1   *Running head:* Demographic consequences of invasion by a native competitor

2

3   **Demographic consequences of invasion by a native, controphic competitor to an insular**

4   **bird population**

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16   *Abstract.* Species invasions and range shifts can lead to novel competitive interactions between

17   historically resident and colonizing species, but the demographic consequences of such

18   interactions remain controversial. We present results from field experiments and 45 yrs of

19   demographic monitoring to test the hypothesis that the colonization of Mandarte Is., BC, Canada,

20   by fox sparrows (*Passerella iliaca*) caused the long-term decline of the song sparrow (*Melospiza*

21   *melodia*) population resident there. Several lines of evidence indicate that competition with fox

22   sparrows for winter food reduced over-winter survival in juvenile song sparrows, enforcing

23   population decline despite an increase in annual reproductive rate in song sparrows over the

24   same period. In contrast, we found no evidence of interspecific competition for resources during

25   the breeding season. Our results indicate that in the absence of a sufficient ecological or

26   evolutionary shift in niche dimension, range expansions by dominant competitors have the

27   potential to cause the extirpation of historically resident species when competitive interactions

28   between them are strong and resources not equitably partitioned.

29   **Word count:** 165

30   **Keywords:** interspecific competition; competitive exclusion; invasive species; range shifts;

31   *Melospiza melodia*; *Passerella iliaca*

32

33   **INTRODUCTION**

34   Exotic species are well-known to affect community composition via competitive, predatory and

35   pathogenic interactions, especially on islands (Reaser et al. 2007; Dhondt 2012; Doherty et al.

36   2016). However, despite many native species undergoing range shifts linked to climate and land

37   use change (e.g., Parmesan 2006; Early and Sax 2014; Krosby et al. 2015; Elmhagen et al. 2015),

38   relatively little is known about the demographic impacts of these colonists on historically extant

39   species (Davis and Shaw 2001; Loarie et al. 2008; Sorte et al. 2010; Rodewald and Arcese

40   2016). Theory suggests that the response of native species to controphic colonists will depend on

41   their overlap in resource use, the demographic effects of resource limitation, the time-frame over

42   which competitive exclusion might occur relative to the rate at which native species can adapt

43   via ecological or evolutionary shifts in niche dimension, and the spatial scale examined (Shea

44   and Chesson 2002; Davis 2003; Gurevitch and Padilla 2004; Reaser et al. 2007; Sax et al. 2007;

45   Bennett et al. 2012; Dhondt 2012; Stuart et al. 2014). Although examples of competitive

46   exclusion by colonist species remain rare, they are thought to be most likely to occur where

47   environmental heterogeneity is low, such as small islands or isolated water bodies (e.g., Chesson

48   2000; Davies et al. 2005; Melbourne et al. 2007; MacDougall et al. 2009). Given the potential for

49   novel competitive interactions to shape species demography and community composition

50   (Simberloff 2005; Reaser et al. 2007), we used a 45 yr study of an island song sparrow

51   (*Melospiza melodia*) population to ask how the colonisation and expansion of a colonist,

52   controphic competitor, the fox sparrow (*Paserella illiaca*) has affected its demography.

53   Although described as migratory throughout its range in North America (Weckstein et al.

54   2002), fox sparrows established resident populations in the San Juan and Gulf Islands of western

55   North America in the latter half of the 20th century, where they now survive and reproduce at

56   rates consistent with rapid population growth (Visty et al. 2017). Because song and fox sparrows

57   are territorial, very similar in life history, but differ in size, we used field experiments and

58   demographic analyses to test for evidence of interspecific competition between song sparrows

59   and this colonist following Dhondt (2012) and Jankowski et al. (2010).

60   Specifically, we first used a life-table response experiment and 45 years of demographic

61   data to identify vital rates contributing most to song sparrow population growth over time, and to

62   test if those rates varied with fox sparrow abundance. We next tested for interspecific

63   competition for breeding habitat by conducting simulated territorial intrusions to quantify

64   interference competition. Because exploitative competition might reduce breeding habitat quality

65   even in the absence of interspecific territoriality, we also tested for long-term declines in site

66   quality following Germain and Arcese (2014). Last, we tested for evidence of interspecific

67   competition for access to winter food by measuring diet overlap and inter-specific dominance.

68

69   **METHODS**

70   *Study system*

71   Mandarte Is. is a *c.* 6 ha islet in southwestern BC, Canada, where a resident, individually-banded

72   song sparrow population was monitored from 1960–63 and 1975–2016 (Tompa 1963; Germain

73   et al. 2015). Song sparrows are a *c.* 24 g passerine that occur over much of North America at

74   densities of ~1–9 pairs/ha (Arcese et al. 2002). On Mandarte Is. song sparrows lay 2–5 eggs in 1-

75   7 open-cup nests annually (Arcese et al. 1992) and defend 200–5000 m^2 territories year-round

76   (Arcese 1989). From April – July 1960–63, 1975-79, and 1981-2016, the territorial status and

77   breeding activity of all song sparrows was monitored at least weekly to locate all nests annually.

78   All nestlings were colour-banded, followed to independence from parental care (~24 days post-

79 hatch) and their recruitment or disappearance from the population was recorded, which provided

80 precise estimates of annual population size, age structure, and reproductive and survival rates

81 (annual re-sighting probability >99%; Wilson et al. 2007). About one immigrant song sparrow

82 settles on Mandarte Is. annually, but because that rate is low and about constant it is not

83 considered here.

84   Fox sparrows are ~19% larger than song sparrows in mass and linear traits and, like song

85 sparrows are territorial, multi-brooded, open-cup nesters that feed mainly on seeds (winter) and

86 insects (breeding; Weckstein et al. 2002, Visty et al. 2017). Fox sparrows are native to BC, but

87 were absent from Mandarte Is. prior to 1975 (Tompa 1963; Drent et al. 1964), when they first

88 bred there (J.N.M. Smith, pers. com.). Fox sparrows were counted systematically in 13 yrs from

89 1960-2016 by spot-mapping singing males, their mates and nest locations, and by mapping their

90 territories in detail in 2010 and 2013–16 when up to 70% of adults were individually identified.

