Predicting migration routes for three species of migratory bats using species distribution models

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Understanding seasonal variation in the distribution and movement patterns of migratory species is essential to monitoring and conservation efforts. While there are many species of migratory bats in North America, little is known about their seasonal movements. In terms of conservation, this is important because the bat fatalities from wind energy turbines are significant and may fluctuate seasonally. Here we describe seasonally resolved distributions for the three species that are most impacted by wind farms (*Lasiurus borealis* [eastern red bat], *L. cinereus* [hoary bat], and *Lasionycteris noctivagans* [silver-haired bat]) and use these distributions to infer their most likely migratory pathways. To accomplish this, we collected 2880 occurrence points from the Global Biodiversity Information Facility over five decades in North America to model species distributions on a seasonal basis and used an ensemble approach for modeling distributions. This dataset included 1,129 data points for *L. borealis*, 917 for *L. cinereus*, and 834 for *L. noctivagans*. The results suggest that all three species exhibit variation in distributions from north to south depending on season, with each species showing potential migratory pathways during the fall migration that follow linear features. Finally, we describe proposed migratory pathways for these three species that can be used to identify stop-over sites, assess small-scale migration and highlight areas that should be prioritized for actions to reduce the effects of wind farm mortality.

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9   **Abstract**

10   Understanding seasonal variation in the distribution and movement patterns of migratory species

11   is essential to monitoring and conservation efforts. While there are many species of migratory

12   bats in North America, little is known about their seasonal movements. In terms of conservation,

13   this is important because the bat fatalities from wind energy turbines are significant and may

14   fluctuate seasonally. Here we describe seasonally resolved distributions for the three species that

15   are most impacted by wind farms (*Lasiurus borealis* [eastern red bat], *L. cinereus* [hoary bat],

16   and *Lasionycteris noctivagans* [silver-haired bat]) and use these distributions to infer their most

17   likely migratory pathways. To accomplish this, we collected 2880 occurrence points from the

18   Global Biodiversity Information Facility over five decades in North America to model species

19   distributions on a seasonal basis and used an ensemble approach for modeling distributions. This

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21   *noctivagans*. The results suggest that all three species exhibit variation in distributions from

22   north to south depending on season, with each species showing potential migratory pathways

23   during the fall migration that follow linear features. Finally, we describe proposed migratory

24   pathways for these three species that can be used to identify stop-over sites, assess small-scale

25   migration and highlight areas that should be prioritized for actions to reduce the effects of wind

26   farm mortality.

27

28   **Keywords**: bats, GBIF, *Lasiurus borealis, Lasiurus cinereus*, *Lasionycteris noctivagans*,

29   migration pathway, species distribution models

30

31 **Introduction**

32 Conservation and management of migratory animals requires knowledge about their seasonal

33 movements across space and time (Webster et al. 2002). In a wide variety of taxa, species

34 migrate when resources vary seasonally (Shaw & Couzin 2013) or temperature variation results

35 in thermal stress (Fleming & Eby 2003). Due to small body sizes it is difficult to track long

36 distance movements of many taxa such as species of bats, birds, and insects reducing our

37 understanding of their migratory behavior. While some progress has been made using light-level

38 geolocators (Åkesson et al. 2012) and various biomarkers (e.g., Hobson & Wassner 2018), these

39 methods have limitations such as requiring recapture and low precision, respectively and as a

40 result are limited in their impact. This is particularly true for bats, small-bodied nocturnal

41 mammals capable of true flight.

42   Although many species of bats migrate, only 12 of 500 Vespertilionid bats undertake

43 long-distance migration and understanding their migration is vital to the conservation of these

44 species (Fleming & Eby 2003; Simmons & Cirranello 2020; Welbergen et al. 2020). By

45 understanding the migration of these species, we can better understand the pressures an

46 individual will face during migration or at home ranges during non-migratory time periods.

47 However, limited information is currently available about the long-distance migration of bats in

48 North America. For example, in most species the approximate direction (north-south), time of

49 year, and some rough estimates of distances travelled are all that is known (Fleming & Eby

50 2003; Pettit & O'Keefe 2019) with much of this information inferred from distribution modeling

51 in these species (e.g., Hayes, Cryan & Wunder 2015) or biomarker studies, such as isotopes (e.g.,

52 Cryan, Stricker & Wunder 2014).

53   Hydrogen isotopes have largely been the focal method for investigations into migration

54   of North American tree bats. For example, Baerwald, Patterson & Barclay (2014) used isotope

55   information to propose that *Lasiurus cinereus* and *Lasionycteris noctivagans* use the eastern

56   slopes of the Rocky Mountains as a migration route. Further, Cryan, Stricker & Wunder (2014)

57   used stable isotope data to suggest that *L. cinereus* has some east-west movement during

58   migration in addition to the north-south, likely toward coastal regions during Autumn migration

59   that potentially contain more suitable winter habitat.

60   In contrast to our understanding of migration in North American bats, there is more

61   known about bats from Europe and other regions. Previous studies have shown repeated and

62   partial migration (Lehnert et al. 2018), and that bats showed site fidelity at stop-over sites during

63   migration (Giavi et al. 2014). One important aspect of research is understanding how bats

64   navigate during migration and some have suggested the tracking of linear features for bat

65   migration (e.g., Voigt et al. 2016; Ahlén et al. 2009), although others have challenged this

66   interpretation (Krauel et al. 2018). Further studies have also shown the impacts of humans during

67   migration. Human activities have the potential to disrupt bat migration via mechanisms such as

68   interfering with magnetic navigation (Voigt et al. 2017), increasing light pollution (Lacoeuilhe et

69   al. 2014), developing wind farms along migration corridors (Hayes, Cryan, & Wunder 2015), or

70   reducing stop-over sites and food availability through deforestation and habitat destruction. To

71   mitigate these effects, a better understanding of migration in bats is needed.

72   A few of these species such as *L. borealis* (Eastern Red bat), *L. cinereus* (Hoary bat), and

73   *L. noctivagans* (Silver-haired bat) have been a focus of understanding these behaviors in North

74   America due to their high mortality at wind farms, with some estimates predicting a 90% species

75   population decline within 50 years due to wind farm interactions (Frick et al. 2017). Bats are the

76   most common animal found dead beneath wind turbines in North America (Kunz et al. 2007)

77   with the majority (~80%) of these individuals consisting of just the three species of migratory

78   listed above (Arnett & Baerwald 2013). Most of the fatalities for these species occur during a

79   period of time coinciding with autumn migration (Kunz et al. 2007), but data linking the act of

80   migration and mortality is lacking. Overall, a more precise delineation of possible migratory

81   corridors (defined here as the most likely path followed during migration) and how these

82   influence wind farm interactions could help to minimize impacts of wind facilities on these

83   species.

