beyond expanding our understanding of avian reservoirs for tick-borne pathogens and generating new hypotheses, our findings also emphasize the need to consider competence in efforts to predict novel hosts of emerging diseases and in the study of multi-host pathogens.

Introduction

As most emerging infectious diseases originate in animals [1], a diverse array of efforts has aimed to predict reservoir hosts and arthropod vectors of zoonotic pathogens [2–4]. Because such predictions can guide surveillance and even interventions, they are necessary steps toward a preemptive approach to minimizing pathogen spillover risks [5,6]. For example, PCR and serological data on Nipah virus from wild bats were leveraged to prioritize field sampling targets across India in response to a novel human outbreak [7], and similar approaches have been successfully applied to identify hosts of filoviruses, rodent zoonoses, and Zika virus [8–10]. However, pathogen detection data likely better reflect host exposure rather than *competence*, which is the ability of a host to transmit a pathogen to a new host or vector [11]. Greater attention to competence could thus improve predictions about novel reservoirs of zoonoses.

Host competence is an inherently individual-level trait driven by immunological and behavioral factors [12,13]. This individual heterogeneity mediates intra- and inter-specific variation in the propensity to transmit pathogens, which is a key determinant of infection dynamics in complex host communities [14]. Species-level variation in competence can produce hosts with disproportionate contributions to pathogen transmission [15]. For example, American robins (*Turdus migratorius*) infect up to 40% of mosquito vectors with West Nile virus despite their lower relative abundance within the avian host community [16], and the transmission of many helminths is often dominated by single host species in small mammal communities [17]. Identifying the broader ecological or evolutionary drivers of competence could in turn illuminate how different host species contribute to the transmission of multi-host pathogens [18,19].

Competence can be difficult to quantify, as infection status of the donor and recipient host must be known or directional transmission events must be inferred [12,20]. However, many

56 tick-borne pathogens provide an useful system to approximate competence, as tick larvae hatch
57 free of some pathogens and only become infectious with their first vertebrate bloodmeal [21].
58 Accordingly, competence can be inferred from the presence of pathogens in engorged larval ticks
59 on the donor host [22]. In this context, inter-specific variation in competence has been best
60 studied for *Borrelia burgdorferi* sensu lato (*Bb*sl), which causes Lyme borreliosis. *Bb*sl is
61 transmitted to humans by nymph *Ixodes* spp. ticks and has infection foci across the northern
62 hemisphere and parts of Latin America [23,24]. Lyme borreliosis is the most common vector-
63 borne disease in the United States (i.e., Lyme disease) [25], where fast-lived rodent species, in
64 particular white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*),
65 infect high proportions of larvae and are the most competent hosts among mammals [26–28].
66 Through infecting the majority of naïve vectors, these host species contribute disproportionally
67 to the production of infectious nymphs and therefore to human Lyme borreliosis risk [29,30].
68 In contrast to mammals, birds likely play an underrecognized role in the global ecology
69 of *Bb*sl, given that the capacity for flight, and especially long-distance migration, can allow avian
70 hosts to disperse infected ticks across entire continents [31–34]. Migratory birds likely transport
71 50–175 million ticks across Canada each spring [35], and the physiological stress of migration
72 itself may help drive reactivation of latent *Bb*sl infection [36]. Individual studies have suggested
73 some birds have important contributions to the enzootic maintenance of *Bb*sl [37,38]. For
74 example, birds play the dominant role in transmission of *B. garinii* and *B. valaisiana* to larvae
75 across Europe [39,40] and contribute to enzootic cycles of the primarily rodent genospecies, *B.*
76 *afzelli* [41]. In North America, *Bb* sensu stricto infects both rodent and avian species; however,
77 as with mammals, birds seemingly also display broad variation in competence. American robins
78 can infect up to 90% of naïve larvae [42], whereas gray catbirds (*Dumetella carolinensis*) and

79 veeries (*Catharus fuscescens*) display lower competence [43–45]. High tick burdens on some
80 avian species, such as ground foragers, may allow some birds to contribute more to community-
81 level *Bb*sl transmission than some rodent hosts [46,47]. Lastly, many bird species capable of
82 infecting larvae are also common in suburban and urban habitats [48,49], which could increase
83 human exposure to infectious nymphal ticks [50]. Yet despite these opportunities for birds to
84 play key roles in the global distribution of *Bb*sl and Lyme borreliosis risk, the inter-specific
85 drivers of reservoir competence across bird species have not yet been systematically identified.
86 Given the potential for birds to play important roles in the dynamics of this tick-borne
87 pathogen, we here compile a comprehensive, global dataset on avian competence for *Bb*sl and
88 assess its ecological and evolutionary drivers. We first describe spatial and temporal patterns in
89 competence, including testing for latitudinal gradients and seasonal variation among species.
90 Next, we characterize phylogenetic patterns in competence and reconstruct its evolution across
91 birds. We lastly use a flexible machine learning algorithm to evaluate the trait profiles associated
92 with competent avian species. For the latter, such data science approaches circumvent many
93 issues associated with traditional hypothesis testing (e.g., a large number of predictors, complex
94 interactions, non-randomly missing covariates) and can uncover new and surprising patterns in
95 data, thereby developing testable hypotheses [51,52]. Our work therefore aims to identify the
96 ecological and evolutionary drivers of avian competence while also generating predictions of
97 likely novel *Bb*sl reservoirs and directions for future studies of tick-borne disease more broadly.
98

99 **Methods**

100 *Competence data*

101 To collate data on avian competence for *Bb*sl, we searched Web of Science, PubMed, and CAB
102 Abstracts with the following string: ("reservoir competence" OR "host competence" OR
103 prevalence) AND (bird* OR Aves) AND (larva* OR tick* OR arthropod*) AND ("Lyme
104 disease" OR *Borrelia* OR "*B. burgdorferi*"). Using a systematic protocol (Fig. S1) [53], we
105 included only studies of experimental trials (e.g., infecting birds and using xenodiagnoses with
106 naïve larvae to test bird-to-tick transmission) or that approximated competence by testing
107 engorged larvae from wild birds for *Bb*sl. We excluded studies that only tested larvae for non-
108 *Bb*sl *Borrelia* (e.g., *B. lonestari*), only tested nymph or adult ticks, pooled ticks by life stage,
109 only tested birds themselves (e.g., blood or tissue), or pooled competence across bird species.
110 We identified 102 studies for inclusion, from which we recorded the sampling country
111 and coordinates (or used centroids of reported regions), sampling months and years, bird and
112 larval tick species, number of sampled and *Bb*sl-positive larvae, the *Bb*sl genospecies, and
113 competence assessment type (experimental trial or testing attached larvae). As most studies had
114 multiple lines of data (88/102), each record (n=1069) was a test of a bird–tick–*Bb*sl association
115 over space and time. Most records were from *Ixodes* ticks (90.11%, mostly *I. ricinus* and *I.*
116 *scapularis*), with the remainder unstated (1.24%) or from *Haemaphysalis* (4.85%), *Hyalomma*
117 (3.71%), or *Amblyomma* (0.10%). Whereas tick genera other than *Ixodes* are unlikely *Bb*sl
118 vectors [54], we retained these records as they still represent transmission from competent birds.
119
120 *Meta-analysis of larval infection prevalence*
121 We first used a phylogenetic meta-analysis to quantify heterogeneity in prevalence of *Bb*sl in
122 bird-fed larvae (n=964, Fig. S2; some studies only reported presence or absence of infected
123 larvae). We obtained a phylogeny of our 183 bird species from the Open Tree of Life with the

