**Title:** Coexistence between similar invaders: The case of two cosmopolitan exotic insects

Matthew B. Arnold[1], Michael Back[1], Michael Daniel Crowell[2], Nageen Farooq[3], Prashant Ghimire[1], Omon A. Obarein[2], Kyle E. Smart[3], Trixie Taucher[1], Erin VanderJeugdt[1], Kayla I. Perry[1], Douglas A. Landis[4], Christie A. Bahlai[1,5]*

[1] Department of Biological Sciences, Kent State University, Kent, Ohio, United States of America, 44242

[2] Department of Geography, Kent State University, Kent, Ohio, United States of America, 44242

[3] Department of Geology, Kent State University, Kent, Ohio, United States of America, 44242

[4] Department of Entomology, and Great Lakes Bioenergy Research Center, Michigan State University, East Lansing, Michigan, United States of America, 48824

[5] Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan, United States of America, 49060

*corresponding author, cbahlai@kent.edu

**Abstract**

Biological invasions have become widespread, threatening native biodiversity and ecosystem services. However, most studies have focused on the impacts of exotic species on natives, and fewer have examined dynamics between invaders, when multiple adventive species successfully coexist in a novel environment. Exotic lady beetle species were introduced into North America for biological control in agricultural systems and have since become dominant species within many native communities. Competitive interactions have been primarily investigated among native and exotic lady beetle species to assess mechanisms of decline and the impact of invasion, and yet two species of invaders, *Harmonia axyridis* and *Coccinella septempunctata* have become co-dominant in many of these communities. In this study, we investigated coexistence via spatial and temporal niche partitioning among *H. axyridis* and *C. septempunctata* using a 31-year dataset from southwestern Michigan, USA. We found evidence of long-term coexistence of these two invaders through a combination of small-scale environmental, habitat, and seasonal mechanisms. Across years, *H. axyridis* and *C. septempunctata* experienced patterns of cyclical dominance likely related to yearly variation in temperatures and precipitation. Within years, populations of *C. septempunctata* peaked early in the growing season around 550 degree days, while *H. axyridis* populations peaked later in the season around 1220 degree days. Habitat preferences for *C. septempunctata* were primarily crops such as soybean, wheat, and alfalfa, whereas *H. axyridis* did not display strong habitat preferences. These findings suggest that within this region *H. axyridis* is a broad habitat and environmental generalist, while *C. septempunctata* has more specific environmental niche preferences. These ecological differences have contributed to the continued coexistence among these two invaders, seemingly via the storage effect. Understanding mechanisms that allow coexistence and success of dominant exotic species contributes to native biodiversity conservation management of invaded ecosystems.

**Keywords**: Biocontrol, biological control, *Coccinella septempunctata*, Coccinellidae, *Harmonia axyridis*, invasion, niche partitioning

## Introduction

The establishment and spread of exotic species is a major driver of global environmental change, threatening native biodiversity, ecosystem services and functions, and human well-being (Vitousek et al. 1996, Wilcove et al. 1998, Millennium Ecosystem Assessment 2005, Ricciardi 2007). Invasions of insect species have occurred on a global scale through intentional or unintentional introductions, resulting in substantial economic and ecological impacts (Kenis et al. 2009, Bradshaw et al. 2016). Ecological impacts of exotic insects are pervasive, affecting native species and ecosystems directly and indirectly (Kenis et al. 2009). For example, when exotic insects can successfully establish and spread within their introduced range, novel communities are formed where native and exotic species may interact directly through herbivory, predation, and parasitism (Liebhold et al. 1995, Boettner et al. 2000, Holway et al. 2002, Snyder and Evans 2006). Additionally, exotic species may cause indirect and/or cascading ecological impacts via various mechanisms such as exploitative and apparent competition, disease transmission, and alteration of habitat or food resources (Louda et al. 1997, Holway et al. 2002, Morin et al. 2007, Gandhi and Herms 2010, Klooster et al. 2018). As the frequency of biological invasions continues to increase globally (Lockwood et al. 2013, Seebens et al. 2017), research investigating novel interactions among native and exotic species is essential for assessing impacts of invaders as well as developing management strategies to conserve biodiversity.

Successful invasion of native communities by exotic species is context dependent and influenced by multiple factors such as abiotic environmental conditions, properties of the native community, and characteristics of the invading species (Blackburn et al. 2011, Lockwood et al.

2013). Because establishment success or failure is influenced by local niche processes and interactions among species, hypotheses that have been proposed to explain the outcome of the establishment stage in the invasion process draw on concepts within niche and coexistence theory (Godoy 2019). For example, the diversity-invasibility hypothesis (i.e. the biotic resistance hypothesis) predicts that more diverse native communities are more stable, and thus more resistant to the establishment of exotic species than less diverse communities (Jeschke 2014). This prediction is based on the premise that less diverse communities have more vacant niches available to invaders and a lower probability of occurrence of strong competitors or predators that could limit coexistence (Levine and D'Antonio 1999, Ricciardi et al. 2013). Long-term coexistence rather than exclusion of exotic species within native communities is determined through stabilizing (niche differences) and equalizing (fitness differences) mechanisms wherein species vary in their environmental responses, resource acquisition, and/or competitive ability (Chesson 2000a, HilleRisLambers et al. 2012). Research has primarily focused on understanding interactions among native and exotic species within invaded communities to discern ecological impacts (e.g. Ricciardi et al. 2013). However, biological invasions have become widespread such that native communities are more commonly invaded by multiple exotic species which then directly or indirectly interact with each other to promote or inhibit coexistence.

Lady beetles (Coleoptera: Coccinellidae) are predatory insects that have been intentionally introduced for biological control in agricultural systems (Caltagirone and Doutt 1989, Obrycki and Kring 1998, Koch 2003, Rondoni et al. 2021). This has led to the successful establishment and spread of several exotic lady beetle species, including the Asian species *Harmonia axyridis* (Pallas) and the European species *Coccinella septempunctata* (Linnaeus) in North America. Both species are considered habitat generalists and primarily aphidophagous (Koch 2003, Hodek and Michaud 2008) but will feed on other arthropod prey and pollen if aphid resources are scarce (Angalet et al. 1979, Ricci et al. 2005, Berkvens et al. 2008, 2010, Evans

2009), making these invaders strong competitors. The establishment and spread of *H. axyridis* and *C. septempunctata* have coincided with declines in several native lady beetle species, while both invaders have been found to coexist (Turnock et al. 2003, Alyokhin and Sewell 2004, Harmon et al. 2007, Roy et al. 2016). For example, *H. axyridis* and *C. septempunctata* were highly abundant within native lady beetle communities that were sampled over 24 years in southwestern Michigan, USA (Bahlai, Colunga-Garcia, et al. 2015). Because *H. axyridis* and *C. septempunctata* have become the dominant lady beetles within many native communities (Alyokhin and Sewell 2004, Harmon et al. 2007, Bahlai, Colunga-Garcia, et al. 2015), direct and indirect forms of competition are hypothesized as drivers of declines in native species (Pell et al. 2008, Li et al. 2021).

Competitive interactions have been primarily investigated among native and exotic lady beetle species to assess mechanisms of decline and the impact of invasion (Pell et al. 2008). These generalist exotic species share similar preferences in habitat and prey as some native lady beetles such that the degree of niche overlap with functionally similar invaders is hypothesized to drive competitive interactions (Snyder 2009). Apparent competition (Smith and Gardiner 2013) and intraguild predation (Gagnon et al. 2011, Thomas et al. 2013) have been observed among native and exotic species in the field, lending some support to this hypothesis. Evidence of exploitative competition also has been observed wherein competition from exotic species for shared prey has shifted the habitat use patterns of native species from agricultural to natural environments such as forests (Grez et al. 2013, Bahlai, Colunga-Garcia, et al. 2015).

Less is known about competitive interactions among the two invaders *H. axyridis* and *C. septempunctata*, both of which are considered efficient competitors and habitat generalists (Koch 2003, Hodek and Michaud 2008) but are known to coexist within similar environments. High levels of intraguild predation among larvae of *H. axyridis* and *C. septempunctata* have been observed in the laboratory (Snyder et al. 2004) and in the field (Gagnon et al. 2011), suggesting this competitive interaction may be common among these exotic species. Outcomes

of competitive interactions such as intraguild predation are influenced by the relative body size, mobility, age, and diet specificity of larvae as well as prey density (Hironori and Katsuhiro 1997, Yasuda et al. 2004). Larvae of *H. axyridis* tend to be larger and more aggressive than other lady beetle species including *C. septempuncata* (Yasuda et al. 2001, Ware and Majerus 2008), which may translate to an asymmetric competitive advantage. For example, larvae of *H. axyridis* were more successful at escaping attacks from *C. septempunctata*, thereby having a greater negative impact on the survival of *C. septempuncata* larvae (Yasuda et al. 2001). If high levels of competition occur asymmetrically among these exotic species in favor of *H. axyridis*, other forms of niche partitioning likely facilitate coexistence of these invaders over time. Research from other locales where these species co-occur have pointed to behaviors leading to differential use of habitats and environment. For instance, *H. axyridis* may have better overwintering survival in very cold environments than *C. septempunctata* due to their behavior of retreating to more temperate locations found in buildings or hibernating under tree bark (Roy et al. 2016, Cheng et al. 2020), leading to more substantial population numbers in spring and earlier reproduction than *C. septempunctata* (Cheng et al. 2020). Improved understanding of the mechanisms that allow coexistence and success of these dominant exotic species will inform biological control programs as well as biodiversity conservation management of invaded ecosystems.

