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Landscape change and alien invasions drive shifts in native lady beetle communities over a century

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Abstract

Understanding causes of insect population declines is essential for the development of successful conservation plans, but data limitations restrict assessment across spatial and temporal scales. Museum records represent a source of historical data that can be leveraged to investigate temporal trends in insect communities. Native lady beetle decline has been attributed to competition with established alien species and landscape change, but the relative importance of these drivers is difficult to measure with short-term field-based studies. We assessed distribution patterns for native lady beetles over 12 decades using museum records, and evaluated the relative importance of alien species and landscape change as factors contributing to changes in communities. We compiled occurrence records for 28 lady beetle species collected in Ohio, USA, from 1900 to 2018. Taxonomic beta-diversity was used to evaluate changes in lady beetle community composition over time. To evaluate the relative influence of temporal, spatial, landscape, and community factors on the captures of native species, we constructed negative binomial generalized additive models. We report evidence of declines in captures for several native species. Importantly, the timing, severity, and drivers of these documented declines were species-specific. Land cover change was associated with declines in captures, particularly for *Coccinella novemnotata* which declined prior to the arrival of alien species. Following the establishment and spread of alien lady beetles, processes of species loss/gain and turnover shifted communities toward the dominance of a few alien species beginning in the 1980s.

Because factors associated with declines in captures were highly species-specific, this emphasizes that mechanisms driving population losses cannot be generalized even among closely related native species. These findings also indicate the importance of museum holdings and the analysis of species-level data when studying temporal trends in insect populations.

KEYWORDS
Coccinellidae, exotic, invasive, ladybird, land cover, land use, non-native, species decline

INTRODUCTION

Global biodiversity loss is a growing threat to the ecosystem services and functions on which humans depend (Cardoso et al., 2020; Ceballos et al., 2015; Dirzo & Raven, 2003; Mace et al., 2012). Given the importance of insects for ecosystem services such as pollination, pest suppression, and nutrient cycling (Losey & Vaughan, 2006; Yang & Gratton, 2014), understanding the causes of documented spatiotemporal changes in insect populations is a critical research focus. Numerous recent studies have pointed to declines in the abundance, richness, and biomass of insects (Hallmann et al., 2017; Seibold et al., 2019), including bees (Grixti et al., 2009; Potts et al., 2010), beetles (Brooks et al., 2012; Homburg et al., 2019), leafhoppers and planthoppers (Schuch et al., 2012), and butterflies and moths (Conrad et al., 2006; Habel et al., 2016; Maes & Van Dyck, 2001; Warren et al., 2021). Although population declines have been frequently reported, relatively stable or increasing populations of insects also have been documented (Fox et al., 2014; Schowalter et al., 2021; Shortall et al., 2009). For example, observations of moths in Great Britain identified highly species-specific temporal patterns over a 40-year period, as 260 species declined in frequency, 160 species increased, and 253 species remained unchanged (Fox et al., 2014). Complexity in the responses of insects has generated scientific debate about whether observed declines are generalizable across insect taxa and guilds and at larger spatial scales (Didham et al., 2020; Saunders et al., 2020; Simmons et al., 2019; Thomas et al., 2019). Although many challenges to studying insect population trends exist (Didham et al., 2020; Montgomery et al., 2020), understanding the magnitude and drivers of declines in insect species is critical for biodiversity conservation management and the maintenance of insect-based ecosystem services and functions.

One primary limitation to understanding insect populations over time stems from data deficiencies such as low taxonomic resolution, geographic restrictions, and short time series (Didham et al., 2020; Sánchez-Bayo & Wyckhuys, 2019; Thomas et al., 2019). However, specimen records from natural history museums and other institutions can be used to investigate trends in insect populations over greater spatial and temporal scales (Kharouba et al., 2019; Lister, 2011). Although specimen record-based data have their own set of biases and challenges such as geographic, taxonomic, and temporal biases that result in nonrandom collections (Boakes et al., 2010; Meineke & Daru, 2021), biological collections represent a unique source of historical data that document the occurrence of species in time and space. For example, museum records revealed that 11 bumble bee species native to eastern North America and Canada have experienced substantial (>50%) declines in captures over the past century, while eight species have remained stable or increased in collections (Colla et al., 2012). Importantly, specimen records can be used as baseline measures for investigating the impacts of anthropogenic stressors such as the establishment of alien species, environmental degradation, and climate change on patterns of biodiversity (Johnson et al., 2011; Kharouba et al., 2019; Suarez & Tsutsui, 2004; Winker, 2004). For instance, moth assemblages collected on Mount Kinabalu in Borneo in 2007 were compared to historical records collected from the same sites in 1965, revealing upward shifts in the altitudinal distribution of species in response to changes in temperature (Chen et al., 2009). Although the use of collections data is limited in its ability to track the absolute abundance of a species due to sampling effort variation (Ries et al., 2019), historical specimen data facilitate understanding of species' responses to anthropogenic change by helping to distinguish signals of decline from natural population variability, especially when considering relative observations in groups of similar taxa. Therefore, specimen records are invaluable resources that can be used to address biodiversity conservation initiatives, including documenting changes in communities of beneficial insects.

Lady beetles (Coleoptera: Coccinellidae) are a family of charismatic insect species that are commonly collected and contribute broadly to pest suppression by consuming aphids, scales, psyllids, mites, fungi, and other pests (Evans, 2009; Hodek et al., 2012; Hodek & Honěk, 2009; Weber & Lundgren, 2009). Because lady beetles are capable of rapidly colonizing habitats to exploit ephemeral prey resources, these species have been used widely in biological control programs in agricultural systems (Caltagirone & Doutt, 1989; Koch, 2003; Obrycki & Kring, 1998; Rondoni

et al., 2021). A number of authors have noted declines in native lady beetle populations across the United States (Alyokhin & Sewell, 2004; Harmon et al., 2007) and Europe (Brown & Roy, 2018; Roy et al., 2012), which may contribute to an overall loss of resilience of the biological control services offered by this community (Bahlai et al., 2021). For example, the historically widespread native aphidophagous species *Hippodamia convergens* Guerin has declined in the US states of Michigan (Gardiner et al., 2009), Ohio (Gardiner et al., 2012), Wisconsin (Steffens & Lumen, 2015), and Minnesota (Steffens & Lumen, 2015), as well as the Canadian Province of Manitoba (Turnock et al., 2003). Likewise, the nine-spotted lady beetle *Coccinella novemnotata* Herbst was once common in eastern North America, but had not been collected for over a decade until a community scientist "rediscovered" it (Losey et al., 2007). Anthropogenic activities such as the establishment of alien species and landscape change have been hypothesized as potential drivers of native lady beetle decline (Alyokhin & Sewell, 2004; Bahlai et al., 2015; Gardiner et al., 2012; Harmon et al., 2007; Honěk et al., 2014; Roy et al., 2016).

