1   **Title:** Landscape change and alien invasions drive shifts in native lady beetle communities over a century

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3   Kayla I Perry [1,2], Christie A Bahlai [2], Timothy J Assal [3], Christopher B Riley [1,4], Katherine J Turo [1,5], Leo

4   Taylor [1,6], James Radl [1], Yvan A Delgado de la flor [1,7], Frances S Sivakoff [8], Mary M Gardiner [1]

5

6   [1] Department of Entomology, The Ohio State University, 2021 Coffey Road, Columbus, Ohio 43210,

7   USA

8   [2] Department of Biological Sciences, Kent State University, 800 E. Summit Street, Kent, Ohio 44242

9   USA

10   [3] Department of Geography, Kent State University, 325 S Lincoln Street, Kent, Ohio 44242, USA

11   [4] Current Address: Bartlett Tree Research Laboratories, 13768 Hamilton Road, Charlotte, North Carolina

12   28278, USA

13   [5] Current Address: Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14

14   College Farm Road, New Brunswick, New Jersey 08901, USA

15   [6] Current Address: The Office of Diversity, Equity, and Inclusion, The Ohio State University, 2120 Fyffe

16   Road, Columbus, Ohio 43210, USA

17   [7] Current Address: Air Program, Environmental Monitoring Branch, California Department of Pesticide

18   Regulation, 1001 I Street, Sacramento, California 95814, USA

19   [8] Department of Evolution, Ecology and Organismal Biology, The Ohio State University, 1465 Mount

20   Vernon Avenue, Marion, Ohio 43302, USA

21

22   *Corresponding Author: Kayla I Perry, kperry34@kent.edu

23

24 **Abstract**

25 **Aim:** Understanding drivers of insect population declines is essential for the development of successful

26 conservation plans, but data limitations restrict assessment across spatial and temporal scales. Museum

27 records represent a unique source of historical data that can be leveraged to investigate temporal trends in

28 insect communities. Native lady beetle decline has been attributed to competition with established alien

29 species and landscape change, but the relative importance of these drivers is difficult to measure with

30 short-term field-based studies. Here we assessed distribution patterns for native lady beetle species over

31 12 decades using museum records and evaluated the relative importance of alien species and landscape

32 change as long-term drivers contributing to changes in lady beetle communities.

33 **Location:** Ohio, USA.

34 **Methods:** We compiled occurrence records for 28 lady beetle species collected in Ohio, USA from 1900-

35 2018. Incidence-based measures of taxonomic beta-diversity were used to evaluate changes in lady beetle

36 community composition over time. To evaluate the relative influence of temporal, spatial, landscape, and

37 community drivers on the captures of native lady beetles, we constructed negative binomial generalized

38 additive models.

39 **Results:** We report evidence of declines in captures for several native species, including *Adalia*

40 *bipunctata*, *Coccinella novemnotata*, *Hippodamia convergens*, and *Coleomegilla maculata*.

41 Importantly, the timing, severity, and drivers of these documented declines were species-specific.

42 Changes in lady beetle species composition began in the 1980s, when processes of species loss/gain and

43 turnover shifted communities towards dominance by a few alien lady beetle species. Land cover change

44 also was associated with declines in captures, particularly for *C. novemnotata* which declined prior to the

45 arrival of alien species in the state.

46 **Main conclusions:** Our study documented shifts in Ohio's lady beetle communities beginning in the

47 1980s as alien species supplanted natives. Drivers of declines in captures of native lady beetle species

48 were highly species-specific, emphasizing that mechanisms driving population losses cannot be

49   generalized even among closely related species. These findings also indicate the importance of museum

50   holdings and the analysis of species-level data when studying temporal trends in insect populations.

51

52   **Keywords:** Coccinellidae, Invasive, exotic, non-native, ladybird, land use, land cover, species decline

53

54   **Introduction**

55   Global biodiversity loss is a growing threat to the ecosystem function and services for which

56   humans depend (Dirzo & Raven, 2003; Mace *et al.*, 2012; Ceballos *et al.*, 2015; Cardoso *et al.*, 2020).

57   Given the importance of insects for ecosystem services such as pollination, pest suppression, and nutrient

58   cycling (Losey & Vaughan, 2006; Yang & Gratton, 2014), understanding the causes of documented

59   spatiotemporal changes in insect populations is a critical research focus. Numerous recent studies have

60   pointed to declines in the abundance, richness, and biomass of insects (Hallmann *et al.*, 2017; Seibold *et

61   al.*, 2019), including bees (Grixti *et al.*, 2009; Potts *et al.*, 2010), beetles (Brooks *et al.*, 2012; Homburg *et

62   al.*, 2019), leafhoppers and planthoppers (Schuch *et al.*, 2012), and butterflies and moths (Maes & Van

63   Dyck, 2001; Conrad *et al.*, 2006; Habel *et al.*, 2016; Warren *et al.*, 2021). Although population declines

64   have been frequently reported, relatively stable or increasing populations of insects also have been

65   documented in some settings (Shortall *et al.*, 2009; Fox *et al.*, 2014; Crossley *et al.*, 2020; Schowalter *et

66   al.*, 2021). For example, observations of moths in Great Britain identified highly species-specific temporal

67   patterns over a 40 year period, as 260 species declined in frequency, 160 species increased, and 253

68   species remained unchanged (Fox *et al.*, 2014). Complexity in the responses of insects has generated

69   scientific debate about whether observed declines are generalizable across insect taxa and guilds and at

70   larger spatial scales (Simmons *et al.*, 2019; Thomas *et al.*, 2019; Didham *et al.*, 2020; Saunders *et al.*,

71   2020). Although many challenges to studying insect population trends exist (Didham *et al.*, 2020;

72   Montgomery *et al.*, 2020), understanding the magnitude and drivers of declines in insect species is critical

73   for biodiversity conservation management and the maintenance of insect-based ecosystem services and

74   function.

75   One primary limitation to understanding insect populations over time stem from data deficiencies

76   such as low taxonomic resolution, geographic restrictions, and short time series (Sánchez-Bayo &

77   Wyckhuys, 2019; Thomas *et al.*, 2019; Didham *et al.*, 2020). However, specimen records from natural

78   history museums and other institutions can be leveraged to investigate trends in insect populations over

79   greater spatial and temporal scales (Lister, 2011; Kharouba *et al.*, 2019). Although specimen record-based

80   data have their own set of biases and challenges (Boakes *et al.*, 2010; Meineke & Daru, 2021), biological

81   collections represent a unique source of historical data that documents the occurrence of species in time

82   and space. For example, museum records revealed that 11 bumble bee species native to eastern North

83   America and Canada have experienced substantial (>50%) declines in captures over the past century,

84   while eight species have remained stable or increased in collections (Colla *et al.*, 2012). Importantly,

85   specimen records can be used as baseline measures for investigating the impacts of anthropogenic drivers

86   such as the establishment of exotic species, environmental degradation, and climate change on patterns of

87   biodiversity (Suarez & Tsutsui, 2004; Winker, 2004; Johnson *et al.*, 2011; Kharouba *et al.*, 2019). For

88   instance, moth assemblages collected on Mount Kinabalu in Borneo in 2007 were compared to historical

89   records collected from the same sites in 1965, revealing upward shifts in the altitudinal distribution of

90   species in response to changes in temperature (Chen *et al.*, 2009). Although the use of collections data is

91   limited in its ability to track the absolute abundance of a species due to sampling effort variation (Ries *et*

92   *al.*, 2019), historical specimen data facilitate understanding of species' responses to anthropogenic change

93   by helping to distinguish signals of decline from natural population variability, especially when

94   considering relative observations in groups of similar taxa. Therefore, specimen records are invaluable

95   resources that can be harnessed to address biodiversity conservation initiatives, including documenting

96   changes in communities of beneficial insects.