84   One explanation for the uncertainty about long-distance migratory pathways of migratory

85   bats is the lack of data on spatial locations through time which is in contrast to such data which

86   are widely available in better-studied migratory species such as birds. One reason for this

87   difference is that observational data on birds can come from a variety of Citizen Science

88   initiatives such as the Breeding Bird and Christmas Bird Surveys and eBird (National Audubon

89   Society 2010; Sullivan et al. 2009). The difference in data quantity is large. For example, a

90   common migratory bird, the yellow warbler (*Setophaga petechia*) has 2.39 million occurrences

91   the Global Biodiversity Information Facility (GBIF; checked 11 Dec 2019) whereas the entire

92   family of Vespertilionidae bats consisting of >400 species have only 1.49 million occurrences

93   recorded. While the causes of this disparity are many, the difference highlights the need to use

94   other sources of data for to study broad scale patterns of bat migration.

95   One approach to better understand seasonal distributions and identify migratory corridors

96   is to generate seasonally explicit species distribution models (SDMs; Fink et al. 2010, Hayes,

97   Cryan, & Wunder 2015; Smeraldo et al. 2018) and use these to infer movement patterns. This

98   approach has been successful in other migratory species, such as birds (Reynolds et al. 2017).

99   While other studies have begun to explore this approach with tree bats (see Findley & Jones

100   1964; Cryan 2003; Hayes, Cryan, & Wunder 2015), much of this work has focused on overall

101   distributions as opposed to seasonal differences in movement. However, seasonal movements

102   can be studied by generating models of bat distributions on a month-by-month basis that allow

103   seasonal variation to be visualized and infer the movement that took place between monthly

104   occurrences.

105   In this study, our objective was to identify possible migratory pathways utilized by

106   migratory bat species in North America (*L. borealis*, *L. cinereus*, and *L. noctivagans*) through

107   modelling their seasonal distributions using SDMs. While not the first study to generate SDMs

108   for these species, it is the first to use them to infer migration patterns for the time between

109   seasonal occurrences. The models generated in this study shed light on the seasonal dynamics for

110   these three species and highlight areas of interest for further study of migratory corridors that

111   could be used to investigate stop-over sites, small scale migration, and be used as a starting point

112   for designing methods to mitigate wind farm mortality.

113   **Methods**

114   *Occurrence data from GBIF*

115   Figure 1 shows an overview of the steps involved in data collection and analysis; more detailed

116   methods are described on Supplemental Material. To begin, all available occurrence data were

117   downloaded for *L. borealis, L. cinereus,* and *L. noctivagans* through the GBIF data portal

118   (http://www.gbif.org) on 11 March 2019 using only 'Preserved Specimens', 'Human

119   Observations', and 'Material Sample' keywords for data from the past 50 years

120   (https://doi.org/10.15468/dl.dpiwzi, https://doi.org/10.15468/dl.irfol0, and

121 https://doi.org/10.15468/dl.viiyt5, respectively). This 50-year period was selected because it

122 allows for more confidence in the call of a species and its locality. While some previous studies

123 have verified occurrence data from older than 50 years ago (see Hayes et al. 2015), we were

124 unable to access the data from the museum collections used in that study. In addition, due to

125 climate change ranges may be shifting as has been observed in some mammal species (MacLeod

126 2009) and so using more recent occurrence data likely provides more accurate current ranges. All

127 downloaded records were screened using several filters (described below) as recommended by

128 others (Feeley & Silman 2011; Carstens et al. 2018). Once data sets were filtered using these

129 criteria, we corrected for over sampling within a 1º region following guidelines given by

130 Hijmans and Elith (2017). In brief, we created a grid of 1º resolution (~111km) and subsampled

131 our occurrence data to one occurrence per grid cell. This was done to reduce the possibility of

132 sampling bias in our data. While there exists a possibility of overthinning data, a larger concern

133 was sampling bias inflating suitability of certain regions especially on these analyses as

134 suitability will determine the inferred pathways. This is especially true for the known spatial bias

135 that exists in GBIF data, due to differences in funding and data sharing of institutions (Razgour

136 et al. 2016). As a result, we took the conservative approach of 1º grid sampling. In addition,

137 other continent-wide studies for some species have used similar scales for filtering and were

138 shown to be an effective filtering approach (Fourcade et al. 2014). Lastly, some have suggested

139 that sampling be limited to an approximate home range for a species (Kramer-Schadt et al.

140 2013). In this case, due to the highly volant nature of bats with the ability to travel long distances

141 of a given night broader filtering is needed. For example, Morningstar and Sandilands (2019)

142 documented an individual *L. cinereus* traveling over 800km in two weeks, finishing ~50km from

143 the initial roost. As a result of this high mobility, a larger grid sample likely produces more

144 accurate distribution models.

145 *Predictor environmental variables*

146 WorldClim version 2 monthly climatic data were used at 2.5-minute resolution (~4.5km; Fick &

147 Hijmans 2017) for our species distribution models and included the following variables:

148 precipitation (mm), solar radiation (kJ m^{-2} day^{-1}), average temperature (^{o}C), maximum

149 temperature (^{o}C), minimum temperature (^{o}C), vapor pressure (kPa), and wind speed (m s^{-1};

150 downloaded on 03 June 2019 from worldclim.org). WorldClim is a database of high spatial

151 resolution global weather and climate data. These data can be used for mapping and spatial

152 modeling. Additionally, elevation maps (Tachikawa et al. 2011; 11 March 2019), and the human

153 influence index (CIESIN, 2005; 11 March 2019) for North America were also downloaded as

154 Jung and Threlfall (2016) showed a negative response to urbanization in the Americas in

155 insectivorous bats in the family Vespertilionidae. Human influence was determined by

156 combining population density, human land use and infrastructure, and human access (WCS,

157 2005). Following Hayes et al. (2015), we also included MODIS Normalized Difference

158 Vegetative Index (Didan et al. 2015) and Global Tree Coverage 2010 (Hansen et al. 2013) as

159 metrics of seasonality and leaf growth, which could impact prey abundance, and be a metric of

160 available roost sites in trees, downloaded on 04 June 2019 and 05 June 2019, respectively. Prior

161 to final selection of predictor variables, correlations between each possible pair of predictor

162 variables were determined and one variable from each pair that was strongly correlated with the

163 other was removed (r > 0.8; Mateo et al. 2013). Any removal of a variable was determined based

164 on biological relevance and previous uses in literature.