91   Rate of annual change in the number of female sparrows on the island in late April was

92 estimated using a generalized linear model with year as a fixed effect (fox sparrow: Poisson

93 distribution, log link; song sparrow, Gaussian distribution). We tested for temporal

94 autocorrelation in the time series (finding none) and employed R 3.1.3 (R Core Team 2015) for

95 all statistical analyses.

96   *Demographic rates*

97 We identified the demographic vital rate contributing most to song sparrow population growth

98 using a stage-structured life table response experiment (LTRE) to estimate the contribution of

99 each vital rate to growth from 1975–2014. We used juvenile and adult age-classes for both sexes

100 because adults differ modestly in survival and reproductive rate after reaching adulthood. Local

101 juvenile survival was estimated as the proportion of offspring surviving from independence (day

102   24 post-hatch) to April 30 the next year. Adult survival was the proportion of individuals alive

103   on April 30 in year t that survived to year $t + 1$. Reproductive rate was the mean number of

104   independent young produced per female annually, excluding birds used in experiments (1979, n

105   = 70; 1985, n = 87; 1988, n = 114; Arcese and Smith 1988; Smith et al. 2006). Juvenile survival

106   was unknown in 1979 and 1980, reproductive rate unknown in 1980, and adult survival unknown

107   in 1975.

108   The LTRE included a treatment matrix parameterized with juvenile and adult survival

109   and adult reproductive rate in each of 37 yrs. Vital rates were arranged in 2 x 2 treatment

110   matrices wherein the 1st and 2nd columns included juvenile and adult vital rates, respectively, and

111   the first and second rows specified reproduction and survival rates, respectively. Because

112   juveniles do not breed, the 1st row of column one always equalled zero. Treatment matrices were

113   compared to a 2 x 2 reference matrix of mean vital rate over all years to determine the

114   contribution (c_{ij}) of each vital rate to annual population growth (*cf* Caswell 1996) such that:

115

116                $$c_{ij} = \left(a_{ij\ ref} - a_{ij\ trt}\right) * s_{ij\ ref}$$ eqn. 1

117

118   where a_{ij} is the (*i,j*) element of *a*, the reference (*ref*) or treatment (*trt*) matrix, and s_{ij} is the

119   sensitivity of the reference matrix, indicating the impact of an absolute change in a vital rate on

120   population growth (de Kroon et al. 1986; Caswell 1996). Analyses were implemented in the

121   *popbio* package (Stubben and Milligan 2007) and trends in vital rate contribution estimated by

122   linear model (Gaussian). Because the LTRE indicated that juvenile survival was a key vital rate,

123   we tested for an effect ($\alpha \leq 0.05$) of fox sparrow abundance on juvenile song sparrow survival

124   using a linear model (Gaussian distribution), with fox and song sparrow numbers as predictors.

125   Song sparrow numbers was included because it was shown previously to predict juvenile

126   survival in that species (Arcese et al. 1992). Estimates of fox sparrow population size and song

127   sparrow juvenile survival were available for 11 years from 1960 to 2016.

128

129   *Competition for winter food*

130   Dhondt (2012) identified space, nesting habitat and food as common limiting factors in bird

131   communities. We tested for interspecific competition for winter food between fox and song

132   sparrows using a seed preference experiment to estimate diet overlap, and two arena experiments

133   to assess behavioral dominance in contests over food. We assessed the breadth of winter food

134   available by characterising the type and abundance of seeds in soil, given that both species feed

135   mainly on seeds in winter (Tompa 1963; Willson 1971; Arcese et al. 1992; Weckstein et al.

136   2002). To do so we excavated 250 ml of soil (10 x 15cm, 2cm deep) at 15 sites across the island

137   in December 2013, extracting all seeds by sieve to estimate abundance by identity. Seeds

138   recovered in soil included 64% blackberry (*Rubus armeniacus*), 17% Oregon grape (*Mahonia*

139   *aquifolium*), 8% Nootka rose (*Rosa nootkensis*), 8% red elderberry (*Sambucus racemosa),* and

140   3% other (bitter cherry, *Prunus emarginata;* choke cherry*, P. virginiana;* snowberry*,*

141   *Symphoricarpos albus; grape, Vitis sp.*) by volume.

142   We estimated fox and song sparrow preference for seeds in March 2015 by cleaning, then

143   freezing blackberry, Nootka rose, elderberry, and snowberry seeds collected from fruits in

144   summer 2014. We chose the seed types that were most abundant in soil samples with the

145   exception of Oregon grape and cherry, which are ~1.5x larger than all other seed types and are

146   likely inedible to song and fox sparrows. Seeds were arranged by species in one of four 98cm^3

147   circular depressions ('cups') in 60 x 12 x 3 cm plywood feeders, and rotated among cups in each

148   trial to avoid location effects. Feeders were placed on the ground at 6 locations on the island used

149   regularly by foraging fox and song sparrows. In each trial we recorded by video the fraction of

150   time a visiting fox or song sparrow fed on each seed type (N=14 trials, including 50 visits by 6

151   different song sparrows and 9 different fox sparrows). A 'visit' comprised the time elapsed from

152   when a focal bird picked up its first seed, to the time the focal bird's lower mandible stopped

153   moving after last seed was eaten, prior to leaving. Seed preference was estimated by recording

154   the total time from when a focal bird picked up a first seed in cup x, to the point its lower

155   mandible stopped moving before selecting a seed from a different cup or leaving. The proportion

156   of total time spent feeding on each seed type during a visit was then used as the dependent

157   variable in a generalized linear mixed model (GLMM, quasibinomial distribution, logit link).

