Landscape composition mediates the relationship between predator body size and pest control

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Abstract. Understanding the mechanisms contributing to positive relationships between predator diversity and natural pest control is fundamental to inform more effective management practices to support sustainable crop production. Predator body size can provide important insights to better understand and predict such predator-pest interactions. Yet, most studies exploring the link between predator body size and pest control have been conducted in species-poor communities under controlled environmental conditions, limiting our ability to generalize this relationship across heterogeneous landscapes. Using the community of naturally occurring ground beetles in cabbage fields, we examined how landscape composition (percent cropland) influences the size structure (mean, variance, and skewness of body size distribution) of predator communities and the subsequent effects on pest control. We found that predator communities shifted their size distribution toward larger body sizes in agriculturally dominated landscapes. This pattern arose from increasing numerical dominance of a few large-bodied species rather than an aggregated response across the community. Such landscape-driven changes in community size structure led to concomitant impacts on pest control, as the mean body size of predators was positively related to predation rates. Notably, the magnitude of pest control depended not only on the size of the dominant predators but was also strongly determined by the relative proportion of small vs. large-bodied species (i.e., skewness). Predation rates were higher in predator assemblages with even representation of small and large-bodied species relative to communities dominated by either large or small-bodied predators. Landscape composition may therefore modulate the relationship between predator body size and pest control by influencing the body size distribution of co-occurring species. Our study highlights the need to consider agricultural practices that not only boost effective predators, but also sustain a predator assemblage with a diverse set of traits to maximize overall pest control.

Key words: biological control; Brassica oleracea; ecosystem services; functional traits; ground beetles; landscape simplification; multi-predator effects; top-down control.

INTRODUCTION

The growing concern over global declines in biodiversity has stimulated research into the consequences of species loss for ecosystem services (Cardinale et al. 2012). Although changes in the number of species is sometimes used as a proxy for explaining certain ecosystem functions and services (Cadotte et al. 2011), the link between predator species diversity and pest control is equivocal, with studies reporting negative, positive, and no relationships (Straub et al. 2008). Similarly, studies examining other facets of predator diversity, such as species evenness and phylogenetic diversity, have also shown

idiosyncratic responses in its relationships with pest control (Crowder et al. 2010, Griffin et al. 2013, Greenop et al. 2018). Understanding the mechanisms underpinning natural pest control could provide better insight into how biodiversity components could be manipulated for maximizing this pivotal ecosystem service.

In this context, extending the analysis beyond species diversity to focus on the functional traits directly linked to prey suppression provides an opportunity to elucidate the mechanisms that drive pest control services. Functional traits, such as body size, often determine the strength of species interactions (Rudolf 2012), and therefore how predator diversity affects pest control. Larger predators usually have higher per capita foraging rates than their small-bodied relatives (Ball et al. 2015), so increasing the average body size of predator communities can potentially induce stronger top-down control of

pest densities (Russell et al. 2017). Research on predatory species also reveals that large individuals are able to reduce functional overlap with heterospecifics due to their ability to access and exploit a broader diversity of food resources (Cohen et al. 1993). Body size is a crucial determinant of niche overlap and intraguild predation within food webs (Woodward and Hildrew 2002), and therefore may increase our ability to predict the circumstances under which predator diversity can lead to positive biocontrol effects. Body size is also tightly linked to other life history traits, such as dispersal ability (Jenkins et al. 2007) and reproductive output (Peters 1983, Honêk 1993), which determines in part, species responses to environmental changes. Understanding variation in body size thus informs not only about ecosystem functioning, but also how species assemblages may change as a result of environmental perturbations.

Relationships between predator body size and pest control are, however, not consistent across systems. Inherent in most of the current trait-based approaches is the assumption that the functional role of species is relatively constant in different ecological contexts and unaffected by the presence of other species in the community assemblage. Yet, there is clear evidence that the functional role of species is not necessarily the same when species are in a mixture, relative to when species are in isolation (Griffin et al. 2013). This is because the presence of interspecific interactions occurring between diverse predator assemblages can positively or negatively affect the trait expression of individual species, altering aggregated contributions to pest control (Sih et al. 1998). While laboratory experiments suggest, for example, that per capita predation rates are positively associated with predator body size (Rouabah et al. 2014), field studies report that communities dominated by large-bodied predators increase the opportunity for intraguild predation on small predators (Rusch et al. 2015), leading to a net decline in pest control. Likewise, small predators might alter the foraging behavior and habitat use of large predators (Prasad and Snyder 2004, Rudolf 2006, Davenport and Chalcraft 2013), in turn influencing pest control. Both the composition of predator body sizes and trophic interactions are likely important in determining the strength of pest control, however, the interplay between them is not well understood.

Another factor that may impact the relationships between predator body size and pest control is landscape context. Landscape context is important because increases in agricultural production have greatly altered land-use patterns, resulting in landscapes that are structurally simplified and dominated by croplands (Tscharntke et al. 2005). Landscape simplification may alter the distribution of predator body sizes not only through changes in species dominance (i.e., when large or small-bodied species become numerically dominant and therefore exert a strong influence on the community mean body size), but also through changes in the functional community composition (i.e., the frequency distribution of different body size classes, herein body size diversity). This may occur because landscape simplification selects for or against species with a distinct set of traits (Gámez-Virués et al. 2015). For example, in Europe, small-bodied ground beetles are more abundant in crop-dominated landscapes than structurally complex landscapes (Kotze and O'Hara 2003). Such changes in body size distributions (i.e., relative proportion of small vs. large species) could have considerable consequences for pest control, particularly as ecosystem services are thought to be largely determined by the functional traits of dominant species (Balvanera et al. 2005, Tolkkinen et al. 2013, Winfree et al. 2015). Furthermore, landscape simplification might lead to changes in predator body size diversity that, in turn, are expected to influence the strength of pest control. The intuitive interpretation that increasing predator size diversity might lead to niche complementarity and better biological control is not always generalizable, as increasing the size range of predators is also likely to increase the strength of indirect interactions among predators that can alter pest control in a landscape-dependent manner (Martin et al. 2013). Thus, land-use changes may modify relationships between predator body size and pest control through multiple pathways, which may not be predicted solely by changes in average body size. Previous research has documented how multiple aspects of body size structure (i.e., mean, diversity, and relative proportion of individuals across size classes) can influence pest control, but often these studies have been performed under controlled, simplified environments (e.g., Rudolf 2012, Rouabah et al. 2014, Jonsson et al. 2018). Information is lacking on how these results scale up into realistic, more species-rich communities observed on farms across heterogeneous landscapes. In addition, few studies have explored the relative importance of concurrent changes on the mean, diversity, and shape of predator body size distributions on the strength of pest control.

