

1 **Migration distance and mating system are not associated with genetic diversity and**
2 **differentiation among bats (Chiroptera)**

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14 **Abstract**

15
16 Genetic variation is critical for evolutionary responses to environmental change. Links between
17 genetic variation and behavioural or life history traits may reveal how varied strategies influence
18 evolutionary trends in speciation and adaptation. Traits associated with movement typically
19 correlate with population genetic structure and could help predict populations' vulnerability to
20 geographic processes such as habitat fragmentation and disease spread. With their wide diversity
21 in behaviours and ecologies, bats provide a useful testing ground for hypotheses about
22 population structure related to species-specific movement patterns. We used a global sample of
23 microsatellite data ($n=233$ sites from 17 bat species) associated with published studies to
24 examine potential links between genetic variation and migration and mating strategies. The
25 genetic measures we tested were population-specific differentiation, gene diversity, and allelic
26 richness. Using Bayesian models that accounted for phylogenetic distances among species, we
27 identified no correlations between migration or mating strategy and genetic variation. Our results
28 do not support long-standing hypotheses about dispersal-mediated genetic structure, and contrast
29 with prior studies on bat genetic diversity and differentiation. We discuss the need for continued
30 research into the complex association of ecological, biogeographical, and behavioural factors
31 that facilitate gene flow among populations, especially in species with diverse movement
32 patterns.

33
34 **Keywords:** allelic richness; dispersal; gene diversity; genetic variation; life history trait;
35 macrogenetics; mammal; population-specific F_{ST}

36

37 **Introduction**

38 While genetic variation is required for evolutionary responses to environmental change and thus
39 population resilience, its connections to behavioural and life history and traits are less clear
40 (Lande, 1980; Mitton & Lewis, 1989; Hamrick & Godt, 1996; Barrett & Schluter, 2008; Schluter
41 & Conte, 2009). These connections may underscore evolutionary processes in population and
42 species-level divergence, as phenotypic variation may contribute to population isolation and
43 ecological speciation (Lande, 1980; Rundle & Nosil, 2005). Behavioural traits related to motility
44 are fundamental to most animals' life histories, and how, when, and where they move during
45 mating and dispersal directs gene flow patterns across the landscape (Cushman & Lewis, 2010)
46 (Cushman and Lewis 2010). For example, geographical, ecological, and behavioural barriers to
47 movement restrict gene flow and can generate structured populations in bats (Moussy *et al.*,
48 2013). Dispersal ability (i.e., the ability to fly, swim, or move across potential barriers) is
49 generally negatively correlated with genetic structure because reproductive individuals from
50 populations of highly motile species are more able to interact and exchange genetic material
51 (Bohonak, 1999; Bradbury *et al.*, 2008; Medina *et al.*, 2018). However, dispersal ability alone
52 has inconsistent correlations with genetic structure among different species (Taylor *et al.*, 2012;
53 Burns & Broders, 2014). With widely-available genetic and ecological data, potential reciprocal
54 links between movement-related traits and genetic variation are becoming more tractable for
55 study across broadly distributed groups of organisms (Schmidt *et al.*, 2020).

56 As the only flying mammals, bats are an interesting group to study connections between
57 movement-related traits and genetic variation. Migration, colonization, and mating systems are
58 often correlated with population structure in bats (Castella & Ruedi, 2000; Burland &
59 Worthington Wilmer, 2001; Kerth & Morf, 2004; Furmankiewicz & Altringham, 2007).
60 However, individual genetic studies are often difficult to compare because of varying marker
61 types and measures of genetic variation (Moussy *et al.*, 2013). A standardized examination of
62 mating systems, migration strategy, and genetic variation can provide insight into how
63 behavioural traits interact with genetic variation in bat species or populations. Bat species
64 worldwide face threats related to climate change, habitat loss, overhunting, and novel fungal
65 pathogens (Lorch *et al.*, 2011; Frick, Kingston, & Flanders, 2020). Defining the traits that best
66 predict genetic structure can help decision-makers identify groups of bats that may be at greater
67 risk of loss of genetic variation, thereby requiring enhanced monitoring or protection.