Several studies have observed that the decline of native aphidophagous species coincided with the establishment and spread of alien lady beetle species, particularly the Asian species *Harmonia axyridis* (Pallas) and the European species *Coccinella septempunctata* (Linnaeus) (Roy et al., 2012, 2016; Steffens & Lumen, 2015; Turnock et al., 2003). Following their establishment, alien lady beetles became the dominant species within many native communities (Alyokhin & Sewell, 2004; Bahlai et al., 2015; Harmon et al., 2007). Because of their numerical and behavioral dominance, direct and indirect competitive interactions with alien species are hypothesized as a cause of declines in native lady beetles (Li et al., 2021; Pell et al., 2008). For example, intraguild predation has been documented among native and alien lady beetles in the field (Brown et al., 2015; Gagnon et al., 2011; Ortiz-Martínez et al., 2020; Thomas et al., 2013), wherein native eggs and larvae were more likely to be the intraguild prey for alien species (Katsanis et al., 2013; Snyder et al., 2004; Turnipseed et al., 2015). In the field, native species experienced greater egg predation from a guild of shared predators than alien lady beetle species, which could translate to apparent competition (Smith & Gardiner, 2013). These asymmetric interactions may largely benefit alien species at the expense of native lady beetle populations, but the extent and context of these effects on native species are difficult to quantify. The short time scales of many studies and the lack of data from lady beetle communities before the establishment of alien species limits understanding of the impacts of these invaders.

Landscape change that results in the loss, fragmentation, and degradation of natural habitat also has been hypothesized as a key driver contributing to population declines of insect species (Potts et al., 2010; Wagner, 2020; Wagner et al., 2021), including lady beetles (Honěk et al., 2017). Land cover change resulting from increased urbanization and agricultural intensification can influence the structure and composition of lady beetle communities (Gardiner et al., 2009, 2021; Grez et al., 2019; Parker et al., 2020; Woltz & Landis, 2014). For example, native and alien species were less abundant in isolated urban greenspaces that were embedded in landscapes dominated by impervious surfaces and built infrastructure (Parker et al., 2020). In agricultural landscapes, native and alien lady beetles were more abundant in fields surrounded by higher crop diversity and more semi-natural habitat types such as grasslands and forests (Woltz & Landis, 2014). Loss and fragmentation of natural habitat in landscapes such as those dominated by urban and agricultural land cover may differentially affect species depending on their life history traits such as phenology, dispersal ability, overwintering biology, and food requirements (Zaviezo et al., 2006). However, the impacts of landscape change on native lady beetle populations may occur gradually over time, making species responses difficult to detect over short time scales. For example, gradual directional change in the species composition of native lady beetle communities was documented over a 118-year period in Missouri, USA, using museum specimen records (Diepenbrock et al., 2016). Because there was no evidence that the establishment of alien lady beetle species affected the rate of change, Diepenbrock et al. (2016) hypothesized that these long-term community changes may be related to altered land use patterns. The substantial year-to-year variation in the abundance of lady beetle species (Elliott et al., 1996; Honěk et al., 2014) requires longer time series data such as those used by Diepenbrock et al. (2016) to detect changes in populations caused by landscape change and to distinguish these effects from other anthropogenic stressors (Bahlai et al., 2021; Bahlai & Zipkin, 2020).

While several hypotheses have been proposed, the causes of declines in native lady beetle populations remain under debate. Importantly, these hypotheses are not mutually exclusive, and it is likely that causes of declines in native species are multifaceted, wherein multiple mechanisms are responsible for the observed patterns in lady beetle populations. Although causes of declines in native species are often studied independently, these drivers may interact to influence native populations (Didham et al., 2007). For example, habitat modification that transitions natural habitat to more highly disturbed urban and agricultural habitats may differentially benefit some lady beetle species over others (Grez et al., 2013), with implications for direct and indirect competitive interactions among native and alien species.

Understanding the magnitude and drivers of declines in native lady beetle populations will require comprehensive

time-series data documenting community responses that can then be used to assess the contribution of the establishment of alien species and landscape change simultaneously. To understand the relative importance of the establishment of alien species and landscape change as contributors of native species decline, we compiled historical occurrence records of lady beetles collected in Ohio, USA, from museums and other institutions across the United States. Although we cannot directly assess changes in abundance with occurrence records, these data allow the investigation of declines in captures of lady beetles over time and the comparison of relative observations among species. Our goals were to: (1) characterize long-term changes in land cover and lady beetle communities which have occurred over time in Ohio by assessing temporal patterns of beta-diversity; and (2) evaluate the relative importance of the establishment and spread of alien lady beetle species and landscape change in Ohio as stressors contributing to patterns of captures in several native lady beetle species over time.

METHODS

Lady beetle specimens and data requests

To investigate long-term changes in native lady beetle communities within Ohio, USA, we used historic occurrence records for native and alien species within the tribe Coccinellini and four additional commonly collected species within the tribes Hyperaspidini, Chilocorini, and Psylloborini. Targeted Coccinellini genera were *Adalia*, *Anatis*, *Anisosticta*, *Aphidecta*, *Calvia*, *Ceratomegilla*, *Coccinella*, *Coelophora*, *Coleomegilla*, *Cycloneda*, *Harmonia*, *Hippodamia*, *Macronaemia*, *Mulsantina*, *Myzia*, *Naemia*, *Neoharmonia*, *Olla*, and *Propylea*, and the four additional species were *Brachiacantha ursina* (Fabricius), *Chilocorus stigma* (Say), *Hyperaspis undulata* (Say), and *Psyllobora vigintimaculata* (Say). We contacted 59 institutions based within the United States, the majority of which are hosted by the Entomological Collections Network (ENC, 2020). Ohio lady beetle records were compiled from 25 institutions with assistance of their curators (see Appendix S1: Table S1 and Section S1).

Specimen loans were requested from museums and institutions that had unidentified lady beetle records from Ohio. Any unidentified lady beetle species that were unaccounted for within the collections of these institutions were not included within our dataset. Lady beetle species identifications were determined using Gordon (1985). All lady beetle species were characterized by their status (native or alien to North America) and their primary diet (aphidophagous, coccidophagous, or fungivorous) which was based on most frequently reported prey (aphids, scales, or fungi) (Angalet et al., 1979; Dixon & Dixon, 2000; Gordon, 1985; Hodek et al., 2012; Majerus, 2016; Michaud, 2001; Staines, 2008).

Land use and land cover change analysis

To assess the influence of landscape change on lady beetle communities, we analyzed historical land use and land cover (LULC) data from four points in time (1938, 1970, 1992, 2016). Annual historical LULC data were obtained from the US Geological Survey (Sohl et al., 2018) for the years 1938, 1970, and 1992. These historical LULC backcasts were modeled using numerous historical datasets and created explicitly to extend the National Land Cover Database (NLCD) to earlier time periods, prior to the availability of remote-sensing data (Sohl et al., 2016). The earliest data available are from 1938, which corresponds with the start of historical reporting in the Agricultural Census (Sohl et al., 2016). The NLCD and historical backcast data were converted into four primary land use classes: agriculture, developed, forest, and other (i.e., non-target; all other land cover classes found in Ohio) (see Appendix S2: Tables S1 and S2). The contemporary landscape of Ohio was assessed with the 2016 NLCD (Dewitz, 2019; Wickham et al., 2021). To assess change over time, we calculated the total area of each of the four cover classes (i.e., agriculture, developed, forest, and other), along with the percentage of area occupied by each class, for each county at each of the four time periods. Although the LULC data have different spatial resolutions (NLCD = 30 m; historical backcasts = 250 m) they were not resampled, as the derived metrics (e.g., total area of cover class, percentage of county area) are relative, and therefore comparable across time. Analyses were completed in R (R Core Team, 2020) using the "raster" and "sf" R packages (Hijmans, 2020; Pebesma, 2018).

