1

2 MR. JEFF J. SHI (Orcid ID : 0000-0002-8529-7100)

3

4

6

7

8 **Ecomorphological and phylogenetic controls on sympatry across extant bats**

9 Running title: Controls on sympatry across bats

10 Jeff J. Shi*[1,2], Erin P. Westeen[1,2], Nathan T. Katlein[3], Elizabeth R. Dumont[4,5], Daniel L.

11 Rabosky[1,2]

12 [1]*Museum of Zoology, University of Michigan, Ann Arbor, MI 48109, USA*

13 [2]*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI*

14 *48109, USA*

15 [3]*Department of Biology, University of South Alabama, Mobile 36688, AL, USA*

16 [4]*School of Natural Sciences, University of California Merced, Merced, CA 95343, USA*

17 [5]*Department of Biology, University of Massachusetts Amherst, Amherst, MA 01003, USA*

18 *Corresponding author: jeffjshi@umich.edu

19

20

21 All code and data will be archived on Dryad upon final acceptance of manuscript.

22

23

24 Abstract word count: 227

25 Total word count (abstract + text + references): 6908

26 Number of figures: 4

27 Number of tables: 2

28 Number of appendices: Narrative Supporting Information document split into 16 sections

29

30 **Abstract**

Aim: Macroecological patterns of sympatry can inform our understanding of how ecological and evolutionary processes govern species distributions. Following speciation, both intrinsic and extrinsic factors may determine how readily sympatry occurs. One possibility is that sympatry most readily occurs with ecological divergence, especially if broad-scale co-occurrence is mediated by niche differentiation. Time since divergence may also predict sympatry if hybridization and gene flow lead to the collapse of species boundaries between closely-related taxa. Here, we test for ecological and phylogenetic predictors of sympatry across the global radiation of extant bats.

Location: Global

Taxon: Bats (Order Chiroptera)

Methods: We used a combination of linear mixed modeling, simulations, and maximum-likelihood modeling to test whether phylogenetic and ecomorphological divergence between species predict sympatry. We further assess how these relationships vary based on biogeographic realm.

Results: We find that time since divergence does not predict sympatry in any biogeographic realm. Morphological divergence is negatively related to sympatry in the Neotropics, but shows no relationship with sympatry elsewhere.

Main conclusions: We find that bats in most biogeographic realms co-occur at broad spatial scales regardless of phylogenetic similarity. Neotropical bats, however, appear to co-occur most readily when morphologically similar. To the extent that pairwise phylogenetic and morphological divergence reflect ecological differentiation, our results suggest that abiotic and environmental factors may be more important than species interactions in determining patterns of sympatry across bats.

Keywords: sympatry; evolutionary ecology; ecomorphology; macroecology; macroevolution; Chiroptera

Introduction

Species' geographic distributions and their ranges reflect the interplay between ecological processes and evolutionary patterns (Ricklefs, 2007; Grossenbacher *et al.,* 2015). In many ways, geographic distributions are unifying units of macroecology and macroevolution, as they are determined by interactions with other species and the environment, and can govern both

62 speciation and extinction. The extent and spatial configuration of species ranges can be

63 controlled by ecological factors, including species interactions (Sexton *et al.*, 2009; Louthan *et*

64 *al.,* 2015), abiotic characteristics of the environment (Terribile *et al.,* 2009), and dispersal

65 (Jønsson *et al.,* 2016). Teasing apart these factors is central to macroecological and

66 macroevolutionary research, especially as researchers strive to understand how ecological

67 processes like competition may change distributions and community compositions over

68 macroevolutionary time (Pigot & Tobias, 2013; 2014).

69   The configuration of species ranges can reflect patterns of sympatry across species,

70 where "sympatry" refers to broad-scale spatial overlap between species regardless of whether

71 they co-occur in local syntopy. Sympatry at this scale can have multiple controlling factors. The

72 probability of broad-scale sympatry could be dependent on competitive interactions that lead to

73 character displacement and niche divergence (Brown & Wilson, 1956; Stuart & Losos, 2013;

74 Cardillo & Warren, 2016), or even to local extinction due to competitive exclusion (Connell,

75 1972; Bengtsson, 1989; Silvestro *et al.,* 2015). These general hypotheses invoke stabilizing

76 mechanisms (*sensu* Chesson, 2000) as a link between divergence and sympatry. Broad-scale

77 sympatry could also be unrelated to resource competition, and instead occurs only in the absence

78 of hybridization, which collapses incipient species (Grant & Grant, 1997; Taylor *et al.,* 2006). If

79 divergence and reproductive isolation generally increase with time, and if those factors are

80 important controls on sympatry, then we should expect to find a positive correlation between

81 phylogenetic divergence and the probability of sympatry (Barraclough & Vogler, 2000).

82   Other models also raise the possibility that greater ecological divergence does not predict

83 extant sympatry. Instead, sympatry can reflect the sorting of regional species pools into

84 communities based on habitat. Species may be more likely to co-occur at low levels of

85 divergence if environmental filtering selects for species with phylogenetically-conserved traits

86 (Webb, 2000; Graham & Fine, 2008; Cavender-Bares *et al.,* 2009) and are thus not structured by

87 present-day competitive interactions (McPeek & Brown, 2000). Some traits may also reflect

88 equalizing mechanisms that reduce fitness differences among organisms (Chesson, 2000; Adler

89 *et al*, 2006), and thus would promote sympatry among more similar taxa.

90   The relationships among sympatry and phylogenetic or phenotypic divergence are

91 unknown across much of the tree of life. Sympatry and divergence are positively related in birds,

92 suggesting a link between local species interactions and broad-scale distributions (Weir & Price,

93   2011; Pigot & Tobias, 2013). Many non-volant mammalian clades, however, exhibit no

94   relationship between sympatry and phylogenetic divergence (Fitzpatrick & Turelli, 2006). Such a

95   pattern could indicate that ecological divergence accumulates rapidly in these groups, or that in

96   many cases, sympatric species are not syntopic and do not interact ecologically.

97   Extant bats (Order Chiroptera) are particularly tractable for exploring the influences of

98   species interactions, phylogeny, and patterns of sympatry at a macroecological scale because of

99   their cosmopolitan distribution and the breadth of their diversity (Jones *et al.,* 2005; Simmons,

100   2005; Shi & Rabosky, 2015). Their potential for high dispersal via flight may mean that species

101   interactions are more important than landscape or edaphic features for predicting spatial patterns.

102   As regional dispersal can also erode any local signals of species interactions, bats may be a

103   system where sorting patterns play a disproportionate role.