To understand how *H. axyridis* and *C. septempunctata* have coexisted within native lady beetle communities over time, this study investigated environmental, habitat, and seasonal niche partitioning among these two dominant exotic species using a 31-year dataset from southwestern Michigan, USA. These long-term data allowed for the spatiotemporal analyses of abundances of both exotic lady beetle species within 9 plant habitats embedded within an agricultural landscape. Our goals were to evaluate environmental and ecological factors that may facilitate coexistence among these two species. We hypothesized that coexistence of these exotic species may occur via: 1) temporal niche partitioning with differing phenology among

species; or 2) spatial niche partitioning with differing habitat and/or environmental preferences among species.

## Methods

*Study system description*

Data for this study were collected at the Kellogg Biological Station Long-Term Ecological Research (KBS LTER) site located in South-West Michigan, United States of America. Our study focuses on data produced in the Main Cropping System Experiment (MCSE) at KBS LTER, a long-term agronomic experiment started in 1989, and incorporates data from the forest plots as well, where an identical monitoring scheme was initiated in 1993 to gain insight into reference conditions adjacent to the MCSE site. The experiment consists of an annual crop rotation (maize, soybean, wheat) maintained under four levels of management intensity, three perennial cropping systems (alfalfa/switchgrass, poplar tree plantation, and early successional vegetation maintained by yearly burnings), and three forest types (successional forest on reclaimed cropland, old growth deciduous fragments, and conifer plantations) to form 9 total plant communities. This research site has supported a wide variety of investigations of long term ecological dynamics of agricultural systems, including agronomic, biogeochemical, and population processes (Bhardwaj et al. 2011, Syswerda et al. 2012, Gelfand and Robertson 2015, Hermann et al. 2016, Cusser et al. 2020), providing unprecedented context for interpretation of subtle ecological trends. Within each research plot, data were collected at five subsampling stations, with most measurements taken within the growing season (May to September of each year). Lady beetle populations are the focus of the insect survey, although several other taxa have also been recorded in more recent years (Colunga-Garcia et al. 1997, Colunga-Garcia and Gage 1998, Hermann et al. 2016).

The present study focused on the dynamics of two species of adventive coccinellids. The KBS LTER insect survey was established in 1989, soon after the arrival of *C.*

*septempuntata* at the site (Maredia et al. 1992). *Coccinella septempunctata* is a large, generalist lady beetle believed to have been intentionally introduced to North America from Europe (Schaefer et al. 1987), but is now Holarctic in distribution (Hodek and Michaud 2008). Soon after its establishment in the eastern United States in the late 1980s, it became the dominant species of Coccinellidae, with its numbers being linked to decreasing numbers of native species in several agroecosystems (Colunga-Garcia 1996, Evans 2004). However, by 1994, another invading lady beetle arrived at KBS LTER. Like *C. septempunctata*, *Harmonia axyridis* is a generalist predator that thrives in many habitat types with a now near-global distribution (Adriaens et al. 2008, Roy et al. 2016). Originally native to the Asian continent from northeastern China to Siberia (Roy et al. 2016), this species has been introduced as a biological control agent since the early 20$^{th}$ century to both North America and Europe (Roy et al. 2016, Sethuraman et al. 2018, Cheng et al. 2020). Although *C. septempunctata* is generally thought to be a European species, some sources note that the natural, or at least naturalized range of both *H. axyridis* and *C. septempunctata* have overlapped, and thus the two species have co-occurred in parts of China for quite some time (Cheng et al. 2020).

Annual insect surveys were performed at the KBS LTER since 1989 using yellow sticky traps, placed at pemanament sampling stations within the MSCE and adjacent forest sites. Yellow sticky traps were placed on T-posts, held at 1.2 m above the ground at each sample station during the growing season. Sample collection periods varied from 8-15 weeks during the sampling period in a year depending upon management intervention (e.g crop management), environmental conditions (e.g weather), and labor availability (Bahlai et al. 2013, Bahlai, Colunga-Garcia, et al. 2015). Traps were inspected weekly, and lady beetles captured were identified to species, and observations were recorded as the number of adults, by species, by date.

In addition to the species count data, we compiled contextual data from the weather station records available from the KBS site (https://lter.kbs.msu.edu/datatables/7). Because

some missing measurements occurred in these data, we adapted a gap-filling algorithm which took the average of the proceeding and immediately following measurement, then substituted this value for any blank observations (Hermann et al. 2016). This manipulation allowed reasonable estimates of cumulative weather data metrics to be calculated.

*Analysis approach*

Insect data were examined at two different temporal resolutions. First, to match the typical sampling frequency during the growing season, data were aggregated into weeks (records taken within each Monday to Sunday period to account for differences in sampling day which may have occurred due to weather, labor, *etc*.). These weekly data were also aggregated across subsamples, and subsample numbers were tallied to account for any variation in sampling effort due to lost traps. A typical sample represented all individuals of each target species captured each week within a treatment by repetition combination, with the total actual traps (usually 5) reported for this time recorded as a sampling effort covariate. Yearly data were compiled in a similar way, except data were aggregated across sampling weeks as well, and reported as total captures of a given species, per treatment by repetition combination, with a covariate per sampling effort (~50 traps per year). Data were culled at the first week of September (week of year = 35) as data collection usually ended by late August at the site over the study period, so records beyond that point were sparse most years.

Weather data were aggregated at complementary resolutions to accompany each temporal resolution of lady beetle data. For weekly data, we computed degree day and precipitation accumulation (after Hermann et al 2016) within each week, and then aggregated over the growing season, using a baseline development threshold of 10°C and a starting date of the beginning of the calendar year (January 1). We also computed several derived weather metrics appropriate to the resolution of the insect data (number of rainy days within an observation week, minimum and maximum temperatures observed within that sampling week).

For yearly data, we computed several derived metrics to characterize weather at a coarser level within a given year, through the growing season. For this, we used four key time points (week of year 20, 25, 30, 35) and computed the degree day and precipitation accumulation at each, allowing us to examine how periods of weather of a given type affect the overall number of each species observed in a given year.

To examine patterns of habitat use between the two species by time period, we conducted 2-D non-metric multidimensional scaling (NMDS) analyses on each data resolution (Oksanen et al. 2013). First, data were subjected to square root transformation and Wisconsin double standardization, and then were subjected to a permutational ANOVA to determine if statistical differences occurred between the two species in their habitat use at either time period (Oksanen et al. 2013). Environmental variables were then fitted to the NMDS for each temporal resolution. Parameters used in the final model were selected from a global model with all computed weather parameters present, subject to backwards selection to simplify a final model with parameters with the strongest explanatory results.

To examine the within-season dynamics between our two lady beetle species and the roles of multiple environmental factors in driving abundances of each species, we constructed a generalized additive model for the number of lady beetles observed, where each parameter tested was allowed to interact with species, allowing us to directly examine how each species response to a given parameter differed. All model structures tested included an offset for trapping effort, used a quasi-Poisson error structure, and smoothing parameters were fitted using restricted maximum likelihood (REML) (Wood 2006). Because of strong autocorrelation between many weather parameters, we used a substitution-based model selection approach by substituting a parameter of each type (temperature, precipitation) and evaluating model performance. Our final model included parameters for degree day accumulation, number of rainy days within the sampling week, and year, as well as a categorical variable for habitat of capture.

Between-year dynamics of the two species were modeled similarly to within-year dynamics, except in this case, because we wanted to allow different conditions to act as drivers for each species, we constructed separate models and corresponding model selections for each species. All models contained offset terms to account for sampling effort, a categorical variable for plant community of capture, and used a quasi-Poisson error structure. Smoothing was performed using REML. Each of these models for the number of adults of a given species also included a covariate for the number of adults of the other species, to assess for apparent competition. Because of collinearity and concurvity between several parameters, we first conducted a Spearman Rank correlation analysis on all weather variables to determine parameters most likely to pose concurvity issues when used simultaneously. Then we completed a forward selection of all environmental variables, first running each parameter on its own in a model, selecting the model containing the parameter with the best performance, adding the next-best parameter that was not correlated with the best parameter ($\rho<0.3$), running the model, and assessing fit and concurvity. This procedure was repeated until there were no more parameters that could be added without causing a concurvity estimate >0.5 for any of the existing parameters. For all environmental parameters tested, smooths were limited to a maximum of three knots to minimize the impact of outlying data points on the overall trends observed and to prevent overfitting.

All data manipulation and aggregation, and quality control, as well as all exploratory and analytical approaches were completed in R 4.1.1.(R Development Core Team 2017). The analysis code and the complete development history are available at https://github.com/ReproducibleQM/space_invader

## Results

*Descriptive*

For conciseness within the results, we have abbreviated *Coccinella septempunctata* as C7 and *Harmonia axyridis* as HA. After culling data in the first week of September in all years and in 1994, after HA arrived, we observed nearly equivalent total captures of the two species, with approximately 20,000 individuals of each species collected at the site (specifically, 19,637 individuals of C7 and 20,412 of HA). Raw abundance and habitat use patterns varied by species but highly overlapped (Fig. 1). At the initiation of the study, C7 dominated at higher numbers but HA steadily increased until the mid 2000s, and then the two species appeared to undergo a cyclical switching off in dominance for the most recent 15 years of the study (Fig. 1A). Both species were present in all habitats examined, although C7 was more commonly captured in wheat than HA, and HA was more common than C7 in all forest treatments (Fig 1B).

