

Agriculturally Intensified Landscapes Are Associated With Reduced Body Condition of Lady Beetles

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2 **body condition of lady beetles**

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25 **ABSTRACT**

26 **Context:** Agricultural intensification is contributing to a global species decline. Underlying mechanisms
27 include toxic effects of pesticides on non-target organisms and reductions in habitat and food availability.
28 However, the effects of agricultural intensification on body condition, particularly of ecosystem service-
29 providing arthropods, are poorly understood.

30 **Objectives:** Here, we investigated whether variations in the body condition of common lady beetle species
31 (Coleoptera: Coccinellidae) can be explained by the composition and configuration of the surrounding
32 landscape. Assuming strong seasonal variation in food availability in intensively farmed regions, we
33 included the entire period of lady beetle activity in our study.

34 **Methods:** Lady beetles were collected from April to September 2011 in 30 landscapes in southern
35 Wisconsin, USA. We examined how body size, body density, and lipid content of the beetles responded to
36 the percentage of intensive cropland, habitat diversity, and edge density in the surrounding landscape.

37 **Results:** The strongest predictor of body condition was the percentage of intensive cropland. For every 10%
38 increase in cropland, body density decreased by about 3.9% and fat content by 6.4%. Landscape diversity
39 and edge density correlated with body condition of individual species.

40 **Conclusions:** In agriculturally intensified landscapes, lady beetles with reduced body condition may
41 produce fewer offspring, have lower survival rates, and exert less effective pest control. Thus, our results
42 suggest a mechanistic link between landscape patterns and observed declines in lady beetle populations.
43 Our results also show that the expansion of monocultures affects even common cropland-associated species
44 such as *Harmonia axyridis*, suggesting a long-term decline in biocontrol services in simplified agricultural
45 landscapes.

46 **KEYWORDS**

47 conservation physiology, natural enemies, body condition, entomology, agroecology, land-use

48 INTRODUCTION

49 Landscape structure affects species' abilities to move, survive, and persist in their environments (Fahrig
50 2007; Tschardt et al. 2012; Gámez-Virúés et al. 2015; Martin et al. 2019; Seibold et al. 2019). This is
51 consequential not only for the conservation of biodiversity generally, but also the maintenance of service-
52 providing organisms such as pollinators and natural enemies of crop pests. Agricultural landscape
53 simplification including loss of semi-natural habitat and reduction of crop diversity is often found to have
54 a negative effect on the abundance and diversity of natural enemies and the biological control services they
55 provide (Chaplin-Kramer et al. 2011; Liere et al. 2015; Rusch et al. 2016; Dainese et al. 2019). However,
56 the count data on natural enemy abundance collected in most studies usually cover only one or a few
57 growing seasons (but see Lamb et al. 2019) and cannot adequately capture population trajectories. This
58 may result in incomplete or misleading conclusions about the effects of landscape structure on species
59 responses in the long-term (Kuussaari et al. 2009). The integration of landscape ecology with conservation
60 physiology constitutes a promising direction for resolving such limitations and advancing from pattern- to
61 process-based understanding of species and service distributions (Ellis et al. 2012; Cooke et al. 2013).

62 Physiological indicators of individual body condition and fitness can offer valuable insights into
63 the status of animal populations in disturbed landscapes before a numerical response is observed. For
64 example, stress biomarkers in birds (Latimer et al. 2020) and limb malformation in amphibians (Guerra and
65 Aráoz 2016) respond to agricultural landscape composition and configuration. For arthropods,
66 characteristics such as body size, mass, and lipid content are important indicators of body condition. Larger
67 individuals are more likely to be better competitors for resources and mates, as well as have higher fecundity
68 and reproductive success (Kajita and Evans 2010; Vargas et al. 2013a; Beukeboom 2018). While body size
69 of holometabolous insects is determined by feeding conditions at the larval stage (Hodek 1973; Vargas et
70 al. 2012), body mass is modulated by food availability to adults and is thought to reflect actual nutrient
71 storage (Knapp and Knappová 2013). Lipid content is an important measure of energy reserves, which
72 determine the ability of individuals to survive during periods of resource scarcity (Arrese and Soulages

73 2009). Direct measurements of body composition, such as lipid content, also tend to be better indicators of
74 body condition than proxy indices such as body size (Knapp and Knappová 2013; Wilder et al. 2016).

75 Relatively few studies have investigated the consequences of landscape structure on arthropod body
76 condition. Early studies showed that the body size and fecundity of a generalist ground beetle was positively
77 correlated with field perimeter-to-area ratio and percentage of perennial crops across cereal farms
78 (Bommarco et al. 1998, Östman et al. 2001). Effects of landscape structure on body condition have also
79 been demonstrated for wolf spiders (Öberg 2009; Drapela et al. 2013) and dung beetles (Salomão et al.
80 2018). Flying organisms are highly mobile and thus may be most susceptible to landscape-related drivers.
81 While there is also a growing literature base examining the effects of landscape on body condition of wild
82 and managed pollinators (Renauld et al. 2016; Alaux et al. 2017; Grab et al. 2019; Dolezal et al. 2019;
83 Mogren et al. 2020), surprisingly little is known about the consequences for flying predators.