97   Lady beetles (Coleoptera: Coccinellidae) are a family of charismatic insect species that are

98   commonly collected and contribute broadly to pest suppression by consuming aphids, scales, psyllids,

99   mites, fungi, and other pests (Evans, 2009; Hodek & Honěk, 2009; Weber & Lundgren, 2009; Hodek *et*

100   *al.*, 2012). Because lady beetles are capable of rapidly colonizing habitats to exploit ephemeral prey

101 resources, these species have been used widely in biological control programs in agricultural systems

102 (Caltagirone & Doutt, 1989; Obrycki & Kring, 1998; Koch, 2003; Rondoni *et al.*, 2021). A number of

103 authors have noted declines in native lady beetle populations across the United States (Alyokhin &

104 Sewell, 2004; Harmon *et al.*, 2007) and Europe (Roy *et al.*, 2012; Brown & Roy, 2018), which may

105 contribute to an overall loss of resilience of the biological control services offered by this community

106 (Bahlai *et al.*, 2021). For example, the historically widespread native aphidophagous species *Hippodamia*

107 *convergens* Guerin has declined in the US states of Michigan (Gardiner *et al.*, 2009), Ohio (Gardiner *et*

108 *al.*, 2012), Wisconsin (Steffens and Lumen 2015), and Minnesota (Steffens and Lumen 2015), as well as

109 the Canadian Province of Manitoba (Turnock et al. 2003). Likewise, the nine-spotted lady beetle

110 *Coccinella novemnotata* Herbst was once common in eastern North America but had not been collected

111 for over a decade until a community scientist "rediscovered" it (Losey *et al.,* 2007). Anthropogenic

112 activities such as the establishment of alien species and landscape change have been hypothesized as

113 potential drivers of native lady beetle decline (Alyokhin & Sewell, 2004; Harmon *et al.*, 2007; Gardiner *et*

114 *al.*, 2012; Honek *et al.*, 2014; Bahlai *et al.*, 2015; Roy *et al.*, 2016).

115 Several studies have observed that the decline of native aphidophagous species coincided with the

116 establishment and spread of alien lady beetle species, particularly the Asian species *Harmonia axyridis*

117 (Pallas) and the European species *Coccinella septempunctata* (Linnaeus) (Turnock *et al.*, 2003; Roy *et al.*,

118 2012; Steffens & Lumen, 2015; Roy *et al.*, 2016). Following their establishment, alien lady beetles

119 became the dominant species within many native communities (Alyokhin & Sewell, 2004; Harmon *et al.*,

120 2007; Bahlai *et al.*, 2015). Because of their dominance, direct and indirect competitive interactions with

121 alien species are hypothesized as a driver of declines in native lady beetles (Pell *et al.*, 2008; Li *et al.*,

122 2021). For example, intraguild predation has been documented among native and alien lady beetles in the

123 field (Gagnon *et al.*, 2011; Thomas *et al.*, 2013; Brown *et al.*, 2015; Ortiz-Martínez *et al.*, 2020), wherein

124 native eggs and larvae were more likely to be the intraguild prey for alien species (Snyder *et al.*, 2004;

125 Katsanis *et al.*, 2013). Apparent competition also has been observed in the field, as native species

126 experienced greater egg predation from a guild of shared predators than alien lady beetle species (Smith

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127 & Gardiner, 2013). These asymmetric interactions may largely benefit alien species at the expense of

128 native lady beetle populations, but the extent and context of these effects on native species are difficult to

129 quantify. The short time scales of many studies and the lack of data from lady beetle communities before

130 the establishment of alien species limits understanding of the impacts of these invaders.

131   Landscape change that results in the loss, fragmentation, and degradation of natural habitat also

132 has been hypothesized as a key driver contributing to population declines of insect species (Potts, *et al.*

133 2010; Wagner, 2020; Wagner *et al.*, 2021), including lady beetles (Honek *et al.*, 2017). Land cover

134 change resulting from increased urbanization and agricultural intensification can influence the structure

135 and composition of lady beetle communities (Gardiner *et al.*, 2009; Woltz & Landis, 2014; Grez *et al.*,

136 2019; Parker *et al.*, 2020). For example, native and alien species were less abundant in isolated urban

137 greenspaces that were embedded in landscapes dominated by impervious surfaces and built infrastructure

138 (Parker *et al.*, 2020). In agricultural landscapes, native and alien lady beetles were more abundant in fields

139 surrounded by higher crop diversity and more semi-natural habitat types such as grasslands and forests

140 (Woltz & Landis, 2014). Loss and fragmentation of natural habitat in landscapes such as those dominated

141 by urban and agricultural land cover may differentially affect species depending on their life history traits

142 such as phenology, dispersal ability, overwintering biology, and food requirements (Zaviezo *et al.*, 2006).

143 However, the impacts of landscape change on native lady beetle populations may occur gradually over

144 time, making species responses difficult to detect over short time scales. For example, gradual directional

145 change in the species composition of native lady beetle communities was documented over a 118-year

146 period in Missouri, USA using museum specimen records (Diepenbrock *et al.*, 2016). Because there was

147 no evidence that the establishment of alien lady beetle species affected the rate of change, Diepenbrock et

148 al. (2016) hypothesized that these long-term community changes may be related to altered land use

149 patterns. The substantial year to year variation in the abundance of lady beetle species (Elliott *et al.*, 1996;

150 Honek *et al.*, 2014) requires longer time series data to detect changes in populations caused by landscape

151 change and to distinguish these effects from other anthropogenic stressors (Bahlai & Zipkin, 2020; Bahlai

152 *et al.*, 2021).

153   While several hypotheses have been proposed, the causes of declines in native lady beetle

154   populations remain under debate. Importantly, these hypotheses are not mutually exclusive, and it is

155   likely that causes of declines in native species are multi-faceted wherein multiple mechanisms are

156   responsible for the observed patterns in lady beetle populations. Although causes of declines in native

157   species are often studied independently, these drivers may interact to influence native populations

158   (Didham *et al.*, 2007). For example, habitat modification that transitions natural habitat to more highly

159   disturbed urban and agricultural habitats may differentially benefit alien species over native lady beetles

160   (Grez *et al.*, 2013), with implications for direct and indirect competitive interactions among native and

161   alien species. In contrast, landscapes with less disturbed perennial grasslands can serve as an important

162   refuge primarily for native lady beetle species, providing prey and habitat requirements necessary for

163   survival and reproduction (Evans, 2004; Diepenbrock & Finke, 2013). Understanding the magnitude and

164   drivers of declines in native lady beetle populations will require comprehensive time series data

165   documenting community responses that can then be used to assess the contribution of the establishment of

166   alien species and landscape change simultaneously.

167   To understand the relative importance of the establishment of alien species and landscape change

168   as drivers of native species decline, we compiled historical occurrence records of lady beetles collected in

169   Ohio, USA from museums and other institutions across the United States. Our goals were to assess long-

170   term patterns in native lady beetle species occurrence and communities within the region, and to evaluate

171   the relative importance of the establishment and spread of alien lady beetle species and landscape change

172   as drivers contributing to native species decline in this community.

173

174   **Methods**

175   *Lady beetle specimens and data requests*

176   To investigate long-term changes in native lady beetle communities within Ohio, USA (Fig. 1),

177   we used historic occurrence records for native and alien species within the tribe Coccinellini and four

178   additional non-Coccinellini species. Targeted Coccinellini genera were *Adalia, Anatis, Anisosticta,*

179   *Aphidecta, Calvia, Ceratomegilla, Coccinella, Coelophora, Coleomegilla, Cycloneda, Harmonia,*

180   *Hippodamia, Macronaemia, Mulsantina, Myzia, Naemia, Neoharmonia, Olla,* and *Propylea*, and non-

181   Coccinellini species were *Brachiacantha ursina* (Fabricius), *Chilocorus stigma* (Say), *Hyperaspis*

182   *undulata* (Say), and *Psyllobora vigintimaculata* (Say). We contacted 59 institutions based within the

183   United States, the majority of which are hosted by the Entomological Collections Network (ENC, 2020).

184   Ohio lady beetle records were compiled from 25 institutions with assistance of their curators (see

185   Appendix 1: Table S1.1 in Supporting Information).

186   Specimen loans were requested from museums and institutions that had unidentified lady beetle

187   records from Ohio. Any unidentified lady beetle species that were unaccounted for within the collections

