1   **Net effects of field and landscape scale habitat on insect and bird damage to sunflowers**

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14

15   **Abstract**

16   Agriculture-dominated landscapes harbor significantly diminished biodiversity, but are also

17   areas in which significant gains in biodiversity can be achieved. Planting or retaining woody

18   vegetation along field margins can provide farmers with valuable ecosystem services while

19   simultaneously benefitting biodiversity. However, when crops are damaged by the biodiversity

20   harbored in such vegetation, farmers are reluctant to incorporate field margin habitat onto

21   their land and may even actively remove such habitats, at cost to both farmers and non-target

22   wildlife. We investigated how damage by both insect pests (sunflower moth, *Homoeosoma*

23   *electellum*) and avian pests to sunflower (*Helianthus annuus*) seed crops varied as a function of

24   bird abundance and diversity, as well as by landscape-scale habitat. Surveys for insect damage,

25   avian abundance, and bird damage were carried out over two years in 30 different fields on

26   farms in California's Sacramento Valley. The mean percentage of moth-damaged sunflowers

27   sampled was nearly four times higher in fields that had bare or weedy margins (23.5%)

28   compared to fields with woody vegetation (5.9%) and decreased in both field types as

29   landscape-scale habitat complexity declined. Birds damaged significantly fewer sunflower seeds

30   (2.7%) than insects, and bird damage was not affected by field margin habitat type, landscape-

31   scale habitat variables, or avian abundance, but was significantly higher along field edges

32   compared to $\geq$ 50m from the field edge. Avian species richness nearly doubled in fields with

33   woody margin habitat compared to fields with bare/weedy margins in both the breeding

34   season and in fall. These results indicate that the benefits of planting or retaining woody

35   vegetation along sunflower field margins could outweigh the ecosystem disservices related to

36   bird damage, while simultaneously increasing the biodiversity value of intensively farmed

37   agricultural landscapes.

38   **Keywords:** agroecology, crop damage, ecosystem services, farm, hedgerow, integrated pest

39   management, pest control, landscape

40

41   **Introduction**

42   In the face of significant losses of both diversity and abundance of avian species (Rosenberg et

43   al. 2019), farming agroecosystems represent a critical frontline for improving vast tracts of land

44   for breeding, migrating, and overwintering birds. Agricultural intensification can drive

45   biodiversity loss, but, paradoxically, agricultural systems rely on the ecosystem services

46   provided by biodiversity (Johnson et al. 2017). Establishing and protecting agroecosystems that

47   take advantage of functional diversity to provide ecosystem services at the farm and landscape

48   level is a way to simultaneously decrease chemical inputs and increase biodiversity (Daily et al.

49   2000, Weier et al. 2018, Kleijn et al. 2019). To this end, there have been calls for biodiversity

50   conservation to be expanded beyond the reserve system, for example by conserving and

51   promoting functional diversity in expansive agricultural settings (Kremen and Merenlender

52   2018, Grass et al. 2019). Bringing together these two mindsets can create a win-win situation

53   for both conservation and agriculture. For example, establishing or maintaining strips of woody

54   vegetation along field margins can increase the diversity, abundance, and corresponding

55   ecosystem services, of pollinators (Garibaldi et al. 2011, M'Gonigle et al. 2015, Sardiñas et al.

56   2016), arthropod predators (Eilers & Klein 2009; Gareau, Letourneau & Shennan 2013), and

57   birds (Heath *et al.* 2017).

58   Farmers are the primary decision makers for land management choices within

59 agricultural regions, and their decisions are mostly based on direct economic returns (Kleijn et

60 al. 2019). Birds are highly detrimental pests to a number of crops worldwide (De Grazio 1978,

61 Gebhardt et al. 2011, Kross et al. 2012, Schäckermann et al. 2014), although the actual costs of

62 bird foraging on crops are rarely quantified because the timing of bird damage often overlaps

63 with crop harvesting. Farmers that perceive birds as detrimental to their crops will take action

64 to deter birds (Kross et al. 2018), often by removing field margin habitat (Gennet et al. 2013) or

65 utilizing commercially available bird deterrents such as gas guns, reflective tape, or netting

66 (Baldwin et al. 2013), all of which can be costly for both farmers and non-target wildlife. Bird

67 depredation of crops therefore not only has direct economic implications for growers, but can

68 lead farmers to oppose conservation programs within agricultural communities and on their

69 own properties (Kross et al. 2018).

70   Studies into the detrimental behaviors of birds rarely focus on potentially beneficial

71 impacts, and similarly, studies into the beneficial pest-control services of birds rarely focus on

72 the fact that the same species may cause damage to crops (Pejchar et al. 2018) with a few

73 recent exceptions (Peisley et al. 2016, Gonthier et al. 2019). The effects of natural vegetation

74 on biological control can vary with crop type, seasonality, farm management, and the

75 demographic effects of interactions between natural enemies and pests (Karp et al. 2018,

76 Settele and Settle 2018). Therefore, disentangling the complex relationships between

77 landscape- and field-level habitat complexity and crop damage from insect and avian pests- and

78 communicating these results to farmers and policymakers- has critical implications for habitat

79 management in agroecosystems.

80   In California, one of the world's most productive and intensive farming regions, less

81   than 4% of potential field margins have been planted with woody vegetation such as

82   hedgerows (Brodt et al. 2009); field margins therefore have significant potential for increasing

83   the biodiversity conservation value of farmland. However, farmers rank uncertainty around the

84   potential benefits of hedgerows and the possibility that these hedgerows could harbor plant,

85   insect and vertebrate pests as constraints to adopting the practice (Brodt et al. 2009). Research

86   to provide information about the costs and benefits of retaining or planting such habitats is

87   therefore critical to inform land management decisions. Here, we present a study to investigate

88   the effects of field-margin and landscape-scale habitat on insect and bird damage to sunflower

89   (*Helianthus annuus)* crops in California.

90   MATERIALS and METHODS

91   *Study Area and Crop*

92   California's Central Valley runs 724 kilometers north-south and covers a total of 10.9

93   million hectares (26.9 million acres). It is one of the most productive agricultural landscapes in

94   the world, producing over 25% of the fresh produce consumed in the United States (USDA

95   2015), and valued at over $45 billion (USD) per year. Over 95% of the Central Valley's riparian

96   and wetland ecosystems have been replaced by highly intensive agriculture and urban

97   development (Katibah 1984, Frayer et al. 1989), with remnant native habitat existing only in

98   fragmented and isolated patches. Nevertheless, some native biodiversity in this region persists

99   despite the highly human-modified landscape (Heath et al. 2017).