104   Bats feed on a wide variety of resources, including arthropods, vertebrates, fruits, and

105   nectar (Nowak, 1994; Simmons & Conway, 2003). Competition for these resources structures

106   many bat communities at local scales, such as within Neotropical savannahs (Aguirre *et al.,*

107   2002; Estrada-Villegas *et al.,* 2012). There is also evidence that some bat communities are

108   structured by echolocation frequency and trophic ecology (Findley & Black, 1983; Siemers &

109   Schnitzler 2004; Moreno *et al.,* 2006). However, we do not know the extent to which

110   competitive interactions for resources among bats are important controls on sympatry, or how

111   these controls may vary across global bat diversity (Figure 1).

112   Bat ecology is tightly coupled with morphology; this is especially well-studied with

113   trophic ecology and skull morphology. The shape and size of bat skulls reflect the link between

114   physiological performance and the ability to capture and process foods with highly variable

115   mechanical properties (Saunders & Barclay, 1992; Dumont, 2004; Nogueira *et al.,* 2009; Santana

116   *et al.,* 2010; Santana & Cheung, 2016), and thus are often used as proxies for ecological metrics

117   in the absence of observational and experimental data. In some families, skull morphology is also

118   closely tied with echolocation ability, another dimension of trophic ecology (Santana & Lofgren,

119   2013; Curtis & Simmons, 2017). While relative performance data among coexisting bat species

120   are rare, morphological divergence is often considered to be at least one predictor of ecological

121   divergence.

122   In this study, we test whether overall, broad patterns of sympatry can be predicted by

123   phylogenetic and/or morphological divergence across extant bats. With range data and museum

124   specimens, we use phylogenetic linear mixed-modeling to test predictors of sympatry, and a

125   maximum-likelihood framework to model the probability of sympatry as a function of age and

126   morphological distance. We explore the influence of phylogenetic dependence on our range data,

127   and propose a general framework for testing if sympatry can be related to various metrics of

128   divergence.

129

130   **Materials and Methods**

131   *Overall framework and scope*

132   We explored how sympatry varies with two pairwise metrics of divergence: time to the

133   most recent common ancestor, and ecomorphological divergence as represented by Euclidean

134   distances between skulls in morphospace. We focused on the binary *presence* (0/1) of broad-

135   scale sympatry, given a threshold of continuous *range overlap* (a percentage) in a species pair.

136   Our framework involved three approaches: (1) pairwise linear mixed-models to test divergence

137   predictors of sympatry, accounting for random effects of phylogeny and species identity; (2)

138   maximum-likelihood modeling of how multiple parameters of sympatry may vary with pairwise

139   divergence among sister taxa (*sensu* Pigot & Tobias, 2013); (3) randomizations that infer the null

140   distributions of sympatry across species pairs given no relationship with divergence. For the

141   pairwise linear mixed models (approach 1), we integrated data from all species pairs. In the

142   maximum-likelihood models (approach 2), we focused on a subset of sister species, where we

143   might expect species interactions to be strongest. All analyses used the species-level Chiroptera

144   phylogeny of Shi & Rabosky (2015) (Appendix S2), which contains 812 of the roughly 1300

145   extant species of bats.

146   All analyses were divided into biogeographic realms, representing regional pools of

147   species that could reasonably co-occur in the absence of constraints on sympatry. We used

148   World Wildlife Fund (WWF) realms (Olson *et al.,* 2001), though we combined the small

149   Oceanic and Australasian realms and excluded bats endemic to Madagascar, Seychelles, and

150   Comoros from the Afrotropics. We divided our analyses to infer how predictors of sympatry

151   vary by region, to capture species pools that sort into communities (Lessard *et al.,* 2012), and to

152   minimize one potential source of biogeographic bias. To illustrate this, consider the different

153   species pools between the Indian Ocean islands and the mainland Afrotropics. Even if taxa in

154   these two regions are rarely found in sympatry due to ancient vicariance, pairwise allopatry

155   states would be repeatedly counted in all comparisons between descendant species of the two

156   regions, regardless of the time since divergence. This would artificially bias relationships

157   between divergence and sympatry in a negative direction (*e.g.* greater divergence being

158   correlated with lower probabilities of sympatry; see Appendix S3).

159

160   *Morphological data*

161   We took 9 linear measurements (Appendix S4: Table S3) from bat skulls at the

162   University of Michigan Museum of Zoology (UMMZ) and the American Museum of Natural

163   History (AMNH). These measurements followed Dumont (2004) and Dumont *et al.* (2012), who

164   linked ecomorphology and diversification in the family Pteropodidae and the superfamily

165   Noctilionoidea. From species-level averaged measurements, we calculated pairwise Euclidean

166   distances in 9-dimensional trait space between all pairs as our metric of pairwise

167   ecomorphological divergence.

168   We targeted 241 species across fourteen of the twenty extant families of bats based on

169   available specimens, representing roughly 30% of the phylogeny.

170

171   *Spatial data and sympatry*

172   We used species ranges from the IUCN's Red List of Threatened Species (IUCN, 2016),

173   though with modifications to the superfamily Noctilionoidea (Appendix S5). We targeted

174   available range polygons based on our phylogeny.

175   With these polygons, we used the *rgeos* and *maptools* R packages to code sympatry state

176   for all pairs of extant bat species in the spatial dataset. We first calculated geographic range

177   overlap with the Szymkiewicz-Simpson coefficient, or the sum area of overlap divided by the

178   range size of the species with the smaller range, for each species pair. We then designated each

179   pair of bat species as sympatric or allopatric based on a threshold of 20% range overlap (as in

180   Pigot & Tobias, 2013), though we also report results from more conservative thresholds

181   (Appendix S6). We decomposed our data into binary states, as opposed to continuous overlap, as

182   the latter metric is more sensitive to assumptions of speciation mode (Phillimore *et al.*, 2008).

183

184   *Phylogenetic linear mixed-modeling*

185   To test if overall pairwise sympatry within biogeographic realms is predicted by

186 divergence, we used phylogenetic linear mixed-models (PLMMs). PLMMs are particularly

187 flexible for their ease of interpretation and implementation in a standard mixed-modeling

188 framework, and the ability to test for distinct fixed and random predictor(s) on response

189 variable(s). Furthermore, they can easily incorporate paired, continuous, and categorical data.

190   We used Markov chain Monte Carlo to simulate posterior distributions of model

191 parameters using the *MCMCglmm* R package (Hadfield, 2010). Our PLMMs took the general

192 form: $S_{i,j} = \beta X_{i,j} + Z_1 u_{i,j} + Z_{2,i} + Z_{2,j}$. Our response variable S corresponded with the

193 probability of sympatry for a given species pair i and j and was related to the observed data

194 (sympatry/allopatry) using a probit ("threshold") link function. We tested for a vector of fixed

195 effects β, given a matrix X of divergence metric(s) between species i and j. We then incorporated

196 two distinct classes of random effects Z into our PLMMs: the hierarchical effect of phylogenetic

197 structure (Z_1), and species identity (Z_2) (Hadfield & Nakagawa, 2010; Tobias *et al.,* 2014). Z_1

198 accounted for the possibility that fixed effects depend on phylogenetic node structure ($u_{i,j}$) and

199 thus subclade identity, while Z_2 accounted for the multiple times each unique species i and j was

200 represented in our datasets. We ran all models with a standard inverse-gamma prior on the

201 variance structure of our random effects (Hadfield, 2010). We checked all MCMC output for

202 autocorrelation at different levels of sample thinning, while also confirming high (variance >

203 1000) effective sample sizes.