We address these knowledge gaps by examining how landscape simplification affects body size structure of predator communities, and how these changes consequently influence pest control. We used the community of ground beetles (Coleoptera: Carabidae) inhabiting cabbage fields as a model system. Ground beetles are sensitive to land-use changes, are taxonomically and functionally diverse, and are considered one of the most important groups of predators of agricultural pests (Lövei and Sunderland 1996, Kromp 1999). Moreover, ground beetle communities differ widely in abundance and body size (2–40 mm) within their constituent species, which makes this group ideal for examining factors affecting body size distribution and subsequent impacts on pest control. Specifically, we asked (1) whether landscape simplification leads to shifts in the mean, diversity, and distribution of predator body sizes, (2) whether body size structure matters for pest control and assessed the relative contribution of individual species in this relationship, and (3) whether landscape context

modulates the strength of the relationship between predator body size and pest control.

Methods

Study site

The study was conducted on 11 farms across a gradient of landscape simplification in the Finger Lakes Region of New York State (USA), during the summers of 2014 and 2015. On each farm, we established two 10 × 10 m plots consisting of 10 rows of cabbage (*Brassica oleracea* var. capitata cv. Capture) with 15 cabbage plants per row. All 44 experimental plots were planted on farms characterized as organic or that used minimal inputs for pest management. Field margin vegetation can affect movement patterns of predator communities (Rouabah et al. 2015). Therefore, to reduce local-scale edge effects, all experimental plots were established within 2 m of a grassy field border (i.e., Poaceae). In addition, plots received no insecticide or fungicide applications, and weeds were removed manually at 2-week intervals. All plots were planted across study areas over two consecutive weeks in mid-June in both years.

Proportions of cropland and semi-natural areas around each plot were calculated using the National Agricultural Statistics Service Cropland Data Layer for New York (USDA-NASS 2016) in ARCGIS 10.3 (ESRI, Redlands, California, USA). Cropland in this region was comprised primarily of corn, soybean, winter wheat, and brassicas; while seminatural habitats included shrubland, deciduous forest, woody wetlands, evergreen forest, and mixed forest. We quantified the cover of cropland and seminatural habitats at three spatial extents: 250, 500, and 1,000 m. By fitting separate linear mixed-effect models (lme) for each response variable and scale, we determined the proportion of cropland at 1,000 m was the scale at which landscape composition provided the best fit to the data (based on the Akaike information criterion corrected for sample size [AIC$_c$] values, see Appendix S1: Table S1). Earlier studies showed that the 1,000 m spatial scale was relevant to understand the dynamics of ground beetle communities (Winqvist et al. 2011, Rusch et al. 2014, Hanson et al. 2016, Rusch et al. 2016).

Ground beetle sampling, community structure, and body size measurement

The activity-density of adult ground beetles in the field was determined using pitfall traps. Each pitfall trap consisted of a 540-mL plastic cup (9 cm diameter openings; Fabri-kal, Kalamazoo, Michigan, USA) filled about one-third with a mixture of odorless detergent (Dr. Bronner's Unscented Pure Castile Soap, Vista, California, USA) and water. The cups were inserted into the soil, with the rim at the soil surface, and protected from direct sunlight and rain with a plastic plate (25 cm diameter) positioned 10 cm above the trap. The traps were placed in the corners and center of each plot, for a total of five traps per plot. All pitfall traps were kept open for 24 h at four different times each year during seedling, pre-cupping, early head formation, and maturation growth stages (Andaloro et al. 1983). Carabid beetles were identified to species using both Lindroth (1961, 1963a, b, 1966, 1968) and Bousquet (2010) taxonomic keys, following the classification of Bousquet and Larochelle (1993). Following taxonomic identification, we gathered information from the literature to further classify carabids into three diet categories according to their predominant feeding habits during the adult stage: carnivorous, omnivorous, or herbivorous (Bousquet 2010, Homburg et al. 2013) (Appendix S1: Table S3).

Plot-specific estimates of species richness, species diversity (Shannon-Wiener), species evenness (Pielou's evenness), and activity-density of all carabid communities were calculated from pooled pitfall catches of each plot and sampling year. In addition, the sex of all specimens collected from each plot and sampling year was determined, and 15 males and 15 females were selected at random to measure body size. If there were fewer than 15 males or females per plot, then all available specimens were measured. Elytra length (i.e., the longest distance from the elytron apex to the elytron base) was digitally measured for all selected specimens using an Olympus SZX10 stereomicroscope connected to a computer installed with the micro imaging software cellSens (Olympus, Tokyo, Japan). Elytra length is considered a good indicator of body size in ground beetle communities and has been used in previous studies (Juliano 1986, Nelemans 1987).

For each plot and sampling year, we calculated three complementary metrics to characterize community body size structure: community weighted mean (CWM), community weighted variance (CWV), and skewness (i.e., frequency distribution of body size classes). Community weighted mean is the mean body size value of the species present per plot weighted by their abundance, and reflects the trait values of dominant species in the community. Community weighted variance is the plot-level variance in body size values weighted by species abundance and represents a measure of size diversity. Community weighted variance was calculated following Gaüzère et al. (2019), with higher values occurring when communities have greater size diversity. Last, skewness was calculated by allocating species into different size categories on the basis of its log-transformed body size (mm). Following the Freedman-Diaconis rule to choose the appropriate number of classes (Birgé and Rozenholc 2006), we grouped individuals into six size categories that spanned the total range of body size in our study (1.5–13.7 mm). Then, we produced a histogram of the number of individuals in each size category and calculated the coefficient of skewness for each plot. Positive skew coefficients indicated right-skewed distributions (i.e., greater number of small-bodied individuals), values

approaching zero indicated symmetric distributions (i.e., similar number of small and large-bodied species), and negative values denoted left-skewed distributions (i.e., greater number of large-bodied individuals). Skew body size distributions can inform whether trait filtering is occurring along the landscape gradient (i.e., shifts in community body size distribution). Metrics were calculated using the FD (Laliberté et al. 2014) and S3cR (Gaüzère et al. 2019) packages in R.