68 One such movement trait that may be related to genetics is migration, the round-trip,
69 seasonal movement of organisms between locations, and is a trait exhibited by numerous taxa to
70 avoid seasonally harsh environments or exploit food resources (Shaw, 2016). It is widely
71 accepted as adaptive, and long-distance migration patterns shaped by competition likely co-
72 evolved with other life history traits (Alerstam, Hedenström, & Åkesson, 2003). Migratory
73 movements have been related to increased genetic diversity in taxa as diverse as butterflies
74 (García-Berro *et al.*, 2023), mammals (Gustafson *et al.*, 2017), and fish (Kovach, Gharrett, &
75 Tallmon, 2013), making migration a potentially important factor in shaping population genetic
76 structure.

77 A species' mating system is another trait that depends on movement patterns (Shuster,
78 2009). Random or promiscuous mating reduces relatedness in family groups and increases
79 genetic diversity (McCauley & O'Donnell, 1984; Gohli *et al.*, 2013). In contrast, monogamy or
80 polygamy theoretically decreases genetic variation in populations, reducing effective population
81 size (Briton *et al.*, 1994). However, work in wild bat populations showed that polygyny may
82 increase genetic variation (Pérez-González, Mateos, & Carranza, 2009; Garg *et al.*, 2012).
83 Explanations for this inconsistency vary, but correlates of harem mating in some polygynous
84 species (e.g., greater male-male competition) may promote increased genetic variation (Pérez-
85 González *et al.*, 2009; Garg *et al.*, 2012).

86 We reasoned that migratory bats (male or female) that travel to swarming sites to breed
87 would have a higher likelihood of interacting with individuals from different populations.
88 Therefore, we classified bat species into three movement classes (long-distance, regional, and
89 non-migrant) to test an association between migration distance and genetic differentiation. We
90 hypothesized that the weakest population-specific genetic differentiation (Weir & Goudet, 2017)
91 would occur in migratory bats, due to increased dispersal ability and greater likelihood of mixing
92 between populations, leading to increased gene flow. We also classified bat species into two
93 mating classes to test an association between mating strategy and genetic differentiation. Bat
94 species can have polygamous (harem-forming), promiscuous (swarming), or (rarely)
95 monogamous mating strategies (McCracken & Wilkinson, 2000). We hypothesized that genetic
96 structure would be stronger in harem-forming species than in swarming species because bats
97 with harems theoretically have fewer mates in a smaller geographic area compared to those that
98 travel to swarming sites. We also hypothesized lower genetic variation (gene diversity and allelic

99 richness) in bat species with shorter migration distances and that use harems. To provide a
100 genetic context for these models of population genetics and life history traits, we assessed
101 differences in the three genetic measures (genetic differentiation, gene diversity, and allelic
102 richness) at a species level.

103

104 **Methods**

105 *Genetic Measurement Collection Methods*

106 The microsatellite data used in the present genetic analyses were compiled in previously
107 published work (Schmidt *et al.*, 2020). They were originally published in multiple research
108 articles (Buchalski, Chaverri, & Vonhof, 2014; Burns, Frasier, & Broders, 2014; Witsenburg *et*
109 *al.*, 2015b; Boston *et al.*, 2015b; Johnson *et al.*, 2015; Moussy *et al.*, 2015b; Razgour *et al.*,
110 2015b; Baird *et al.*, 2015; Vesterinen *et al.*, 2016b; Günther *et al.*, 2016b; Afonso *et al.*, 2017b;
111 Cleary, Waits, & Finegan, 2017b; Davy *et al.*, 2017; Lausen *et al.*, 2019) and several online
112 repositories (Buchalski, Chaverri, & Vonhof, 2013; Boston *et al.*, 2015a; Burns, Frasier, &
113 Broders, 2015; Moussy *et al.*, 2015a; Razgour *et al.*, 2015a; Witsenburg *et al.*, 2015a; Baerwald
114 & Barclay, 2016; Günther *et al.*, 2016a; Johnson *et al.*, 2016; Vesterinen *et al.*, 2016a; Afonso *et*
115 *al.*, 2017a; Cleary, Waits, & Finegan, 2017a; Santos & Meyer, 2017; Davy *et al.*, 2018; Lausen
116 *et al.*, 2018). In total, we attained data from 17 bat species, representing 233 populations and
117 8,095 individuals (Table S1). We used all individuals for gene diversity and allelic richness
118 metrics, and due to one population for some groups, we used a subset of samples to estimate
119 genetic differentiation which included 12 species (228 populations with 7,618 individuals)
120 (Figure 1; Table S2). Gene diversity was calculated with Adegnet v2.1.5 (Jombart, 2008), while
121 genetic differentiation and allelic richness were calculated with hierfstat v0.5.7 (Goudet, 2005).