188   of these institutions were not included within our dataset. Lady beetle species identifications were

189   determined using Gordon (1985). All lady beetle species were characterized by their status (native or

190   alien to North America) and their primary diet (aphidophagous, coccidophagous, or fungivorous) which

191   was based on most frequently reported prey (aphids, scales, or fungi) (Angalet *et al.*, 1979; Gordon, 1985;

192   Dixon & Dixon, 2000; Michaud, 2001; Staines, 2008; Hodek *et al.*, 2012; Majerus, 2016).

193

194   *Land use and land cover change analysis*

195   To assess the influence of landscape change on lady beetle communities, we analyzed historical

196   land use and land cover (LULC) data from four points in time (1938, 1970, 1992, 2016). Annual

197   historical LULC data were obtained from the US Geological Survey (Sohl *et al.*, 2018) for the years 1938,

198   1970, and 1992. These historical LULC backcasts were modeled using numerous historical data sets and

199   created explicitly to extend the National Land Cover Database (NLCD) to earlier time periods, prior to

200   the availability of remote-sensing data (Sohl *et al.*, 2016). The NLCD and historical backcast data were

201   crosswalked into four primary land use classes: agriculture, developed, forest, and non-target (i.e., all

202   other land cover classes found in Ohio) (see Appendix 2: Table S2.1, Table S2.2 in Supporting

203   Information). The contemporary landscape of Ohio was assessed with the 2016 NLCD (Dewitz, 2019;

204   Wickham *et al.*, 2021). To assess change over time, we calculated the total area of each cover class, along

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205   with the percentage of area occupied by each class, for each county at each of the four time periods.

206   Although the LULC data have different spatial resolutions (NLCD = 30 m; historical backcasts = 250 m)

207   they were not resampled, as the derived metrics (e.g. total area of cover class, percentage of county area)

208   are relative, and therefore comparable across time. Analyses were completed in R (R Core Team, 2020)

209   using the 'raster' and 'sf' R packages (Pebesma, 2018; Hijmans, 2020).

210   There was an increase in forest cover from 1938 to 1970, and it has held steady since the early

211   1990s (see Appendix 2: Fig. S2.6). Most of the increase occurred in the Appalachian Plateau and Lake

212   Erie Glaciated Plateau regions in the eastern and southern portions of the state (Fig. 2). There was a

213   steady increase in developed land around existing population centers, with a larger increase in suburban

214   areas since the early 1990s. The increase in forest and developed lands came at the expense of agricultural

215   lands, yet this cover class remains the dominant land cover in many counties of the state (Fig. 2; see

216   Appendix 2: Fig. S2.6). During each time period, there was high variability in the amount of agricultural

217   and forested land across Ohio counties (see Appendix 2: Fig. S2.6).

218   Land cover data were compiled at the county and decade resolution to align with the spatial and

219   temporal resolution available for the museum specimen data. For each county, we used an assumed linear

220   progression between available timepoints to estimate the percentage land cover of a given class in each

221   decade. The 1930 land cover data were extrapolated using the same procedure with available data from

222   1938-1970. Because lady beetle data were generally recorded at the county level, we computed the

223   geographic centroids of each Ohio county based on present-day county boundaries as defined by the Ohio

224   Department of Transportation (http://ogrip-eohio.opendata.arcgis.com/datasets/odot-county-boundaries).

225

226   *Statistical analysis*

227   Lady beetle museum records were included in the analyses if they were collected within Ohio,

228   and we could obtain county-level location data and the year of collection. All analyses were conducted in

229   R (R Core Team, 2020).

230   Changes in total lady beetle and aphidophagous lady beetle community composition over time

231   were assessed using incidence-based measures of taxonomic beta-diversity. Due to low county-level

232   counts, county records of lady beetle species were pooled by Ohio geographic region (Fig. 1; Lake Erie

233   Glaciated Plateau (LEGP) in the northeast, Appalachian Plateau (AP) in the southeast, Indiana-Ohio Till

234   Plain (IOTP) in the southwest, and Western Lake Erie Basin (WLEB) in the northwest) and across ten-

235   year intervals such that patterns of community composition were assessed across 11 decades from the

236   1900s through the 2010s. First, descriptive patterns of total and aphidophagous lady beetle taxonomic

237   beta-diversity were evaluated within geographic regions among decades by calculating total Sorenson

238   dissimilarity (β_{SOR}) using the *beta.temp* function in the R package 'betapart' (Baselga & Orme, 2012).

239   Total Sørensen dissimilarity was decomposed into a turnover component (β_{SIM}; reflects species

240   replacement) and a nestedness component (β_{SNE}; reflects species loss or gain) (Baselga, 2010). Next,

241   pairwise dissimilarity matrices for Sørensen dissimilarity (β_{sor}) and the respective components of species

242   turnover (β_{sim}) and nestedness (β_{sne}) were calculated using the *beta.pair* function in the R package

243   'betapart' (Baselga & Orme, 2012). Then, permutational multivariate analysis of variance

244   (PERMANOVA) and analysis of multivariate homogeneity of group dispersions (BETADISPER) were

245   used to compare β_{sor}, β_{sim}, and β_{sne} pairwise dissimilarity matrices for total lady beetles and aphidophagous

246   lady beetles among decades. PERMANOVA tests whether the centroid of communities differs among

247   groups in multivariate space, while BETADISPER tests whether groups differ in the amount of dispersion

248   from its spatial median among communities within a group. Differences in total and aphidophagous lady

249   beetle community composition among decades were visualized using non-metric multidimensional

250   scaling (NMDS). PERMANOVA, BETADISPER, and NMDS analyses were conducted using the 'vegan'

251   package (Oksanen *et al.*, 2011).

252   To determine the relative influence of temporal, landscape, spatial, and community drivers on the

253   captures of five key species (*A. bipunctata*, *C. novemnotata*, *C. maculata*, *H. convergens*, the four most

254   abundant native aphidophagous species, and *C. stigma*, the most abundant coccidophagous species), we

255   constructed negative binomial generalized additive models (GAMs) to describe spatial and temporal

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256   patterns for each species using the 'mgcv' package (Wood, 2017), and then used an adaptive model

257   selection procedure for each species in combination with available contextual data to determine the

258   relative importance of the drivers. Response data took the form of total captures of each species in a given

259   county, in a given decade. Because the absolute number of records was very sparse earlier in our study

260   period, we restricted these analyses to specimens captured in or after 1930 for these analyses. For *A.*

261   *bipunctata* and *C. novemnotata*, which were extremely rare or absent from collections in later decades,

262   data were culled at 1990 to restrict these analyses of drivers to times when these species were present. We

263   computed several community variables for each decade-county combination; in addition to absolute

264   captures of each coccinellid species, including the abundance of two dominant invaders, *C.*

265   *septempunctata* and *H. axyridis*, the total lady beetles captured, total alien species captured, and the

266   proportion of the community captures belonging to alien species. All GAMs constructed included an

267   offset variable of the structure $\log(1 + \text{total lady beetles captured})$ to account for variability in sampling

268   effort (with the exception of the model describing sampling effort over time).