There was an increase in forest cover from 1938 to 1970, and it has held steady since the early 1990s (see Appendix S2: Figure S2). Most of the increase occurred in the eastern and southeastern regions of the state (Figure 1). There was a steady increase in developed land around existing population centers, with a larger increase in suburban areas since the early 1990s. The increase in forest and developed lands came at the expense of agricultural lands, yet this cover class remains the dominant land cover in many counties of the state (Figure 1; see Appendix S2: Figure S2). During each time period, there was high variability in the amount of agricultural and forested land across Ohio counties (see Appendix S2: Figure S2).

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

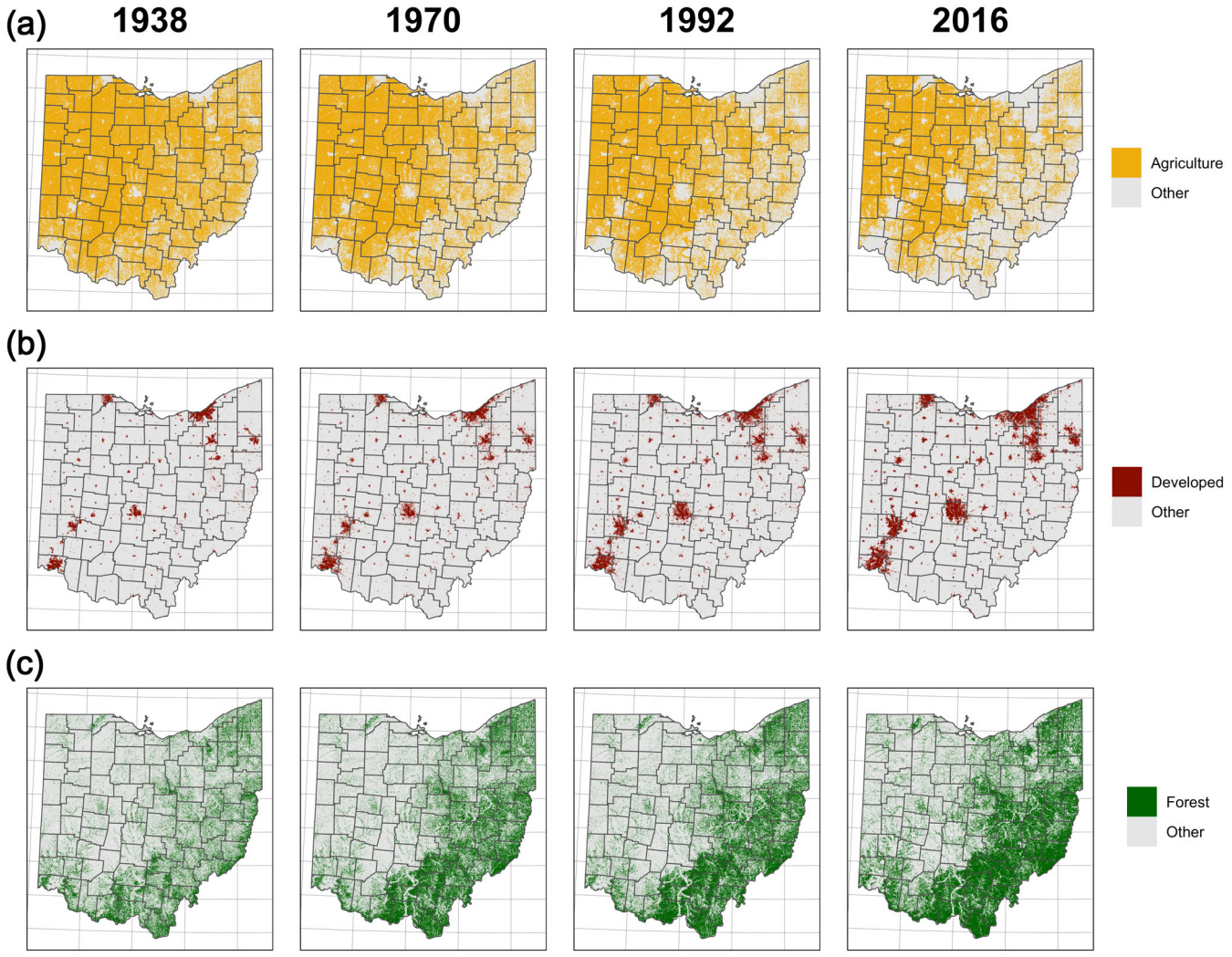

FIGURE 1 Spatial extent of agriculture (a), developed land (b), and forest (c) in Ohio for each time period (columns).

resolution available for the museum specimen data. For each county, we used an assumed linear progression between available timepoints to estimate the percentage land cover of a given class in each decade. The 1930 land cover data were extrapolated using the same procedure with available data from 1938 to 1970. Because lady beetle data were generally recorded at the county level, we computed the geographic centroids of each Ohio county based on present-day county boundaries as defined by the Ohio Department of Transportation (http://ogrip-eohio.opendata.arcgis.com/datasets/odot-county-boundaries).

Statistical analysis

Lady beetle museum records were included in the analyses if they were collected within Ohio, and we could obtain county-level location data and the year of collection. All analyses were conducted in R (R Core Team, 2020). The analysis code and development history are available in Bahlai and Perry (2024).

To characterize changes in land cover and lady beetle communities over time, differences in land cover and lady beetle community composition were visualized using nonmetric multidimensional scaling (NMDS) analyses. Raw land cover composition data (agriculture, developed, forest, and other/non-target) were compiled at the county level for the four time periods collected (i.e., 1938, 1970, 1992, 2016). Lady beetle specimen data were compiled at the county level and pooled across decades to create four time periods that corresponded with the available landscape data (before 1938, 1939–1970, 1971–1992, 1993–2016). Two lady beetle analyses were conducted, one with all species and one with native species only. NMDS analyses were conducted using the "vegan" package (Oksanen et al., 2011).

To further investigate long-term changes in native lady beetle communities within the region, community

composition was assessed by partitioning incidence-based measures of taxonomic beta-diversity for total and aphidophagous lady beetle species. Aphidophagous lady beetles were investigated separately because the established alien species primarily feed on aphid prey, and it is hypothesized that native aphidophagous species would experience strong competition with alien species due to this overlap in resource use. Due to low county-level counts, county records of lady beetle species were pooled across 10-year intervals such that patterns of community composition were assessed at the spatial scale of the state of Ohio across 11 decades from the 1900s through the 2010s. Descriptive patterns of total and aphidophagous lady beetle taxonomic beta-diversity were evaluated by calculating total Sorenson dissimilarity (β_{SOR}) using the *beta.temp* function in the R package "betapart" (Baselga & Orme, 2012). Total Sorensen dissimilarity was decomposed into a turnover component (β_{SIM}; reflects species replacement) and a nestedness component (β_{SNE}; reflects species loss or gain) (Baselga, 2010).

To evaluate the relative importance of temporal, spatial, landscape, and community factors on the captures of five key native lady beetle species (*Adalia bipunctata*, *C. novemnotata*, *Coleomegilla maculata*, *H. convergens*, the four most abundant native aphidophagous species, and *C. stigma*, the most abundant coccidophagous species), we constructed negative binomial generalized additive models (GAMs) for each species using the "mgcv" package (Wood, 2017), and then used an adaptive model selection procedure in combination with available contextual data to determine the relative importance of the factors. For all GAMs, lady beetle records were pooled at the county spatial scale and the decade temporal scale. Because the absolute number of records was very sparse earlier in our study period, we restricted these analyses to specimens captured in or after 1930 for these analyses. For *A. bipunctata* and *C. novemnotata*, which were extremely rare or absent from collections in later decades, data were culled at 1990 to restrict these analyses to times when these species were present. We computed several community variables for each decade-county combination, in addition to absolute captures of each coccinellid species, including the captures of two dominant invaders, *C. septempunctata* and *H. axyridis*, the total lady beetles captured, total alien species captured, and the proportion of the community captures belonging to alien species. All GAMs constructed included an offset variable of the structure log(1 + total lady beetles captured) to account for variability in sampling effort (with the exception of the model describing sampling effort over time).