84 Lady beetles (Coleoptera: Coccinellidae) are highly mobile predators that provide valuable
85 biological control services in agricultural landscapes (Obrycki et al. 2009). Despite their association with
86 crops, population sizes are often reduced in regions that are dominated by intensive agriculture (Gardiner
87 et al. 2009a, b; Grez et al. 2014; Woltz and Landis 2014). Tiede et al. (2017) showed that the gut microbiome
88 of native and introduced lady beetle species in Wisconsin (USA) varied by species, prey diversity, local
89 habitat type, and landscape context. They also found that landscape context mediated the effect of gut
90 microbiota on beetle lipid content, but the study's relatively small sample size and qualitative measurement
91 of lipid content makes it difficult to draw strong conclusions and left other aspects of body condition
92 unexplored.

93 Here we ask whether variation in lady beetle body condition can be explained by features of the
94 surrounding landscape. Specifically, we investigated how body size, body density, and lipid content
95 responded to variation in landscape composition (percentage of intensive cropland, landscape diversity)
96 and configuration (edge density) in agricultural landscapes. In a mensurative field experiment (Hadley &
97 Betts 2016), we sampled populations of five lady beetle species at 30 sites along a gradient from low to
98 high agricultural intensification in southern Wisconsin, USA. The sampling period extended from beetle

99 emergence from hibernation in May to September when they allocate energy for hibernation, thus including
100 periods when the region's large-scale row crops (corn and soybeans) are not yet present or are already
101 harvested, and thus do not provide food resources. We assumed that lady beetles in agriculturally intensified
102 landscapes—characterized by a high percentage of row crops, a low diversity of habitat types, and a low
103 density of habitat edges—have less access to food resources than conspecifics in more complex landscapes,
104 especially in the early and late seasons. We therefore predicted that lady beetles sampled in landscapes with
105 high agricultural intensification will have a reduced body condition compared to beetles collected in less
106 intensified landscapes. Because different lady beetle species have different habitat preferences and food
107 requirements (Lundgren and Wiedenmann 2004; Berkvens et al. 2008; Gardiner et al. 2009a; Diepenbrock
108 and Finke 2013), we also expected species-specific differences in the strength of response and relative
109 importance of different landscape factors.

110 **METHODS**

111 *Sampling locations & collection*

112 Adult lady beetles were sampled in 30 locations in Wisconsin, USA, between April and September 2011
113 (Fig. 1). The beetles were collected opportunistically based on the phenology of local vegetation and the
114 abundance of food resources. In the early growing season when lady beetles emerged from hibernation,
115 beetles were collected by sweep netting and hand collection in alfalfa fields, grasslands, and field margins.
116 In June beetles were collected in small grain crops (wheat, oats, rye), and from late June onwards in corn
117 and soybean fields. In addition, yellow sticky traps (Great Lakes IPM GL-3310-00, Vestaburg, MI, USA)
118 were placed in semi-natural habitats such as hedgerows for 48 hours in June. The sampling method had no
119 effect on body condition metrics (data not shown) and therefore was not addressed in the statistical analysis.
120 In total we collected individuals of five aphidophagous lady beetle species (Table 1). Beetles were placed
121 in a cooler to limit their activity during transport to the lab, where they were preserved at -20 °C.

122 *Analysis of body condition*

123 Beetles were sexed and dissected under a stereoscopic microscope (10-40x magnification). The presence
124 of mite or fungus parasites was documented in 153 individuals (11.9% of samples). Excluding these
125 specimens did not qualitatively change the results (data not shown), so we present results based on the
126 analysis of all samples. Additionally, 92 beetles (7.7% of the samples) had soft and pale elytra and were
127 recorded as teneral (newly hatched). The presence or absence of eggs was also noted for female beetles.

128 We assessed the body condition of beetles by analyzing body size, body density, and lipid content.
129 As an indicator of structural body size, we measured elytra length and pronotum width to the nearest 0.001
130 mm (ProgRes camera and CapturePro imaging system, JenOptik, Jena, Germany) and multiplied them. The
131 use of multiple size measurements has been shown to be more informative of body condition than single
132 size measurements (Knapp and Knappová 2013). In preparation for the measurement of lipid content, the
133 elytra, wings, head and pronotum were removed from the torso (thorax and abdomen) and processed
134 separately. All samples were dried at 50°C for 72 hours and cooled to room temperature in a desiccator for
135 at least 1 hour before being weighed to the nearest 0.001 mg (Mettler Toledo MT5, Mettler-Toledo,
136 Columbus, OH, USA) (Anderson 1981). The torso was weighed separately from the other body parts, and
137 the values were added to obtain the total dry mass. Body mass was corrected for individual size to
138 standardize body condition, as the two measures are closely correlated (Knapp and Knappová 2013). We
139 divided mass by size to determine "body density" (i.e., size-corrected dry mass).

