1   **100+ years of bird survey data reveal changes in functional fingerprints indexing ecosystem health**

2   **of a tropical montane forest through time**

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22   excellent feedback; The following scientific collections allowed access to bird specimens: IAvH, ICN,

23   Museo de La Salle, Museo Univalle, AMNH.

24   **Abstract**

25   Ecologically relevant traits of organisms inhabiting an ecosystem determine its functional fingerprint.

26   Quantifying changes in the shape, volume and shifts in the position of functional fingerprints can provide

27   information about the effects of diversity loss or gain through time, and is a promising means to monitor

28   ecological integrity. This, however, is seldom possible owing to limitations in historical surveys and lack

29   of data on organismal traits, particularly in diverse tropical regions. Using detailed bird surveys from four

30   time periods across more than one century and morphological traits of 233 species, we quantified changes

31   in the avian functional fingerprint of a tropical montane forest site in the Andes of Colombia. We found

32   that 79% of the variation in functional space, regardless of time period, was described by three major axes

33   summarizing body size, dispersal ability, and habitat breadth. Changes in species composition caused

34   significant alterations of the functional fingerprint of the assemblage, with 35 – 60% reductions in

35   functional richness and dispersion. Owing to species extirpations and to novel additions to the

36   assemblage, functional space is currently smaller and at least 11% different to what it was a century ago,

37   with fewer large-sized species, more good dispersers, and fewer habitat specialists. Extirpated species had

38   high values of functional uniqueness and distinctiveness, resulting in large reductions of functional

39   richness and dispersion after their loss, implying potentially important consequences for ecosystem

40   functioning. Conservation efforts aimed at maintaining ecosystem function must move beyond

41   maintaining species numbers to designing strategies for the maintenance of ecological function by

42   identifying and conserving species with traits conferring high vulnerability.

43   **Key words:** *birds, Colombia, ecological integrity, fragmentation, functional richness, functional*

44   *uniqueness*

45   **Introduction**

46   Determining how changes in the natural world affect ecosystems and the biodiversity within them is

47   essential, especially if we are to maintain ecosystem function and restore degraded habitats to regain

48   services they once provided (Cadotte et al. 2011; Dirzo et al. 2014). First, however, we must understand

49   what defines healthy ecosystems in terms of function, and how ecosystems change naturally or in

50   response to human intervention. Functional traits, defined as ecological, morphological or behavioral

51   traits influencing fitness and survival of organisms (Violle et al. 2007), mediate ecosystem processes, and

52   determine the responses of populations to environmental conditions, biotic interactions and nutrient

53   cycling in ecological assemblages (Bregman et al. 2016; Funk et al. 2017). Therefore, measures of

54   diversity in functions provide information about ecosystem health because higher functional diversity is

55   associated with greater plasticity, productivity, and resilience when facing disturbances or climatic

56   fluctuations (Mason et al. 2005; Cadotte et al. 2011). Examining changes in functional diversity within

57   assemblages known to have changed in species composition through time offers an opportunity to

58   understand the consequences that impacts on biodiversity have on the functions and services it provides.

59   Measures of functional diversity are often quantified as a multidimensional volume, where each

60   species occupies a position depending on its similarity to others. In this volume, species with similar trait

61   values (i.e. functionally redundant species) are located in the center close to other species, whereas

62   functionally distinctive species are far from the rest in the periphery (Mason et al. 2005; Ricklefs 2012;

63   Kuebbing et al. 2018). The shape of the multi-dimensional trait space formed by organisms inhabiting an

64   ecosystem hence determines a unique "functional fingerprint". Quantifying changes in the shape, volume

65   and shifts in the position of functional fingerprints can therefore provide information about the effects of

66   diversity loss or gain, and is a promising means to monitor ecological integrity (Carmona et al. 2016;

67   Pigot et al. 2016; Cooke et al. 2019b).

68   In response to environmental changes, the functional fingerprint of an assemblage may remain

69   unchanged, shift in different directions, or change in shape and volume. For instance, if an assemblage

70   loses or gains species far from others in functional space, then its functional richness (i.e. the total

71   functional space it occupies) would change more drastically than if it lost or gained species occupying

72   similar areas of trait space relative to other members of the assemblage (Carmona et al. 2016; Grenié et al.

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73   2017; Kuebbing et al. 2018). Similarly, whether lost or gained species are located close or far from the

74   centroid of trait space will determine the effect of changes on functional dispersion (i.e. the mean distance

75   of each species to the centroid of trait space; Laliberte & Legendre 2010), with extirpations of species in

76   the periphery of functional volume causing greater decreases in functional dispersion (Laliberte &

77   Legendre 2010). Finally, changes in abundance of species in an assemblage can also impact its functional

78   dispersion by shifting the center of gravity towards the most abundant traits (Laliberte & Legendre 2010).

79   Changes in functional shape or volume would therefore depend on characteristics of the species changing

80   in abundance relative to the rest of the assemblage (Carmona et al. 2016).

81   Birds are good indicators of ecosystem health because they rapidly respond to environmental

82   changes, and because variations in bird assemblages can be readily assessed by human observers (e.g.

83   Gregory & van Strien 2010; Bregman et al. 2016). Furthermore, the link between avian functional traits

84   and ecosystem processes is well documented (Maglianesi et al. 2015; Ikin et al. 2019; Pigot et al. 2020).

85   Although many studies have documented changes in bird assemblages through time as a response to

86   habitat or climate change (e.g. Renjifo 1999; Robinson 1999; Freeman et al. 2018; Rosenberg et al. 2019),

87   determining whether ecosystem health is affected by changes in species diversity and abundance requires

88   assessing whether changes extend to functional spaces.

89   Studies of the temporal dynamics of functional diversity within ecological assemblages indicate

90   that extinctions and colonizations of species are not random in terms of their functional traits (Petchey et

91   al. 2007), and changes in functional space characterize succession in ecological assemblages (Purschke et

92   al. 2013). Responses to habitat and landscape changes also affect functional groups differentially and

93   produce changes in interspecific interactions which affect ecosystem function at different scales

94   (Chalmandrier et al. 2015; Jarzyna & Jetz 2018; Stouffer 2020). Furthermore, changes in functional

95   diversity after habitat fragmentation may homogenize traits within assemblages, implying loss of unique

96   functions (Clavel et al. 2011; Jarzyna & Jetz 2017). However, studies quantifying long-term changes in

97   the multidimensional functional fingerprint of tropical assemblages are lacking.

