Assessing migration patterns in *Passerina ciris* using the world's bird collections as an aggregated resource

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Natural history museum collections (NHCs) represent a rich and largely untapped source of data on demography and population movements. NHC specimen records can be corrected to a crude measure of collecting effort and reflect relative population densities with a method known as abundance indices. We plot abundance index values from georeferenced NHC data in a 12-month series for the new world migratory passerine *Passerina ciris* across its molting and wintering range in Mexico and Central America. We illustrate a statistically significant change in abundance index values across regions and months that suggests a quasi-circular movement around its non-breeding range, and use enhanced vegetation index (EVI) analysis of remote sensing plots to demonstrate non-random association of specimen record density with areas of high primary productivity. We demonstrate how abundance indices from NHC specimen records can be applied to infer previously unknown migratory behavior, and be integrated with remote sensing data to allow for a deeper understanding of demography and behavioral ecology across space and time.

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3

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13

14 ABSTRACT

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16 Natural history museum collections (NHCs) represent a rich and largely untapped source of data

17 on demography and population movements. NHC specimen records can be corrected to a crude

18 measure of collecting effort and reflect relative population densities with a method known as

19 abundance indices. We plot abundance index values from georeferenced NHC data in a 12-

20 month series for the new world migratory passerine *Passerina ciris* across its molting and

21 wintering range in Mexico and central America. We illustrate a statistically significant change in

22 abundance index values across regions and months that suggests a quasi-circular movement

23 around its non-breeding range, and use enhanced vegetation index (EVI) analysis of remote

24 sensing plots to demonstrate non-random association of specimen record density with areas of

25 high primary productivity. We demonstrate how abundance indices from NHC specimen records

26 can be applied to infer previously unknown migratory behavior, and be integrated with remote

27 sensing data to provide a deeper understanding of demography and behavioral ecology across

28 time and space.

29 INTRODUCTION

30

31   Natural history museum collections (NHCs) represent a rich and largely untapped source

32   of data on demography, behavioral ecology, and population movements. (Lister and Group 2011,

33   Suarez and Tsutsui 2004). Housed in museums and herbaria worldwide, NHCs are unique among

34   extant biological datasets in their breadth, depth, and, for the most part, in lacking biases intrinsic

35   to data collected for a specific research goal. NHCs are particularly valuable in that the oldest

36   specimens in collections predate even the longest running ecological surveys (Magurran et al.

37   2010), and that the majority of specimens are associated with detailed provenance data (Lister

38   and Group 2011). The combination of these records into sortable databases spanning multiple

39   institutions provides an invaluable resource in approaching a wide range of biological questions

40   through careful scrutiny and meta-analysis.

41   NHCs have traditionally been used to assess biogeographic range changes (Boakes et al.

42   2010), phenological shifts (Robbirt et al. 2011), hybridization (Rohwer and Wood 1998) and

43   evolutionary change in morphology. Applications of molecular techniques to NHCs have

44   extracted DNA from historic specimens to use in phylogenetic analyses (Paabo et al. 2004),

45   performed stable isotope analyses to track diet and migration in birds (Inger and Bearshop 2008),

46   and examined environmental contamination through trace element analysis (Berg et al. 1966,

47   Hickey and Anderson 1968). While specimen collections have obvious utility in addressing

48   questions of population biology, particularly in gaining access into otherwise-unknown historical

49   population dynamics, a major shortcoming of these data is the absence of information on

50   collecting effort associated with any individual specimen.

51   One method of overcoming this shortcoming is the application of indices that are

52   corrected to a crude measure of effort (Miki et al. 2000, Barry et al. 2009). These abundance

53   indices are calculated by use of electronic natural history museum catalogs (such as VertNet.org)

54   to aggregate records of specimens from a particular region and time period that are expected to

55   have been collected in a similar manner to the focal species of a study. Abundance indices have

56   been successfully applied to show molt migration (Barry et al. 2009), population dynamics in

57   medicinal plants (Miki et al. 2000), and in assessing migratory double-breeding (Rohwer et al.

58   2012) and changes in community composition from massive environmental pertubations

59   (Rohwer et al. 2015). A logical extension of these analyses is to examine spatial and temporal

60   changes in abundance index values to infer month-to-month population-level movements, where

61   technology, cost and unpredictable behavior often prohibit geotagging individuals. However,

62   such use of aggregated collection records remains untested.