122

123 *Behaviour Classification Methods*

124 Migration strategies were classified by species into non-migrants, regional migrants, and
125 long-distance migrants based on their known life histories. Species observed to migrate between
126 summer and winter roosts within the same region (movements may be tens to hundreds of km)
127 were considered regional migrants, and migrants travelling between different regions
128 (movements commonly greater than 1,000 km) were considered long-distance migrants. These

129 categories roughly correspond to the distance categories used by Burns and Broders (2014).
130 Similarly, where we could not find an explicit reference to a species' migratory status, we
131 classified them as non-migratory. Bat species were also classified by mating system, determined
132 by whether or not they used harems in their reproduction. The full list of behaviour
133 classifications is in Table S3, using several databases and research articles (Davis & Hitchcock,
134 1965; Fenton, 1969; Bradbury & Vehrencamp, 1977; Nagorsen & Brigham, 1993; Leu, 2000;
135 Caceres & Barclay, 2000; Anderson, 2002; Vingiello, 2002; Wang, 2002; Keinath, 2004;
136 Wohlgenuth *et al.*, 2004; McGuire *et al.*, 2012; Boston *et al.*, 2012; Moussy *et al.*, 2013; Cryan,
137 Stricker, & Wunder, 2014; Ibáñez & Juste, 2016; Bentley, 2017; Fraser, Brooks, & Longstaffe,
138 2017; Taylor & Tuttle, 2019; Godlevska, Gazaryan, & Kruskop, 2021; Elliott, 2022; GBIF
139 Secretariat, 2022a,b,c,d; Encyclopedia of Life, 2023; Jarso, 2023; NBN Atlas, 2023;
140 UNEP/EUROBATS Secretariat, 2023).

141

142 *Population Genetics Across Species*

143 Prior to modeling correlations between population genetic measures and behaviours, we
144 examined differences in population genetic measures among species without modeling other
145 variables. In the statistical computing environment R v4.2.1, the package brms v2.18.0 was used
146 for Bayesian modeling, while tidyverse v2.0.0, tidybayes v3.0.3, ggbeeswarm v0.7.1, and
147 patchwork v1.1.2 were useful for data management and model visualization (Bürkner, 2018;
148 Wickham *et al.*, 2019; Pedersen, 2022; R Core Team, 2022; Kay, 2023). We first examined
149 differences in population genetic measures across species by fitting a series of models with
150 species identity as a fixed effect.

151 The three population genetic measures used were genetic differentiation, gene diversity
152 (also called expected heterozygosity), and allelic richness (Nei & Chesser, 1983; Weir & Goudet,
153 2017). Each Bayesian model was fit with a Gaussian distribution, using four independent
154 Hamiltonian Monte Carlo chains across 5,000 warm-up and 15,000 sampling iterations each
155 (60,000 sampling iterations total). For the models analyzing genetic differentiation or gene
156 diversity, normal priors of mean 0 and standard deviation 1 were used for global intercepts and
157 model coefficients. For the model analyzing allelic richness, we used normal priors of mean 0
158 and standard deviation 5. In all models, adapt delta was raised to 0.99 and maximum tree depth

159 raised to 16. Model fit was assessed with the potential scale reduction statistic R^2 , visual
160 inspection of trace plots, and visual inspection of posterior predictive checks over 100 draws in
161 each model. Models were accepted only if R^2 was 1.00 for all parameters. The R package
162 emmeans v1.8.4-1 (Searle, Speed, & Milliken, 1980) was used to both gather posterior draws for
163 visualization and for estimating marginal means to compare 95% highest posterior density
164 (HPD) in a pairwise manner between species.