100   Each year, sunflower is grown for hybrid seed production on an average of 20,234ha

101   (50,000 acres) across California's Sacramento Valley, producing over 31,750 tons valued at

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102   approximately $70 million/year (Long et al. 2019). California's Central Valley produces over 95%

103   of the United States' hybrid sunflower seeds, and over 25% of global sunflower seeds (Long et

104   al. 2019). Sunflowers grown for seed are valued at five to ten times that of the commercial oil

105   crops for which they are used (Long et al. 2019), and growers therefore have a low threshold

106   for damage. All sunflower fields in our study were grown for the same seed company and

107   therefore were grown using the same field-management practices. This study was conducted

108   within conventional fields (i.e. non-organic fields), but no growers reported utilizing insecticides

109   on their fields over the duration of this study.

110   The predominant insect pest for sunflowers in North America is the sunflower moth

111   (*Homoeosoma electellum*). Female sunflower moths lay eggs among the florets of sunflowers in

112   early bloom, and eggs take 2-5 days to hatch. After hatching, larvae remain on the face of

113   flowers for 8 days before boring into the developing seeds where they can cause losses of 30-

114   60% of a crop (Long et al. 2019). Birds are also a key pest of sunflower crops around the world

115   (De Grazio 1978, Schäckermann et al. 2014, Long et al. 2019, Ernst et al. 2019). Within a field,

116   bird damage to sunflowers is often concentrated to the edges nearest to habitat that can act as

117   shelter for birds. For example, in Israel, bird damage within a field was highest in areas close to

118   trees (>5m in height), but increasing the number of trees within a 1-km radius of fields was not

119   associated with higher damage (Schäckermann et al. 2014), suggesting that presence of habitat

120   along edges of crops prone to bird damage is more important than the presence of habitat in

121   the landscape overall.

122   *Field- and Landscape- Habitat Complexity*

6

123   We conducted bird counts and collected sunflower damage data from six fields with

124   woody margin habitat and seven fields with bare or weedy field margins in 2014, and from 12

125   complex fields and 5 simple fields in 2015, for a total of 30 fields sampled. To quantify local

126   (field) habitat complexity, we collected data on the height, width, and number of canopy layers

127   of field margin vegetation at 5 locations along each transect (see Heath et al. 2017 for details).

128   To quantify and incorporate landscape habitat complexity into our study design, we selected

129   fields at varying distances from natural habitat, which in our study area consists mainly of

130   remnant and restored riparian areas (Figure 1). We used pre-existing habitat data for our study

131   area (CA DWR 2008, Geographic Information Center 2009), and added by hand any trees within

132   800m of each transect that were not included in the existing dataset (e.g. trees lining

133   driveways, trees around homesteads). To calculate the distance to riparian area, we used

134   ArcGIS 10.1 (ESRI 2010) to create a distance raster that encompassed the entire study area by

135   using the Euclidean distance algorithm. We used the riparian vegetation GIS dataset (habitats

136   classified as native riparian, blue oak woodland, valley foothill riparian, fresh emergent

137   wetland, saline emergent wetland, and valley foothill riparian) as the 'source' input for the

138   algorithm and set the output grid cell size to 10 meters. Each field's transect center point was

139   then buffered by 50 meters, and we calculated the distance from each grid cell within the

140   buffer to the nearest riparian vegetation polygon. The mean distance for all cells within each

141   buffer was calculated as the distance value for each field. We also calculated the mean

142   proportion area consisting of natural habitat (Appendix 1) at concentric buffer distances of

143   100m, 200m, 400m, and 800m, which have been shown to be relevant scales for riparian bird

144   species in the Central Valley (Seavy et al. 2009).

145   *Vertebrate Exclosures*

146   In 2015, we created exclosures to prevent vertebrates (birds and bats) from accessing

147   sunflowers (see Maas et al. 2019 for a review of exclosure methods). Enclosures consisted of

148   nylon bird netting (No-Knot Bird Netting ¾" polypropylene mesh, Bird B Gone Inc®, Irvine, CA)

149   draped over an area 4 rows of sunflowers in width and approximately 20 flowers in length and

150   secured to cover the tops of the flowers to a height of approximately 2-4 feet above the

151   ground. Exclosures were installed in late spring, prior to the onset of bloom (which is when

152   sunflower moth typically lay eggs on the flowers), and were checked and maintained over the

153   entire growing season until final damage estimates were made. We set up four exclosures in

154   each field, with the closest end of each exclosure located 5m, 10m, 50m, and 100m from the

155   edge of the field. Due to last minute changes in the harvest schedule at some fields, we were

156   able to collect damage data from the exclosures at nine different fields. All experiments were

157   carried out in accordance with the University of California's Institutional Animal Care and Use

158   Committee approved protocol #18033

159

160   *Sunflower damage*

161   We quantified both bird and insect damage by visually inspecting each of ten sunflowers

162   within each sampling area. Sunflowers were chosen by reaching out to select a plant stalk, so

163   the seed-bearing area of each plant was not seen until after the plant was selected (most

164   sunflowers were at or above head-height for observers). Observers moved a few steps along

165   and between rows to select each new flower. Bird damage was characterized by missing seeds.

166   We were careful to avoid classifying wind-damaged seeds that had been rubbed off of

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167   sunflowers by a neighboring flower as bird damage. These seeds were generally removed from

168   larger continuous areas of the sunflower head, whereas seeds removed by birds were in patchy

169   sections or removed singularly. Wind-damaged seeds were also often seen whole on the

170   ground underneath the plants. Insect damage was characterized by an area of visible frass

171   (insect excrement and webbing) on the surface of multiple sunflower seeds. Seeds under the

172   frass were often shrunken or visibly damaged. All areas that were under frass were classified as

173   insect-damaged.

174   To estimate the percent of seeds on each sunflower that were damaged, we used a pre-cut

175   circular piece of galvanized steel chicken-wire that was marked to allow for easy measurement

176   of the flowers. Sunflower heads were classified into different size classes based on the diameter

177   (to the nearest 1.3 cm, or 0.5 inches) of the seed-bearing area on each plant. We then

178   estimated the number of hexagons on the wire (to the nearest ¼ hexagon) that was damaged

179   by birds or damaged by insects on each sunflower head. Using the flower circumference and

180   the known area within each hexagon of our grid, we were then able to calculate the percent of

181   each sunflower head that was damaged by birds, and the total that was damaged by insects. To

182   estimate yield, damage from insects and damage from birds were summed for a total percent

183   damage to each sunflower, since both types of damage result in a direct loss of yield for

184   growers.

185   We sampled from 10 sunflowers at distances from 0m to 200m from the field edge. In 2014,

186   we collected observations of both insect and bird damage from each site at 0, 10, 20, 30, 40, 50,

187   75, 100, 150, and 200m from the field edge. In 2015, we collected observations from each site

188   at 5, 10, 50, and 100m from the field edge because we found in 2014 that bird damage dropped

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189   to close to 0 at distances beyond 50m, and that insect damage was largely unchanged by

190   distance from the field edge (see Figure 2). Estimates for insect and bird damage in 2015 were

191   taken from sunflowers within exclosures and from sunflowers that were approximately 10m

192   from the exclosures (parallel to the field margin), but only data from non-enclosed sunflowers

193   was used in our comparative analysis of insect damage.