140 Lipid content was determined gravimetrically by the difference in dry mass before and after total
141 lipid extraction (Plastow and Siva-Jothy 1996; Östman et al. 2001; Östman 2005). Only the torso was used
142 (pronotum and abdomen without wings, elytra and legs) as wings and elytra contain no measurable amount
143 of fat, and no metabolically usable fat is stored in the head (Plastow and Siva-Jothy 1996). As a lipid
144 solvent, 1 mL of dichloromethane-methanol solution (2:1) was added to the torso in individual glass vials.
145 After 72 hours at room temperature, the lipid-containing solution was discarded, and the torso was washed
146 in another 1 ml of dichloromethane-methanol solution for 10 min and dried for 72 hours at 50°C before re-
147 weighing. Percentage lipid content was calculated by dividing the lipid-free dry weight by the total dry

148 weight of the torso and multiplying by 100 (Morita et al. 1999). Lipid content data was collected for all
149 species except *Coccinella septempunctata*. Although there were significant correlations between body
150 condition metrics (especially size and density), sufficient variation existed to test the effects of landscape
151 on each metric separately (see Online Supplement 1 Figure S1).

152 *Landscape metrics*

153 All landscape analyses were conducted at a 1 km radius around sampling sites. Landscape features within
154 a 0.5 km to 2 km radius have been ecologically most informative for population-level numerical responses
155 of lady beetles in previous studies (Gardiner et al. 2009a; Woltz and Landis 2014; Yang et al. 2018). While
156 lady beetles migrate between habitats and patches during the season to find ephemeral prey, foraging within
157 a patch is characterized by short-distance movements (Hodek et al. 1993; Evans 2003; Schellhorn et al.
158 2014). We therefore assume that a rather local scale is most relevant for physiological effects at the
159 individual level.

160 We used the 2011 USDA Cropland Data Layer (CDL, NASS 2011) and the landscape metrics
161 package in R (Hesselbarth et al. 2019) to obtain measures of landscape composition and configuration at a
162 resolution of 30 m. We calculated the percentage of land categorized as corn and soybean, the dominant
163 crops in the region, as a metric of intensively-managed annual monoculture (hereafter “intensive
164 cropland”). Intensive cropland was negatively correlated (Pearson’s $r = -0.91$, $p < 0.001$) with semi-natural
165 habitat (grassland and woodland classes) and was used in our analysis because this type of habitat is easier
166 to categorize unambiguously than semi-natural habitats.

167 Landscape diversity was quantified as the diversity of land cover classes using Simpson’s diversity
168 index (Simpson 1949), which is less sensitive to rare classes than other metrics such as Shannon’s diversity
169 index (McGarigal 1995). Edge density was calculated as the length of the habitat boundaries of all land
170 cover classes. Pearson correlation coefficients between pairs of these three landscape metrics used in our
171 analysis were $r < 0.4$ (see Online Supplement 1 Figure S2 for Pearson’s correlation coefficient distributions
172 of landscape metrics).

173 *Statistical analyses*

174 We used R (v4.0.5; R Core Team 2020), and RStudio (v1.4.1103; RStudio Team 2020) for all statistical
175 analysis and the ggplot2 package (Wickham 2016) for the visualization of results. Data and code are
176 provided (Online Supplement 2).

177 We tested the effects of landscape metrics on the body condition of lady beetles with linear mixed-
178 effects models (lme function, nlme package; Pinheiro et al. 2021). For each combination of body condition
179 measurements (body size, body density, and lipid content) and landscape metrics (percentage of intensive
180 cropland, landscape diversity, and edge density) we used separate models, resulting in nine predictor and
181 response variable combinations.

182 For each response variable, we tested whether the data fitted a normal or lognormal distribution
183 using the fitdistrplus package (function fitdist; Delignette-Muller and Dutang 2015) in combination with
184 Akaike's information criterion (AIC). In addition, we visually checked the error distribution of the models
185 to verify whether a ln-transformation reduced heteroskedasticity compared to untransformed response
186 variables. Body size data was analyzed untransformed, while body density and lipid content data were ln-
187 transformed. For models with body density as a response variable, teneral beetles (newly emerged adults)
188 were excluded since they were significantly lighter than non-teneral beetles (data not shown). In models of
189 body size or lipid content teneral beetles were statistically indistinguishable and were thus included (data
190 not shown).