269   First, to describe the relative abundance of each key species over time, corrected for varied

270   sampling intensity, a simple GAM was constructed for each species with decade of capture as the

271   independent variable, constrained to 3 knots and a smoothing parameter of 0.5. For the spatial analyses,

272   data were aggregated into three-decade groups, and the captures of each species were modeled using a

273   negative binomial GAM with a gaussian process smooth and a combination of latitude and longitude,

274   both in aggregate and then by decade group. Latitude and longitude were included in the model to control

275   for differences in the spatial distribution of lady beetle collections within the state and to account for

276   spatial autocorrelation. To examine the interaction of temporal, spatial, landscape, and community factors

277   on captures of each species, we used a modified backwards-stepping model selection applied to negative

278   binomial GAMs. First, a global model was constructed that included decade, longitude, latitude,

279   percentage land cover in agriculture, forest, and developed uses, the total captures of alien species, and

280   the sampling offset. Because of a high-degree of autocorrelation between the aggregate alien species

281   metrics, each of these variables was substituted into the model separately, and the variables with the best

282   performance (determined by AIC) were selected for further analysis. Absolute numbers of *C.*

283   *septempunctata* and *H. axyridis* were considered together in the same model to test if target species were

284   exhibiting differential responses to the two alien species. After the substitution-based model selection was

285   completed, the remaining model selection was completed using backwards selection by systematically

286   dropping each variable with the lowest explanatory power, using AIC as the decision criterion. The

287   selected model was then subjected to concurvity analysis and if the 'worst case' concurvity estimate

288   exceeded 0.8 for any parameter, the parameter was eliminated from the model and backwards model

289   selection was resumed (Ross, 2019). Complete data manipulation, community analyses, model

290   specifications, model selection, and construction of prediction intervals, as well as the development

291   history of our analyses are available on Github: https://github.com/BahlaiLab/Ohio_ladybeetles

292

293   **Results**

294   We compiled 4,194 lady beetle museum records representing 28 species collected in Ohio, USA

295   from 1900-2018 (Table 1; see Appendix 2: Table S2.3, Figs. S2.1-S2.4). Total collections of native

296   species varied from year to year, with high numbers collected in the 1930s and 1980s (Fig. 3A). The most

297   common native species represented in these collections were *Coleomegilla maculata* (Degeer) (16.4% of

298   total records), *Hippodamia convergens* Guerin (9.5%), *Hippodamia parenthesis* (Say) (8.4%), *Psyllobora*

299   *vigintimaculata* (Say) (7.6%), *Cycloneda munda* (Say) (7.2%), *Brachiacantha ursina* (Fabricius) (6.1%),

300   and *Adalia bipunctata* (Linnaeus) (5.2%). Records documented the presence of the aphidophagous alien

301   species *Coccinella septempunctata* (Linnaeus) (2.4% of total records; first detected in 1978), *Coccinella*

302   *undecimpunctata* Linnaeus (0.02%; single record in 1953), *Harmonia axyridis* (Pallas) (11.2%; first

303   detected in 1993), *Hippodamia variegata* (Goeze) (0.2%; first detected in 2000), and *Propylea*

304   *quatuordecimpunctata* (Linnaeus) (0.6%; first detected in 2003). Collections of alien species began to

305   increase in the 1980s, with numbers surpassing natives in the 2000s and 2010s (Fig. 3A).

306

307   *Lady beetle species composition*

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308   The proportion of native lady beetles comprising collections, including *A. bipunctata*, *C.*

309   *novemnotata*, and *H. convergens*, has decreased in Ohio since the 1970s as alien lady beetles such as *C.*

310   *septempunctata* and *H. axyridis* have increased (Fig. 3B). Descriptive patterns of lady beetle taxonomic

311   beta-diversity (β_{SOR}) within geographic regions across decades were the result of species turnover (β_{SIM})

312   and nestedness (β_{SNE}), but the strongest contributor to changes in lady beetle community composition

313   shifted over time (Fig. 4A, B). Nestedness was the primary contributor to patterns of lady beetle beta-

314   diversity until the 1980s. From 1980-2018, species turnover increasingly became the stronger contributor,

315   especially for aphidophagous species, and was the dominant driver of lady beetle beta-diversity by the

316   2010s (Fig. 4A, B). PERMANOVA and NMDS analyses of pairwise beta-diversity matrices identified

317   decades when significant shifts occurred in lady beetle community composition, primarily driven by

318   aphidophagous species (see Appendix 2: Table S2.4, Fig. S2.5). Lady beetle beta-diversity (β_{sor}) differed

319   between the 1920s and 1930s ($F = 3.88$; $P = 0.014$) and between the 1930s and 1940s ($F = 3.12$; $P =$

320   0.003), with species composition in the 1930s being highly similar across geographic regions in Ohio and

321   nested within the more variable collections from the 1920s and 1940s (see Appendix 2: Fig. S2.5A, B).

322   Lady beetle beta-diversity (β_{sor}) also differed between the 1980s and 1990s ($F = 2.94$; $P = 0.021$) and

323   between the 1990s and 2000s ($F = 3.36$; $P = 0.009$), with communities similarly variable among decades,

324   but collections shifting in species composition (see Appendix 2: Fig. S2.5C, D).

325

326   *Drivers of lady beetle populations*

327   Relative captures of all lady beetle species varied with time, indicating that all species had some

328   form of temporal dependence in the number of individuals captured when accounting only for sampling

329   effort and using a normal error structure. However, these simple negative binomial models explained

330   limited variation in the data. Using these simple models, native species were captured less per sampling

331   effort later in the study period, but the steepness and timing of declines in captures varied by species. The

332   two alien species exhibited more variable patterns. Captures of *C. septempuncata* initially increased in

333   residual captures but then decreased during the four decades it has been present in Ohio. Conversely,

334 captures of *H. axyridis* increased over the three decades since its establishment. For *A. bipunctata* and *C.*

335 *novemnotata*, statistically significant temporal patterns were not observed within the modeled time period,

336 as both species had relatively stable capture frequency prior to the 1980s but became extremely rare and

337 then absent in later years of data collection. To provide meaningful model fits for the time when these

338 species were present, years with zero-biased data were not included in their respective models. Sampling

339 effort varied dramatically by year and location. Patterns of captures over time were not spatially static, as

340 several native species also exhibited spatiotemporal dependencies over the study (i.e. changing spatial

341 distributions with time; see Appendix 3: Table S3.1, Fig. S3.1-S3.5).

342 Species-specific patterns emerged in the negative binomial models that accounted for landscape,

343 invasion, and spatiotemporal drivers, and model fit was much improved in all cases (Fig. 5; see Appendix

344 3: Table S3.1). *Adalia bipunctata* exhibited a steep negative response to the increasing proportion of alien

345 species in the community but also was positively associated with agriculture and developed land covers.

346 *Coccinella novemnotata* had a strong negative population trend over time as well as spatial dependencies

347 in its captures but only appeared to respond negatively to agricultural cover as a landscape driver. Since

348 this native species had already begun to decline prior to invasions by *C. septempunctata* and *H. axyridis*,

349 there was limited co-occurrence of *C. novemnotata* and any of the alien species (only 5 captures of *C.*

350 *novemnotata* were recorded after 1980). *Coleomegilla maculata* populations were relatively net stable

351 over time, with an increase peaking in the 1970s and 1980s, but a net decrease since. Our models suggest

352 a relatively neutral effect of small numbers of alien lady beetles on *C. maculata*, but a negative impact as

353 alien species become dominant (i.e. >50% of the lady beetles collected). Additionally, agricultural land

354 cover had a slight positive association with captures of *C. maculata*. Captures of *H. convergens* had a

355 negative trend over time and exhibited a differential response to the two dominant alien species: a positive

356 association with *C. septempunctata* and a negative association with *H. axyridis*, as well as a positive

357 association with higher values of developed land cover. *Chilocorus stigma* exhibited spatial dependencies

358 and a positive association with forested habitats, and a negative association with the proportion of alien

359 lady beetles in the community.

14

360

Discussion

362   Specimen records can be harnessed to understand long-term biodiversity trends across various

363   spatial scales in response to anthropogenic threats (Shaffer *et al.*, 1998; Suarez & Tsutsui, 2004; Lister,

364   2011; Meineke *et al.*, 2019). Using historic occurrence records of lady beetles collected in Ohio, USA, we

365   report evidence of declines in captures for several native species, but the timing and severity of declines

366   as well as the relative importance of alien species and land cover change as long-term drivers were

367   species-specific. Observed changes in species composition that began in the 1980s indicated processes of

368   species loss/gain and turnover that shifted communities towards dominance of a few alien lady beetle

369   species.