194   *Bird counts*

195   We conducted four bird surveys at each site, two in summer (June 9- July 2) and two in

196   fall (August 5- September 16). All bird surveys were conducted by trained observers and timed

197   to coincide with sunflower bloom in the summer (when sunflower moths typically lay eggs on

198   the flowers), and immediately prior to the seed harvest in the fall. All counts were conducted

199   between dawn and 10am and were not conducted in very cold (<3C) or very hot weather

200   (>24C), in high winds or heavy precipitation. Counts were also re-scheduled if there were any

201   farm workers or machinery in our focal field. We conducted two counts per visit at each field:

202   one to quantify the birds utilizing the field margin habitat, and another to quantify the birds

203   utilizing the field interior. These methods provide relative values for comparing inter-site bird

204   communities. To count birds utilizing field margin habitat, observers walked a 200m transect

205   slowly over 10 minutes, counting all detectable birds by sight or sound within 20m of the field

206   margin, but not within the field itself. To count birds utilizing the field interior, observers

207   returned to the mid-point of the transect, allowed five minutes for birds to settle, and then

208   conducted a 10-minute point count focused only on birds that were observed within the field.

209   We counted all birds detected within each field because each species was assumed to have

210   similar detectability in all fields, since sunflowers were at similar levels of maturation and

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211 height at the time of each count, and since fields were all of a similar size. We used different

212 methods for the edge and interior transects to maximize our detection of birds utilizing each

213 type of habitat. While these methods may result in counting the same individual in both

214 habitats on the same visit, this is relevant since birds at our study sites were regularly observed

215 using both the field margin and field interior habitats.

216

217 *Statistical Analyses*

218   Because the variables describing field margin habitat (height, width, and number of

219 vegetation layers) were highly correlated, we used a Principle Components Analysis (PCA) to

220 reduce these into two orthogonal axes that explained over 95.5% of the variance among them.

221 The two axes, PC1 and PC2, were included as predictor variables in our candidate models for

222 sunflower damage and for bird abundance and richness. PC1 explained 86.2% of the variability

223 among habitat variables and was negatively associated with all three variables, whereas PC2

224 was positively associated with habitat width and height, and negatively associated with habitat

225 layers. Therefore, if PC1 is a positive predictor of damage, we would expect less damage at sites

226 with habitat that is taller, wider and has more layers (because of the inverse relationship). If

227 PC2 is a positive predictor of damage, we would expect less damage at sites with more habitat

228 layers and more damage at sites with taller/wider habitat. We also found collinearity among

229 the predictor variables for landscape-scale habitat complexity, so constructed separate models

230 for each landscape-scale habitat complexity variable. Model selection revealed that the

231 variable for mean distance to natural habitat was most parsimonious in our sunflower damage

232 models (Tables S1-2), so we present the results from that model in the main text of this paper.

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233   We used a Wilcoxon rank-sum test to compare the total insect damage observed inside

234   exclosures and in adjacent non-exclosure locations. For all other analyses, only the data from

235   the non-exclosure locations were used for investigating the effects of habitat variables on

236   sunflower damage.

237   For both damage categories, we used generalized linear models with a negative

238   binomial family of errors to analyze our data on percent damage to sunflowers in R v.3.3.1 .

239   Sunflower moth damage and bird damage were analyzed in separate models. For our bird

240   abundance and richness data, we ran eight separate linear regressions for avian species

241   richness and abundance along the field edge and within the field interior for data collected in

242   summer and in fall. For all analyses, we included as predictor variables in our maximal models

243   the continuous variables for the distance from the nearest riparian habitat, PC1, and PC2, as

244   well as the categorical variable for whether the field had a weedy or bare edge (simple edge

245   habitat) or had woody field margin habitat (complex edge habitat). We simplified the maximal

246   models by removing interactions, then main effects, until no further reduction in residual

247   deviance (measured using Akaike's Information Criterion) was obtained. For all regression

248   analyses, we considered candidate models with ΔAIC $\leq$ 2 and chose the most parsimonious

249   model.

250   *Economic Estimates*

251   We used published data on the range and mean sunflower yields and economic value for the

252   Sacramento Valley from 2015-2018 (Long et al. 2018) to calculate the reduction in gross

253   earnings for farmers as a result of insect and bird damage in response to significant predictor

254   variables. Mean sunflower yields were 1,260 lbs/acre (1,412kg/ha; range 1,076-1,748 kg/ha)

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255   after seed companies clean and remove nonviable seeds and non-seed material from field

256   harvests (Long et al. 2018). Seeds were valued at a mean value of $1.2/lb ($0.54/kg; range of

257     $0.41-0.68/kg (Long et al. 2018)). We calculated the economic effect size of insect or bird

258   damage by multiplying the scaled effect sizes from our model estimates.

259

260   **RESULTS**

261   *Vertebrate Exclosures*

262   There was no significant difference between sunflower damage from insects inside exclosures

263   (mean= 3.40 ± 0.61% damage) compared to areas outside of exclosures that birds and bats

264   could access (mean= 3.08 ± 0.47% damage).

265

266   *Sunflower damage*

267   Sunflower moth damage was almost four-times higher at sites with bare or weedy field margin

268   habitat (23.46 ± 1.41%) compared to sites with woody vegetation along field margin habitat

269   (5.89 ± 1.16%; z= 7.12, p < 0.001). There was a slight decrease in sunflower moth damage as

270   PC2 increased (z= -2.75, p = 0.005; Figure 2a), and a significant reduction in damage as distance

271   from natural habitat increased (z= -2.25, p = 0.02; Figure 2b). Bird damage was highest at the

272   edge of fields, regardless of the presence of field margin habitat, and dropped quickly to near

273   0% within 50m of the field edge (Figure 2c). This effect was driven entirely by distance from

274   field edge, with only the linear (z= -4.45, p < 0.001) and quadratic values (z= 2.98, p = 0.003) for

275   distance from field edge retained in the final model.

276

277   *Economic Estimates*

278   Our models estimate that at sites adjacent to natural vegetation, farmers would expect to lose

279    $877/ha in lost yields due to sunflower moth damage at sites with bare/weedy vegetation

280   along the field margin, compared to $220/ha in lost yields due to sunflower moth damage at

281   sites with woody vegetation. To put this into perspective, the mean cost of applying insecticides

282   to treat for sunflower moth is $292/ha, so our results suggest that fields in this scenario would

283   be likely to remain under an economic threshold to trigger growers to apply insecticides. In the

284   same scenario, bird damage at the field edge would result in $100 in lost yields but that would

285   decline to negligible damage within 50m of the field edge.

286

287   *Bird results*

288   Species richness of complex fields was higher in fields with woody margins in both

289   summer (19.70 ± 0.91) and fall (16.0 ± 1.04) compared to fields with bare/weedy margins in

290   summer (10.4 ± 0.96) and fall (8.17 ± 0.67). We observed 70 different avian species during our

291   summer counts, and 74 species during our fall counts. These included California 'Bird Species of

292   Special Concern' (Shuford & Gardali 2008) like northern harrier (*Circus hudsonius*), yellow

293   warbler (*Setophaga petechia),* and California 'Threatened' species like Swainson's hawk (*Buteo*

294   *swainsoni*), and tri-colored blackbird (*Agelaius tricolor*, 13 individuals observed at one site).