191 In all models the explanatory variables were beetle species, collection date and their interactions
192 with the landscape metrics as fixed effects, and species, sex, and sampling site as nested random intercepts
193 to account for repeated measures and beetle-specific responses. In the body density and lipid content
194 models, a quadratic term was used for the collection date (allowing for a peak in mid-season), as this
195 improved model fitting (lower AICc values; <http://christoph-scherber.de/stepAICc.txt>). A variance function
196 with different estimates for each species was also used to account for variance heterogeneity between
197 species.

198 We applied weighted effects coding using the `wec` package (Nieuwenhuis et al. 2017) to test the
199 effects of landscape variables and their interactions with lady beetle species on body condition metrics.
200 Weighted effects coding is an alternative to conventional “dummy coding” of categorical variables in
201 regression analysis and is well-suited to analyzing unbalanced observational data. In weighted effects
202 coding, the effect of each category (here, beetle species) represents the deviation of that category from the
203 sample mean (te Grotenhuis et al. 2017). This allowed us to test whether there is an overall effect of each
204 landscape variable on the body condition of all beetles sampled, as well as whether there are species for
205 which the relationship between body condition and landscape metric is statistically different from the
206 overall trend. The significance of all predictor terms in the linear mixed-effects models was assessed at $\alpha =$
207 0.05 using type II Wald chi-square tests (`Anova` function, `car` package; Fox and Weisberg 2018). These
208 tests follow the principle of marginality, where each term is tested after all others, but ignores each term’s
209 interactions.

210 A graphical overview of all effects of landscape predictors and body condition metrics of all
211 individual lady beetle species (Fig. 2) was generated based on regression coefficients calculated with the
212 generic summary function of R that is based on t-statistic using type-III sums of squares. The significance
213 of predictor terms did not differ from the ones determined by Wald chi-square tests. Because the scales of
214 different landscape and body condition metrics varied considerably, we standardized the regression
215 coefficients by transforming the predictor (% intensive cropland, Simpson’s diversity index, and edge
216 density) and response variables (body size, body density, and lipid content) to z-scores. Regression
217 coefficients are thus displayed in units of standard deviations.

218 For four beetle species with sufficient numbers of non-teneral female individuals for statistical
219 analysis (*C. maculata*, $n = 83$; *C. munda*, $n = 32$; *C. septempunctata*, $n = 51$; *H. axyridis*, $n = 247$) we
220 examined the relationship between body condition metrics and the presence of eggs. To do this, we used
221 logistic regression models using the `glmmTMB` package (Brooks et al. 2017). Models included egg
222 presence/absence (1/0) as a response variable and one of the body condition metrics (body size, body
223 density, and lipid content), collection date and their interactions with species as fixed effects, and sampling

224 location as a random intercept. We used the weighted effects coding described above to determine the
225 overall effect of body density on egg presence and possible interactions with the species. The significance
226 of predictor terms was assessed using Wald chi-square tests (Anova function, car package; Fox and
227 Weisberg 2018) as described above.

228 **RESULTS**

229 All three landscape predictors studied had a significant effect on the body condition of at least one lady
230 beetle species (Table 2; Fig. 2, 3). As the percentage of intensively managed cropland in a landscape
231 increased there was a small, but significant decrease in body density and lipid content of lady beetles. For
232 every 10% increase in landscape area covered by intensively managed cropland, there was an approximately
233 3.9% decrease in beetle body density and 6.4% decrease in beetle fat content (Table 2; Figure 2a, b). At the
234 species level, body density of two introduced species, the multicolored asian lady beetle *Harmonia axyridis*
235 (Fig. 2; orange dots) and the variegated lady beetle *Hippodamia variegata* (Fig. 2, blue dots) and fat content
236 of *H. axyridis* were significantly negatively influenced by an increasing amount of intensively managed
237 cropland. Landscape diversity and edge density did not have an overall effect for any of the body condition
238 metrics (Table 2) but had effects on individual species. The native pink spotted lady beetle
239 *Coleomegilla maculata* (Fig. 2; green points) had reduced fat content in more diverse landscapes. Finally,
240 *C. maculata* and *H. variegata* collected from landscapes with higher edge density had greater body density.
241 See Online Supplement 1 Table S1 for summary statistics on deviations of species-specific responses from
242 the overall effect for all combinations of landscape predictors and body condition metrics.

243 Lady beetle species was a strong and significant predictor of body condition in all models (Table
244 2). That is, there were inherent differences among species after accounting for landscape metrics. For
245 collection date, a quadratic term was used in the body density and lipid content models to account for the
246 higher body density and higher lipid content in mid-season. The collection date itself had an effect on body
247 density, with higher body density in the middle of the season. The interaction between collection date and

248 beetle species was a significant predictor of body density and fat content (Table 2), indicating that these
249 body condition metrics increased in some species and decreased in others over the season.