Predation rates in the field

Concurrently with carabid sampling, we conducted a sentinel prey experiment to determine the relationship between ground beetle community structure and predation rates. Predation rates were quantified using pupae of the economically important pest the diamondback moth (*Plutella xylostela*) obtained from a colony collected from cabbage fields, and maintained on a wheat germ-casein artificial diet (Shelton et al. 1991).

In each plot, 10 circular plastic plates (9 cm diameter) were placed on the ground at least 1.5 m apart from each other in a 5×2 formation in the center of the plot. The plates were positioned so that the surface of each plate was level with the ground. A group of 10 pupae was then placed in the center of each plate and left in the field for 24 h. At the end of this period, the number of removed pupae was recorded. We repeated this experiment three times per plot each year at 15, 30, and 45 d after transplanting, which covered crop development from seedling to early head-formation stage.

Because other arthropods and small vertebrates might also be involved in pupal predation, we monitored one of the sentinel prey arenas per plot with a video camera to determine the relative contribution of ground beetles to overall predation rates (see Appendix S1: Supplementary Methods S1 for more details on the video surveillance of predation events). Video data revealed that ants (37%), carabid beetles (22%), and opiliones (18%) accounted for the majority of visits to sentinel prey, while prey visits by other predatory taxa collectively accounted for only 23% of the total visits (Appendix S1: Fig. S1). Predation rates attributable to carabid beetles (P_{cb}) for each sentinel prey arena were calculated as

$$P_{cb} = P_T \times V_{cb}/10$$

where P_T is the total number of removed pupae on a given sentinel prey arena, V_{cb} is the proportion of total prey visits made by carabid beetles calculated from video observations of a given plot (see Appendix S1: Supplementary Methods S1), and 10 is the initial number of pupae per sentinel prey arena. We believe that our P_{cb} calculations represent a conservative estimate of the biocontrol potential exerted by carabid beetles. *Plutella xylostella* is not the only pest in these landscapes (e.g., aphids, flea beetles, and cabbage root flies), and crops other than cabbage have additional pests that may be attacked by carabid beetles (Clark et al. 1997, Suenaga and Hamamura 2001). Indeed, carabid beetles are polyphagous predators that have the potential to maintain a wide range of pest species below outbreak levels (Kromp 1999, Menalled et al. 1999). As such, our predation rate estimates provide a proxy measure of pest control that is easily comparable across experimental plots. Whether increased predation on sentinel prey translated into final service delivery (e.g., reduction in pest density and higher crop yield) is an open question. There is evidence, however, that increased predation rates may lead to decreased pest density or reduced plant damage across a range of cropping systems (Karp et al. 2013, Perez-Alvarez et al. 2019, Thomine et al. 2020). Regardless, it is safer to interpret our predation rate estimates as comparative measures of biocontrol potential rather than absolute magnitudes of pest regulation by carabid beetles. Most importantly, our video analysis revealed no significant differences in the relative proportion of predation visits by carabid beetles along the landscape gradient (Appendix S1: Fig. S3), indicating that any potential bias in the accuracy of the method to estimate predation by carabid beetles is the same in all communities and thereby does not invalidate relationships found in our study.

Statistical analysis

Landscape effects on the mean, variation, and body size distribution.—To determine whether species with a particular body size are specialized in some portions of the landscape gradient, we carried out a multivariate technique of constrained ordination, the Outlying Mean Index (OMI; Doledec et al. 2000). OMI used a plot-by-species abundance matrix as the response and the proportion of cropland at 1,000 m radius as the predictor. This provided information regarding the niche position (i.e., mean conditions of occurrence) of each carabid species along the landscape gradient. Species with positive values along the OMI axis tended to occur in simple landscapes, and those with negative values tended to occur in complex landscapes. OMI also provided a measure of niche breadth (variance around the niche position). Species with high niche breadth values occur across a broad range of landscape conditions, whereas species with low niche breadth occur in a limited range of conditions. To test whether the mean body size of each species was significantly associated with its niche position (i.e., niche position on OMI axis) and niche breadth, we performed linear regression analyses. Calculations were performed using the package ade4 (Dray and Dufour 2007).

To evaluate the effect of landscape simplification on the mean (CWM), diversity (CWV), and symmetry (skewness) of community body size distributions, we used linear mixed-effect models (nlme) with proportion of cropland in a 1,000-m radius as a predictor variable. Farm identity and year were included as random effects

in all models to account for any environmental differences across sites and years. Model assumptions were checked according to the graphical validation procedures recommended by Zuur et al. (2009). Significance of the models was assessed by conditional F tests (Pinheiro and Bates 2000). No spatial autocorrelation was found in residuals of these models (Appendix S1: Table S2).

Species-specific contributions to community body size change across the landscape gradient.—To quantify the contribution of individual carabid species to community weighted mean (CWM), we followed the method proposed by Gaüzère et al. (2019). This method is based on a Jackknife procedure, where species are removed one by one from the data set and then the CWM is iteratively recalculated. The contribution of each species is estimated as the difference between CWM of the whole dataset and CWM values without a given species. Species with positive values contribute toward the CWM global trend, while negative values indicate species contributing against the overall trend. Furthermore, major contributors to the CWM trend are species with large fluctuation in relative abundance and extreme body sizes (e.g., an exceptionally large or small species; Gaüzère et al. 2019).

To characterize the relative contribution of small and large species to community mean body size, we divided species into two discrete size categories based on a cluster analysis: small (1.5–6.2 mm) and large (7.3–13.7 mm; see Appendix S1: Supplementary Methods S2 for details on the cluster analysis). Similarly, we categorized species according to functional group (i.e., carnivorous, herbivorous, and omnivorous) and estimated the collective contribution of each group to overall CWM trends across the landscape gradient.