295   During our summer counts, 64 different bird species utilized sunflower field edges and 49

296   species utilized field interiors. During our fall counts, we observed 69 species utilizing sunflower

297   field edges and 46 species utilizing field interiors. Further details of bird species observed can

298   be found in Bourbour et al. (In prep).

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299   For our summer counts, avian species richness (t = -5.44, p <0.001, Figure 3a) and

300   abundance (t = -5.47, p <0.001, Figure 3b) along field edges had a strong negative correlation

301   with PC1. Since PC1 was negatively associated with all three measures of field margin habitat

302   complexity (habitat height, width, and number of canopy layers), our results predict that as

303   field margin habitat becomes more complex, avian richness and abundance along field edges

304   increased. For summer field interiors, avian species richness was uncorrelated with PC1 (t = -

305   1.83, p = 0.08, Figure 3c). None of our predictor variables were retained in the model for avian

306   abundance within the field interior in summer.

307   In the fall, field edge richness, field edge abundance, and field interior abundance were

308   all positively associated with increasing field margin habitat complexity. Field edge avian

309   species richness was negatively associated with PC1 (t = -9.82, p <0.001, Figure 3e), PC2 (t = -

310   2.80, p <0.01) and average distance to nearest riparian habitat (t = -2.30, p = 0.03). Avian

311   abundance at the field edge in fall was negatively associated with PC1 (t = -23.40, p <0.001,

312   Figure 3f). Avian species richness in field interiors during the fall was not correlated with edge

313   complexity or distance to riparian habitat. Avian abundance was significantly higher at sites

314   with weedy/bare edges, compared to sites with woody vegetation (mean of 109 more birds at

315   simple sites; t = 2.33, p = 0.03), but increased in both bare/weedy and woody vegetation field

316   margin types with increasing field margin habitat complexity (negatively association with PC1; t

317   = -2.31, p = 0.03, Figure 3h).

318

319   DISCUSSION

320   Our results suggest that sunflower growers would benefit from planting or maintaining

321   woody vegetation alongside their fields since sunflower moth damage was significantly higher

322   at sites without field margin vegetation, while bird damage was not driven by field margin

323   habitat. Furthermore, within sunflower fields across all distances from the field margin,

324   sunflower moth damage was significantly higher than bird damage, and was therefore the main

325   source of yield loss for sunflower growers in our area. The pest control service benefits that

326   farmers receive from field margin vegetation therefore outweigh the potential ecological

327   disservices associated with bird damage to sunflowers. In fact, bird damage at our 30 fields was

328   similar across sites with and without field margin habitat. Our results also indicate a clear

329   benefit for biodiversity, with significantly higher species richness and avian abundance along

330   field edges that had woody habitat. Combined, these results support the assertion that

331   diversified farming systems can provide both farmers and broader society with multiple

332   additive ecosystem services (Kremen & Miles 2012).

333   Our exclosures did not reveal an effect of bird foraging on sunflower moth damage. This

334   could be the result of small sample size (n=36 exclosures in 9 fields), or these results could

335   indicate that foliage-gleaning birds and bats are not a major predator of sunflower moth. We

336   predict that the patterns of sunflower moth damage we observed were driven by either

337   increased predation pressure from invertebrates or from aerially-hunting bats and birds. If

338   adult moths are depredated in flight, prior to ovidepositing on flowers, our exclosures would

339   not have detected an effect of aerially-hunting vertebrate predators such as bats and birds.

340   Whereas if most depredation occurs to adult moths as they lay eggs, to the eggs themselves, or

341   to larvae, our exclosures would have indicated if vertebrate predators were the cause. Because

342   of their nocturnal nature, sunflower moth adults are likely to be targeted more by nocturnal

343   arthropod predators and/or bats (both of which would not be affected by the presence of

344   exclosures) than by the predominantly diurnal avian predators. There is also a possibility that

345   the presence of woody vegetation creates a physical barrier to fields or that sunflower moths

346   avoid areas near woody vegetation because of the potential for higher predation. Further

347   research is clearly needed in this system.

348   The value of insect pest control provided to US farmers by beneficial insects was

349   estimated at $4.5 billion per year in 2006 (Losey and Vaughan 2006), and the value of insect

350   pest control provided to farmers of corn globally was estimated to be worth over $1 billion per

351   year in 2015 (Maine and Boyles 2015). Studies in California have shown that the presence of

352   habitat along field margins is associated with increased diversity and abundance of beneficial

353   insects including natural enemies (Eilers and Klein 2009, Gareau et al. 2013, Morandin et al.

354   2014), and with increased bat activity (Kelly et al. 2016). For example, in almond orchards,

355   higher proportions of natural habitat surrounding orchards resulted in higher parasitoid and

356   vertebrate control of the naval orangeworm (Eilers and Klein 2009, Morandin et al. 2014).

357   Our model selection process revealed that the distance to nearest natural vegetation

358   was the strongest of our landscape-scale predictors of sunflower damage (Table S2). This

359   variable has been shown to be a significant predictor of bird use of agricultural fields in our

360   study region (Kross et al. 2016, Heath et al. 2017) since the landscape is largely dominated by

361   farm fields, with widely spaced corridors of natural habitat along riparian areas, and farmsteads

362   acting as small islands of natural habitat (Figure 1). In this landscape, hedgerows themselves are

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363   an important sources of pollination services (Sardiñas et al. 2016) and for supporting pollinator

364   metacommunity dynamics (Ponisio et al. 2019)

365   The benefits and costs of bird presence on farms are complicated (Pejchar et al. 2018).

366   Individual species can be beneficial to a crop in some seasons and detrimental in others, or may

367   benefit one crop and cause damage to another. Birds may also disrupt other natural trophic

368   cascades that benefit farmers (Grass et al. 2017). Seasonality of avian foraging guilds is

369   important, and often overlooked by either those interested in describing only pest-control

370   services or those interested in describing only damage from pest bird species. For example, red-

371   winged blackbirds (*Agelaius phoeniceus*) are a notorious pest of sweet corn crops in the North

372   American Midwest in late summer and early fall when corn kernels are ripening, but these

373   abundant birds also consume large quantities of a number of insect pests of corn in spring and

374   early summer (Dolbeer 1990; Tremblay, Mineau & Stewart 2001). In sunflowers, some species

375   considered to be major pests of sunflower crops, including blackbird species (Icteridae) and

376   European starlings (*Sturnus vulgaris*), are insectivorous during the breeding season - the time of

377   year that sunflowers are attacked by insect pests, including sunflower head moth. These

378   species later become pests when they switch to a primarily granivorous diet in the fall. Farmers

379   may therefore want to retain, or even encourage, blackbird populations on their land in spring

380   and summer, and then utilize bird deterrent techniques, alternative food sources, and bird-

381   resistant cultivars to reduce damage from birds once crops become susceptible. Importantly,

382   while our results indicate a net benefit of hedgerows for both sunflower yields and avian

383   diversity in California, sunflowers in other regions (Schäckermann et al. 2014, Ernst et al. 2019)

384   suffer from economically significant bird-damage to the same crop. Therefore, we caution that

385   land managers and scientists should consider local climate, habitat availability, agricultural

386   practices, and avian communities before translating our findings into management changes in

387   other regions.