158   Each visit was numbered and included in the model as a random effect, as was fox or song

159   sparrow identity. We used the glht function in the *multcomp* package (Hothorn et al. 2008) to

160   assess statistical significance of all pairwise comparisons of fox or song sparrow with each seed

161   species using Tukey contrasts for unequal groups (Tukey 1949; Kramer 1956).

162   We conducted arena experiments in October 2013 to assess interspecific dominance at

163   winter food sources by piling 250ml of commercial bird seed at 5 sheltered locations across the

164   island and using video cameras to record interactions. We recorded 19 fox and 19 song sparrows

165   in 68 aggressive interactions. The wining individual stayed in the arena (datum = 1); the loser

166   was chased (datum = 0; Arcese and Smith 1985). We tested the null expectation of equality

167   among species using two GLMMs (binomial distributions, logit links), each including fox and

168   song sparrow identity as random effects. In the first model, we estimated the displacement rate

169   using maximum likelihood; in the second model, we tested the hypothesis of displacement rate

170   equal to 0.5 for both species. Finding a significant effect of 'species' on displacement is

171   consistent with a hypothesis of interspecific dominance. We replicated the arena experiment in

172   March 2015 using 20 feeders (15 x 20cm plastic tray on ~20cm stake; 250ml of commercial

173   birdseed), distributed in sheltered sites across the island. We monitored, scored and analysed 31

174   interactions between 20 song and 16 fox sparrows.

175

176   *Competition for space*

177   To test whether fox and song sparrows compete for breeding space, we first calculated the spatial

178   overlap of song and fox sparrow territories in 2010, 2013, 2014 using ArcMap (ESRI 2011). We

179   also conducted playback experiments prior to breeding in April 2014 to quantify the response of

180   song sparrows to fox sparrow, song sparrow, and Swainson's thrush (*Catharus ustulatus*) (a

181   control species) following Jankowski et al. (2010). Playback experiments involved placing a

182   taxidermic mount on an artificial perch at the center of 27 song sparrow territories, and playing

183   species-appropriate song from a speaker placed below the mount. In each 12 min trial we

184   recorded the closest approach of the territorial male and female song sparrow to the mounts,

185   during: 2 min of pre-trial observation, 5 min of playback, and 5 min follow-up observation. All

186   mounts were presented in random order and prepared in a neutral, perched position. Swainson's

187   thrushes are similar to fox sparrows in size but do not breed on Mandarte Is. Trials were

188   conducted throughout the day but separated by ≥ 1 hour on focal and neighboring territories.

189   Closest approach to the mount was used as a dependent variable to indicate aggression (*cf*

190   Jankowski et al. 2010) and compared among mounts using a GLMM (negative binomial

191   distribution, log link), and including the identity of focal male song sparrows as a random effect.

192   Time of day (categorical effect: morning, <10am, n = 22; midday, 10–1pm, n = 27; afternoon, 1–

193   4pm, n = 6; evening, >4pm, n = 22), whether or not the focal male was singing prior to playback

194   (1/0 fixed effect), and whether one or more neighbor males sang in response to playbacks were

195   also recorded and included as covariates (1/0 fixed effect).

196

197   *Competition for nesting habitat*

198   We followed Germain and Arcese (2014) to estimate site quality as the mean number of

199   independent song sparrow young produced annually in each of 146 20 x 20 m grid cells

200   distributed continuously over the island. Doing so allowed us to test the prediction that site

201   quality for song sparrows declined as fox sparrow abundance increased over time, as expected

202   given competition by song and fox sparrows for breeding resources. Specifically, we regressed

203   site quality on year using a linear mixed model (year of study included as a fixed effect, grid cell

204   identity as a random effect). We also tested for a decline in the mean number of independent

205   young produced by female song sparrows over the study using a GLMM (negative binomial

206   distribution, log link) with year as a fixed effect and female identity as a random effect to

207   account for repeat observations across years.

208

209   **RESULTS**

210   *Population size and demography*

211   Female song sparrow population size varied widely over 45 years (range = 4–71, mean = 35.0 $\pm$

212   17.1 SD), but declined on average (β = -0.60 $\pm$ 0.14 SE, $t(43)$ = -4.19, p < 0.001, R^2 = 0.29;

213   figure 1). In contrast, fox sparrow abundance increased after 1975 (range = 1–30 females, β =

214   0.06 $\pm$ 0.01 SE, $z(11)$ = 9.13, p < 0.001; figure 1).

215   Juvenile song sparrow survival also varied widely over the 37 yrs it was recorded from

216   1960 to 2016 (range = 0.04–0.88, mean = 0.37 $\pm$ 0.18 SD, n_{yrs} = 37; figure 2), as did adult annual

217   survival (range = 0.07–0.88, mean = 0.59 ± 0.17 SD, n_{yrs} = 38), and annual reproductive rate

218   (range = 1.10–6.90, mean = 3.25 ± 1.32 SD, n_{yrs} = 38). However, despite wide variation in song

219   sparrow vital rates over time, when contribution (as determined from the LTRE) was regressed

220   on year, juvenile survival was the only vital rate to increase in influence over time (β = -0.01 ±

221   0.004 SE, $t(35)$ = -3.37, R^2 = 0.25, p = 0.002; figure 3a). Variation in annual reproductive rate

222   had no detectable effect on long-term change in song sparrow population size ($t(35)$ = -1.29, p =

223   0.21, R^2 = 0.05; figure 3b). Similarly, the contributions of annual adult survival to change in

224   population size were smaller and unrelated to long-term decline in song sparrow abundance

225   ($t(35)$ = 1.29, p = 0.20, R^2 = 0.05; figure 3c).