First, to describe the relative abundance of each key species over time, corrected for varied sampling intensity, a negative binomial GAM was constructed for each species with decade of capture as the independent variable, constrained to 3 knots and a smoothing parameter of 0.5. For the spatial analyses, data were aggregated into three-decade groups, and the captures of each species were modeled using a negative binomial GAM with a Gaussian process smooth and a combination of latitude and longitude, both in aggregate and then by decade group. Latitude and longitude were included in the model to control for differences in the spatial distribution of lady beetle collections within the state and to account for spatial autocorrelation. To examine the interaction of temporal, spatial, landscape, and community factors on captures of each species, we used a modified backward-stepping model selection applied to negative binomial GAMs. First, a global model was constructed that included decade, longitude, latitude, percentage land cover in agriculture, forest, and developed uses, the total captures of alien species, and the sampling offset. Because of a high degree of autocorrelation and non-independence between the aggregate alien species metrics, each of these variables was substituted into the model separately, and the variables with the best performance (determined by Akaike information criterion [AIC]) were selected for further analysis. Captures of *C. septempunctata* and *H. axyridis* were considered together in the same model to test if target native species were exhibiting differential responses to the two alien species. After the substitution-based model selection was completed, the remaining model selection was completed using backward selection by systematically dropping each variable with the lowest explanatory power, using AIC as the decision criterion. The selected model was then subjected to concurvity analysis and if the "worst case" concurvity estimate exceeded 0.8 for any parameter, the parameter was eliminated from the model and backward model selection was resumed (Ross, 2019).

RESULTS

We compiled 4194 lady beetle museum records representing 28 species collected in Ohio, USA, from 1900 to 2018 (Table 1; see Appendix S2: Table S3 and Figures S3–S6). Total collections of native species varied from year to year, with high numbers collected in the 1930s and 1980s (Figure 2a). The most common native species represented in these collections were *C. maculata* (Degeer) (16.4% of total records), *H. convergens* Guerin (9.5%), *Hippodamia parenthesis* (Say) (8.4%), *P. vigintimaculata* (Say) (7.6%), *Cycloneda munda* (Say) (7.2%), *B. ursina* (Fabricius) (6.1%), and *A. bipunctata* (Linnaeus) (5.2%). Records documented the presence of the aphidophagous alien species

TABLE 1 Ohio lady beetle species records from 1900 to 2018 compiled from 25 institutions across the United States.

Tribe	Lady beetle species	Records	First record	Last record	Status	Primary diet
Hyperaspidini	*Brachiacantha ursina* (Fabricius)	255	1902	2015	Native	Aphidoidea, Coccoidea
	Hyperaspis undulata (Say)	61	1905	2014	Native	Coccoidea
Chilocorini	*Chilocorus stigma* (Say)	111	1901	2016	Native	Coccoidea, Aphidoidea
Coccinellini	*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
Psylloborini	*Psyllobora vigintimaculata* (Say)	321	1902	2016	Native	Fungi (Erisyphaceae)

Note: Data collection focused on native and alien species within the tribe Coccinellini and four additional species in the tribes Hyperaspidini, Chilocorini, and Psylloborini. Lady beetle species were characterized based on their status (native or alien to Ohio, USA) and their primary diet (aphids, scales, or fungi).

C. septempunctata (Linnaeus) (2.4% of total records; first detected in 1978), *Coccinella undecimpunctata* Linnaeus (0.02%; single record in 1953), *H. axyridis* (Pallas) (11.2%; first detected in 1993), *Hippodamia variegata* (Goeze) (0.2%; first detected in 2000), and *Propylea quatuordecimpunctata* (Linnaeus) (0.6%; first detected in 2003). Collections of alien species began to increase in the 1980s, with numbers surpassing natives in the 2000s and 2010s (Figure 2a). The proportion of native lady beetles in collections, including *A. bipunctata*, *C. novemnotata*, and *H. convergens*, has decreased in Ohio since the 1970s as alien lady beetles such as *C. septempunctata* and *H. axyridis* have increased (Figure 2b).

Temporal patterns of landscape and lady beetle community change

NMDS analyses identified parallel shifts in land cover and lady beetle composition that occurred from 1992 to 2016 (Figure 3). Land cover composition was similar among the 1938, 1970, and 1992 time periods, until substantial changes occurred in the 2016 time period (Figure 3a).

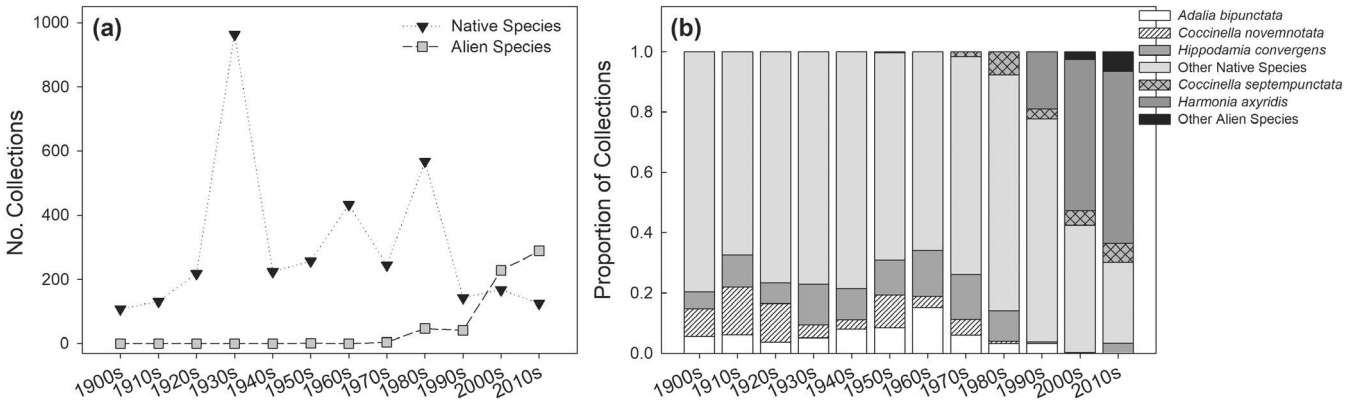

FIGURE 2 Number of collections (a) and proportion of collections (b) of native and alien lady beetle records from Ohio by decade from 1900 to 2018.

This shift corresponded to a decrease in agricultural land cover and an increase in forest and developed land cover across these time periods. Total and native lady beetle communities displayed a similar temporal response. Lady beetle species composition was similar among the first two time periods (before 1938 and 1938–1970), shifted slightly from 1971 to 1992, and then substantially changed in the final time period from 1993 to 2016 (Figure 3b,c).