*Multivariate analysis*

Habitat use patterns varied between the two species at both the yearly ($F=14.25$, $R^2=0.04$, $p=0.001$) and weekly ($F=21.93$, $R^2=0.03$, $p=0.001$) temporal resolution. Non-metric multidimensional scaling (Fig 2) suggested a distinct but overlapping pattern of spatio-temporal distribution between the two species at both temporal resolutions. Some measures of precipitation and degree day accumulation were included in the best model for environmental drivers of the distribution of observations in both cases, suggesting these drivers both impacted the within-season and between-season dynamics of the two species. At the yearly resolution, the final variables included in the environmental model were degree day accumulation at 35 weeks ($r^2=0.086$, $p=0.001$), precipitation accumulation at 35 weeks ($r^2=0.064$, $p=0.001$), and the year (treated as a continuous variable; $r^2=0.025$, $p=0.017$). At the weekly resolution, the environmental model included within-season degree day accumulation ($r^2=0.0328$, $p=0.001$), within-season precipitation accumulation ($r^2=0.014$, $p=0.001$), and the year (treated as a continuous variable; $r^2=0.011$, $p=0.045$). In both cases, year and precipitation accumulation plotted as nearly perfectly collinear, but moving in opposite directions, but the degree day

accumulation factor plotting with a larger orthogonal component, more closely corresponding to the axis of differentiation between the distributions of the two species.

*Within-season GAM model*

The final model for within season captures of lady beetles (-REML=27394, n=27432, Deviance explained = 33.3%) included terms for the categorical variables of habitat (F= 144.42, df=8, p<0.001), species (F= 15.04, df=1, p<0.001), and the interaction between habitat and species (F= 79.09, df=8, p<0.001), as well as smoothing terms for degree day accumulation, number of rainy days, and year, each interacting with species (Table 1, Fig. 3).

**Table 1: Within-season multivariate model results explaining the spatio-temporal distribution of the two lady beetle species from relative capture counts.**

| Term | Effective degrees of freedom | F | p-value |
|---|---|---|---|
| Degree days : C7 | 6.28 | 169.63 | <0.001 |
| Degree days : HA | 6.84 | 94.75 | <0.001 |
| Rain days : C7 | 1.97 | 28.56 | <0.001 |
| Rain days : HA | 1.96 | 1.04 | 0.349 |
| Year : C7 | 8.21 | 120.41 | <0.001 |
| Year : HA | 8.18 | 121.10 | <0.001 |

The majority of within-season variation in both species was attributable to habitat of capture and degree day accumulation. Both species exhibited strong, differential within-season

responses to degree day accumulation (Fig 3A). Using the instantaneous rate of change of the line of best fit, we computed the approximate degree day accumulations where activity peaks occurred. C7 had a large activity peak early in the season at approximately 550 degree days accumulated, and a slight peak later in the season at an accumulation of 1210 degree days. HA had a major late season activity peak near 1220 degree days accumulation, and populations remained high thereafter, and we observed two lesser early season activity peaks near 410 and 690 degree days respectively. Although model selection favored the inclusion of a term describing the number of rainy days in the week when observations were taken, this term explained very little variation for HA, and suggested perhaps a slight increase in C7 activity in weeks that were consistently rainy (Fig 3B). Once other factors were controlled for in the model, residual habitat use patterns between the two species became strikingly differential: residual captures of HA were relatively consistent in all habitats, but C7 was much more variable (Fig 3C). Finally, once within-year factors were controlled for, year-to-year dynamics of both species still contributed considerable variation to the captures (Fig 3D).

*Between-year model*

In the examination of between-year dynamics of the two species, model selection favored GAM models with four environmental parameters for both species (Table 2), with three of these factors overlapping between models. The C7 model explained more variation in the year-to-year abundance of this species (-REML=2092, n=1353, Deviance explained = 69.7%) than the model for HA abundance (-REML=2219, n=1353, Deviance explained = 40.0%). In general, relationships between HA and environmental parameters were slight, and HA abundance peaked near the mean values of each parameter in 3 out of 4 environmental parameters included in the model (Figure 4), suggesting that while HA is not affected strongly by environmental conditions, it generally is most abundant in years when conditions are near the mean. C7 was observed to have both generally stronger responses to environmental

conditions, but also, was more negatively associated with mean conditions, i.e. having higher numbers in years associated with cooler later summer conditions and dryer conditions prior to and early in the growing season.

**Table 2: Between-year multivariate model results explaining the spatio-temporal distribution of the two lady beetle species from relative capture counts.**

| Term | Effective degrees of freedom | F | p-value |
|---|---|---|---|
| C7 model | | | |
| HA counts | 2.35 | 16.34 | <0.001 |
| Degree days at 35 weeks | 2.85 | 36.18 | <0.001 |
| Precipitation at 20 weeks | 2.89 | 20.25 | <0.001 |
| Precipitation at 25 weeks | 2.99 | 183.45 | <0.001 |
| Precipitation at 35 weeks | 2.99 | 84.29 | <0.001 |
| Habitat (parametric term) | 8 | 110.5 | <0.001 |
| HA model | | | |
| C7 counts | 2.86 | 13.66 | <0.001 |
| Degree days at 20 weeks | 1.99 | 5.00 | <0.001 |
| Degree days at 35 weeks | 1.97 | 39.46 | <0.001 |

| | | | |
|---|---|---|---|
| Precipitation at 20 weeks | 1.98 | 15.36 | <0.001 |
| Precipitation at 25 weeks | 1.99 | 92.65 | <0.001 |
| Habitat (parametric term) | 8 | 41.41 | <0.001 |

## Discussion

Following their establishment and spread within North America, the dominant exotic lady beetle species *H. axyridis* and *C. septempunctata* have been commonly collected within similar environments, but how these species are able to coexist is poorly understood. In this study, we used a 31-year dataset from an agricultural landscape in southwestern Michigan, USA to investigate environmental, habitat, and seasonal niche partitioning to understand mechanisms of coexistence among these dominant species. We found evidence of long-term coexistence, as both species were collected in similar abundance overall and found in all habitat types. Our findings indicated that a combination of small-scale niche partitioning via environmental, habitat, and seasonal mechanisms contributed to coexistence among these species. Overall, *H. axyridis* seems to be a broad generalist in terms of habitat and abiotic environmental preferences, while *C. septempunctata* tends to thrive under more specific ecological conditions which are not the average for this region.

Evidence of temporal niche partitioning among *H. axyridis* and *C. septempunctata* was observed when patterns of abundance were assessed within and between years. Following the arrival and establishment of *H. axyridis* within the region, these two species experienced patterns of cyclical dominance in abundance across years, suggesting there is some degree of overlap in their niches. This finding aligns with research that has documented overlap in preferences for aphid prey among the two species (Koch 2003, Hodek and Michaud 2008, Roy et al. 2016) as well as evidence of antagonistic competitive interactions in some environments

(Snyder 2009, Gagnon et al. 2011). These patterns of between year partitioning may suggest coexistence of these two competitively dominant species via the storage effect. The storage effect hypothesis posits that competitors may coexist if overlapping generations experience temporal fluctuations in the recruitment of individuals due to species-specific responses to the environment (Chesson and Huntly 1997, Chesson 2000b). Yearly fluctuations in environmental conditions over the course of this long-term study may have differentially benefited one species over the other, resulting in the patterns of cyclical dominance. This is supported by our findings that populations of *H. axyridis* and *C. septempunctata* responded differentially to abiotic environmental conditions in relation to precipitation and temperature. Strong responses to these environmental factors were observed with populations of *C. septempuncata*, as the abundance of this species was more negatively associated with means of several different metrics describing environmental conditions. Instead, populations of *C. septempunctata* were more successful in years characterized by dryer conditions early in the growing season and cooler temperatures in late summer. A study conducted over 28 years in northern China found that daily minimum temperatures were important for populations of *C. septempunctata*, with reductions in overwintering survival observed as minimum temperatures declined during the winter months (Cheng et al. 2020). In comparison to *C. septempuncata*, *H. axyridis* was not strongly affected by the abiotic environmental variables investigated in this study and was generally most abundant in years when temperatures and the amount of precipitation were near the mean. Within this region of the midwestern US, our findings suggest that *H. axyridis* may be an environmental generalist, while *C. septempuncata* has more specific environmental niche requirements, and these differences have resulted in cyclical patterns of species dominance over time. These environmental niche responses may have implications for within-year partitioning and tropic dynamics of the two species.