165

166 *Genetic-Life History Trait Correlations*

167 We used a Bayesian approach to model potential relationships between migration strategy
168 or mating system, and population genetic measures. The same statistical programs and packages
169 were used for these models as in the models of population genetics across species. Bayesian
170 models were fit with the following model structure in R:

171 $population\ genetic\ measure \sim (migration\ strategy\ or\ mating\ system) +$
172 $(1\ | \ species) + (1\ | \ phylogenetic\ correlation\ matrix) +$
173 $(spatial\ simultaneous\ autoregressive\ structure)$

174 Here, genetic differentiation, gene diversity, and allelic richness were also used as population
175 genetic measures. Thus, six models were run: three population genetic measures compared
176 against either migration strategy or mating system.

177 Both migration strategy and mating systems were modeled as fixed effects. Species was
178 included as a random intercept in each model to address factors independent of phylogenetic
179 relatedness that may cause differences in species means for each genetic metric, such as niche or
180 environmental effects (Hadfield & Nakagawa, 2010). A phylogenetic correlation matrix was also
181 included as a random effect to address evolutionary relatedness among the bat species used in the
182 present analyses. This phylogeny was created by using the R package taxize v0.9.00 to retrieve
183 the taxonomic classifications and hierarchy for the list of species used against the National
184 Center for Biotechnology Information database using the functions *classification* and *class2tree*
185 (Figure S1) (Chamberlain & Szöcs, 2013). With this taxonomic tree, the R package ape v5.7 was
186 used to calculate the phylogenetic correlation matrix used in each model with *vcv.phylo* (Paradis

187 & Schliep, 2019). Model priors, distributions, sampling parameters, and contrasts were set and
188 assessed with the same methods as in the models of population genetic measures across species.

189 To address the potential for spatial autocorrelation to affect model results, we used spatial
190 autoregressive terms in brms with the *sar* function. Specifically, a K=4 nearest neighbors
191 connection network of sampling locations was created with the R package *adespatial* v0.3-21.
192 This network was used for specifying the spatial weighting matrix in the spatial simultaneous
193 autoregressive structure, with type 'lag' chosen to model response variables.

194 We used the *hypothesis* function in brms to identify evidence ratios and posterior
195 probabilities of differences between groups in several models with contrasts that were not
196 significant in terms of HPD intervals. These models were run without global intercepts (unlike
197 the overall models) to draw explicit comparisons among all variable levels, thus no prior was set
198 for intercept, but priors remained the same for model coefficients (i.e., normal distributions with
199 mean 0 and standard deviation 1 for genetic differentiation and gene diversity, and a normal
200 distribution with mean 0 and standard deviation 5 for allelic richness). The models run in this
201 manner were the genetic differentiation mating model to compare non-harem to harem mating
202 strategies, and the gene diversity and allelic richness migration models, to quantify higher values
203 for the long-distance migrants versus the non-migrants and regional migrants. Model fits were
204 evaluated using the same metrics as the other models in the present study.

205

206 **Results**

207 Across species, the serotine bat (*Eptesicus serotinus*) (Schreber, 1774) and common bent-
208 wing bat (*Miniopterus schreibersii*) (Kuhl, 1817) tended to have higher genetic differentiation,
209 and lower gene diversity and allelic richness than certain other species, such as the Jamaican fruit
210 bat (*Artibeus jamaicensis*) (Leach, 1821) or chestnut short-tailed bat (*Carollia castanea*) (Allen,
211 1890) (Figure 2; Tables S4-S6). Overall, these results revealed species-specific differences in
212 population-specific differentiation and genetic variation.

213 We observed no differences in any comparison between migration or mating strategies
214 using 95% HPD intervals (Figure 3; Tables S7-S8). Within the genetic differentiation model of
215 mating strategies, the non-harem groups had a slightly higher genetic differentiation (0.01, -0.03

216 to 0.05 95% credible interval) than harem groups with an evidence ratio of 2.61 and posterior
217 probability of 0.72 (Table S9). In the gene diversity model of migration strategies, long-distance
218 migrants had higher gene diversity estimates than the regional and non-migrants with evidence
219 ratios of 7.53 and 1.86, and posterior probabilities of 0.88 and 0.65, respectively (Table S9). In
220 the allelic richness model of migration strategies, long-distance migrants had higher allelic
221 richness estimates than the regional and non-migrants with evidence ratios of 3.84 and 1.19, and
222 posterior probabilities of 0.79 and 0.54, respectively (Table S9). We emphasize, however, that
223 these differences were slight and none of the contrasts were ‘significant’ in the typical statistical
224 sense of significance level α at 0.05.