Lady beetle species composition

Descriptive patterns of lady beetle taxonomic beta-diversity (β_{SOR}) across decades within the state of Ohio were the result of species turnover (β_{SIM}) and nestedness (β_{SNE}), but the strongest contributor to changes in lady beetle community composition shifted over time (Figure 4). Nestedness was the primary contributor to patterns of lady beetle beta-diversity before the establishment of alien species. Following the establishment of *C. septempunctata* and *H. axyridis* in the late 1970s and early 1990s, respectively, an increase in total beta-diversity was observed driven by increased species nestedness. From 1980 to 2018, species turnover increasingly became the stronger contributor, especially for aphidophagous species, and was the dominant driver of lady beetle beta-diversity by the 2010s (Figure 4).

Responses of native lady beetle species

Relative captures of all lady beetle species varied with time in models accounting only for sampling effort and using a normal error structure (see Appendix S3: Figure S1). However, these simple negative binomial models explained limited variation in the data. Native species were captured less per sampling effort later in the study period, but the steepness and timing of declines in captures varied by species (see Appendix S3: Figure S1A–E). The two alien species exhibited more variable patterns. Captures of *C. septempunctata* initially increased in effort-corrected captures but then decreased during the four decades it has been present in Ohio (see Appendix S3: Figure S1F). Conversely, captures of *H. axyridis* increased over the three decades since its establishment (see Appendix S3: Figure S1G). For *A. bipunctata* and *C. novemnotata*, statistically significant temporal patterns were not observed within the modeled time period, as both species had relatively stable capture frequency prior to the 1980s, but became extremely rare and then absent in later years of data collection. To provide meaningful model fits for the time when these species were present, years with zero-biased data were not included in their respective models. Sampling effort varied dramatically by year and location. Patterns of captures over time were not spatially static, as several native species also exhibited spatiotemporal dependencies over the study (i.e., changing spatial distributions with time; see Appendix S3: Table S1 and Figures S2–S6).

Species-specific patterns emerged in the negative binomial models that accounted for landscape change, invasion, and spatiotemporal factors, and model fit was much improved in all cases compared with models that did not account for these potential factors (Figure 5; see Appendix S3: Table S1). Captures of *A. bipunctata* exhibited a steep negative response to the increasing proportion of alien species in the community but also were positively associated with agriculture and developed land covers. Captures of *C. novemnotata* had a strong negative trend over time as well as spatial dependencies but only appeared to respond negatively to agricultural cover. Since captures of this native species had already begun to decline prior to invasions by *C. septempunctata* and *H. axyridis*, there was limited co-occurrence of *C. novemnotata* and any

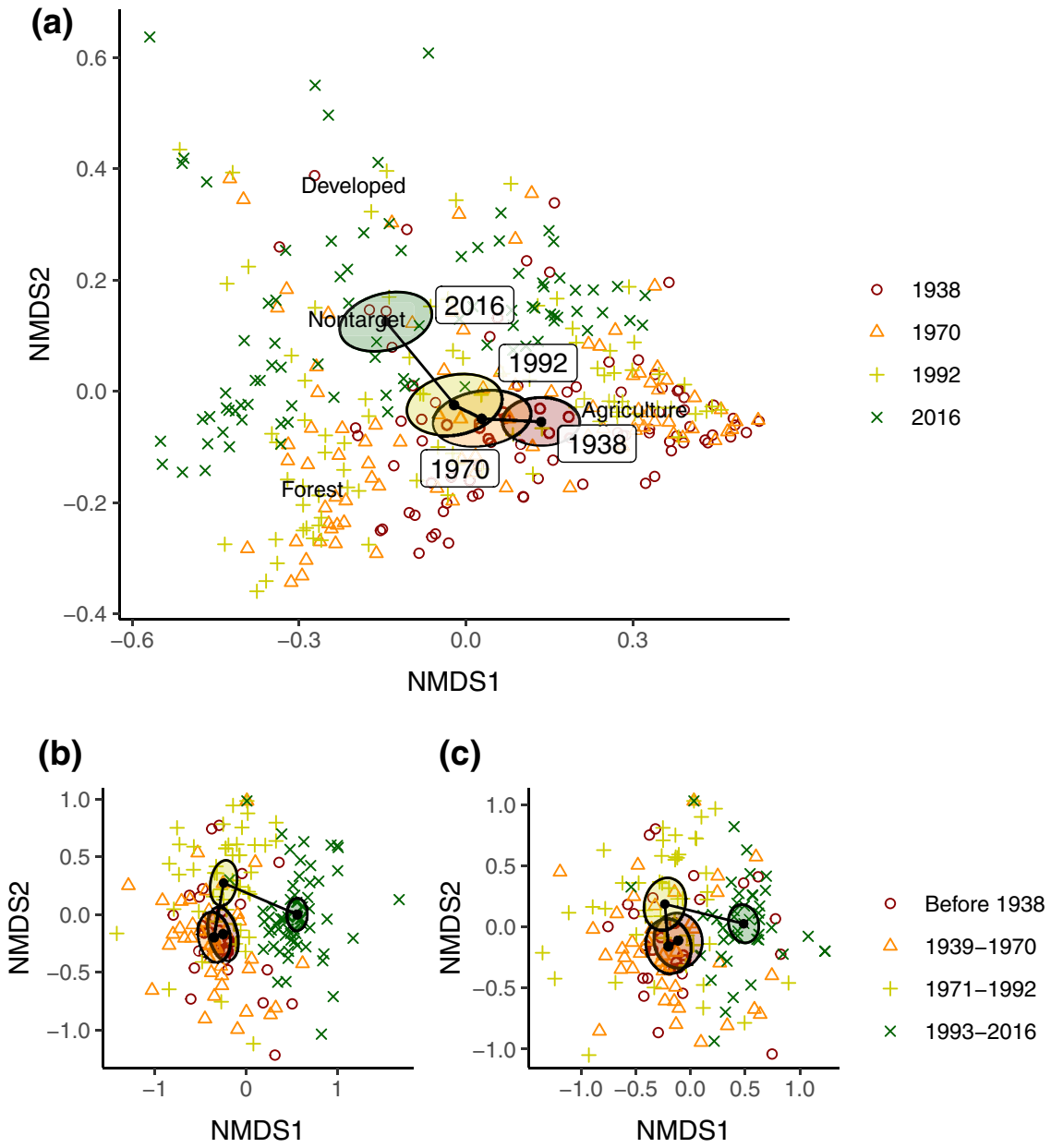

FIGURE 3 Changes in land cover composition by county (a), total lady beetle species composition by county (b), and native lady beetle species composition by county (c) across four time periods in Ohio. Shaded ellipses represent 99% confidence intervals around centroids. Centroids adjacent in time to each other are connected with a solid black line.

of the alien species (only five captures of *C. novemnotata* were recorded after 1980). Captures of *C. maculata* were relatively consistent in the earlier period of the study, with a slight increase peaking in the 1970s and 1980s, but a net decrease since. Our models suggest a relatively neutral effect of small numbers of alien lady beetles on *C. maculata*, but a negative impact as alien species become dominant (i.e., >50% of the lady beetles collected). Additionally, agricultural land cover had a slight positive association with captures of *C. maculata*. Captures of *H. convergens* had a negative trend over time and exhibited a differential response to the two dominant alien species: a positive association with *C. septempunctata* and a negative association with *H. axyridis*, as well as a positive association with higher values of developed land cover. Captures of *C. stigma* exhibited spatial dependencies, a positive association with forested habitats, and a negative association with the proportion of alien lady beetles in the community.