98   The avifauna of San Antonio, a montane forest locality in the Andes of Colombia, poses an

99   unprecedented opportunity to examine shifts in functional fingerprints through time in a highly diverse

100   tropical ecosystem, and thereby to infer how species extirpations and recolonizations may have influenced

101   ecosystem health. San Antonio was first surveyed by naturalists in the 1910's (Chapman 1917). Since

102   then, exhaustive resurveys conducted in the 1950's, 1990's and 2000's have allowed researchers to

103   document substantial changes in composition of the bird assemblage over more than a century of

104   landscape change (Kattan et al. 1994; Palacio et al. 2019). We combined morphological and ecological

105   data for the complete bird assemblage of San Antonio, comprising 233 species, to test the hypothesis that

106   functional fingerprints changed as a result of gains, losses and changes in abundance of functionally

107   distinctive species. We expected functional richness and dispersion to have decreased between the early

108   1910's and the 1990's when several species extirpations occurred (Kattan et al. 1994), and to have

109   increased following recovery of some species and colonization by formerly absent species in the 2000's

110   (Palacio et al. 2019). We also evaluated whether colonization by novel species caused changes in the

111   functional fingerprint of the San Antonio assemblage, filling areas of functional space not occupied by the

112   set of species coexisting in the area in the 1910's. If extirpated species were functionally unique, then this

113   system may have lost functions provided by those species and potentially gained others from the novel

114   colonizers. Alternatively, if extirpated species or novel colonizers were functionally redundant, then the

115   overall functionality of the system may not have changed significantly.

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117   **Methods**

118   *Study site.-* The *Cerro de San Antonio* is a mid-elevation mountain ridge (1700 - 2200 m), located in

119   Colombia's Western Andes (3.4960 N, -76.6305 W) approximately 15 km west of Cali, Valle del Cauca

120   (Kattan et al. 1994; Palacio et al. 2019). This region (covering ~7000 ha) originally harbored extensive

121   tropical montane and cloud forests, which suffered widespread fragmentation from the 1930's to the

122   1960's resulting in a ~46% reduction in forest cover (Kattan et al. 1994; Palacio et al. 2019). Since then,

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123   the remaining matrix of forest fragments, small farms and country houses has remained relatively stable,

124   with an estimated ~10% increase in forest cover between 1995 and 2016 (Palacio et al. 2019).

125   ***Historical and contemporary bird survey data.-*** We analyzed data based on published bird lists from San

126   Antonio compiled by Palacio et al. (2019), which comprise a total of 233 species detected across surveys

127   conducted between 1907 and 2016 (Appendix S1). We divided data into 4 periods: (1) the 1910's,

128   corresponding to surveys led by Frank M. Chapman and Mervin G. Palmer; (2) the 1950's, by Alden H.

129   Miller; (3) the 1990's, by Gustavo Kattan et al.; and (4) the 2000's, by Ruben Palacio et al. Detailed

130   methodologies for these surveys can be found in the original publications (Chapman 1917; Miller 1963;

131   Kattan et al. 1994; Palacio et al. 2019) and together they comprise an accurate representation of the

132   avifauna of San Antonio and its compositional changes over 100+ years. For details on changes in the

133   avifauna during these time periods see Appendix S3.

134   Surveys in the 1910's consisted exclusively of collecting expeditions (Chapman 1917) but from

135   the 1950's onwards, surveys combined standardized observations with collecting, and the most recent

136   surveys in the 2000's also integrated citizen-science data (Kattan et al. 1994; Palacio et al. 2019).

137   Methodological differences between surveys imply that we have strong certainty about species

138   extirpations occurring between time periods but are less certain about novel species colonizations because

139   the older surveys were more likely to have missed species which were actually present but not identified

140   or collected due to limited knowledge of bird songs, lack of good binoculars, etc.. To address this issue,

141   we analyzed our data considering two scenarios. The first assumes that all surveys accurately describe the

142   avifauna present and that any records of species not detected in prior surveys of San Antonio represent

143   real colonizations. The second, more conservative scenario, assumes that all the 'novel species', i.e. those

144   detected for the first time after the 1910's, were false absences and so we added them to the 1910's list.

145   Therefore, under Scenario 2 any changes in the avifauna consisted exclusively of extirpated species or re-

146   colonization of previously extirpated species. What actually occurred likely lies somewhere in the middle

147   of our two scenarios.

148   *Functional traits.-* For all 233 species, we compiled information on 9 traits describing functional

149   morphospace and ecological strategies (Cooke et al. 2019b; Habel et al. 2019; Pigot et al. 2020; Sheard et

150   al. 2020): body mass, bill length, bill width, wing chord, tail length, tarsus length, hand-wing index (i.e. a

151   measure of wing shape), habitat breadth and generation time (BirdLife International 2018; Appendix S1).

152   We also made sure most of the traits considered had low values of correlation within our assemblage

153   (72% of traits have correlation coefficients < 0.6, supplementary Fig. S3.1 in Appendix S3; Cadotte et al.,

154   2011). For additional details on functional trait compilation see Appendix S3.

155   *Estimation of functional diversity metrics and temporal comparisons.-* Body mass was $\log_{10}$

156   transformed, and all traits were scaled and centered to have zero mean and unit variance (Cadotte et al.

157   2011; Carmona et al. 2016; Cooke et al. 2019a). To obtain a reduced set of uncorrelated variables

158   explaining variation in functional traits, we ran a principal components analysis using data from all

159   species (R Development Core Team 2019). Out of nine principal components, the first three explained

160   78% of the variation in functional trait values. Loadings suggested that PC1 described mostly variation in

161   body size (55%), PC2 was related to dispersal ability through the hand-wing index (13%) and PC3

162   described habitat breadth (11%; Appendix S3). The first 3 PC scores were then used as axes to compare

163   functional spaces among time periods and groups of species (Carmona et al. 2016; Cooke et al. 2019b).

164   We adopted methods from Cooke et al. (2019) to construct functional spaces and evaluate

165   temporal shifts in the San Antonio avifauna since the 1910's. Two and three-dimensional trait spaces are

166   constructed by comparing different combinations of trait-space values, in this case PC1, PC2 and PC3

167   (Cooke et al., 2019). Multivariate kernel density estimates (Duong 2019) were used to calculate the 0.5,

168   0.95 and 0.99 probability contours for trait spaces (Cooke et al. 2019b). Scores from PC's comprising

169   ~95% of variance were used to construct a trait hypervolume to visualize temporal shifts in functional

170   space and to calculate changes in volume and overlap between time periods. The hypervolume was

171   constructed following Cooke et al. (2019) using a 'one-class support vector machine (SVM)' method

172   (Blonder & Harris 2019).

173   Historical and contemporary relative abundances of species from San Antonio were extracted

174   from Palacio et al. (2019). We assigned a value between 0 and 1 to each abundance category where 0 =

175   absent or extirpated, 0.2 = rare, 0.4 = uncommon, 0.6 = fairly common, 0.8 = common, and 1 = abundant.

176   We constructed a period-by-species matrix with these relative abundance values, and a species-by-trait

177   matrix with the standardized values of our 9 functional traits. We then estimated functional richness and

178   dispersion using function *'dbFD'* in R package '*FD*' (Villeger et al. 2008; Laliberte & Legendre 2010;

179   Laliberté et al. 2014). Functional richness (*FRic*) was estimated as the volume of the minimum convex

180   hull (Villeger et al. 2008). For ease of interpretation, the functional richness of each time period was

181   standardized by the global *FRic,* thus constraining values to range between 0 and 1 (Laliberté et al. 2014).