124 *rotl* package in R and used the *ape* package to calculate branch lengths [55,56]. We then used the
125 *metafor* package to estimate logit-transformed proportions and sampling variances [57]. We next
126 used restricted maximum likelihood to fit a random-effects model (REM), which included a
127 species-level random effect (the covariance structure used the phylogenetic correlation matrix),
128 observation nested within a study-level random effect, and weighting by sampling variances.
129 Resulting estimates of the variance components were used to derive I^2, the contribution of true
130 heterogeneity to the total variance in larval *Bb*sl prevalence, and to partition variance attributed
131 to each random effect. For avian species, we calculated phylogenetic heritability (H^2) [58].
132 To assess spatial and temporal variation in avian competence, we fit mixed-effects
133 models (MEMs) with the same random effects to the data subset describing *Bb*sl prevalence in
134 engorged larvae derived only from wild birds (n=922). Covariates included geographic region
135 (n=922), latitude (n=778), year (n=917), and season (n=654). As many studies pooled *Bb*sl
136 prevalence across time, we used either the given sampling year or the mid-point sampling year.
137 Similarly, we coded season as four binary covariates (winter, spring, summer, fall; only 10
138 prevalence estimates were from the southern hemisphere), as studies often reported data per
139 single season or pooled across multiple seasons. Given the differences in sample size between
140 predictors, we used Akaike information criterion corrected for small sample sizes (AICc) to
141 compare two sets of MEMs [59]: (*i*) space and year and (*ii*) space and season. Comparisons
142 included an intercept-only model, and we derived a pseudo-R^2 as the proportional reduction in
143 the summed variance components per MEM compared with that of an equivalent REM [60].
144
145 *Phylogenetic analyses*

We next aggregated tick–*Bb*sl data per avian species to assess phylogenetic patterns in binary competence. Using the *caper* package, we calculated the *D* statistic, where a value of 1 indicates a phylogenetically random trait distribution and a value of 0 indicates phylogenetic clustering under a Brownian motion model of evolution [61]. Significant departure from either model was quantified using a randomization test with 1000 permutations. However, because traits such as competence may also arise under a punctuated equilibrium model of evolution, we next used a graph-partitioning algorithm, phylogenetic factorization, to flexibly identify clades with significantly different propensity to be competent at various taxonomic depths. We used the *taxize* package to obtain a taxonomy from the NCBI database [62] and used the *phylofactor* package to partition competence as a Bernoulli-distributed response in a generalized linear model [63]. To account for variable study effort, we used the *rwos* package to quantify the number of citations per species in Web of Science and used the square-root transformed values as weights [7,8]. We determined the number of significant phylogenetic factors (clades) using a Holm's sequentially rejective 5% cutoff for the family-wise error rate. Lastly, to assess if phylogenetic patterns in competence could stem from study effort alone, we performed a secondary analysis to partition Web of Science citation counts for each avian species as a quasi-Poisson response.

To investigate the evolution of competence along the avian phylogeny, we next used the *ape* package and maximum likelihood to reconstruct the ancestral character state [56]. We compared an equal-rate and an all-rates-different model of evolution using Akaike information criterion (AIC) [64] and used the most competitive model to perform stochastic character mapping with Markov chain Monte Carlo (n=1000) using the *phytools* package [65]. We displayed the mean posterior probabilities of competence across our sampled avian phylogeny.

169 *Trait-based analyses*

170 We compiled avian trait data from EltonTraits [66], the Amniote Life History database [67],
171 International Union for the Conservation of Nature [68], and HormoneBase [69]. Traits included
172 diet composition and breadth, foraging strata (e.g., ground foraging), pace of life (e.g., maximum
173 lifespan, clutch size, fledging age, clutches per year), morphology (e.g., adult body mass,
174 hatching weight), maximum elevation, global population trend, and physiology (i.e., baseline
175 corticosterone; CORT). Using distribution maps from BirdLife International and the Handbook
176 of the Birds of the World [70], we derived total range size, latitude of the centroids of breeding
177 and non-breeding ranges, and mean migration distance (greater circle distance between these
178 centroids). We also quantified migratory dispersion, the extent to which species inhabit larger
179 (positive) or smaller (negative) areas in the non-breeding season relative to breeding range size,
180 and categorized migratory strategy (resident, full migrant, partial migrant) [71]. For resident
181 species, mean migration distance and dispersion were set to zero. To represent phylogeny, we
182 included binary covariates for each avian family and any clades identified by phylogenetic
183 factorization; we also had a binary covariate for Passeriformes given their overrepresentation in
184 our data (166/183 species). We also derived the degree of evolutionary isolation per species in
185 the avian phylogeny with the *picante* package [72]. We again used Web of Science citations per
186 species to approximate study effort. We transformed continuous predictors that spanned orders
187 of magnitude and excluded those with zero variance or missing values for over 75% of birds. We
188 compiled features for our 183 sampled birds and all remaining avian species to predict likely but
189 unsampled competent hosts. We limited out-of-sample species to the 39 families included in our
190 *Bb*sl dataset (approximately 4700 birds). Feature definitions and coverage are given in Table S1.

We used boosted regression trees (BRTs) to fit a predictive model relating binary competence to a predictor matrix of all avian traits [73]. In our analysis, BRTs were trained to maximize classification accuracy by learning patterns of features that best distinguish competent and non-competent avian species. This generates recursive binary splits for randomly sampled predictor variables, and successive trees are built using residuals of the prior best-performing tree as the new response. Boosting generates an ensemble of linked trees, where each achieves increasingly more accurate classification. Prior to analysis, we randomly split data into training (80%) and test (20%) datasets while preserving the proportion of positive labels. Models were trained with the *gbm* package [74], with the maximum number of trees set to 50000, a learning rate of 0.0001, and an interaction depth of three [73]. BRTs used a Bernoulli error distribution and 10-fold cross-validation, and we used the *ROCR* package to quantify classification accuracy as area under the receiver operator curve (AUC) [75]. As BRT results can depend on random splits between training and test data, we used five partitions to generate a model ensemble [76]. To diagnose if trait profiles of competent birds are driven by study effort, we ran a secondary BRT ensemble that modeled Web of Science citation counts as a Poisson-distributed response.

After assessing accuracy of our BRTs against test data, we applied our model ensemble to the full trait dataset to generate mean probabilities of *Bb*sl competence per avian species. To assess potential phylogenetic signal in predictions, we estimated Pagel's λ in logit-transformed mean probabilities with the *caper* package [77]. To guide surveillance for likely competent avian reservoirs, we mapped the distributions of non-positive bird species with mean probabilities of over 50%. We stratified distributions by avian phenology to emphasize when these unsampled *Bb*sl reservoirs are most likely to encounter questing larvae (i.e., breeding and resident ranges).