225

226 **Discussion**

227 Despite species-level differences in population genetic measures, we did not find a
228 relationship between migratory distance or mating system and population-specific differentiation
229 and genetic variation among the bat populations studied. These results are consistent with work
230 that identified high connectivity in bats over large regional scales, such as in the little brown bat
231 (*Myotis lucifugus*) (Le Conte, 1831) (Burns *et al.*, 2014). However, we had expected populations
232 of species that exhibit larger dispersal distances to mix more, resulting in weaker population
233 structure.

234 Our results did not support the hypothesis that long-distance migratory tendency results
235 in genetic mixing. Wing morphology, which is correlated with migratory behaviour in birds,
236 bats, and insects (Burns & Broders, 2014; Flockhart *et al.*, 2017; Vincze *et al.*, 2018), has
237 emerged as a predictor of population structure in bats (Miller-Butterworth, Jacobs, & Harley,
238 2003; Olival, 2012; Burns & Broders, 2014). High wing loading allows fast flying with low
239 maneuverability, and high wing aspect ratio allows efficient flights, which facilitates energy-
240 efficient long-distance movements. However, long-distance migration dispersal (or the ability to
241 do so) does not necessarily mean that homogeneous mixing of populations will occur. Regardless
242 of the distance that a population migrates, a key assumption is that the migration movement
243 results in breeding dispersal (Petit & Mayer, 2000); if strongly migratory species mate on the
244 summer breeding grounds, as non-migrants do, their genetic structure would not be expected to
245 differ from that of non-migrants’ (Moussy *et al.*, 2013). It is possible that bat species with

246 morphological features designed for use fast and efficient flights to mix far and wide on the
247 breeding grounds, regardless of their migration behaviour. Studies that directly track migration
248 movements, and discern the mating locations, of specific populations are required to reconcile
249 the influences of morphological and behavioural traits.

250 Predicting genetic structure based on harem-forming and swarming behaviour may also
251 be too simplistic, because a complex set of morphological, physiological, and behavioural traits
252 combine with biogeographical features to impede or facilitate population mixing (Olival, 2012).
253 Morphological characteristics such as brain size, testis size, and baculum length are correlated
254 with female promiscuity or male fertilization success (Hosken & Stockley, 2004; Pitnick, Jones,
255 & Wilkinson, 2006); all of which may contribute to shaping geographic genetic patterns among
256 species. Some species of harem-forming bats exhibit high variation in levels of promiscuity (by
257 both males and females) (Campbell, 2008; Garg *et al.*, 2012), which could lead to weakened
258 genetic structure among populations. Availability of food resources may influence short-term
259 dispersal patterns on the breeding grounds; for instance frugivorous or nectivorous bats may
260 need to move farther or more frequently than insectivorous bats, because insects are typically a
261 more stable food source (Webb & Tidemann, 1996; Moreno-Valdez, Honeycutt, & Grant, 2004;
262 Bontadina *et al.*, 2008). Thus, for two species with similar mating strategies, frugivorous bats
263 might incidentally have more genetic mixing because they are exposed to more individuals
264 outside their populations while moving around to find food.

265 In addition to using relatively simplified models, some information on bats in the
266 literature may not be accurate, leading to misclassification of the migratory or mating status for
267 some of the species in our samples. Some bat species classified as non-migratory may move
268 farther than we assume. Conversely, not all populations of species that we considered migratory
269 actually migrate, which would result in a small average effect size in our analysis. For example,
270 stable isotope analysis revealed high variation in the migratory movements of *Lasionycterus*
271 *noctivagans* (Le Conte, 1831) (Fraser *et al.*, 2017). Within species that are partially migratory,
272 non-migratory populations can have greater genetic structure (e.g., *Eidolon helvum* (Kerr, 1792)
273 (Juste, Ibáñez, & Machordom, 2000; Peel *et al.*, 2013)). Even in species where all populations
274 are migratory, those populations with low migratory connectivity can have greater genetic
275 structure, possibly reflecting genetic isolation by distance (e.g., *M. lucifugus* (Vonhof, Russell, &
276 Miller-Butterworth, 2015; Wilder, Kunz, & Sorenson, 2015)). While misclassification may have

277 prevented us from detecting some genetic differences between migratory and non-migratory
278 species, our null results also highlight the need for more studies on bat movement behaviour, as
279 data on migration strategy is sparse among bats.