182   Functional dispersion (*FDis*) is the mean distance of each species to the centroid of trait space, weighted

183   by its relative abundance (Laliberte & Legendre 2010). *FDis* increases as the most abundant trait values

184   are further from the center of gravity of trait space (Laliberté et al. 2014). The relative abundance

185   categories for the historical datasets may be inaccurate because they do not account for collecting bias,

186   i.e. an uncommon species in the collection might have been common in the assemblage. We therefore

187   also estimated *FDis* without considering abundances.

188   To evaluate whether functional metrics for each time period were different from what might be

189   expected through random processes, we compared observed values to those generated by null models. We

190   randomly reordered the species-identity column of the abundance matrix 999 times (thus breaking

191   associations between traits and species' identities), and then recalculated *FRic*, and *FDis* for each random

192   assemblage (Van de Perre et al. 2020). To assess the magnitude of the difference between observed and

193   null values of *FRic* and *FDis,* we estimated standard effect sizes as: $SES = \frac{obs - meanNull}{SD\ Null}$ (Van de Perre

194   et al. 2020) and assessed significance with *P* values as: $\frac{(Number\ F_{null} \le F_{obs} + 1)}{(999 + 1)}$ (Cooke et al. 2019a).

195   ***Functional characteristics of extirpated species and novel colonizers.-*** To describe functional

196   differences among 1. extirpated species, 2. novel additions to the assemblage as of the 2000's, and 3.

197   shared species maintained through time, we constructed trait probability density curves (TPD), using the

198   first three PC axes as traits, and the aforementioned species groups as ecological units for comparison in

199   package 'TPD' (Carmona et al. 2016, 2019). We used a two-sample Kolmogorov-Smirnov test to assess

200   whether there were differences between TPD's of extirpated species and novel additions to the

201   assemblage.

202   Additionally, to evaluate whether extirpated species and those establishing new populations in

203   San Antonio were functionally redundant or unique, we calculated functional distinctiveness and

204   uniqueness using package 'funrar' in R (Grenié et al. 2017; Pimiento et al. 2020). Functional

205   distinctiveness (D_i) measures how uncommon a species' trait value is compared to other species in the

206   assemblage, weighted by the species' relative abundance, and has values between 0 (high functional

207   redundancy), and 1 (low functional redundancy; Grenié et al. 2017). Functional uniqueness (U_i) is the

208   distance of each species to its nearest neighbor in the assemblage (Grenié et al. 2017). The closer U_i is to

209   1, the further species i is to its closest neighbor (Grenié et al. 2017). We ran permutation tests to evaluate

210   whether extirpated species and new additions to the assemblage were more functionally unique or

211   distinctive than expected by chance (Pimiento et al. 2020), and carried out pairwise comparisons to assess

212   differences between time periods (Cooke et al. 2019a).

213

214   **Results**

215   Under both assumed scenarios (1 – species were both extirpated and colonized the assemblage; and 2 –

216   there were no novel colonizers), the center of abundance of two-dimensional morpho-spaces has remained

217   in the same position, but both the shape and extent of trait space have changed over 100+ years (Fig. 1

218   and supplementary Fig. S3.2). Extirpated species (both scenarios), as well as new colonizers (Scenario 1),

219   are spread over functional space, but those located towards the periphery have been responsible for the

220   most noticeable shape changes in functional space (Fig. 1 and supplementary Fig. S3.2).

221   Changes in functional space were also evident in trait density curves comparing extirpated

222   species, novel additions, and shared species through time. Trait density curves for Scenario 1 showed that

223   the San Antonio assemblage has seen a shift towards smaller-sized birds (k-s test D = 0.34, P = 0.03, Fig.

224   2A), and towards species with higher dispersal ability (k-s test D = 0.48, P = 0.0008, Fig. 2B) and wider

225   habitat breadths (i.e. fewer habitat specialists; k-s test D = 0.44, P = 0.003, Fig. 2C). These shifts resulted

226   in 34% of the functional hypervolume present in the 1910's being absent from the 2000's. In turn, 11% of

227   the volume occupied by the 2000's assemblage was not occupied in the 1910's, and 55% has remained

228   constant (Figure 2D). For Scenario 2, trait density curves for body size and dispersal ability showed

229   similar shifts to those of Scenario 1 with the assemblage loosing larger-sized birds (k-s test D = 0.39, P =

230   0.0003) and some species with relatively low dispersal ability (k-s test D = 0.43, P = 0.000), but showing

231   no significant shifts in habitat breadths of species (i.e. PC3; k-s test D = 0.24, P = 0.08) (supplementary

232   Fig. S3.3). Under Scenario 2, 29% of the trait hypervolume from the 1910's was lost, whereas only 1% of

233   the hypervolume was unique to the 2000's and 70% remained constant across periods.

234   Changes in the hypervolume of all traits were comparable to measures of functional richness

235   (*FRic*) using the minimum convex hull. Under Scenario 1, between the 1910's and 1950's, functional

236   richness decreased by ~36%, and it recovered ~22% between the 1990's and 2000's (Table 1, Figure 3A).

237   Under Scenario 2, there was a ~66 % decrease in functional richness between the 1910's and 1990's

238   (Table 1) and then a recovery of 12% during the 2000's (Table 1). Functional dispersion (*FDis*) followed

239   a similar pattern in both scenarios (Table 1) with a decrease of ~8% between 1910's and 1950's and an

240   increase of ~3% between the 1990's and 2000's (Table 1, Fig. 3B). The difference between values of

241   *FDis* estimated with and withought weighting for abundance were negligible (mean difference = 0.02,

242   range = 0.003 – 0.05). All observed values of *FRic* and *FDis* were lower than expected by chance, with

243   negative standard effect sizes ranging from -0.87 to -2.81 (Fig. 3C).

244   Finally, we found that the San Antonio assemblage has lost a higher number of functionally

245   unique and distinctive species than would have been expected by chance (Figs. 4A-B), and pairwise

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246   comparisons between groups of species showed significant differences in functional distinctiveness and

247   uniqueness between extirpated species and species remaining in the assemblage across time periods. For

248   example, large frugivores, a group especially sensitive to extirpation, were among the highest ranked in

249   functional distinctiveness and uniqueness (Fig. 4. and Appendix S3). Nine out of 32 novel additions to the

250   assemblage (Scenario 1) also had relatively high values of functional distinctiveness and uniqueness, with

251   the Ornate Hawk-Eagle (*Spizaetus ornatus*), which was first recorded during the 1990's, having the

252   highest value (Fig. 4).

253

Discussion

255   We showed that changes in species composition caused significant shifts in the functional fingerprint of a

256   montane bird assemblage from the western Andes of Colombia. Due mostly to species extirpations,

257   functional space in the 2000's was considerably smaller and at least 11% different to what it was 100

258   years before, containing fewer large-sized species, more species with high dispersal ability, and fewer

259   habitat specialists. However, the core of functional space, which holds most of the species (~65%), has

260   remained in the same position, suggesting a portion of the system's original functionality remains intact.