388

389   CONCLUSIONS

390   Contrary to common assumptions about avian pests, we found that sunflower fields with

391   woody vegetation along their margins did not suffer from significantly higher bird damage

392   compared with fields that had weedy or bare edges. Instead, overall sunflower seed yield was

393   driven by insect damage, which was lower in fields with vegetated margins. Our results show

394   that planting or retaining woody vegetation along field margins can simultaneously decrease

395   insect pest damage to crops (Figure 2) and increase the biodiversity value of sunflower fields for

396   birds (Figure 3), adding to the growing body of scientific studies that demonstrate the benefits

397   of planting or retaining habitat for wildlife along field margins. These results are particularly

398   important for avian conservation in intensive agricultural landscapes, where little natural

399   habitat remains and significant gains in habitat may be made through restoration activities

400   along the ~96% of field margins in California that are currently bare. Our results demonstrate

401   one case where increasing the habitat value of non-production areas in intensive, conventional

402   farming systems may simultaneously increase yield and benefit biodiversity.

403

404   AUTHOR'S CONTRIBUTIONS

405   SMK, TRK and JMT conceived the ideas and designed methodology; SMK, BLM, RPB and field

406   assistants collected the data; CM performed the landscape analysis; SMK analyzed the data;

19

407   SMK led the writing of the manuscript. All authors contributed critically to the drafts and gave

408   final approval for publication.

409

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418

419   DATA ACCESSIBILITY

420   Data will be made available from the Columbia University Library Digital Repository.
421
422   Online Appendices:
423   Supplementary Table 1: Model selection for candidate models explaining sunflower moth

424   damage to sunflower seeds using the distance to nearest natural habitat as a measure of

425   landscape-scale habitat complexity.

426   Supplementary Table 2: Model selection for candidate models explaining sunflower moth
427   damage to sunflower seeds using, as a measure of landscape-scale habitat complexity, the
428   proportion of natural habitat within concentric distance buffers from each site.
429

430

431   LITERATURE CITED

432

433   Baldwin, R. A., T. P. Salmon, R. H. Schmidt, and R. M. Timm. 2013. Wildlife pests of California

434   agriculture: Regional variability and subsequent impacts on management. Crop

435   Protection 46:29–37.

436   Brodt, S., K. Klonsky, L. Jackson, S. B. Brush, and S. Smukler. 2009. Factors affecting

437   adoption of hedgerows and other biodiversity-enhancing features on farms in

438   California, USA. Agroforestry Systems 76:195–206.

439   CA DWR. 2008. Department of Water Resources: Yolo County Land Use GIS dataset.

440   Sacramento, CA.

441   Daily, G. C., T. Soderqvist, S. Aniyar, K. Arrow, P. Dasgupta, P. R. Ehrlich, C. Folke, A. Jansson,

442   B. O. Jansson, N. Kautsky, S. Levin, J. Lubchenco, K. G. Maler, D. Simpson, D. Starrett,

443   D. Tilman, and B. Walker. 2000. Ecology - The value of nature and the nature of

444   value. Science 289:395–396.

445   De Grazio, J. W. 1978. World bird damage problems. Proceedings of the 8th Vertebrate Pest

446   Conference.

447   Eilers, E. J., and A. M. Klein. 2009. Landscape context and management effects on an

448   important insect pest and its natural enemies in almond. Biological Control 51:388–

449   394.

450   Ernst, K., J. Elser, G. Linz, H. Kandel, J. Holderieath, S. DeGroot, S. Shwiff, and S. Shwiff. 2019.

451   The economic impacts of blackbird (*Icteridae*) damage to sunflower in the USA.

452   Pest Management Science.

453   ESRI. 2010. ArcGIS Desktop 10.1. Environmental Systems Research Institute, Redlands, CA.

454   Frayer, W. E., D. D. Peters, H. R. Pywell, and U. S. Fish and Wildlife Service. 1989. Wetlands

455   of the California Central Valley: status and trends.

456   Gareau, T. L. P., D. K. Letourneau, and C. Shennan. 2013. Relative Densities of Natural

457   Enemy and Pest Insects Within California Hedgerows. Environmental Entomology

458   42:688–702.

459   Garibaldi, L. A., I. Steffan-Dewenter, C. Kremen, J. M. Morales, R. Bommarco, S. A.

460   Cunningham, L. G. Carvalheiro, N. P. Chacoff, J. H. Dudenhöffer, S. S. Greenleaf, A.

461   Holzschuh, R. Isaacs, K. Krewenka, Y. Mandelik, M. M. Mayfield, L. A. Morandin, S. G.

462   Potts, T. H. Ricketts, H. Szentgyörgyi, B. F. Viana, C. Westphal, R. Winfree, and A. M.

463   Klein. 2011. Stability of pollination services decreases with isolation from natural

464   areas despite honey bee visits: Habitat isolation and pollination stability. Ecology

465   Letters 14:1062–1072.

466   Gebhardt, K., A. M. Anderson, K. N. Kirkpatrick, and S. A. Shwiff. 2011. A review and

467   synthesis of bird and rodent damage estimates to select California crops. Crop

468   Protection 30:1109–1116.

469   Gennet, S., J. Howard, J. Langholz, K. Andrews, M. D. Reynolds, and S. A. Morrison. 2013.

470   Farm practices for food safety: an emerging threat to floodplain and riparian

471   ecosystems. Frontiers in Ecology and the Environment 11:236–242.

472   Geographic Information Center. 2009. Vegetation – Central Valley Riparian and Sacramento

473   Valley [ds1000].

474   Gonthier, D. J., A. R. Sciligo, D. S. Karp, A. Lu, K. Garcia, G. Juarez, T. Chiba, S. Gennet, and C.

475   Kremen. 2019. Bird services and disservices to strawberry farming in Californian

476   agricultural landscapes. Journal of Applied Ecology.

477 Grass, I., K. Lehmann, C. Thies, and T. Tscharntke. 2017. Insectivorous birds disrupt

478   biological control of cereal aphids. Ecology 98:1583–1590.

479 Grass, I., J. Loos, S. Baensch, P. Batáry, F. Librán-Embid, A. Ficiciyan, F. Klaus, M. Riechers, J.

480   Rosa, J. Tiede, K. Udy, C. Westphal, A. Wurz, and T. Tscharntke. 2019. Land-sharing/-

481   sparing connectivity landscapes for ecosystem services and biodiversity

482   conservation. People and Nature.