226   The fraction of juvenile song sparrows surviving overwinter also declined as fox sparrow

227   abundance increased (figure 4), amounting to a 40% decline in the expected value of survival

228   from 1960 to 2015 (0.39 ± 0.06 SE and 0.23 ± 0.07 SE, respectively). Juvenile song sparrow

229   survival was also inversely related to fox sparrow population size (β = -0.009, ± 0.004 SE, $t(8)$ =

230   -2.46, p = 0.04, R^2 = 0.44), but unrelated to song sparrow population size ($t(8)$ = -0.63, p = 0.55).

231

232   *Competition for winter food*

233   Fox and song sparrows exhibited a strong preference for elderberry (mean proportion of time

234   spent feeding 0.34 ± 0.05 SE and 0.34 ± 0.12 SE, respectively), and against blackberry (mean

235   0.05 ± 0.02 SE and <0.01 ± 0.003 SE, respectively). But we found no differences in the time

236   spent feeding by each species on blackberry, Nootka rose, red elderberry or snowberry seeds

237   (blackberry: $z(59)$ = -0.81, p = 1.0, elderberry: $z(59)$ = -0.19, p = 1.0, rose: $z(59)$ = -0.37, p =

238   1.0, snowberry: $z(59)$ = -0.18, p = 1.0), implying complete overlap in preference for these seed

239   species (figure 5).

240   Our observations of song and fox sparrows at experimental arenas baited with

241   commercial bird seed revealed that song sparrows were displaced by fox sparrows in 91% of 68

242   contests ($X^2 = 25.6$, df = 1, p < 0.001) in October. In a replicate experiment in early March fox

243   sparrows displaced song sparrows in 100% of 31 interactions, obviating further analysis.

244

245   *Competition for space and nest sites*

246   We observed no evidence of competition for space or nest sites during the breeding period. Fox

247   and song sparrow breeding territories overlapped 100% in 2010, 2013 and 2014, and no

248   aggressive interactions between them were observed despite regularly perching or singing within

249   1 m of each other. Territorial song sparrows approached conspecific mounts in simulated

250   intrusions much more closely than fox sparrow or Swainson's thrush mounts ($t(41) = -7.83$, p <

251   0.001 and $t(41) = -8.28$, p < 0.001; respectively). Song sparrows also responded similarly to fox

252   sparrows and Swainson's thrush mounts ($t(41) = -0.82$, p = 0.42; figure 6), indicating that song

253   sparrows did not respond to territorial intrusions by fox sparrows as expected if these species

254   compete for breeding space.

255   We observed no evidence of a long-term decline in nest site quality (expected number of

256   song sparrow young produced per nest; $t(2671) = -1.29$, p = 0.20) evaluated in 147 grid squares

257   distributed continuously over the island and monitored annually over the study (see Methods).

258   However, we observed a statistically significant increase in the mean annual reproductive

259   success of female song sparrows from 1975 to 2014 ($\beta = 0.014$, SE = 0.002, $t(643) = 6.63$, p <

260   0.001). These results are opposite to the hypothesis that fox and song sparrows compete during

261   the breeding period.

262

DISCUSSION

263

264 We tested whether the colonization of Mandarte Is. by fox sparrows in 1975 led to the decline of

265 the song sparrow population resident there (figure 1). Song sparrows have, on average, declined

266 over the past 46 years whilst fox sparrows increased from 0 to 30 breeding pairs. Demographic

267 analyses indicate that juvenile survival was the most influential of three vital rates affecting

268 population growth in song sparrows and that it declined as fox sparrows increased (figure 4). In

269 comparison, adult survival and reproductive rate had no detectable effect on the long-term

270 decline in song sparrow abundance (figure 3). These findings mirror analyses conducted at much

271 larger scales which indicate a long-term, regional decline in song sparrow abundance (Jewell and

272 Arcese 2008), but increases in fox sparrow abundance, particularly in winter (Visty et al. 2017).

273 Because these results are consistent with the hypothesis that interspecific competition may be

274 contributing to song sparrow declines on Mandarte Is. and regionally, we conducted additional

275 tests to discover potential mechanisms, focusing on competition during breeding and overwinter

276 periods.

277 Contrary to the idea that fox and song sparrows compete for breeding space, we observed

278 complete overlap in song and fox sparrow territories. Moreover, territorial song sparrows largely

279 ignored simulated intrusions by fox sparrows (and the control), despite responding strongly to

280 simulated intrusions by song sparrows (figure 6). These results are opposite to expectation if fox

281 and song sparrows compete by interference for breeding space (Jankowski et al. 2010; Dhondt

282 2012).

283 We also found no evidence of exploitative competition between fox and song sparrows in

284 the breeding period. First, annual reproductive rate in female song sparrows increased as song

285 sparrow population size declined and fox sparrows increased (figure 3c), opposite to

286 expectations under exploitative competition (Dhondt 2012), but consistent with earlier reports of

287 density-dependent reproductive success in song sparrows (Arcese and Smith 1988; Arcese et al.

288 1992). Second, we detected no change in habitat quality for song sparrows (*cf* Germain and

289 Arcese 2014; Crombie et al. 2017), contrary to the expectation that sharing habitat with fox

290 sparrows might reduce food or nest site availability during breeding.

291   Intraspecific competition for winter food and space are well-known to affect juvenile

292 survival and population growth in song sparrows (Nice 1943; Arcese 1989; Arcese et al. 1992;

293 Wilson and Arcese 2008), raising the possibility that interspecific competition with fox sparrows

294 may also reduce survival in juvenile song sparrows sufficient to cause population decline.