261   On average, extirpated species had higher values of functional distinctiveness and uniqueness relative to

262   the whole assemblage, and groups known to be globally prone to extirpation, such as large frugivores,

263   were ranked high in uniqueness and distinctiveness. Therefore, despite the stability of the core functional

264   space, important ecological functions performed by relatively few species may have been

265   disproportionately affected by changes in assemblage composition.

266   We detected substantial (i.e. 30 – 60%) declines in functional richness in the San Antonio

267   assemblage over 100 years. These values are high given that declines in functional richness in the 11-25%

268   range are considered to cause substantial loss of functionality in highly diverse ocean and forest

269   assemblages (Mcwilliam et al. 2018; Newbold et al. 2020; Pimiento et al. 2020), and that some systems

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270   with 40% difference in tree cover, such as agriculture vs old growth forest, differ by only ~5% in the

271   functional richness of their bird assemblages (Ikin et al. 2019). Furthermore, we found that extirpated

272   species had higher than expected values of functional uniqueness and distinctiveness, and therefore their

273   loss was mostly responsible for the decreasing trend in functional diversity over 100 years. The joint

274   substantial reduction in functional diversity and loss of unique species suggests that the San Antonio

275   assemblage has likely lost important ecological functions.

276   Our approach can enable conservation managers to move beyond simple quantifications of losses

277   and gains through time to identify areas of functional space in need of attention owing to negative effects

278   on ecosystem function. For example, the loss of functionally unique large frugivores from the San

279   Antonio assemblage likely increased the potential for collapse of mutualistic networks of bird and plant

280   species in which previous work revealed they play a critical role (Palacio et al. 2016). Loss of large

281   frugivores can further have negative cascading effects on ecosystem health by reducing seed dispersal,

282   affecting the survival of native trees, influencing the potential for forest regeneration, and even

283   constraining the vegetation's ability to respond to climate change (Cordeiro & Howe 2003; Moran et al.

284   2009; McConkey et al. 2012; Mokany et al. 2014; Ribeiro da Silva et al. 2015; Bovo et al. 2018).

285   Although the San Antonio bird assemblage has changed in functional volume, the core of its

286   functional fingerprint (concentrating a majority of species which are arguably functionally redundant) has

287   retained its position. High functional redundancy may be just as important as richness extending to the

288   periphery of functional space for ecosystem health, being one of the mechanisms helping to maintain high

289   diversity and ecosystem function (Wohl et al. 2004), reducing negative effects of natural enemies of

290   species (Philpot et al. 2012), and facilitating niche packing within assemblages (Ricklefs 2012; Pigot et

291   al. 2016; Cooke et al. 2019a). Our finding that the core of the San Antonio bird assemblage has seemingly

292   not lost functions nor shifted in position suggests that there are still important attributes of the system's

293   functionality that mirror the pre-disturbance assemblage of 100+ years ago. Hopefully, given the right

294   conditions (i.e. time, continued forest recovery and increased connectivity between remaining forest

295   fragments), San Antonio may still recover more of its lost functionality provided by extirpated species,

296   some of which are are still found in the wider region (Palacio et al. 2016, 2019).

297   Our study provides the first example of an assessment of temporal changes in funcional

298   fingerprints from a highly diverse tropical ecosystem, and both our findings and the methods we

299   employed have wide applications particularly for tropical ecosystem study and conservation (Stroud &

300   Thompson 2019). For instance, restoration objectives aimed at replicating previous states of a system,

301   could use measures of functional fingerprints to quantify how much change is needed and to direct efforts

302   to areas of functional space in particular need of recovery (Meli et al. 2014). Similarly, conservation

303   actions aimed at maintaining or recovering functionality can use functional fingerprints to assess routes to

304   recovery and to prioritize species with a particular combination of traits which should be preserved or

305   potentially re-introduced (Chazdon 2008). Future studies could explore whether the San Antonio

306   functional fingerprints can be used as a basis for comparison to other tropical localities lacking long-term

307   data (Stroud & Thompson 2019), and other historical suveys (e.g. Miller et al. 1957) can be used to carry

308   out comparisons over larger scales.

309   Certain species traits, such as being large, specialized, social, having low dispersal ability and

310   being at the top end of food webs, make animal species more vulnerable to local extirpation (Kattan et al.

311   1994; Davies et al. 2000; Pearson et al. 2009; Habel et al. 2019). Our results highlight that some of these

312   traits, namely body size, dispersal ability and habitat breadth, are responsible for ~78% of the variation in

313   functional diversity within a tropical bird assemblage. This means that species with trait values at the

314   extremes of these axes of variation (size, dispersal and habitat specialization) likely also account for a

315   large proportion of the functional richness and dispersion in ecological assemblages. Thus, when a system

316   loses species at the extremes of these axes, it likely also loses unique functionality. In San Antonio, the

317   extirpation of species combining some of these traits associated with vulnerability resulted in significant

318   decreases in functional richness and dispersion, hence arguably making the assemblage less healthy and

319   potentially more susceptible to further changes (Mouillot et al. 2013). In agreement with our results,

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320   species vulnerability to extinction is positively correlated to functional uniqueness and specialization in a

321   wide range of organisms (Pimiento et al. 2020), and the functions provided by these unique species may

322   be particularly prone to disappear (Mouillot et al. 2013; Teichert et al. 2017). Therefore, conservation

323   efforts aimed at maintaining ecosystem health must move beyond just maintaining species numbers to

324   designing strategies for the maintenance of ecological function by identifying and conserving species with

325   traits conferring high vulnerability (Cadotte et al. 2011; McConkey et al. 2012; Pimiento et al. 2020).

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470   **Tables and Figures**

471   **Table 1.** Values of functional richness and functional dispersion estimated for two possible Scenarios of

472   changes in species assemblages during 100 years in San Antonio – Colombia.

Period	Functional Richness		Functional Dispersion	
	Scenario 1[a]	Scenario 2[b]	Scenario 1	Scenario 2
1910's	0.60	1.00	2.39	2.45
1950's	0.24 (- 36%)[c]	0.41 (- 59%)	2.19 (- 8%)	2.28 (- 7%)
1990's	0.28 (+ 4%)	0.34 (- 7%)	2.27 (+ 3%)	2.32 (+ 2%)
2000's	0.46 (+ 18%)	0.46 (+ 12%)	2.35 (+ 3%)	2.35 (+ 2%)

[a] Scenario 1 assumes there were novel species which joined the assemblage as well as extirpations and re-colonizations.
[b] Scenario 2 assumes there were no novel species, just extirpations and re-colonizations.
[c] Numbers are estimates for each time period and in parenthesis the equivalent change from the previous period as a percentage.