Within an average year, the population dynamics of *H. axyridis* and *C. septempunctata* showed differing responses to seasonal change, as abundances of each species peaked at

different times during the growing season. Both species responded strongly to degree day accumulation, with the abundance of *C. septempunctata* peaking earlier in the growing season, while *H. axyridis* became more abundant later in the season. The differing phenological responses likely allow these two competitors to locally coexist on short time scales by creating temporal niche differences. Differences in phenology strongly influence when and at which developmental stage species interactions occur within a community, and thus patterns of coexistence among species (Rudolf 2019, Blackford et al. 2020). Unlike *H. axyridis*, *C. septempuncata* requires aphid prey to successfully develop and reproduce (Berkvens et al. 2008, Hodek and Michaud 2008), and therefore, the phenology of this species may be strongly tied to this prey resource. For example, in Europe where *C. septempuncata* is native, this species exploits immigrating aphid populations in cereals beginning in May until the crop matures in July (Honek et al. 2019). The breeding period of *H. axyridis* is greatly extended compared to other lady beetle species, and populations will continue to grow into late summer as individuals reproduce even at risk of later generations not completing development (Honek et al. 2018). Indeed, work examining dynamics of *H. axyridis* to regional populations of soybean aphid found that late season abundance was linked to prey availability early in the growing season (Bahlai, vander Werf, et al. 2015). Although phenological differences among species may promote local coexistence through increased niche differences (i.e. stabilizing mechanisms) (Albrecht and Gotelli 2001), it is also possible that greater phenological differences can lead to increased fitness differences (i.e. equalizing mechanisms) that promote competitive exclusion (Godoy and Levine 2014, Blackford et al. 2020). For instance, in years where *C. septempunctata* activity is favored early in the growing season, this species may deplete local prey resources (Bianchi and Van der Werf 2004), negatively impacting early generations of *H. axyridis*. A depletion of local prey resources by *C. septempuncata* may reduce later season activity peaks of *H. axyridis*, resulting in the year-to-year tradeoffs in dominance we observed between the two species.  Additional research is needed to understand the relative

importance of these two temporal scales (between or within years) for contributing to niche partitioning and coexistence among these exotic species.

Patterns of abundance of *H. axyridis* and *C. septempuncata* varied among plant communities, indicating spatial niche partitioning among habitat types. Abundance of *C. septempunctata* was highest in soybean, wheat, and alfalfa, which suggests a habitat preference for these crop types. Other studies have reported high abundances of *C. septempuncata* on various herbaceous plants, including cereals (Honek et al. 2014, 2019), potato (Alyokhin and Sewell 2004), alfalfa, and maize (Elliott et al. 1996). Conversely, the abundance of *H. axyridis* was more consistent across all plant communities, which aligns with studies that have identified this exotic species as a habitat generalist (Koch 2003, Adriaens et al. 2008). Although *H. axyridis* did not show a preference for a particular habitat type, this species was more abundant than *C. septempuncata* in forests. Populations of *H. axyridis* have been commonly reported in arboreal habitats in Europe (Adriaens et al. 2008, Vandereycken et al. 2012, Honek et al. 2014, Panigaj et al. 2014), wherein their abundance was found to be 7.5x higher on trees than other herbaceous plants including crops (Honek et al. 2019). Larvae of *H. axyridis* are morphologically adapted for exploiting canopy environments compared to *C. septempuncata* due to their well-developed anal disc for adhering to plant surfaces (Eigenbrode et al. 2009). Although *C. septempuncata* displayed clear preferences for soybean, wheat, and alfalfa, individuals of *H. axyridis* also were found in these habitat types. There is some evidence that when these two species overlap in habitat, they partition resources at a finer spatial scale. For example, *C. septempunctata* did not change its habitat use patterns on apple trees in the presence of *H. axyridis*, and instead, these species limited niche overlap by vertically partitioning resources (Lucas et al. 2002). Moreover, *C. septempunctata* has been shown to remain in preferred habitats such as alfalfa and soybean for extended periods, while *H. axyridis* frequently disperses among habitats especially later in the growing season (Forbes and Gratton 2011).

Anthropogenic disturbances such as climate change may alter the coexistence mechanisms among these dominant exotic lady beetles via direct and indirect effects. Phenological responses of species and the seasonal timing of interactions are not static but vary yearly with environmental conditions (Singer and Parmesan 2010, Rudolf 2019). Climate change is causing gradual increases in temperature on a global scale as well as altered patterns of precipitation (IPCC 2014). Our findings documented that lady beetle activity and thus, the interactions between these two dominant species were strongly related to temperatures via daily degree day accumulation, and to a lesser extent, precipitation accumulation. Warmer temperatures affect lady beetles directly by increasing metabolism and rates of egg and larval development, but also require higher rates of prey consumption (Banfield-Zanin and Leather 2016, Speights and Barton 2019). Although warmer temperatures are generally associated with increased activity, there is evidence that increased temperatures may cause high mortality of eggs, larvae, and some adults above a heat stress threshold (Acar et al. 2001, Knapp and Nedvěd 2013, Auad et al. 2014). Prey responses to climate change also are complex and can be affected by physiological tolerances and host plant quality, which may indirectly affect interactions with natural enemies such as predators and parasitoids (Honek et al. 2017, Sloggett 2021). Responses of aphids are often species-specific but warming temperatures and milder winters generally shift aphid phenology such that early season flight activity occurs sooner in the season (Bell et al. 2015, Wu et al. 2020). Under laboratory simulated drought conditions, aphids tended to be less nutritious and smaller in size, requiring higher consumption rates by lady beetle species to meet dietary requirements (Banfield-Zanin and Leather 2016). Therefore, climate change may lead to directional shifts in species phenology and the timing of trophic interactions such that predatory-prey interactions may become more synchronous or asynchronous, with implications for biological control. Adding complexity, future land use practices that continue to promote simplification rather than diversification of landscapes may interact with climate change to influence coexistence

outcomes among lady beetle species and their ecosystem services (Schulte et al. 2021). Opportunistic generalist species such as *H. axyridis* may be better adapted to respond to environmental shifts associated with anthropogenic disturbances, which likely will give these species a competitive advantage.

*Conclusions*

Lady beetles contribute broadly to biological control as predators of key arthropod pests (Obrycki and Kring 1998, Evans 2009, Weber and Lundgren 2009, Rondoni et al. 2021), but the introduction and establishment of exotic lady beetle species threaten native species and the long-term resilience of this ecosystem service (Bahlai et al. 2021). Following their establishment and spread within North America, the exotic species *H. axyridis* and *C. septempunctata* have become dominant within many native lady beetle communities (Alyokhin and Sewell 2004, Harmon et al. 2007, Bahlai, Colunga-Garcia, et al. 2015, Gardiner et al. 2021). In this study, we found that these two dominant exotic species can coexist within agricultural landscapes in the midwestern US due to a combination of spatial and temporal niche partitioning. Our findings indicated that *H. axyridis* is a broad habitat and abiotic environmental generalist, while *C. septempunctata* has more specific niche preferences. Ecological differences among these species have promoted niche partitioning via environmental, seasonal, and habitat mechanisms that have contributed to the continued coexistence of these two invaders within the region. Understanding mechanisms that allow coexistence and success of dominant exotic species contributes to native biodiversity conservation management of invaded ecosystems in the face of global change.

## Acknowledgements

This manuscript was prepared in part as a class project by students in CB's Reproducible Quantitative Methods graduate class at Kent State University. We thank Lama Tawk for leading

a discussion of coexistence theory in the class. This work was supported by National Science Foundation grants OAC 1838807 and DBI 2045721 to CB. Support for this research was also provided by the NSF Long-term Ecological Research Program (DEB 1832042) at the Kellogg Biological Station and by Michigan State University AgBioResearch. DAL acknowledges support from The Great Lakes Bioenergy Research Center, U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research (Award DE-SC0018409). The Mozilla Foundation supported CB during the development of the course where this work was completed. The long-term lady beetle experiment at KBS-LTER was initiated in 1989 by Stuart Gage and Manuel Colunga-Garcia. The authors sincerely thank the ongoing efforts of the research staff supporting the long-term study, particularly: Stacey Van Der Wulp, Sven Bohm, Julia Perrone, Elizabeth D'Auria, and countless undergraduate assistants over the project's three decade history.

## References


Acar, E. B., B. N. Smith, L. D. Hansen, and G. M. Booth. 2001. Use of calorespirometry to determine effects of temperature on metabolic efficiency of an insect. Environmental Entomology. 30: 811–816.

Adriaens, T., G. San Martin y Gomez, and D. Maes. 2008. Invasion history, habitat preferences and phenology of the invasive ladybird *Harmonia axyridis* in Belgium, pp. 69–88. *In* Roy, H.E., Wajnberg, E. (eds.), From Biological Control to Invasion: The Ladybird *Harmonia axyridis* as a Model Species. Springer Netherlands, Dordrecht.

Albrecht, M., and N. J. Gotelli. 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia. 126: 134–141.

Alyokhin, A., and G. Sewell. 2004. Changes in a lady beetle community following the establishment of three alien species. Biological Invasions. 6: 463–471.

Angalet, G. W., J. M. Tropp, and A. N. Eggert. 1979. *Coccinella septempunctata* in the United States: Recolonizations and notes on its ecology. Environmental Entomology. 8: 896–901.

Auad, A. M., J. C. Santos, and M. G. Fonseca. 2014. Effects of temperature development and survival of *Harmonia axyridis* (Coleoptera: Coccinellidae) and *Chrysoperla externa* (Neuroptera: Chrysopidae) fed on *Rhopalosiphum padi* (Hempitera: Aphididae). The Florida Entomologist. 97: 1353–1363.

Bahlai, C. A., M. Colunga-Garcia, S. H. Gage, and D. A. Landis. 2013. Long term functional dynamics of an aphidophagous coccinellid community are unchanged in response to repeated invasion. PLoS One. 8: e83407.

Bahlai, C. A., M. Colunga-Garcia, S. H. Gage, and D. A. Landis. 2015. The role of exotic ladybeetles in the decline of native ladybeetle populations: evidence from long-term monitoring. Biological Invasions. 17: 1005–1024.

Bahlai, C. A., C. Hart, M. T. Kavanaugh, J. D. White, R. W. Ruess, T. J. Brinkman, H. W.

Ducklow, D. R. Foster, W. R. Fraser, H. Genet, P. M. Groffman, S. K. Hamilton, J. F. Johnstone, K. Kielland, D. A. Landis, M. C. Mack, O. Sarnelle, and J. R. Thompson. 2021. Cascading effects: insights from the U.S. Long Term Ecological Research Network. Ecosphere. 12: e03430.