214 **Results**

215 *Avian competence on a global scale*

216 Half of all sampled bird species were competent for *Bb*sl (91/183). Only nine species had
217 experimental evidence of competence, and all 91 competent species (with the exception of
218 *Gallus gallus*) had larvae from wild hosts test positive (Fig. S2). For records reporting *Bb*sl
219 genospecies from positive bird-fed larval ticks, our global-scale data were dominated by *B.*
220 *garinii* (31%), *B. valaisiana* (20%), *B. burgdorferi* sensu stricto (16%), and *B. afzelii* (15%),
221 representing the geographic skew of the data toward Europe (59%) and North America (37%);
222 3% of our data were from Eastern Asia, whereas 1% were from South America (Fig. 1A).
223 However, these 91 competent avian species were more broadly distributed across the Americas,
224 Africa, Asia, and Oceania, representing a mixture of resident, breeding, or wintering ranges.

225 We observed significant heterogeneity in bird-fed larval tick *Bb*sl prevalence (I^2=0.75,
226 Q_{963}=2970, p<0.0001). Avian species accounted for more of this variation ($I^2_{species}$=0.30) than
227 study (I^2_{study}=0.19) or individual record ($I^2_{observation}$=0.26), resulting in moderate phylogenetic
228 signal (H^2=0.40). Given the stronger effect of avian phylogeny, we found no effect of study-level
229 predictors such as space (Fig. 1B) or year (Fig. 1C) on the proportion of larval ticks infected by
230 wild birds (Table S2). Seasons were also generally uninformative (Table S3), but prevalence in
231 bird-infected larvae was lower for sampling conducted in summer (w_i=0.44, R^2=0.01; Fig. 1D).

232

233 *Evolutionary patterns in donor transmissibility*

234 We next considered competence as an intrinsic binary trait per avian species. We estimated
235 intermediate phylogenetic signal in the ability of birds to transmit *Bb*sl to larvae (D=0.78),
236 indicating significant phylogenetic clustering between randomness (p<0.001) and a Brownian

motion model of evolution ($p<0.001$). After controlling for study effort, phylogenetic factorization identified one clade, the genus *Turdus*, as having a significantly greater likelihood of including competent species when compared to other avian taxa (Fig. 2). In particular, all but one member of this clade demonstrated the ability to infect larval ticks with *Bb*sl (92%).

Our secondary analysis identified seven taxa as having significantly different Web of Science citation counts (Fig. S3), five of which were heavily studied single species: *Gallus gallus* (4139), *Parus major* (3736), *Sturnus vulgaris* (2509), *Passer domesticus* (2162), and *Ficedula hypoleuca* (1500). Disproportionately studied taxa also included the Phasianidae ($\bar{x}$=609) and a subclade of the Icteridae (genera *Quiscalus*, *Molothrus*, and *Agelaius*; $\bar{x}$=545). These taxonomic patterns in Web of Science citation counts did not overlap with taxonomic patterns in avian competence, suggesting the latter were not driven by study effort (Fig. S3).

The evolution of avian competence was best described by an equal-rate model (w_i=0.73). Stochastic character mapping suggested equal transitions from non-competent to competent and from competent to non-competent (Fig. 2), with the ancestral state being equivocal. Competence was gained in the Turdidae as well as the Mimidae, Passerellidae, and Troglodytidae, with both gains and losses in the Parulidae. We also observed a clear loss of competence within the majority of the Carduelinae as well as within the Corvidae, Picidae, and Strigidae (Fig. 2).

Trait profiles of competent birds

Our BRT models distinguished competent from non-competent birds with a mean 76% accuracy (AUC=0.76 ± 0.02 SE; Fig. 3A). The top features for describing *Bb*sl-competent avian species included those relevant to life history (i.e., fledging age, maximum lifespan, birth and adult weight, egg mass, incubation time, clutch size), physiology (i.e., baseline CORT), migration

260 (dispersion, distance), geography (breeding latitude, maximum elevation, geographic range size),
261 evolutionary isolation, and study effort. The family Turdidae was the only taxonomic feature
262 with non-trivial importance, and foraging was generally uninformative (Fig. 3B, Table S4).
263 *Bb*sl-competent bird species were partly described by a faster life history (Fig. 4).
264 Competent avian reservoirs have shorter incubation times and young that are smaller and fledge
265 earlier than their non-competent counterparts. However, competent birds also have longer
266 lifespans, lay smaller clutches, and have larger eggs and adults. Physiologically, competent birds
267 have lower baseline concentrations of CORT, the main avian glucocorticoid. Competent birds
268 also tend to breed at higher latitudes, have larger geographic ranges, occupy lower elevations,
269 and have stable or increasing population trends. The likelihood of competence was also greater
270 for species with negative migratory dispersion, indicating such hosts have larger breeding ranges
271 and greater diversity of migratory movements from their wintering to their breeding grounds.
272 Competence was less strongly related to mean migratory distance, with intermediate-distance
273 migrants being most likely to transmit *Bb*sl to larvae. Lastly, well-studied species are also more
274 likely to be competent. However, our secondary BRTs showed that Web of Science citations
275 were not predictable by these same traits (AUC=0.50 ± 0 SE), suggesting that the trait profile of
276 a competent bird is not confounded by the ecological traits associated with well-studied hosts.
277 Applying our BRT ensemble to trait and taxonomic data across the 39 sampled avian
278 families revealed at least 127 species that could be prioritized for *Bb*sl surveillance based on
279 feature similarity to known competent reservoirs, including six birds not currently known to be
280 competent and 121 unsampled birds (Fig. 5A). We observed strong phylogenetic signal in mean
281 predicted probabilities of competence (λ=0.95), indicating the influential traits revealed by our
282 BRTs are likely driven by lineages with high potential for being competent for *Bb*sl (Fig. 5B).

The geography of likely high-probability reservoirs revealed potential hotspots of competent birds across their breeding (Fig. 5C), non-breeding (Fig. 5D), and resident (Fig. 5E) ranges. Likely false negatives included the Indigo bunting (*Passerina cyanea*) [78–80], yellow-breasted chat (*Icteria virens*) [81,82], common reed bunting (*Emberiza schoeniclus*) [39,83,84], eyebrowed thrush (*Turdus obscurus*) [85], garden warbler (*Sylvia borin*) [86], and European pied flycatcher (*Ficedula hypoleuca*) [86]. Likely but unsampled reservoirs included the American goldfinch (*Spinus tristis*), Townsend's warbler (*Setophaga townsendi*), Abert's towhee (*Melozone aberti*), Harris's sparrow (*Zonotrichia querula*), grasshopper sparrow (*Ammodramus savannarum*), yellow-headed blackbird (*Xanthocephalus xanthocephalus*), northern mockingbird (*Mimus polyglottos*), and eastern bluebird (*Sialia sialis*) in North America; Acadian flycatcher (*Empidonax virescens*), red-eyed vireo (*Vireo olivaceus*), alder flycatcher (*Empidonax alnorum*), Louisiana waterthrush (*Parkesia motacilla*), great crested flycatcher (*Myiarchus crinitus*), and clay-colored thrush (*Turdus grayi*) across the Americas; corn bunting (*Emberiza calandra*) and horned lark (*Eremophila alpestris*) in Eurasia; and thick-billed murre (*Uria lomvia*) and rhinoceros auklet (*Cerorhinca monocerata*) across pelagic zones. The names and propensity scores of bird species in the top 50th percentile of BRT predictions are provided in Table S2.