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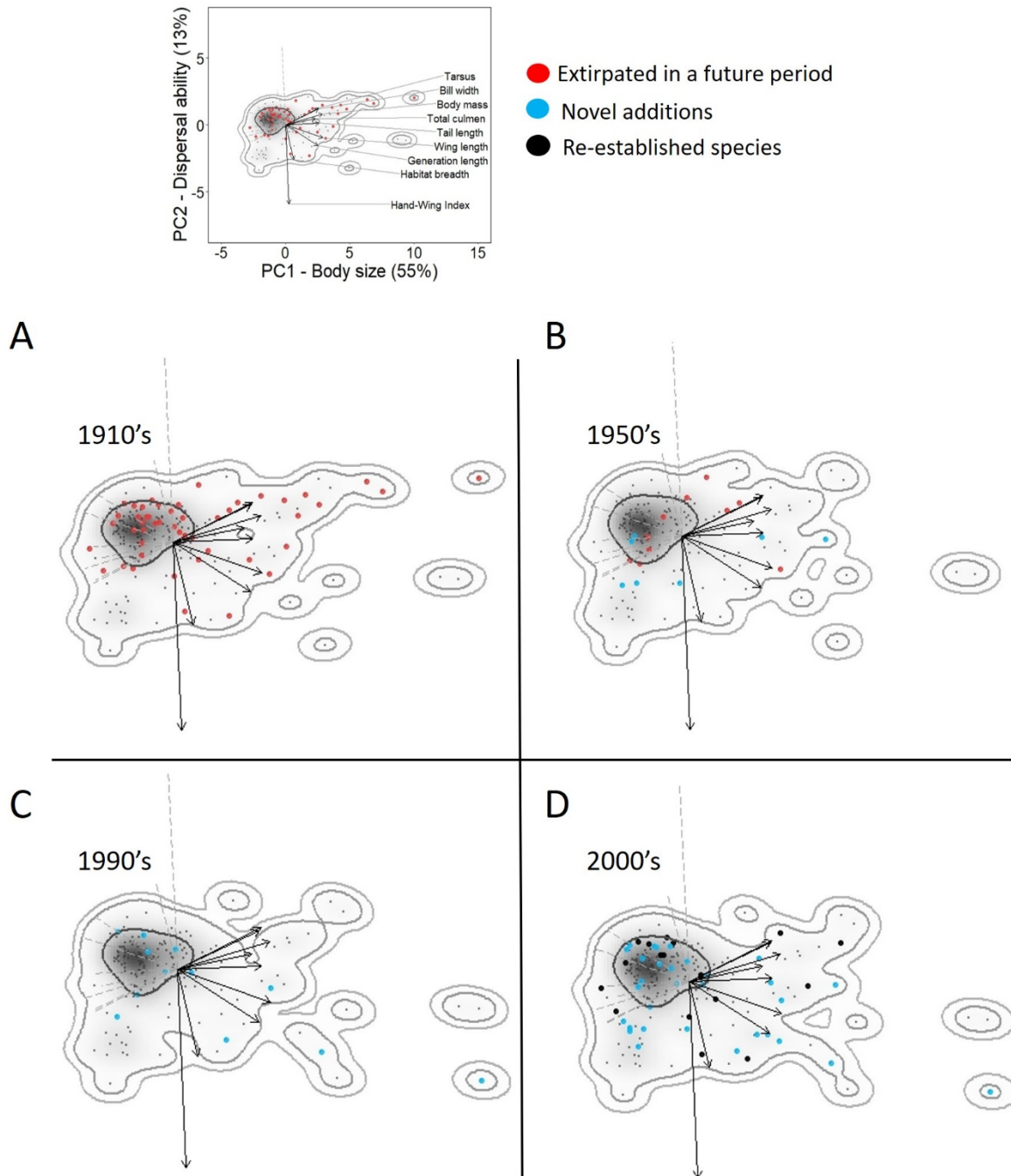
Figure 1. Species extirpations, novel additions and re-establishments have caused changes in the shape

and extent of the functional space of the San Antonio avian assemblage in 100+ years, but the centroid of

trait space (gray shading) has not shifted. Two-dimensional functional space is represented by PC scores

of functional traits during 4 time periods (**A-D**). PC1 reflects largely variation in body size whereas PC2

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479   correlates with dispersal ability of birds and habitat breadth. Small dots are species present in each time

480   period, with larger red dots representing species which became extirpated in a future period and larger

481   blue dots representing new additions which were absent in previous periods. In **D**, the larger black dots

482   are species which re-established populations after being extirpated. Arrows are scaled to represent the

483   loadings and direction of each trait in functional space and the insert above shows the scale and the traits

484   represented by each arrow. Gray shading represents the kernel density estimates for each time period and

485   curved lines show the 50, 95 and 99% probability contours.

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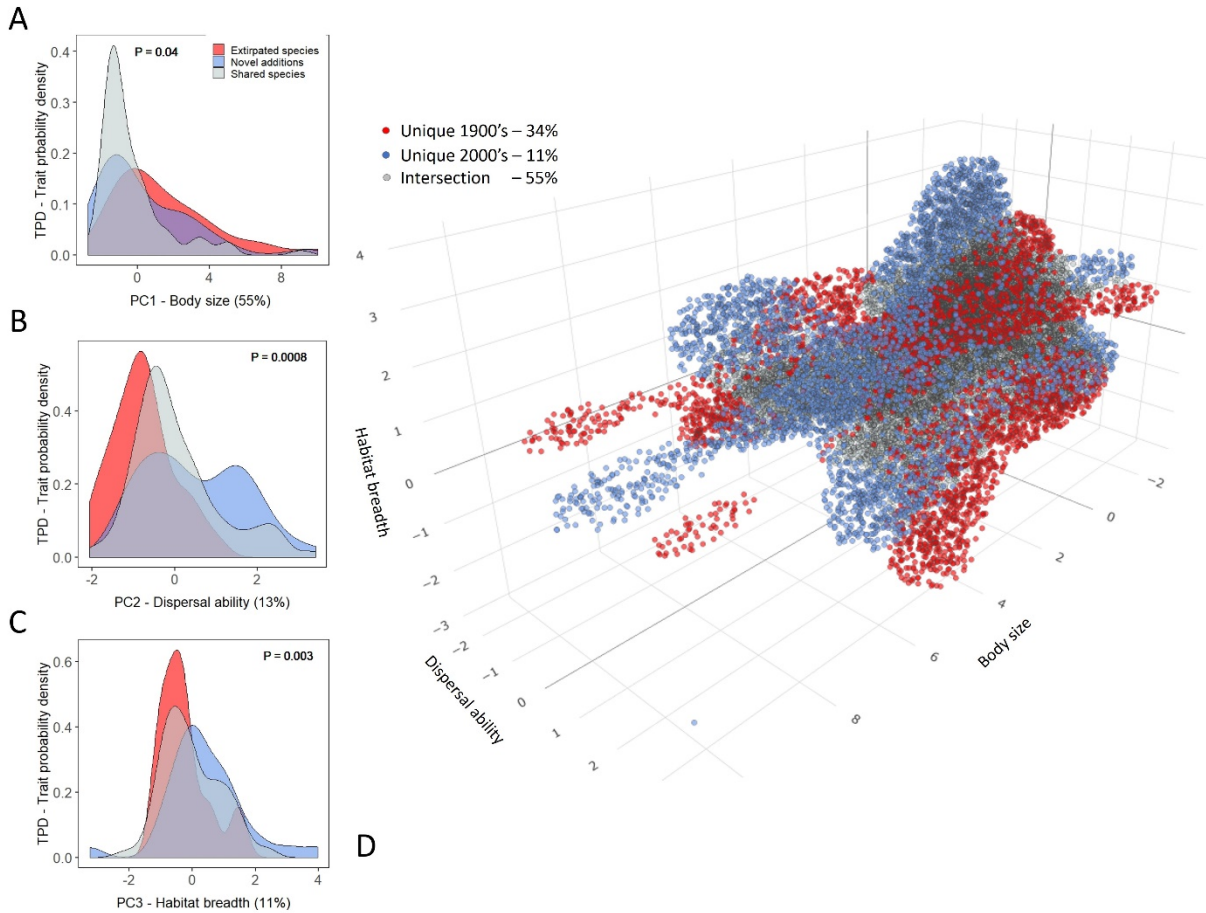
Figure 2. Probability density curves of extirpated species and novel additions to the avifauna between 1910's and 2000's (Scenario 1), show that San Antonio's functional fingerprint has shifted towards **A.** Smaller birds, **B.** Species with higher dispersal ability and **C.** Species with wider habitat breadths. *P* values were obtained through Kolmogorov-Smirnov tests comparing the distributions of extirpated and novel species. **D.** An overlap of the 9-dimension hypervolumes of the 1900's and 2000's suggests that 35% of the volume occupied in 1910's (in red) has been lost and replaced by 11% of new functional space (in blue) provided by the novel additions to the San Antonio assemblage during the 2000's. 55% of the functional hypervolume has remained constant in time. Only the first 3 dimensions are used for visualization.