295 Specifically, Dhondt (2012) notes that competitive exclusion becomes more likely when, in the

296 presence of intraspecific competition for a limiting resource, the addition of an interspecific

297 competitor further reduces the fitness of subordinate competitors by further reducing access to

298 those resources. Consistent with these expectations, we observed a strong overlap in preference

299 for native seeds in fox and song sparrows, mirroring the results of Willson (1971) who reported

300 strong overlap in preference for commercial seed in Illinois, USA, and also found fox sparrows

301 to be significantly more efficient at handling seeds on average. Moreover, on Mandarte Is., fox

302 sparrows excluded song sparrows from access to supplemental food in 91 and 100% of contests

303 in October and March, respectively. Because these periods correspond with annual peaks in

304 intraspecific aggression and dispersal in song sparrow (Arcese 1989; Wilson and Arcese 2008),

305 these findings suggest that fox sparrows limit song sparrow abundance on Mandate Is. via

306 aggressive competition for winter fool. Overall, therefore, our findings are consistent with the

307 hypothesis that range shifts in colonizing species have the potential to drive community

308 composition via interspecific competition.

309   The coexistence of interspecific competitors has been shown to depend in part on the

310   ability of species to partition resources in ways that allow each to maintain positive growth rates.

311   In ground finches (*Geospiza* spp) on the Galapagos Islands, a drought-mediated decline in seed

312   abundance intensified competition between a resident and colonist species, but also facilitated

313   their rapid morphological divergence and coexistence (Grant and Grant 2006). Stuart et al.

314   (2014) also reported the rapid evolution of feeding behavior and morphology in a native lizard

315   following the invasion of its habitat by a competitively dominant congener. Similarly, Jankowski

316   et al. (2010) demonstrated a strong role for interspecific competition in maintaining elevational

317   range boundaries in congeneric Andean forest birds, but noted that as ranges shift upwards, the

318   species at the top may be limited in their response. These studies illustrate a potential for

319   'evolutionary rescue' to facilitate co-existence via rapid adaptation (e.g., Carlson et al. 2014),

320   and imply that song and fox sparrows are most like to co-exist where sufficient heterogeneity in

321   habitat type or resource use allows each species to diverge sufficiently in its use of limiting

322   resources to maintain positive growth rates.

323   In contrast, low habitat heterogeneity on Mandarte Is. (Lameris et al. 2016; Crombie et al.

324   2017), small population size and low juvenile survival rates in song sparrows all increase the

325   likelihood of their local extirpation on Mandarte Is. (Arcese et al. 1992; Arcese and Marr 2006).

326   Although divergence in quantitative traits potentially affecting co-existence is possible (Schluter

327   and Smith 1986), small population size, random genetic drift and gene swamping are likely to

328   limit rapid local adaptation in the Mandarte Is. song sparrow population (Keller et al. 2001; Marr

329   et al. 2002). Given regional increases in fox sparrow abundance (Visty et al. 2017) and declines

330   in song sparrow abundance (Jewell and Arcese 2008; National Audubon Society 2010; Sauer et

331   al. 2017), it remains an open question as to how competition between these species may be

332   affecting abundance at larger spatial scales.

333   Alternative explanations for the decline of our focal song sparrow population seem

334   unlikely. Jewell and Arcese (2008) showed that brown-headed cowbirds (*Molothrus ater*) can

335   limit song sparrow population growth by reducing reproductive success, but cowbirds were

336   absent from Mandarte Is. in 16 of 17 yrs since 2000, and female reproductive success increased

337   over the course of our study. Severe weather can also decimate sparrow populations (Arcese et

338   al. 1992; Keller et al. 1994; Smith et al. 2006) but has been ameliorated by climate warming (P.

339   Arcese and R. Norris, unpubl. res). Despite changes in vegetation cover, we detected no

340   reduction in the cover of fruiting shrubs (Lameris et al. 2016) or increases in nest failure

341   (Crombie et al. 2017). Overall, therefore, our results strongly support the hypothesis that fox

342   sparrows caused the Mandarte Is. song sparrow population to decline, but more work is needed

343   to understand how fox sparrows may limit song sparrow abundance and distribution regionally.

344   Shifts in species distribution could have far-reaching effects on plant and animal

345   communities via their effects on predation, pathogens and competition (e.g., Simberloff 2005;

346   Parmesan 2006; Early and Sax 2014; Elmhagen et al. 2015; Rodewald and Arcese 2016).

347   Although the threat of competitive exclusion by colonizing species is sometimes downplayed

348   (Davis 2003; Gurevitch and Padilla 2004; Krosby et al. 2015), novel competitive interactions can

349   be expected to increase as climate and habitat change promote shifts in species ranges further.

350   Because interspecific competition can act subtly in communities (Dhondt 2012), long-term and

351   experimental studies of the competitive exclusion of native species by colonists undergoing

352   range expansion will be needed to predict community dynamics in the future. Our results

353   indicate that in the absence of ecological or evolutionary shifts in niche dimension, range

354   expansions by dominant competitors have the potential to cause the extirpation of historically

355   resident species when competitive interactions between them are strong and resources not

356   equitably partitioned.

357

358   **ACKNOWLEDGEMENTS**

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505

506   **Figure Legends**

507   FIGURE 1. Number of breeding female song sparrows in 45 years from 1960–63 and 1975–2016

508   (black circles) and fox sparrow breeding females in 13 years from 1960–2016 (grey diamonds).

509   Song sparrow population size has declined significantly over the study period while fox sparrow

510   population size has increased. Shaded areas represent predicted values ± 1 SE.

511

512   FIGURE 2: Percent of yearling male and female song sparrows surviving from the end of

513   parental care (day 24 after hatching) to April 30th of the following year (juvenile survival) from

514   1975-2016 (excluding 1979 and 1980 when juvenile survival was unknown).