Effects of ground beetle community structure on predation rates.—Relationships between ground beetle community structure and predation on sentinel prey were examined using mixed effect models (nlme) with Gaussian error distributions. Response variable was defined as the mean proportion of sentinel prey removed by carabid beetles across the season for a given plot and a given year. We fit separate models for each relevant component of community structure as explanatory variables of predation rates: species richness, activity-density, species diversity, evenness, CMW, CWV, and size skewness. The initial fixed effects included a community descriptor, proportion of cropland in the landscape in a 1,000 m radius, and their interaction. Farm identity and year were included as random effects in all models. We then simplified the fixed-effects structure using backward stepwise model simplification, where non-significant predictors were removed ($P > 0.05$). Statistical significance of fixed effects and their interactions were assessed by conditional F tests (Pinheiro and Bates 2000). To evaluate which aspects of community structure better predicted predation rates, we selected models with the highest explanatory power by comparing the AIC values of the minimum adequate models (Burnham and Anderson 2002). We also conducted an analysis to test whether models excluding non-predatory carabids better predicted predation rates than models that included the full carabid community. We only report results for the overall carabid community because analysis excluding non-predatory carabids did not indicate any systematically higher predictive power or affect any of our conclusions (Appendix S1: Fig. S7).

Last, we took advantage of the natural differences in body size distributions across the landscape to examine how changes in the relative proportion of small vs. large species influenced the relationship between body size and predation rates. Local carabid communities were grouped into three discrete classes on the basis of the shape of the body size distribution: (1) right skewness (i.e., communities dominated by small-bodied species), (2) left skewness (i.e., communities dominated by large-bodied species), and (3) symmetrical distribution (similar number of small and large-bodied species). To determine if the local body size distributions were significantly skewed, they were tested against normality using Shapiro-Wilks tests. Sample sizes for each group were as follows: right skewness ($n == 19$), left skewness ($n == 11$), and symmetrical distribution ($n == 12$). For each group, we then calculated the slopes of the relationships between CWM of body size and predation rates using simple linear regression analysis. We also evaluated whether predation rates between the three size distribution groups were significantly different using a one-way ANOVA followed by a Tukey's multiple comparison test at $P < 0.05$. All analyses were conducted using R version 3.5.3 (R Development Core Team 2019).

RESULTS

A total of 3,378 carabids belonging to 47 species and 22 genera were collected in cabbage fields (Appendix S1: Table S3). Of these, 29 were small-bodied species (elytra length <7.3 mm), which made up 58% of individuals collected, while the remaining 18 species were categorized as large (elytra length ≥7.3 mm) representing 42% of the total capture (Appendix S1: Fig. S4).

The OMI analysis revealed different occupancy requirements and patterns of specialization between large- and small-bodied beetles (Fig. 1). Large-bodied beetles tended to occur in more simple landscapes (i.e., positive niche values) and exhibited a narrower niche breadth than small-bodied beetles (Fig. 1b,c). On average, niche breadth for small beetles was 2.4 times higher than for large beetles, indicating that small beetles are distributed along a wider variety of landscape conditions (Fig. 1c). These overall patterns were followed for some, but not all, species. In fact, species within the same size class displayed great variation in both niche position and niche breadth (Fig. 1a).
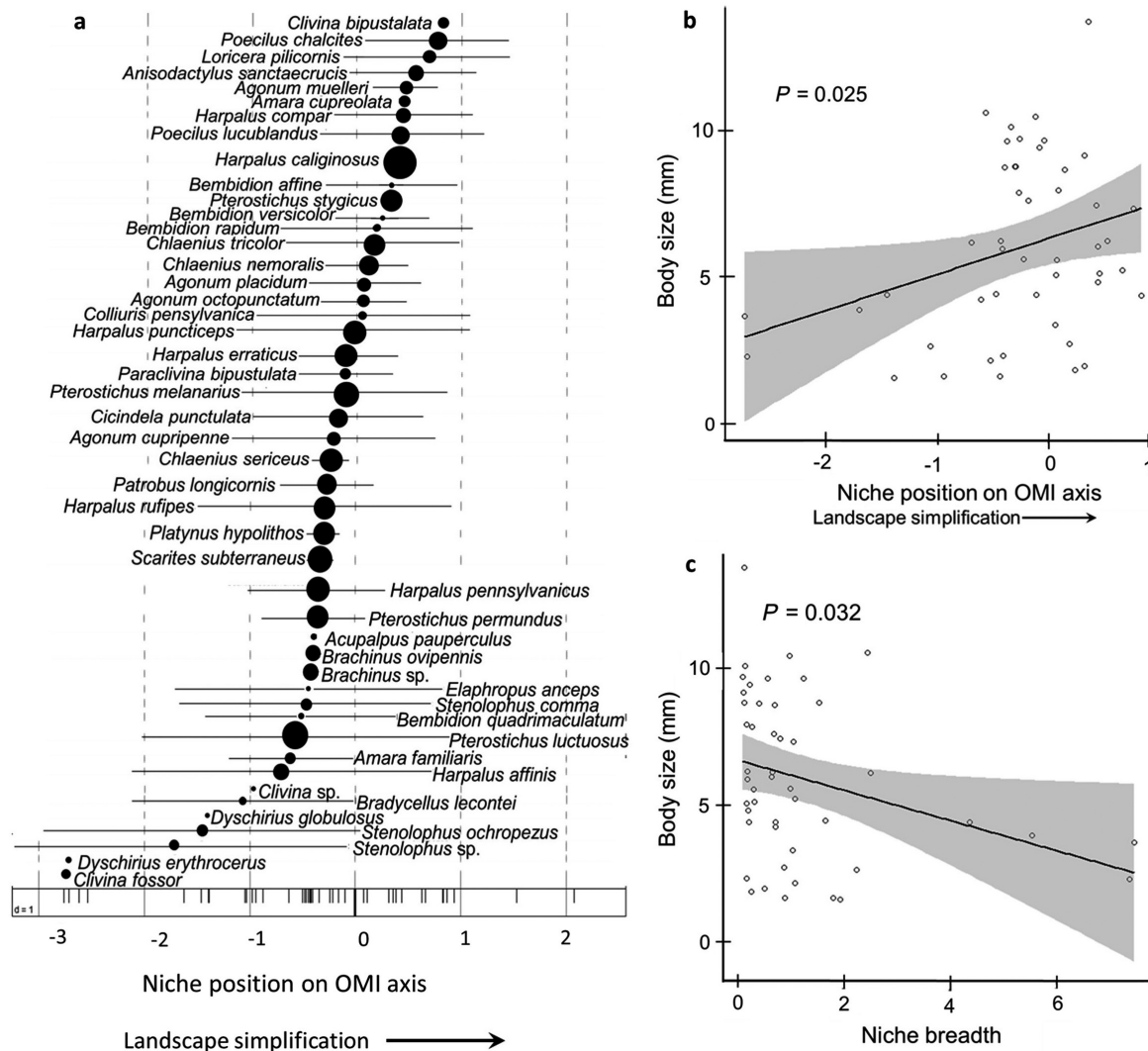
FIG. 1. (a) Species' niche position and niche breadth for all carabid species along the landscape simplification gradient. This analysis was based on the Outlying Mean Index (OMI). Circles represent the average position along the landscape gradient used by every species and the horizontal bars correspond to ±SD as a measure of niche breath. Values near zero indicate proportion of agriculture near the available mean for the study region (i.e., ~30%), whereas values far from this origin indicate marginal environments, that is, complex (negative values) or simple (positive values) landscapes. Small vertical bars at the bottom of the panel correspond to the position of the experimental plots. The size of the circles is proportional to the relative body size of each species. (b) Relationship between species body size and landscape niche position (outlying mean index). (c) Relationship between species body size and niche breadth along the gradient of landscape simplification. Regression lines and 95% confidence intervals shown.