63   Here, we demonstrate how abundance indices can be applied to infer population-level

64   movements from month to month across a migratory species' non-breeding range. We plot

65   abundance index values from georeferenced NHC data in a 12-month series for the new world

66   migratory passerine *Passerina ciris* across its molting and wintering range in Mexico and central

67   America. We illustrate a statistically significant change in abundance index values across regions

68   and months that suggests a quasi-circular movement around its non-breeding range, and use

69   enhanced vegetation index (EVI) analysis of remote sensing plots to demonstrate non-random

70   association of specimen record density with areas of high primary productivity.

71

72   METHODS

73

74   *Study species.* The Painted Bunting (*Passerina ciris*) is a migratory New World

75   passerine in the family Cardinalidae. Current taxonomy recognizes two subspecies of Painted

76   Bunting but the boundary between these races does not coincide with a nearly 500km gap

77   separating the east coast and the Midwestern breeding populations of Painted Buntings

78   (Thompson 1991). Further, these isolated breeding populations differ dramatically in their molt

79   scheduling, with the eastern population molting on its breeding range prior to migration and the

80   Midwestern population moving to the monsoon region of the southwestern United States and

81   northwestern Mexico where it pauses to molt before proceeding to its wintering range in

82   southern Mexico and Central America (Thompson 1991, Rohwer et al. 2005, V.G. Rohwer et al.

83   2009).

84   Across their range, Painted Buntings favor ecotones, brushy, weedy habitats in second

85   growth, and dense forest understory. Relatively little is known in detail about the species'

86   movements following molt stopover, but progressive southward movements of populations along

87   the west coast of Mexico have been observed in the autumn (Rohwer 2014, pers. comm.; Contina

88   et al. 2013).

89   *Calculating Abundance Indices.* To track spatial and temporal changes in Painted

90   Bunting population densities during the wintering season, we employed a method of inferring

91   relative population densities from specimen collections data known as Abundance Indices. The

92 method, proposed in Rohwer et al. 2011 and developed independently by Miki et al. (2000),

93 adjusts for a major shortcoming of specimen collections data -- the absence of associated

94 information on collecting effort -- by producing an index that is corrected to a crude measure of

95 effort. This index is calculated by using electronic natural history museum catalogs (such as

96 VertNet.org) to aggregate records of specimens from a particular region and time period that are

97 expected to have been collected in a manner similar to the methods used to collect the focal

98 species of a study.

99   We used the formula for abundance index calculation proposed in Rohwer et al. (2015):

$$AI_{kr} = 100 \frac{x_{kr}}{\sum_{j=1}^{n} x_{jr}}$$

100

101 where x_{kr} is number of specimens of the kth species collected in *r*, the region and time period of

102 interest, and *n* is the number of specimens of all species that would be "expected" to be collected

103 using the same methods in that region and time period of interest.

104   *Reference data.* In order to calculate abundance indices for Painted Buntings, we

105 accessed two databases of specimen collection records: the Mexican Bird Atlas, and VertNet.

106 The Mexican Bird Atlas began compilation by A. Navarro and T. Peterson in the 1990s, and now

107 represents the most complete reference of study skins of Mexican birds residing in natural

108 history museums worldwide (Navarro et al 2003). The Atlas now contains records of more than

109 370,000 specimens from 71 museums, and is completely georeferenced. We used records for the

110 Mexican Bird atlas for all indices calculated within the political boundaries of Mexico. The

111 VertNet data portal (vertnet.org) is an NSF-funded collaborative project to make biodiversity

112 information, including specimen collections records, freely and easily accessible to the public.

113 We also used records from VertNet to examine raw bunting counts by month for the Central

114 American countries of Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama.

115   *Subsetting and data cleaning.* We produced abundance indices for Painted Buntings for

116 each month of the year. These indices were produced on a relatively fine spatial scale for Mexico

117 (see section *GIS* below), but were only produced on a country-wide level for Central America,

118 due to limitations in properly georeferenced in the VertNet data. To calculate abundance indices,

119 we referenced Painted Bunting collections against the combined records of species collected

120   using similar methods, as in Rohwer et al. 2012: Passerines (order Passeriformes), Cuckoos

121   (order Cuculiformes), and Woodpeckers (order Piciformes; family Picidae).