370

Shifts in lady beetle species composition

372   As collections of some native species declined over time in Ohio, captures of alien lady beetle

373   species increased following their establishment and spread. Beginning in the 2000s, alien species

374   comprised over 60% of the total specimens collected, suggesting a shift in lady beetle community

375   structure and alien species dominance within the state. This shift was further supported by changes in

376   patterns of total beta-diversity within geographic regions of the state that began in the 1980s. From the

377   1980s to the 2010s, beta-diversity of lady beetle species increased across decades, and the contribution of

378   species turnover to these patterns increased compared to previous decades, becoming the dominant driver

379   of beta-diversity by the 2010s. This finding indicates that lady beetle communities within a geographic

380   region became increasingly dissimilar over time due to processes of species loss or gain (i.e. species

381   nestedness) and species replacement (i.e. species turnover) during the period that coincides with alien

382   lady beetle establishment and spread. Changes in lady beetle species composition from the 1900s to the

383   1970s were primarily driven by species nestedness. These patterns were the result of the loss and gain of

384   uncommon native species in collections throughout the state, as well as the loss of common native species

385   such as *A. bipunctata* and *C. novemnotata* which began to decline prior to alien species arrival. Species

15

386   composition shifted in the 1980s as dissimilarity of communities increased substantially and the

387   contribution of species replacement to these patterns increased. High species replacement indicates that a

388   similar number of lady beetle species were collected within geographic regions among these decades, but

389   a low number were shared as species were replaced over time.

390   A combination of species nestedness and species turnover that resulted in high dissimilarity in

391   lady beetle species composition during the 1980s, 1990s, and 2000s is indicative of spatiotemporal loss

392   and replacement of native species. By the 2010s, lady beetle communities had become more similar to

393   each other in terms of species composition and were dominated by alien lady beetle species. Similar shifts

394   in lady beetle communities have been observed in response to the establishment of alien species (Elliott *et*

395   *al.*, 1996; Alyokhin & Sewell, 2004; Bahlai *et al.*, 2013). For example, a shift in species dominance with

396   the establishment of *C. septempunctata* in the 1980s was observed in potato fields in Maine, USA

397   (Alyokhin & Sewell, 2004). Within four years of its establishment in southwestern Michigan, USA, *H.*

398   *axyridis* was the dominant lady beetle species collected and was found in diverse habitats, including

399   agricultural and old fields, and poplar plantations (Colunga-Garcia & Gage, 1998). Although the

400   composition of lady beetle communities has become dominated by exotic species, Bahlai et al. (2013)

401   documented that their potential to suppress pest populations in agricultural and natural habitats had

402   remained relatively consistent over time. As significant shifts in lady beetle communities have occurred

403   across the Midwestern US, reliance on alien species to maintain pest suppression may be required for

404   management, but further declines of native species may affect long-term resilience of this ecosystem

405   service (Bahlai *et al.*, 2021).

406

407   *Drivers of native lady beetle decline*

408   Using museum specimens collected over twelve decades, we documented declines in captures of

409   the native species *A. bipunctata*, *C. novemnotata*, *H. convergens*, *C. maculata*, and *C. stigma*. The native

410   species *A. bipunctata*, *C. novemnotata*, and *H. convergens* were once widely distributed across much of

411   the United States (Gordon, 1985), with early surveys in Ohio recording these species across the state

16

412   (Dury, 1879; Bubna, 1902). Now, these species are considered rare or potentially extirpated in much of

413   eastern North America (Wheeler Jr & Hoebeke, 1995; Elliott *et al.*, 1996; Gardiner *et al.*, 2012). For

414   example, no captures of *C. novemnotata* or *A. bipunctata* were found after 1985 and 1996, respectively,

415   suggesting their populations were below the detection threshold or extirpated within the state. While

416   declines in captures of these native species were observed, the relative importance of alien lady beetles

417   and land cover change as drivers was species-specific.

418

419   *Adalia bipunctata*

420   We found evidence that declines in captures of the aphidophagous species *A. bipunctata* began in

421   the 1960s, prior to the arrival and dominance of alien lady beetle species. The last collection of *A.*

422   *bipunctata* in Ohio occurred in 1996, and since the arrival of *C. septempunctata* in 1978, there were only

423   13 individuals of this native species collected from the state. During this period of overlap with alien

424   species, collections of *A. bipunctata* decreased as the proportion of captures of alien species increased

425   within the community. Reports from southwestern Michigan also observed declines in *A. bipunctata* over

426   24 years with increasing dominance of alien species (Bahlai *et al.*, 2015). *Harmonia axyridis* was first

427   collected in Ohio in 1993 and shares an affinity for arboreal habitats with *A. bipunctata* (Colunga-Garcia

428   & Gage, 1998; Honek *et al.*, 2019). Although our findings indicate that alien species likely contributed to

429   declines in captures of *A. bipunctata* to some degree, declines in captures prior to the arrival of alien

430   species suggests other contributing factors such as landscape change. We found that collections of *A.*

431   *bipunctata* increased with percentage of agricultural and developed land cover. Land cover change

432   analyses showed agricultural land cover decreased, while developed land cover increased over time. We

433   hypothesize that declines in captures of this native species could be related to reductions in aphid prey

434   availability due to a combination of landscape stressors such as reductions in agricultural land cover

435   paired with improved pest management practices as well as improved air and/or habitat quality in urban

436   environments that reduce pest outbreaks (Sloggett, 2017).

437

438 *Coccinella novemnotata*

439   We found no evidence that declines in captures of the aphidophagous species *C. novemnotata* in

440 Ohio were related to alien lady beetles, as this species was nearly absent from collections by the time *C.*

441 *septempunctata* was recorded in 1978. Captures of *C. novemnotata* began to decline in the 1950s prior to

442 the arrival of alien species, with the last Ohio collection occurring in 1985. Since the arrival of *C.*

443 *septempuncata* in Ohio, only 12 individuals of this native species were recorded. This finding contrasts

444 with many studies that have hypothesized declines of *C. novemnotata* were related to competitive

445 displacement by *C. septempunctata* (Staines Jr *et al.*, 1990; Wheeler Jr & Hoebeke, 1995; Snyder &

446 Evans, 2006). For instance, declines of *C. novemnotata* have been widely reported during the 1970s and

447 1980s, which coincides with the establishment and spread of *C. septempunctata* (Wheeler Jr & Hobeke,

448 1995 and references therein). We found that captures of *C. novemnotata* decreased with increasing

449 agricultural land cover, with declines beginning around the 1950s. Since the 1930s, the amount of

450 agricultural land cover has decreased within the state, but the spatial extent of these changes was highly

451 variable and not consistent across all Ohio counties. This loss of agriculture was primarily in the eastern

452 region of the state, while western Ohio remained dominated by agricultural land cover throughout the

453 study period. Along with these changes in the extent of agricultural land cover, landscapes have

454 experienced a shift from more diversified cropping systems to highly managed crop monocultures since

455 the mid-1900s (Crossley *et al.*, 2021). *Coccinella novemnotata* has a broad ecological niche (Losey *et al.*,

456 2007), and populations have been found in a variety of cultivated crops (Wheeler Jr & Hoebeke, 1995),

457 including alfalfa (Goodarzy & Davis, 1958; Pimentel & Wheeler, 1973), corn (Smith, 1971), cotton (Bell

458 & Whitcomb, 1964), soybeans (Dumas *et al.*, 1964), and fruit trees (Oatman *et al.*, 1964; Putman, 1964).

459 Simplification of agricultural landscapes due to loss of natural habitat and reductions in crop diversity

460 may impact temporal prey availability and diversity as well as refuge and overwintering habitats that are

461 required for predatory insect species such as *C. novemnotata* (Rusch *et al.*, 2016).

462

463 *Coleomegilla maculata*

18

464   Captures of the aphidophagous species *C. maculata* increased slightly and then declined with

465   increasing dominance of alien species within the community. *Coleomegilla maculata* is known to be a

466   strong aphidophagous competitor (Long & Finke, 2014), and this species remains one of the most

467   frequently collected native lady beetles in croplands and grasslands (Smith and Gardiner 2013). For

468   example, *C. maculata* was commonly collected in residential gardens across the state of Ohio by

469   community scientists (Gardiner *et al.*, 2012; Gardiner *et al.*, 2021). However, declines in *C. maculata*

470   populations were reported during a long-term study in southwestern Michigan (Bahlai *et al.*, 2015).