Bahlai, C. A., W. vander Werf, M. O'Neal, L. Hemerik, and D. A. Landis. 2015. Shifts in dynamic regime of an invasive lady beetle are linked to the invasion and insecticidal management of its prey. Ecological Applications. 25: 1807-1818.

Banfield-Zanin, J. A., and S. R. Leather. 2016. Prey-mediated effects of drought on the consumption rates of coccinellid predators of *Elatobium abietinum*. Insects. 7.

Bell, J. R., L. Alderson, D. Izera, T. Kruger, S. Parker, J. Pickup, C. R. Shortall, M. S. Taylor, P. Verrier, and R. Harrington. 2015. Long-term phenological trends, species accumulation rates, aphid traits and climate: five decades of change in migrating aphids. Journal of Animal Ecology. 84: 21–34.

Berkvens, N., J. Bonte, D. Berkvens, K. Deforce, L. Tirry, and P. De Clercq. 2008. Pollen as an alternative food for *Harmonia axyridis*, pp. 201–210. *In* Roy, H.E., Wajnberg, E. (eds.), From Biological Control to Invasion: The Ladybird *Harmonia axyridis* as a Model Species. Springer Netherlands, Dordrecht.

Berkvens, N., C. Landuyt, K. Deforce, D. Berkvens, L. Tirry, and P. De Clercq. 2010. Alternative foods for the multicoloured Asian lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). Eur. J. Entomol. 107: 189–195.

Bhardwaj, A. K., P. Jasrotia, S. K. Hamilton, and G. P. Robertson. 2011. Ecological management of intensively cropped agro-ecosystems improves soil quality with sustained productivity. Agriculture, Ecosystems & Environment. 140: 419–429.

Bianchi, F. J. J. A., and W. Van der Werf. 2004. Model evaluation of the function of prey in non-crop habitats for biological control by ladybeetles in agricultural landscapes. Ecological Modelling. 171: 177–193.

Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, and D. M. Richardson. 2011. A proposed unified framework for biological invasions. Trends in Ecology & Evolution. 26: 333–339.

Blackford, C., R. M. Germain, and B. Gilbert. 2020. Species differences in phenology shape coexistence. The American Naturalist. 195: E168–E180.

Boettner, G. H., J. S. Elkinton, and C. J. Boettner. 2000. Effects of a biological control introduction on three nontarget native species of saturniid moths. Conservation Biology. 14: 1798–1806.

Bradshaw, C. J. A., B. Leroy, C. Bellard, D. Roiz, C. Albert, A. Fournier, M. Barbet-Massin, J.-M. Salles, F. Simard, and F. Courchamp. 2016. Massive yet grossly underestimated global costs of invasive insects. Nature Communications. 7: 12986.

Caltagirone, L. E., and R. L. Doutt. 1989. The history of the vedalia beetle importation to California and its impact on the development of biological control. Annu. Rev. Entomol. 34: 1–16.

Cheng, J., P. Li, Y. Zhang, Y. Zhan, and Y. Liu. 2020. Quantitative assessment of the contribution of environmental factors to divergent population trends in two lady beetles. Biological Control. 145: 104259.

Chesson, P. 2000a. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics. 31: 343–366.

Chesson, P. 2000b. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology. 58: 211–237.

Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. The American Naturalist. 150: 519–553.

Colunga-Garcia, M. 1996. Interactions between landscape structure and ladybird beetles (Coleoptera: Coccinellidae) in field crop agroecosystems. Michigan State University.

Colunga-Garcia, M., and S. H. Gage. 1998. Arrival, establishment, and habitat use of the

multicolored Asian lady beetle (Coleoptera: Coccinellidae) in a Michigan landscape. Environmental Entomology. 27: 1574–1580.

Colunga-Garcia, M., S. H. Gage, and D. A. Landis. 1997. Response of an assemblage of Coccinellidae (Coleoptera) to a diverse agricultural landscape. Environmental Entomology. 26: 797–804.

Cusser, S., C. Bahlai, S. M. Swinton, G. P. Robertson, and N. M. Haddad. 2020. Long-term research avoids spurious and misleading trends in sustainability attributes of no-till. Global Change Biology. 26: 3715–3725.

(Ecosystems and human well-being) . 2005. Ecosystems and human well-being. Island Press, Washington, DC.

Eigenbrode, S. D., W. E. Snyder, G. Clevenger, H. Ding, and S. N. Gorb. 2009. Variable attachment to plant surface waxes by predatory insects, pp. 157–181. *In* Gorb, S.N. (ed.), Functional Surfaces in Biology: Adhesion Related Phenomena Volume 2. Springer Netherlands, Dordrecht.

Elliott, N., R. Kieckhefer, and W. Kauffman. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. Oecologia. 105: 537–544.

Evans, E. W. 2004. Habitat displacement of North American ladybirds by an introduced species. Ecology. 85: 637–647.

Evans, E. W. 2009. Lady beetles as predators of insects other than Hemiptera. Biological Control. 51: 255–267.

Forbes, K. J., and C. Gratton. 2011. Stable isotopes reveal different patterns of inter-crop dispersal in two ladybeetle species. Ecological Entomology. 36: 396–400.

Gagnon, A.-È., G. E. Heimpel, and J. Brodeur. 2011. The ubiquity of intraguild predation among predatory arthropods. PLOS ONE. 6: e28061.

Gandhi, K. J. K., and D. A. Herms. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biological

Invasions. 12: 389–405.

Gardiner, M. M., K. I. Perry, C. B. Riley, K. J. Turo, Y. A. Delgado de la flor, and F. S. Sivakoff. 2021. Community science data suggests that urbanization and forest habitat loss threaten aphidophagous native lady beetles. Ecology and Evolution. 11: 2761–2774.

Gelfand, I., and G. P. Robertson. 2015. Mitigation of greenhouse gases in agricultural ecosystems, pp. 310–339. *In* Hamilton, S.K., Doll, J.E., Robertson, G.P. (eds.), The Ecology of Agricultural Landscapes: Long-Term Research on the Path to Sustainability. Oxford University Press, New York.

Godoy, O. 2019. Coexistence theory as a tool to understand biological invasions in species interaction networks: Implications for the study of novel ecosystems. Functional Ecology. 33: 1190–1201.

Godoy, O., and J. M. Levine. 2014. Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. Ecology. 95: 726–736.

Grez, A. A., T. A. Rand, T. Zaviezo, and F. Castillo-Serey. 2013. Land use intensification differentially benefits alien over native predators in agricultural landscape mosaics. Diversity and Distributions. 19: 749–759.

Harmon, J. P., E. Stephens, and J. Losey. 2007. The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada, pp. 85–94. *In* New, T.R. (ed.), Beetle Conservation. Springer Netherlands, Dordrecht.

Hermann, S. L., S. Xue, L. Rowe, E. Davidson-Lowe, A. Myers, B. Eshchanov, and C. A. Bahlai. 2016. Thermally moderated firefly activity is delayed by precipitation extremes. Royal Society open science. 3: 160712.

HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. Rethinking community assembly through the lens of coexistence theory. Annu. Rev. Ecol. Evol. Syst. 43: 227–248.

Hironori, Y., and S. Katsuhiro. 1997. Cannibalism and interspecific predation in two predatory

ladybirds in relation to prey abundance in the field. Entomophaga. 42: 153–163.

Hodek, I., and J. P. Michaud. 2008. Why is *Coccinella septempunctata* so successful? (A point-of-view). EJE. 105: 1–12.

Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002. The causes and consequences of ant invasions. Annu. Rev. Ecol. Syst. 33: 181–233.

Honek, A., A. F. Dixon, A. O. Soares, J. Skuhrovec, and Z. Martinkova. 2017. Spatial and temporal changes in the abundance and composition of ladybird (Coleoptera: Coccinellidae) communities. Current Opinion in Insect Science. 20: 61–67.

Honek, A., Z. Martinkova, A. F. G. Dixon, J. Skuhrovec, H. E. Roy, M. Brabec, and S. Pekar. 2018. Life cycle of *Harmonia axyridis* in central Europe. BioControl. 63: 241–252.

Honek, A., Z. Martinkova, P. Kindlmann, O. M. C. C. Ameixa, and A. F. G. Dixon. 2014. Long-term trends in the composition of aphidophagous coccinellid communities in Central Europe. Insect Conservation and Diversity. 7: 55–63.

Honek, A., Z. Martinkova, H. E. Roy, A. F. G. Dixon, J. Skuhrovec, S. Pekár, and M. Brabec. 2019. Differences in the phenology of *Harmonia axyridis* (Coleoptera: Coccinellidae) and native coccinellids in central Europe. Environmental Entomology. 48: 80–87.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Jeschke, J. M. 2014. General hypotheses in invasion ecology. Diversity and Distributions. 20: 1229–1234.

Kenis, M., M.-A. Auger-Rozenberg, A. Roques, L. Timms, C. Péré, M. J. W. Cock, J. Settele, S. Augustin, and C. Lopez-Vaamonde. 2009. Ecological effects of invasive alien insects. Biol Invasions. 11: 21–45.

Klooster, W. S., K. J. K. Gandhi, L. C. Long, K. I. Perry, K. B. Rice, and D. A. Herms. 2018. Ecological impacts of emerald ash borer in forests at the epicenter of the invasion in

North America. Forests. 9.