122   While the majority of specimen collections records accessed from the Mexican Bird Atlas

123   were both dated and georeferenced, a subset (<10% in both Painted Bunting and reference

124   specimen data) had either missing or obviously erroneous values for date or latitude and

125   longitude coordinates. These were excluded from all subsequent analyses.

126   *Analyzing migration patterns.* We used a Geographic Information Systems (GIS)

127   approach to plot all specimen collections records from the Mexican Bird Atlas, for both Painted

128   Buntings and reference specimens. A 5' raster grid was initially overlayed on plotted reference

129   specimens, which were then transformed into a scaled density map of all collected specimens in

130   a particular region and month. In any grid square where Painted Bunting specimens were

131   collected, an abundance index was calculated and plotted as a circle, its diameter proportional to

132   the value of the index. While abundance indices were produced for Central America, we did not

133   incorporate these into our geospatial analysis due to exceedingly few Painted Bunting specimens

134   and corresponding low AI values.

135   To determine the statistical significance of any observed patterns of spatial and temporal

136   change, we divided Mexico into three regions corresponding with contiguous bands of Painted

137   Bunting habitat, (NW, NE, and S, defined by the 20th parallel north and the 103rd meridian West,

138   respectively; **Figure 1**). Among these regions, we performed four Pearson's chi-square tests for

139   changes in abundance indices in Painted Buntings and reference specimens during three time

140   periods: the molt-stopover period (July-October), winter (November-April), and spring migration

141   (May and June). Specifically, we asked 1) whether Painted Bunting records were significantly

142   more numerous than expected by chance (relative to reference specimens) in NW Mexico during

143   the molting season; 2) whether Painted Bunting records were significantly more numerous than

144   expected by chance in Southern Mexico during the winter; and 3) whether Painted Bunting

145   records were significantly more numerous than expected by chance along the Gulf of Mexico

146   during spring migration. While lacking resolution, this aggregated measure of abundance change

147   allowed us to more rigorously test our interpretation of the direction of migration (**Figure 1**).

148   Additionally, we performed a chi-square test to determine whether Painted Bunting records were

149   significantly more numerous below 500m in elevation.

150   Finally, to provide additional ecological context to our findings, and offer evidence of a

151   possible explanatory factor for population movement, we investigated the correlation between

152   bunting abundance and primary productivity. We downloaded monthly means for the Enhanced

153   Vegetation Index (EVI) compiled from 2000 to 2010 from the North American Vegetation Index

154   and Phenology Lab website (http://vip.arizona.edu). We used EVI, as opposed to the more

155   widely used Normalized Difference Vegetation Index (NDVI), as an index of primary

156   productivity because of EVI's enhanced sensitivity in high biomass regions (such as the Painted

157   Buntings' wintering sites) and its robustness against atmospheric influences (Liu and Huete,

158   1995; Matsushita et al., 2007). The downloaded data for each monthly mean consisted of a

159   georeferenced HDF raster file at a 0.05° resolution. We extracted the EVI data layer and clipped

160   it to the area of interest (Latitude: 10 to 40°, Longitude: -125 to -70°).

161   For each month, we extracted EVI values for pixels within a 10 km radius of each

162   collection site. We included data from each specimen such that locations from which multiple

163   specimens were collected were represented multiple times in the data set. We assume that

164   collection sites that yielded multiple birds are indicative of the most suitable or desirable habitat

165   for Painted Buntings, and that they should be overrepresented among all the collection sites

166   when evaluating the correspondence between EVI and Painted Bunting distributions. The data

167   extraction yielded an average of 10.3 pixels per collecting location (range = 3 to 14). Locations

168   near coastlines often had fewer pixels than inland site as the EVI data did not extend into water

169   bodies.

170   To test the simple null hypothesis that specimen locations for Painted Buntings were

171   random with respect to EVI, we generated 500 uniformly random locations within the borders of

172   Mexico and repeated the extraction process described above with each monthly EVI map and the

173   500 random points. Extractions from random locations yielded an average of 11.1 EVI pixels

174   (range: 2 to 15).