Discussion

Competence is increasingly recognized to be an important trait governing infectious disease dynamics, especially in multi-host communities [11,12,27]. Efforts to predict new reservoirs of zoonotic pathogens would be improved by identifying the ecological or evolutionary drivers of the capacity for species to successfully transmit to recipient hosts or vectors [18,19]. To do this, we examined Lyme borreliosis, a model system to study competence for a tick-borne disease.

306 Whereas inter-specific variation in this trait has been well-characterized for mammals [26–28],
307 competence has been comparatively understudied across avian hosts, despite their ability to
308 disperse infected ticks across large spatial scales and mounting evidence of high competence
309 across multiple species [42,43,87]. We show that taxonomic and life history traits of *Bb*sl
310 competence are likewise predictable across avian hosts. Our phylogenetic analyses demonstrate
311 that competence has evolved multiple times across birds and is pronounced in the genus *Turdus*.
312 Trait-based analyses distinguished competent avian hosts with 76% accuracy and emphasized
313 that such species fledge early, have low baseline CORT, breed at high latitudes, and have diverse
314 migratory movements into their breeding range. These trait profiles can be leveraged to prioritize
315 surveillance of likely but unsampled *Bb*sl-competent avian species and emphasize birds display
316 underrecognized variation in their contributions to the enzootic cycles of this zoonotic pathogen.
317 Although pathogen transmission inherently occurs from individual hosts, variation in
318 competence can arise across broader biological scales such as space or species [11,14,15]. Our
319 meta-analysis identified substantial heterogeneity in *Bb*sl prevalence from bird-fed larval ticks
320 (i.e., high I^2) that was better explained by bird phylogeny rather than space, and this intermediate
321 phylogenetic signal was also confirmed in our species-level analysis. Although intraspecific
322 variation in *Bb*sl competence may be high in some contexts (e.g., latitudinal gradients in Europe
323 [34]), the strong contribution of phylogeny likely obscured such patterns at a global scale across
324 bird assemblages. These analyses thus suggest that the ability to transmit *Bb*sl to larval ticks can
325 be considered an intrinsic trait of avian species. However, we note that most of our data only
326 inferred competence from presence of infected larvae on wild birds, and future experimental
327 infections and tests of bird-to-tick transmission are necessary to improve inference [43,87].
328 Our moderate estimates of phylogenetic signal in avian competence were reflected in

329 numerous gains and losses of this trait across the phylogeny, suggesting that competence has
330 evolved multiple times to form lineages of highly competent birds. Phylogenetic factorization
331 identified one of these clades, the genus *Turdus*, as being especially competent, even after
332 accounting for variable study effort across birds. Of the12 sampled *Turdus* species, all but one
333 (*T. obscurus*) had engorged larvae test positive for *Bb*sl [85], and two (*T. migratorius* and *T.*
334 *merula*) have experimentally infected naïve larvae [42,87]. Given the more extensive *Turdus*
335 clade (approximately 85 species), this result suggests the other remaining true thrushes could
336 also be competent reservoirs for *Bb*sl. *Turdus* thrushes are globally distributed owing to their
337 evolutionary origins in the eastern Palearctic before dispersal to Africa and radiation through
338 trans-Atlantic movements [88]. The genus displays wide variation in migratory strategy, with
339 resident, migrant, and partial migrants. However, most of the European *Turdus* are complete or
340 partial migrants [89], and photoperiod manipulations suggest annual migrations of at least one
341 species (*Turdus iliacus*) can reactivate latent *Bb*sl infections [36]. Future comparative studies
342 across *Turdus* thrushes that vary in both geography and migratory strategy could elucidate the
343 generality of this pattern and the broader inter-specific drivers of competence across this clade.
344 Prior work on competence for *Bb*sl in mammals suggests interspecific variation is shaped
345 by life history strategy. Fast-lived species, which display rapid development and high fecundity
346 at the expense of longevity, are more competent than slow-lived counterparts [26–28]. This
347 pattern is likely drive by tradeoffs with host immunity, such that fast-lived mammals invest more
348 in developmentally inexpensive innate defenses and in turn have weaker developmentally
349 expensive adaptive defenses [90]. Although host defense against *Bb*sl involves both innate and
350 adaptive mechanisms, robust *Bb*sl-specific antibody titers limit pathogen transmission to naïve
351 ticks [91]. This immunological basis to competence is likely to also occur in avian hosts, as fast-

352 lived bird species similarly invest less in adaptive defenses such as antibodies [92]. Our BRTs
353 provide some support for fast life histories shaping competence across avian hosts. Competent
354 birds had short incubation times and young that are small and fledge early, patterns consistent
355 with weaker antibody defenses that would facilitate *Bb*sl transmission to larvae. Yet competent
356 birds also had long lifespans, small clutches, and large eggs, which are consistent with a slow life
357 history that would support stronger adaptive immunity and thus weaker competence. Such
358 discrepancies could stem from competence occasionally occurring in families with slow life
359 histories, such as the Alcidae (i.e., *Fratercula arctica*) and Phasianidae (i.e., *Gallus gallus* and
360 *Phasianus colchicus*). While our sample size limited applying BRTs to only the passerines,
361 explicit comparisons of life history, antibody defense, and competence across the Passeriformes
362 could provide more robust and mechanistic tests of how pace of life shapes avian competence.
363 Our BRTs also identified CORT as an important predictor of avian competence for *Bb*sl.
364 Glucocorticoids such as CORT orchestrate physiological changes that allow animals to cope with
365 acute stressors; however, because elevated CORT can have deleterious effects over long
366 timescales, prolonged stressors can be immunosuppressive [93]. For example, prior work on
367 West Nile virus has shown that persistently elevated CORT can amplify competence by
368 increasing pathogen loads in birds and prolonging their infectious periods [94]. However, we
369 found that competent bird species were more likely to have lower baseline concentrations of this
370 hormone. At baseline, CORT has mostly metabolic functions that regulate energy storage and
371 mobilization, allowing animals to meet energetic demands and respond to adverse conditions
372 [93]. Low baseline CORT could also be linked to *Bb*sl competence by its association with
373 breeding latitude. Birds tend to display lower baseline CORT at high latitudes, which could
374 facilitate continued breeding in the face of suboptimal environments [95]. Such a mechanism