204   As we did not have representative morphological data for every species, we ran two

205 groups of PLMMs with varying β and X vectors. The first set of PLMMs only tested for β_1, the

206 effect of phylogenetic divergence (in mya) on pairwise sympatry, with separate models for each

207 realm. For each model, we simulated the posterior distributions of model parameters using 20

208 million generations of MCMC simulation, sampling every 10,000 generations, with 10%

209 discarded as a burnin.

210   The second set of PLMMs tested for three fixed effects: (1) β_1, (2) β_2: the effect of

211 ecomorphological divergence, and (3) β_3: the interaction of both divergence metrics. β_3

212 accounted for the possibility that the strength of ecomorphological control depends on time since

213 divergence. Given the limited sampling of our morphological data, this second set was divided

214 into just the Nearctic and Neotropical realms, as well as the combined New World. We simulated

215 this second set of posterior distributions of model parameters using 10 million generations of

216　MCMC simulation, sampled every 5,000 generations, with 10% discarded as burnin, as these

217　were much smaller datasets.

218

219　*Modeling the probability of sympatry*

220　　　　We further used a maximum-likelihood (ML) framework to compare models where

221　multiple parameters that govern the relationship between sympatry and divergence can be

222　estimated. We fit models in which the probability of sympatry explicitly varies with phylogenetic

223　(*t*, time in mya) and/or morphological (*d*, pairwise Euclidean distance) divergence (Figure 2). We

224　tested covariates independently, and also in interaction (*td*), to account for scenarios where

225　morphological divergence has the most dramatic effect in close relatives. We restricted these

226　analyses to sister taxa represented in the tree, as we may expect to find the strongest signal of

227　divergence among young pairs. Although these pairs may not be true sisters, this restriction

228　accounted for phylogenetic nonindependence of data; this general approach was analogous to

229　that of Pigot & Tobias (2013). We performed the following analyses for all measured sister

230　species pairs, and for the subset composed of New World pairs, where the bulk of our

231　morphological data are represented.

232　　　　For these analyses, we treated the probability of sympatry as a binomially distributed

233　random variable with a single parameter θ. The likelihood L of observing any combination of

234　allopatry (0) and sympatry (1) states across pairs of species *i* and *j*, in a set of *n* species Y, was

235　thus denoted by $L = \prod_{i,j=1}^{n} Pr(Y_{i,j}|\theta)$, where $Pr(Y_{i,j}|\theta) \sim binom(\theta)$. θ, in turn, was

236　governed by three potential models of sympatry (Figure 2). For M1, θ was treated as a constant.

237　This model served as our null hypothesis: under this model, the ML estimate for the probability

238　of sympatry is simply the percentage of sympatric pairs in a given set Y.

239　　　　In M2, θ varied as an exponential decay function with *t*, *d*, or *td* as follows (written for *t*

240　alone): $\theta = \alpha(1 - e^{-kt})$. M2 reflected scenarios in which pairwise sympatry varied with

241　divergence. Because θ approaches an unfixed asymptote α, which is a parameter estimated from

242　the data, the model also accounted for the biological reality that some species pairs will simply

243　never become sympatric due to geographic or historical constraints (Figure 2). The rate

244　parameter *k*, which reflects how rapidly θ approaches α, was also estimated from the data, where

245　M2 reduces to M1 as *k* approaches infinity.

246   In our final model (M3), θ varied logistically with t, d, or td as follows (written for t

247 alone): $\theta = \dfrac{\alpha}{1 + e^{-k(t-w)}}$. M3 represented a scenario analogous to one proposed by Pigot &

248 Tobias (2013, 2014), where θ is correlated with time and/or ecomorphology, but includes a lag or

249 delay parameter (w) before sympatry is readily attained (Figure 2). This w parameter may

250 represent a minimum threshold of morphological divergence to avoid competition, or a minimum

251 age threshold to avoid hybridization, among other possibilities. In this case, α, w, and the rate

252 parameter k were all estimated from the data, where M3 will also reduce to M1 when $w = 0$ and k

253 approaches infinity.

254   We fitted all seven potential models to sister species data using the *bbmle* R package. We

255 tested overall model fit using the corrected Akaike Information Criterion (AICc). Our model

256 setup also allowed us to explicitly test hypotheses using likelihood-ratio tests within the three

257 groups of related models (one group for each metric of divergence t, d, or td, where M1 was

258 always the null hypothesis of no relationship between divergence and θ). Given our sample sizes

259 of sister species pairs, we also explored false positive rates using randomly simulated datasets

260 (Appendix S7).

261

262 *PLMM and ML model validation*

263   We applied both our PLMM and ML model-fitting approaches to the phylogenetic,

264 morphological, and spatial data of sister species pairs of Neotropical ovenbirds (Family

265 Furnariidae) from Pigot & Tobias (2013), who concluded that ecomorphological and

266 phylogenetic divergence affected the rate at which species pairs became sympatric (Appendix

267 S9). By using the same data as Pigot & Tobias (2013), we tested whether our analytical

268 framework could recover similar relationships between divergence and sympatry as reported in

269 their study.

270

271 *Sympatry-age relationships*

272   Finally, we inferred a null distribution of the relationship between pairwise sympatry

273 state and time since divergence by using a set of randomizations (Figure 3). We randomly

274 assigned species (and thus ages) to ranges, for each extant bat, and then fit a logistic model for

275 sympatry as a function of age. This randomization process, representing a model where the

276 pattern of sympatry across bats is random with respect to divergence time, was repeated 500

277 times. These randomizations established a distribution of randomized log-odds from logistic

278 models, and we compared this to the empirical age-overlap relationship. We performed these

279 randomization tests for each of the 6 WWF biogeographic realms.

280

281 **Results**

282 *Data summary*

283   Overall, we report results for 696 bats with spatial data that are included in our

284 phylogenetic tree. We measured 1073 adult specimens at the UMMZ and combined these data

285 with the previously published AMNH data of Dumont *et al.* (2012) (mean specimens/species =

286 3.86, *sd* = 3.53) .

287   Regional pairwise sympatry among bats is consistently high, given a 20% threshold of

288 overlap (Table S1; weighted average: 42.2% of pairs are sympatric). This does not appear to be

289 correlated with regional species diversity or realm size, as even the relatively low diversity but

290 large Nearctic realm has over 50% of its species pairs in sympatry. In both New World realms

291 (the Neotropics and the Nearctic), 50% or more of species pairs are sympatric, with average

292 overlap percentages near 40%. We note that in all realms but the Palearctic, average overlap is

293 above our base threshold for sympatry.