515

516   FIGURE 3. Contributions of (a) juvenile survival, (b) adult reproductive rate and (c) adult

517   survival to song sparrow population growth from 1975–2014, derived from a stage-structured

518   life table response experiment (see Methods). The contribution of juvenile survival changed

519   significantly over time, but reproductive rate and adult survival remained approximately zero,

520   indicating that the observed decline in song sparrows is best explained by the decrease in

521   juvenile survival (Figure 3). The shaded areas around the line indicate predicted values ± 1 SE.

522

523   FIGURE 4. Juvenile song sparrow survival declined as the number of fox sparrow breeding

524   females increased. The shaded areas around the line indicate predicted values ± 1 SE. The black

525   circles are observed juvenile song sparrow survival in each study year for which fox sparrow

526   population size was known ($N_{yrs} = 11$).

527

528   FIGURE 5. Proportion of time song (dark) and fox (light) sparrows fed on each seed type during

529   feeder visits (see Methods). Seeds were presented by type in identical circular depressions in

530   plywood feeders dispersed across Mandarte Island. Fox and song sparrow seed preference

531   overlapped completely. Whiskers represent approximate 95% confidence intervals around the

532   median (solid line), and the box spans the lower and upper quartiles (25%–75%).

533

534   FIGURE 6. Closest approach by territorial male and female song sparrows to taxidermic mounts

535   presented at the center of song sparrow territories during playback trials. Song sparrows (SOSP)

536   came closer to the conspecific mount than to the fox sparrow (FOSP) or control (Swainson's

537   thrush) mounts, and there was no difference in song sparrow response to the fox sparrow and

538   control mounts, indicating that song sparrows do not respond to simulated territorial intrusions

539   by fox sparrows. Whiskers represent approximate 95% confidence intervals around the median