At the community level, landscape simplification had a clear effect on the functional composition of the dominant species (Fig. 2a). Landscape simplification promoted a shift to communities dominated by large-bodied species (i.e., negative skewness), while complex landscapes were numerically dominated by small-bodied species (i.e., positive skewness) ($F_{1,19} == 9.09$, $P == 0.007$). Importantly, we detected no change in body size diversity (i.e., community-weighted variance) across the landscape gradient ($F_{1,19} == 0.73$, $P == 0.405$; Fig. 2b), indicating that the observed shifts in body size distributions arose from changes in the relative proportion of small vs. large species, rather than a

net change in the number of species. Indeed, we found no significant differences in species richness, i.e., the number of species, across the landscape gradient ($F_{1,19} == 3.80$, $P == 0.066$; Appendix S1: Fig. S5).

The community-weighted mean (CWM) for predator body size increased with the proportion of cropland in the surrounding landscape ($F_{1,19} == 5.21$, $P == 0.034$; Fig. 2c). Overall, predator body size increased by about 35% from complex to simple landscapes. When considering the contributions of each species separately, we found that 16 of the 47 species collected shaped CWM trends, whereas the remaining species exhibited negligible contributions (Fig. 3a). These results indicated that
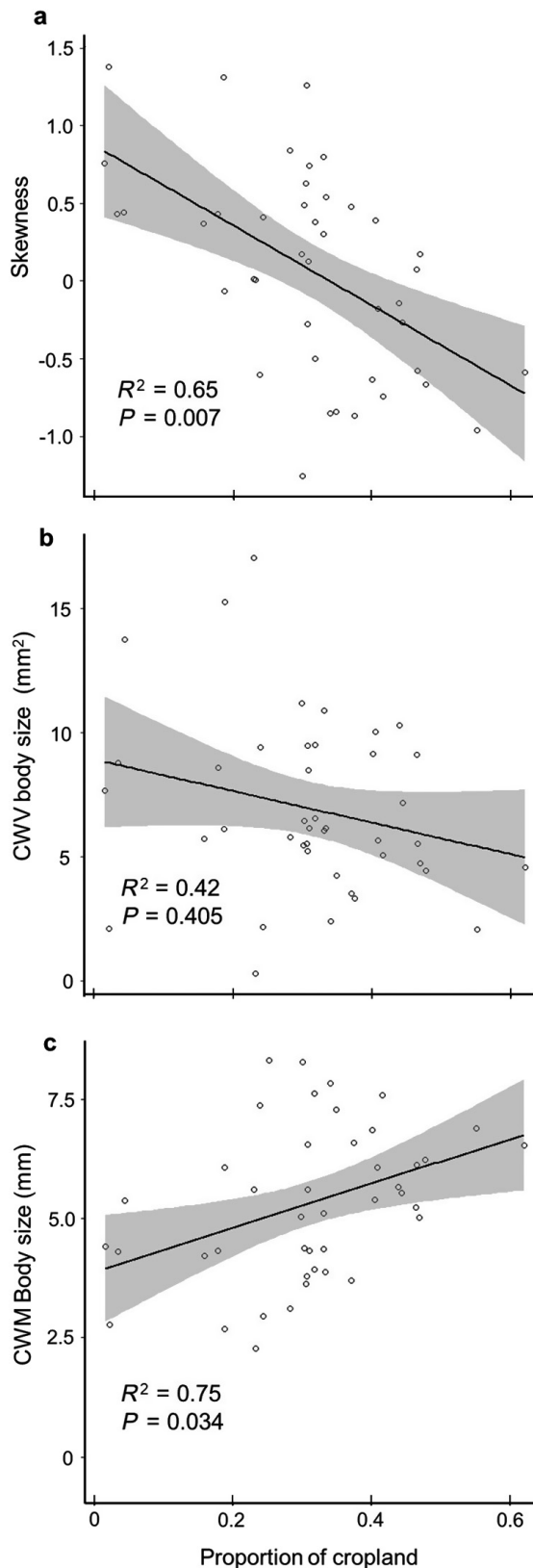
FIG. 2. Relationships between the proportion of cropland in a 1,000 m radius around the experimental plots and (a) skewness coefficients of body size distribution, (b) community weighted variance of body size (CWV), and (c) community weighted mean body size (CWM). Each data point represents a single community (plot). Positive and negative skewness indicate dominance by species with small and large-bodied size, respectively. Lines depict predicted trends from linear mixed-effects models and associated 95% confidence intervals (gray shaded). Conditional coefficient of determination (R^2) and significance of fixed effects are shown.

the overall trend toward increasing mean body size as landscapes became simpler was largely driven by changes in the relative proportion of a few dominant species, rather than a community-wide shared response. Species driving this overall trend were large-bodied species whose abundances increased in simple landscapes (e.g., *Poecilus chalcites* and *Pterostichus melanarius*) and small-bodied species with decreased abundance across the landscape simplification gradient (e.g., *Elaphropus anceps* and *Bembidion quadrimaculatum*) (Fig. 3a,b). Specifically, *Poecilus chalcites* and *Elaphorus anceps* were the top two species that together accounted for 50% of the community mean increase in body size in simple landscapes (Fig. 3a). Other species tended to decrease CWM along the landscape simplification gradient (i.e., large-bodied species with decreased abundance in simple landscapes or small-bodied species with increased abundance in simple landscapes), and therefore had a negative contribution to overall trends. As with positive contributors, only a few species were substantially contributing against the global CWM trends (i.e., *Harpalus puncticeps* and *Harpalus rufipes*). Carabid functional groups also made different contributions to CWM trends, with carnivorous and omnivorous species having net positive contributions, while phytophagous species were largely responsible for negative contributions (Fig. 3c).