175   We averaged the pixels from each location and then compared the set of EVI values for

176   each month from the specimen locations to the corresponding EVI values associated with the

177   random locations. We performed a t-test for each monthly data set and calculated 95%

178   confidence intervals for each overall mean. Initial manipulation of EVI data was performed using

179   the gdal translator library (http://www.gdal.org). All subsequent analysis were performed in R

180   version 3.1.0 (R Core Team, 2014) with extensive use of the following packages: raster (Bivand

181 and Rundel, 2015), maptools (Bivand and Lewin-Koh, 2015), plyr (Wickham, 2011), rgeos

182 (Bivand and Rundel, 2015), and ggplot2 (Wickham, 2009).

183

184 RESULTS

185

186   *Migration analysis.* Our plotted monthly abundance indices for *P. ciris* confirm a pattern

187 of population-level movement across Mexico throughout the year (Figure 2). AI values plotted

188 for July illustrate an east-west split during mid-summer*,* with high AI values forming two

189 clusters in Northern Mexico: an eastern cluster in Nuevo Leon and Tamalpais, and a western

190 cluster in Sinaloa and Durango. In August and September, these associations persist, with the

191 western cluster increasing both by number of raster grid squares reporting an abundance index,

192 and by value of plotted abundance indices. October, November, and December show the

193 southward movement and diffusion of plotted AI values on both coasts of Mexico. Abundance

194 indices again hug the states of both coasts, forming a loose western cluster in Guerrero,

195 Michoacán, Oaxaca, Jalisco, and Colima, and a loose eastern cluster in the Veracruz, Tabasco,

196 Campeche, and Yucatán. There is then no observable pattern in plotted AI values from January

197 to April within or among these clusters, followed by a strong association of AI values in

198 northeast Mexico (Coahuila, Nuevo Leon, Tamalpais) and an absence of values elsewhere in the

199 month of May. South of Mexico, specimen records indicate the presence of Painted Buntings at

200 extremely low densities, mostly restricted to the winter months of November to March. Pooled

201 raw counts of buntings for all records in this region (including Belize, El Salvador, Honduras,

202 Guatemala, Nicaragua, Costa Rica, and Panama) confirm the near absence (n<10 per month) of

203 bunting specimens collected during the July-October stopover period (**Figure 3**).

204   *Statistical tests.* Our chi-sq tests confirm significantly higher Painted Bunting record

205 density than expected for all four analyses. Painted Buntings were significantly more numerous

206 in NW Mexico during the molt-stopover period than expected, compared to reference specimens

207 (question 1; X-squared = 108.8395, df = 1, p-value < 2.2e-16), were significantly more numerous

208 in southern than NW Mexico in the winter than reference specimens (question 2; X-squared =

209 122.772, df = 1, p-value < 2.2e-16), were significantly more numerous along the Gulf of Mexico

210 than along the west coast of Mexico, compared to reference specimens during spring migration

211   (question 3; X-squared = 63.6554, df = 1, p-value = 1.482e-15), and were significantly more

212   numerous below 500m elevation (question 4; X-squared = 122.772, df = 1, p-value < 2.2e-16).

213   *Remote sensing.* For almost every month of the year, Painted Bunting collection sites in

214   Mexico had higher EVI scores (i.e. higher primary productivity) than randomly generated

215   locations within Mexico (**Figure 4**, p < 0.01). The only exceptions were May and June, when

216   Painted Buntings are on their breeding grounds and are relatively scarce in Mexico. The highest

217   monthly EVI average associated with the specimen data was from the month of October, which

218   corresponds with high Painted Bunting densities in the states of Sinaloa and Sonora, where many

219   if not most Painted Buntings undergo feather molt. It is also in the month of October that we

220   observed the greatest difference between the mean EVI value for collection sites and for random

221   sites.

222

223   DISCUSSION

224

225   The spatial and temporal changes in plotted abundance indices presented in **Figure 2**

226   illustrate that an abundance index approach can be applied to NHC datasets to infer population-

227   level movements across a species' range from month to month. The advantages of this approach

228   in determining general trends within or among taxa are numerous. Analyzing spatial and

229   temporal changes in abundance indices allows for the repurposing of a comprehensive and pre-

230   existing source of species occurrence data into a tool for investigating questions about behavior

231   and population movement. In doing so, the approach also circumvents the need for costly and

232   potentially error-prone geologger tagging studies (Contina et al. 2013). Perhaps most

233   importantly, the use of NHC datasets allows for the potential of describing *historical* population-

234   level movements, phenomena that might otherwise go undescribed due to an absence of

235   contemporary observers, and the disturbance of decades of anthropogenic pressure on

236   populations and land-use change that may have changed historic movement patterns.