294

295 *PLMM results*

296   *MCMCglmm* returns pMCMC-values, which are two-tailed calculations of the proportion

297 of simulations where fixed effects differ from zero. We use these to assess the significance of

298 fixed effects in PLMMs, and find that time since divergence does not significantly predict

299 sympatry in any realm (Table 1). We can also use highest posterior density intervals and

300 credibility intervals to evaluate our posterior distribution, but in our analyses all these methods

301 are concordant (see Supporting Information).

302   In the New World bats, when we incorporate ecomorphological divergence, we find that

303 there are notable differences between Nearctic and Neotropical bats. There are no significant

304 effects of divergence in the Nearctic. However, we recover significant evidence for a negative

305 relationship between ecomorphological divergence and binary sympatry state in the Neotropics

306 (Table 2; Figure 4). While there is some uncertainty in the specific relationship - particularly in a

307 threshold of ecomorphological divergence that makes sympatry less likely - there is extremely

308 strong support for a negative signal in the data (Figure 4b). This negative relationship does not

309 appear to be driven by divergent outliers, as we recover concordant results with an analysis on a

310 smaller subset of our data (Figure 4c, Appendix S15). Across the entire New World (Nearctic +

311 Neotropics), the interaction of phylogeny with ecomorphology has a negative effect on sympatry,

312 though the two variables are not significant predictors independently (Table 2). These negative

313 relationships imply that sympatry is actually less likely as divergence increases.

314   If we subsample by varying the threshold overlap percentage for sympatry, we generally

315 recover concordant results in our PLMMs, implying that our main analyses are conservative in

316 estimating predictors of sympatry (Appendix S6).

317

318 *ML models of the probability of sympatry*

319   We fit our ML models of sympatry to 67 sister species pairs, as well as 53 New World

320 sister species pairs. A simple, null model where all species pairs share a common probability of

321 sympatry, regardless of any type of divergence, was the best-fitting model (Appendix S7).

322

323 *PLMM and ML model validation*

324   We recover, as do Pigot & Tobias (2013), positive effects of both divergence time and

325 ecomorphology on sympatry in furnariid sister species with both PLMMs and our ML models

326 (Appendix S9). We specifically find strong evidence for models with a lagtime, further

327 suggesting that species interactions mediate sympatry.

328

329 *Sympatry-age relationships*

330   In each WWF biogeographic realm, the null distributions of age-sympatry relationships

331 (calculated from range randomizations as log-odds from logistic regressions between sympatry

332 state and time since divergence, as described in Figure 3) are centered around 0, as expected. The

333 empirical age-sympatry relationship does not appear to significantly deviate from the null

334 distribution in any realm, though it skews slightly negative in the Afrotropics (Appendix S11).

335

336 **Discussion**

337 *Divergence time and sympatry*

338   We find no significant effects of age on pairwise patterns of sympatry (Table 1). We also

339   find that there is no significant difference between a process-neutral null model and any ML

340   model where the probability of sympatry varies with age (Appendix S7). Age is often intrinsic to

341   any explanation for patterns of sympatry, especially given correlations of divergence with time.

342   However, our finding is consistent across all biogeographic realms. Therefore, even though one

343   explanation for this null pattern is that divergence and time are simply not well-correlated in

344   bats, it is unlikely this is true across all families and realms (Appendix S16).

345

346   *Ecomorphology and sympatry in the New World*

347   We find no evidence for ecomorphological controls on sympatry among the measured

348   Nearctic bat species, but find that there is a negative relationship between ecomorphological

349   divergence and sympatry among Neotropical bats (Figure 4b, c). We also find a negative

350   interaction effect of age and ecomorphology on sympatry across New World bats as a whole in

351   our PLMMs (Table 2). As noctilionoids are characterized by strong relationships between

352   ecology and highly specialized morphology (Dumont *et al.*, 2012), we may have expected to see

353   the strongest link between divergence and sympatry in this realm. Nevertheless, Neotropical

354   species pairs are more likely co-occur when they are morphologically similar. Multiple

355   hypotheses could explain this pattern, including community assembly via environmental

356   filtering, or within-realm sorting that biases where similar species are most likely to be found

357   (Webb 2000; Leibold & McPeek, 2006; Graham & Fine 2008; Cavender-Bares *et al.,* 2009).

358   Within noctilionoids, there are numerous examples both of clades that are filtered by resource

359   availability, leading to sympatry among the most similar pairs, and those that assemble into

360   communities based on stabilizing mechanisms (Villalobos & Arita 2010). As our morphological

361   data are partial proxies for ecological divergence, a deeper dataset that addresses feeding

362   mechanics and performance may yield a fine-grained picture of how functional divergence

363   relates to co-occurrence within communities.

364   Despite the significant negative effect of ecomorphology in our PLMMs, our best-fitting

365   ML model is a simple one in which all pairs share a common probability of sympatry regardless

366   of phylogenetic or morphological divergence (Appendix S7). This discrepancy likely reflects a

367   fundamental difference between the two datasets. It is possible that the shorter timescales

368   associated with sister taxa are insufficient for accumulating enough ecomorphological

369 divergence to influence the processes governing sympatry. Our sister species dataset is also

370 relatively small, and it thus possible that statistical power was lower for these analyses.

371   The significant New World interaction effect of divergence metrics on sympatry in our

372 PLMMs (Table 2) likely reflects scale and differences between Nearctic and Neotropical bats.

373 Nearctic bats are predominantly insectivorous vespertilionoids, while the Neotropics are

374 dominated by their high richness of noctilionoid bats, which span the full breadth of bat feeding

375 diversity (Nowak, 1994; Simmons, 2005). We can interpret this significant effect as evidence

376 that, at the scale of the entire New World, we are most likely to find morphologically similar and

377 closely-related bats in sympatry. This is likely compounded by the fact that morphological

378 divergence among many Neotropical species can be relatively large, and is recent compared with

379 the relatively ancient (~50 mya) divergence of noctilionoids from Nearctic vespertilionoids (Shi

380 & Rabosky, 2015).

381

382 *Sympatry-divergence relationships across extant bats and potential causes*

383   Multiple interactions beyond resource competition can drive patterns of sympatry.

384 Mutualistic interactions with plants, or predation and parasitism (McIntire & Farjado, 2014;

385 Spiesman & Inouye, 2014) can govern spatial patterns. Some bat communities, their

386 distributions, and abundances are non-randomly structured with respect to other phenotypic

387 traits, including flight ability and echolocation (Norberg & Rayner, 1987; Schoeman & Jacobs,

388 2003; Siemers & Schnitzler, 2004; Santana & Lofgren, 2013; Corcoran *et al.,* 2014), as well as

389 available foraging and roosting habitats (Schoeman & Jacobs, 2011; Voss *et al.,* 2016). These

390 multiple pressures existing in conjunction could mask relationships between skull morphology

391 and sympatry. The framework we develop here is flexible to the integration of other metrics of

392 divergence, including measures of ecological performance that more directly test for

393 competition.