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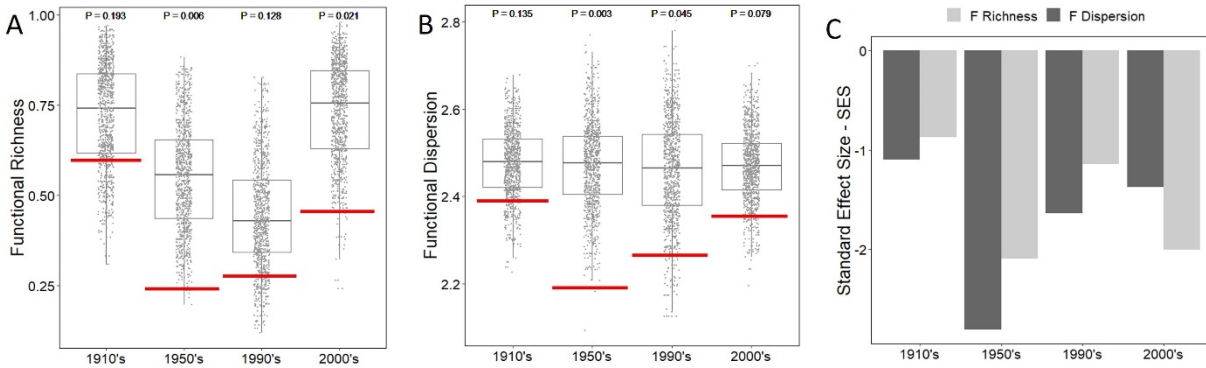
Figure 3. Functional richness (**A**), and dispersion (**B**) decreased significantly between the 1910's and the 1950's, appeared to increase slightly thereafter until the 1990's and then increased significantly until the 2000's. Red lines show the empirical values of functional richness and dispersion estimated for each time period, and boxplots show the distribution of these values generated by 999 iterations of a null model with randomized species identities. Deviance from random expectation, measured as standard effect sizes (**C**) were all negative suggesting that the assemblages at different time periods have lower than expected values of functional richness and dispersion, i.e. extirpated species were more functionally unique than expected by chance.

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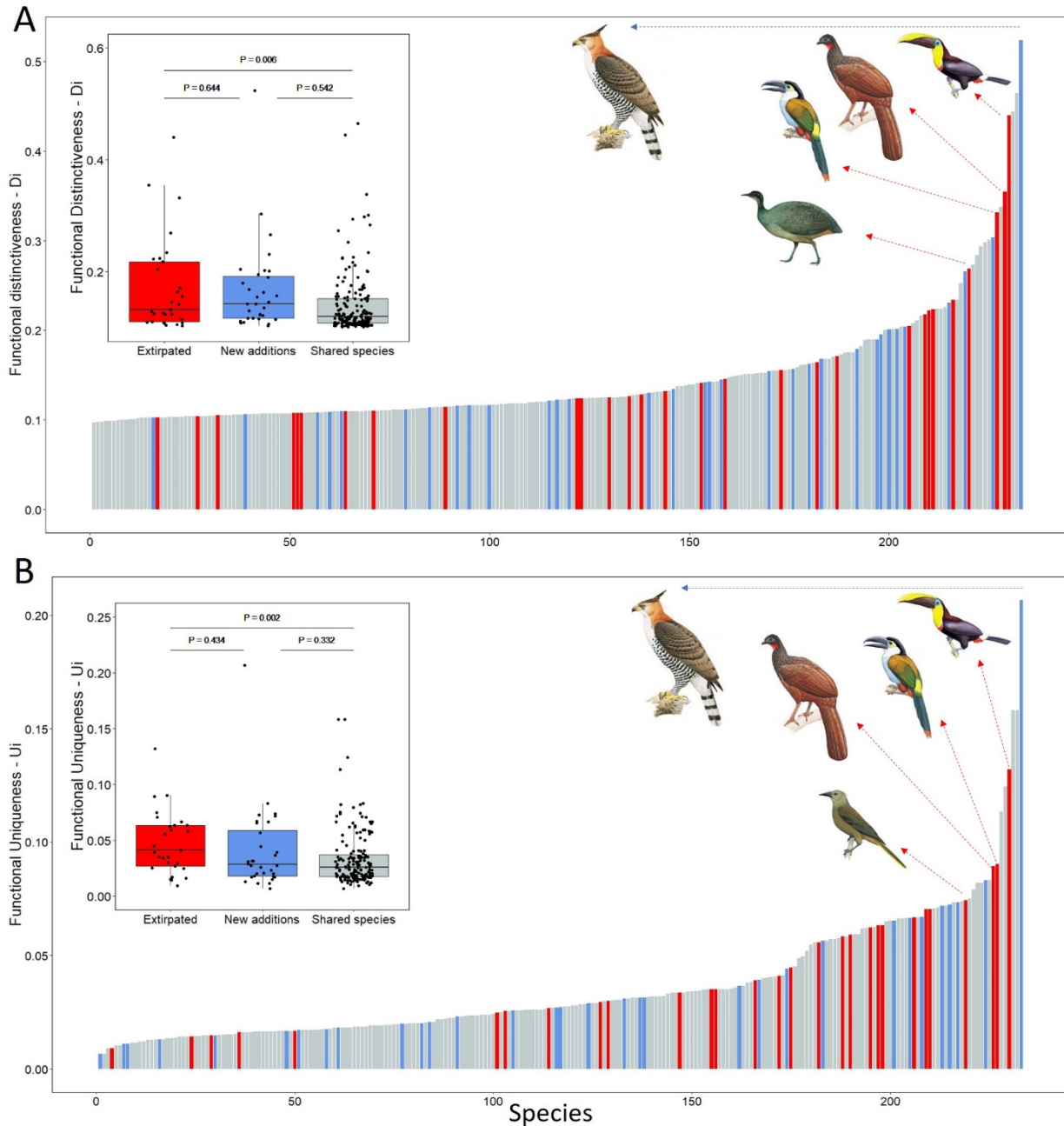
Figure 4. Figure 4. Both extirpated species and novel additions to the San Antonio assemblage had