165 *Species distribution modeling*

166 Species distribution models were generated for each species using five different methods: four

167 specific model algorithms and an ensemble approach (see below). Specific algorithms included:

168 generalized linear model (GLM; Guisan, Edwards, & Hastie 2002), BIOCLIM model (BC;

169 Booth et al. 2014), random forest (RF; Breiman 2001; Mi et al. 2017), and maximum entropy

170 (MaxEnt; Phillips, Dudik, & Schapire 2017). These four approaches, while good predictors

171 individually, can be made more effective through an ensemble method. This approach accounts

172 for the problems of each model and can allow for better performing models (Araújo & New,

173 2006; Marmion et al. 2009) and is becoming more common (Razgour et al. 2016). Due to this

174 and our results (see below), we used the ensemble models for all analyses.

175   All SDM analyses were carried out in R using the packages "randomForest" (Liaw &

176 Wiener 2018), "raster" (Hijmans et al., 2019), "rgeos" (Bivand et al. 2019), "maptools" (Bivand

177 et al. 2019), "dismo" (Hijmans et al. 2017), "sp" (Pebesma, Bivand, & Pebesm, 2012),

178 "ecospat" (Di Cola et al. 2016), and "rJava" (Urbanek 2019). We created 1000 pseudo absence

179 points for each month from random points in the background layers and partitioned the model

180 into testing (80%) and training data (20%) using the "kfold" function.

181   Each model was then assessed using the Area under the ROC (receiver operating

182 characteristic) curve (AUC) and the True Skill Statistic (TSS). These values were then used to

183 weigh each layer and were then combined into a single ensemble SDM. Following generation of

184 our ensemble models, they were assessed using the same AUC and TSS metrics as outlined

185 above and data points used for all other models for comparison to determine which model to use

186 for further analysis. These layers were then used to predict migratory pathways.

187   The importance of individual variables was assessed using different methods for each

188 model. For RF we used the 'importance' function in the "randomForest" R package to measure

189   the importance of a variable in a model. With MaxEnt, variable importance was assessed using

190   'var.importance' function in "ENMeval" to determine the importance of each variable

191   (Muscarella et al., 2014). For the GLM model, we used the 'varImp' function present in "caret"

192   (Kuhn et al., 2020).

193   *Migratory pathways*

194   To identify migratory pathways using SDMs we used three complementary methods: circuit

195   theory (McRae & Beier 2007; Shah & McRae 2008), 95th percentile suitability (Poor et al. 2012),

196   and least cost path analyses (LCP; Howey 2011). Since each of these methods have advantages

197   and disadvantages, results from these three methods were compared to generate a consensus

198   delineation of possible corridors (Bond et al. 2017; Marrotte & Bowman 2017). While some

199   authors have argued for selecting the single best hypothesized approach (Marrotte & Bowman

200   2017), as we do not know if these species follow linear features as has been observed in some

201   species (Ahlén et al. 2009) or exhibit more erratic movements, we could not confidently select a

202   single approach. Multiple authors (Dutta et al. 2015; Medley, Jenkins & Hoffman 2015) show

203   that circuit and least-cost based analyses complement each other and can give more insight into

204   the movement of a species. In addition, the use of circuit theory and least-cost-path allow for

205   some movement through less suitable areas. In least-cost-path analyses an individual's path may

206   go through less suitable areas as the model weighs both distance and suitability of the areas

207   traveled through. For example, the model would give preference for travel through a single less

208   suitable cell if the cumulative cost is less than four more suitable cells. Similarly, in circuit

209   theory it is possible for the "current" (an individual movement likelihood) to pass through less

210   suitable cells as long as the total resistance to do so is less than adjacent alternative paths.

211   For circuit theory, the protocol of Burke et al. (2019) was followed. In brief, we

212   aggregated our winter month occurrences (December – February) into a single dataset and did

213   the same for summer months (June-July), using Hayes et al., (2015) to determine the appropriate

214   months for each season. As SDMs can be interpreted as conductance maps, we used an average

215   of both spring and fall months (March, April, May; and August, September, October,

216   respectively) to assess potential corridors between winter and summer occurrences. These time

217   periods are based on previously published distributions of occurrences (Cryan 2003), previous

218   SDM modeling (Hayes, Cryan, & Wunder 2015), wind farm fatality data (Arnett et al. 2008),

219   radio telemetry (Walters et al. 2006), and acoustic data (Muthersbaugh et al. 2019). Using

220   Circuitscape (Shah & McRae 2008), we set our start ("source") and end ("ground") points based

221   on the hypothesized direction of migration. To identify patterns of spring migration, we set our

222   start as winter occurrences and end as summer points, with the spring SDMs as the conductance

223   raster; and summer as start and winter as end with fall SDMs as the fall migration conductance

224   raster; this was repeated for each species.

225   To use least cost path analysis to predict migratory pathways we used the R function

226   'shortestPath' implemented in 'gdistance' (Van Etten 2017). The analysis was done iteratively

227   between all points previously designated as "Winter" and "Summer" points for Circuitscape, and

228   spring/fall conductance surfaces for cost determination. As single pathways are likely not

229   informative for species-wide migratory pathways, we combined each least cost path to create a

230   density of pathways. A high density of overlapping paths was used to identify a potential

231   migratory pathway. Additionally, while we are unable to infer if a proposed path is true, we used

232   Moran's I (Moran 1950) and Geary's C (Geary 1954) to quantify if these proposed pathways are

233   positively clustered, as would be expected in a migratory corridor. We also quantified the

234   distance traveled compared to straight-line distance to determine if the proposed pathways would

235   be biologically relevant (i.e., if not following straight line, other factors influence where bats

236   migrate through). Next, binary rasters identifying potential migratory pathways using the 95th

237   percentile approach was generated to identify areas where bats are more likely to be concentrated

238   compared to background (Poor et al. 2012). This was to identify areas where suitability is higher

239   and therefore a potential migratory pathway. Finally, overlaps between Circuitscape, least cost

240   path, and 95th percentile approaches were identified to highlight locations where they agreed and

241   those were inferred to be potential migratory pathways.