280 Several genetic reasons may underlie the present null results. Genetic variation was found
281 to have a small to moderate influence on variance in migration timing in purple martins (*Progne*
282 *subis*) (Linnaeus, 1758) (de Greef *et al.*, 2023), and it is possible that migration and mating
283 strategies are only weakly related to genetics in bats. Therefore, the population-level analyses
284 conducted in the present study may have missed subtle, population-specific, and individual-level
285 connections between the observed traits and genetics. Microsatellite data used for genetic
286 differentiation is effective for testing overall patterns of genetic variation, it makes up small
287 portions of the genome (Fischer *et al.*, 2017). With increasing use of tools gaining larger
288 representation of the genome (e.g., RAD-seq, whole genome sequencing), and improvements in
289 methods to track bat movements, studying bat differentiation with increasing genome coverage
290 may be useful for detecting linkages between movement-related life history traits and genetic
291 variation. Alternatively, there may be no biological connection between the genetic variation and
292 the observed traits in bats at the time these data were collected. Widespread phenotypic shifts
293 may have induced prior shifts in gene flow or related processes in bats because of environmental
294 change (Smeraldo *et al.*, 2021), which may have altered the dynamics of how genotypes reflect
295 phenotypes.

296 The differing sampling distribution and quantity across species in our study could affect
297 the representation of different types of migration or mating systems. For example, some species
298 were sampled more than others (ranging between 3104 bats across 66 sampling populations for
299 *M. lucifugus*, and 6 bats across 1 sampling population for *M. thysanodes* (Miller, 1897)). This
300 would change the spatial extent of the samples corresponding to each species' respective ranges
301 and artificially reduce genetic differentiation if few populations were sampled. We also assumed
302 that distances moved during migration relative to range sizes did not affect the categorization of
303 migratory strategies. Additionally, describing genetic structure in populations requires
304 consideration of multiple seasons, such as summer maternity roosts, swarming sites, and
305 hibernacula (Davy *et al.*, 2015). Variation in the timing of sampling collection across species
306 made it difficult to parse out seasonal effects on population structure overall, and we assumed
307 samples came from discrete genetic populations. However, we can at least conclude that site-

308 specific genetic differentiation and variation was not associated with migration or breeding
309 strategy. These results show that bats potentially maintain genetic variation despite differences in
310 behavioural strategies.

311

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317

318 **Data Availability Statement**

319 All data used in the present study were downloaded from publicly available resources
320 detailed in the methods, with specific repositories listed in the references.

321

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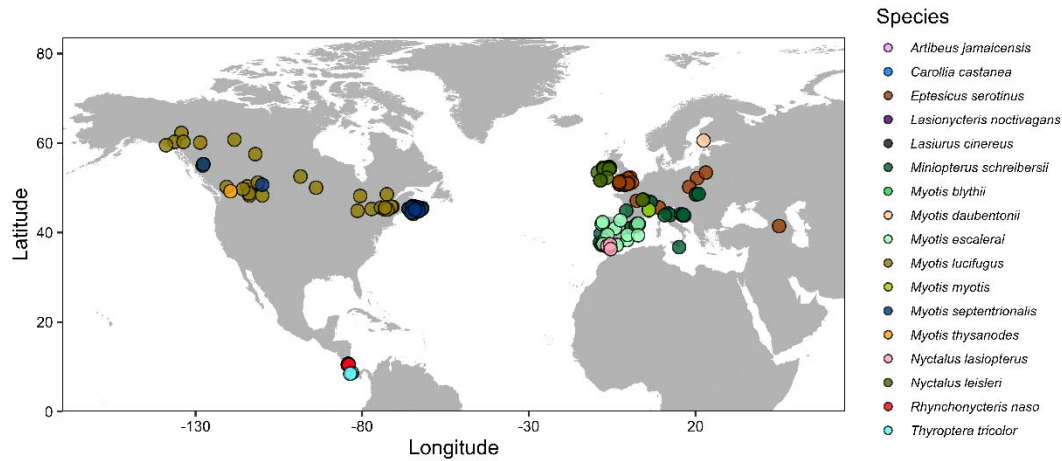
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625 **Figures and tables**