DISCUSSION

Specimen records can be harnessed to understand long-term biodiversity trends across various spatial scales in

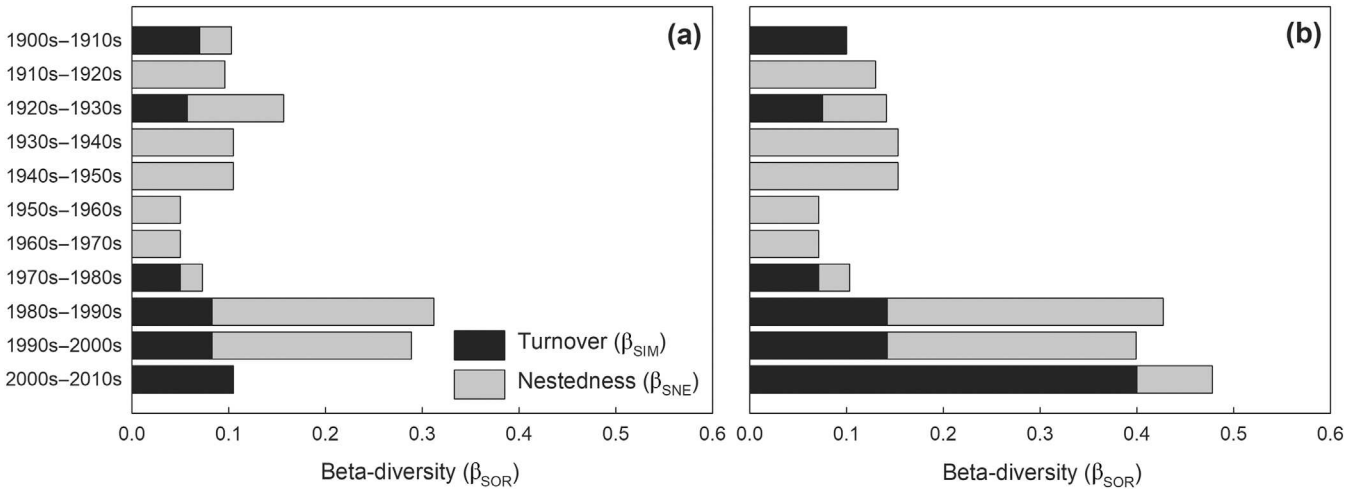

FIGURE 4 Descriptive patterns of taxonomic beta-diversity across decades for all lady beetle species (a) and aphidophagous lady beetle species (b) collected in Ohio. Total Sorensen dissimilarity (β_{SOR}) among decades was partitioned into two additive components: Turnover (β_{SIM}; reflects species replacement) and nestedness (β_{SNE}; reflects species loss or gain). Therefore, $\beta_{SOR} = \beta_{SIM} + \beta_{SNE}$.

response to anthropogenic threats (Lister, 2011; Meineke et al., 2019; Shaffer et al., 1998; Suarez & Tsutsui, 2004). Using historic land cover data and occurrence records of lady beetles collected in Ohio, USA, we documented parallel shifts in land cover and lady beetle composition that occurred from 1992 to 2016, aligning with decreased agricultural land cover and the establishment and spread of alien lady beetle species. Investigation of these patterns revealed evidence of declines in captures for several native species, but the timing and severity of declines as well as the relative importance of alien species and land cover change as long-term factors were species-specific. Observed changes in species composition that began in the 1980s indicated processes of species loss/gain and turnover that shifted communities toward dominance of a few alien lady beetle species.

Shifts in lady beetle species composition

As collections of some native species declined over time in Ohio, captures of alien lady beetle species increased following their establishment and spread. Beginning in the 2000s, alien species comprised over 60% of the total specimens collected, indicating a shift in lady beetle community structure and alien species dominance within the state. This shift in total and native lady beetle species composition first became evident in the 1971–1992 time period, which coincided with the establishment and spread of *C. septempunctata*, and this was followed by a more substantial shift in species composition during the 1993–2016 time period when *H. axyridis* became established and dominant. These patterns were further supported by changes in lady beetle beta-diversity across the state that began in the 1980s. From the 1980s to the 2000s, total beta-diversity of lady beetle species increased across decades, indicating that lady beetle communities became increasingly dissimilar within the state during the period that coincided with alien lady beetle establishment and spread. This increase in beta-diversity was initially driven by processes of species loss or gain (i.e., species nestedness), which is consistent with the establishment and spread of alien species within native lady beetle communities. From the 2000s to 2010s, the contribution of species turnover to patterns of beta-diversity increased compared with previous decades, especially for aphidophagous species, which suggests replacement of natives by alien species. High species replacement indicates that a similar number of lady beetle species were collected during these decades, but a low number were shared as species were replaced over time. Changes in lady beetle species composition from the 1900s to the 1970s were primarily driven by species nestedness. These patterns were likely the result of the loss and gain of uncommon native species in collections throughout the state, as well as the loss of common native species such as *A. bipunctata* and *C. novemnotata* which began to decline prior to alien species arrival.

A combination of species nestedness and species turnover that resulted in high dissimilarity in lady beetle species composition during the 1980s, 1990s, and 2000s is indicative of spatiotemporal loss and replacement of native species. By the 2010s, lady beetle communities had become more similar to each other in terms of species