394   Low competition for resources among bats may also decouple divergence from sympatry,

395 especially if resources like aerial insects are ubiquitous and plentiful at night (Fenton & Thomas

396 1980; Fleming, 1986). Studies that test for resource competition among bats are uncommon, and

397 there is mixed evidence depending on guild, body size, and seasonality (Heithaus *et al.*, 1975;

398 Swift & Racey, 1983; Kingston *et al.*, 2000). Divergence may also occur in situations when

399 species historically co-occurred, but exist presently in allopatry, thereby masking the signature of

400 the sympatry-divergence relationship (Anacker & Strauss, 2014). Furthermore, we must also

401 acknowledge that ranges themselves are inherited and non-independent properties of species.

402 While we partially account for this in the random effects of our PLMMs, there is considerable

403 room for the integration of models that simulate range heritability and evolution.

404   Divergence may also be unrelated to sympatry if abiotic filtering is the dominant process

405 shaping species assemblages at the spatial scales considered here. For example, elevation and

406 water availability (Henry *et al.,* 2004; McCain, 2007a; 2007b) control syntopy at local scales, but

407 this fine-grained spatial structuring might not translate to regional range overlap. Bat diversity in

408 the Afrotropics, for instance, appears to be highest in the wettest and most humid regions (Figure

409 1); this pattern may underlie co-occurrence in sympatry. Bat distributions can also vary with

410 temporal and seasonal variation in resource use (Kronfeld-Schor & Dayan, 2003; Adams &

411 Thibault, 2006). Abiotic, environmental conditions can also mediate ecological interactions,

412 eroding clear relationships between divergence and sympatry (Chesson, 1986; Dunson & Travis,

413 1991). If traits actually underlie fitness differences as opposed to niche differences, then

414 equalizing mechanisms may be the most important promoters of coexistence, which can also

415 result in null or negative relationships between divergence and sympatry (Chesson, 2000; Adler

416 *et al*., 2006). This seems less likely in bats, where morphological differences are linked to major

417 trophic categories, but is a possibility for other taxa characterized by generally low divergence.

418   It is also possible that there are trade-offs between mechanisms of divergence and habitat

419 filtering that scale with community and range sizes (Kneitel & Chase, 2003). Local communities

420 can be overdispersed without this pattern manifesting at the regional scale (*e.g.* Rabosky *et al.,*

421 2011). Local and regional scales are also not consistent across organisms and biomes, given

422 differences in dispersal ability (Warren *et al.*, 2014). Finally, processes that control the degree of

423 overlap may be distinct from those that preclude co-occurrence altogether. Even given no

424 relationship between divergence and the *presence* of sympatry, there may still be a relationship

425 between divergence and the *degree* of overlap in a subset of sympatric pairs, indicating that once

426 requirements for sympatry are met, range overlap is readily increased.

427   Our results indicating weak or null effects of phylogenetic distance on regional co-

428 occurrence could also be evidence for alternative modes of speciation, including speciation in

429 sympatry. While speciation in allopatry is often assumed to be the most prevalent mode,

430 sympatric speciation could cloud any signals of divergence upon sympatry (Fitzpatrick &

431 Turelli, 2006), especially if extant ranges largely reflect the geography of speciation.

432 Reproductive sorting by echolocation frequency has been suggested as a driver of sympatric

433 speciation in some clades of bats (Kingston & Rossiter, 2004). Considering the generally coarse

434 nature of available range data, allopatric pairs may even appear sympatric, as in cases where

435 isolation depends on microhabitat availability like roosts (Voss *et al.,* 2016). Spatial patterns of

436 bat diversity may also be unrelated to divergence if larger ranges are simply more likely to

437 overlap when constrained by continental geography, analogous to the mid-domain explanation

438 for the latitudinal diversity gradient (Colwell & Lees, 2000). This would also be evidence for

439 dispersal ability as a driver of sympatry across bats, though testing would require higher-

440 resolution data on range limits. Dispersal could even erode signals of local competitive

441 exclusion, leading to the appearance of widespread sympatry.

442 One of the biggest limiting factors to macroecological studies is the quality and accuracy

443 of data. Uncertainty in divergence time estimation can impede efforts to infer the effects of age

444 on extant diversity. The presence of cryptic species may make identification of syntopic species

445 difficult. Furthermore, all studies that use spatial data are sensitive to the accuracy of range

446 maps, which have not been systematically reviewed across Chiroptera, to our knowledge.

447 Ultimately, it is unlikely that ecological interactions scale to macroecological patterns and

448 macroevolutionary dynamics equally across the tree of life. The negative relationship between

449 divergence and co-occurrence across bats is potentially evidence that their diversity is

450 unsaturated (Shi & Rabosky, 2015), and that they are continuing to radiate into a diversity of

451 ecological niches and biomes.

452

453 **Acknowledgments**

459

460 **Biosketch**

461   **Jeff J. Shi** performed this research as part of his Ph.D. in Ecology and Evolutionary

462 Biology at the University of Michigan. His dissertation evaluates how extant patterns of diversity

463 reflect dynamic histories of diversification and species interactions; he focuses on extant bats as

464 a model study system.

465   Author contributions: J.J.S. and D.L.R. designed this study and its methods and analyses,

466 and led the writing of the manuscript. J.J.S., E.P.W., N.T.K., and E.R.D. contributed to data

467 collection. E.P.W. and E.R.D. reviewed, added to, and commented on the manuscript throughout

468 the writing process.

469

470 **Literature Cited**

471 Adams, R.A. & Thibault, K.M. (2006) Temporal resource partitioning by bats at water holes.

472   *Journal of Zoology,* **270**, 466–472.

473 Adler, P.B., HilleRisLambers, J. & Levine, J.M. (2007) A niche for neutrality. *Ecology*

474   *Letters,* **10**, 95–104.

475 Aguirre, L.F., Herrel, A., van Damme, R. & Matthysen, E. (2002) Ecomorphological analysis of

476   trophic niche partitioning in a tropical savannah bat community. *Proceedings of the*

477   *Royal Society B: Biological Sciences,* **269**, 1271–1278.

478 Anacker, B.L. & Strauss, S.Y. (2014) The geography and ecology of plant speciation: range

479   overlap and niche divergence in sister species. *Proceedings of the Royal Society B:*

480   *Biological Sciences*, **281**, 20132980.

481 Barraclough, T.G. & Vogler, A.P. (2000) Detecting the geographical pattern of speciation from

482   species-level phylogenies. *The American Naturalist*, **155**, 419–434.