237   Our results also shed light on previously unconfirmed migratory behavior in *P. ciris.* The

238   initial clustering of high AI values in July-September in northwestern Sinaloa (**Figure 2**)

239   correlate to evidence of molt-migration stopover in agricultural habitats in NW Sinaloa for

240   subspecies *P. c. pallidor* (Contina et al. 2013, Rohwer 2013, Rohwer et al. 2009, Rohwer et al

241   2005)*.* We believe subsequent southward progression and diffusion visible in abundance index

242   values across the southern half of Mexico from October to April is consistent with anecdotal

243   observations by Rohwer (2015, pers comm) describing a complete absence of wintering Painted

244   Buntings in regions where they had been previously been abundant during the molting period, as

245   well as geologger tag and isotope evidence from Contina et al. (2013) of similar movement. The

246   limited number of specimen records elsewhere in Central America provides additional support

247   for this movement, as the timing of Painted Bunting presence in countries south of Mexico is

248   consistent with a post molt-migration stopover arrival to the southern extent of the species' range

249   (**Figure 3**). A reduction in individual grid-square AI values and increase in overall number of

250   grid squares filled also correlates with expected migratory behavior: in the absence of sedentary

251   behavior associated with molt stopover sites during molt-migration, and associated high

252   population densities during this time period, individuals should move independently and avoid

253   competition for limited resources. Finally, plotted AI values in May and June illustrate the high

254   population densities in NE Mexico in the Gulf Coast migration corridor to be expected during

255   spring migration through this region to breeding grounds in the United States.

256   Taken in sum, monthly plotted abundance indices (**Figure 2**) indicate a quasi-circular

257   movement of *P. ciris* populations around coastal and Southern Mexico. We believe these

258   patterns can be partially explained by the EVI analysis of remote sensing data presented in

259   Figure 3. A period of peak live green vegetation in Mexico in the months of July - September

260   correlates with the cluster of abundance indices representing the molt-migration stopover site in

261   Sinaloa for *P. c. pallidor* identified for the same period in Figure 1. After a period of reduction in

262   green vegetation from October - March, a second peak in live green vegetation in Mexico

263   correlates with the location of *P. ciris* abundance indices in NE Mexico representing an increase

264   in population densities in a migration corridor immediate prior to spring arrival on their principle

265   midwestern breeding grounds in the United States.

266   EVI plots indicating peaks in live green vegetation can be thought of as a rough indicator

267   of primary productivity and corresponding resource availability. *P. ciris* population densities

268   therefore appear to shift in tangent with precipitation and plant growth, a logical correlation

269   given *P. ciris* feeds primarily on grass seeds during the winter, and supported by our comparison

270   with randomly generated localities. The comparison of EVI data associated with collection sites

271   and randomly generated sites (**Figure 4**) confirms that the dynamic distribution of Painted

272   Buntings as evinced by museum collection data corresponds in a non-random manner with

273 increased primary productivity across the landscape. Numerous studies have documented similar

274 associations including studies of Painted Buntings (Bridge et al, in press) and various tests of the

275 green-wave hypothesis (Drent et al., 1978; Owen, 1980, Shariatinajafabadi et al., 2014, Si et al.,

276 2015). Therefore, we present this finding as validation that our specimen based distribution

277 mapping yields rather than a novel correlative observation. Likely also due to resource

278 limitation, our finding that Painted Bunting specimen records were significantly more numerous

279 below 500m supports claims that *P. ciris* primarily winters in the lowlands (Rohwer 2015, pers.

280 comm.; Howell and Webb 2007).

281   While we demonstrate the utility of NHC abundance indices in inferring population level

282 movements, we reiterate that the technique in no way reflects the movements of individual birds.

283 AI values represent stationary population densities at a particular time and place, and as such,

284 caution must be taken not to over interpret findings, while keeping an open mind to alternate

285 hypotheses. These include the existence of sedentary populations with geographically distinct

286 distributions, and the potential of results being an historical artifact of a particular collecting

287 expedition in regions with limited collecting effort. However, assuming thorough background

288 collecting, the absence of target species at a particular time and place almost certainly represents

289 the mass movement of individuals (rather than huge die-offs). In light of this, we believe the

290 method can be applied to significantly more complex cases than the one described above. We are

291 particularly interested to see studies with well-sampled species in regions where anthropogenic

292 disturbance has substantially altered migratory corridors in recent years. We hope in the future

293 AI values will shed light on avian demographics, behavior, and distribution, and continue to

294 illustrate the immense value of NHCs worldwide.