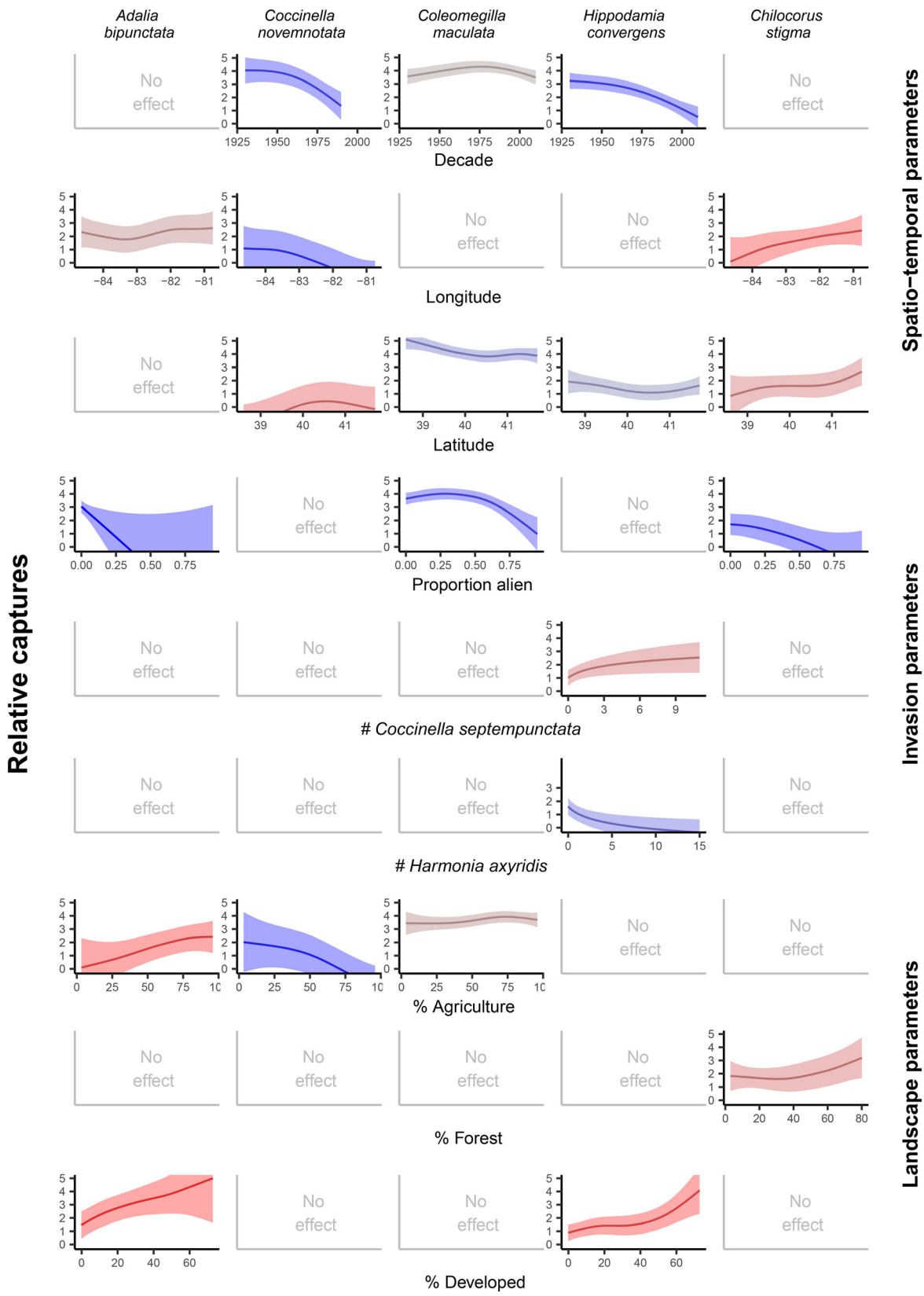

FIGURE 5 Matrix of partial generalized additive model (GAM) predictions of responses for five key native species to spatiotemporal, invasion, and landscape parameters. Negative binomial GAMs used Ohio museum collections, 1930–2018 data on lady beetle captures, and were adjusted for sampling effort. Predictions 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 (see Appendix S3: Table S1). Solid lines, shading represent 95% confidence intervals.

composition as indicated by the decrease in total beta-diversity and were dominated by alien lady beetle species. Similar shifts in lady beetle communities have been observed in response to the establishment of alien species (Alyokhin & Sewell, 2004; Bahlai et al., 2013; Elliott et al., 1996). For example, a shift in species dominance with the establishment of *C. septempunctata* in the 1980s was observed in potato fields in Maine, USA (Alyokhin & Sewell, 2004). Within 4 years of its establishment in southwestern Michigan, USA, *H. axyridis* was the dominant lady beetle species collected and was found in diverse habitats, including agricultural and old fields, and poplar plantations (Colunga-Garcia & Gage, 1998). Although the composition of lady beetle communities has become dominated by alien species, Bahlai et al. (2013) documented that their potential to suppress pest populations in agricultural and natural habitats had remained relatively consistent over time. As significant shifts in lady beetle communities have occurred across the Midwestern US, reliance on alien species to maintain pest suppression may be required for management, but further declines of native species may affect long-term resilience of this ecosystem service (Bahlai et al., 2021).

Drivers of native lady beetle decline

Using museum specimens collected over 12 decades, we documented declines in captures of the native species *A. bipunctata*, *C. novemnotata*, *H. convergens*, *C. maculata*, and *C. stigma*. The native species *A. bipunctata*, *C. novemnotata*, and *H. convergens* were once widely distributed across much of the United States (Gordon, 1985), with early surveys in Ohio recording these species across the state (Bubna, 1902; Dury, 1879). Now, these species are considered rare or potentially extirpated in much of eastern North America (Elliott et al., 1996; Gardiner et al., 2012; Wheeler & Hoebeke, 1995). For example, no captures of *C. novemnotata* or *A. bipunctata* were found after 1985 and 1996, respectively, suggesting their populations were below the detection threshold or extirpated within the state of Ohio. Major drivers of declines in native biodiversity remain the establishment and spread of alien species and habitat loss from land use change (Lövei, 1997; Newbold et al., 2015; Seibold et al., 2019; Vitousek et al., 1997; Wilcove et al., 1998). Our findings revealed that captures of native lady beetles responded to both stressors.

As alien lady beetle species increased in dominance, declines in captures of *C. maculata*, *H. convergens*, and *C. stigma* were associated with these invaders, although the magnitude and timing of the effects were species-specific. For example, collections of *H. convergens* declined with captures of *H. axyridis* but increased with captures of *C. septempunctata*. These divergent patterns highlight that alien lady beetle species are not ecologically equivalent, and instead, can have different impacts on native species. Moreover, *C. stigma* is coccidophagous, and declines in captures of this native species suggests that aphidophagous alien lady beetles may affect non-aphidophagous native species to some extent. The magnitude of decline in native lady beetles is predicted to be linked to competitive interactions and degree of niche overlap with alien lady beetle species (Bahlai et al., 2015). The competitive exploitation hypothesis posits that decline in populations of native species would occur following the establishment of functionally similar alien species that are superior competitors (Snyder, 2009). In this study, collections of alien species were predominantly *C. septempunctata* and *H. axyridis*, both of which feed on a wide variety of aphid prey and are efficient competitors (Angalet et al., 1979; Bahlai et al., 2013; Hodek et al., 2012; Koch, 2003). Decline of *C. stigma* immediately following the establishment of *H. axyridis* has been reported in southwestern Michigan, USA, further suggesting potential competitive interactions among these species (Colunga-Garcia & Gage, 1998). Although *H. axyridis* is primarily aphidophagous (Koch, 2003), this species also feeds on scale insects in arboreal environments (Mcclure, 1986), which suggests some degree of dietary and habitat overlap with *C. stigma*. *C. maculata* is known to be a strong aphidophagous competitor (Long & Finke, 2014), and this species remains one of the most frequently collected native lady beetles in croplands, grasslands, and home gardens (Gardiner et al., 2021; Smith & Gardiner, 2013). For example, *C. maculata* was the most commonly collected native lady beetle in residential gardens across the state of Ohio by community scientists (Gardiner et al., 2012, 2021). However, decline in *C. maculata* populations were reported during a long-term (two decadal-scale) study in southwestern Michigan (Bahlai et al., 2015). *C. maculata* feeds on pollen in addition to aphid prey (Dixon & Dixon, 2000; Hodek et al., 2012; Majerus, 2016), and this pollen feeding was hypothesized to reduce competition with alien species (Bahlai et al., 2015). However, there is evidence that *H. axyridis* and *C. septempunctata* also feed on pollen as a supplemental food resource when arthropod prey is scarce (Berkvens et al., 2008, 2010; Ricci et al., 2005), which may suggest the competitive impacts of alien species on *C. maculata* have been underestimated.

We found evidence that declines in captures of the aphidophagous species *A. bipunctata* and *C. novemnotata* began prior to the arrival and dominance of alien lady beetle species. Declines in captures of *A. bipunctata* began in the 1960s, with the last collection in Ohio in

1996. Since the arrival of *C. septempunctata* in 1978, there were only 13 individuals of *A. bipunctata* collected from the state. Although our findings indicated that alien species likely contributed to declines in captures of *A. bipunctata* to some degree, declines in captures prior to the arrival of alien species suggests other contributing factors such as landscape change. Captures of *C. novemnotata* began to decline in the 1950s, with the last Ohio collection occurring in 1985. Since the arrival of *C. septempunctata* in Ohio, only 12 individuals of *C. novemnotata* were recorded. This finding contrasts with many studies across the United States that have hypothesized declines of *C. novemnotata* were related to competitive displacement by *C. septempunctata* (Snyder & Evans, 2006; Staines et al., 1990; Ugine et al., 2018; Wheeler & Hoebeke, 1995).