483 Bengtsson, J. (1989) Interspecific competition increases local extinction rate in a

484   metapopulation system. *Nature,* **340**, 713–715.

485 Brown Jr., W.L. & Wilson, E.O. (1956) Character displacement. *Systematic Zoology*, **5**, 49–64.

486 Cardillo, M. & Warren, D.L. (2016) Analysing patterns of spatial and niche overlap among

487   species at multiple resolutions. *Global Ecology and Biogeography,* **25**, 951–963.

488 Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of

489   community ecology and phylogenetic biology. *Ecology Letters,* **12**, 693–715.

490 Chesson, P.L. (1986) Environmental variation and the coexistence of species. *Community*

491   *ecology* (ed. by Diamond, J. & Case, T.J.), Harper and Row, New York, New York,

492   USA, 240-256.

493 Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology*

494   *and Systematics*, **31**, 343-366.

495 Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the

496   geography of species richness. *Trends in Ecology and Evolution*, **15**, 70-76.

497 Connell, J.H. (1972) Interactions on marine rocky intertidal shores. *Annual Review of Ecology*

498   *and Systematics,* **3**, 169–192.

499 Corcoran, A.J. & Conner, W.E. (2014) Bats jamming bats: Food competition through sonar

500   interference. *Science,* **346**, 745–747.

501 Curtis, A.A. & Simmons, N.B. (2017) Unique turbinal morphology in horseshoe bats

502   (Chiroptera: Rhinolophidae) *The Anatomical Record,* **300**, 309–325.

503 Dumont, E.R., Dávalos, L.M., Goldberg, A., Santana, S.E., Rex, K. & Voigt, C.C. (2012)

504   Morphological innovation, diversification and invasion of a new adaptive zone.

505   *Proceedings of the Royal Society B: Biological Sciences,* **279**, 1797–1805.

506 Dumont, E.R. (2004) Patterns of diversity in cranial shape among plant-visiting bats. *Acta*

507   *Chiropterologica,* **6**, 59–74.

508 Dunson, W. & Travis, J. (1991) The role of abiotic factors in community organization. *The*

509   *American Naturalist,* **138**, 1067–1091.

510 Estrada-Villegas, S., McGill, B.J. & Kalko E.K.V. (2012) Climate, habitat & species

511   interactions at different scales determine the structure of a Neotropical bat community.

512   *Ecology,* **93**, 1183–1193.

513 Fenton, M.B. & Thomas, D.W. (1980) Dry-season overlap in activity patterns, habitat use &

514   prey selection by sympatric African insectivorous bats. *Biotropica,* **12**, 81–90.

515 Findley, J.S. & Black, H.A.L. 1983. Morphological and dietary structuring of a Zambian

516   insectivorous bat community. *Ecology,* **64**, 625–630.

517 Fitzpatrick, B.M. & Turelli, M. (2006) The geography of mammalian speciation: mixed signals

518   from phylogenies and range maps. *Evolution*, **60**, 601–615.

519 Fleming, T.H. (1986) Opportunism versus specialization: the evolution of feeding strategies in

520   frugivorous bats. *Frugivores and seed dispersal* (ed. by Estrada, A. & Fleming, T.H.), Dr

521   W. Junk Publishers, Dordrecht, South Holland, Netherlands, 105-118.

522 Graham, C.H. & Fine, P.V.A. (2008) Phylogenetic beta diversity: linking ecological and

523   evolutionary processes across space in time. *Ecology Letters,* **11**, 1265–1277.

524 Grant, P.R. & Grant, B.R. (1997) Genetics and the origin of bird species. *Proceedings of the*

525   *National Academy of Sciences of the United States of America,* **94**, 7768–7775.

526 Grossenbacher, D., Briscoe Runquist, R., Goldberg, E.E. & Brandvain, Y. (2015) Geographic

527   range size is predicted by plant mating system. *Ecology Letters,* **18**, 706–713.

528 Hadfield, J.D. (2010) MCMC methods for multi-response generalized linear mixed models: the

529   MCMCglmm R package. *Journal of Statistical Software,* **33**, 1–22.

530 Hadfield, J.D. & Nakagawa, S. (2010) General quantitative genetic methods for comparative

531   biology: phylogenies, taxonomies and multi-trait models for continuous and categorical

532   characters. *Journal of Evolutionary Biology,* **23**, 494–508.

533 Heithaus, E.R., Fleming, T. H. & Opler, P. A. (1975) Foraging patterns and resource utilization

534   in seven species of bats in a seasonal tropical forest. *Ecology*, **56**, 841–854.

535 Henry, M., Barrière, P., Gautier-Hion, A. & Colyn, M. (2004) Species composition, abundance

536   and vertical stratification of a bat community (Megachiroptera: Pteropodidae) in a West

537   African rain forest. *Journal of Tropical Ecology,* **20**, 21–29.

538 IUCN. (2016) *The IUCN red list of threatened species. Version 2016-2.*

539 Jones, K.E., Bininda-Emonds, O.R.P. & Gittleman, J.L. (2005) Bats, clocks & rocks:

540   diversification patterns in Chiroptera. *Evolution,* **59**, 2243–2255.

541 Jønsson, K.A., Tøttrup, A.P., Borregaard, M.K., Keith, S.A., Rahbek, C. & Thorup, K. (2016)

542   Tracking animal dispersal: from individual movement to community assembly and global

543   range dynamics. *Trends in Ecology and Evolution,* **31**, 204-214.

544 Kingston, T., Jones, G., Zubaid, A. & Kunz, T.H. (2000) Resource partitioning in rhinolophoid

545   bats revisited. *Oecologia*, **124**, 332-342.

546 Kingston, T., & Rossiter, S.J. (2004) Harmonic-hopping in Wallacea's bats. *Nature*, **429**,

547   654-657.

548 Kneitel, J.M. & Chase, J.M. (2004) Trade-offs in community ecology: Linking spatial scales

549   and species coexistence. *Ecology Letters,* **7**, 69–80.

550 Kronfeld-Schor, N. & Dayan, T. (2003) Partitioning of time as an ecological resource. *Annual*

551   *Review of Ecology, Evolution & Systematics,* **34**, 153–181.

552 Leibold, M.A. & McPeek, M.A. (2006) Coexistence of the niche and neutral perspectives in

553   community ecology. *Ecology,* **87**, 1399–1410.

554 Lessard, J.P., Belmaker, J., Myers, J.A., Chase, J.M., & Rahbek, C. (2012) Inferring local

555   ecological processes amid species pool influences. *Trends in Ecology and Evolution,*

556   **27**, 600–607.

557 Louthan, A.M., Doak, D.F., & Angert, A.L. (2015) Where and when do species interactions set

558   range limits? *Trends in Ecology and Evolution,* **30**, 780-792.

559 McCain, C.M. (2007a) Area and mammalian elevational diversity. *Ecology.* **88**, 76–86.

560 McCain, C.M. (2007b) Could temperature and water availability drive elevational species

561   richness patterns? A global case study for bats. *Global Ecology and Biogeography,*

562   **16**, 1–13.