483 Heath, S. K., C. U. Soykan, K. L. Velas, R. Kelsey, and S. M. Kross. 2017. A bustle in the

484   hedgerow: Woody field margins boost on farm avian diversity and abundance in an

485   intensive agricultural landscape. Biological Conservation 212:153–161.

486 Johnson, C. N., A. Balmford, B. W. Brook, J. C. Buettel, M. Galetti, L. Guangchun, and J. M.

487   Wilmshurst. 2017. Biodiversity losses and conservation responses in the

488   Anthropocene. Science 356:270–275.

489 Karp, D. S., R. Chaplin-Kramer, T. D. Meehan, E. A. Martin, F. DeClerck, H. Grab, C. Gratton, L.

490   Hunt, A. E. Larsen, A. Martínez-Salinas, M. E. O'Rourke, A. Rusch, K. Poveda, M.

491   Jonsson, J. A. Rosenheim, N. A. Schellhorn, T. Tscharntke, S. D. Wratten, W. Zhang, A.

492   L. Iverson, L. S. Adler, M. Albrecht, A. Alignier, G. M. Angelella, M. Zubair Anjum, J.

493   Avelino, P. Batáry, J. M. Baveco, F. J. J. A. Bianchi, K. Birkhofer, E. W. Bohnenblust, R.

494   Bommarco, M. J. Brewer, B. Caballero-López, Y. Carrière, L. G. Carvalheiro, L.

495   Cayuela, M. Centrella, A. Ćetković, D. C. Henri, A. Chabert, A. C. Costamagna, A. De la

496   Mora, J. de Kraker, N. Desneux, E. Diehl, T. Diekötter, C. F. Dormann, J. O. Eckberg, M.

497   H. Entling, D. Fiedler, P. Franck, F. J. Frank van Veen, T. Frank, V. Gagic, M. P. D.

498   Garratt, A. Getachew, D. J. Gonthier, P. B. Goodell, I. Graziosi, R. L. Groves, G. M. Gurr,

499   Z. Hajian-Forooshani, G. E. Heimpel, J. D. Herrmann, A. S. Huseth, D. J. Inclán, A. J.

500   Ingrao, P. Iv, K. Jacot, G. A. Johnson, L. Jones, M. Kaiser, J. M. Kaser, T. Keasar, T. N.

501   Kim, M. Kishinevsky, D. A. Landis, B. Lavandero, C. Lavigne, A. Le Ralec, D. Lemessa,

502   D. K. Letourneau, H. Liere, Y. Lu, Y. Lubin, T. Luttermoser, B. Maas, K. Mace, F.

503   Madeira, V. Mader, A. M. Cortesero, L. Marini, E. Martinez, H. M. Martinson, P.

504   Menozzi, M. G. E. Mitchell, T. Miyashita, G. A. R. Molina, M. A. Molina-Montenegro, M.

505   E. O'Neal, I. Opatovsky, S. Ortiz-Martinez, M. Nash, Ö. Östman, A. Ouin, D. Pak, D.

506   Paredes, S. Parsa, H. Parry, R. Perez-Alvarez, D. J. Perović, J. A. Peterson, S. Petit, S. M.

507   Philpott, M. Plantegenest, M. Plećaš, T. Pluess, X. Pons, S. G. Potts, R. F. Pywell, D. W.

508   Ragsdale, T. A. Rand, L. Raymond, B. Ricci, C. Sargent, J.-P. Sarthou, J. Saulais, J.

509   Schäckermann, N. P. Schmidt, G. Schneider, C. Schüepp, F. S. Sivakoff, H. G. Smith, K.

510   Stack Whitney, S. Stutz, Z. Szendrei, M. B. Takada, H. Taki, G. Tamburini, L. J.

511   Thomson, Y. Tricault, N. Tsafack, M. Tschumi, M. Valantin-Morison, M. Van Trinh, W.

512   van der Werf, K. T. Vierling, B. P. Werling, J. B. Wickens, V. J. Wickens, B. A.

513   Woodcock, K. Wyckhuys, H. Xiao, M. Yasuda, A. Yoshioka, and Y. Zou. 2018. Crop

514   pests and predators exhibit inconsistent responses to surrounding landscape

515   composition. Proceedings of the National Academy of Sciences 115:E7863–E7870.

516 Katibah, E. E. 1984. A brief history of riparian forests in the Central Valley of California.

517   Page *in* R. E. Warner and K. M. Hendrix, editors. California riparian systems.

518   University of California Press, Berkeley, CA.

519 Kleijn, D., R. Bommarco, T. P. M. Fijen, L. A. Garibaldi, S. G. Potts, and W. H. van der Putten.

520   2019. Ecological Intensification: Bridging the Gap between Science and Practice.

521   Trends in Ecology & Evolution 34:154–166.

522   Kremen, C., and A. M. Merenlender. 2018. Landscapes that work for biodiversity and

523   people. Science 362:eaau6020.

524   Kross, S. M., K. P. Ingram, R. F. Long, and M. T. Niles. 2018. Farmer Perceptions and

525   Behaviors Related to Wildlife and On-Farm Conservation Actions. Conservation

526   Letters 11:e12364.

527   Kross, S. M., T. R. Kelsey, C. J. McColl, and J. M. Townsend. 2016. Field-scale habitat

528   complexity enhances avian conservation and avian-mediated pest-control services

529   in an intensive agricultural crop. Agriculture, Ecosystems & Environment 225:140–

530   149.

531   Kross, S. M., J. M. Tylianakis, and X. J. Nelson. 2012. Effects of Introducing Threatened

532   Falcons into Vineyards on Abundance of Passeriformes and Bird Damage to Grapes.

533   Conservation Biology 26:142–149.

534   Long, R. F., S. E. Light, M. Galla, and J. Murdock. 2018. Sample Costs to Produce Sunflowers

535   for Hybrid Seed in the Sacramento Valley, 2018:19.

536   Long, R., T. Gulya, S. Light, K. Bali, K. Mathesius, and R. D. Meyer. 2019. Sunflower Hybrid

537   Seed Production in California. University of California, Agriculture and Natural

538   Resources.

539   Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by

540   insects. Bioscience 56:311–323.

541   Maas, B., S. Heath, I. Grass, C. Cassano, A. Classen, D. Faria, P. Gras, K. Williams-Guillén, M.

542   Johnson, D. S. Karp, V. Linden, A. Martínez-Salinas, J. M. Schmack, and S. Kross. 2019.

543   Experimental field exclosure of birds and bats in agricultural systems —

544   Methodological insights, potential improvements, and cost-benefit trade-offs. Basic

545   and Applied Ecology 35:1–12.

546 Maine, J. J., and J. G. Boyles. 2015. Bats initiate vital agroecological interactions in corn.

547   Proceedings of the National Academy of Sciences 112:12438–12443.

548 M'Gonigle, L. K., L. C. Ponisio, K. Cutler, and C. Kremen. 2015. Habitat restoration promotes

549   pollinator persistence and colonization in intensively managed agriculture.