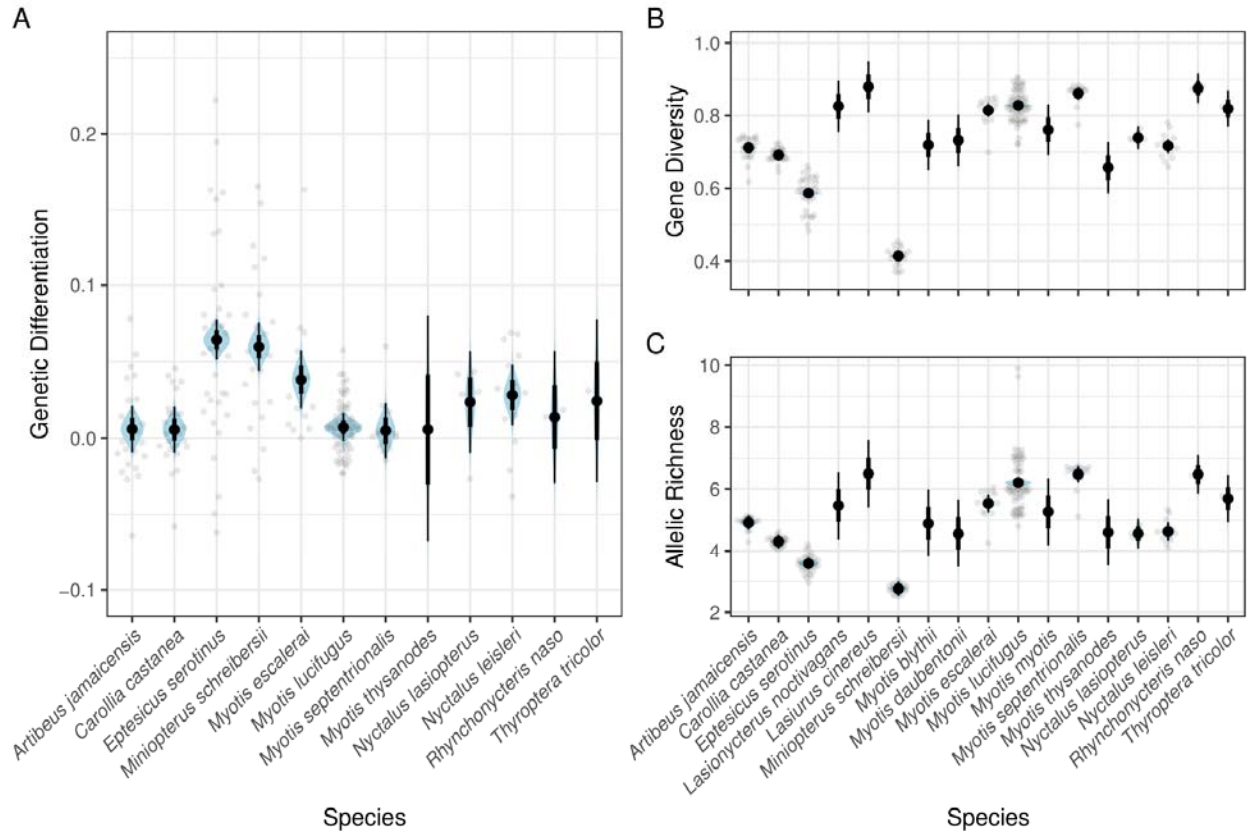
626 **Figure 1.** Map of bat genetic data and sampling locations used in the present analyses. Sampling
627 locations are coloured by species. A total of 12 species, 228 sampling groups, and 7618
628 individuals were used for analyses of genetic differentiation (genetic differentiation) while 17
629 species, 233 sampling groups, and 8095 individuals were used for analyses of gene diversity
630 (gene diversity) and allelic richness.