295

296 CONCLUSIONS

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298 Our study illustrates the utility of NHC specimen collection records in inferring population-level

299 movement through abundance index analysis. We find evidence of quasi-circular movement

300 from month to month in *Passerina ciris* populations across its non-breeding range, with

301 abundance index values non-randomly distributed in regions with high EVI values (indicating

302 high primary productivity).

303

304   ACKNOWLEDGEMENTS

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1

Diagram of Chi-square tests of seasonal changes in *Passerina ciris* specimen record densities

Figure 1. Chi-square analysis of *Passerina ciris* population movements around Mexico. 2x2 grids illustrate Pearson's chi-square tests asking whether Painted Bunting ("PABU") populations were significantly greater in a particular region (NW, NE, and S, divided by 20 degrees N and 103 degrees west and marked on the plot) and a particular time (molting period, wintering period, and spring migration) than expected with respect to reference specimen populations ("Other").
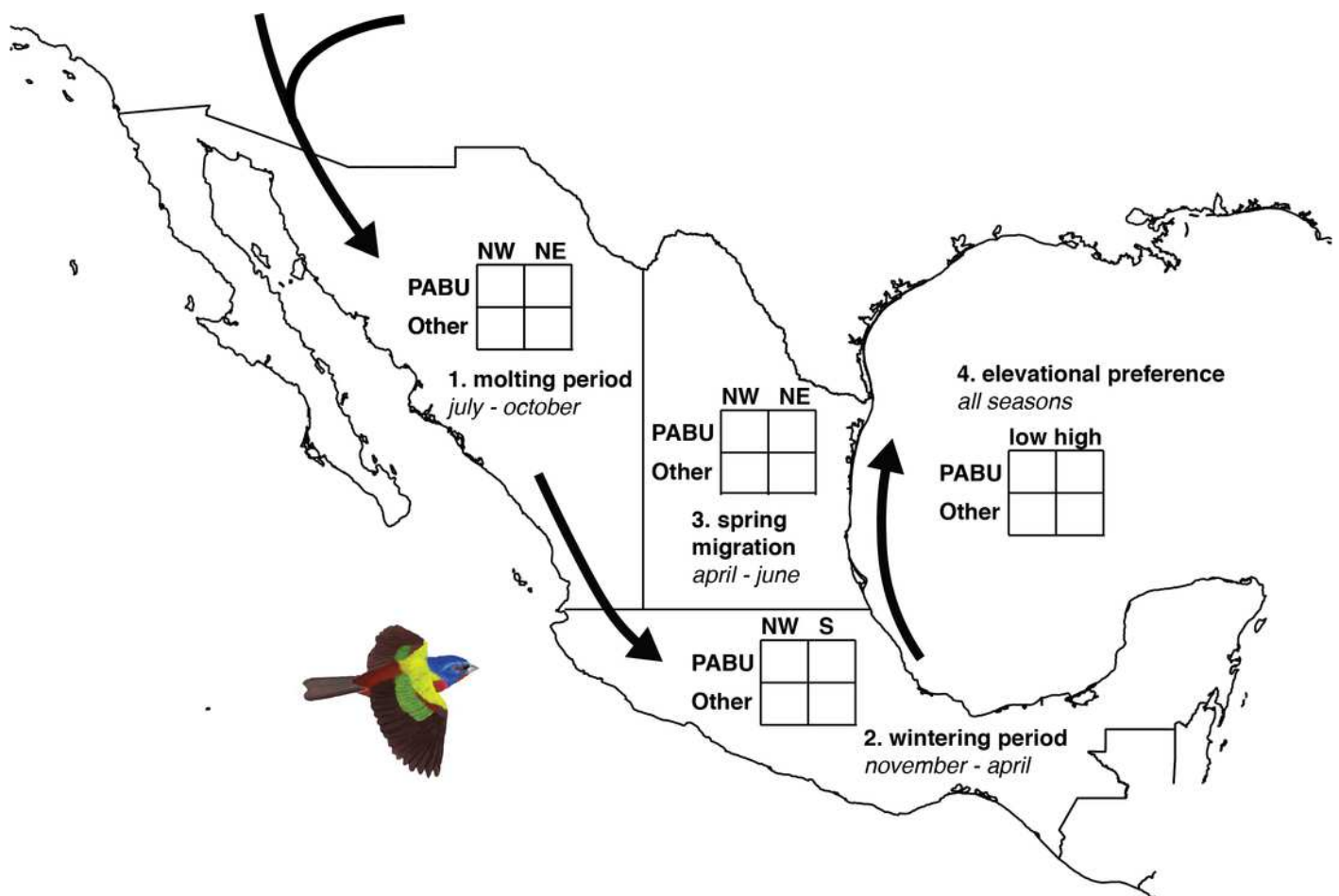
2