242   To ensure we are tracking migration and not simply sampling bias, a comparison between

243   the results for migratory pathways above and those from two non-long-distance migratory

244   species (*Myotis lucifugus* and *Eptesicus fuscus*) following the same methods above was carried

245   out. If the pathways are similar to those from these two species it is possible that we are tracking

246   the ability to capture bats during the winter instead of actual movement. On the other hand, if

247   pathways are different, then it is more likely that we are identifying true pathways. Occurrence

248   data for these additional species were collected from GBIF on 31 January 2020

249   (https://doi.org/10.15468/dl.fphagx) and were treated in the same manner as the three migratory

250   species to generate SDMs and test migratory pathways.

251   **Results**

252   *GBIF Occurrence Data*

253   A total of 20,697 occurrences were downloaded from the GBIF database: 8,362 for *L. borealis*,

254   7,649 for *L. cinereus*, and 4,686 for *L. noctivagans*. After filtering, there were 10,743 data points

255   remaining: 4,380 for *L. borealis*, 3,736 for *L. cinereus*, and 2,627 for *L. noctivagans*. Finally,

256   after accounting for sampling bias there were 1,129 data points for *L. borealis*, 917 for *L.*

257   *cinereus*, and 834 for *L. noctivagans* (Figure 2). For each month numbers of data points ranged

258   between 21 and 205 (Table 1). All months were above the minimum of 13 observations

259   suggested by van Proosdij et al. (2016) (based on simulated data) as necessary for SDM analyses

260   for wide ranging species. Further, only December for two species had occurrences below a

261   higher secondary minimum threshold of 25 data points based on empirical data (per van Proosdij

262   et al. 2016). SDM analyses were conducted with each subset of data using each of the 5

263   modeling approaches: GLM, BC, RF, MaxEnt, and ensemble, for a total of 60 model runs for

264   each species. While we acknowledge the presence of other datasets (see NABat

265   [https://www.nabatmonitoring.org/] and/or American Wind/Wildlife Institute [https://awwi.org/]),

266   we found that we had sufficient data available via GBIF for all months given that we had over

267   25 occurrences for 11 months, and the only month below this threshold is also deficient in other

268   datasets. Further these other datasets are not comprehensive across North American for all

269   months and/or are not readily available to the public.

270   *Predictor variables*

271   Following removal of variables that were highly correlated (r>0.8), eight variables were retained:

272   elevation, forest coverage, NDVI, precipitation, solar radiation, average temperature, vapor

273   pressure and wind speed. The variables that were removed were minimum and maximum

274   temperature which were highly correlated with average temperature (r=0.98 and 0.99,

275   respectively). Average temperature was selected due to the ability of bats to regulate their body

276   temperature and energy expenditure through torpor (Baloun & Guglielmo 2019). While relative

277   importance of variables fluctuated between the four original models implemented (GLM,

278   MaxEnt, RF, and BC), in general, average temperature, solar radiation, and vapor pressure were

279 the most important variables (Table 2; specific weights Table S1). In contrast, NDVI, percent

280 forest, wind, and precipitation were consistently the least important variables.

281 *Species distribution models*

282 AUC scores range from 0.50 to 0.99, while TSS values range from 0.44 to 0.95 across all 5 types

283 of models. When evaluated by both AUC and TSS, the consistently best performing species

284 distribution model was the TSS weighted ensemble model (Figure S1), with this model having a

285 minimum AUC of 0.94 and TSS of 0.78 (Table S2), indicating a high predictive performance

286 (e.g. Smeraldo et al., 2018). In addition, these high values indicate sufficient sampling (both

287 number and spatial scale) present for the analyses completed. With the exception of the model

288 for *L. borealis* for July, our TSS weighted ensemble model was always determined to be the best

289 model by both AUC and TSS. As a result of the ensemble models consistently high performance,

290 it was used for all subsequent analyses. We now describe the results for each of the three species.

291   While we did not explicitly explore the seasonal variation present in each species

292 generated SDM's, this variation can be observed in Figure 3 (each species detailed in Figure S2-

293 4). In short, we observe trends that are similar to those found in previous studies (e.g. Baerwald

294 & Barclay 2011; Johnson et al. 2011; Hayes, Cryan, & Wunder 2015). For *L. borealis* and *L.*

295 *cinereus* we observe concentration of habitat suitability in the southern portions of their range

296 during winter months with a northward movement during the summer into early fall. This is

297 followed by a contraction again to the south. On the other hand, *L. noctivagans* exhibits a

298 different pattern: while it has suitable habitat further north during the winter and expands

299 northward it doesn't appear to do so to the same extent as the other two species. With these

300 results being similar to expected, we can use them to predict the most likely migratory pathways.

301   *Potential migratory pathways*

302   Using three methods (Circuitscape, LCP, and 95ᵗʰ percentile), we find potential migratory

303   pathways for each species that vary between the spring and fall seasons (Figure 4; Circuitscape

304   maps are shown in Figure S5). In terms of spring migration patterns, *L. borealis* shows highest

305   density of LCP along the Eastern coast of the U.S. and near the Mississippi River suggesting an

306   avoidance of the Appalachian Mountains and using coasts and rivers as guidance during

307   migration (Figure 4). This pattern is also present in the 95ᵗʰ percentile maps. For *L. cinereus*,

308   higher LCP densities occur along Western Mexico into the Southern U.S., after which the higher

309   probability pathways lie on either side of the Rocky Mountains pattern and along the Atlantic

310   coast suggesting a lack of resolved pathway during this time period (Figure 4). This is also

311   supported by the 95ᵗʰ percentile map showing higher suitability scores being present in both

312   these regions before the paths would extend further north. Finally, *L. noctivagans* shows two

313   different patterns: LCP maps suggest movement from south to north in the Western U.S. along

314   the Pacific coast and along the western edge of the Rocky Mountains (Figure 4). In the Eastern

315   U.S. there appears to be more of an east-west movement during which individuals would split off

316   to move north or south, likely indicating a partial or incomplete migration in this species. For

317   each of these species we see significant positive clustering in our pathways when using both

318   Moran's I and Geary's C (Table 3). We can also observe that these potential pathways are

319   significantly longer than straight line distance by hundreds of kilometers meaning these

320   pathways would be biologically important, or in other words, that the most likely paths found

321   here follow some biologic aspect of the area.