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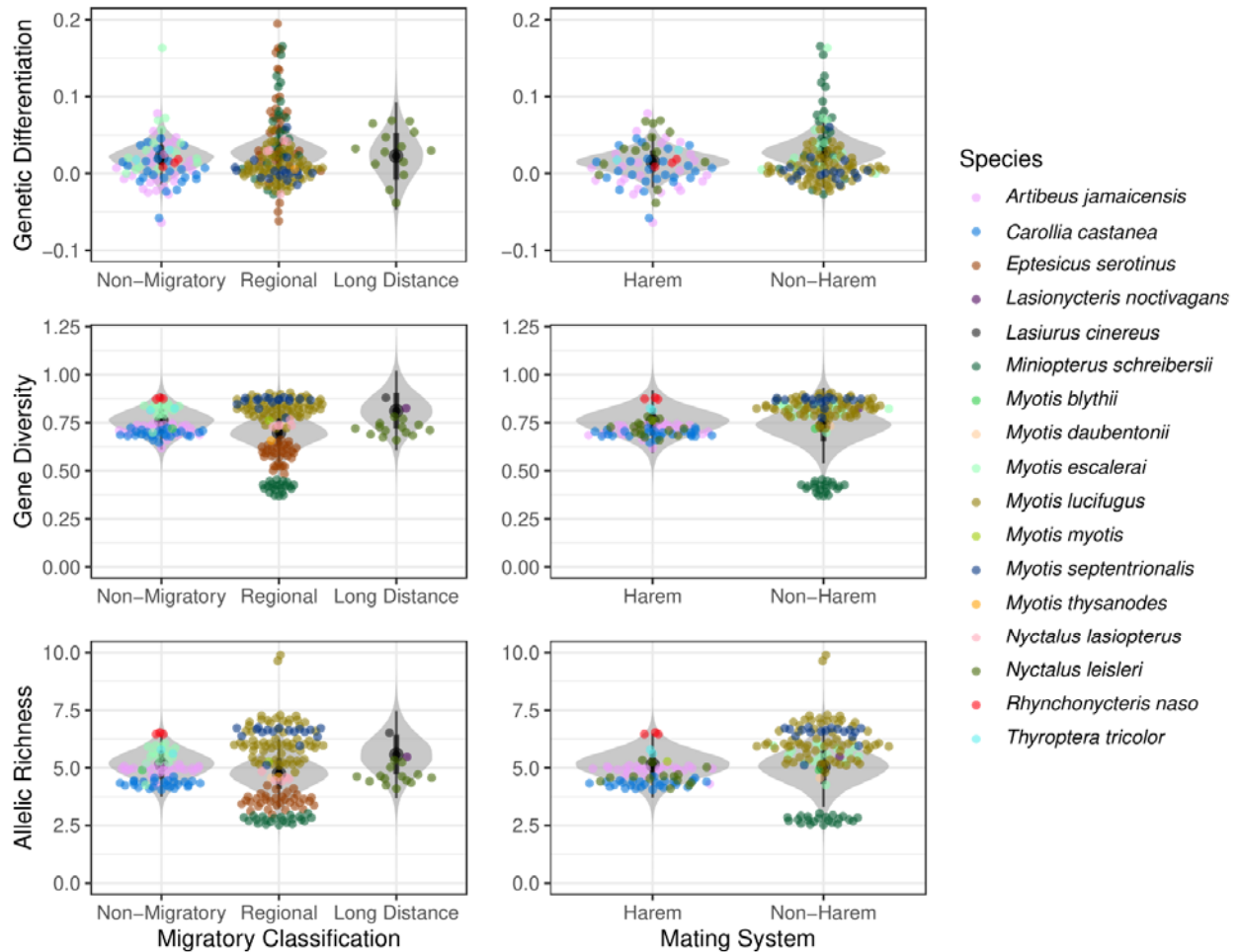
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635 **Figure 2.** Estimates of population differentiation (genetic differentiation), gene diversity (gene
636 diversity), and allelic richness across species. Posterior distributions are provided in blue,
637 95% credible intervals in thin black lines, and 66% credible intervals in bold black lines. Group-level
638 data points used for modeling genetic measures across species are also provided.
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642 **Figure 3.** Estimates of population differentiation (genetic differentiation), gene diversity (gene
643 diversity), and allelic richness compared between migration strategies (non-migratory, regional,
644 long-distance) and mating systems (harm, non-harem) in bats. Posterior distributions are in gray,
645 while group-level datapoints used for modeling genetic measures are coloured by species.



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