550   Ecological Applications 25:1557–1565.

551 Morandin, L. A., R. F. Long, and C. Kremen. 2014. Hedgerows enhance beneficial insects on

552   adjacent tomato fields in an intensive agricultural landscape. Agriculture,

553   Ecosystems & Environment 189:164–170.

554 Peisley, R. K., M. E. Saunders, and G. W. Luck. 2016. Cost-benefit trade-offs of bird activity in

555   apple orchards. PeerJ 4:e2179.

556 Pejchar, L., Y. Clough, J. Ekroos, K. A. Nicholas, O. Olsson, D. Ram, M. Tschumi, and H. G.

557   Smith. 2018. Net Effects of Birds in Agroecosystems. BioScience.

558 Ponisio, L. C., P. de Valpine, L. K. M'Gonigle, and C. Kremen. 2019. Proximity of restored

559   hedgerows interacts with local floral diversity and species' traits to shape long-term

560   pollinator metacommunity dynamics. Ecology Letters 22:1048–1060.

561 Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton,

562   A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American

563   avifauna. Science 366:120–124.

564 Sardiñas, H. S., K. Tom, L. C. Ponisio, A. Rominger, and C. Kremen. 2016. Sunflower (

565   *Helianthus annuus*) pollination in California's Central Valley is limited by native bee

566   nest site location. Ecological Applications 26:438–447.

567   Schäckermann, J., N. Weiss, H. von Wehrden, and A.-M. Klein. 2014. High trees increase

568   sunflower seed predation by birds in an agricultural landscape of Israel. Frontiers in

569   Ecology and Evolution 2.

570   Seavy, N. E., J. H. Viers, and J. K. Wood. 2009. Riparian bird response to vegetation structure:

571   a multiscale analysis using LiDAR measurements of canopy height. Ecological

572   Applications 19:1848–1857.

573   Settele, J., and W. H. Settle. 2018. Conservation biological control: Improving the science

574   base. Proceedings of the National Academy of Sciences 115:8241–8243.

575   Weier, S. M., I. Grass, V. M. G. Linden, T. Tscharntke, and P. J. Taylor. 2018. Natural

576   vegetation and bug abundance promote insectivorous bat activity in macadamia

577   orchards, South Africa. Biological Conservation 226:16–23.

578

579   FIGURE LEGENDS

580   Figure 1: Map showing sunflower field locations at varying distances from natural habitat (blue)

581   across an intensive agriculture landscape. Sunflower fields had either bare/weedy field margin

582   habitat (red points), or had woody vegetation field margin habitat (white points).
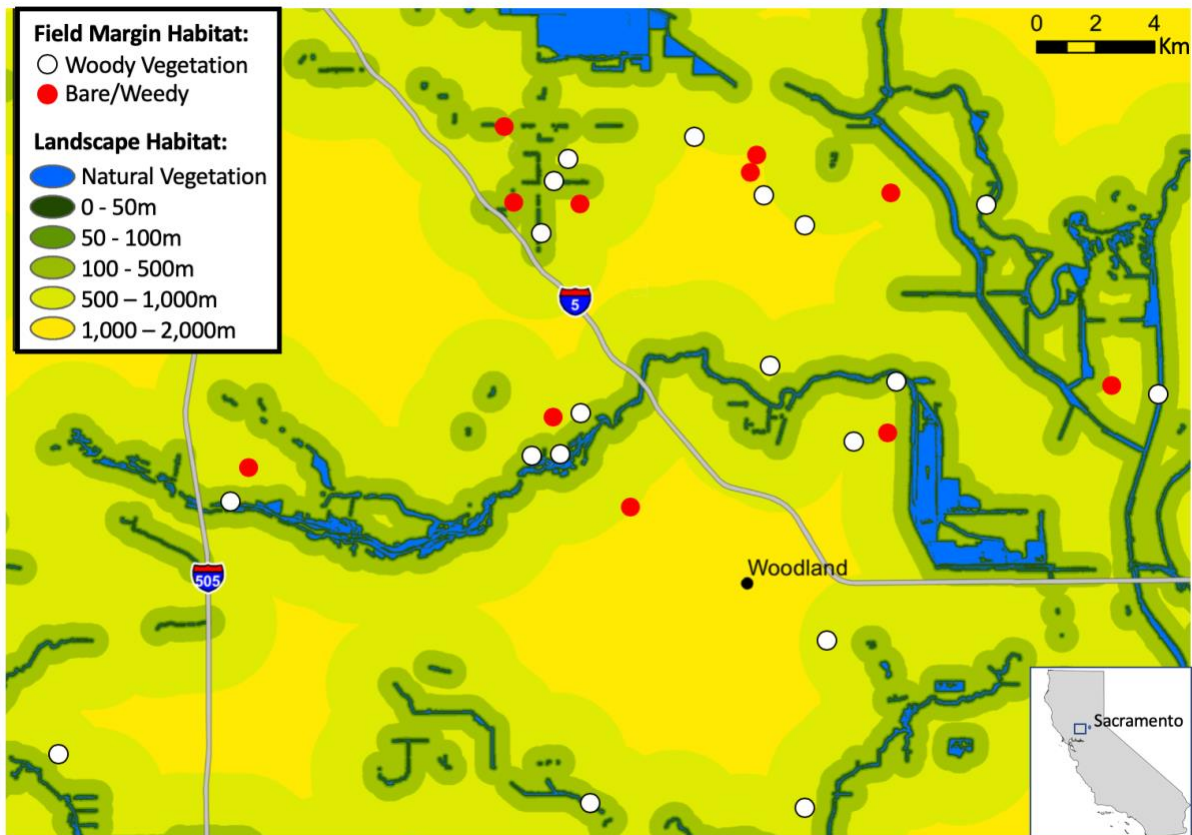
583

584   Figure 2: Model estimates of percent of sunflower seeds damaged as a function of the presence

585   (darker colored lines) or absence (lighter colored lines) of woody vegetation along field edges

586   and, a) an orthogonal axis for field margin habitat type, b) the distance to the nearest natural

587   habitats; and c) percent seeds damaged by birds as a function of the distance of sampling

588   points within each field from the nearest field margin.

589

590   Figure 3: Avian species richness and abundance along sunflower field edges and within

591   sunflower field interiors in Summer (top row) and Fall (bottom row) as a function of increasing

592   field margin habitat height, width, and number of canopy layers (-PC1). Statistical significance

593   of PC1 variable as a predictor in a linear regression for each response variable is shown bottom

594   right in each panel.

595   FIGURE 1

596

597   Figure 1: Map showing sunflower field locations at varying distances from natural habitat (blue)

598   across an intensive agriculture landscape around the city of Woodland in the Sacramento Valley

599   of California. Sunflower fields had either bare/weedy field margin habitat (red points), or had

600   woody vegetation field margin habitat (white points).