540   (solid line), and the box spans the lower and upper quartiles (25%–75%).
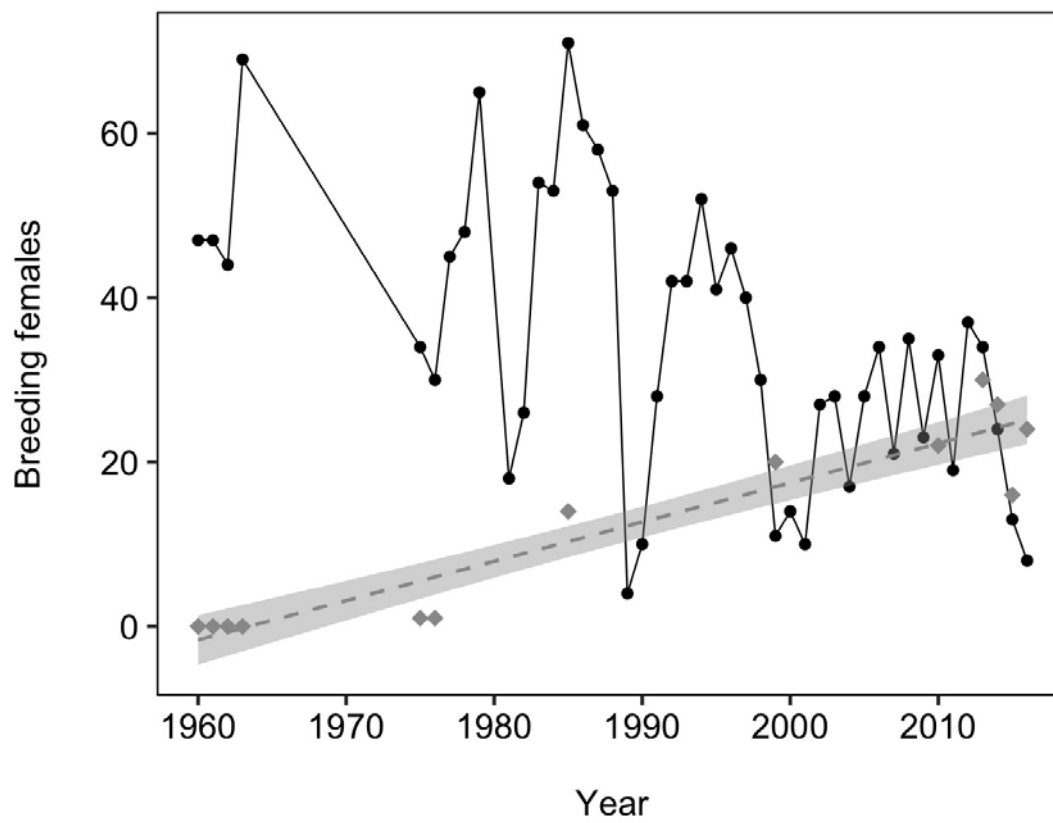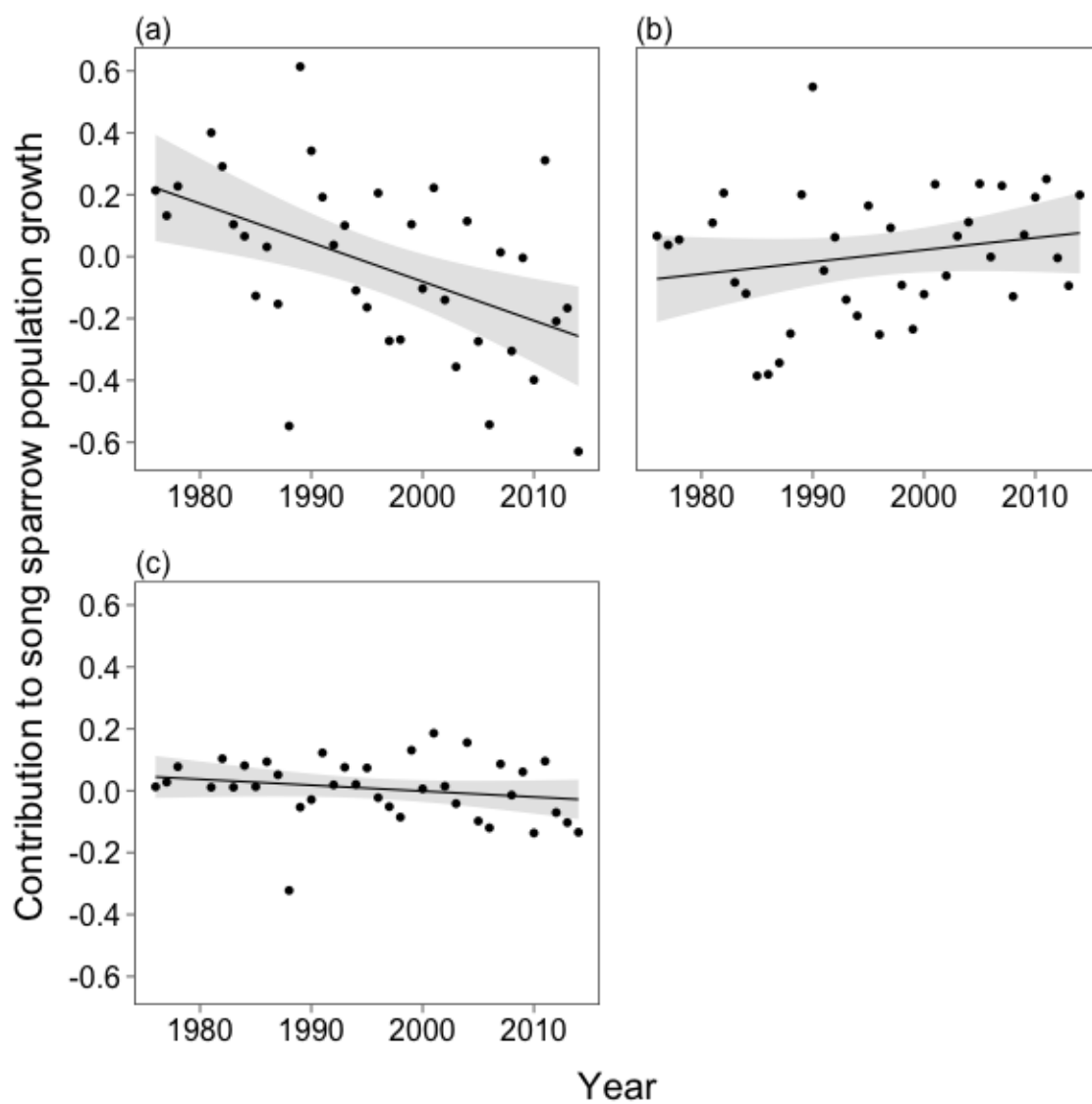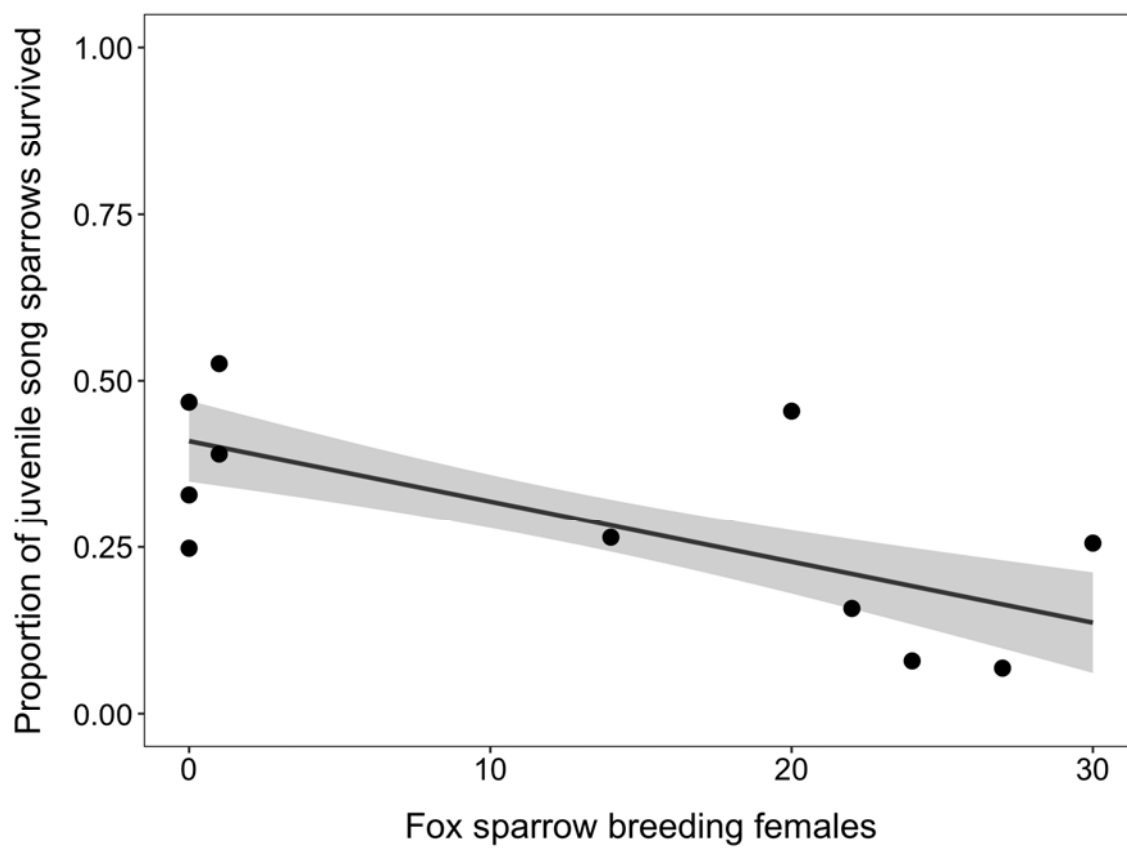
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542   FIGURE 1
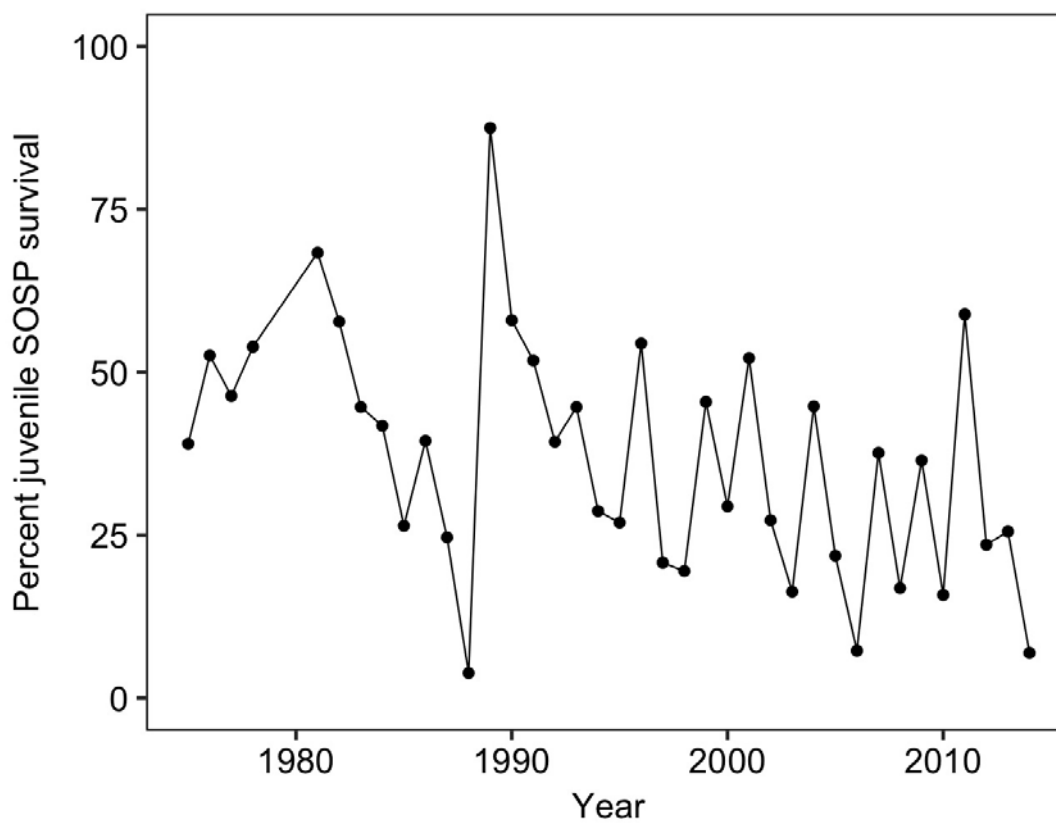
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544   FIGURE 2