Predation on sentinel prey was not predicted by any of the taxonomic-based indices (i.e., species richness, evenness, species diversity), activity-density, size diversity (CWV) or by size distribution (skewness) of ground beetle communities (Appendix S1: Fig. S6 and Table S4). In contrast, we found a positive relationship between community weighted mean body size (CWM) and the number of sentinel pupae predated in the field ($F_{1,19}$ == 9.19, P == 0.006; Fig. 4a). Predation rates were, on average, two-fold greater in plots with higher CWM predator body size (i.e., >6 cm) relative to plots with lower CWM (i.e., <4 cm). While we detected an overall positive relationship between increasing body size and predation rates, this pattern was not consistent across communities (Fig. 4b). Communities dominated by large-bodied species or with similar number of small and large individuals, showed a significant positive relationship between increasing predator body size and
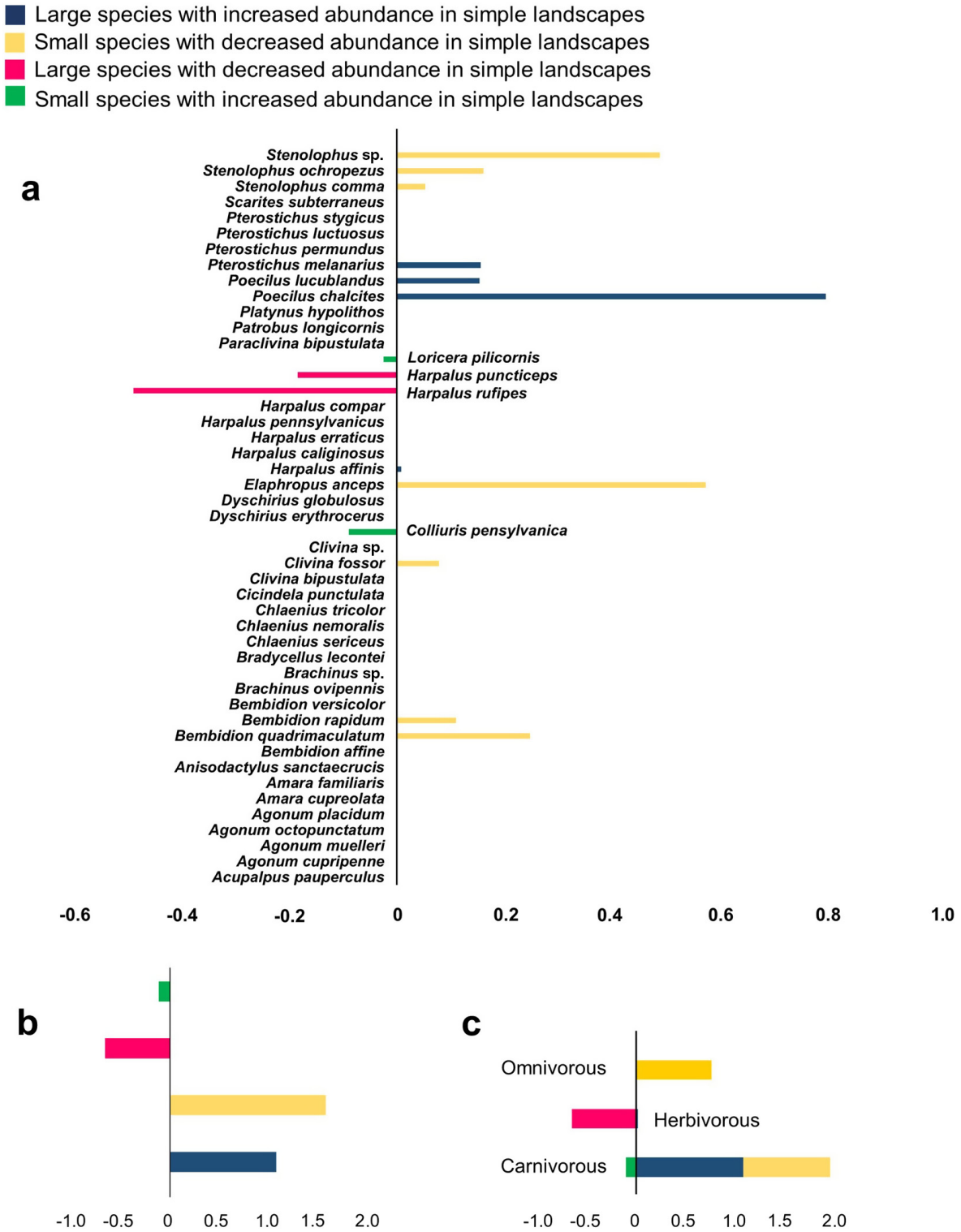
FIG. 3. (a) Species-specific contributions to community weighted mean (CWM) shifts in body size along the landscape simplification gradient. A positively contributing species tends to increase CWM along the landscape simplification gradient whereas negatively contributing species tends to decrease it. Species positively contributing are shown on the right side and negatively contributing species on the left side. Bar colors indicate the interaction between size category (i.e., small vs. large) and population trend (i.e., increased vs. decreased abundance along the landscape gradient). (b) Cumulative contribution by size category and population trend. (c) Cumulative contributions by trophic group.
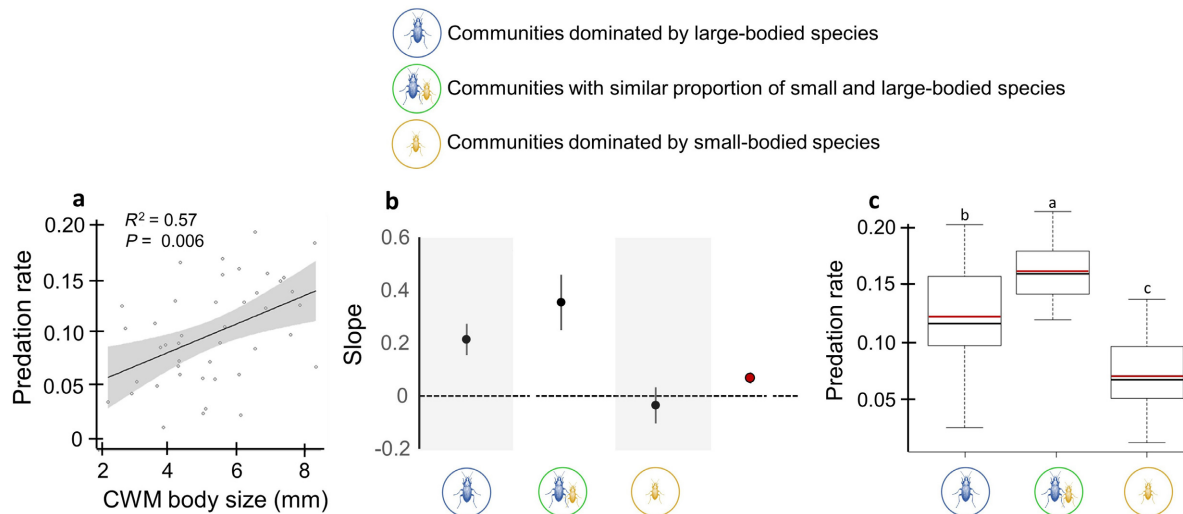
Fig. 4. (a) Relationship between community weighted mean body size (CWM) and predation rates on sentinel diamondback moth pupae in the field. Line depicts predicted trend from the linear mixed-effects model and associated 95% confidence intervals (gray shaded). Conditional coefficients of determination (R^2) and significance of fixed effects are shown. (b) Slopes of the CWM body-size–predation relationships in communities with different patterns of body size distribution: left skewed (communities dominated by large-bodied species), symmetric (similar number of small and large species), and right skewed (communities dominated by small-bodied species). Values are mean ± SE. Overall mean slope for the whole community in red. (c) Box plots of predation rates for communities with different patterns of body size distribution (sample sizes are left skewed == 11, symmetric == 12, and right skewed == 19). Lines within each box represent the median (black) and mean (red) values. Box plot whiskers extend to 1.5 times the interquartile range. Different letters above boxplots indicate significant differences between groups (one-way ANOVA followed by a Tukey HSD test, $P < 0.05$).