322   In terms of fall patterns, *L. borealis* show*s* two apparent migration paths: one along the

323   East coast, and the other near the Mississippi River and into the Southern plains (Figure 4).

324   These paths are supported by the 95th percentile map, which shows suitable habitat in these areas

325   at the same time of year. These two paths again indicate a potential following of coastline and

326   rivers as linear guides during migration. *L. cinereus* shows evidence for multiple pathways

327   (Figure 4). Two possible pathways are present along the coasts of the Atlantic and Pacific, again

328   indicating a possible following of coastlines during migration. While the Pacific is the clearer

329   pathway of the two there is still a high density of lines along the Atlantic, which could be a

330   minor pathway for those individuals navigating around the Appalachian Mountains. In addition,

331   a pathway appears in our LCP map and is supported by the 95th percentile map along the

332   Mississippi River. There is also evidence for movement through the Great Plains between the

333   eastern slopes of the Rocky Mountains and the interior highlands near Missouri and Arkansas.

334   Finally, *L. noctivagans* shows similar patterns for fall as those observed during spring migration

335   periods (Figure 4). We see a north-south pathway west of the Rocky Mountains, and east of

336   those, a more east-west pathway is observed, with movements extending north or south, which

337   again potentially indicates a partial or incomplete migration. With fall migration, we also

338   observe positively clustered pathways that are significantly longer than Euclidean distance

339   (Table 3).

340   The two bats that are not long-distance migrants show less variation in seasonal

341   distribution as compared to the three migrant species discussed earlier (Figure 4). In particular,

342   both *E. fuscus* and *M. lucifugus* show a consistent east-west distribution pattern that does not

343   change throughout the year. This supports the idea that changes in distributions of the migratory

344   species likely reflect migratory behavior. Of interest is that the pathways determined by LCP for

345   *E. fuscus* are similar to *L. noctivagans,* providing additional support that silver-haired bats

346   undergo only a partial migration, that being some individual migrant while others overwinter in

347   northern portions of the range. This seems possible as it has been documented silver-haired bats

348   can overwinter at Northern latitudes (Cryan, 2003).

349   **Discussion**

350   Other studies have used SDMs and occurrence to model seasonal distributions of wide-ranging

351   migratory bats including those studied here (e.g., Cryan 2003; Hayes, Cryan, & Wunder 2015).

352   This study extends this approach by using SDMs to predict migratory corridors, in this case the

353   most likely path used. In essence, while others have used these data to delineate where bats are at

354   a given time, we expand on this by attempting to understand what is happening between these

355   occurrences. Below we discuss limitations of our analyses and then expand on the conservation

356   implications of our results.

357   *Analysis limitations*

358   Using species occurrence data to generate species distribution models can be impacted by

359   sampling biases present in the data (Feng et al. 2019). We attempted to minimize these biases by

360   following guidelines described in Feng et al. (2019). Specifically, we took steps to reduce

361   oversampling of regions by subsampling our dataset to 1 point per 1º grid cell. Additionally,

362   because occurrence records only represent presence points, and not true absences, we included

363   models that require only presence data or can be adapted for use with presence only data. Despite

364   these measures, it is possible biases remain in our models and so we stress that our models

365   represent hypothetical species distributions and migratory pathways for any point in time.

366   Another potential limitation with this approach is ability of bats to traverse unsuitable habitat.

367   This could lead to some true pathways we are unable to predict as our models "prefer" suitable

368   areas for inferring patterns of movement. However, the approaches used allow for some level of

369 traversing areas of unsuitable habitat prior to using suitable stop-over sites (as noted above). As a

370 result, we further stress that the pathways presented are only the most likely to be used and

371 should be investigated further via other sources of data for inferring individual movements such

372 as biomarkers and GPS tags.

373 *Migratory Pathways*

374 Our analyses identify potential migratory pathways across modelling approaches, although we

375 observed some differences that likely result from features of the data that are given different

376 weight by different methods (McClure, Hansen, & Inman 2016). For example, we were unable to

377 identify clear pathways using Circuitscape despite using multiple transformations of our data

378 (square root, log, natural log, and cube-root transformations). The lack of identifiable paths using

379 Circuitscape may indicate a true lack of clear migratory pathways yet still reflect the general

380 patterns shown by the other methods. This is supported by the least cost path analysis, as while

381 the figures present the most likely paths (Figure 4), many other paths were evident (see Figure

382 S6). Diffusion or a wandering migration, across the landscape has been proposed for these

383 species in previous studies (Weller et al. 2016; McGuire 2019). As noted in Baerwald et al.

384 (2021) for some species of migratory bats, more erratic 'wandering' movements in opposite

385 direction of typical seasonal movements may be observed. While we find some evidence for this

386 in our data, the Circuitscape maps identity areas of higher possible movement are also predicted

387 by the LCP and 95th percentile threshold methods, providing support for specific proposed

388 pathways. We emphasize that our results are not definitive delineations of a single migratory

389 corridor followed by all individuals for the entire duration of migration. Rather, they identify the

390 general paths followed during spring and fall migration while allowing for individual variation.

391   We note that specific features of our most likely migration pathways match patterns

392   proposed by others. For example, in *L. cinereus* we find support movement along the eastern

393   slope of the Rocky Mountains. The same pattern was proposed by Baerwald, Paterson & Barclay

394   (2014) as a likely route followed by spring and fall migrants of the same species to and from

395   Alberta, Canada based on isotope data. In addition, consistent with our study, results from GPS

396   tagging work suggest that *L. cinereus* uses the west of the Rocky Mountains during Autumn

397   migration (Weller et al. 2016), although the sample size was limited. Finally, further work in *L.*

398   *cinereus* using isotopes by provides strong support for predominantly north-south movement

399   (especially in the Autumn) with some east-west movement (Cryan, Stricker & Wunder (2014).