Monthly changes in *Passerina ciris* abundance index values with EVI analysis of remote sensing data

Figure 2 (also provided as .gif animation in supplemental files). Abundance index (AI) values for *Passerina ciris* specimens in Mexico by month, plotted against EVI analysis of remote sensing data. Red circles indicate the occurrence of *P. ciris* specimens, with the diameter of the circle proportional to value of Abundance Index. Green areas indicate high EVI values, correlated with regions with a high density of live green plants (photosynthetically active vegetation).
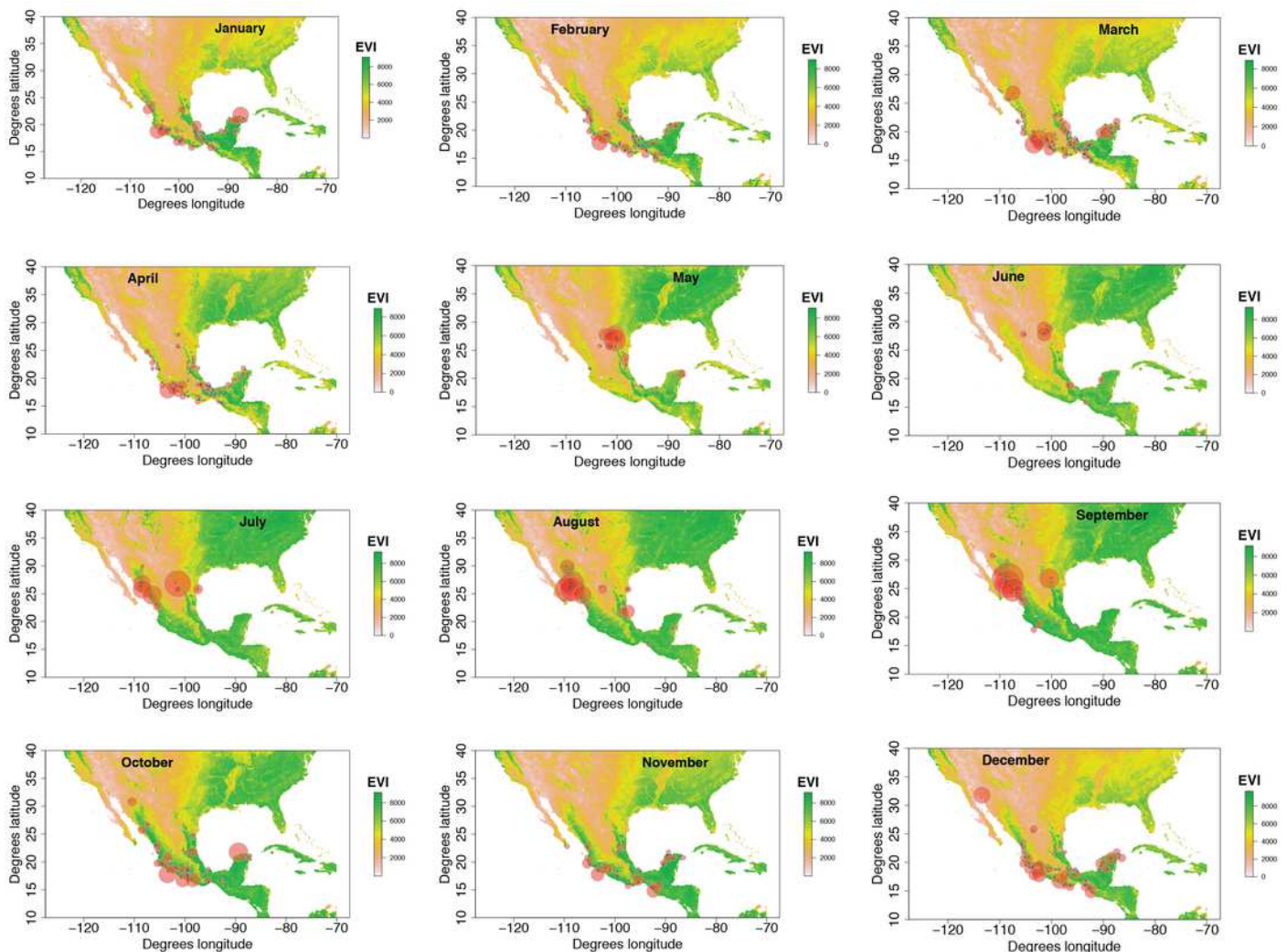
3