471   *Coleomegilla maculata* feeds on pollen in addition to aphid prey (Dixon & Dixon, 2000; Hodek *et al.*,

472   2012; Majerus, 2016), and this pollen feeding was hypothesized to reduce competition with alien species

473   (Bahlai *et al*., 2015). However, there is evidence that *H. axyridis* and *C. septempunctata* also feed on

474   pollen as a supplemental food resource when arthropod prey is scarce (Ricci *et al.*, 2005; Berkvens *et al.*,

475   2008; Berkvens *et al.*, 2010). Therefore, the dietary niche overlap and thus the impacts of alien species on

476   *C. maculata* may have been underestimated.

477

478   *Hippodamia convergens*

479   Our findings isolated *H. axyridis* as the major driver of declines in captures of the aphidophagous

480   species *H. convergens*. *Hippodamia convergens* was last collected in Ohio in 2015, although only 18

481   individuals are recorded from 1990-2015. Collections of *H. convergens* declined with captures of *H.*

482   *axyridis* but increased with captures of *C. septempunctata*. These divergent patterns highlight that alien

483   lady beetle species are not ecologically equivalent, and instead, can have different impacts on native

484   species. *Hippodamia convergens* also was positively associated with percentage of developed land. The

485   effects of urbanization on lady beetles are highly context dependent, as previous studies have reported

486   positive (Egerer *et al.*, 2017; Honek *et al.*, 2018; Liere *et al.*, 2019) and negative (Rocha *et al.*, 2018; Grez

487   *et al.*, 2019; Parker *et al.*, 2020) associations. However, as *H. convergens* has widely declined within the

488   study region over the past several decades while urban habitat has increased, this observed positive

489   association does not appear to be a major driver of their population status and could reflect a sampling

490   bias wherein this rare species was more likely to be collected in densely populated areas.

491

492   *Chilocorus stigma*

493   Collections of the coccidophagous species *C. stigma* declined as the proportion of alien species

494   increased in the community, suggesting that aphidophagous alien lady beetles may affect non-

495   aphidophagous native species to some extent. Likewise, decline of *C. stigma* immediately following the

496   establishment of *H. axyridis* has been reported in southwestern Michigan, USA, further suggesting

497   potential competitive interactions among these species (Colunga-Garcia & Gage, 1998). Although *H.*

498   *axyridis* is primarily aphidophagous (Koch, 2003), this species also feeds on scale insects in arboreal

499   environments (Mcclure, 1986), which suggests some degree of dietary and habitat overlap with *C. stigma*.

500   *Chilocorus stigma* was the only native lady beetle associated with forest land cover, with captures

501   increasing as the percentage of forest increased at the county level. This response is likely linked with the

502   ecology of this species. Scale insects are common pests of trees in managed and natural forests. Further,

503   *C. stigma* is reported to oviposit eggs in bark cracks and crevices as well as overwinter as adults in the

504   leaf litter layer (Mayer & Allen, 1983). Similar patterns have been found in other native lady beetle

505   surveys. For instance, the amount of forest habitat at a 2 km landscape scale was positively associated

506   with native lady beetle abundance and species diversity within residential gardens (Gardiner *et al.*, 2021).

507   The conservation value of forests for native lady beetles may be underestimated, but additional research is

508   required to understand when and how native species are utilizing these habitats.

509

510   *Conclusions*

511   Using specimen records collected over 118 years in Ohio, USA, we documented shifts in lady

512   beetle species composition beginning in the 1980s as communities became increasingly dominated by

513   alien species. Because of uneven sampling inherent to museum collections, total records of native lady

514   beetles varied from year to year, which made it difficult to detect any changes in absolute abundance at

515   the community-level. Therefore, our methodology and results cannot provide evidence that all native lady

516   beetles are in decline. Such stochasticity may be inherent to lady beetle biology as native populations are

517   known to experience boom-bust cycles (Bahlai *et al.*, 2015) and other studies have reported similar year

518   to year variability in their numbers (Elliott & Kieckhefer, 1990; Kieckhefer & Elliott, 1990; Elliott *et al.*,

519   1996; Harmon *et al.*, 2007). Despite patterns of annual variation, we detected evidence of declines in

520   captures of several native lady beetle species, including several aphidophagous species and a

521   coccidophagous species, via decreasing representation in the sampled community of lady beetles.

522   The use of long-term specimen records facilitated investigation of the relative importance of the

523   establishment of alien species and landscape change as drivers of native lady beetle decline. Drivers of

524   declines in captures of native lady beetles were highly species-specific, emphasizing that mechanisms

525   driving population losses cannot be generalized even among closely related species. Additionally, this

526   finding highlights the importance of species-level data when investigating temporal trends in insect

527   populations. Although the establishment of exotic species and landscape change have been identified as

528   major drivers of spatiotemporal patterns in insect populations (Fox *et al.*, 2014; Sánchez-Bayo &

529   Wyckhuys, 2019; Seibold *et al.*, 2019), the causes of declines are likely more complex and multifaceted

530   (Homburg *et al.*, 2019; Wagner, 2020; Wagner *et al.*, 2021). Our study underscores this complexity by

531   documenting how closely related native lady beetle species displayed opposing, species-specific

532   responses to alien species and land cover change. For several native species investigated, the dominance

533   of alien lady beetles was identified as a major contributor to declines in captures, but other native species

534   began to decline prior to alien species establishment. The importance of landscape change as a driver

535   structuring the distributions of lady beetle populations suggests biodiversity conservation management is

536   required at the landscape scale. Landscape scale management will need to balance the opposing needs of

537   native species to be effective. Importantly, we are unable to disentangle the effects of historical changes

538   in land cover with more recent intensification and simplification of agricultural landscapes on these

539   observed trends in captures. Native lady beetle species are key predators of aphids, scales, psyllids, mites,

540   fungi, and other pests (Evans, 2009; Hodek & Honěk, 2009; Weber & Lundgren, 2009), contributing

21

541   broadly to biological control in agricultural systems (Caltagirone & Doutt, 1989; Obrycki & Kring, 1998;

542   Rondoni *et al.*, 2021). Increased dominance of alien lady beetles indicates that these species may be

543   required to maintain successful pest management in the future. Understanding how these major

544   anthropogenic drivers influence long-term trends in native lady beetle populations will inform the

545   conservation of this ecologically and economically important family of insects.

546

570

Author Contributions

572   M.M. Gardiner, K.I. Perry, and C.A. Bahlai conceived, designed, and implemented the study; K.I. Perry,

573   C.B. Riley, K. J. Turo, L. Taylor, J. Radl, Y.A. Delegado de la flor, and F. S. Sivakoff compiled the

574   specimen data; K.I. Perry, C.A. Bahlai, and T.J. Assal analyzed and interpreted the data; K.I. Perry wrote

575   the first draft of the manuscript; all authors reviewed and edited the manuscript.

576

Data availability statement

578   The data and analyses code that support the findings of this study are openly available on GitHub:

579   https://github.com/BahlaiLab/Ohio_ladybeetles

580

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Table 1. Ohio lady beetle species records from 1900-2018 compiled from 25 institutions across the United States. Data collection focused on native and alien species within the tribe Coccinellini and four additional species (*B. ursina, C. stigma, H. undulata,* and *P. vigintimaculata*). Lady beetle species were characterized based on their status (native or alien to Ohio, USA) and their primary diet (aphids, scales, or fungi).