400   These patterns are also observed in our data.

401   In addition, while some differences between this study and those observed in Cryan,

402   Stricker & Wunder (2014) such as apparent crossing of the Rocky Mountains, these could be in

403   part due to how the pathways are presented. In Cryan, Stricker & Wunder (2014) they represent

404   movement using straight lines, whereas in nature bats may follow less direct, linear paths which

405   are better captured by our approach. Further differences can be observed for *L. cinereus* in that

406   Cryan, Stricker & Wunder (2014) find less support for north-south movement during spring than

407   we do. This difference could be an artifact of the use of isotope data which can lack precision, or

408   it's possible our current understanding of spring migration is different than previously expected

409   and tested here. Weller et al. (2016) also found some differences between our proposed pathways

410   and their data. While their sample sizes were limited, they found some support for a more

411   'wandering' migration in this species (at least west of the Rocky Mountains).

412   Finally, in *L. borealis*, there have been numerous reports of individuals being captured

413   offshore during migratory time periods (e.g., Sjollema et al. 2014; Hatch et al. 2013). These

414   reports support our findings suggesting bats use linear features, such as coastlines, during

415   migration. Lastly, *L. noctivagans* is regularly captured during winter months in the northern

416   portions of their range (Falxa 2007; Barnhart & Gillam 2017) supporting the interpretation of

417   this species as a partial migrant. However, as noted in Baerwald, Paterson & Barclay (2014),

418   some individuals are likely migratory and may follow some portion of the Rocky Mountains, a

419   path not strongly supported in our data for *L. noctivagans*.The lack of clear pathways for *L.*

420   *noctivagans* also support the 'wandering' migration proposed by McGuire (2018). In summary,

421   while some differences do exist between our results and others, the broader trends in terms of

422   patterns of movements in these bats appear to be mostly consistent with previous studies.

423   The most likely pathways found here for bats match migratory patterns of many other

424   species in North America including waterfowl and insects (e.g., Lincoln 1935; Westbrook et al.

425   2016; Tracy et al. 2019). Of interest is the similarity to insect migrations which is consistent with

426   an idea proposed by Rydell et al. (2010) that bat deaths at wind farms may be related to feeding

427   on migratory insects near turbines. Bats may be tracking the migration of insects to determine

428   their pathways and are feeding on them during migration leading to turbine mortality of bats (but

429   see Reimer, Baerwald, & Barclay 2018).

430   Another possible explanation for the paths in the results are that bats use linear features,

431   such as rivers, coastlines, and mountain ranges, as guides during migration (Wang et al. 2007;

432   Ijäs et al. 2017). For example, in *L. borealis* we observe apparent tracking of the Mississippi

433   river and Atlantic Coast/eastern edge of Appalachian Mountains, while *L. cinereus* tracks the

434   previous two mentioned and the Pacific Coast. One proposed rationale for the tracking of water

435   bodies is that these features support a higher abundance of prey to feed upon during migration,

436   allowing for more rapid travel (Furmankiewicz & Kucharska 2009). We note, however, that

437   other studies have failed to support this idea. For example, Krauel, McGuire & Boyles (2017) did

438   not find evidence that another species of bat (*Myotis sodalis*) used rivers as a navigation guide

439   during migration. Likewise, based on data from acoustic surveys, Cortes and Gillam (2020) did

440   not find support for the use of the Missouri River as a migration guide for multiple species.

441   These differences may be due to the geographic scale at which the studies were conducted

442   compared to the results presented here. For example, Cortes and Gillam (2020) was conducted

443   over a ~100km of the Missouri River while our study focuses on much larger scales. It's possible

444   that the 100km portion of the river studied by Cortes and Gillam (2020) is not widely used as a

445   linear feature for navigation but the use of rivers is common when looking more broadly. The

446   last possibility for the apparent tracking of rivers and coasts is that increased tree cover also

447   appears to follow these same features (i.e., near river = more trees; as observed in tree cover

448   maps from Hansen et al. 2013). While there are multiple hypotheses for the tracking of linear

449   features, we are not able to distinguish between them, and it could even be some combination of

450   them all. Further, the rationale for use of linear features likely vary among and between species

451   of bats. As noted above, while all this may be true, we only present the most likely path for

452   migration but that does not mean it is the only path. While individuals likely vary, the broad

453   trends observed in our data can inform the conservation of these species.

454   Conservation for migratory bat species needs to be politically and geographically broad

455   to be effective (Fleming 2019). Conservation plans need to include protecting roost sites (during

456   all stages of life), stop-over sites, and conserving foraging habitat around these sites (Fleming

457   2019). Our results give direction as to where to look for stopover sites during migration, provide

458   a starting point to identify areas where protecting habitat for migration is needed, and supply

459   information as to where to best implement smart-curtailment mitigation methods during fall

460   migration (Hayes et al. 2019).

461   In addition, there has been a recent focus on understanding the small-scale patterns of the

462   movement that are embedded in larger migration patterns of these bats to develop effective

463   conservation measures at small spatial scales (e.g., Baerwald, Patterson, & Barclay 2014). Our

464   results contribute to this effort by providing specific hypothesis with which to direct future

465   studies that focus on understanding small-scale aspects of the larger migration movements. For

466   example, researchers could look for migration through regions highlighted here by using acoustic

467   detectors or other methods along areas of the Mississippi River or in areas moving between

468   coastal and nearby mountain ranges, similar to the work done by Cortes and Gillam (2020) along

469   the Missouri River. This type of research could identify areas of high bat activity during

470   migration periods where mitigation efforts could be focused to have the largest impact through

471   reduction of mortality due to wind farms and other causes.

472   *Conclusions*

473   Developing a better understanding about how these species move to and from summer

474   habitat may be key in reducing the number of bats killed at wind farms. With bats making

475   significant contributions to the economy of the United States through ecosystem services (Boyles

476   et al. 2011) and provide valuable ecological services (Ghanem & Voigt 2012) effective and

477   practical measures are necessary to reduce the number of bat deaths annually at wind farms

478   (Frick et al. 2017). By understanding migration, we can better mitigate and conserve species that

479   are currently of concern in many states (e.g. Ohio Division of Wildlife 2015). Our study provides

480   SDMs that can be used as priors in conjunction with isotopic or other biomarker models for

481   determining movement and more importantly, establish a proof of concept of how SDMs can be

482   used to predict migratory pathways. We further provide more information on the movements of

483   migratory bats, thereby informing researchers on where to focus our efforts towards the goal of

484   reducing bat mortality due to wind farms.