250 In all four species analyzed, female beetles with greater body density were more likely to have
251 developing eggs (Online Supplement 1 Fig S3, Table S2, S3). This suggests that body density (i.e.,
252 standardized body mass) is a meaningful index of fecundity. No relationship was found between the
253 presence of eggs and body size or lipid content (Online Supplement 1 Table S2, S3).

254 **DISCUSSION**

255 Landscape composition and configuration explained small but significant portions of the variation in the
256 body condition of multiple lady beetle species across southern Wisconsin's agricultural landscapes. Lady
257 beetles were generally lighter and leaner in simplified agricultural landscapes dominated by annual row
258 crop fields. Previous studies have shown that coccinellid abundance and biological control services decline
259 in simplified landscapes in the midwestern United States and other regions of the world (Gardiner et al.
260 2009b; Grez et al. 2014; Woltz and Landis 2014; Yang et al. 2018, 2019). Our results provide a possible
261 mechanistic link for the observed relationship between landscape structure and lady beetle numeric
262 response, and consequently ecosystem services.

263 Likely reasons for the effects of landscape composition and configuration on lady beetle body
264 condition include differences in spatial and temporal resource continuity and quality. Corn and soybean
265 fields can be heavily colonized by aphids and thus provide abundant prey for lady beetles, but this is only
266 the case during limited time periods; over long periods such fields are characterized by resource scarcity,
267 e.g., before crop emergence, after crop maturity, or after pesticide application (Rand et al. 2006; Schellhorn
268 et al. 2014; Iuliano and Gratton 2020). In landscapes that are strongly dominated by a few crop
269 monocultures, these periods are synchronized over large areas and habitat patches with alternative food
270 sources are often far away and only accessible at high energetic costs (Bonte et al. 2012; Stowe et al. 2021b).
271 In contrast, in more heterogeneous landscapes where a variety of annual and perennial crops are grown and
272 natural or semi-natural habitat patches are available, landscape complementation (in the sense of Dunning

273 et al. 1992) for mobile natural enemies may occur. Landscapes with more intensive cropland may also mean
274 greater risk of pesticide exposure (Meehan et al. 2011), which has potential lethal and sublethal
275 consequences for lady beetles and other beneficial insects (Santos et al. 2017, Stuligross and Williams et
276 al. 2021), though little is known about pesticide effects at the landscape scale (Mancini et al. 2020).

277 Landscape structure also shapes the diversity and composition of plants and arthropods (Jonsen and
278 Fahrig 1997; Clough et al. 2007; Seibold et al. 2019; Le Provost et al. 2021) and consequently the quality
279 of food resources for lady beetles, which in turn may influence their performance. Nutritional studies
280 conducted in the laboratory have shown that growth rate, body composition, and fecundity can vary
281 significantly depending on the prey and non-prey foods consumed. For example, *C. maculata* can complete
282 its life cycle entirely on corn pollen, but then achieved a lower body weight and laid fewer eggs than
283 conspecifics that feed on aphids (Lundgren and Wiedenmann 2004). In *H. axyridis*, known primarily as
284 aphid predators, a diet of Lepidoptera eggs (*Ephestia kuehniella* Zeller) resulted in higher body weight, fat
285 content, reproductive output, and longevity compared to a diet of pea aphids (*Acyrtosiphon pisum* Harris)
286 (Specty et al. 2003; Berkvens et al. 2008). In this context, it appears to be species-specific which food types
287 are best suited for predators to achieve high body condition. However, a mixed diet of complementary foods
288 has been shown to be beneficial for several generalist predators and is actively sought by them (Soares et
289 al. 2004; Raubenheimer et al. 2007; Harwood et al. 2009; Marques et al. 2015; Stowe et al. 2021a). As
290 such, landscapes with fewer diversity of crops or landscape diversity may manifest as decreases in the
291 physiological condition of mobile predatory arthropods such as lady beetles, leading to longer-term
292 population declines, as has been found for other beneficial insects (Hemberger et al. 2021).

293 Generalist natural enemies are likely to achieve a balanced diet more easily in landscapes with high
294 resource diversity. Locally high plant diversity and habitat heterogeneity increased the dietary diversity and
295 composition of generalist predatory ground arthropods (Tiede et al. 2016; Staudacher et al. 2018; Macé et
296 al. 2019). In a study from Germany and Switzerland, *H. axyridis* and another common aphid predator, the
297 lacewing *Chrysoperla carnea* (Stephens), supplemented their diets throughout the season with pollen that,
298 even in agriculture-dominated landscapes, came largely from non-crop plants (Bertrand et al. 2019). Local

299 semi-natural habitats can supplement the food supply for natural enemies of plant pests, but the availability
300 of resources also depends on the surrounding landscape. Seibold et al. (2019) demonstrated a decline in
301 arthropods over nine years in grasslands that was particularly pronounced when the areas were embedded
302 in intensively farmed landscapes.