375 would be compatible with our finding that *Bb*sl competent species also generally breed at high
376 latitudes. Birds breeding further from the equator can have stronger tradeoffs between arms of
377 the immune system, such that high-latitude avian hosts mount weaker adaptive responses [96].
378 Birds breeding at high latitudes could thus display weaker antibody-mediated defenses that
379 increase *Bb*sl competence. Sampling *Bb*sl-competent birds across latitudinal gradients could
380 characterize such immunity tradeoffs and test if these restrict bird-to-tick transmission [97].
381 Alongside breeding latitude, our trait-based analyses identified several other predictors
382 related to bird geography and annual cycles, including low elevation, large distributions, and
383 negative migratory dispersion. For the latter, such values indicate avian species with a greater
384 diversity of migratory movements from their wintering to breeding grounds [71]. Associations
385 between more diverse spring migrations and competence could be driven by the physiological
386 changes incurred during this phase of the annual cycle, as long-distance movements demand
387 large energy expenditures that can in turn impair immune function [98]. These energetic costs
388 and shifts in immunity could cause latent *Bb*sl infections to reactivate, as previously illustrated
389 for redwings (*Turdus iliacus*) at the onset of migratory restlessness [36]. Such a mechanism
390 could facilitate competent birds arriving at their breeding grounds especially primed to infect
391 larval ticks. The generally positive association between migratory distance and competence
392 likewise supports the idea that longer biannual movements, in being more energetically costly,
393 could further promote these relapse events. Future work could explicitly test this hypothesis by
394 longitudinally sampling *Bbs*l-competent bird species across their annual cycles [99]. Similarly,
395 mathematical models of latent and relapsing infections could be expanded into a migratory
396 network to further understand the contexts when "migratory relapse" increases risk [100,101].

397 Results of our clade- and trait-based analyses also inform the surveillance of specific
398 species of wild birds for their contribution to the enzootic cycle of *Bb*sl and possibly other tick-
399 borne pathogens. In particular, phylogenetic factorization suggested unsampled *Turdus* thrushes
400 are especially likely to be competent, and our BRTs identified at least 14 unsampled species of
401 this genus as having a greater than 50% probability of being capable of infecting larvae (Table
402 S5). Similarly, this analysis suggested *T. obscurus* to be a likely false negative in our dataset
403 [85]. Some species such as *T. grayi* are known to be parasitized by ticks [102], whereas others
404 such as *T. torquatus* and *T. nigriceps* have had engorged nymphs test positive for *Bb*sl [83,103].
405 More broadly, the predicted probabilities from our BRTs displayed high phylogenetic
406 signal, suggesting general lineages of competent birds. Alongside the *Turdus*, the Parulidae
407 (New World warblers), Laridae (seabirds), Emberizidae (buntings), and Icteridae (icterids) had
408 relatively large numbers of likely but unsampled reservoirs. As with the *Turdus*, several species
409 in these families have had blood or nymphal ticks test positive for *Bb*sl, such as *Parkesia*
410 *motacilla* [81] and *Rissa tridactyla* [104]. Because some of these likely competent birds can be
411 common in suburban or urban habitats and could have unrecognized contributions to human
412 Lyme borreliosis risk [48,49], we suggest they be prioritized for spatiotemporal studies of
413 infection dynamics to identify when and where these species are most likely to infect ticks [105].
414 Experimental *Bb*sl infections and xenodiagnosis could also confirm competence of such species.
415 In addition to intrinsic factors, extrinsic environmental change could play an important
416 role in shaping how known and likely competent birds contribute to *Bb*sl dynamics and human
417 disease risk. Climate shifts and urbanization could alter bird geographic distributions and within-
418 host processes that influence intra-specific variation in competence. For the former, the breeding
419 distributions of many North American bird species are shifting north with climate change [106],

420 which could synchronize phenologies of competent birds and questing ticks if vectors also
421 expand northward [107]. Alternatively, warmer temperatures could facilitate shifts toward
422 residency, as observed for *Bb*sl-competent bird species such as *Turdus merula* [108]. If such
423 species become resident in parts of their range where ticks are abundant, sedentary behavior
424 could increase vector exposure and amplify bird–tick transmission cycles. Similarly, several
425 *Bb*sl-competent bird species (e.g., *Sylvia atricapilla*, *Turdus migratorius*, *Junco hyemalis*) and
426 unsampled but likely reservoirs (e.g., *Spinus tristis*) have shortened migration or become entirely
427 resident owing to abundant food in urbanized habitats [109–111]. However, urban residency
428 could also decrease host competence (e.g., if supplemental food increases antibody defense
429 [112]) or facilitate bird-to-tick transmission (e.g., if artificial night at light extends infectious
430 periods [113]). Combining sampling of known or likely competent birds across urban–rural
431 gradients or their historic and recent range with mathematical models could help forecast how
432 environmental change will alter bird distributions, competence, and contribution to *Bb*sl risk.
433 In conclusion, we demonstrate that host ability to transmit pathogens to new hosts or
434 vectors is predictable on the basis of ecological and evolutionary characteristics of bird species
435 within the Lyme borreliosis system. By combing flexible phylogenetic and trait-based analyses,
436 our work generates testable hypotheses for future comparative and theoretical studies of tick-
437 borne disease (e.g., how life history and migratory strategies shape competence) alongside
438 predictions that can inform bird surveillance efforts for *Bb*sl and similar pathogens (e.g.,
439 *Anaplasma*, *Ehrlichia*, *Babesia*) in the context of environmental change. Moving forward,
440 greater attention to the factors that shape competence within and between species could improve
441 our ability to predict and manage wild reservoirs for emerging infectious diseases more broadly.
442

Acknowledgments

We thank BirdLife International for providing avian distribution data, Tao Huang for assistance with data processing, and JP Schmidt for technical advice on BRTs. We also thank Ellen Ketterson, Alex Jahn. and members of the Ketterson lab for feedback on this manuscript.

Data availability

All spatiotemporal bird-fed larvae *Bb*sl infection prevalence data and binary competence per sampled avian species are available in Dryad Digital Depository [114]: https://datadryad.org/stash/share/4shvYd0_lCUkjEFhO5g1yc95sSLUfq3zbrd79_1J-0Q. All bird species feature data used in the BRTs are available from their original sources [66–70].

Funding

DJB was supported by an appointment to the Intelligence Community Postdoctoral Research Fellowship Program, administered by Oak Ridge Institute for Science and Education through an interagency agreement between the U.S. Department of Energy and the Office of the Director of National Intelligence. BAH was supported by the National Science Foundation Ecology and Evolution of Infectious Diseases program (DEB-1717282 and DEB-1619072).

Competing interests

We declare no competing interests.

Figures and legends

Figure 1. Global distribution of *Bb*sl infection prevalence in tick larvae sampled from wild birds. (A) Sampled countries are shown with a black border alongside spatiotemporal bird–tick–*Bb*sl prevalence estimates, which are sized by magnitude and colored by georegion. Shapefiles of the 91 competent species are overlaid in black and are from BirdLife International and the Handbook of the Birds of the World [70]. Larval infection prevalence is plotted by absolute latitude (B), year (C), and season (D), with each point representing a sampled bird–tick–*Bb*sl association; points are colored by region and jittered to reduce overlap. Black points and lines (D) display back-transformed predicted means and 95% confidence intervals from the MEM (Table S3).