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494

495 **References**

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Table 1(on next page)

GBIF Occurrence Data

Number of GBIF occurrence points per month for each species analyzed after filtering

	January	February	March	April	May	June	July	August	September	October	November	December
L. borealis	45	33	44	75	99	151	205	192	123	86	49	27
L. cinereus	29	38	44	80	99	108	125	138	110	86	36	24
L. noctivagans	25	24	28	62	110	111	104	131	106	74	38	21
Total	99	95	116	217	308	370	434	461	339	246	123	72

1

Table 2 (on next page)

Variable Importance

Variable importance rank for three of the four SDM models implemented in these analyses. 1 – indicates the most important variable, while 9 – represents the least important. Each importance was found by the following: RF we used the 'importance' function in the "randomForest" R package, MaxEnt, variable importance was assessed using 'var.importance' function in "ENMeval", GLM model, we used the 'varImp' function present in "caret".

	Precipitation	Solar Radiation	Temperature	Vapor Pressure	Wind Speed	Human Influence	Elevation	NDVI	Forest Cover
Random Forest	5	2	1	3	8	7	4	6	9
MaxENT	6	2	1	3	8	4	5	7	9
GLM	6	1	2	3	7	4	5	8	9

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Table 3(on next page)

Spatial Clustering of Paths

Moran's I and Geary's C to determine if clustering among potential migratory pathways is present. For Moran's I, values range between -1 and 1, with values above 1 indicating positive clustering. Geary's C values range between 0 and 2, with values below 1 indicating positive clustering. Results given for paired t-tests comparing Euclidean and Least-Cost distances.
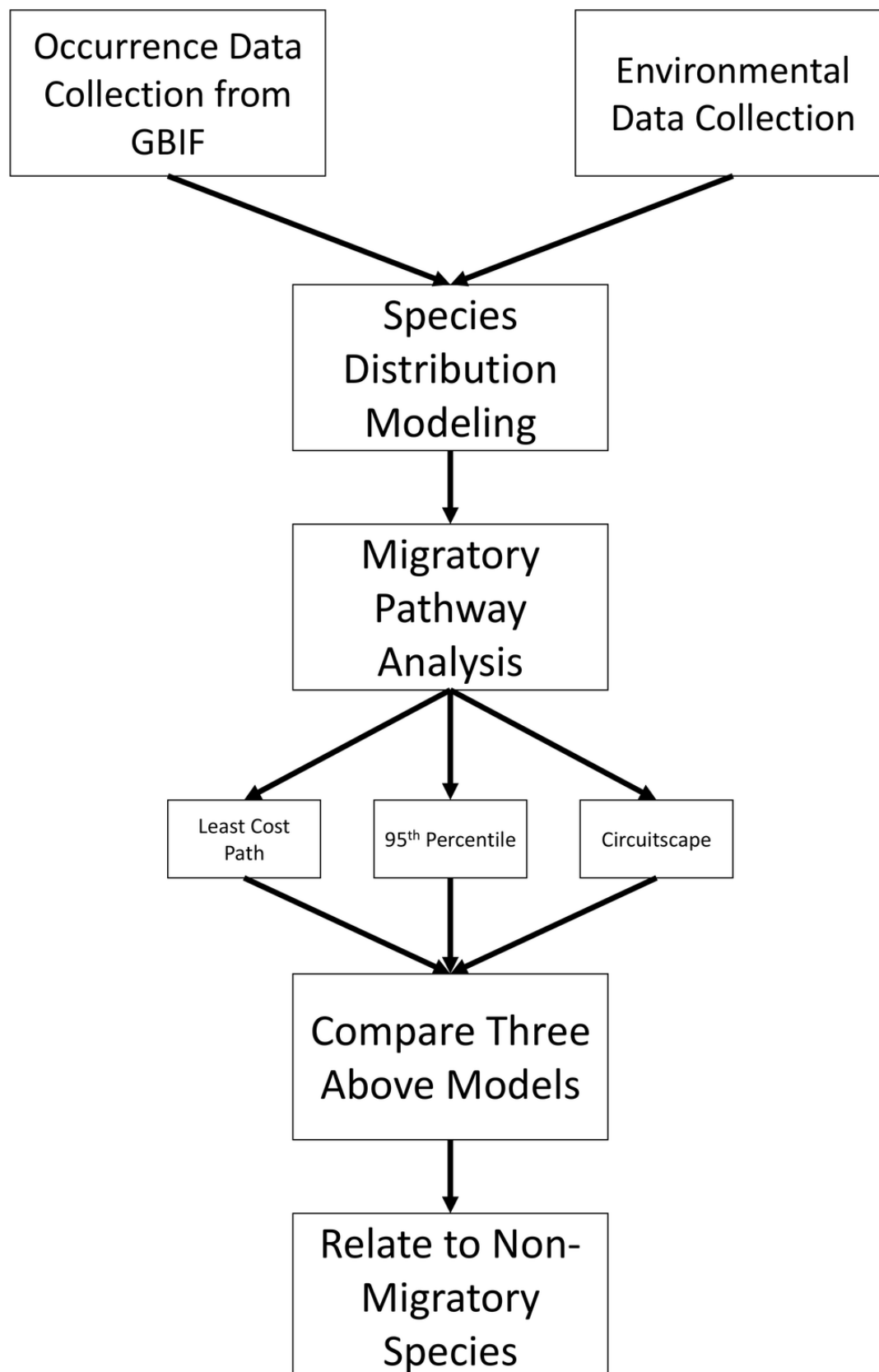
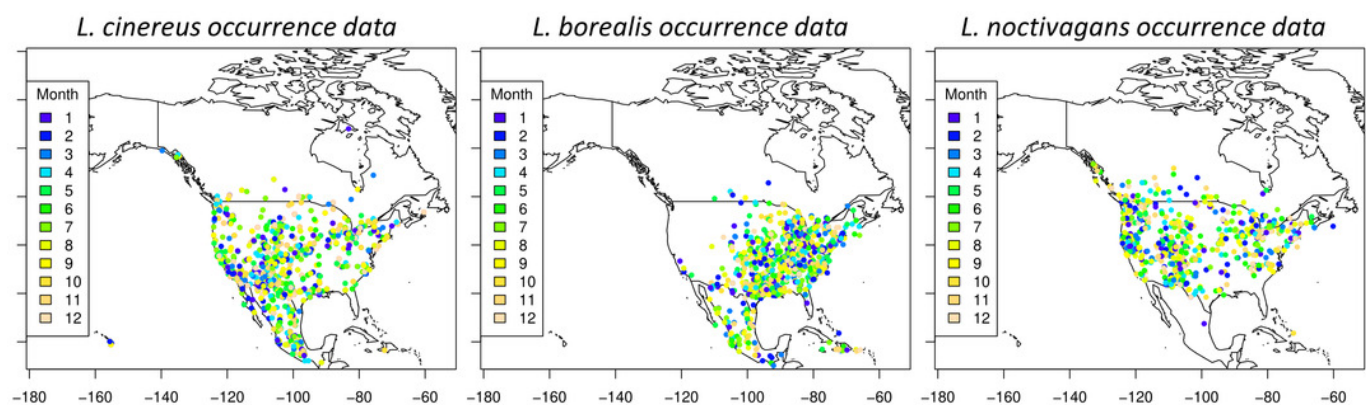|	Spring						Fall					
	Moran's I		Geary's C		Paired t-test		Moran's I		Geary's C		Paired t-test	
	I	p-value	C	p-value	Mean Increase	p-value	I	p-value	C	p-value	Mean Increase	p-value
L. noctivagans	0.39	0.01	0.60	0.01	880.40	< 0.001	0.34	0.01	0.67	0.01	767.16	< 0.001
L. borealis	0.45	0.01	0.54	0.01	348.33	< 0.001	0.42	0.01	0.56	0.01	325.39	< 0.001
L. cinereus	0.36	0.01	0.65	0.01	721.51	< 0.001	0.37	0.01	0.63	0.01	526.85	< 0.001