303 In our study, we examined the correlation of three different aspects of landscape simplification with
304 three different characteristics of coccinellid body condition. The two measures of landscape composition,
305 the percentage of predominant annual monocultures of soybean and corn, and landscape diversity were not
306 correlated. This means that a landscape with few soybean and corn crops is not necessarily a landscape with
307 many different other habitat types, and vice versa. The third metric, edge density, is a measure of landscape
308 configuration and provides information about the size of fields and other habitats. Its independence from
309 the other two landscape metrics implies that, for example, landscapes with a high percentage of intensively
310 used farmland may consist of many small fields with correspondingly high edge density, and high edge
311 density is not necessarily associated with high diversity of habitat types (see also Martin et al. 2019).

312 Of these three factors, the percentage of intensive cropland was the strongest predictor of lady
313 beetle body condition and the only one for which a general effect on all species was found. A high
314 percentage of intensive cropland was generally negatively correlated with lipid content and body density
315 of coccinellids. In a former study, lady beetles collected from semi-natural habitats had qualitatively higher
316 lipid content than conspecifics from monocultures, but a direct effect of the amount of intensive cropland
317 in the surrounding landscape could not be demonstrated (Tiede et al. 2017). The survey period of our present
318 study exceeds that of the former one by far, and thus covers a larger part of the activity period of
319 coccinellids, ranging from awakening from hibernation to reproduction of (multiple) new generations to
320 preparation for overwintering. This includes periods when annual row crops may be productive food
321 sources for natural enemies, as well as periods when crop pests are not yet or no longer present. While high
322 pest abundance can have a positive short-term effect on the development of natural enemy populations
323 (Rand et al. 2006), our results suggest longer-term negative consequences of agricultural intensification for
324 beneficial insect populations.

325 While the percentage of soybean and corn fields can be easily and unambiguously categorized,
326 landscape diversity as a measure of heterogeneity is less straightforward, as the composition of habitat types
327 can vary greatly even with the same level of diversity. Some habitat types, although contributing to greater
328 diversity at the landscape level, may not provide many resources for coccinellids, e.g., impervious surfaces,
329 water bodies, or intensively pesticide-treated crops. In addition, preferences for cultivated plants or semi-
330 natural habitats are often species-specific for coccinellids. For example, native species are often found in
331 grasslands, whereas forests play a more important role for introduced species (Gardiner et al. 2009a;
332 Werling et al. 2011; Diepenbrock and Finke 2013). Species-specific preferences may also have contributed
333 to the absence of a general effect of landscape diversity in our study. We detected a significant negative
334 effect of landscape diversity on lipid content only for the native *C. maculata*. For this species, higher
335 population densities have previously been found in low-diversity landscapes with abundant grasslands and
336 corn. However, overall coccinellid abundance and biological control performance were supported by high
337 landscape diversity (Gardiner et al. 2009a; Gardiner et al. 2010).

338 High edge density had a positive effect on the body density of *C. maculata* and *H. variegata*, but
339 again no overall effect could be detected. Landscape classification using the USDA Cropland Data Layer
340 (CDL, NASS 2011) provides a relatively coarse 30 m x 30 m resolution of land cover classes. A finer-
341 grained landscape analysis that also captures small edge structures and habitat islands, as well as field
342 margins between the same habitat types could potentially reveal stronger impacts of edge density on
343 coccinellid performance. Small-scale structures that can be accessed with minimal energy expenditure such
344 as field margins can be an attractive source of food and shelter for coccinellids (Hodek et al. 2012). Recent
345 studies have found that edge density increases abundance of many pollinators and natural enemy species,
346 improves pollination and pest control, and increases yields in arable landscapes (Martin et al. 2019).
347 Alternatively, other measures of landscape configuration such as connectivity may reveal additional
348 landscape features that translate to physiological outcomes for lady beetles (Koh et al. 2013).

349 We used three different physiological parameters to estimate body condition in lady beetles to
350 account for the fact that an animal's phenotype is a consequence of many integrated and interdependent

351 traits (Wilder et al. 2016). Body density and lipid content were more informative for the influence of
352 landscape structure on body condition than body size. This is of little surprise given that body size is
353 determined during larval development (Vargas et al. 2013b). Lady beetle individuals often migrate multiple
354 times over longer distances after hatching in search of suitable food, egg-laying or overwintering sites
355 (Hodek et al. 1993; Schellhorn et al. 2014). The landscape at a 1 km radius around collection sites is thus
356 most likely not representative of the larval feeding habitat that could have primarily influenced body size.
357 Body density and lipid content are better predictors of recent access to resources. Lipid content is a direct
358 measure of body composition and a good estimate of energy reserves in arthropods (Lease and Wolf 2011;
359 Knapp and Knappová 2013). Body density, calculated as size-corrected body weight, also comprises total
360 lipid weight, but in addition includes the content of other body substances, e.g., protein. Protein is not
361 directly related to the energy reserves of individuals but has been shown to be of considerable importance
362 for insect reproductive fitness (Knapp and Knappová 2013; Wilder et al. 2016). Consistently, body density
363 was also the only body parameter we measured that was correlated with the presence of eggs. We conclude
364 that, taken together, the chosen parameters provide good insight into the effects of landscape simplification
365 on the body condition and fitness of coccinellids.