545

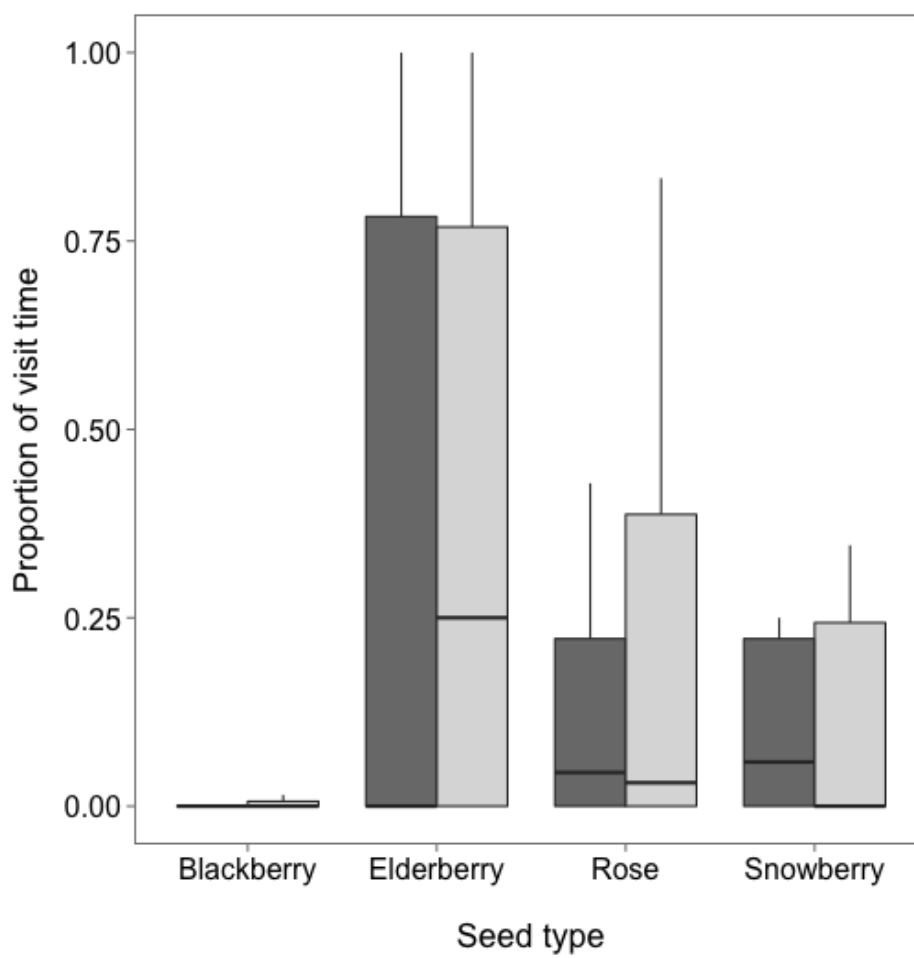546   FIGURE 3

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FIGURE 5

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