Land cover change was an important factor for several native lady beetles, although responses were highly species-specific. For example, positive, neutral, and negative responses to the percentage of agricultural land cover were documented. Captures of *C. novemnotata* decreased with the percentage of agricultural land cover, while collections of *A. bipunctata* increased. Since the 1930s, the amount of agricultural land cover has decreased within the state, but the spatial extent of these changes was highly variable and not consistent across all Ohio counties. This loss of agriculture was primarily in the eastern region of the state, while western Ohio remained dominated by agricultural land cover throughout the study period. Along with these changes in the extent of agricultural land cover, landscapes have experienced a shift from more diversified cropping systems to highly managed crop monocultures since the mid-1900s (Crossley et al., 2021). *C. novemnotata* has a broad ecological niche (Losey et al., 2007), and populations have been found in a variety of cultivated crops (Wheeler & Hoebeke, 1995), including alfalfa (Goodarzy & Davis, 1958; Pimentel & Wheeler, 1973), corn (Smith, 1971), cotton (Bell & Whitcomb, 1964), soybeans (Dumas et al., 1964), and fruit trees (Oatman et al., 1964; Putman, 1964). Simplification of agricultural landscapes due to loss of natural habitat, reductions in crop diversity, and insecticide use may impact temporal prey availability and diversity as well as refuge and overwintering habitats that are required for predatory insect species such as *C. novemnotata* (Rusch et al., 2016).

Of the species investigated, *C. stigma* was the only native lady beetle associated with forest land cover, with captures increasing as the percentage of forest increased at the county level. This response is likely linked with the ecology of this species. Scale insects are common pests of trees in managed and natural forests. Further, *C. stigma* is reported to oviposit eggs in bark cracks and crevices as well as overwinter as adults in the leaf litter layer (Mayer & Allen, 1983). Similar positive associations with forests have been reported in other native lady beetle surveys. For instance, the amount of forest habitat at a 2 km landscape scale was positively associated with the abundance and species diversity of native lady beetles within residential gardens (Gardiner et al., 2021). We hypothesize that the conservation value of forests for native lady beetles may be underestimated, but additional research is required to understand when and how native species are utilizing these habitats.

Conclusions

Using specimen records collected over 118 years in Ohio, USA, we documented shifts in lady beetle species composition beginning in the 1980s as communities became increasingly dominated by alien species. Additionally, we documented a parallel shift in land cover composition during the same time periods that resulted from the replacement of agriculture by forest and developed land. Because of uneven sampling inherent to museum collections, total records of native lady beetles varied from year to year. Therefore, we were unable to make inferences about changes in absolute abundance for a given species, and instead, make our interpretations from proportional capture rates at the community-level. Unknown sampling effort in early museum records is a limitation of any studying utilizing museum data (Bartomeus et al., 2013), and species records are often more numerous within recent decades (Colla et al., 2012), with some evidence that this is due to increased sampling effort (Jeppsson et al., 2010). Our method likely provides a conservative estimate of individual species decline, as it assumes the net community of lady beetles, inclusive of alien species, has remained roughly stable, and changing rates of captures across the community through time are associated with sampling effort. Although occupancy models have been used to attempt to account for wide variation in sampling intensity in similar museum records (Erickson & Smith, 2021), these methods are generally dependent on large amounts of metadata to properly parameterize the models to give authentic estimates of absolute abundance (Guzman et al., 2021). Likewise, comprehensive land cover data at the spatial and temporal resolution required for other modeling techniques are not readily available for studies focused on time periods before contemporary remote sensing technology. Given the limitations to the available specimen and land cover data in our case, our methodology and results were constrained and must be interpreted with these constraints in mind, including that they cannot provide evidence that native lady beetle populations are declining in abundance.

Despite these data limitations, we detected evidence of shifts in dominance of lady beetle communities from native to alien species and declines in captures of several native lady beetle species, including several aphidophagous species and a coccidophagous species, via decreasing representation in the collected community of lady beetles.

The use of long-term specimen records facilitated investigation of the relative importance of the establishment of alien species and landscape change as contributing factors to the decline in captures of native lady beetles. Although the establishment of alien species and landscape change have been identified as major drivers of spatiotemporal patterns in insect populations (Fox et al., 2014; Sánchez-Bayo & Wyckhuys, 2019; Seibold et al., 2019), the causes of declines are likely more complex and multifaceted (Homburg et al., 2019; Wagner, 2020; Wagner et al., 2021). Our study underscores this complexity by documenting how captures of closely related native lady beetle species displayed opposing, species-specific responses to alien species and land cover change, as well as variation in captures over time and space that were not well explained by either of these factors. For several native species investigated, the dominance of alien lady beetles was identified as a major contributor to declines in captures, but other native species responded strongly to land cover change and captures began to decline prior to alien species establishment. Importantly, we are unable to disentangle the effects of historical changes in land cover with insecticide use and more recent intensification and simplification of agricultural landscapes on these observed trends in captures. Some native lady beetle species also responded strongly to spatiotemporal factors which may be the manifestation of climate change signals on the community, although this driver cannot be explicitly tested due to the resolution at which historical specimen data are available.

Although alien species and landscape change were important predictors, declines in captures of native lady beetles were highly species-specific, emphasizing that mechanisms driving population losses cannot be generalized even among closely related species. Additionally, this finding highlights the importance of species-level data when investigating temporal trends in insect populations. Species-specific responses of native lady beetles to these factors have important implications for conservation management programs. Increased dominance of alien lady beetles in native communities suggests that reliance on these species may be required to maintain successful pest management in the future (Bahlai et al., 2021). The importance of landscape change as a driver structuring the distributions of lady beetle populations suggests biodiversity conservation management is required at the landscape scale. Landscape scale management will need to balance the opposing needs of native species to be effective, as there is not one inclusive strategy that will aid in native lady beetle conservation. Due to the differential responses of native species to land cover type, prioritizing habitat diversity at the landscape scale, especially in agricultural systems, may be an important component in future conservation management. Native lady beetle species are key predators of aphids, scales, psyllids, mites, fungi, and other pests (Evans, 2009; Hodek & Honěk, 2009; Weber & Lundgren, 2009), contributing broadly to biological control in agricultural systems (Caltagirone & Doutt, 1989; Obrycki & Kring, 1998; Rondoni et al., 2021). Further declines of native species in response to alien lady beetles, landscape change, or other drivers such as climate change may disrupt the long-term resilience of this ecosystem service. Understanding how these major anthropogenic drivers influence long-term trends in native lady beetle populations will inform the conservation of this ecologically and economically important family of insects.

AUTHOR CONTRIBUTIONS

Mary M. Gardiner, Kayla I. Perry, and Christie A. Bahlai conceived, designed, and implemented the study. Kayla I. Perry, Christopher B. Riley, Katherine J. Turo, Leo Taylor, James Radl, Yvan A. Delgado de la flor, and Frances S. Sivakoff compiled the specimen data. Kayla I. Perry, Christie A. Bahlai, and Timothy J. Assal analyzed and interpreted the data. Kayla I. Perry wrote the first draft of the manuscript. All authors reviewed and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Bahlai & Perry, 2024) are available in Zenodo at https://doi.org/10.5281/zenodo.11263088. Ohio lady beetle records were compiled from the 25 institutions listed in Appendix S1: Table S1, with query details for obtaining these data in Appendix S1: Section S1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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