Knapp, M., and O. Nedvěd. 2013. Gender and timing during ontogeny matter: Effects of a temporary high temperature on survival, body size and colouration in *Harmonia axyridis*. PLOS ONE. 8: e74984.

Koch, R. L. 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. Journal of Insect Science. 3: 32.

Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: A review of evidence linking diversity and invasibility. Oikos. 87: 15–26.

Li, H., B. Li, G. L. Lövei, T. J. Kring, and J. J. Obrycki. 2021. Interactions among native and non-native predatory Coccinellidae influence biological control and biodiversity. Annals of the Entomological Society of America. 114: 119–136.

Liebhold, A. M., W. L. MacDonald, D. Bergdahl, and V. C. Mastro. 1995. Invasion by exotic forest pests: A threat to forest ecosystems. Forest Science. 41: a0001-z0001.

Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2013. Invasion Ecology. John Wiley & Sons.

Louda, S. M., D. Kendall, J. Connor, and D. Simberloff. 1997. Ecological effects of an insect introduced for the biological control of weeds. Science. 277: 1088–1090.

Lucas, É., I. Gagné, and D. Coderre. 2002. Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). Eur. J. Entomol. 99: 457–463.

Maredia, K., S. Gage, D. Landis, and T. Wirth. 1992. Ecological observations on predatory Coccinellidae (Coleoptera) in southwestern Michigan. The Great Lakes Entomologist. 25: 265–270.

Morin, R. S., A. M. Liebhold, P. C. Tobin, K. W. Gottschalk, and E. Luzader. 2007. Spread of beech bark disease in the eastern United States and its relationship to regional forest composition. Can. J. For. Res. 37: 726–736.

Obrycki, J. J., and T. J. Kring. 1998. Predaceous Coccinellidae in biological control. Annu. Rev. Entomol. 43: 295–321.

Oksanen, J., F. G. Blanchet, R. Kindt, M. J. Oksanen, and M. Suggests. 2013. Package 'vegan.' Community ecology package Version. 2: 0–0.

Panigaj, L., P. Zach, A. Honěk, O. Nedvěd, J. Kulfan, Z. Martinková, D. Selyemová, S. Viglášová, and H. E. Roy. 2014. The invasion history, distribution and colour pattern forms of the harlequin ladybird beetle *Harmonia axyridis* (Pall.) (Coleoptera, Coccinellidae) in Slovakia, Central Europe. Zookeys. 89–112.

Pell, J. K., J. Baverstock, H. E. Roy, R. L. Ware, and M. E. N. Majerus. 2008. Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. BioControl. 53: 147–168.

R Development Core Team. 2017. R: A Language and Environment for Statistical Computing 3.3.3. R Foundation for Statistical Computing.

Ricci, C., L. Ponti, and A. Pires. 2005. Migratory flight and pre-diapause feeding of *Coccinella septempunctata* (Coleoptera) adults in agricultural and mountain ecosystems of Central Italy. European Journal of Entomology. 102: 531.

Ricciardi, A. 2007. Are modern biological invasions an unprecedented form of global change? Conservation Biology. 21: 329–336.

Ricciardi, A., M. F. Hoopes, M. P. Marchetti, and J. L. Lockwood. 2013. Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs. 83: 263–282.

Rondoni, G., I. Borges, J. Collatz, E. Conti, A. C. Costamagna, F. Dumont, E. W. Evans, A. A. Grez, A. G. Howe, E. Lucas, J.-É. Maisonhaute, A. Onofre Soares, T. Zaviezo, and M. J. W. Cock. 2021. Exotic ladybirds for biological control of herbivorous insects – a review. Entomologia Experimentalis et Applicata. 169: 6–27.

Roy, H. E., P. M. J. Brown, T. Adriaens, N. Berkvens, I. Borges, S. Clusella-Trullas, R. F.

Comont, P. De Clercq, R. Eschen, A. Estoup, E. W. Evans, B. Facon, M. M. Gardiner, A. Gil, A. A. Grez, T. Guillemaud, D. Haelewaters, A. Herz, A. Honek, A. G. Howe, C. Hui, W. D. Hutchison, M. Kenis, R. L. Koch, J. Kulfan, L. Lawson Handley, E. Lombaert, A. Loomans, J. Losey, A. O. Lukashuk, D. Maes, A. Magro, K. M. Murray, G. S. Martin, Z. Martinkova, I. A. Minnaar, O. Nedved, M. J. Orlova-Bienkowskaja, N. Osawa, W. Rabitsch, H. P. Ravn, G. Rondoni, S. L. Rorke, S. K. Ryndevich, M.-G. Saethre, J. J. Sloggett, A. O. Soares, R. Stals, M. C. Tinsley, A. Vandereycken, P. van Wielink, S. Viglášová, P. Zach, I. A. Zakharov, T. Zaviezo, and Z. Zhao. 2016. The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology. Biological Invasions. 18: 997–1044.

Rudolf, V. H. W. 2019. The role of seasonal timing and phenological shifts for species coexistence. Ecology Letters. 22: 1324–1338.

Schaefer, P. W., R. J. Dysart, and H. B. Specht. 1987. North American distribution of *Coccinella septempunctata* (Coleoptera: Coccinellidae) and Its mass appearance in coastal Delaware. Environmental Entomology. 16: 368–373.

Schulte, L. A., B. E. Dale, S. Bozzetto, M. Liebman, G. M. Souza, N. Haddad, T. L. Richard, B. Basso, R. C. Brown, J. A. Hilbert, and J. G. Arbuckle. 2021. Meeting global challenges with regenerative agriculture producing food and energy. Nature Sustainability.

Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, P. Pyšek, M. Winter, M. Arianoutsou, S. Bacher, B. Blasius, G. Brundu, C. Capinha, L. Celesti-Grapow, W. Dawson, S. Dullinger, N. Fuentes, H. Jäger, J. Kartesz, M. Kenis, H. Kreft, I. Kühn, B. Lenzner, A. Liebhold, A. Mosena, D. Moser, M. Nishino, D. Pearman, J. Pergl, W. Rabitsch, J. Rojas-Sandoval, A. Roques, S. Rorke, S. Rossinelli, H. E. Roy, R. Scalera, S. Schindler, K. Štajerová, B. Tokarska-Guzik, M. van Kleunen, K. Walker, P. Weigelt, T. Yamanaka, and F. Essl. 2017. No saturation in the accumulation of alien species worldwide. Nature Communications. 8: 14435.

Sethuraman, A., F. J. Janzen, M. A. Rubio, Y. Vasquez, and J. J. Obrycki. 2018. Demographic histories of three predatory lady beetles reveal complex patterns of diversity and population size change in the United States. Insect Science. 25: 1065–1079.

Singer, M. C., and C. Parmesan. 2010. Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? Philosophical Transactions of the Royal Society B: Biological Sciences. 365: 3161–3176.

Sloggett, J. J. 2021. Aphidophagous ladybirds (Coleoptera: Coccinellidae) and climate change: a review. Insect Conservation and Diversity. 14: 709–722.

Smith, C. A., and M. M. Gardiner. 2013. Biodiversity loss following the introduction of exotic competitors: Does intraguild predation explain the decline of native lady beetles? PLOS ONE. 8: e84448.

Snyder, W. E. 2009. Coccinellids in diverse communities: Which niche fits? Biological Control. 51: 323–335.

Snyder, W. E., G. M. Clevenger, and S. D. Eigenbrode. 2004. Intraguild predation and successful invasion by introduced ladybird beetles. Oecologia. 140: 559–565.

Snyder, W. E., and E. W. Evans. 2006. Ecological effects of invasive arthropod generalist predators. Annu. Rev. Ecol. Evol. Syst. 37: 95–122.

Speights, C. J., and B. T. Barton. 2019. Timing is everything: Effects of day and night warming on predator functional traits. Food Webs. 21: e00130.

Syswerda, S. P., B. Basso, S. K. Hamilton, J. B. Tausig, and G. P. Robertson. 2012. Long-term nitrate loss along an agricultural intensity gradient in the Upper Midwest USA. Agriculture, Ecosystems & Environment. 149: 10–19.

Thomas, A. P., J. Trotman, A. Wheatley, A. Aebi, R. Zindel, and P. M. J. Brown. 2013. Predation of native coccinellids by the invasive alien *Harmonia axyridis* (Coleoptera: Coccinellidae): Detection in Britain by PCR-based gut analysis. Insect Conservation and Diversity. 6: 20–27.

Turnock, W. J., I. L. Wise, and F. O. Matheson. 2003. Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. The Canadian Entomologist. 135: 391–404.

Vandereycken, A., D. Durieux, É. Joie, É. Haubruge, and F. Verheggen. 2012. Habitat diversity of the Multicolored Asian ladybeetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in agricultural and arboreal ecosystems: a review. Biotechnologie, Agronomie, Societé et Environnement. 16: 553–563.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist.

Ware, R. L., and M. E. N. Majerus. 2008. Intraguild predation of immature stages of British and Japanese coccinellids by the invasive ladybird *Harmonia axyridis*, pp. 169–188. *In* Roy, H.E., Wajnberg, E. (eds.), From Biological Control to Invasion: The Ladybird *Harmonia axyridis* as a Model Species. Springer Netherlands, Dordrecht.

Weber, D. C., and J. G. Lundgren. 2009. Assessing the trophic ecology of the Coccinellidae: Their roles as predators and as prey. Biological Control. 51: 199–214.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience. 48: 607–615.