366 Continuous sampling of local lady beetle populations is challenging because the highly mobile
367 beetles move between different habitat patches in search of food or egg-laying sites. We often found that a
368 collection site that previously had high lady beetle abundance was devoid of lady beetles on the next visit.
369 In the resulting dataset, landscape structure and collection date are somewhat confounded. As such, for
370 species that could only be collected at a limited subset of sites or dates, the full extent of landscape effects
371 on body metrics may not have been fully measured. In addition, samples were dominated by the native
372 *C. maculata* and the introduced *H. axyridis*, while other species comprised < 20 % of the specimens.
373 However, this is consistent with species distributions in agricultural landscapes of the upper Midwestern
374 United States (Werling et al. 2011; Lamb et al. 2019). The dramatic decline of native coccinellid species in
375 the United States, (Harmon et al. 2007; Gardiner et al. 2011; Lamb et al. 2019), Europe (Brown and Roy
376 2018) and South America (Grez et al. 2013, 2014) since the late 20th century has often been linked to the

377 introduction of invasive competitors such as *H. axyridis*, but an important mediating effect of landscape
378 structure has also been emphasized (Gardiner et al. 2009a, 2011; Werling et al. 2011; Grez et al. 2013;
379 Bahlai et al. 2015). Our results demonstrate that even highly mobile species closely associated with
380 cropland and pest control, such as *H. axyridis*, exhibit the effects of agricultural intensification on
381 physiological performance.

382 While the landscape effects on lady beetle body condition documented here are modest, they
383 suggest the potential loss of biological pest control due to a yet-to-be fully realized numerical response,
384 since lighter and leaner beetles may be less effective predators, produce fewer offspring and have a lower
385 chance of survival (Arrese and Soulages 2009; Kajita and Evans 2010; Beukeboom 2018). These results
386 are consistent with arguments for maintaining semi-natural habitats, diversifying cropping systems, and
387 increasing the number of edges (e.g., by reducing the size of fields) in agricultural landscapes where
388 conservation of beneficial arthropods such as lady beetles and their ecosystem services are desirable.

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393 *Conflicts of interest*

394 The authors declare no conflict of interest.

395 *Ethics approval*

396 None required.

397 *Consent to participate*

398 None required.

399 *Consent for publication*

400 All authors agree to the content of this manuscript.

401 **DATA AVAILABILITY**

402 Data is available in Online Supplement 2.

403 **CODE AVAILABILITY**

404 Code is available in Online Supplement 2.

405 **AUTHORS' CONTRIBUTIONS**

406 JT and CG conceived of the study. JT conducted field sampling and laboratory analysis. BI and JT analyzed
407 the data. BI wrote the first manuscript draft. All authors contributed to subsequent drafts.

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655 **FIGURES & TABLES**

656 **Fig. 1** Location of the 30 sites (black points) sampled across the state of Wisconsin from April to September
657 2011. Inset maps show examples of 1 km buffers around the sampling locations with the corresponding
658 land cover classification based on USDA data.

659 **Fig. 2** Effect of landscape predictors (% intensive cropland, landscape diversity, and edge density) on lady
660 beetle body condition (body size, body density, and lipid content). The x-axis shows standardized (z-scored)
661 beta coefficients of the specific landscape predictors in linear mixed effects models. Black diamonds
662 represent the overall effect of the landscape predictor on the body condition metric. Colored dots represent
663 species-specific effects, whose estimates were calculated from interaction terms between landscape
664 predictor and species. Error bars represent 95% confidence intervals. Filled symbols and lines highlight
665 confidence intervals that do not cross the zero line, representing significant landscape effects. All species-
666 specific confidence intervals overlap with confidence intervals for the overall effect, indicating that there
667 were no species for which the relationship between body condition and landscape metric was statistically
668 different from the all-species mean (see also Online Supplement S1).

669 **Fig. 3** Effect of landscape predictors within 1 km of sampling locations on the body condition metrics of
670 lady beetles, presented as partial residual plots (back-transformed from ln-transformation for illustrative
671 purposes). The panels show: (a) the relationship between the amount of intensive cropland and body
672 density; (b) the relationship between habitat edge and body density; (c) the relationship between the amount
673 of intensive cropland and lipid content; (d) the relationship between landscape diversity and body density.
674 Species-specific effects (individual lines) are shown for illustrative purposes only; the interaction between
675 landscape metrics and lady beetle species was not significant in any model (see also Table 2 and Online
676 Supplement Table S1).