predation rates. In contrast, there was no significant relationship in communities dominated by small-bodied species. Furthermore, there was a 2.3-fold variation among communities in the magnitude of the effect on how changes in predator body size affected predation rates ($F_{2,39}$ == 22.73, $P < 0.001$; Fig. 4c). Interestingly, predation rates peaked in places that harbored communities with even representation of small and large species. These results indicated that the consequences of increasing predator body size on the strength of top-down control depended upon the body size distributions of co-occurring species that, in turn, were influenced by landscape context.

DISCUSSION

We found that landscape simplification, associated with increasing cropland, influenced the body size distribution of predator communities. Overall, predator communities shifted their size distribution toward larger body sizes with increasing landscape simplification. This pattern arises from increasing numerical dominance of a few large-bodied species rather than an aggregated response across multiple species in the community. Indeed, only three species (6% of the total 47 species collected) were responsible for 54% of the community body size changes across the landscape gradient (i.e., *P. chalcites*, *P. lucublandus*, and *P. melanarius*). Such landscape-driven changes in community body size structure may

lead to concomitant impacts on ecosystem functioning, as the average body size was positively related to predation rates on sentinel prey. Thus, our results highlight body size as a key predictor of pest control, as it affects both the way species respond to land-use changes and mediate the strength of trophic interactions.

Landscape simplification had clear effects on predator body size. We found that plots in complex landscapes favored a greater abundance of small-bodied species, while plots from simple landscapes were numerically dominated by large-bodied species. Contrary to our findings, previous studies have shown that increased landscape simplification lead to lower average body size of multiple invertebrate taxa (Tsiafouli et al. 2015). Instead, our results are in line with results of recent studies showing that ground beetle communities can benefit from landscape simplification (Winqvist et al. 2011, Rusch et al. 2016). In fact, several of the large-bodied species collected in this study are relatively well adapted to habitats with open and sparse vegetation such as croplands (e.g., *Pterostichus* spp. and *Poecilus* spp.; Bousquet 2010), where they can overwinter and take advantage of the high prey availability (Rand and Tscharntke 2007). Importantly, this variation in body size distribution of predator communities occurred without any detectable change in predator richness along the landscape gradient. This suggests that landscape variation in body size distributions may serve as an early indicator for detecting potential changes in pest control

provision that occur before, or even in the absence of, declines in species richness.