Wood, S. N. 2006. Generalized additive models: an introduction with R. chapman and hall/CRC.

Wu, Y., J. Li, H. Liu, G. Qiao, and X. Huang. 2020. Investigating the impact of climate warming on phenology of aphid pests in China using long-term historical data. Insects. 11.

Yasuda, H., E. W. Evans, Y. Kajita, K. Urakawa, and T. Takizawa. 2004. Asymmetric larval interactions between introduced and indigenous ladybirds in North America. Oecologia. 141: 722–731.

Yasuda, H., T. Kikuchi, P. Kindlmann, and S. Sato. 2001. Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. Journal of Insect Behavior. 14: 373–384.

## Figure captions

**Figure 1: Raw trends in the abundance of two adventive lady beetle species at Kellogg Biological Station in Southwestern Michigan, 1994-2020.** A) abundance of adult lady beetles of each species, captured per repetition treatment combination (*ca*. 5 traps per week) B) the same data given by plant community treatment, aggregated over time.*Coccinella septempunctata* (C7) captures are given in red, *Harmonia axyridis* (HA) in orange.

**Figure 2: Non-metric multidimensional scaling of habitat use patterns by two adventive lady beetle species at Kellogg Biological Station in Southwestern Michigan, 1994-2020, at two temporal aggregations.** A) yearly resolution, 2-D stress= 0.21 B) weekly resolution, 2-d stress= 0.226. *Coccinella septempunctata* observations are given by red X, *Harmonia axyridis* observations are given by orange O.

**Figure 3: Partial effects of terms included in a within-season Generalized Additive Model for two adventive lady beetle species at Kellogg Biological Station in Southwestern Michigan, 1994-2020**, using weekly observations of lady beetles captured in nine plant communities. A) Within-season degree day accumulation (base 10°C); B) Rainy days, ie number of days in the observation week when precipitation was recorded); C) residual habitat effects; and D) remaining year-to-year population variation. *Coccinella septempunctata* (C7) effects are given in red, *Harmonia axyridis* (HA) in orange.

**Figure 4: Partial effects of environmental parameters from a between-season Generalized Additive Models for two adventive lady beetle species at Kellogg Biological Station in Southwestern Michigan, 1994-2020**. Each species was modelled, and subjected to model

selection separately. *Coccinella septempunctata* (C7) model effects are given in red, *Harmonia axyridis* (HA) in orange(left). Models also included terms for between-habitat variation and captures of the other species of lady beetle.

**Figure 1**

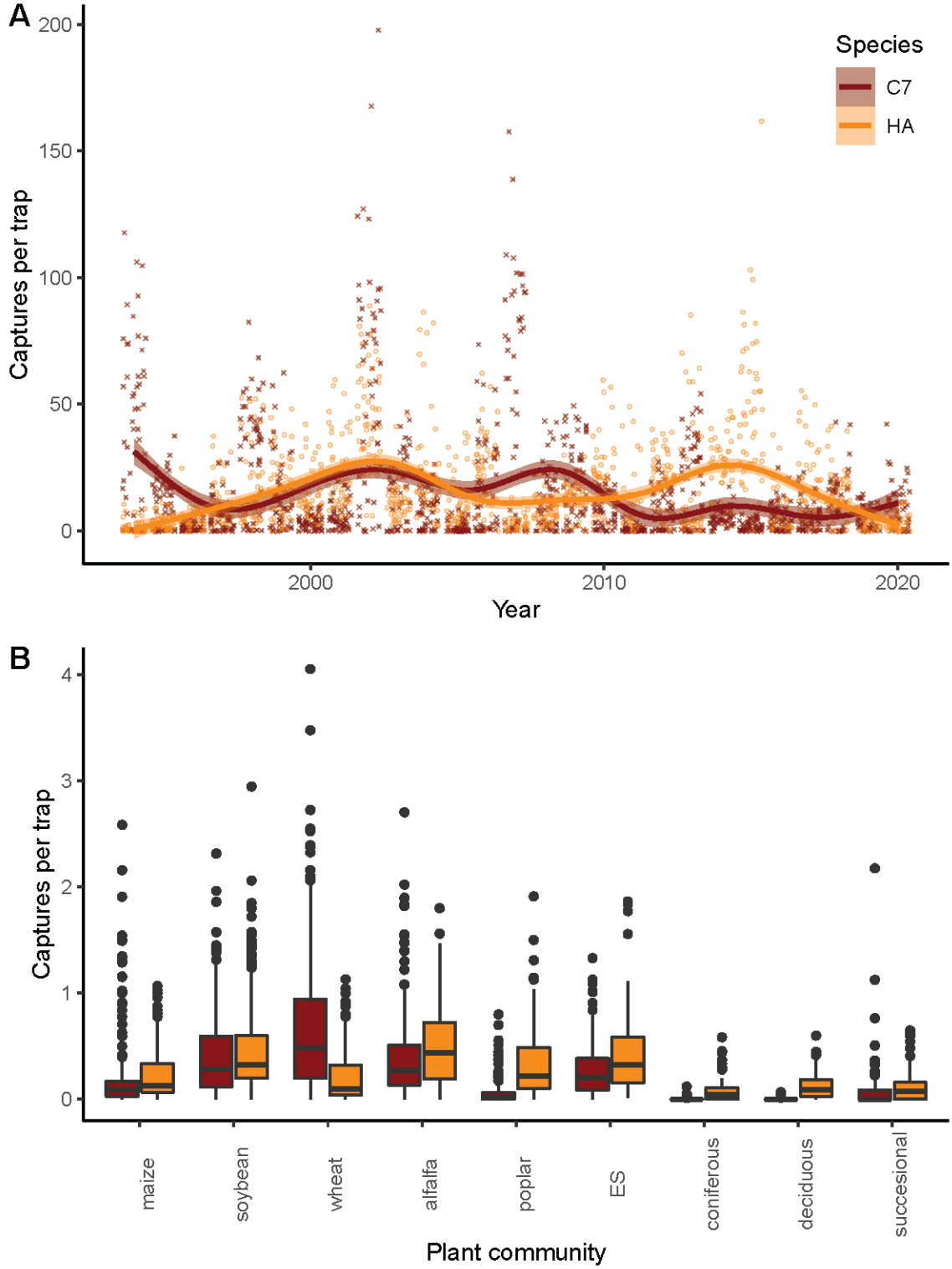

A
Species
C7
HA
Captures per trap
200
150
100
50
0
2000
2010
2020
Year
B
Captures per trap
4
3
2
1
0
maize
soybean
wheat
alfalfa
poplar
ES
coniferous
deciduous
succesional
Plant community

**Figure 2**

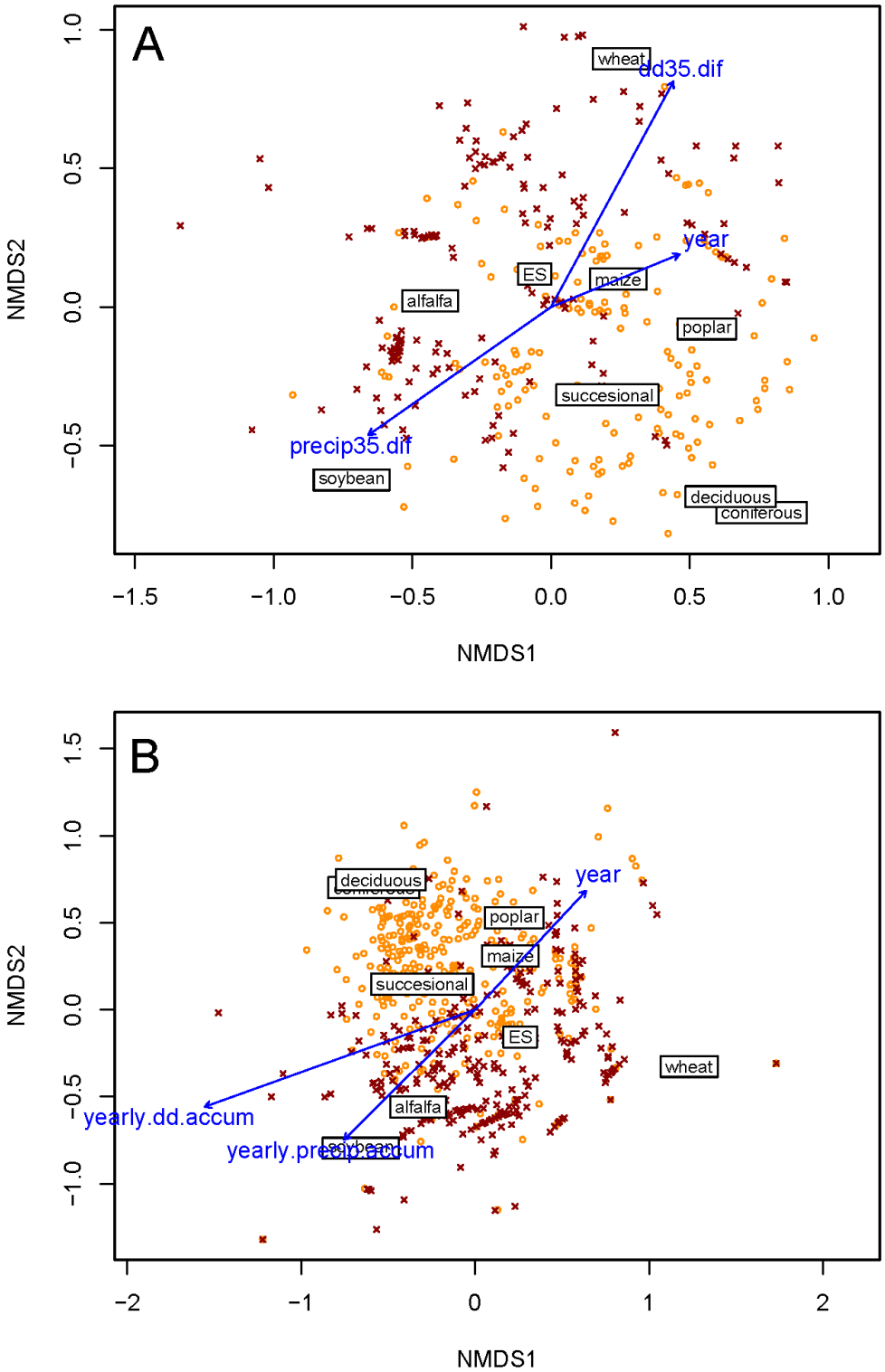

A
wheat
dd35.dif
year
ES
maize
alfalfa
poplar
succesional
precip35.dif
soybean
deciduous
coniferous
NMDS2
NMDS1
B
deciduous
year
poplar
maize
succesional
ES
wheat
alfalfa
yearly.dd.accum
yearly.precip.accum
NMDS2
NMDS1