563 Mcintire, E.J.B. & Fajardo, A. (2014) Facilitation as a ubiquitous driver of biodiversity. *New*

564   *Phytologist,* **201**, 403–416.

565 McPeek, M.A. & Brown, J.M. (2000) Building a regional species pool: diversification of the

566   Enallagma damselflies in eastern North America. *Ecology,* **81**, 904–920.

567 Moreno, C., Arita, H. & Solis, L. (2006) Morphological assembly mechanisms in Neotropical

568   bat assemblages and ensembles within a landscape. *Oecologia,* **149**, 133–140.

569 Nogueira, M.R., Peracchi, A.L. & Monteiro, L.R. (2009) Morphological correlates of bite

570   force and diet in the skull and mandible of phyllostomid bats. *Functional Ecology,*

571   **23**, 715–723.

572 Norberg, U.M. & Rayner, J.M.V. (1987) Ecological morphology and flight in bats

573   (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and

574   echolocation. *Philosophical Transactions of the Royal Society B: Biological Sciences,*

575   **316**, 335–427.

576 Nowak, M.D. (1994) *Walker's bats of the world*. Johns Hopkins University Press, Baltimore,

577   Maryland, USA.

578 Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood,

579   E.C., D'amico, J.A., *et al.* (2001) Terrestrial ecoregions of the world: a new map of life

580   on Earth. *BioScience,* **51**, 933-938.

581 Phillimore, A.B., Orme, C.D.L., Thomas, G.H., Blackburn, T.M., Bennett, P.M., Gaston, K.J. &

582   Owens, I.P.F. (2008) Sympatric speciation in birds is rare: insights from range data and

583   simulations. *The American Naturalist*, **171**, 646–657.

584   Pigot, A.L. & Tobias, J.A. (2014) Dispersal and the transition to sympatry in vertebrates.

585   *Proceedings of the Royal Society B: Biological Sciences,* **282**, 20141929.

586   Pigot, A.L. & Tobias, J.A. (2013) Species interactions constrain geographic range expansion

587   over evolutionary time. *Ecology Letters,* **16**, 330–338.

588   Rabosky, D.L., Cowan, M.A., Talaba, A.L. & Lovette, I.J. (2011) Species interactions mediate

589   phylogenetic community structure in a hyperdiverse lizard assemblage from arid

590   Australia. *The American Naturalist,* **178**, 579–595.

591   Ricklefs, R.E. (2007) History and diversity: explorations at the intersection of ecology and

592   evolution. *The American Naturalist,* **170 Suppl**, S56-70.

593   Santana, S.E. & Lofgren, S.E. (2013) Does nasal echolocation influence the modularity of the

594   mammal skull? *Journal of Evolutionary Biology,* **26**, 2520–2526.

595   Santana, S.E. & Cheung, E. (2016) Go big or go fish: morphological specializations in

596   carnivorous bats. *Proceedings of the Royal Society B: Biological Sciences,*

597   **283**, 20160615.

598   Santana, S.E., Dumont, E.R. & Davis, J.L. (2010) Mechanics of bite force production and its

599   relationship to diet in bats. *Functional Ecology,* **24**, 776–784.

600   Saunders, M.B. & Barclay, R.M.R. (1992) Ecomorphology of insectivorous bats: a test of

601   predictions using two morphologically similar species. *Ecology,* **73**, 1335–1345.

602   Schoeman, M.C. & Jacobs, D.S. (2011) The relative influence of competition and prey

603   defences on the trophic structure of animalivorous bat ensembles. *Oecologia,* **1**, 493–506.

604   Schoeman, M.C. & Jacobs, D.S. (2003) Support for the allotonic frequency hypothesis in an

605   insectivorous bat community. *Oecologia,* **134**, 154–162.

606   Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and ecology of species

607   range limits. *Annual Review of Ecology, Evolution, and Systematics,* **40**, 415–436.

608   Shi, J.J. & Rabosky, D.L. (2015) Speciation dynamics during the global radiation of extant

609   bats. *Evolution,* **69**, 1528–1545.

610   Siemers, B.M. & Schnitzler, H.-U. (2004) Echolocation signals reflect niche differentiation in

611   five sympatric congeneric bat species. *Nature,* **429**, 657–661.

612   Silvestro, D., Antonelli, A., Salamin, N. & Quental, T.B. (2015) The role of clade competition in

613   the diversification of North American canids. *Proceedings of the National Academy of*

614   *Sciences of the United States of America,* **112**, 8684–8689.

615 Simmons, N.B. & Conway, T.M. (2003) Evolution of ecological diversity in bats. *Bat ecology*

616   (ed. by Kunz, T.H. & Fenton, M.B.), University of Chicago Press, Chicago, Illinois,

617   USA, 493-535.

618 Simmons, N.B. (2005) Order Chiroptera. *Mammal species of the world: a taxonomic and*

619   *geographic reference, 3rd edition* (ed. by Wilson, D.E. & Reeder, D.M.) Johns Hopkins

620   University Press, Baltimore, Maryland, USA, 312-529.

621 Spiesman, B.J. & Inouye, B.D. (2014) The consequences of multiple indirect pathways of

622   interaction for species coexistence. *Theoretical Ecology,* **8**, 225–232.

623 Stuart, Y.E. & Losos, J.B. (2013) Ecological character displacement: glass half full or half

624   empty? *Trends in Ecology and Evolution*, **28**, 402–408.

625 Swift, S.M. & Racey, P.A. (1983) Resource partitioning in two species of vespertilionid bats

626   (Chiroptera) occupying the same roost. *Journal of Zoology*, **200**, 249–259.

627 Taylor, E.B., Boughman, J.W., Groenenboom, M., Sniatynski, M., Schluter, D. & Gow, J.L.

628   (2006) Speciation in reverse: morphological and genetic evidence of the collapse of a

629   three-spined stickleback (Gasterosteus aculeatus) species pair. *Molecular Ecology,*

630   **15**, 343–355.

631 Terribile, L.C., Diniz-Filho, J.A.F., Rodríguez, M.Á. & Rangel, T.F.L.V.B. (2009) Richness

632   patterns, species distributions and the principle of extreme deconstruction. *Global*

633   *Ecology and Biogeography,* **18**, 123–136.

634 Tobias, J.A., Cornwallis, C.K., Derryberry, E.P., Claramunt, S., Brumfield, R.T. & Seddon, N.

635   (2014) Species coexistence and the dynamics of phenotypic evolution in adaptive

636   radiation. *Nature,* **506**, 359–363.

637 Villalobos, F. & Arita, H.T. (2010) The diversity field of New World leaf-nosed bats

638   (Phyllostomidae) *Global Ecology and Biogeography,* **19**, 200-211.