601   FIGURE 2
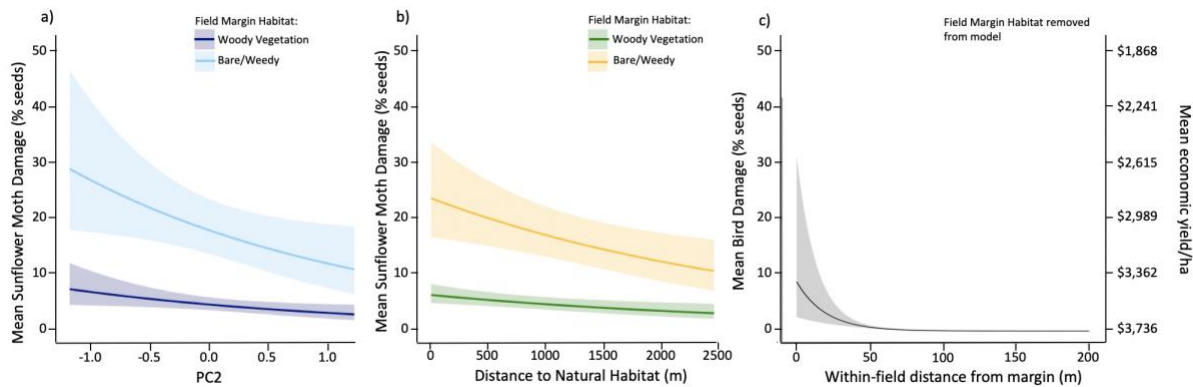
602

603   Figure 2: Model estimates of percent of sunflower seeds damaged as a function of the presence

604   (darker colored lines) or absence (lighter colored lines) of woody vegetation along field edges

605   and, a) an orthogonal axis for field margin habitat type, b) the distance to the nearest natural

606   habitats; and c) percent seeds damaged by birds as a function of the distance of sampling

607   points within each field from the nearest field margin. The mean economic yield per hectare is

608   shown as a secondary y-axis and applies to all three panels.

609　　FIGURE 3
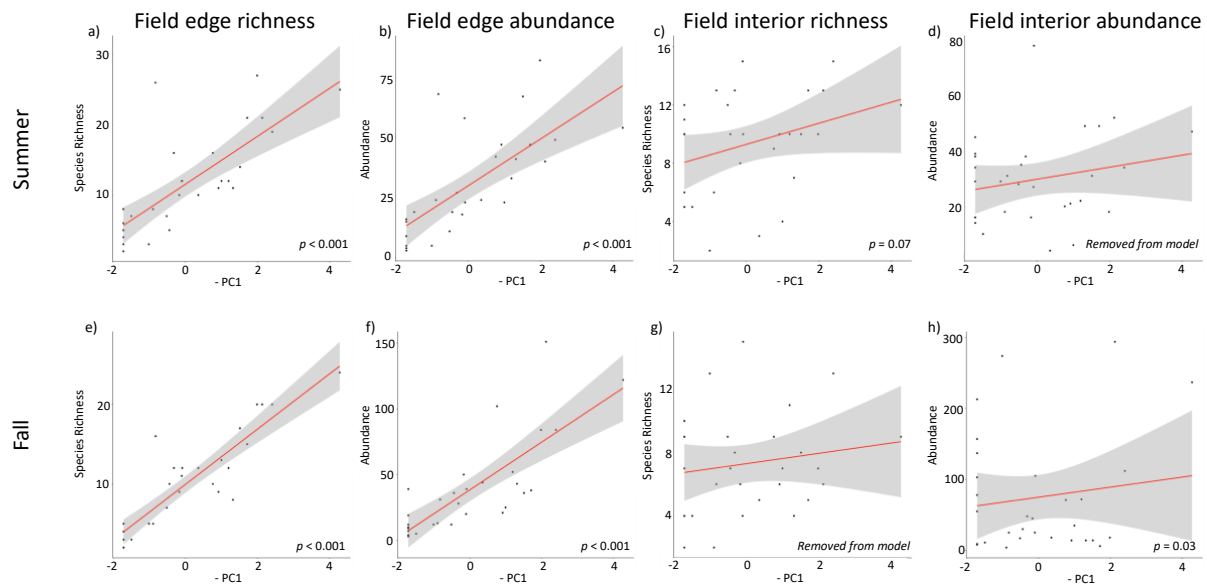
610

611　　Figure 3: Avian species richness and abundance along sunflower field edges and within

612　　sunflower field interiors in Summer (top row) and Fall (bottom row) as a function of increasing

613　　field margin habitat height, width, and number of canopy layers (- PC1). Statistical significance

614　　of PC1 variable as a predictor in a linear regression for each response variable is shown bottom

615　　right in each panel.

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623 **Supplementary Material**

624 Supplementary Table 1: Model selection for candidate models explaining sunflower moth

625 damage to sunflower seeds using the distance to nearest natural habitat as a measure of

626 landscape-scale habitat complexity. A principal components analysis was used to consolidate

627 local habitat complexity variables into two orthogonal axes (PC1 and PC2). Field margins for

628 each site were categorically defined based on the presence or absence of woody vegetation

629 along the field margin. The 'Distance into Field' measure is the number of meters within the

630 field for each sampling location from the nearest field edge.

631

632

Name	Residual df	Residual Deviance	Δ AIC	w_i
Field Margin + Distance to Natural + PC2	190	218	0	0.48
Field Margin + Distance to Natural + PC1 + PC2	189	218	1.7	0.2
Field Margin + Distance to Natural + PC1	190	219	3.1	0.1
Field Margin + Distance to Natural	191	219	3.2	0.09
Field Margin + Distance to Natural + Distance into field + PC1 + PC2	188	218	3.3	0.09
Field Margin * Distance to Natural + Distance into field + PC1 + PC2	187	218	5.3	0.03
Null	193	222	42.4	0

633

634 Supplementary Table 2: Model selection for candidate models explaining sunflower moth

635 damage to sunflower seeds using, as a measure of landscape-scale habitat complexity, the

636 proportion of natural habitat within concentric distance buffers from each site. Only the

637 landscape-scale habitat variable is shown changed in this table based on the most parsimonious

638 model above. A principal components analysis was used to consolidate local habitat complexity

639   variables into two orthogonal axes (PC1 and PC2). Field margins for each site were categorically

640   defined based on the presence or absence of woody vegetation along the field margin.

Model Terms	Residual df	Residual Deviance	Δ AIC	w_i
Field Margin + Distance to Natural + PC2	190	218	0	0.59
Field Margin + Prop. Natural 800m + PC2	190	219	1.9	0.23
Field Margin + Prop. Natural 200m + PC2	190	219	4.8	0.05
Field Margin + Prop. Natural 100m + PC2	190	219	5	0.05
Field Margin + Prop. Natural 50m + PC2	190	219	5.4	0.04
Field Margin + Prop. Natural 400m + PC2	190	219	5.5	0.04
Null	193	222	42.4	0

641