Histogram of raw *Passerina ciris* specimen counts in Central America

Figure 3. Raw Painted Bunting specimen records pooled from Belize, Guatemala, El Salvador, Honduras, Nicaragua, Panama, and Costa Rica, and totaled by month of collection.

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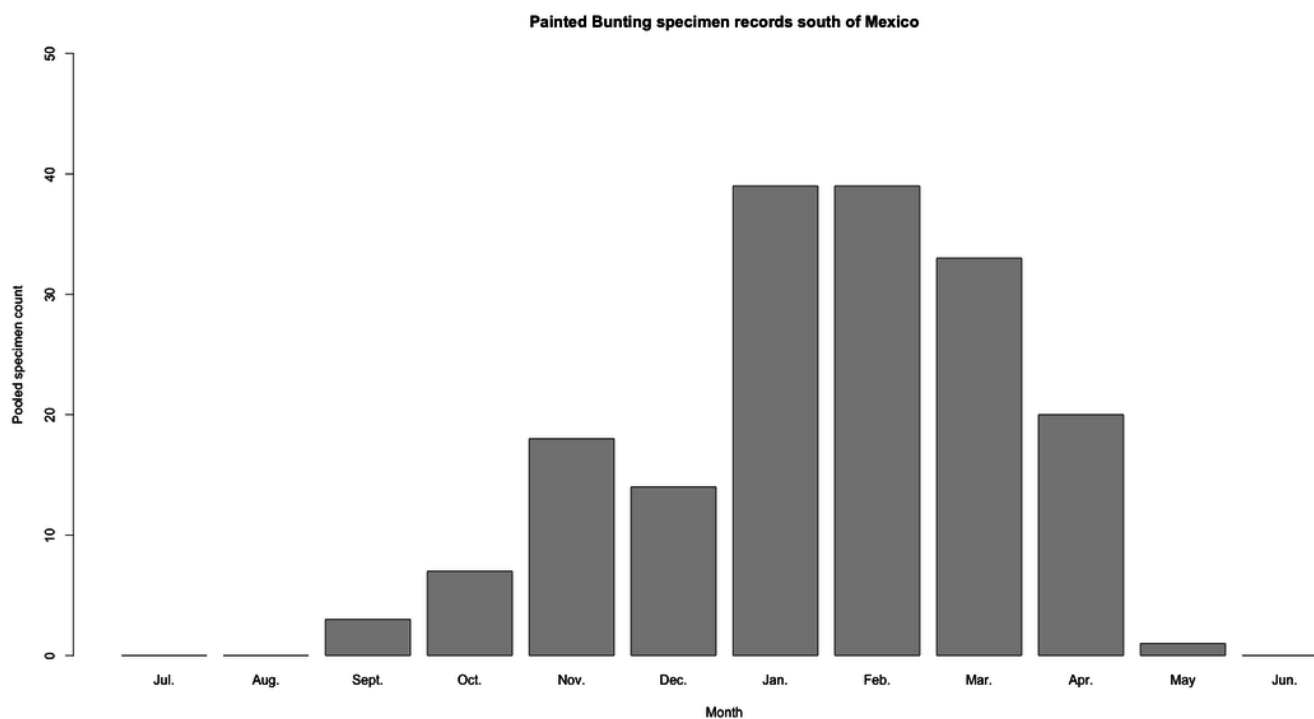
Mean EVI values of specimen data compared to mean EVI values of randomly distributed points, by month

Figure 4. Mean EVI values of specimen records compared to mean EVI values of 500 randomly distributed points within Mexico.