639 Voss, R.S., Fleck, D.W., Strauss, R.E., Velazco, P.M. & Simmons, N.B. (2016) Roosting

640   ecology of Amazonian bats: evidence for guild structure in hyperdiverse mammalian

641   communities. *American Museum Novitates,* **3870**, 1–43.

642 Warren, D.L., Cardillo, M., Rosauer, D.F., & Bolnick, D.I. (2014) Mistaking geography for

643   biology: inferring processes from species distributions. *Trends in Ecology and Evolution*,

644   **29**, 572–580.

645 Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example

646   for rain forest trees. *The American Naturalist,* **156**, 145–155.

647 Weir, J.T. & Price, T.D. (2011) Limits to speciation inferred from times to secondary sympatry

648   and ages of hybridizing species along a latitudinal gradient. *The American Naturalist,*

649   **177**, 462–469.

650

651

652 **Table 1.** PLMM results for the effect of age (β_1) alone on pairwise patterns of sympatry (at a

653 20% overlap threshold) for all pairs of bat species with spatial data, divided into WWF

654 biogeographic realms. Posterior means and pMCMC values (see Results) are included.

Realm (*N*)	β_1 posterior mean	β_1 pMCMC
Afrotropics (78 species)	-0.016	0.060
Indomalaya (175 species)	-0.008	0.083
Nearctic (40 species)	-0.018	0.182
Neotropics (235 species)	-0.012	0.336
Oceania & Australasia (82 species)	-0.008	0.481
Palearctic (70 species)	-0.009	0.209

655

656 **Table 2.** PLMM results for the effects of age (β_1), ecomorphological divergence (β_2), and

657 combined age and ecomorphological divergence (β_3) on pairwise patterns of sympatry (at a 20%

658 overlap threshold) for all pairs of bat species with both types of divergence data. These pairs are

659 divided according to realm. Posterior means and pMCMC values are included, and bolded when

660 pMCMC < 0.05. Note that some species are part of the species pools of both realms.

Realm (N)	β_1 posterior mean	β_1 pMCMC	β_2 posterior mean	β_2 pMCMC	β_3 posterior mean	β_3 pMCMC
Nearctic (34 species)	-0.029	0.380	-0.015	0.958	-0.002	0.800
Neotropics (135 species)	-0.018	0.203	**-0.091**	**0.009***	< 0.001	0.621
New World (161 species)	-0.026	0.330	-0.029	0.360	**-0.002**	**0.004***

661

662

663 **Figure 1.** Global richness of extant bats, based on 696 range polygons used for this study.

664 Warmer colors represent higher species richness. Regional diversity of bats is highest in the

665 tropics and peaks in the western Amazon basin and eastern slopes of the Andes.

666

667 **Figure 2.** Three models for how the probability of sympatry (θ) can vary as a function of either

668 phylogenetic or morphological divergence. From top to bottom: M1, a model where θ is

669 independent of the evolutionary or morphological divergence between taxa; M2, where θ

670 approaches a limiting value α; M3, where θ logistically varies with divergence and also

671 asymptotically approaches a limiting value α.

672

673 **Figure 3.** A schematic of our range randomization approach used to test the relationship between

674 sympatry and the time since divergence. For each realm, we took the (a) phylogeny of all bat

675 species endemic to that realm, and (b) randomized species and range identity while holding the

676 tree constant. For each of these randomizations, we calculated (c) the logistic regression and

677 associated log-odds between divergence time and sympatry state. Repeating (b) and (c) 500

678 times created (d) a null distribution of relationships, shown here as the logarithm of the odds-
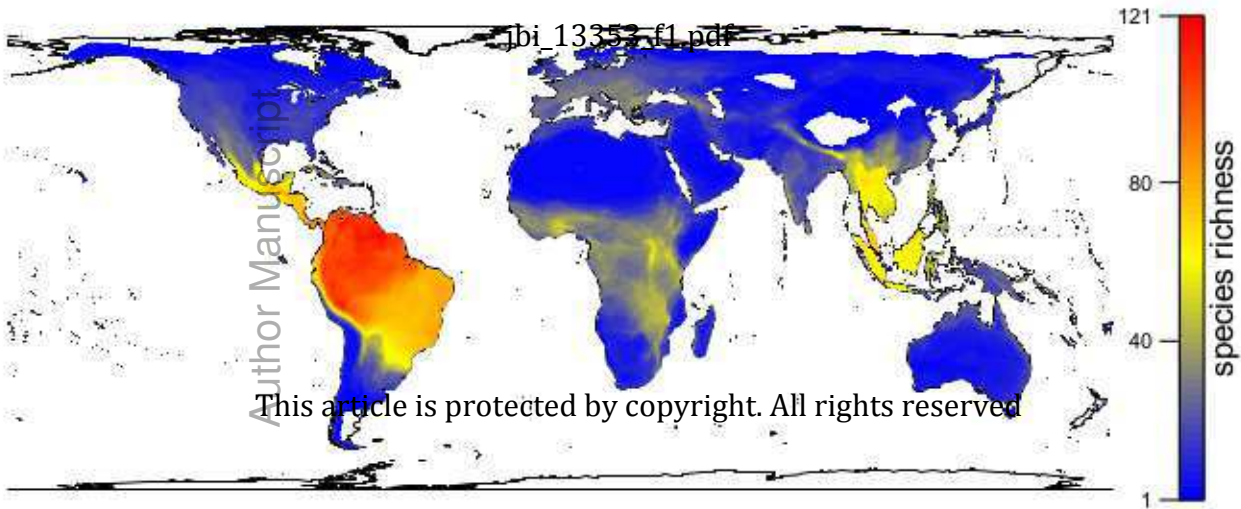
679 ratio between divergence time and sympatry state. This null distribution was then compared to

680 the empirical value for that realm, indicated by the dashed line.

681

682   **Figure 4.** (a) Pairwise Euclidean distances (ecomorphology) versus percentage range overlap for

683   all pairs of Neotropical bat species considered in this study ($N = 8967$ pairs). Pairs above the

684   dotted threshold are considered sympatric for the main analyses of this study. (b) Points denote

685   the same dataset, decomposed into binary sympatry or allopatry states. The curve is the posterior

686   mean PLMM estimate of the relationship between pairwise ecomorphological distance and the

687   probability of sympatry. Progressively darker polygons highlight the 90%, 75%, 50%, 25%, and

688   10% credibility intervals around the mean. There is a significant negative relationship between

689   the probability of sympatry and ecomorphological distance, although credible intervals are wide.

690   (c) The same relationship as (b), but fitting the model only to species pairs with morphological

691   distances less than 6.0, which accounts for 95.8% of all species pairs. This analysis was

692   performed to ensure that the overall negative relationship was not driven by the small number of

693   pairs with very high ecomorphological distance values.

(a)

(b)

(c)

sympatry state

divergence time

(d)

log-odds