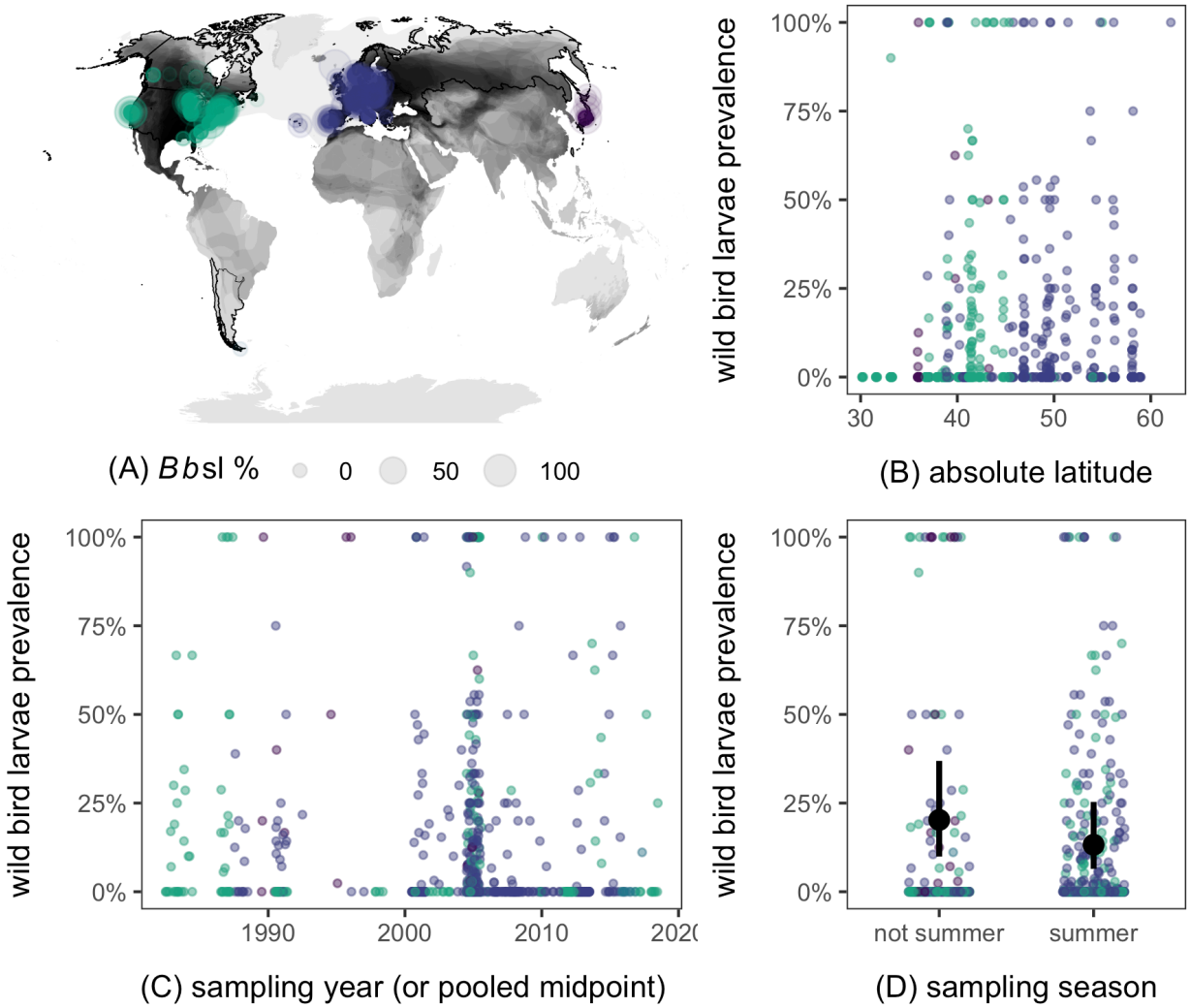
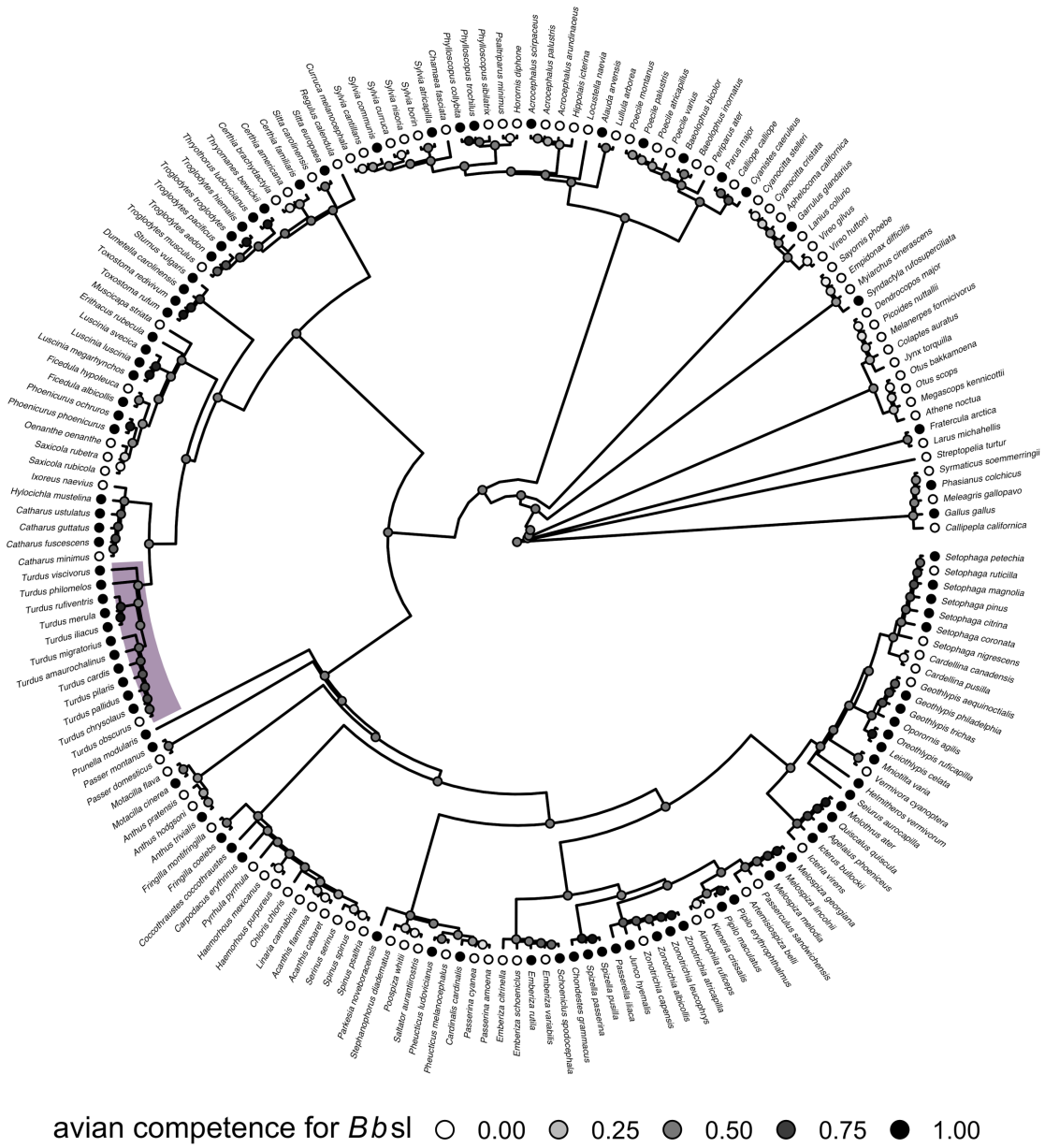