677 **Table 1. Overview of the five lady beetle species collected, their origin and body condition**
 678 **metrics (mean and standard deviation SD) with number of individuals (n) analyzed for each.**

Species (origin)	Body condition metric	n	mean	SD
<i>Coleomegilla maculata</i> , De Geer (native)	Size index (mm ²)	559	8.92	1.22
	Density (mg/mm ²)	544	0.47	0.09
	Lipid content	558	28.75	7.06
	Egg presence	83	-	-
<i>Harmonia axyridis</i> , Pallas (non-native)	Size index (mm ²)	486	16.61	2.25
	Density (mg/mm ²)	415	0.71	0.13
	Lipid content	486	31.92	10.29
	Egg presence	247	-	-
<i>Cycloneda munda</i> , Say (native)	Size index (mm ²)	114	9.61	1.35
	Density (mg/mm ²)	113	0.46	0.10
	Lipid content	114	27.43	7.02
	Egg presence	32	-	-
<i>Coccinella septempunctata</i> , L. (non-native)	Size index (mm ²)	65	19.01	2.85
	Density (mg/mm ²)	65	0.67	0.20
	Lipid content	-	-	-
	Egg presence	51	-	-
<i>Hippodamia variegata</i> , Goeze (non-native)	Size index (mm ²)	58	6.85	1.04
	Density (mg/mm ²)	52	0.42	0.10
	Lipid content	58	31.92	7.16
	Egg presence	-	-	-

679

680 **Table 2. Summary of landscape effects on lady beetle body condition.**

Explanatory variables	Body size			ln (Body density)			ln (Lipid content)		
	χ^2	df	P ($>\chi^2$)	χ^2	df	P ($>\chi^2$)	χ^2	df	P ($>\chi^2$)
<i>% Intensive cropland models</i>									
Intens. cropland	1.0	1	0.318	4.4	1	0.036	4.6	1	0.032
Species	1987.7	4	<0.001	460.0	4	<0.001	27.1	3	<0.001
Date	1.0	1	0.318	16.2	2	<0.001	5.0	2	<i>0.081</i>
Intens. cropland:Species	5.4	4	0.250	4.2	4	0.373	1.78	3	0.641
Date:Species	4.5	4	0.337	46.6	8	<0.001	118.9	6	<0.001
<i>Landscape diversity models</i>									
Landsc. diversity	0.5	1	0.471	0.4	1	0.518	0.7	1	0.401
Species	1883.0	4	<0.001	488.6	4	<0.001	24.8	3	<0.001
Date	1.4	1	0.239	18.4	2	<0.001	4.8	2	<i>0.093</i>
Landsc. diversity:Species	1.3	4	0.861	6.3	4	0.188	4.8	3	0.185
Date:Species	5.0	4	0.283	49.6	8	<0.001	122.0	6	<0.001
<i>Edge density models</i>									
Edge density	1.3	1	0.260	2.9	1	<i>0.087</i>	1.1	1	0.292
Species	2038.4	4	<0.001	509.6	4	<0.001	27.9	3	<0.001
Date	1.7	4	0.203	18.4	2	<0.001	5.5	2	<i>0.063</i>
Edge density:Species	1.6	4	0.811	5.8	4	0.213	0.5	3	0.925
Date:Species	4.9	4	0.300	49.1	8	<0.001	120.4	6	<0.001

681 Results of linear mixed-effects models testing the effects of landscape predictors (% intensive cropland,
682 landscape diversity, edge density), beetle species and collection date (in the body density and lipid content
683 models, a quadratic term was used for collection date) on body condition metrics (body size, ln-transformed
684 body density and ln-transformed lipid content) of coccinellids. Test statistics are based on type II Wald chi-
685 square tests at $\alpha = 0.05$. *P* values <0.05 are reported in bold numbers and *P* <0.10 in italics. The
686 corresponding coefficients of variation, standard errors, and *P* values for taxon contrasts are reported in the
687 Online Supplement Table S1. Abbreviations: *df* = degrees of freedom.

Figures

Figure 1

Location of the 30 sites (black points) sampled across the state of Wisconsin from April to September 2011. Inset maps show examples of 1 km buffers around the sampling locations with the corresponding land cover classification based on USDA data.

Figure 2

Effect of landscape predictors (% intensive cropland, landscape diversity, and edge density) on lady beetle body condition (body size, body density, and lipid content). The x-axis shows standardized (z-scored) beta coefficients of the specific landscape predictors in linear mixed effects models. Black diamonds

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Figure 3

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