higher functional distinctiveness (**A**. $P_{ext} = 0.009$, $P_{new} = 0.002$) and uniqueness (**B**. $P_{ext} = 0.002$, $P_{new} = 0.017$), than expected by chance. Differences between pairs of groups were only significant between

extirpated and shared species. The highest ranked extirpated species are all large frugivores, but the

514   species with the highest rank is the Ornate Hawk-eagle, a novel addition which appeared in the 1990's in

515   San Antonio.

516   **Supporting information**

517   Appendix S1 contains the complete trait dataset used in this tudy plus the PC scores and the values of

518   functional Uniqueness and Distinctiveness estimated for each species. Appendix S2 contains the R code

519   used for all analyses, and Appendix S3 contains supplementary methods, tables and figures.

520

521   **Appendix S3.** Supplementary methods, figures and tables.

522   *Functional trait dataset.-* Our trait dataset contains a combination of measurements taken from almost

523   1900 bird specimens housed at seven ornithological collections in Colombia, compiled mainly by

524   Montoya et al. (2018) and complemented with secondary information from other published trait datasets

525   (Claramunt et al. 2012; Cooke et al. 2019; Pigot et al. 2020). For 93 species which did not have complete

526   information, we measured additional specimens (see acknowledgements). Where possible, at least 2

527   males and 2 females of each species were measured (mean = 8, range = 1 - 124 individuals). Habitat

528   breadth (the number of habitats listed in IUCN accounts) and generation time (years), were extracted from

529   the IUCN List of Threatened Species accounts (BirdLife International 2018). Mean trait values for each

530   species were estimated and used in all subsequent analyses. The impact of measurement error due to

531   multiple observers on our analysis is negligable due to the large disparity in body sizes in our dataset (eg.

532   *Coragyps atratus* `~1,600 g vs. *Ocreatus underwoodii* ~2,5 g).

533   **Historical changes in the San Antonio Avifauna.-** The original avifauna, which contained 201 species

534   in the 1910's, suffered the extirpation of 47 species between the 1930's and 1990's due to extensive forest

535   fragmentation and hunting (Kattan et al. 1994). However, 17 species were reestablished in the 2000's

536   after forest regeneration (Palacio et al. 2019). Additionally, since the 1990's the site has been colonized

537   by 32 species not recorded in the 1910's (Kattan et al. 1994; Palacio et al. 2019). Large canopy

538   frugivores, understory insectivores, habitat specialists and species at their elevational limits were more

539   prone to extirpation in San Antonio (Kattan et al. 1994), in agreement with work in other tropical areas

540   experiencing forest fragmentation (Renjifo 1999; Sodhi et al. 2006; Ferraz et al. 2007; Pearson et al.

541   2009; Stouffer 2020).

542

543 **Supplementary Table S3.1.** Summary of PCA showing standard deviation, variance explained and

544 loadings for 9 PC axes. 79% of the variation in functional traits was explained by the first 3 PC. PC1

545 describes body size, PC2 dispersal ability and PC3 habitat breadth.

|	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9
Standard deviation	2.23	1.09	0.98	0.90	0.64	0.54	0.45	0.35	0.28
Proportion of variance	0.55	0.13	0.11	0.09	0.05	0.03	0.02	0.01	0.01
Cumulative proportion	0.55	0.68	0.79	0.88	0.92	0.96	0.98	0.99	1.00
Loadings	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**
Weight	0.41	0.12		0.22		0.11	0.58	0.20	0.62
Bill length	0.33			-0.66		0.44	-0.32	0.37	0.12
Bill width	0.36	0.17	-0.19	-0.48		-0.25	0.41	-0.53	-0.24
Wing length	0.41	-0.14	0.12	0.22			0.22	0.47	-0.69
Tail length	0.37			0.17	-0.71	-0.41	-0.37		0.16
Tarsus	0.37	0.18		0.39	0.14	0.56	-0.28	-0.49	-0.11
HWI		**-0.85**	0.31	-0.15	-0.19	0.20	0.13	-0.26	
Habitat breadth		-0.37	**-0.89**	0.20					
Generation time	0.36	-0.22	0.17		0.65	-0.46	-0.35		0.16

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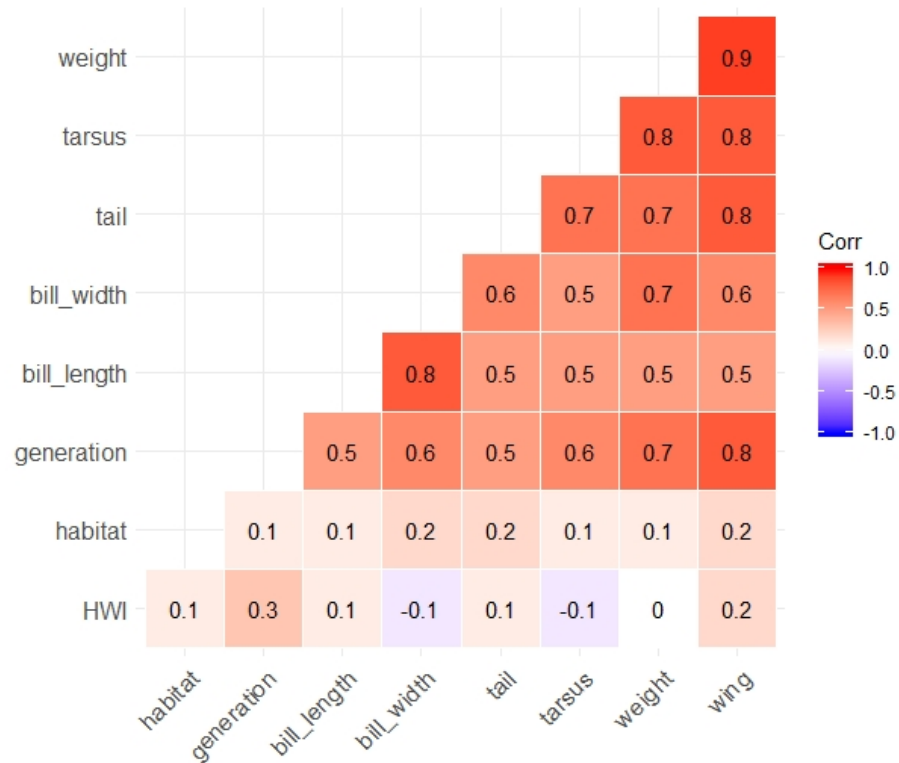
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548   **Figure S3.1.** Correlation matrix of the 9 functional traits used in this study. 72% of our traits have

549   correlation values equal to or below ±0.6.