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Figure 1

Methods Overview

Flowchart showing how occurrence data were analyzed and used to infer migratory pathways for each bat species.

Figure 2

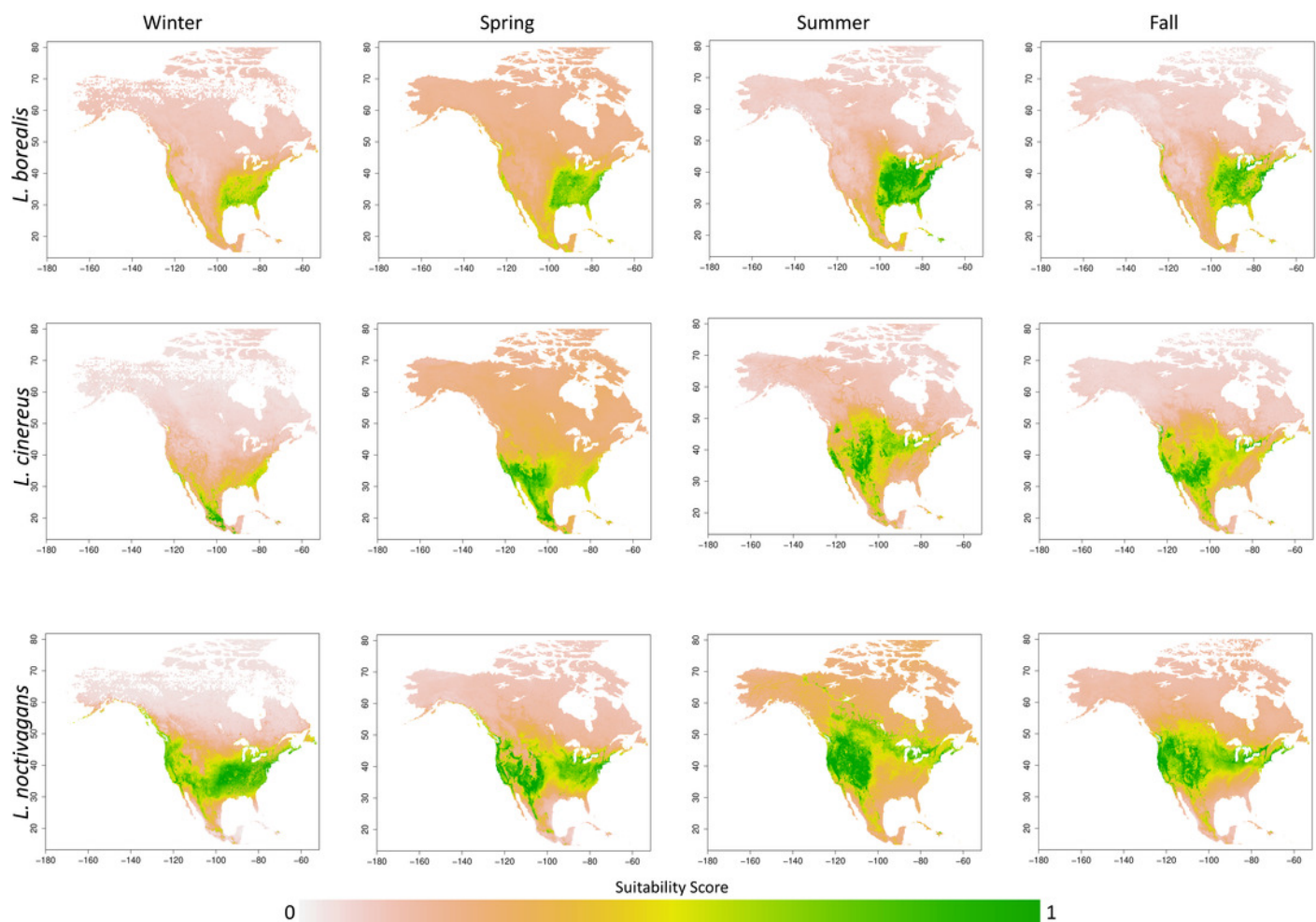Occurrences Used for Species Distribution Models

Each dot indicates a filtered occurrence for a migratory species. Each of these points are then given a color based on the month when the occurrence was detected. These points were then used in order to generate species distribution models for each season of a species.

Figure 3

Seasonal Suitability for Three Species of Migratory Bat Species

Seasonal SDMs for all three species (*L. borealis*, *L. cinereus*, and *L. noctivagans*). Colors identify either individual species or groups of species that occur in a given area. Outlier cells have been removed, and all rasters rescaled to range from 0 to 1. For more detailed figures for each species, see supplemental Figures S2-S4.

Figure 4

Potential Migratory Pathways

Migration pathways determined using two approaches: binary models determined from TSS

weighted ensemble model using 95th percentile threshold determined for each species

(shown in grey and white), and least-cost-path density (shown as color gradient) for *L.*

borealis, *L. cinereus*, and *L. noctivagans, M. lucifugus*, and *E. fuscus*.