**Figure 3**

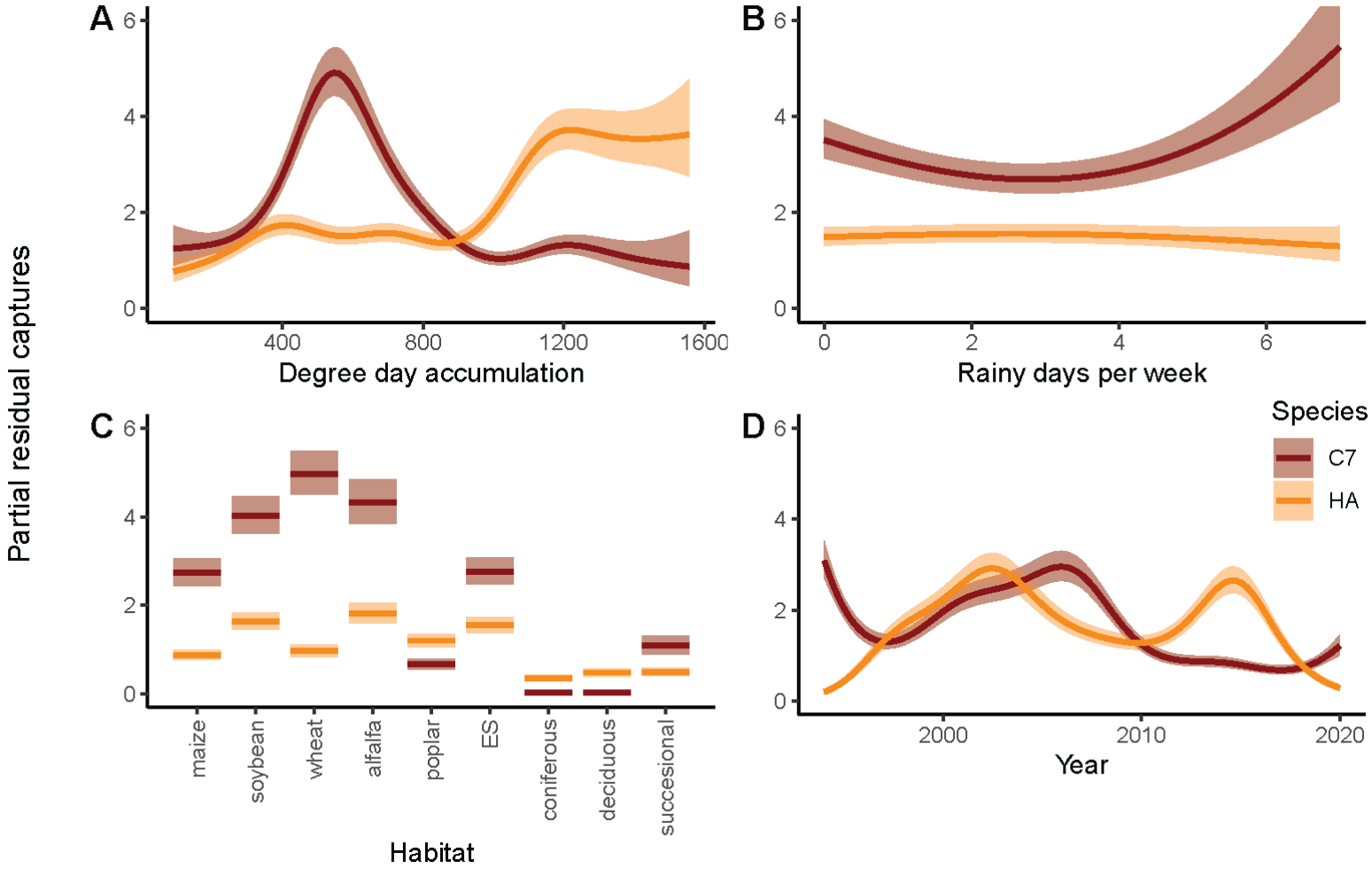
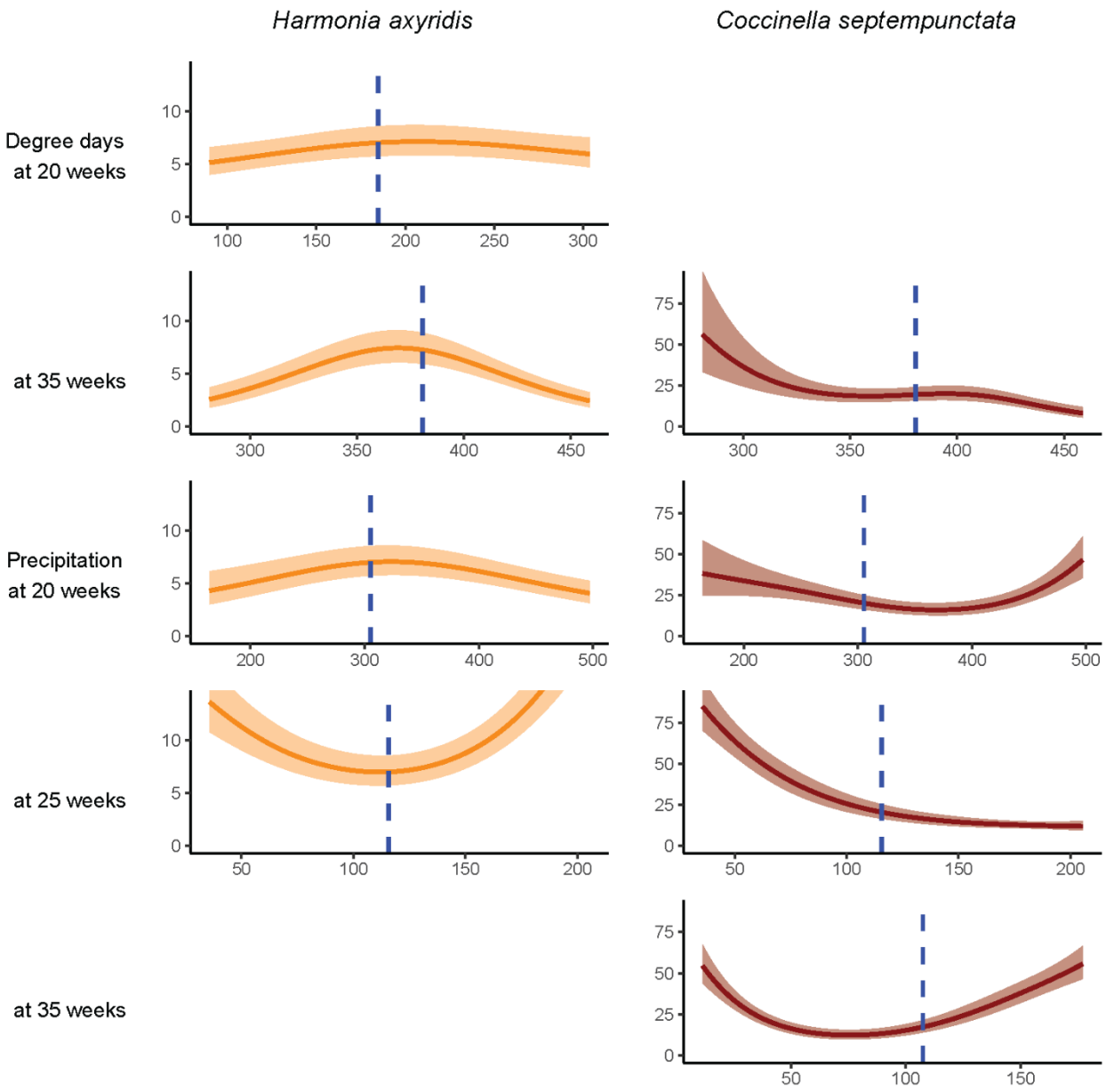

A
B
C
D
Partial residual captures
Degree day accumulation
Rainy days per week
Habitat
Year
maize
soybean
wheat
alfalfa
poplar
ES
coniferous
deciduous
succesional
Species
C7
HA

**Figure 4**


Harmonia axyridis
Coccinella septempunctata
Degree days at 20 weeks
at 35 weeks
Precipitation at 20 weeks
at 25 weeks
at 35 weeks