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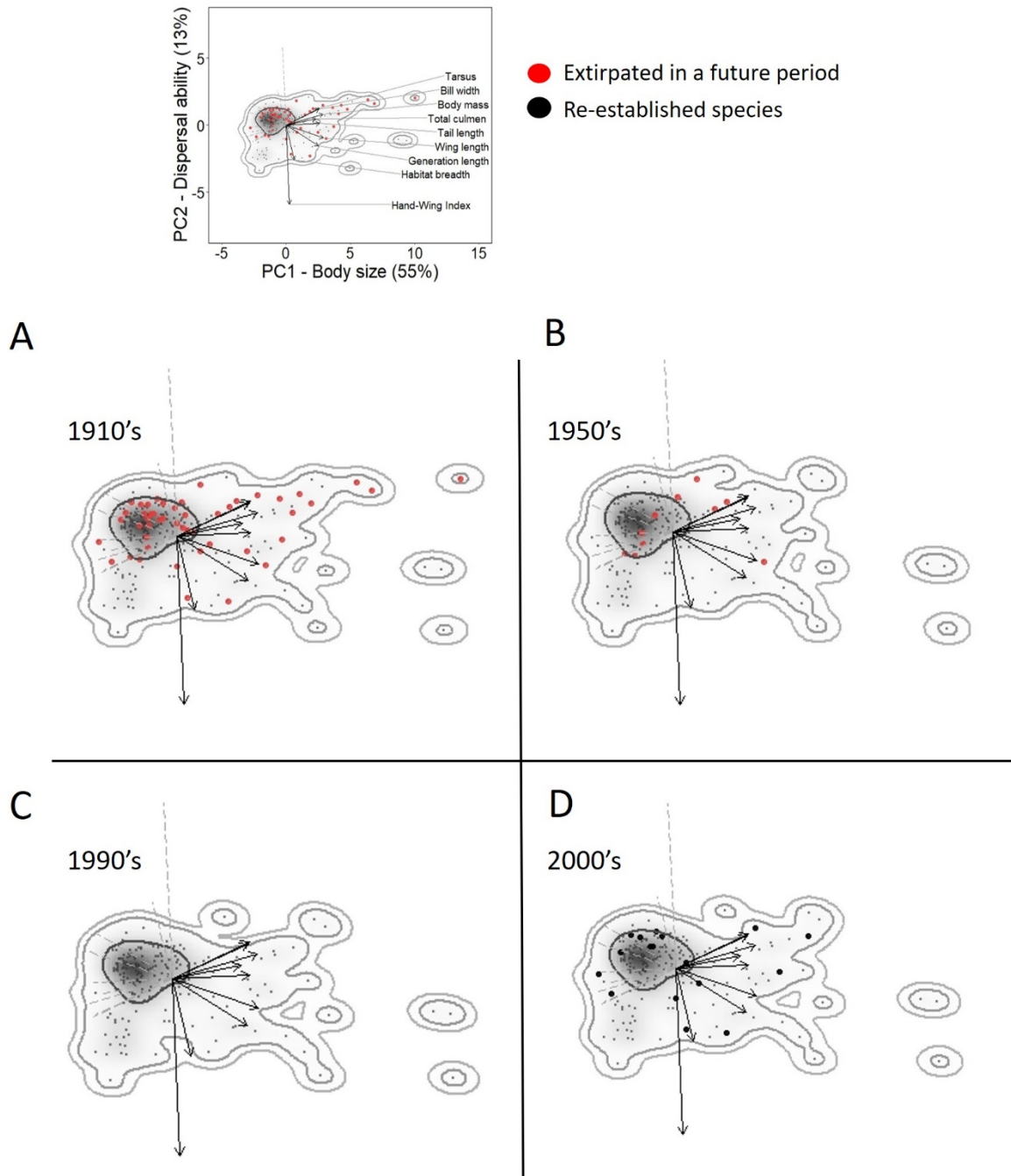
**Figure S3.2.** Species extirpations and re-establishments (Scenario 2) have caused changes in the shape and extent of the functional space of San Antonio in 100 years, but the centroid of trait space (gray shading) has not shifted. Two-dimensional functional space is represented by PC scores of functional traits during 4 time periods (**A-D**). PC1 reflects largely variation in body size while PC2 correlates with

556   dispersal ability of birds and habitat breadth. Small dots are species present in each time period, with

557   larger red dots representing species which became extirpated in a future period and larger black dots are

558   species which re-established populations after being extirpated. Arrows are scaled to represent the

559   loadings and direction of each trait in functional space and the insert above shows the scale and the traits

560   represented by each arrow. Gray shading represents the kernel density estimates for each time period and

561   curved lines show the 50, 95 and 99% probability contours.

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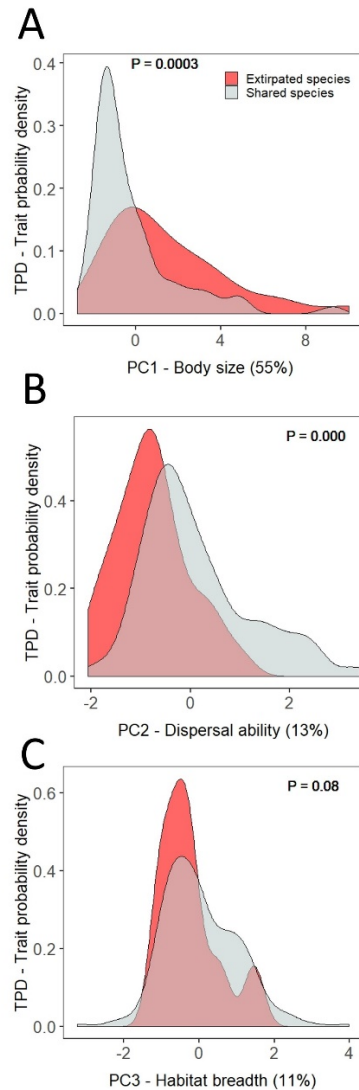
Figure S3.3. Under Scenario 2, assuming there were no novel species joining the San Antonio bird assemblage, the probability density curves of extirpated species between 1910's and 2000's, show that the functional fingerprint has shifted towards **A.** Smaller birds, and **B.** Species with higher dispersal ability. **C.** Contrasting with scenario 1, in scenario 2 species habitat breadths did not change significantly as a consequence of species extirpations. *P* values were obtained through Kolmogorov-Smirnov tests comparing the distributions.

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