Lady beetle species	Records	First Record	Last Record	Status	Primary Diet
Brachiacantha ursina (Fabricius)	255	1902	2015	Native	Aphidoidea, Coccoidea
Hyperaspis undulata (Say)	61	1905	2014	Native	Coccoidea
Chilocorus stigma (Say)	111	1901	2016	Native	Coccoidea, Aphidoidea
Adalia bipunctata (Linnaeus)	218	1901	1996	Native	Aphidoidea
Anatis labiculata (Say)	176	1907	2012	Native	Coccoidea, Aphidoidea
Anatis mali (Say)	23	1932	2013	Native	Coccoidea, Aphidoidea
Anisosticta bitriangularis (Say)	16	1923	2012	Native	Aphidoidea, Pollen
Coccinella novemnotata Herbst	169	1901	1985	Native	Aphidoidea
Coccinella septempunctata (Linnaeus)	102	1978	2017	Alien	Aphidoidea
Coccinella transversoguttata Mulsant	51	1921	1986	Native	Aphidoidea
Coccinella trifasciata Linnaeus	19	1911	1971	Native	Aphidoidea
Coccinella undecimpunctata Linnaeus	1	1953	1953	Alien	Aphidoidea
Coleomegilla maculata (Degeer)	690	1901	2018	Native	Aphidoidea, Pollen
Cycloneda munda (Say)	302	1901	2017	Native	Aphidoidea
Harmonia axyridis (Pallas)	470	1993	2018	Alien	Aphidoidea
Hippodamia convergens Guerin	400	1903	2015	Native	Aphidoidea
Hippodamia glacialis (Fabricius)	39	1905	2016	Native	Aphidoidea
Hippodamia parenthesis (Say)	353	1900	2017	Native	Aphidoidea
Hippodamia quindecimmaculata Mulsant	3	1905	1935	Native	Aphidoidea
Hippodamia tredecimpunctata (Linnaeus)	155	1903	2014	Native	Aphidoidea
Hippodamia variegata (Goeze)	10	2000	2016	Alien	Aphidoidea
Mulsantina luteodorsa J. Chapin	1	2008	2008	Native	Aphidoidea
Mulsantina picta (Randall)	51	1924	2015	Native	Aphidoidea

| *Myzia pullata* (Say)	30	1934	2012	Native	Aphidoidea
Neoharmonia venusta (Melsheimer)	119	1902	2012	Native	Coccoidea
Olla v-nigrum (Mulsant)	21	1932	2004	Native	Aphidoidea, Psylloidea
Propylea quatuordecimpunctata (Linnaeus)	27	2003	2016	Alien	Aphidoidea
Psyllobora vigintimaculata (Say)	321	1902	2016	Native	Fungi (Erisyphaceae)