Figure 2. Phylogenetic patterns in avian competence for *Bb*sl. The avian phylogeny displays observed species binary competence, and highlighted clades are those with significantly different competence from the paraphyletic remainder using phylogenetic factorization. Nodes show the mean posterior probabilities of being competent estimated from stochastic character mapping.



479 Figure 3. BRT performance in identifying traits predictive of avian competence for *Bb*sl and

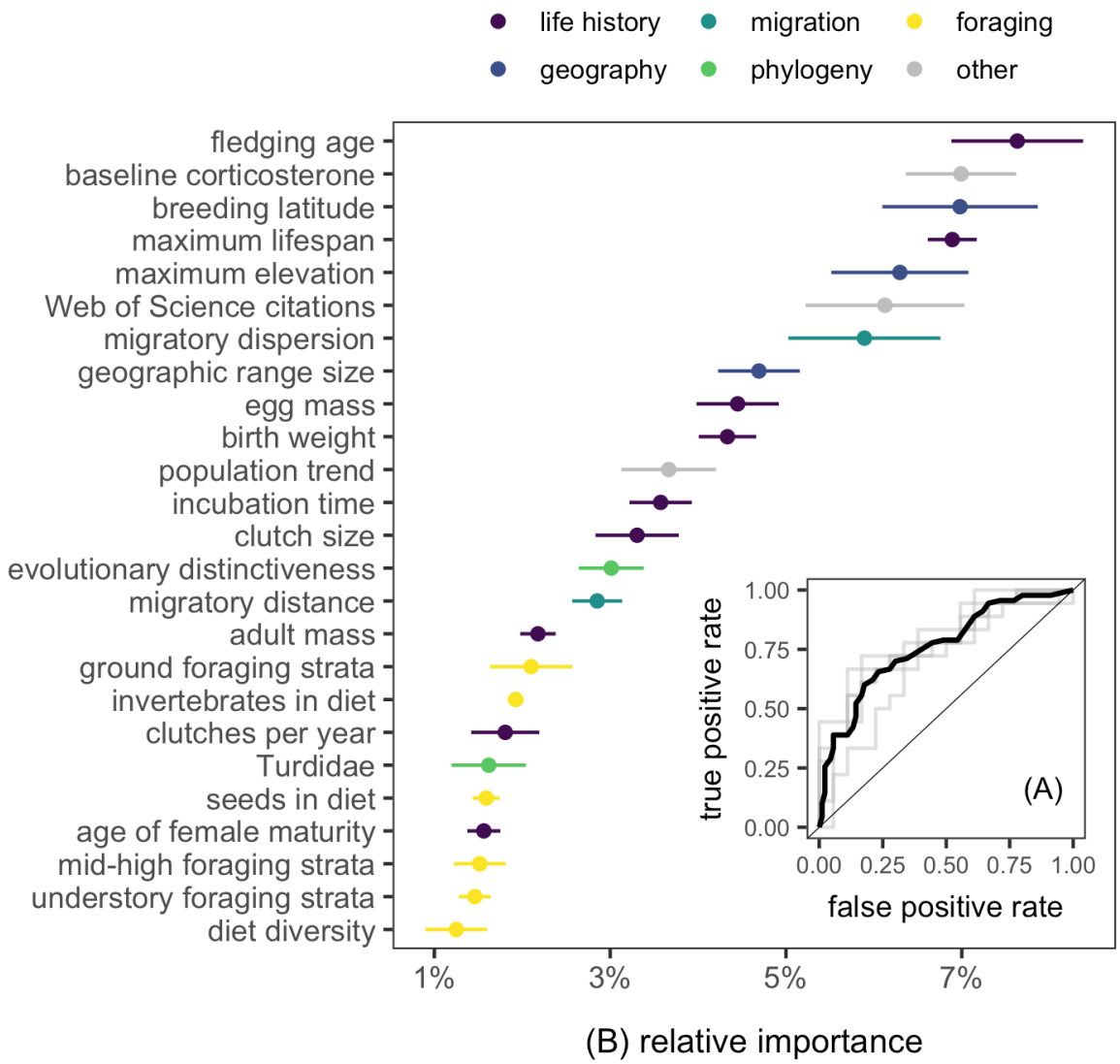
480 their relative importance across five random partitions of training and test datasets. (A) Accuracy

481 is shown by the receiver operator curves obtained from 10-fold cross-validation on test data.

482 Grey lines show curves from each partition, whereas the black line displays the mean. (B)

483 Relative importance per feature is shown as the mean and standard error across partitions. Only

484 features with mean importance greater than 1% are shown (Table S4).



485

486

Figure 4. Trait profile of a *Bb*sl-competent avian species. Partial dependence plots of the top predictors across BRTs applied to five random partitions of training and test data are shown in order of mean relative importance. Grey lines or point show the marginal effect of a given variable for predicting *Bb*sl competence from each random data partition, whereas the black lines or squares display the average marginal effect. Histograms and rug plots display the distribution of continuous and categorical predictor variables, respectively, across the 183 sampled birds.