Quantifying the contribution of individual predator species to overall prey suppression within a multispecies assemblage would be a formidable undertaking. Rather, current practice is to assess the ecological role of species indirectly via their functional traits (Díaz et al. 2013, Perović et al. 2017). Here, we demonstrated that body size is indeed an important determinant of species' functional significance for pest control. That is, communities dominated by large-bodied species exhibited, on average, greater predation rates. This result might be explained by increasing strength of per capita trophic interactions with body size (Berlow et al. 2009). Nevertheless, increasing the numerical dominance of large-bodied species was not, by itself, sufficient to explain the magnitude of pest control. Indeed, our study suggests that changes in the relative proportion of different size classes (i.e., body size frequency distributions) are also likely to alter the strength of top-down control. Specifically, we found that predation rates were highest in communities with even representation of small and large-bodied species compared to communities dominated by either large or small-bodied species. This might occur because individuals of different size classes interacted in fundamentally different ways that, in turn, influenced their collective impact on pest control. Competitive interactions among similar-sized predators may lead to a decline in pest control provision (Dayan et al. 1990, Niemelä 1993, Gianuca et al. 2016). Conversely, a shift toward a more even size distribution is likely to promote species complementarity and elevate the level of pest control (Rudolf 2012, Ye et al. 2013). Though it is possible that increasing the size range of predators could promote intraguild predation as well (e.g., Krenek and Rudolf 2014), our work supports previous findings showing that increasing size diversity may enhance prey mortality despite the potential for antagonistic interactions among dissimilar sized predators (Rudolf 2012). In fact, different sized predators often differ to some extent in other traits such as microhabitat use and diel activity patterns (e.g., day vs. night foragers) that may underpin differences in their exploitation of a shared prey (Rudolf 2006, Kamenova et al. 2015). In turn, these finer-scale niche differences among size classes may lead to relaxation of interspecific competition and, by extension, strengthen pest control through niche complementarity (Northfield et al. 2010). More symmetric body size distributions within a predator community thus might have consequences analogous to those of predator species evenness (Crowder et al. 2010). Consequently, the strength of pest control depends not only on the size of the dominant predators but is also strongly determined by the body size distribution of co-occurring species. This also implies that the performance of particular species is likely to be influenced by interactions with other predators in the community assemblage, not functional capacity alone.

The context dependency of species interactions may, at least in part, explain why variable outcomes in the interaction between predator diversity and pest control are often reported (Straub et al. 2008). Thus, while former studies already stressed the importance of targeting high-performing species (e.g., large-bodied species in our study) for achieving effective biological control (Straub and Snyder 2006, Long and Finke 2014), our analysis highlights that suboptimal species (i.e., small-bodied species) cannot be disregarded as they can strongly affect the performance of more efficient species and/or can drive different processes (e.g., complementarity) that contribute to an overall effect (see predation rates in Fig. 4c). As such, conservation strategies that only target a limited number of effective predators are not always an appropriate approach to promote pest control. Considering individual species in isolation when designing schemes to maintain agricultural biodiversity may be detrimental to other, important predators in the system, but also ultimately influence the performance to the very species we are targeting to maximizing biocontrol. Further, relying on the performance of a few dominant predators undermines the resilience of the system, making it more susceptible to sudden environmental changes, and can translate into greater variability in pest control services over time (Macfadyen et al. 2011). Hence, for biological control to be maximized at the landscape scale and simultaneously for several pest species, the functional diversity of the predator community would have to be increased. In support of this view, we found that a shift toward a more diversified carabid community (in terms of body size distribution) resulted in stronger top-down control. This does not preclude the role of particular species being of key importance for effective pest control (i.e., species identity), especially in homogeneous landscapes where the high effectiveness of particular biocontrol agents has been linked to the simplified nature of the food web (Hawkins et al. 1999). Likewise, the presence of a particularly effective predator does not rule out the potential for positive or negative interactions among predators, as reported here.

Another important finding of this study is that body size alone does not explain the strength of top-down control. That is, the mere presence of a species with large body size did not always lead to increased pest control. Instead, our results show that species' food preferences can also influence their performance as biocontrol agents. Carnivorous species were largely responsible for top-down control (i.e., large species with increased abundance in simple landscapes, Fig. 3c), whereas herbivores and omnivores had little or no contribution. Although it might seem obvious that pest control was mainly driven by carnivorous species, this aspect is often ignored in studies examining the effects of body size on ecosystem functioning (Rudolf et al. 2014). Yet, we found clear evidence that similar-sized species (e.g., *Pterostichus* spp., *Harpalus* spp.) can have different diets, and accounting for this variation related to diet breadth may improve

the capacity of body size as a predictor of pest control provision. Indeed, we show that although body size alone (i.e., CWM) explained a significant amount of the variance in predation rates ($R^2 == 0.57$), there is still substantial variation that remains to be explained. This is not surprising given that realized levels of pest control in natural communities depend on numerous abiotic and biotic processes including interactions between multiple predators. This indicates that we need to consider other traits if we are to accurately predict how changes in predator body size influence the outcome of species interactions and the emergent impacts on pest control. Our results suggest that diet breadth is also an important underlying driver of species-based contributions to pest control, and it might help to explain why similar size predators differ in their relative contribution. Further research should also investigate the predictive capacity of body size when combined with other traits such as hunting mode and predator's microhabitat use that are well known to affect trophic interaction strengths (Schmitz 2007, Woodcock and Heard 2011). Similarly, other species-specific traits such as predator origin (i.e., native vs. exotic) may play an important role in predicting pest suppression by influencing the outcomes of predator–predator interactions (Snyder and Evans 2006, Gardiner et al. 2011). Despite obvious shortcomings of purely size-based approaches, our findings show that body size better predicted top-down control than other components of predator community structure (i.e., activity-density, species richness, and evenness), in accordance with previous work (Rusch et al. 2015, Gianuca et al. 2016).

In conclusion, our results show that landscape simplification influences the body size structure of ground beetle communities, with potential implications for pest control services. On the surface, our results suggest that management strategies to maximize pest control should be aimed toward increasing predator body size by targeting specific species. However, changes in size distribution (i.e., skewness) within predator communities could also alter the strength of top-down control. Thus, communities with the same mean body size, but varying in the relative proportion of different size classes may have different effects on pest control. Given that both mean body size and size distributions are subject to landscape-driven variation, this suggests that there is no universal relationship between predator body size and pest control. Instead, our study shows that the relationship between predator body size and pest control is landscape dependent and that the resulting magnitude of pest control is not always deducible from averaging body size of predators. Moreover, apart from body size, predator species differ in other traits like diet breadth, which may also affect the extent of pest regulation in a landscape-dependent manner given that different trophic groups vary in their sensitivity to land-use changes (Purtauf et al. 2005). Consequently, future schemes will need to adopt not only local practices to boost populations of effective predators suited to specific pests, but also landscape management to sustain a carabid assemblage with a diverse set of traits to maximize overall pest control. In this regard, the adoption of practices such as conservation tillage, reduced pesticide pressure, organic farming, and maintenance of non-crop refuges are promising management options that can be implemented at local and landscape scales to optimize pest control by ground beetles (Holland and Luff 2000, Landis et al. 2000).

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