Figure 1. The study area is congruent with the state of Ohio; inset shows the relative location of Ohio in the conterminous United States. Ohio counties within the four geographic regions of the state are color-coded, Lake Erie Glaciated Plateau (LEGP; top right), Appalachian Plateau (AP; bottom right), Indiana-Ohio Till Plain (IOTP; bottom left), and Western Lake Erie Basin (WLEB; top left).
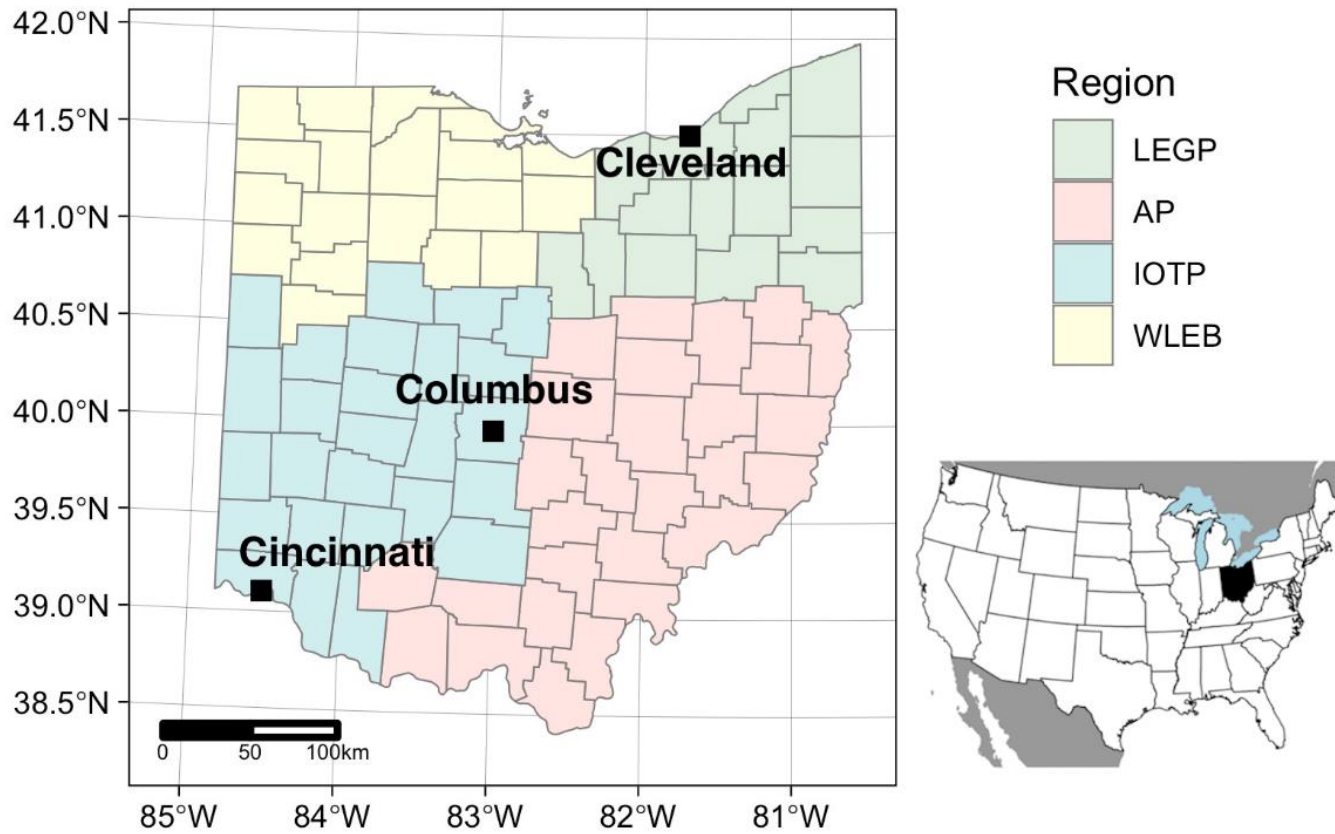
Figure 2. Spatial extent of agriculture (row A), developed land (row B), and forest (row C) in Ohio for each time period (columns).
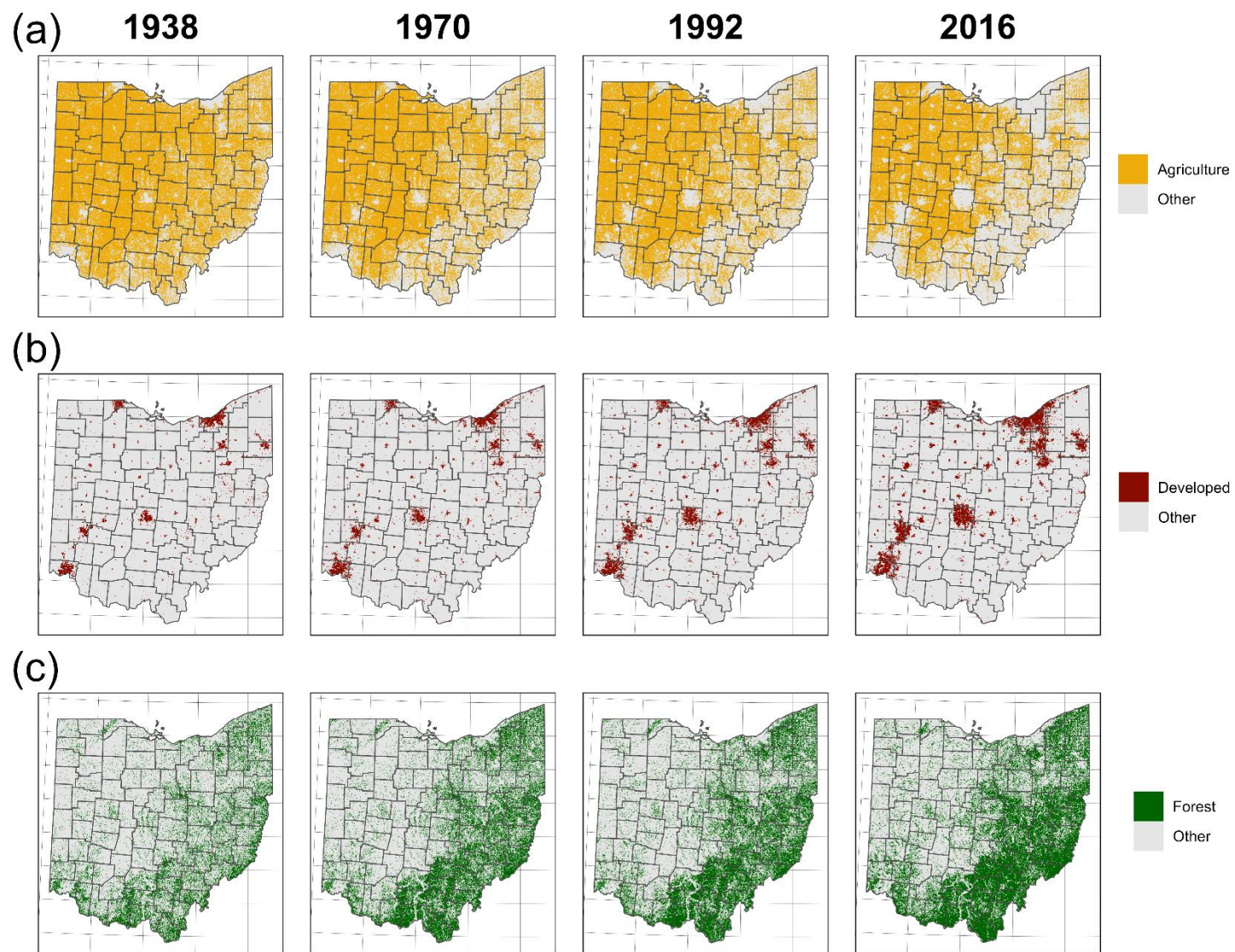
Figure 3. Number of collections (A) and proportion of collections (B) of native and alien lady beetle records from Ohio by decade from 1900 to 2018.
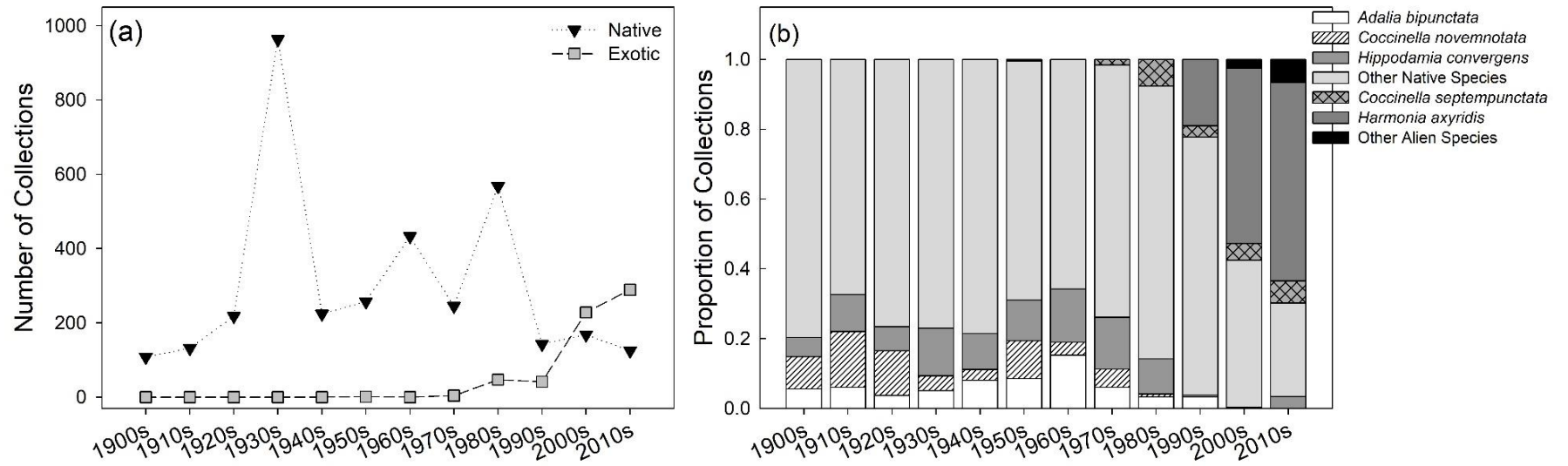
Figure 4. Descriptive patterns of taxonomic beta-diversity across decades for all lady beetle species (A) and aphidophagous lady beetle species (B) collected in Ohio. Total Sorensen dissimilarity (β_{SOR}) among decades was partitioned into two additive components: turnover (β_{SIM}; reflects species replacement) and nestedness (β_{SNE}; reflects species loss or gain). Therefore, $\beta_{SOR} = \beta_{SIM} + \beta_{SNE}$.
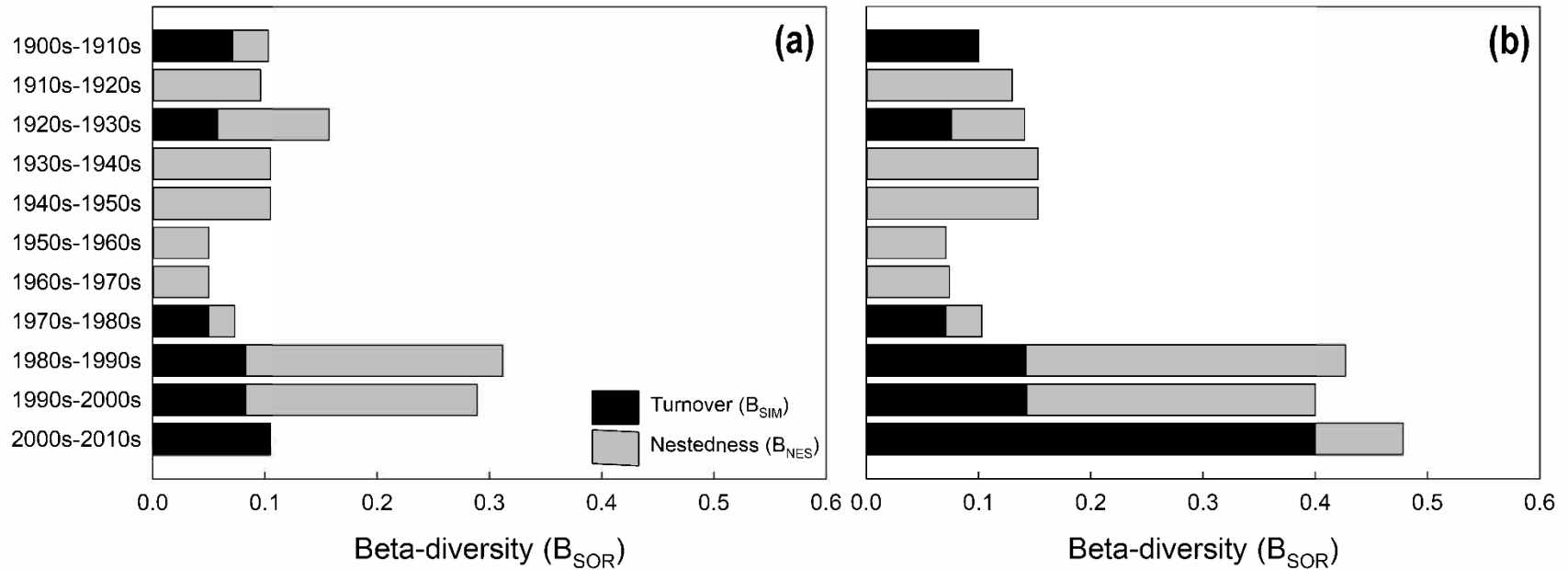
Figure 5. Matrix of partial GAM predictions of responses for five key native species to spatiotemporal, invasion, and landscape parameters. Negative binomial generalized additive models used Ohio museum collections, 1930-2018 data on lady beetle captures and were adjusted for sampling effort. Predictions were constructed by generating data that held all other parameters constant and varying the parameter of interest, and then substituting these data into the best-fit model determined by model selection (Appendix 2, Table 1). Solid lines, shading represent 95% confidence intervals.