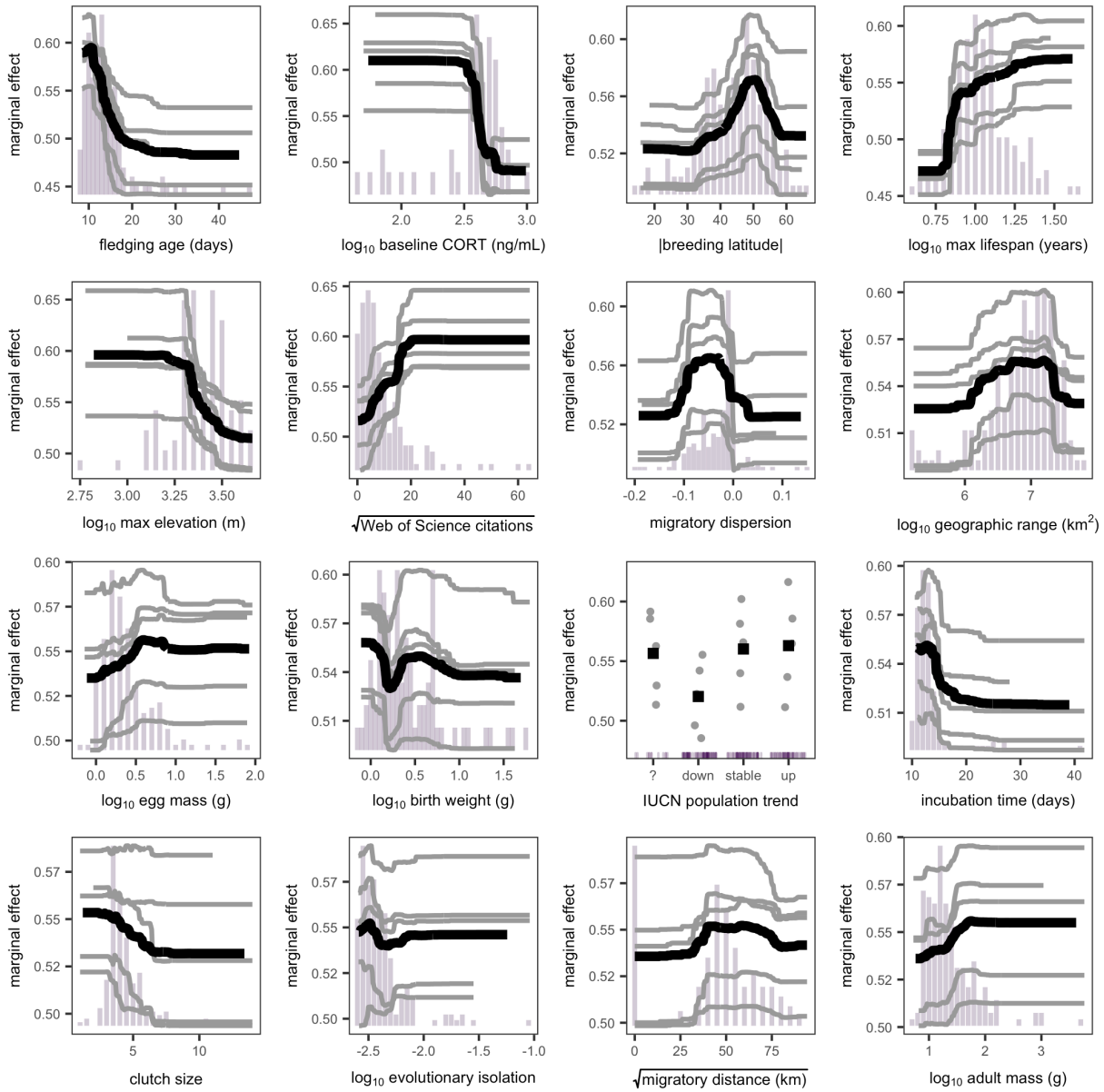
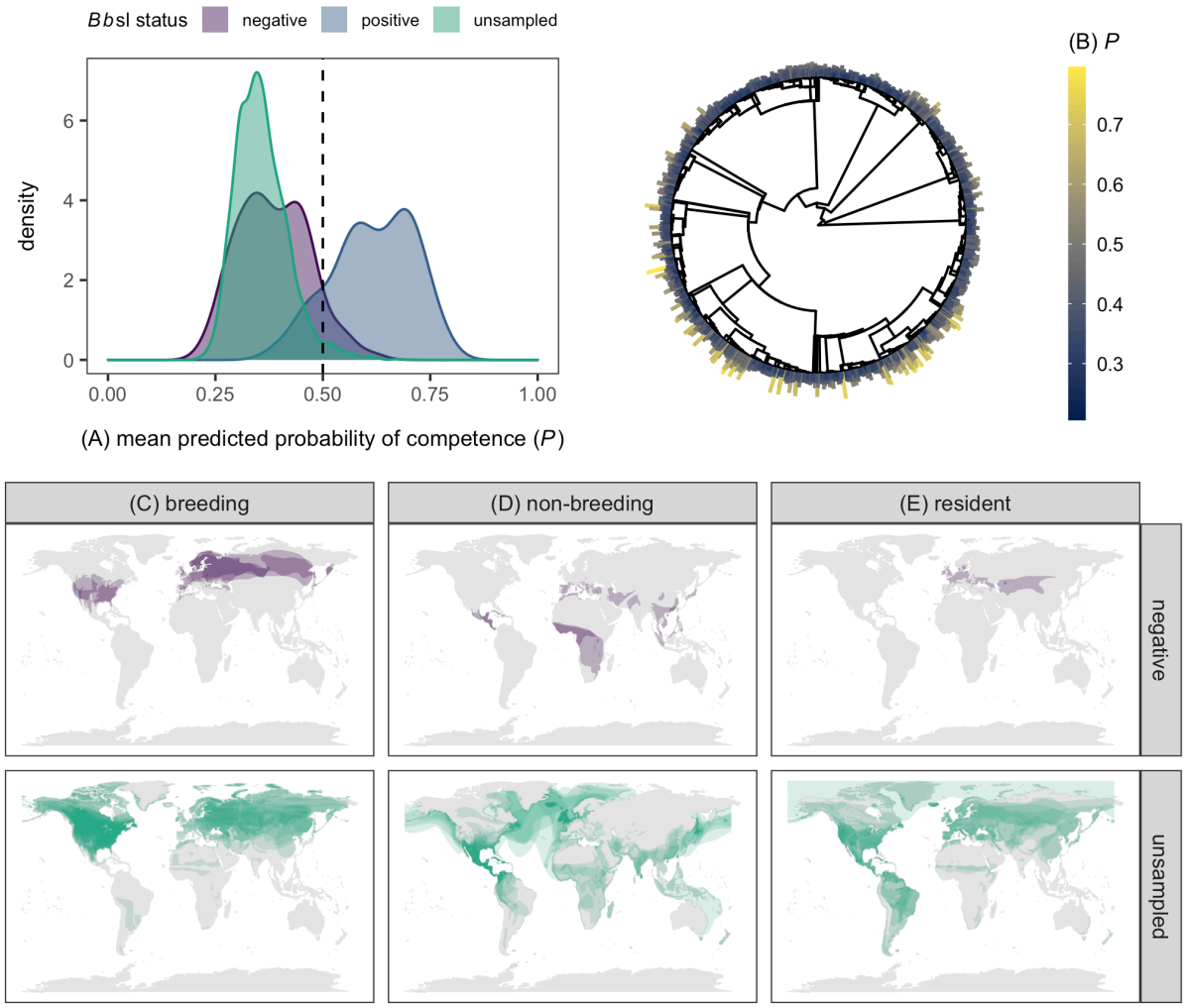


Figure 5. Distribution of the mean predicted probabilities of *Bb*sl competence across the 39 sampled avian families. (A) Density plots show mean predicted probabilities for currently negative, positive, and unsampled species, and these propensity scores are also shown across the avian phylogeny (B). The geographic distributions of species within a mean probability of over 50% are shown across by their breeding (C), non-breeding (D), and resident ranges (E). Shapefiles are from BirdLife International and the Handbook of the Birds of the World [70].



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